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The first records of *Pictonautilus* Branger, 2004 (Cephalopoda: Nautiloidea) from the Upper Bathonian – ? Lower Callovian (Middle Jurassic) of Germany and Poland

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Key words: Nautiloids, Paracenoceratidae, Bathonian, Callovian, biostratigraphy, palaeobiogeography.

Abstract. The rare Middle Jurassic nautilid genus *Pictonautilus* Branger, 2004 is reported for the first time from Upper Bathonian strata of SW Germany and from Upper Bathonian – ? Lower Callovian beds of S Poland. The new specimens can be assigned to the type species *P. verciacensis* (Lissajous, 1923) and point to a larger maximum size than previously expected. Although the new findings expand the geographic range of this genus, its phyletic origin remains unknown. From its original description and illustration, *Nautilus* (*Paracenoceras*) *wilmae* Jeannet, 1951, from the Lower Callovian of Switzerland, was suspected to represent another species of *Pictonautilus*. After study of the holotype, however, this taxon is considered a junior subjective synonym of "*Paracenoceras*" *calloviense* (Oppel, 1857). Another specimen from the Lower Callovian of SW Germany cited as *Nautilus* (*Paracenoceras*) *wilmae* Jeannet, 1951 was misidentified and represents the first hitherto recognized record of the dwarfish *Paracenoceras dorsoexcavatum* (Parona, Bonarelli, 1895) from Europe besides the holotype from Savoy.

INTRODUCTION

After a severe ecological crisis at the end of the Triassic, nautilids recovered and diversified again in the course of the Jurassic (Kummel, 1956, 1964; Dzik, 1984; Tintant, 1990). The post-Triassic phylogeny of nautilids is still poorly understood and speculative due to preservation biases and lack of data over large areas. From the Middle Jurassic of Southern Germany, adjacent Switzerland and extra-Carpathian Poland, all of these otherwise very well-studied Jurassic areas, only relatively few nautilid taxa have been reported yet (*e.g.*, Quenstedt, 1856–1858; Oppel, 1857; Neumayr, 1871; Engel, 1908; Jeannet, 1951; Schweigert, 2020, 2021; Dietze *et al.*, 2021; Jain *et al.*, 2023; Weis *et al.*, 2023). In most of the older papers nautilids are only listed but not illustrated. This is in sharp contrast to the much better documentation of Middle Jurassic nautilids in other European countries mainly due to the works of the eminent French palaeontologist Henri Tintant and his followers (*e.g.*, Branger, 2004, 2023; Rulleau, 2008, and literature cited therein).

In this study we report for the first time occurrences of the very rare Middle Jurassic nautilid genus *Pictonautilus* Branger, 2004 in the Upper Bathonian of southwestern Germany and Upper Bathonian or Lower Callovian of southern Poland. We take the opportunity to discuss the temporal and spatial distribution of this genus as well as its possible ancestry.

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GEOLOGICAL SETTINGS

The newly identified *Pictonautilus* specimen from SW Germany presented below was discovered in the fossil collection of Eberhard Rosswog (Wittnau). The exact finding level within a temporarily exposed very fossiliferous section in the township of Geisingen (Fig. 1) was reconstructed by direct comparison of the rock matrix and preservation with biostratigraphically well-dated samples from each bed of the same locality (Dietl, Niederhöfer, 2018, fig. 1). The bed that had yielded the nautilid is a finely iron-oolitic nodular marly limestone that is safely dated into the Orbis/Retrocostatum Zone of the Upper Bathonian by a few age-diagnostic ammonites (Dietl, Niederhöfer, 2018, p. 98), *e.g.*, *Procerites eichbergensis*. The intensively red-coloured iron-oolitic bed following immediately above yields very rich and high-diverse ammonite assemblages of Early Callovian age, with *Alcidia subdiscus*, *Cadoceras quenstedtiforme*, *C. suevicum*, *Choffatia* aff. *recuperoi*, *Homoeoplanulites* spp., *Kheraiceras bullatus*, *Macrocephalites jacquoti*, *Parachoffatia subbackeriae*, *Phlycticeras mexicanum*, among others (Fig. 2). Originally termed as "Orbis-Oolith" the Bathonian-age bed is the lowermost bed in the Geisingen section yielding iron ooids and is included here in the Rotes Erzlager Member of the Wutach Formation. Nautilids have never been reported before from the Bathonian of this section nor elsewhere in the area; some Callovian ones from higher-up in the section are under study.

The Polish *Pictonautilus* specimen was purchased by one of us (T.H.) from a Polish fossil trader. According to his communication the specimen originated from a temporary Middle Jurassic excavation in the forest area of the village Bolęcin, *ca.* 7.5 kilometres east of the town of Chrzanów.

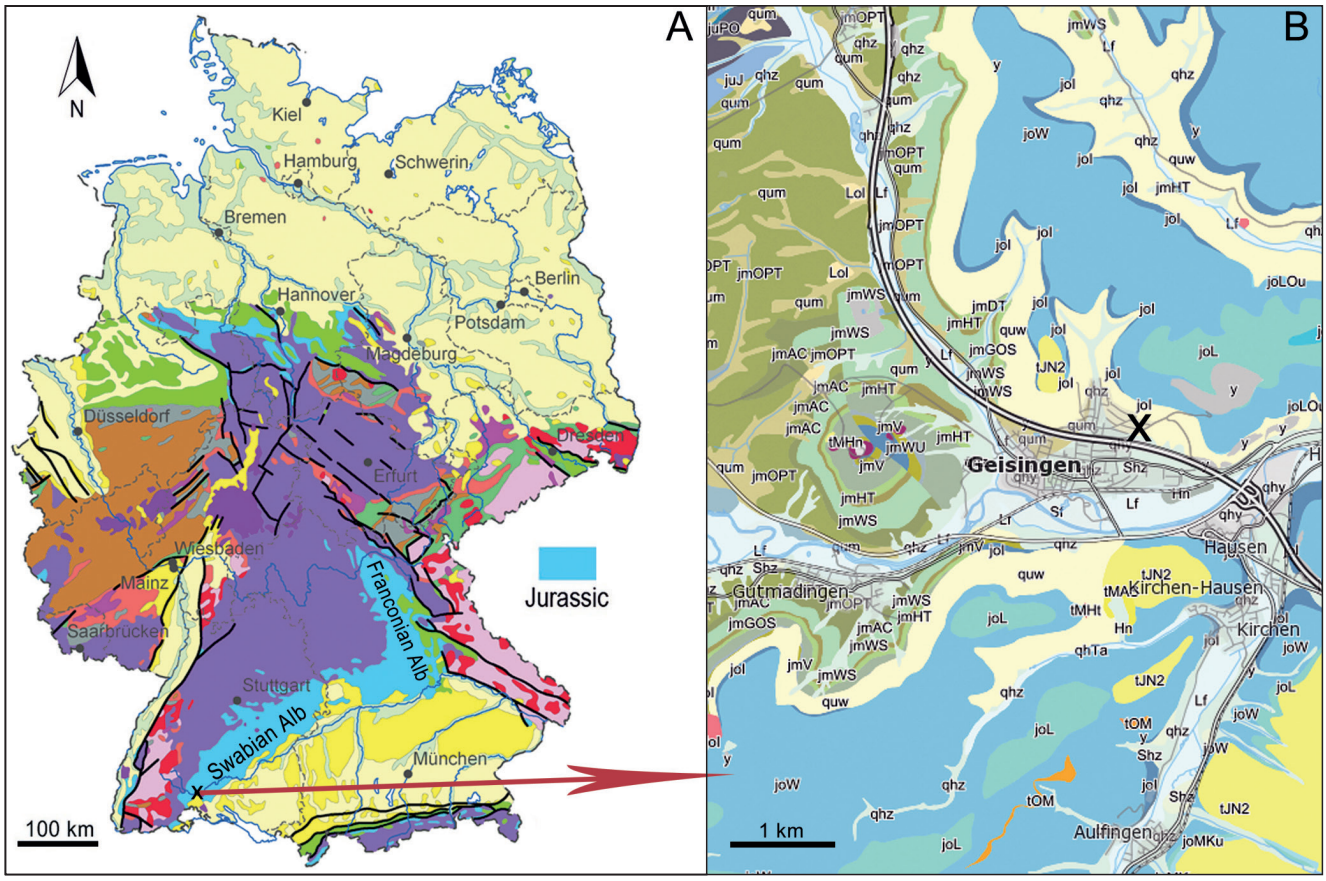

Fig. 1. Locality in SW Germany, where the specimen of *Pictonautilus verciacensis* (Lissajous, 1923) was found

A. Generalized geological map of Germany (modified from https://www.bgr.bund.de/). **B.** Detailed geological map of the vicinity of Geisingen in the westernmost part of the Swabian Alb (modified from https://maps.lgrb-bw.de/). The "X" marks the locality within the township of Geisingen. Olive and greenish colours – Middle Jurassic; blueish colours – Upper Jurassic; yellow and orange colours – Neogene; red-violet – Neogene volcanic rocks; white and grey colours – Quaternary and anthropogenic deposits

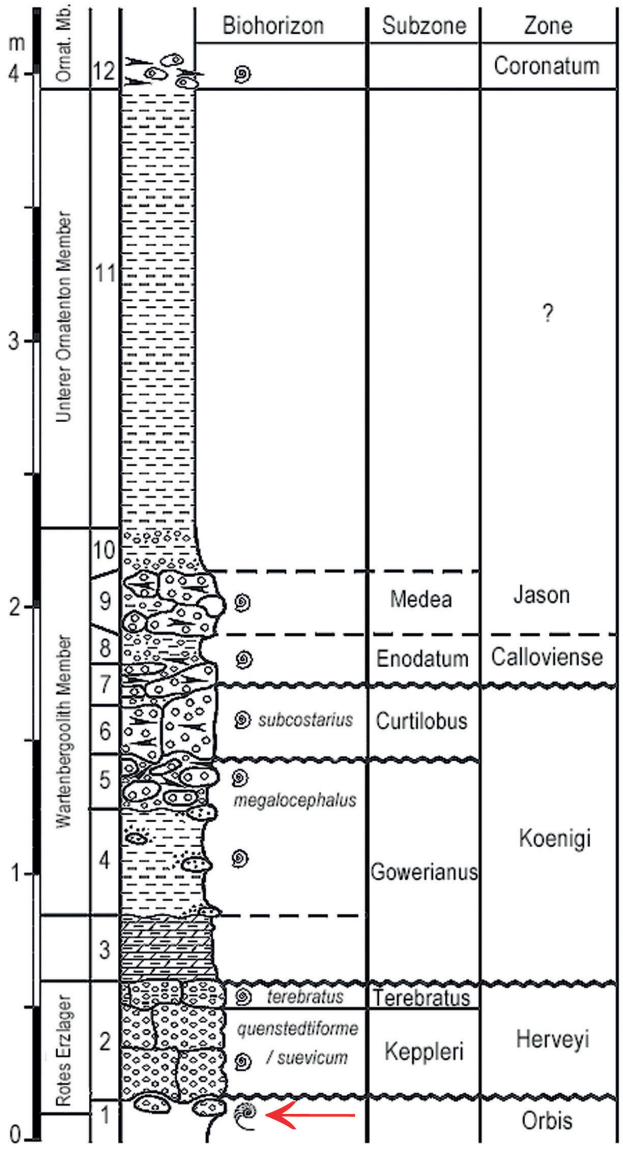

Fig. 2. Stratigraphy of the Wutach Formation at Geisingen with the finding level of *Pictonautilus verciacensis* (Lissajous, 1923) highlighted by a red arrow

Ornat. Mb. = Ornatenoolith Member. Section modified from Dietl, Niederhöfer (2018)

The iron-oolitic Bathonian–Callovian section of this area corresponds to the rock unit historically well-known as "Oolithe de Balin". This ferruginous oolite is highly condensed and ranges from the Upper Bathonian Orbis Zone at least to the Lower Callovian Gracilis Zone (Tarkowski *et al*., 1994). Numerous ammonite taxa indicative of a Late Bathonian age (*e.g.*, *Bullatimorphites suevicus*, *Clydoniceras discus*, *Epistrenoceras contrarium*, *Hemigarantia julii*, *Paroecotraustes maubeugei*) have been reported from there (Neumayr, 1871; Tarkowski *et al*., 1994; Mangold *et al*., 1996). Since all previously published records of *Pictonautilus verciacensis* come from beds of Middle to Late Bathonian age (Branger, 2023), a Late Bathonian age of the specimen from the "Oolithe de Balin" is very likely also for the Polish specimen. Moreover, a visual comparison with the preservation of ammonites from the same locality fits better with Bathonian ones, but an Early Callovian age cannot be totally excluded due to the lack of precise sampling data. Neumayr (1871) had listed two nautilid taxa within the Bathonian–Callovian cephalopod assemblage described from that area, *Nautilus calloviensis* Oppel, 1857 and *Nautilus subtruncatus* Morris and Lycett, 1850, but did not illustrate them. Due to their poor preservation, Neumayr (1871) himself stated he was not sure about the correctness of his determinations.

MATERIAL AND METHODS

The new specimens of *Pictonautilus* reported herein were prepared mechanically using fine chisels and scrapers and/or airbrasive blasting with iron powder.

The Jurassic nautilids illustrated herein are housed in the collections of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich, Germany (acronym SNSB-BSPM), of the ETH Zürich, Switzerland, of the Paläontologisches Institut und Museum der Universität Zürich, Switzerland (acronym PIMUZ), and of the Staatliches Museum für Naturkunde in Stuttgart, Germany (acronym SMNS), respectively. A photo of the holotype of *Nautilus verciacensis* Lissajous, 1923 stored in the palaeontological collection of Université Claude Bernard 1 in Lyon, France, was assessed via RECOLNAT (https://www.recolnat.org/).

SYSTEMATIC PALAEONTOLOGY

The high-level classification follows the suggestions of King, Evans (2019).

Subclass **Nautilia** Wade, 1988

Order **Nautilida** Agassiz, 1847

Superfamily **Nautiloidea** Blainville, 1825

Family **Paracenoceratidae** Spath, 1927
in Spath, 1927–1933

Genus ***Pictonautilus*** Branger, 2004

Type species. *Nautilus verciacensis* Lissajous, 1923, by original designation.

Included species. *Nautilus verciacensis* Lissajous, 1923. *Somalinautilus* ex gr. *clavifer* Tintant, 1994 and some specimens originally placed in *Pictonautilus* by Branger (2004) are excluded from this taxon and assigned to *Somalinautilus* Spath, 1927 (see Schweigert, 2020, 2021) and *Micronautilus* Branger, 2023, respectively (see Branger, 2023). See also discussion below.

Emended diagnosis. Medium-sized nautilid with high-trapezoidal whorl section; venter tabulate, bordered by prominent lateral carinae; marginal or median ventral sulci absent; umbilical wall well-rounded, umbilical width increasing with growth; Suture line with prominent widely expanding lateral lobe and rounded ventral lobe.

Distribution. Western and extra-Alpine eastern France (Lissajous, 1923; Branger, 2004, 2023), SW Germany (herein), extra-Carpathian Poland (herein).

Range. Middle Bathonian – Lower Callovian. Branger (2023, fig. 7) signalled the presence of "*Pictonautilus* sp." in the Lower Callovian but did not yet provide further information.

Pictonautilus verciacensis (Lissajous, 1923)
Figs. 3, 4

*1923. *Nautilus verciacensis* Lissajous, p. 48, pl. 2, fig. 1, 1a

2004. *Pictonautilus verciacensis* (Lissajous, 1923). – Branger, p. 143, pl. 1, figs. 1, 2 only

2016. *Pictonautilus verciacensis* Lissajous, 1923. – Grulke, p. 141, unnumbered figure bottom left

2023. *Pictonautilus verciacensis* (Lissajous, 1923). – Branger, appendix 2, fig. B

Holotype. Specimen illustrated by Lissajous (1923, pl. 2, fig. 1, 1a), Université Claude Bernard Lyon 1 – UCBL, Collections de paléontologie, Laboratoire de Géologie, no. UCBL-FSL 18692; Fig. 3A.

Type locality. Verzé, Dpt. Saône-et-Loire, France.

Type horizon and age. After Lissajous (1923) from the Bathonian "*Zigzagiceras arbustigerum* Zone" which approximately correlates with the Middle Bathonian (Hahn, 1972, p. 15). Ammonites from Verzé identified as *Zigzagiceras arbustigerum* by Lissajous (1923) were partly revised as *Prevalia kysylalmensis* (Besnosov, in: Besnosov, Mitta, 1993) and are of late Middle Bathonian age (Bremeri Zone, Bullatimorphus Subzone) (Mangold *et al.*, 2012).

Material studied. One specimen (SMNS 70692; Fig. 3B–E) from the Upper Bathonian "Orbisoolith" Bed at the base of the Wutach Formation at Geisingen, SW Germany and one specimen (PIMUZ 39863; Fig. 4A–D) from the Upper Bathonian (? or Lower Callovian) part of the "Oolithe de Balin" in the vicinity of Chrzanów, Poland.

Measurements.

Specimen	D [mm]	H [mm]	W [mm]	U [mm]	W/D	W/H
Holotype	123	72	55	10	0.45	0.76
SMNS 70692	105	62	52	6	0.50	0.84
2021.BR.N.050	110	58	64	7	0.58	1.10
PIMUZ 39863	170	70	80	18	0.47	1.14

Abbreviations: D = diameter; H = whorl height; W = whorl width; U = umbilical width.

Descriptions: SMNS 70692 (Fig. 3B–E) is an uncompressed internal mould preserved in a very finely iron-oolitic rock matrix with some indication of reworking and abrasion prior to final burial. The specimen is completely septate without showing any crowding of the septa. The whorl section is high-trapezoidal and relatively narrow. The venter becomes more and more flattened during ontogeny and is tabulate in the latest preserved state. The suture line shows a widely expanded lateral lobe and a relatively deep, well-rounded ventral lobe. The saddle between the lateral and the ventral lobe culminates in the ventrolateral edge. Position of the siphuncle is subcentral, not ventral as in *Pseudaganides* Spath, 1927.

PIMUZ 39863 (Fig. 4A–D) is an uncompressed, excellently preserved internal mould with some remains of the shell on one flank. The rock matrix is an iron-oolitic limestone. The shell remains are smooth, apart from growth lines. The absence of a spiral striation confirms the systematic placement in Paracenoceratidae Spath, 1927. The conch is completely septate lacking the body-chamber. There is no crowding of the septa discernible so that it remains unclear whether the specimen was adult or still subadult. The whorl section is high-trapezoidal but significantly broader than in SMNS 70692. The venter is tabulate and laterally bordered by marked angular crests. The suture line exhibits an expanded lateral lobe spanning almost the entire flank. On the venter a shallow ventral lobe is developed. It is slightly less deep and rounded than in SMNS 70692 probably as a result of the wider whorl section. The saddle between the lateral and ventral lobes coincides exactly with the position of the angular crests. The umbilicus is rather narrow but not closed and widens during growth.

The measurements of the newly recorded specimens fit well within the somewhat variable ranges reported for this species (cf. Branger, 2004). Interestingly, the W/H ratio of the new specimen from Germany (SMNS 70692; Fig. 3B–E) is very close to that of the holotype of *P. verciacensis* (Fig. 3A), whereas in the Polish specimen (PIMUZ 39863; Fig. 4A–D) this ratio is much closer to the best-reported and multiple illustrated French specimen from the Patrick

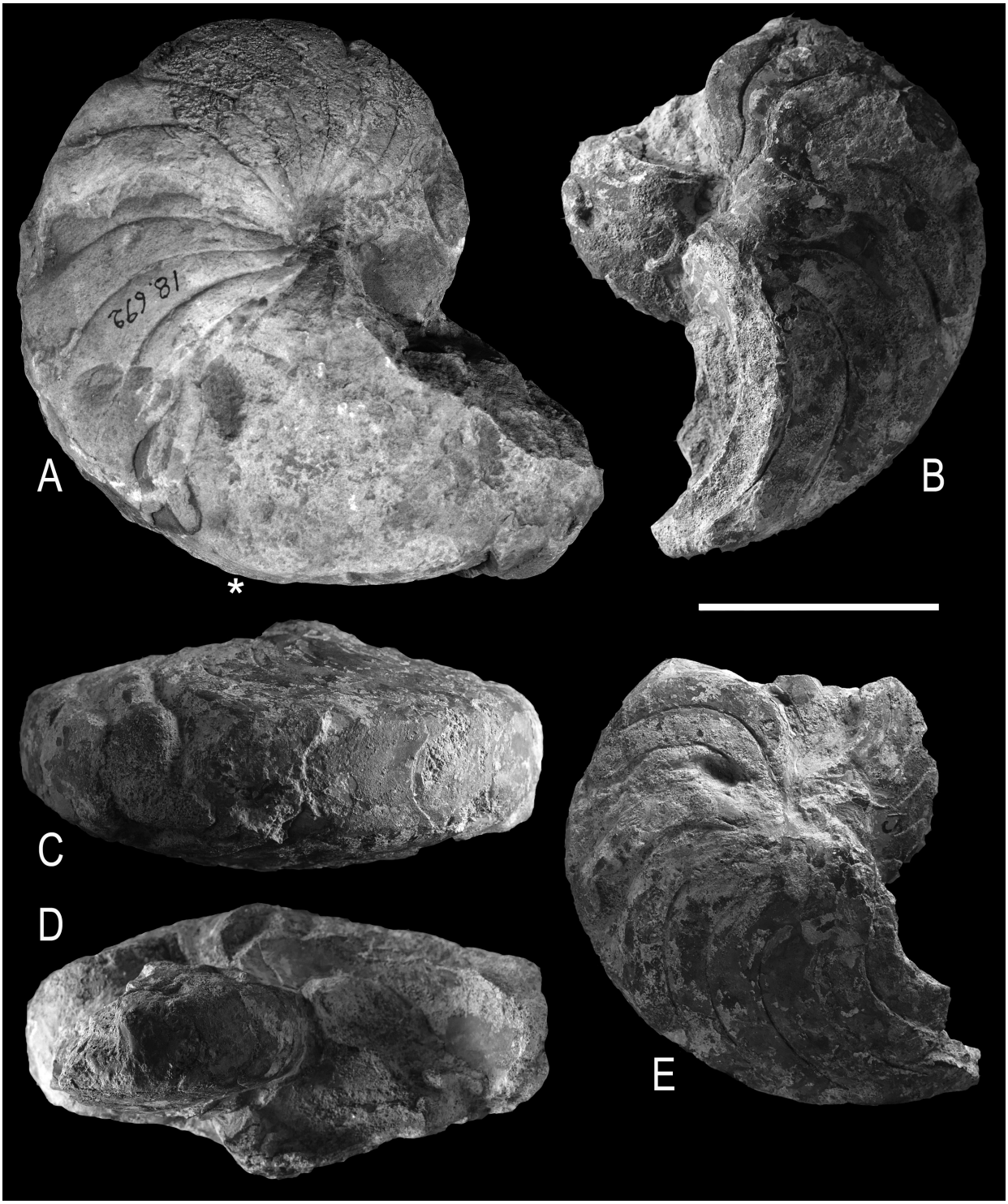

Fig. 3. ***Pictonautilus verciacensis*** **(Lissajous, 1923)**

A. Specimen UCBL-FSL 18692 (Marcel Lissajous collection), holotype, ? ♀, Middle Bathonian, Verzé, France; photo by courtesy of RECOLNAT (ANR-11-INBS-0004). **B–E.** Specimen SMNS 70692 (legit Eberhard Rosswog), ? ♀, in lateral (B, E) and ventral (C, D) views; Middle Jurassic, basalmost bed of Wutach Formation (Rotes Erzlager Member, "Orbisoolith"); Upper Bathonian, Orbis/Retrocostatum Zone; Geisingen, SW Germany.
Asterisk marks last septum. Scale bar equals 5 cm

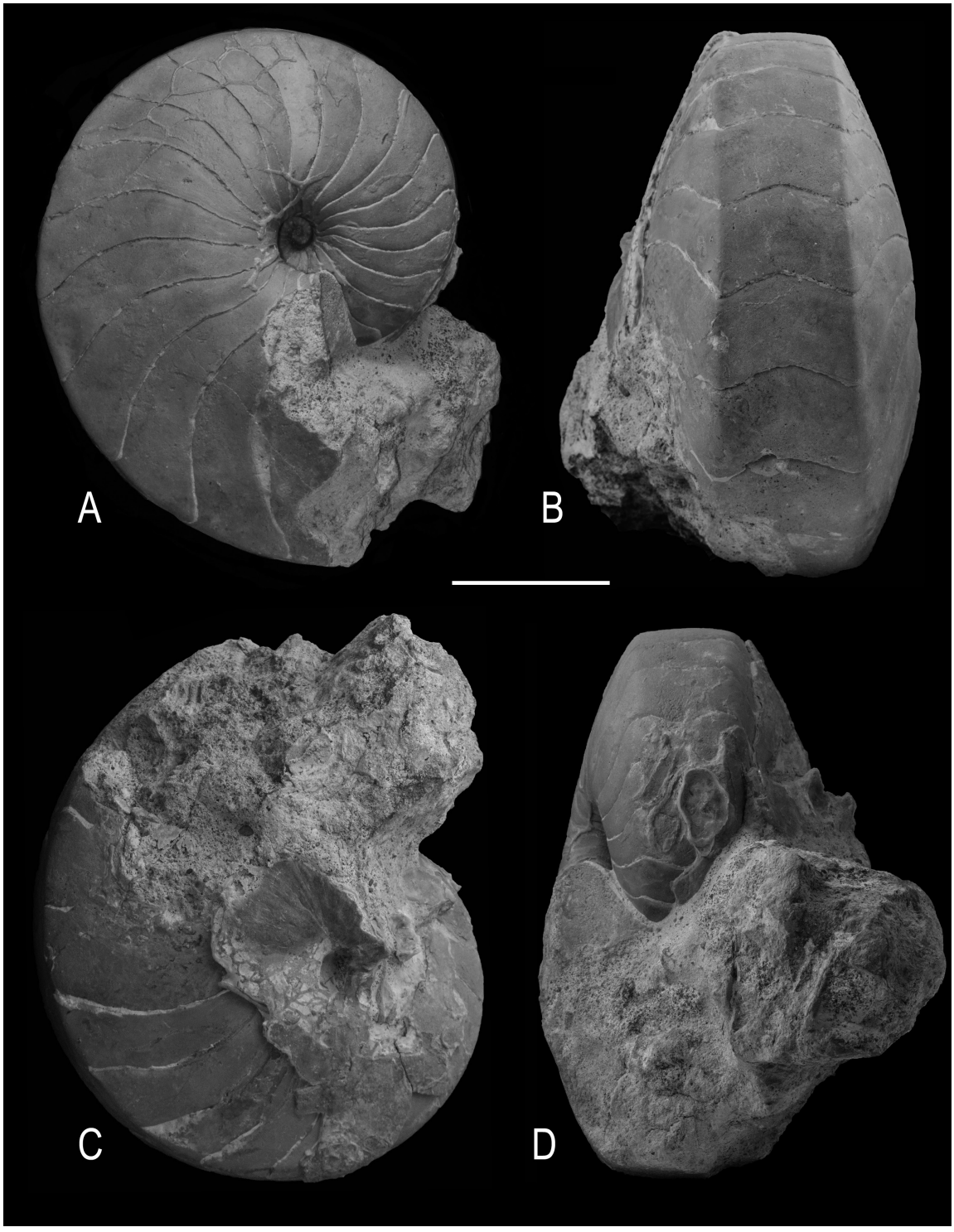

Fig. 4. A–D. *Pictonautilus verciacensis* (Lissajous, 1923)

Specimen PIMUZ 39863, ? ♂; "Oolithe de Balin" (Upper Bathonian or ? Lower Callovian); *ca.* 7.5 km E of Chrzanów, Poland. Scale bar equals 5 cm

Branger collection. Of course the small number of specimens available does not allow statistics, however, these very distant ratios can be easily explained by sexual dimorphism, which is reported both from modern (Saunders, Landman, 1987; Dunstan *et al.*, 2011) and Jurassic nautilids (*e.g.*, Crick, 1898; Schairer, Barthel, 1977; Schweigert, 2021). The dimorphism in nautilids is mainly expressed by significantly greater widths of the male shells. Great differences in shell diameter between the sexes as reported for ammonites with their so-called macroconchs and microconchs (Makowski, 1962; Callomon, 1963) were also thought to be adopted by fossil nautilids (Tintant, 1969, 1981), but we strongly concur with Branger (2023) and Jain *et al.* (2023) that this view was erroneous in the light of their modern analogues having similar diameters for males and females. The hitherto largest known specimen of *Pictonautilus verciacensis*, still lacking its body-chamber, is PIMUZ 39863 showing a remarkably wide whorl section. It is therefore considered a male, whereas the smaller holotype with its narrower whorl section at comparable respective diameters is considered a female. In the holotype, however, there is no crowding of the last septa behind the body-chamber so that this specimen was probably not adult either and even the females could reach somewhat larger diameters.

Occurrence. Extra-Alpine France (Poitou, Maconnais), SW Germany (herein), extra-Carpathian Poland (herein).

Stratigraphic range. Middle Bathonian – Early Callovian (Branger, 2023; this paper and personal communication by P. Branger).

DISCUSSION

In this study we report for the first time occurrences of the rare monotypic nautilid genus *Pictonautilus* Branger, 2004 from SW Germany and S Poland. As reported for other rare Jurassic nautilids, transgressions and high sea-levels as well as favorable environmental conditions have led to short-term spreads over large distances (Schweigert, 2020, 2022; Jain *et al.*, 2023). In this sense, the presence of *Pictonautilus* in the European epicontinental seas (Fig. 5) either results from post-mortem transport of empty floating shells by currents (*e.g.*, Chamberlain *et al.*, 1981; Reyment, 2008; Yacobucci, 2018) or from active immigration, possibly via

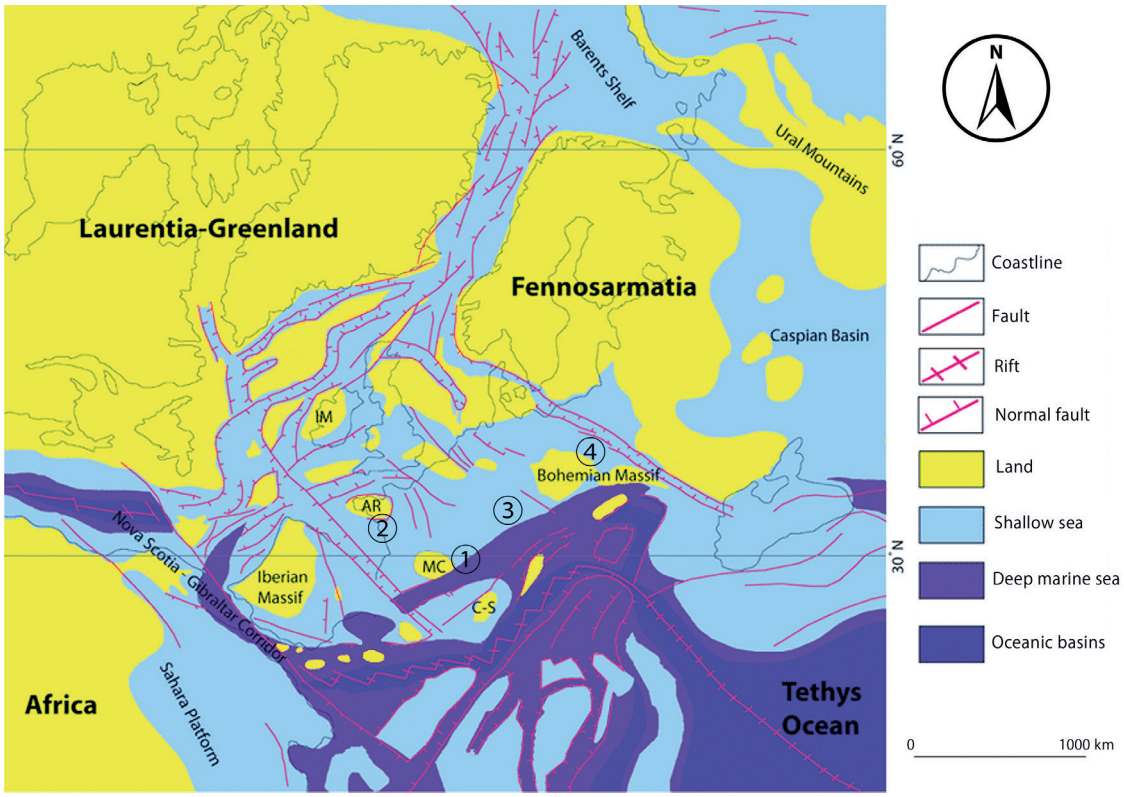

Fig. 5. Palaeobiogeography in the late Middle Jurassic with records of *Pictonautilus verciacensis* (Lissajous, 1923)

Abbreviations: IM – Irish Massif; AR – Armorican Massif; MC – Massif Central; C-S – Corsica-Sardinia Massif; 1 – Verzé, France (Lissajous, 1923; type locality); 2 – Western France (Branger, 2004, 2023); 3 – Geisingen, Germany (herein); 4 – Chrzanów, Poland (herein). Map modified from Kettle (2016)

a southern Tethyan route (Jain *et al.*, 2023). The preservation of the studied shells does not allow us to clearly distinguish between these possibilities. The absence of epizoans (except a few small oysters on the venter of the Polish specimen) and numerous co-occurring exotic ammonite taxa (*e.g.*, *Epistrenoceras contrarium*, *Hemigarantia julii*, *Bullatimorphites suevicus*, *Macrocephalites* spp.) in the Upper Bathonian of France and Poland as well as in the coeval beds of SW Germany, however, point to living populations.

Recently, a new paracenoceratid genus, *Micronautilus* Branger, 2023, was described from the Bathonian of western France. It was suggested that both *Micronautilus* and *Pictonautilus* derived from the "*Cenoceras*" *fuscum* group in the Late Bajocian. The latter is a representative of the long-ranging genus *Somalinautilus* Spath, 1927 and very close to the Early Bathonian *S. clavifer* Tintant, 1994. Both taxa, however, differ from *Pictonautilus verciacensis* in their adult whorl section showing a steep angular umbilical wall with an umbilical edge and characteristic shallow sulci bordering the ventrolateral crests on each side towards the slightly convex venter (cf. Tintant, 1994, figs. 3a, 6a). Moreover, they differ from *P. verciacensis* in their smaller size, and a narrowing of the umbilicus during ontogeny. This is why we hesitate to include *S.* ex gr. *clavifer* in *Pictonautilus* as practiced by Branger (2023) although we fully concur that all of them must originate from the same stock. To resolve the ancestry of *Pictonautilus*, *Somalinautilus* and their allies further data is needed from the still unknown evolutionary center of this family, possibly located somewhere in the Southern Tethys or Palaeopacific.

The new findings from Poland and southern Germany suggest that *Pictonautilus* may also be present in the Middle Jurassic of Switzerland (*e.g.*, in the basal Late Bathonian part of the Anwil Bed); however, there is no evidence yet. The Middle Jurassic nautilid *Nautilus (Paracenoceras) wilmae* Jeannet, 1951, from the Lower Callovian of Switzerland, was suspected to be assignable to *Pictonautilus*. The medium-size diameter, narrow umbilicus, suture line and tabulate venter reported for this species (Jeannet, 1951) as well as the ventrolateral crests marked by dashed lines in Jeannet's (1951, fig. 6) line drawing of the specimen point to such an identification. However, a study of the holotype (Fig. 6) clearly indicates that the venter is not tabulate but well-rounded and ventrolateral crests do not exist at all. Moreover, the umbilicus is nearly closed and the suture line crosses the venter almost straight thus lacking the distinct ventral lobe typical of *Pictonautilus verciacensis*. Because of this combination of characters we interpret *Nautilus* (*Paracenoceras*) *wilmae* as a junior subjective synonym of *Nautilus calloviensis* Oppel, 1857, the lectotype of which from the Alcide d'Orbigny collection was designated by Tintant (1969). Tintant (1969), however, erroneously included true *Paracenoceras*, *P. blakei* Jeannet, 1951, as its supposed "macroconchiate" sexual partner in "*Paracenoceras*" *calloviensis*. He also mixed up this species with specimens of *Somalinautilus* sp. and *Metacenoceras* sp. (Jain *et al.*, 2023). The traditional assignment of *Nautilus calloviensis* to *Paracenoceras* is challenged by the report of a spiral striation of the shell in related species from India (see discussion in Jain *et al.*, 2023).

Nautilus (*Paracenoceras*) *wilmae* Jeannet has been additionally cited from the Lower Callovian Koenigi Zone in the Wutach area of SW Germany (Zeiss, 1955: 246). The referred specimen (Fig. 7) is very small but complete. Its body-chamber widens at the distal end forming the aperture. The venter shows a weak median depression. These characters as well as the marked ventrolateral edges are clearly distinct from the taxon introduced by Jeannet (1951); it seems that Zeiss (1955) was misled by the poor and size-reduced line-drawings. The general outline, whorl section, suture line and size fits perfectly with *Nautilus dorsoexcavatus* Parona and Bonarelli, 1895, originally described from Lower Callovian beds at Chanaz in Savoy, today part of France. Tintant (1984) had assigned this taxon to *Paracenoceras* Spath, 1927 and interpreted it as a miniaturized species of this otherwise very large-growing genus. The specimen from the Wutach area is the sole record of this species from Germany and the only one from Europe besides the holotype. Further records of *Paracenoceras dorsoexcavatum* come from Lower Callovian beds of Saudi Arabia (Tintant, 1987) and namely from India (Halder, 2000a, b).

CONCLUSIONS

In this study we report for the first time occurrences of the rare monotypic nautilid genus *Pictonautilus* Branger, 2004 from SW Germany and S Poland. These records expand significantly the known palaeogeographic range of this genus previously only reported from France. The German record is firmly dated into the Late Bathonian Orbis Zone; a similar age is also likely for the Polish specimen, but we cannot fully exclude an Early Callovian age of the latter. The discontinuous stratigraphic range and the apparent absence of direct ancestors in the same area point to immigration events from the Tethys during favourable environmental conditions.

Nautilus (*Paracenoceras*) *wilmae* Jeannet, 1951, from the Lower Callovian of Switzerland, is definitely not a representative of *Pictonautilus* and is demonstrated to be synonymous with "*Paracenoceras*" *calloviense* Oppel, 1857. The sole report of *Nautilus* (*Paracenoceras*) *wilmae* besides the holotype is restudied here as well and could be identified as *Paracenoceras dorsoexcavatum* (Parona, Bonarelli, 1895).

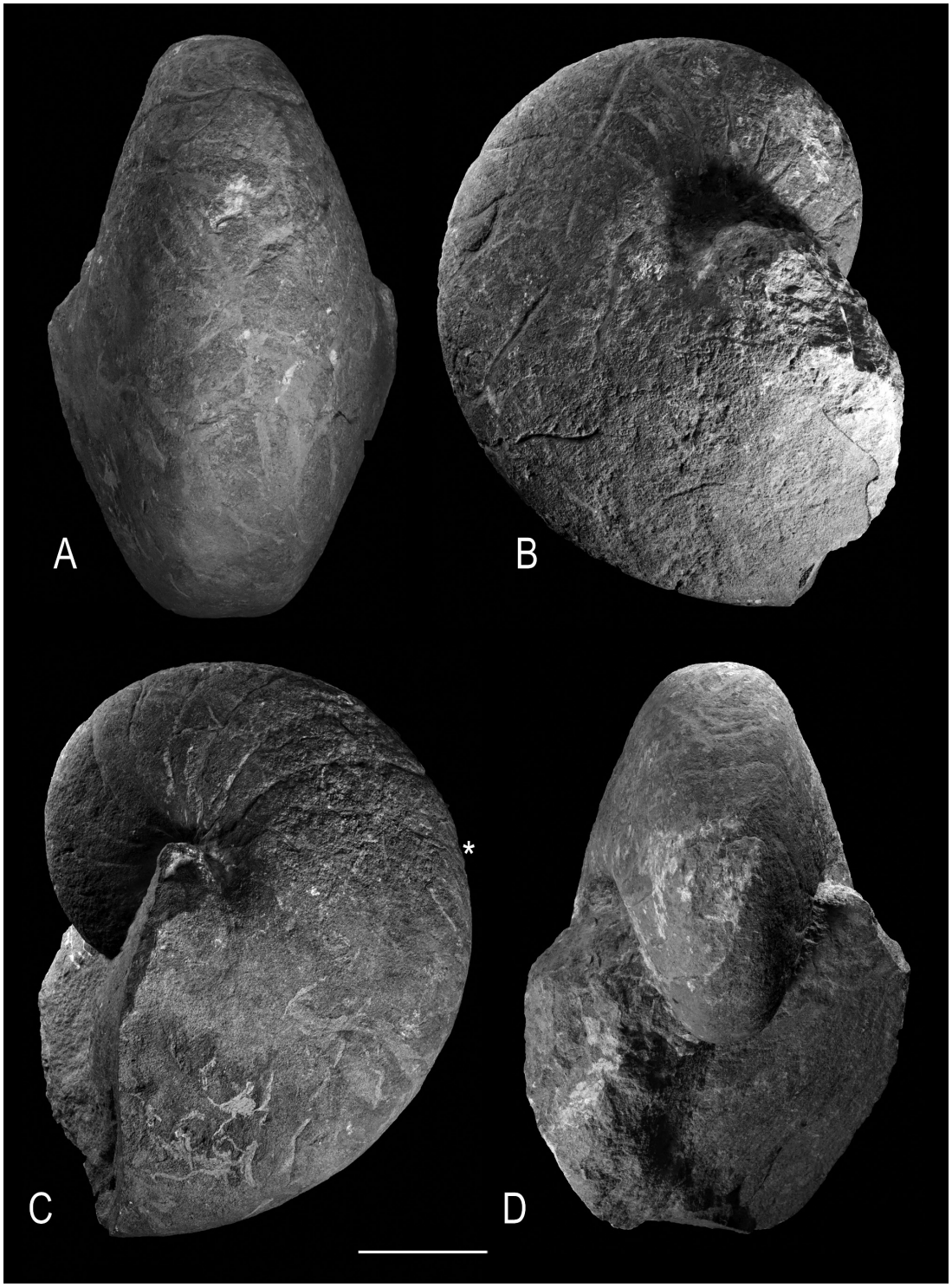

Fig. 6. A–D. "*Paracenoceras*" *calloviense* (Oppel, 1857) (=holotype of *Nautilus* (*Paracenoceras*) *wilmae* Jeannet, 1951), Alphonse Jeannet collection at ETH Zürich, no. eth000015366. Ifenthal Formation, Ängistein Member, lower part of "Unter-Erli-Bank" (formerly "Kornberg-Sandstein", see Bitterli-Dreher, 2019); Lower Callovian, Calloviense Zone; Herznach, Switzerland

Asterisk marks last septum. Scale bar equals 5 cm

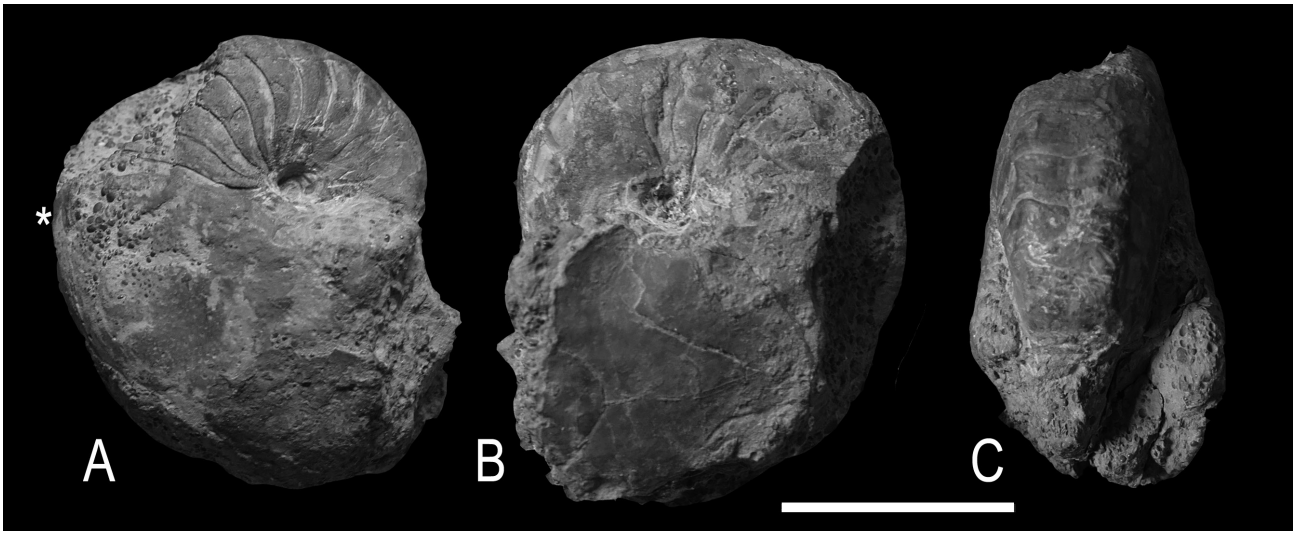

Fig. 7. A–C. "*Paracenoceras*" *dorsoexcavatum* (Parona, Bonarelli, 1895) (=Orig. *Nautilus* (*Paracenoceras*) *wilmae* Jeannet in Zeiss, 1955, p. 246); specimen SNSB-BSPG 1950 XXX 86; Wutach Formation, Graublaues Erzlager Member; Lower Callovian, Koenigi Zone; Blumberg, Germany

Asterisk marks last septum. Scale bar equals 2 cm

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