

Middle Anisian (Bithynian to Illyrian?, Middle Triassic) Ammonoidea from Rüdersdorf (Brandenburg, Germany) with a revision of *Beneckeia* Mojsisovics, 1882 and notes on migratory pathways

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Bithynian and Pelsonian (Anisian, Middle Triassic) Ammonoidea are generally rare in the Germanic Basin. Here, we describe ammonoids from the Jena and Rüdersdorf formations (Lower Muschelkalk) of Rüdersdorf (Brandenburg, Germany). This locality is peculiar in its isolated situation and its comparatively high diversity in ammonoids. This outcrop yielded several assemblages encompassing eight species: *Balatonites ottonis* (Buch, 1849), *B. balatonicus* (Mojsisovics, 1873), *B. egregius* (Arthaber, 1896), *Beneckeia buchi* (Alberti, 1834), *Bulogites zoldianus* (Mojsisovics, 1882), “*Ceratites*” *antecedens* (Beyrich, 1858), *Discoptychites dux* (Giebel, 1853) and *Noettingites strombecki* (Griepenkerl, 1860). When the geographic distribution of these species are compared, it becomes evident that immigrants from the southeast and the southwest met in that region. Such immigrations were only possible during transgressions. *Balatonites balatonicus*, *B. egregius* and *B. zoldianus* are recorded from the area for the first time. *Beneckeia* is revised with a focus on *Ben. buchi*, one of the few true endemites of the Germanic Basin, using synchrotron data to describe its early ontogeny. The holotype of “*Ceratites*” *antecedens* is figured for the first time and a lectotype for *Balatonites egregius* is designated. • Key words: Ammonoidea, Triassic, Anisian, Lower Muschelkalk, palaeobiogeography, ontogeny, synchrotron.

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Ammonoidea are usually absent to rare in most outcrops of the marine deposits of the terminal Buntsandstein and the Lower Muschelkalk (Triassic, Anisian) of the epicontinental Germanic Basin (Fig. 1). Although a number of taxa are recorded (see compilation in Urlichs & Mundlos 1985, Hagdorn 2020a), endemism, their scarce record and often poor documentation delimit their potential value for stratigraphy and palaeobiogeographic reconstructions. Only *Beneckeia buchi* (Alberti, 1834) is reasonably well documented, because it occurs comparatively frequently, locally even in larger numbers (e.g. Wagner 1921, Müller 1981, Schaumberg 1995). Following a number of early works on early Anisian ammonoids from the Germanic Basin (e.g. Wissmann 1840; Dunker 1851; Giebel 1853; Beyrich 1854, 1858; Griepenkerl 1860; Wagner 1888; Fritsch 1902; Frech 1903–1908; Rassmuss 1914; Schmidt 1907b, 1935; Assmann 1937),

later contributions are rare (e.g. Urlichs & Mundlos 1985, Dzik 1990, Kaim & Niedźwiedzki 1999, Klug *et al.* 2005). A continuously ongoing discussion concerns the question, which of these Lower Muschelkalk taxa represent species endemic to the Germanic Basin, and which species can be used for correlations outside the Germanic Basin (Claus 1955, Urlichs & Mundlos 1985, Urlichs 1999).

Here, we present an Anisian ammonoid fauna (Bithynian to Illyrian? age) from the Rüdersdorf quarry near Berlin (52° 28' N, 13° 47' E; Fig. 1). Located in a palaeogeographic position between the main part of the Germanic Basin and its southwestern gateway to the Tethys (Burgundy Gate) and the Silesian Muschelkalk in the southeast and its connection to the Tethys (East Carpathian and Silesian Main gates), the Rüdersdorf ammonoid assemblage reflects faunal incursions from both areas (Fig. 1).

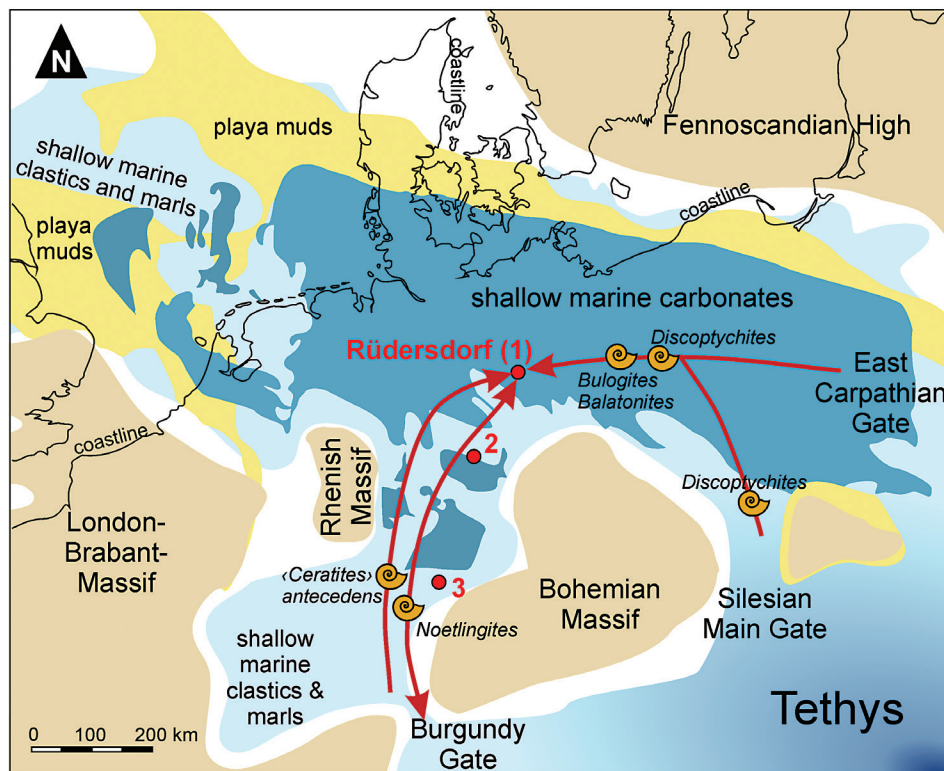


Figure 1. Simplified palaeogeographic map of the Germanic Basin including information from maps of Bachmann *et al.* (2010) as well as McKie & Williams (2009). The numbers 1–3 relate to the areas considered in Figure 2.

The first record of an unidentified ammonoid from the Lower Muschelkalk of the Rüdersdorf quarry date back to Overweg (1849), which was later identified as *Ammonites dux* Giebel, 1853 by Beyrich (1854). The author listed five specimens of *D. dux*, together with *Balatonites ottonis* (Buch, 1849), “*Ceratites*” *antecedens* (Beyrich, 1858) and *Beneckeia buchi* (Alberti, 1834) (Beyrich 1858, 1859a, b). Much later, Hardt (1952) described two specimens of *Noetlingites strombecki* (Griepenkerl, 1860) from the middle parts of the Jena Formation. Since then, no further data were contributed to the Ammonoidea of the area. Here, we describe the Rüdersdorf ammonoid fauna based on historical specimens and new finds. We revise the known taxa and put their Rüdersdorf occurrence into a palaeobiogeographic context.

Geological background

In the Rüdersdorf area, sediments of the Lower Muschelkalk Subgroup are exposed in the form of the Jena and Rüdersdorf formations, the latter interfingering towards the west with the Jena Formation, which itself – close to the southern limits of the Germanic Basin – grade into the marginal Freudenstadt Formation (Hagdorn & Simon 2020; Fig. 2). The occurrence of Triassic sediments within Quaternary deposits east of Berlin is related to a diapir, on top of which Buntsandstein and Muschelkalk sediments rest (Zwenger 1993, Jubitz 1994, Schroeder 1995a). This

explains its rather isolated position, quite far away from the next surface outcrops of the Lower Muschelkalk.

In the Rüdersdorf working quarry, strata from the Upper Buntsandstein (Röt Formation) to the Upper Muschelkalk (lower Meißner Formation) with a thickness of *c.* 270 m are exposed (Bithynian to Fassanian; Middle Anisian to Ladinian). A compilation of the geology of Rüdersdorf is found in Schroeder (1995a, b). Detailed logs of the Lower Muschelkalk from Rüdersdorf, applying to some extent the technical lithostratigraphic subdivision into lithounits A–L of Schwahn & Böttcher (1974), are found in Zwenger (1985), Kędzierski (2000), Zwenger & Koszinski (2009), and Kramm & Hagdorn (2020). A correlation of the Rüdersdorf Lower Muschelkalk with that of the central Germanic Basin was undertaken by Kędzierski (2000), Zwenger & Koszinski (2009) and Kramm & Hagdorn (2020). Our Figure 3 gives an overview on the lithostratigraphy of the Rüdersdorf section and is based on Zwenger & Koszinski (2009).

The top of the uppermost Röt Formation (terminal Buntsandstein) is formed by the Dornburg Member, the former *Myophoria* Beds (unit A), which represent the renewed flooding of the Germanic Basin from the east after a continental episode. It correlates in part with the top of the Lower Gogolin beds of Silesia, Poland (Hagdorn & Simon 2020, p. 436, fig. 1). This storm depositional setting is represented by a 13 to 14 m thick alternation of grey, thin, often tempestitic limestone and yellowish grey to slightly greenish grey intercalated marl (Streicher 1980).

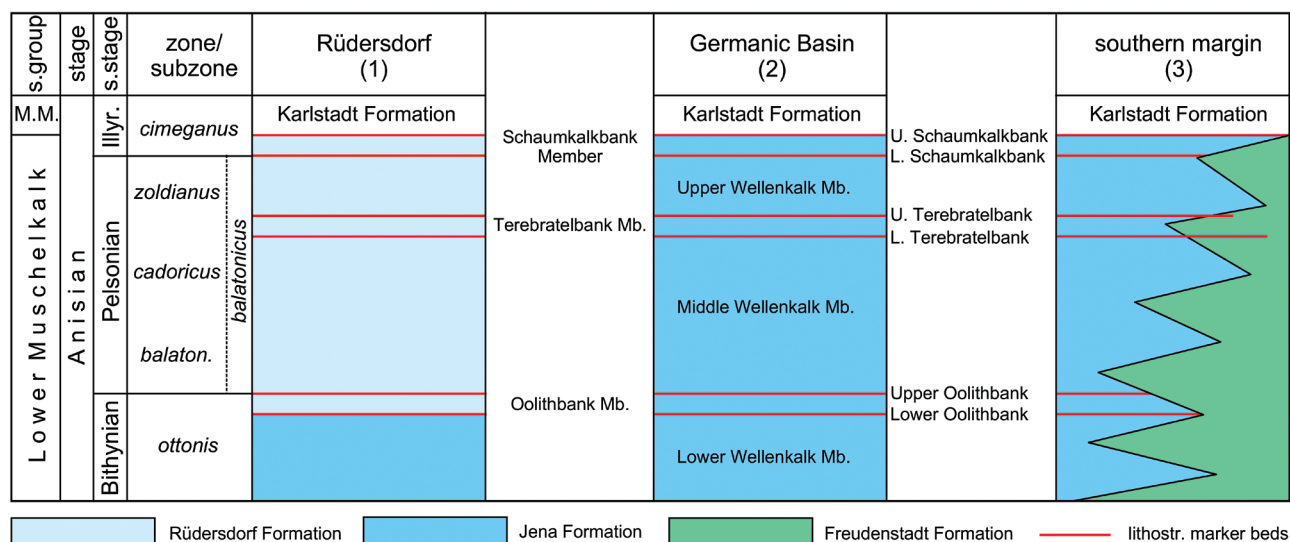


Figure 2. Generalized lithostratigraphic overview of the Lower Muschelkalk Subgroup in the Germanic Basin (modified after Hagdorn & Simon 2020). The biostratigraphic subdivision bases on Vörös (2003a) with modifications of Monnet *et al.* (2008); see also Jenks *et al.* (2015).

Few limestone beds exceed 10 cm in thickness and aid as marker horizons within the quarry (“5m-Bank”, “9m-Bank”, Zwenger & Koszinski 2009). The base of the Jena Formation (base unit B) is taken at an increase in the CaCO_3 content up to 78–88%, but sedimentologically, the transition is gradual. Only the lowermost part of the Jena Formation, the Lower Wellenkalk Member, is developed here. As in other parts of the Germanic Basin, it consists of an alternation of grey marl, intercalated with lighter grey to blue grey, shell-detrital limestone beds, most of which represent storm depositional events. Graded bedding and current-related sedimentary structures such as gutter and pot casts are frequent (Schroeder 1995b, 2015). The amount of tempestites and bed thickness increases progressively towards the top. The base of unit G has traditionally been taken as the base of the “Schaumkalk” (“foamy limestone”), a term used since Overweg (1849). The name derives from its high porosity due to dissolution of aragonitic ooids, and today, the “Schaumkalk” corresponds to the c. 73 m thick Rüdersdorf Formation. The Rüdersdorf Fm. (see Kramm & Hagdorn 2020 for details) reflects deposits of ooidal shoals with frequent shell-detrital beds and large-scale, shallow angle cross stratification. Lithostratigraphically, it correlates with the higher Jena Formation of the central Germanic Basin (Oolithbank Member to the base of the Karlstadt Fm., Fig. 2). Intervals with hardgrounds and burrowed surfaces with open burrow systems (“madige Schichten”: maggoty beds) represent periods of low sea-level and can be correlated with the classical marker beds of the Jena Formation in the central Germanic Basin (Oolithbank, Terebratelbank, Schaumkalkbank Member; Zwenger & Koszinski 2009, p. 44, fig. 15; Fig. 2).

Biostratigraphy, ammonoid fauna and palaeobiogeography

Comprehensive data on lithology and the integrated biostratigraphic subdivision of the Muschelkalk deposits of the Germanic Basin were given by Kozur (1974), Bachmann & Kozur (2004) and Kozur & Bachmann (2006). Recent biostratigraphic compilations are presented by Hagdorn (2020b), and an overview on the ammonoid stratigraphy and assemblages is given by Hagdorn (2020a). Here, we apply the ammonite biostratigraphic subdivision of the Anisian for the Balaton Highland (Hungary) of Vörös (2003a) with modifications of Monnet *et al.* (2008) (Fig. 3). The terminal Bithynian is represented by the *ottonis* Zone. The Pelsonian is characterized by the *balatonicus* Zone, further subdivided into the (in ascending order) *balatonicus*, *cadoricus* and *zoldianus* subzones. For the Rüdersdorf section, the application of the subzones is impossible due to the rarity of ammonoids, but some more general statements are possible, which have also been compiled in parts by Hagdorn (2020a) for the Germanic Basin.

The basal Muschelkalk of the Rüdersdorf section (Lower Wellenkalk and Oolithbank members) falls into the upper Bithynian *ottonis* Zone, which yields an assemblage of *B. buchi*, *N. strombecki* and *B. ottonis*. From Poland, *Acrochordiceras damesi* (Noetling, 1880) is known from this stratigraphic level. The rich *Balattonites* fauna without *B. balatonicus* from Raciborowice (Groß Hartmannsdorf, Lower Silesia, Poland; e.g. Rassmuss 1914, Holdefleiß 1915, Assmann 1937) represents possibly the terminal Bithynian (Vörös 2003b). *Balattonites spinosus* Picard, 1899 could be of the same age. This is a further *Bala-*

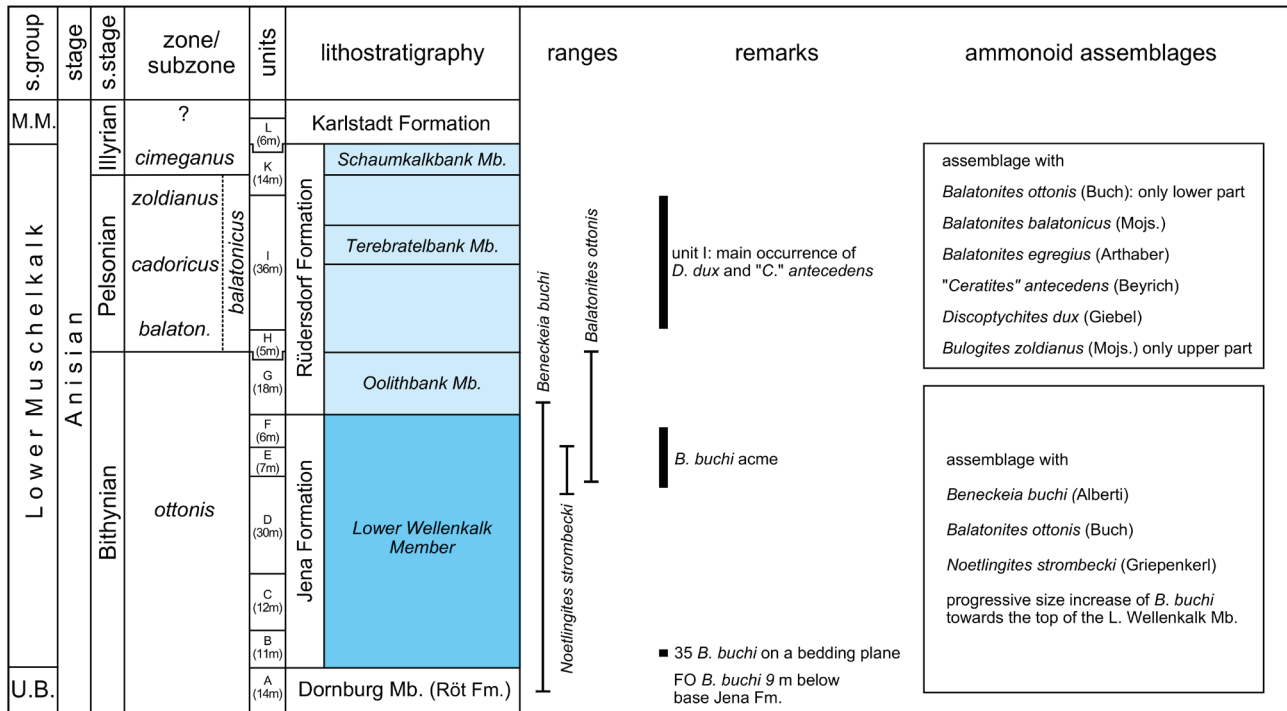


Figure 3. Lithostratigraphic subdivision of the Ruedersdorf Lower Muschelkalk Subgroup based on Zwenger & Koszinski (2009), with known ammonoid ranges and assemblages (please note: there exists no unit J in the original subdivision).

tonites, which is not from the *ottonis* but rather from the *egregius* group from just below the Oolithbank Member of Sondershausen (Thuringia, Germany). We re-interpret the inferred Pelsonian *Balatonites* fauna of Israel (Parnes 1986), together with *Pronoetlingites arifensis* (Parnes, 1962) and *Beneckeia* sp. cf. *B. wogauana posterior* Fritsch *sensu* Parnes (1986) stratigraphically as late Bithynian due to the absence of *B. balatonicus* (see below) and its resemblance to the the terminal Bithynian fauna from the Germanic Basin.

Lacking a good record of the index taxon, the base of the Pelsonian *balatonicus* Zone cannot be reliably determined in the Germanic Basin. Following Kozur (1974), an alternative ammonoid marker for the base of the *balatonicus* Zone is the first occurrence (FO) of "*C.*" *antecessens*, entering the stratigraphic record only 1 m above the Oolithbank Member (Wagner 1922). We, therefore, take – following Kozur (1974) as well as Bachmann & Kozur (2004) – the base of the *balatonicus* Zone tentatively at the top of the Oolithbank Member. This is in contrast to Hagdorn (2020a), who places the base of the Pelsonian at the base of the Oolithbank Member. The *balatonicus* Zone ammonoid assemblage of Ruedersdorf consists of *Balatonites balatonicus*, *B. egregius*, "*C.*" *antecessens*, *Discoptychites dux* and *Bulogites zoldianus*, the latter indicative of the Pelsonian *zoldianus* subzone.

The base of the Illyrian is taken with the FO of *Paraceratites trinodosus* by Ogg & Chen (2020), but this

datum is not in agreement with the use in Europe. We follow Monnet *et al.* (2008) by taking the base of the Illyrian with the FO of *Rieppelites cimeganus* (Mojsisovics, 1882), which likewise marks the FO of the genus *Judicrites* (Stiller & Bucher 2008, p. 556, fig. 7). Because *Bulogites* occurs in the Terebratelbank Member and *Judicrites* in the Schaumkalkbank Member (Hagdorn 2020a), the base of the Illyrian is best placed above the first and below the latter. The unclear situation becomes apparent in Hagdorn (2020a, p. 238, fig. 2), who puts the base of the Illyrian at the base of the Schaumkalkbank Member, while it is shifted to the top of the Terebratelbank Member in Hagdorn (2020b, p. 255, fig. 4). Because the Schaumkalkbank Member represents the FO of *Judicrites*, we take its base as the base of the Illyrian.

Judging from abundance and distribution of the recorded ammonoid species in the Germanic Basin (Urlichs & Mundlos 1985, Urlichs 1999, Hagdorn 2020a), *Balatonites ottonis*, *B. balatonicus*, *B. egregius* and *Bulogites zoldianus* reached the Ruedersdorf area most likely from the east, which might as well be true for *Discoptychites dux* (Fig. 1). Vice versa, "*Ceratites*" *antecessens* and *Noetlingites strombecki* play almost no roll in the eastern part of the basin and thus, an immigration *via* the Burgundy Gate is more likely (Fig. 1). The situation is less clear for *Beneckeia*. Given the rarity of *B. tenuis* and *B. buchi* in Poland (e.g. Assmann 1937, Kaim & Niedzwiedzki 1999), the abundance of *B. tenuis* in Thuringia (e.g. Passarge 1891)

and the locally great abundance of *B. buchi* in the entire Germanic Basin, in Rüdersdorf, and further southwest (e.g. Schmidt 1907a, Murr 1957, Hagdorn 2020a), the migrational pathway of the genus remains unclear. The distribution of *B. buchi* in the Germanic Basin suggests that it could be a descendant of *B. tenuis*, which persisted in relict habitats in the terminal Buntsandstein (Roetian). If correct, *B. buchi* would be a truly endemic species, which evolved in the Germanic Basin. Nevertheless, the questions for the origin of *B. tenuis* and from where it entered the Germanic Basin cannot be answered with the available data. This is also true for the migration route of *Beneckeia* to Israel.

Material and methods

Most specimens were collected in situ, and the stratigraphic position of historical specimens was re-assessed by plotting the technological stratigraphic subdivision of Schwahn & Böttcher (1974) against the lithostratigraphic subdivision of Zwenger & Koszinski (2009).

Institutional abbreviations are as follows: BT/X – Bundesanstalt für Geowissenschaften und Rohstoffe Berlin (X = “Originalesammlung”); FS – Frank Siegel collection; MB.C. – Museum für Naturkunde Berlin (C = “Cephalopodensammlung”); MHI – Museum Hagdorn Ingelfingen; MPRC – Museumspark Rüdersdorf (C = “Cephalopodensammlung”); NHMS-WT – Naturhistorisches Museum Schloss Bertholdsburg Schleusingen; JW – Jens Wiedenbeck collection; TB – Thomas Billert collection.

Abbreviations of main conch parameters and ratios based on Klug *et al.* (2015) are as follows: dm – diameter; bcl – body chamber length; ah – apertural height; wh – whorl height; ww – whorl width; uw/dm – umbilical width index; wh/dm – whorl height index; WER – whorl expansion rate; IZR – imprint zone rate.

The suture terminology (ELUI) follows Schindewolf (1929, 1951, 1954): external lobe E; lateral lobe L; umbilical lobe U; internal lobe I. The classification follows Tozer (1981).

Pyritized internal moulds of the initial whorls of *Beneckeia* were scanned by F. Marone at the TOMCAT beamline (Stampanoni *et al.* 2007) of the Swiss Light Source (SLS), Paul Scherrer Institut, Switzerland using synchrotron-radiation X-ray tomographic microscopy (SRXTM). The image stack obtained from the complete three-dimensional recordings (voxel size width = 2130, height = 1731, 1421 slices) were rendered by Serena Jobbins using Mimics v.19 software (<https://www.materialise.com/en/medical/software/mimics>, Materialise, Leuven, Belgium). The resulting 3D models were used to visualize the morphology of the initial chamber, the

embryonic conch, and the first whorls of *Beneckeia*. Tomographic data and 3D models are available on Figshare with the DOI 10.6084/m9.figshare.19576444.

Systematic palaeontology

Order Ceratitida Hyatt, 1884

Superfamily Ceratitoidea Mojsisovics, 1879

Family Hedenstroemiidae? Waagen, 1895

Genus *Beneckeia* Mojsisovics, 1882

(non *Beneckeia* Uhlig, 1882 = *Silesites* Uhlig, 1883)

Type species. – Type species is *B. buchi* (Alberti, 1834), subsequently designated by Spath (1934, p. 234).

Diagnosis. – Juveniles up to a size of ca. 5 mm moderately involute and more depressed than compressed, constrictions can occur. With increasing size and shift towards an involute and highly oxycone conch with a funnel-like umbilicus, first a keel and then an acute venter develops. Adults show a late egressive coiling in the last whorl. Broad flexuose ribs can occur on the body chamber. The undenticulated suture line with simple elements shows E and L and a number of up to 3–9 auxiliary lobes. Adventitious elements can occur.

Remarks. – The atypically developed suture line with unserrated elements makes it difficult to relate *Beneckeia* reliably to any concomitant ammonoid family. Originally, Mojsisovics (1882) included *Beneckeia* into the Pinacoceratinae Mojsisovics 1879. Spath (1934) gave an overview on the taxonomic odyssey of *Beneckeia*, excluded any relation to *Hedenstroemia* and kept a relation to a primitive *Lecanites* stock as possible. Finally, Parnes (1962) hypothesized that *Beneckeia* could derive from a common stock with the Hedenstroemiidae. Interestingly, serrations of the lobes can occur as atavistic features (*B. denticulata* Fritsch 1902, *B. subdenticulata* Pohl 1914; see below). Among more than 400 specimens of *B. buchi* from the Jena Formation of Rüdersdorf, only four fragments show serrations at the lateral and the adjacent umbilical lobe, but such serrations are well-documented (e.g. Seebach 1861; Eck 1879; Wagner 1888; Fritsch 1902; Schmidt 1907a, 1928). Wagner (1891) described even a multi-denticulated suture without any non-denticulated lobes in a *B. buchi* from the *Myophoria* Beds of Löbstedt/Rauhthale near Jena. From *Beneckeia levantina* of Israel, Parnes (1962) describes “lobes simple or feebly divided or denticulated” and “subdivision of the lobes by inflections on their bases is a constant character of the new levantine species and may also represent a new development”. The idea of

Diener (1915) to interpret the denticulation of the external lobation as an adventitious element is, therefore, possibly obsolete. Assuming that the serrations and denticulations reflect “atavistic” characters, genetically inherited from the immediate root of *Beneckeia*, its occurrence might be instead interpreted to be expression of developmental instability (environmental stress-induced “deviations of the actual phenotype from the target phenotype for the respective genotype and environment”, Klingenberg 2019, p. 3). Instable salinities in a storm-depositional system, such as typical of the Triassic Germanic Basin, potentially provide the environmental stress (see Ulrichs & Mundlos 1985). Noteworthy is the observation that comparably simplified suture lines with entire lobes and saddles occur also in some Cretaceous ammonite genera such as *Flickia* (Wright & Kennedy 1979, p. 695, text-fig. 2), *Libycoceras* (Zaborski 1982, 1983) or *Neolobites* (e.g. Wiese & Schulze 2005). In particular, fragments of *Neolobites* Fisher, 1882 (Fig. 4) can easily be confused with *Beneckeia* at first sight due to the overall similar conch morphology with a funnel-like umbilicus, faint ribbing as in *B. buchi* and its sutural development. This similarity was repeatedly reported (e.g. Spath 1934). *Beneckeia*, *Neolobites* and *Libycoceras* have in common that they occurred preferably in agitated, shallow water or nearshore settings, which raises the question whether or not the reduction of lobe/saddle incisions and the

development of numerous auxiliary lobes reflect an adaption to such an environment.

Eleven species and subspecies of *Beneckeia* have been described in the literature: *B. buchi* (Alberti, 1834), *B. cognata* Wagner, 1891, *B. denticulata* Fritsch, 1902, *B. levantina* Parnes, 1962, *B. levantina* sp. nov. var. Parnes, 1962, *B. majiashanensis* Guo, 1982, *B. sinensis* Frech, 1911, *B. subdenticulata* Pohlig, 1914, *B. tenuis* (von Seebach, 1857), *B. wogauana* (von Meyer, 1848) and *B. wogauana posterior* Fritsch, 1902.

We consider only *B. tenuis*, *B. buchi* and *B. levantina* as valid species. *Beneckeia subdenticulata* from the Röt Formation (Upper Buntsandstein) of Raciborowice (Groß Hartmannsdorf, Poland) is based on a single, unfigured specimen, in which the E lobe is described to show a serration. This is merely an atavistic feature as also observed in *B. tenuis*, why the specimen is best included in *B. tenuis*.

Beneckeia denticulata is a *B. buchi* with a serrated lobe (see below); *B. wogauana* shows no differences from *B. buchi* and is synonymized (see below); *B. wogauana posterior* corresponds to larger specimens of *B. buchi* (see below); *B. cognata* Wagner, 1891 was interpreted as *Beyrichites* by Frech (1903–1908) and Trammer (1972), but is now included in the genus *Intornites* (*Intornites cognata*; e.g. Hagdorn 2020a); *B. levantina* sp. nov. var. Parnes (1962) is included in *B. levantina* (Parnes 1962).

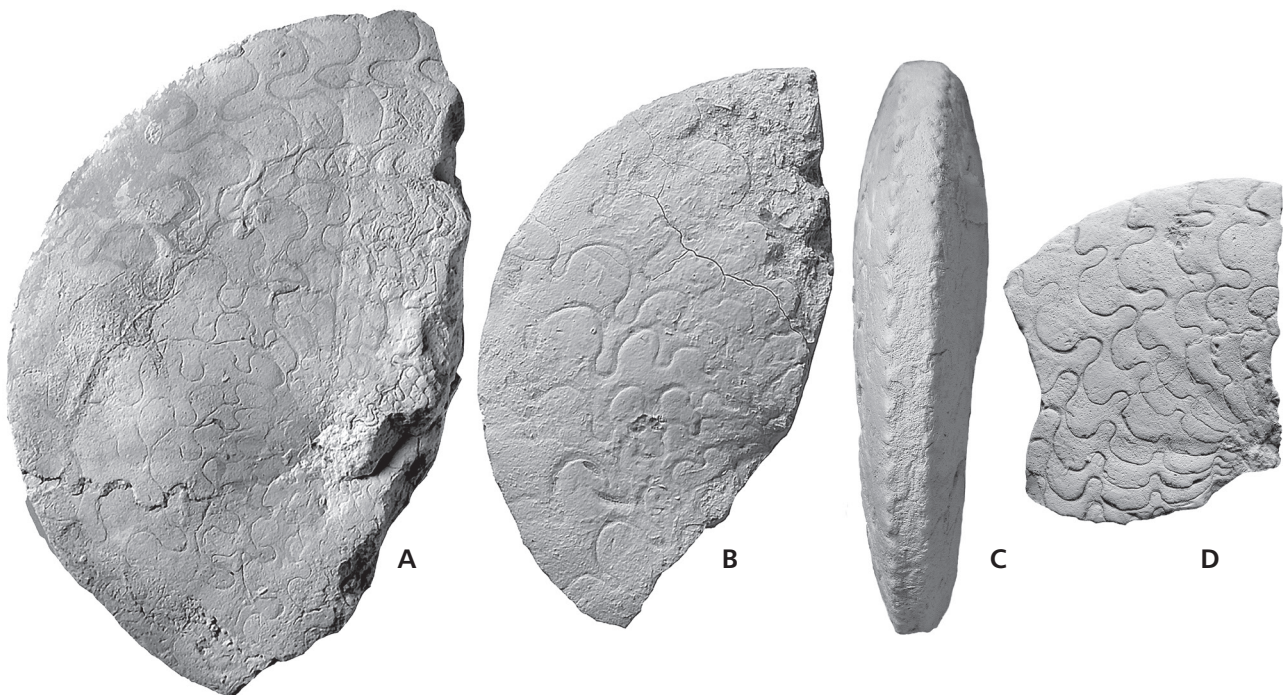


Figure 4. *Neolobites vibrayeanus* (d’Orbigny, 1841) from the Upper Cenomanian (Upper Cretaceous). A – MB.C. 3399 from Wadi Mujib, Jordan. B – MB.C. 5431 from Wadi Mor, Egypt. C – ventral view showing the typical flat venter and tuberculated ventral shoulder of *N. vibrayeanus* (MB.C. 3394, Wadi Mujib, $\times 0.7$). D – MB.C. 3404 from Wadi Mujib, Jordan (originals of Wiese & Schulze 2005, natural size).

here; *B. sinensis* Frech (1911, pl. 30, fig. 13) appears to be a corroded specimen. It shows a suture line with *ca.* three shallow and broad lobes and almost equally developed saddles, which does not fit that of *Beneckeia*. Thus, we exclude this taxon from *Beneckeia*. *Beneckeia majiashanensis* Guo (1982) from China is poorly preserved and the figured suture line cannot be related to *Beneckeia*.

Occurrence. – *Beneckeia* is known from The Netherlands, Germany, Poland and Bulgaria (see below). There are further records from the Lower to Middle Anisian of Palestine and Israel (Parnes 1962, 1986), Jordan and Egypt (Avnimelech 1958).

***Beneckeia buchi* (Alberti, 1834)**

Figures 5–10, Table 1

- 1834 *Ammonites Buchii* Alberti's.v.; Alberti, p. 52.
 1840 *Ammonites Buchi* Alb. – Wissmann in Leonhard & Bronn, pp. 533–536.
 1848 *Ammonites (Ceratites) Wogauanus*. – v. Meyer in Leonhard & Bronn, p. 465.
 1846–1849 *Ammonites Buchii* v. Alberti. – Quenstedt, p. 70.
 1849 *Ammonites Buchii* v. Alberti. – Quenstedt, pl. 3, fig. 12 a/b.
 1851 *Ammonites (Ceratites) Buchii*, v. Alb. – Dunker, pp. 335–336; pl. 42, figs 3–5.
 1853 *Ammonites Buchi* Alberti. – Schmid, p. 19.
 1854 *Ammonites (Goniatites) Buchii* v. Alb. – Beyrich, p. 515.
 1861 *Ceratites Buchii* v. Alberti. – Seebach, pp. 648, 650.
 1864 *Goniatites Buchii* v. Alberti sp. – Alberti, p. 182.
 1872 *Ammonites Buchii* Alb. – Eck, p. 57.
 1879 *Ammonites Buchi* Alb. – Eck, pp. 274–276.
 1880 *Ammonites (Ceratites) Buchii* v. Alb. – Noetling, pp. 332, 333.
 1882 *Beneckeia Buchi* (Alberti). – Mojsisovics, pp. 183, 184.
 1888 *Beneckeia Buchi* v. Alb. – Wagner, pp. 30–35; pl. 4, figs 1–4; pl. 5, figs 3–5.
 1888 *Ceratites Buchi* v. Alberti spec. – Picard, pp. 120–122; pl. 3, figs 1–2c.
 1891 *Beneckeia Buchi* v. Alb. – Wagner, p. 899, fig. 4.
 1902 *Beneckeia Wogauana* H. v. Meyer sp. – Fritsch, pp. 47, 48; pl. 4, fig. 1.
 1902 *Beneckeia Wogauana* mut. *Posterior*. – Fritsch, p. 47.
 1902 *Beneckeia denticulata* Fr. – Fritsch, pp. 48, 49.
 1902 *Beneckeia Buchii* (v. Alb.) Dunk. sp. – Fritsch, pp. 50–53; pl. 4, figs 2, 4, 5, 11.
 1903–1908 *Beneckeia Buchii* Dunker. – Frech, pl. 1, figs 6a–c.
 1906 *Beneckeia Buchi*. – Walther, p. 70, fig. 60.
 1907a *Beneckeia Buchi* (v. Alb.) Dunk. – Schmidt, pp. 83–89, figs 4–8; pl. 2, figs 1–3.
 1921 *Beneckeia Buchi* Alb. sp. – Wagner, pp. 425–428.
 1927 *Beneckeia Buchi* v. Alb. – Walther, p. 40; pl. 9, figs 60, 60 a.
 1928 *Beneckeia Buchi* v. Alberti sp. – Schmidt, p. 288, fig. 796.
 1928 *Beneckeia wogauana* H. v. Meyer sp. – Schmidt, pp. 288, 289, fig. 797.
 1934 *Beneckeia buchi* (Alberti), Quenstedt sp. – Spath, pp. 232–235, fig. 79a.
 1952 *Beneckeia buchi* v. Alb. – Hardt, pp. 97, 98, fig. 52.
 1955 *Beneckeia buchi* v. Alberti. – Claus, p. 37; pl. 1, fig. 4a, b.
 1955 *Beneckeia wogauana* H. v. Meyer. – Claus, p. 37; pl. 2, fig. 1a, b.
 1957 *Beneckeia buchi* Alb. – Murr, pp. 33–36.
 1959 *Beneckeia buchi* v. Alb. – Rothe, p. 68, fig. 4.
 1965 *Beneckeia buchi* (v. Alb.). – Müller, p. 189, fig. 253.
 1972 *Beneckeia buchii* Dunker. – Dertien, p. 132, unnumb. fig.
 1972 *Beneckeia wogauana* H. v. Meyer. – Schaumberg, p. 269, unnumb. fig.
 1975 *Beneckeia spec.* – Tjalkens, p. 192, unnumb. fig.
 1975 *Beneckeia spec.* – Dertien & Dertien-te Voortwis, pp. 93, 94, fig. 1.
 1980 *Beneckeia buchi*. – Streichan, p. 1034, fig. 3.
 1981 *Beneckeia buchi* (v. Alb.). – Müller, p. 214, fig. 273.
 1986 *Beneckeia buchi* (Alberti). – Baumgarte & Schulz, p. 89, fig. 3.
 ? 1986 *Beneckeia* sp. cf. *B. wogauana posterior* Fritsch. – Parnes, pl. 2, fig. 1.
 1986 *Beneckeia buchi* (Alberti, 1834). – Malinowska, pl. 20, fig. 3.
 1988 *Beneckeia buchi*. – Knappe & Tröger, p. 26, fig. 19.1.
 1990 *Beneckeia buchi*. – Streichan, p. 73, unnumb. fig.
 1991 *Beneckeia buchi* (Alberti, 1834). – Senkowiczowa, pp. 118, 119, figs 10, 11; pl. 3, fig. 3.
 1994 *Beneckeia buchi* (v. Alb.). – Müller, p. 239, fig. 268.
 1995 *Beneckeia buchi* (v. Alberti). – Schaumberg, pp. 169–175, figs 1–5b.
 1999 *Beneckeia buchi* (Alberti, 1834). – Kaim & Niedźwiedzki, pp. 109–110, fig. 12a, b.
 2004 *Beneckeia buchi*. – Hagdorn, p. 35, fig. 82.
 2012 *Beneckeia buchi* (von Alberti, 1834). – Ackermann & Mulder, p. 64, fig. 65; pl. 9.
 2012 *Beneckeia buchi* (v. Alberti). – Wannenmacher & Stappenbeck, p. 224, fig. 3, p. 225, fig. 6.
 2014 *Beneckeia buchi*. – Müller et al., fig. 27.2.
 2015 *Beneckeia buchi*. – Schroeder, p. 16, fig. 5.5–6.
 2019 *Beneckeia buchi* (von Alberti, 1834). – Eldijk et al., p. 189, fig. 3c.
 2019 *Beneckeia buchi*. – Gümbel, p. 41, fig. 31 a–d.
 2020a *Beneckeia buchi* (v. Alberti, 1834). – Hagdorn, p. 248, fig. 1a–c; p. 249.
 ? 2021 *Beneckeia* sp. – Niedźwiedzki et al., fig. 5.

Table 1. Conch parameters in mm and ratios of *Beneckeia buchi*.

Specimen	dm	bcl	ah	wh	uw	ww _{min}	ww _{max}	uw/dm	wh/dm	WER	IZR
NHMS-WT2908	23				2.6?			0.11?			
NHMS-WT2911	72	155?			3.0?			0.04?			
NHMS-WT2904	53	90	17	31	1.2?			0.02?	0.58	2.17	0.45
NHMS-WT2891	60	112?		32		7	13		0.53		
NHMS-WT2896	62	88	20	38					0.61	2.18	0.47
NHMS-WT2897	21	37	8	13					0.62	2.61	0.38
NHMS-WT2900	40	75	16	25?					0.63?	2.78	0.36?
NHMS-WT2898	88	110	25	55					0.63	1.95	0.55
NHMS-WT2894	90	108	26	52	2.0	10	15	0.02	0.58	1.98	0.50
NHMS-WT2895	68	90	20	38					0.78	2.01	0.47
NHMS-WT2893	40				2.2?			0.06?			
NHMS-WT2892	76	115	24	43	3.2			0.04	0.57	2.14	0.44
NHMS-WT2906	60	80	18	35					0.58	2.86	0.49
MPRC 05	61	80	16	33	2.0?			0.03?	0.54	2.22	0.52
MPRC 07	45	80	14	24	1.0?			0.02?	0.53	2.90	0.42
MPRC 12	59	115	18	30	1.3?			0.02?	0.51	2.88	0.40
MPRC 21	58	90	16	33					0.57	2.76	0.55
MPRC 24	41	77	13	25					0.67	2.93	0.48
MPRC 28	42	80	16	25?	1.2?			0.03?	0.6?	3.23	0.36?
MPRC 33	44	78	15	27?					0.61?	3.00	0.44?
MPRC 34	61	125	18?	34?					0.56?	2.84?	0.47?
MPRC 35	62	85	17	35		6	10		0.56	2.76	0.51
MPRC 36	47	78	15	28	1.2			0.03	0.60	2.94	0.46
MPRC 37	44	82	17	25					0.57	3.26	0.32
MPRC 38	56	90	17	34					0.61	2.87	0.50
MPRC 39	24	42	7?	13					0.54	2.82?	0.46?
MPRC 40	65	90?	14?	40?					0.62?	2.55?	0.65?

Type. – The specimens mentioned by Alberti (1834, p. 52) from “Horgen, Niedereschach, Dunningen, Seedorf, auf den 24 Höfen” were never figured, but parts of the collection survived in the Naturkundemuseum Stuttgart. However, the type series consists of pyritized, partly poorly preserved inner whorls of juveniles, none of which is suitable to serve as a type. Thus, a neotype with better material from the type area needs to be selected.

Material. – From the 400 specimens available to us, the following were used in this study: NHMS-WT2908, NHMS-WT2911 (unit A, higher *Myophoria* Beds); NHMS-WT2891, 2892–2898, 2900–2902, 2904, 2908, 2909, 2911, 2914–2934, 2937, 2938, 2940, 2941, 2943–2947, 2951, 2953–2956, 2958, 2963–2983, 2985–2991 (units B–F, Lower Wellenkalk Member); NHMS-WT2906 (unit

G, Oolithbank Member); MPRC01–MPRC16, MPRC20–MPRC41 (units B–F, Lower Wellenkalk Member); X-06082 (higher Lower Wellenkalk Member); BT-51816/55, BT-51758, BT-51759, BT-51766, BT-51780, BT-51782 (units B–F, Lower Wellenkalk Member). Because no juvenile material was available, we used some material from the “buchi Mergel” [*buchi* Marls] of the type locality “24 Höfe” (Freudenstadt Formation, Baden Württemberg) to convey the complete ontogenetic development of *B. buchi* (NHMS-WT3062–3068).

Description. – *Beneckeia buchi* is a medium-sized species of *Beneckeia* with an adult diameter between ca. 50 and max. 110 mm. Small variants carry an acute keel. The conch is extremely involute, compressed, with gently vaulted flanks, which are slightly inclined towards the

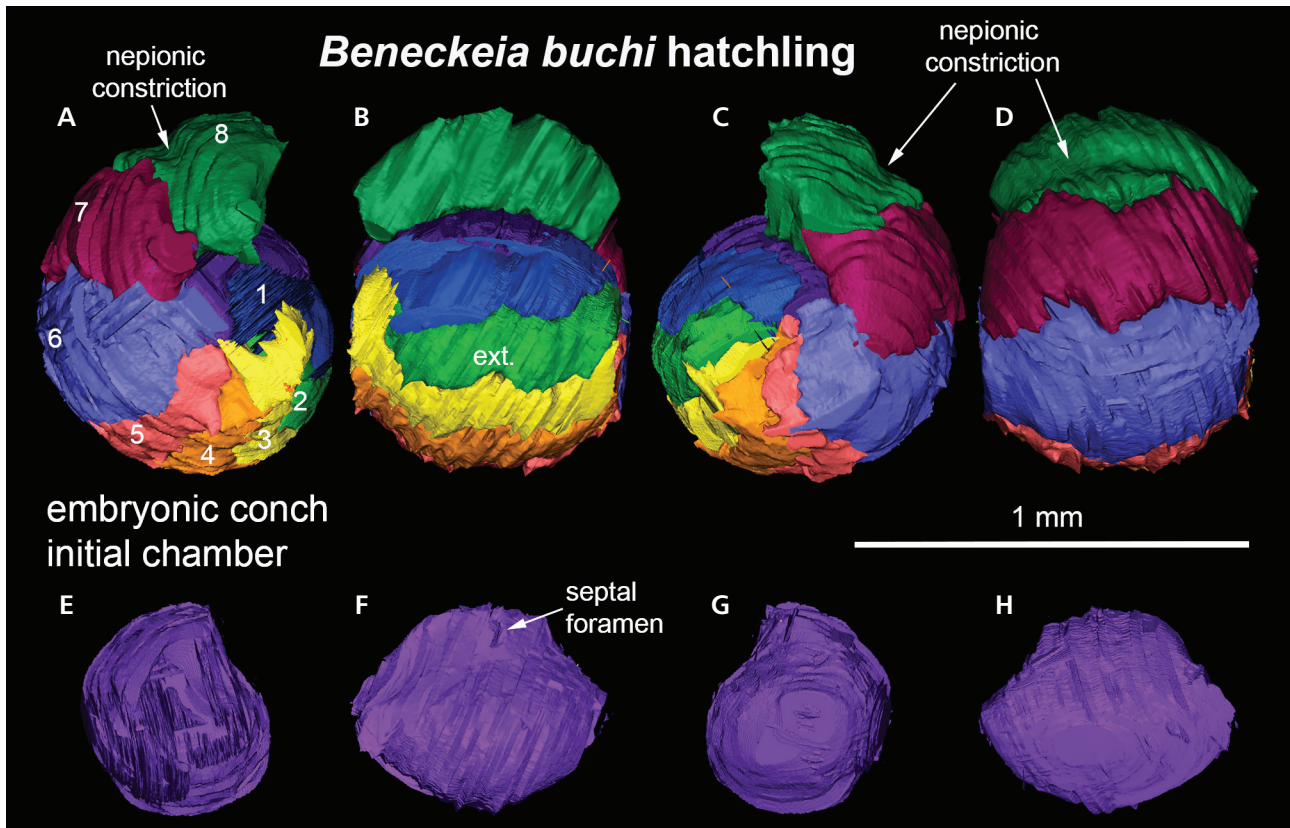


Figure 5. Initial chamber and ammonitella (conch of the hatchling) of *Beneckeia buchi* (Alberti, 1834), Freudenstadt Fm., «24 Höfe», district Loßburg, specimen NHMS-WT3066 (see also Figs 6 & 7E). Renderings based on an image stack obtained through synchrotron-radiation X-ray tomographic microscopy (SRXTM). A–C – embryonic conch; A – left side, all chambers are numbers; note that the initial chamber is almost completely covered by the first whorl; B – apertural (dorsal) view; note the external lobes and the septal perforation in septum 8; C – right side, note the nepionic constriction. D – ventral view. E, F – initial chamber; E – left side; F – apertural (dorsal) view; note the septal perforation and the very broad geometry. G – right side. H – ventral view.

umbilicus. Juveniles are almost subspherical with constrictions; quickly becoming oxyconic at diameters over 5 mm. Lobes harmonically rounded with wide bases, flanks of lobes nearly parallel, saddles significantly wider than lobes; up to 9 visible lobes on the flanks. Our material represents most growth phases, and we discern five developmental stages (measurements and ratios in Tab. 1):

1) Initial chamber and embryonic conch (not represented in the Rüdersdorf material): The embryonic conchs are known from pyritic internal moulds of minute specimens from the Kocher valley (southern Germany). Synchrotron revealed details of the initial chamber and first whorl of specimen NHMS-WT3066 (Figs 5, 6, 7E). In this specimen, the broadly ovoid initial chamber (Fig. 5E–H) has a diameter of about 0.55 mm, it is 0.65 mm wide, and the first septum (protoseptum) is 0.15 mm high. Although visible (Fig. 5F), the size of the septal foramen cannot be determined exactly, it is probably nearly 0.1 mm wide. The first septum is only slightly folded, with gently vaulted external, lateral and internal lobes.

The nepionic constriction is well visible in Figures 5C and D. Accordingly, the embryonic conch measures

about 0.95 mm in diameter and it is 0.75 mm wide. The aperture at the nepionic constriction of this specimen has an apertural height of about 0.25 mm and the whorl height is slightly over 0.4 mm. The embryonic conch is subspherical and the umbilicus is very narrow, although the resolution of the scan is not sufficient to quantify this.

2) Hatchling, early juvenile/neoconch (not represented in the Rüdersdorf material). The earliest whorls of *B. buchi* are involute and inflated with a gently rounded venter without keel. 3–4 constrictions/whorl occur on the flanks. NHMS-WT3067 (dm 3.5 mm, Fig. 7F) shows early growth stages without constrictions, but with a rounded aperture and a broad umbilicus. NHMS-WT3068 (dm 4 mm, Fig. 7G) displays also the evolute coiling of the inner whorls, while NHMS-WT3066 (dm 4.5 mm, Figs 6, 7E) shows the first shallow constrictions. Ontogenetically early sutures are visible in NHMS-WT3068 (Fig. 7G), where the lobes are widely open and septal distances are wide. The umbilicus is evolute in all these specimens and represents nearly one-third of the conch diameter. In NHMS-WT3065 (Fig. 7D), the umbilicus is already more narrow and the body chamber accordingly longer. A keel

is still missing in this ontogenetic stage. These growth stages range from the ammonitella with a diameter of around 1 mm to early juvenile (neanic) conchs of about 5 mm.

3) Juvenile (not represented in the Rüdersdorf material): At diameters of around 5 mm, the conch section becomes oxyconic. Body chamber and phragmocone become flattened, increasing simultaneously in apertural height, and the umbilical width becomes smaller. The body chamber increases proportionally in size, and the constrictions on the flanks become weaker before they disappear (NHMS-WT3064, Fig. 7C). A keel develops, which is not bordered by depressions or furrows. At diameters between 8 and 10 mm, the typical features of a keeled oxyconic conch are more (NHMS-WT3062, Fig. 7A) or less (NHMS-WT3063, Fig. 7B) well developed. The external lobes begin to extend beyond the venter onto the flanks (NHMS-WT3062, Fig. 7A).

4) Preadult (10 to 40 mm): Specimen NHMS-WT2897 (Fig. 8B) is the smallest conch currently known from Rüdersdorf. At a diameter of 21 mm, it displays all characters of the species. Specimen NHMS-WT2900 (Fig. 8F) is preserved with a body chamber that occupies almost 220° of the terminal whorl at a diameter of 40 mm. In specimen NHMS-WT2893 (Fig. 8D), the body chamber measures 275° at the same diameter 40 mm. Conchs of this size range still have body chambers that form more than half a whorl. At this growth stage, the conchs still appear slightly inflated compared to the adults; they display slightly vaulted flanks and a moderately acute keel (specimen NHMS-WT2900 at 40 mm diameter, Fig. 8F). The umbilicus is still wider than in mature conchs (uw 2 mm in specimen NHMS-WT2900 at 40 mm diameter, up to 4 mm in specimen NHMS-WT2893 at diameter of 40 mm). The concavity on the flanks adjacent to the umbilicus is not or weakly discernible in this growth stage (e.g. in specimen NHMS-WT2904; Fig. 9F).

5) Maturity: Our material contains two different groups of supposedly adult conchs. The smallest adult morphs have about 40–50 mm in diameter and are sharply keeled, and the flanks are not entirely flat. The morphological transition from the preadult to the mature stage is not distinct (e.g. NHMS-WT2896, Fig. 8E). The sickle-shaped aperture is rectiradiate to slightly prorsiradiate (an impression that originates in the broad ventrolateral projection), near the umbilicus the apertural margin turns slightly posteriorly (e.g. NHMS-WT2904, NHMS-WT2891; Fig. 9C to F). The body chamber occupies 50 to 65% of the terminal whorl. Adult specimens exceeding 60 mm in diameter are stronger compressed, with a sharp keel and a narrower umbilicus (e.g. $uw/dm = 0.03$ in specimen NHMS-WT2894; 0.02 in specimen MPRC12; NHMS-WT2898 dm 88 mm, NHMS-WT2894 dm 90 mm). By contrast, smaller specimens

(e.g. NHMS-WT2891, Fig. 9C, D) show a more bloated body chamber with slightly rounded flanks at diameters below 60 mm. Overall, there is a trend from moderately wide platyconic to oxyconic shells with initially narrow umbilicus and a closed umbilicus in adults. The maximum whorl width with *ca.* 15 mm is near the terminal aperture of the largest conchs with diameters between 90 and 100 mm (13 mm in smaller conchs like NHMS-WT2891, 15 mm in NHMS-WT2894). The body chamber occupies about half a whorl in adult specimens. In the largest specimens, the body chamber is even shorter at around 160 degrees (e.g. NHMS-WT2898, NHMS-WT2894, Fig. 9A, B, J). In some adult specimens, the inner flanks become nearly flat to faintly concave in the part of the whorl overlap (e.g. NHMS-WT2898, NHMS-WT2894; Figs 8E; 9A, B, J). The conch is smooth except weakly developed bulges near the aperture as adult modifications in some specimens (NHMS-WT2904, NHMS-WT2891, NHMS-WT2896; Fig. 9C–F). Few well-preserved larger specimens display fine growth lirae (NHMS-WT2904, NHMS-WT2891, NHMS-WT2896, NHMS-WT2894; Figs 8E, 9A–F), one specimen shows spiral lines on the body chamber (NHMS-WT2894, Fig. 9A, B) and some show faint ribbing (NHMS-WT2900, NHMS-WT2895; Fig. 8F, G).

Sutural elements of the adult suture are well rounded, the lobes are only moderately open and the openings themselves are usually only slightly wider than the basis. The saddles show similar properties. Their bases are usually more narrow than the opening or similarly wide (NHMS-WT2911, NHMS-WT2898, NHMS-WT2894; Figs 8C; 9B, J; 10). Only the E-lobes show a reduced width, which are not more than 1 mm wide and slightly serrated in small specimens (e.g. NHMS-WT2894, Fig. 9B). In smaller morphs, this lobe is mostly well rounded with a very wide opening (e.g. NHMS-WT2904, Figs 9F, 10C) and the flanks of the lobes are not parallel anymore. The edges of the L-lobes can be narrow at their base; the L-lobe is always the largest. The umbilical lobes become shallower towards the umbilicus, but their flanks remain relatively close. The visible suture shows a maximum of 6 to 7 U-lobes (e.g. 7 in NHMS-WT2894). I-lobes are not visible among the available specimens. The saddles are much wider than the lobes (Figs 9B, 10A). In large morphs, the saddles are usually twice as wide as the lobes (e.g. NHMS-WT2894). In several specimens (NHMS-WT2902, NHMS-WT2894), the saddles are slightly bent towards the umbilicus, thus giving the flanks of the saddles an asymmetric appearance. The outermost saddles are well rounded, but from the middle of the flank they flatten rapidly (e.g. NHMS-WT2902). The saddles may as well keep their form (NHMS-WT2892). In rare cases, serrations of the lateral lobes occurs (NHMS-WT2902, MPRC41; Fig. 9G).



Figure 6. Juvenile *Beneckeia buchi* (Alberti, 1834), Freudenstadt Fm., «24 Höfe», district Loßburg, specimen NHMS-WT3066 (see also Figs 5 & 7E); max. diameter 2.8 mm. Renderings based on an image stack obtained through synchrotron-radiation X-ray tomographic microscopy (SRXTM). A – venter. B – left side. C – dorsal view (apertural). D – right side. E – one slice from near the plain of symmetry; the body chamber contains some bioclasts. F – virtual section perpendicular to the plain of symmetry; note the ontogenetic change from the very broad initial chamber via depressed to increasingly compressed whorls.

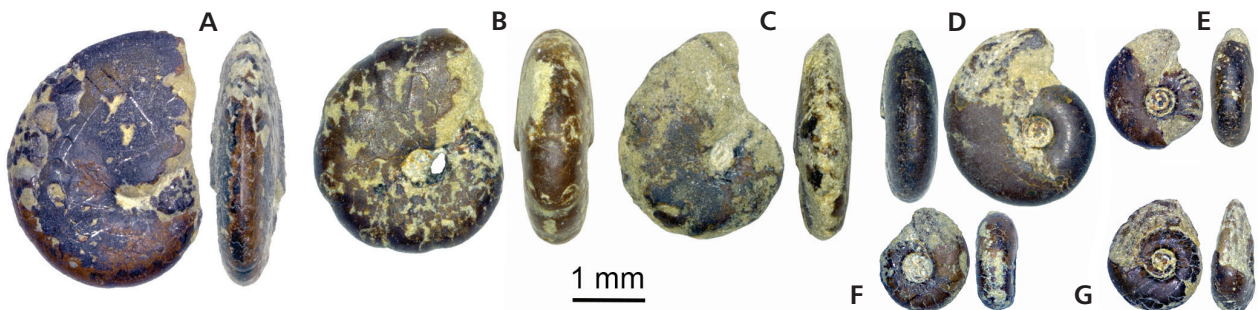


Figure 7. *Beneckeia buchi* (Alberti, 1834), Freudenstadt Fm. from type locality «24 Höfe», district Loßburg, Baden-Württemberg. Juvenile specimens and phragmocons of various developmental stages. A – NHMS-WT3062, phragmocone with fully developed “*buchi-habitus*”, i.e. involute with compressed whorls. B – NHMS-WT3063, phragmocone with distinct constrictions on the flanks and not keeled. C – NHMS-WT3064, eroded specimen, probably phragmocone, with constrictions. D – NHMS-WT3065, smaller specimen without constrictions, but with a rather wide umbilicus. Note the large and irregular distance between the septa. E – NHMS-WT3066, small specimen with comparatively wide umbilicus and very evolute (see also Figs 5, 6). F – NHMS-WT3067, small specimen, with a well rounded aperture and a wide umbilicus. G – NHMS-WT3068, quite evolute in this early ontogenetic stage.

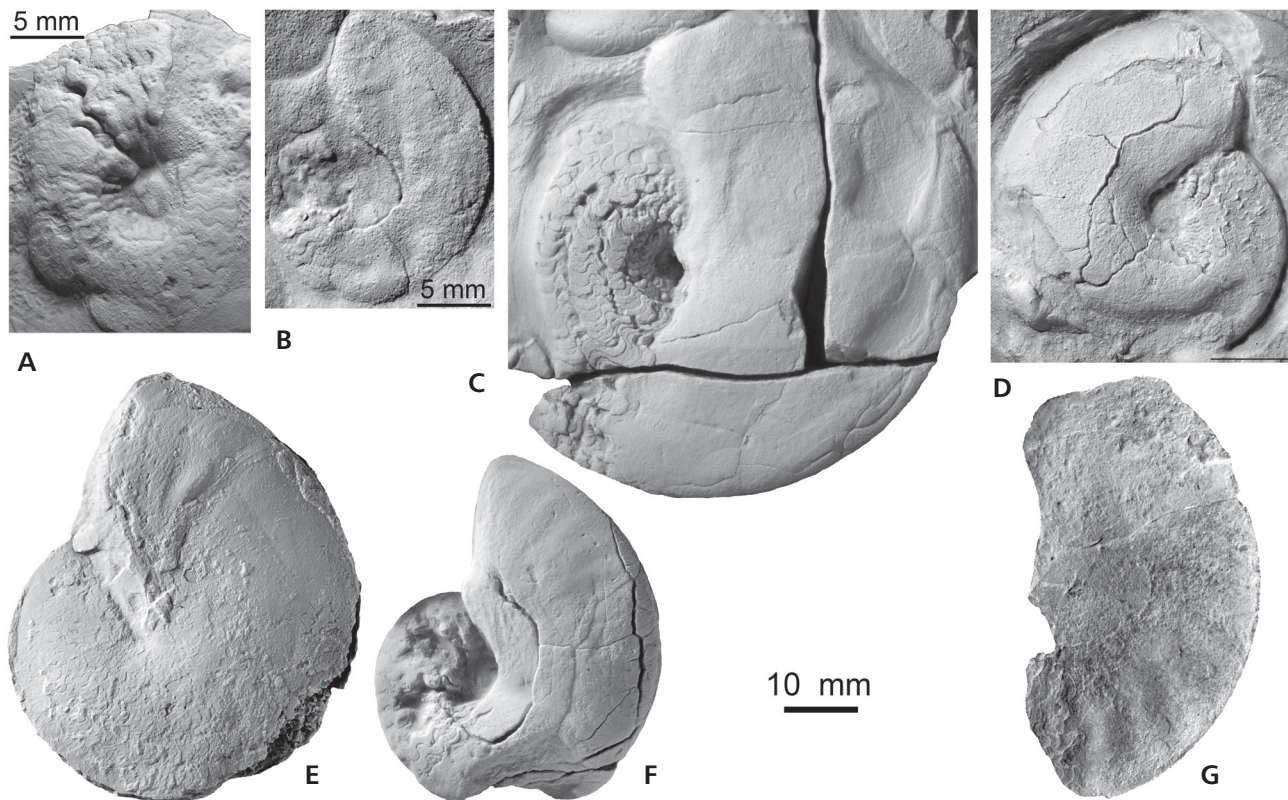


Figure 8. Preadult specimens of *Beneckeia buchi* (Alberti, 1834), Jena Fm. from Rüdersdorf. A – NHMS-WT2908, phragmocone, oldest known specimen from Rüdersdorf, unit A (‘5 m Bank’). B – NHMS-WT2897, juvenile specimen, unit B. C – NHMS-WT2911, large conch, unit A (‘9 m Bank’). D – NHMS-WT2893, conch found 3 metres below Oolithbank alpha, unit F. E – NHMS-WT2896, conch with irregular swellings near the aperture, possibly pathological and caused by an injury of the body chamber, unit B. F – NHMS-WT2900, specimen with faint ribbing near the aperture, unit B. G – NHMS-WT2895, body chamber with clearly pronounced ribbing, base of unit E.

Discussion. – The growth stages described above were in part already recognized by Wissmann (1840), and *B. buchi* from Rüdersdorf differs morphologically and in its size range by no means from the well-documented and described occurrences from other parts of the Germanic Basin (e.g. Dunker 1851; Wagner 1888; Picard 1888, 1899; Fritsch 1902; Frech 1903–1908; Schmidt 1907a; Claus 1955; Schaumberg 1995). The globulose earliest stages occur also in *B. levantina* (see Parnes 1962, pl. 2, fig. 1). The suture of *B. buchi* was already documented by Eck (1879), Mojsisovics (1882), Fritsch (1902) and Schmidt (1907a, 1928), who also reported the rare occurrence of denticulated lobes, and its significance was already discussed above.

There is a trend through time towards more compressed and larger specimens and the progressive development of a sharp keel towards the lower Oolithbank Member (units B to D: NHMS-WT2904, NHMS-WT2891, NHMS-WT2896), and the morphotypes from units E to F (e.g. NHMS-WT2898, NHMS-WT2894) are similar to those of other regions (e.g. Fritsch 1902, Frech 1903–1908, Claus 1955, Schaumberg 1972). Because this size increase can be observed in the entire Germanic Basin, we

tentatively suggest that it could be an expression of Cope’s rule as described by Monnet *et al.* (2012) for the Triassic ammonoid family Acrochordiceratidae. By contrast, the sea-level fall towards the Oolithbank Member could have induced a phase of ventilation of the entire basin and a basinwide equalization of salinity, terminating a period of locally restricted environments with elevated salinities.

Beneckeia wogauana (Meyer, 1848) is based on three specimens from the *Myophoria* Beds of Wogau near Jena: “Dieser schöne Ceratit liegt in drei Exemplaren vor; er steht dem Ammonites (Ceratites) enodis Quenst. am nächsten, ist aber kleiner, hat statt des gewölbten Rückens einen scharfen, wodurch auch die Seiten-Flächen anders gestaltet erscheinen, ist vollkommen glatt, und auch in Betreff der Suturen stimmt er nicht mit der damit verglichenen Spezies überein” (Meyer 1848, p. 464) [This beautiful ceratite is represented by three specimens, it is closest related to *Ammonites* (...) *enodis*... but is smaller, has an acute instead of an arched venter, why the flanks are different, it is completely smooth and with reference to the sutures, it does not agree with the species compared to]. The interpretation of *B. wogauana* as a link between *B. tenuis* and *B. buchi* with an intermediate number of

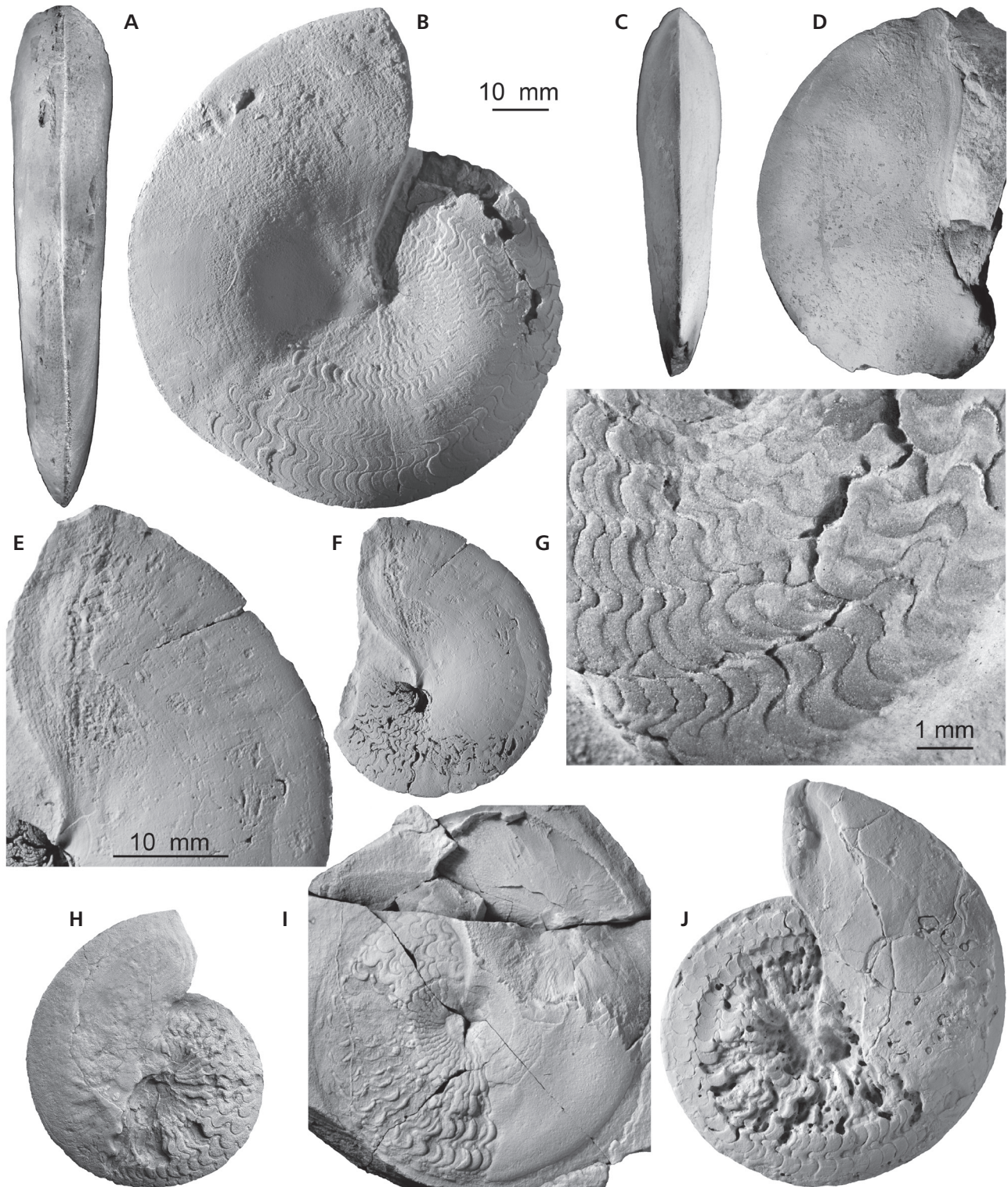


Figure 9. *Beneckeia buchi* (Alberti, 1834), Jena and Rüdersdorf Fm. from Rüdersdorf. A, B – NHMS-WT2894, large specimen, conch with a sharp keel and spiral ornamentation on the body chamber, base of unit E. C, D – NHMS-WT2891, body chamber with a sharp keel, which occupies almost 220° of the terminal whorl, typical for the more or less adult growth stage, base of unit B. E, F – NHMS-WT2904, conch with weakly developed swellings near the typical sickle-shaped aperture, base of unit B. G – NHMS-WT2902, fragment of a phragmocone with well-developed serrations of the lateral lobes, unit B. H – NHMS-WT2906, specimen found 3 m below the top of the lower Oolithbank, youngest known specimen from Rüdersdorf, unit G. I – NHMS-WT2892, large conch with septal crowding, found 3 m below the lower Oolithbank, unit F. J – NHWS-WT2898, large and sharply keeled conch, typical shape from deeper water (original Streichan 1990, p. 73, unnumb.fig.), unit E or F.

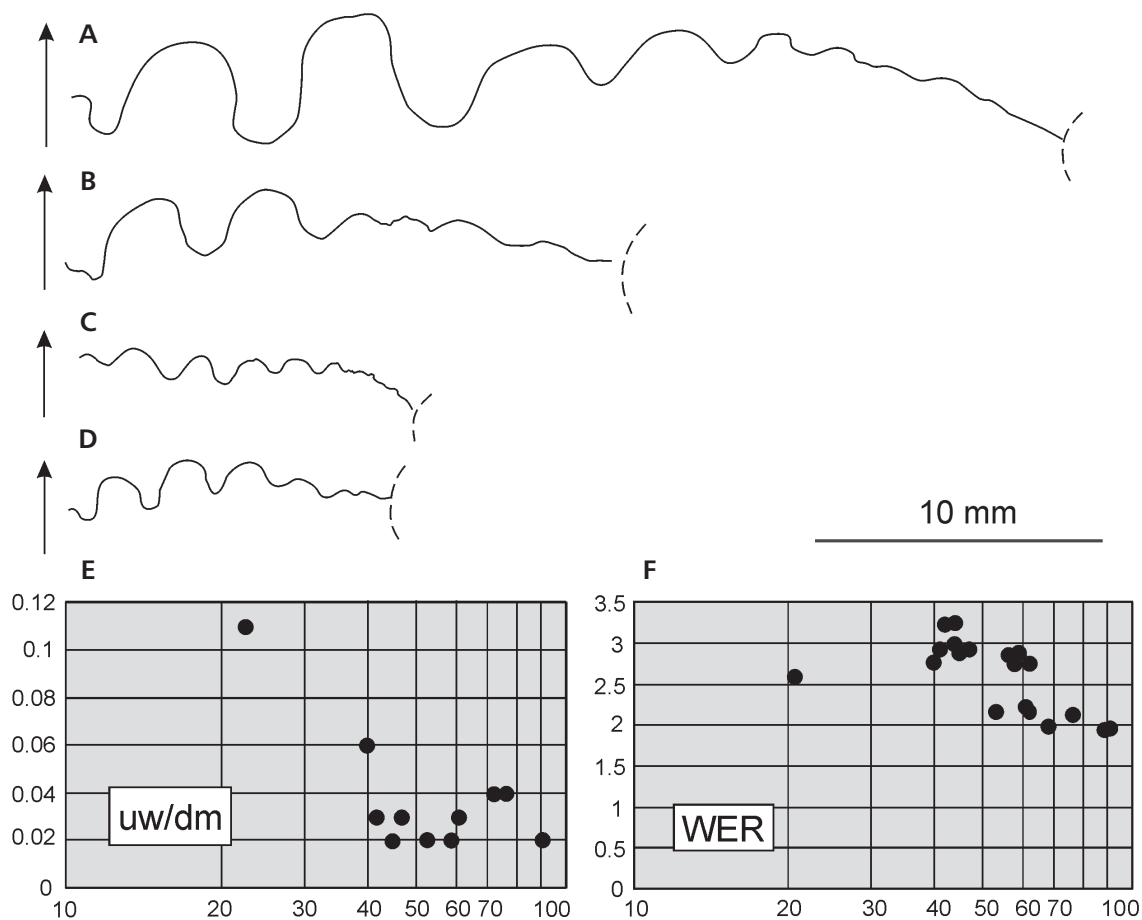


Figure 10. Suture lines and conch parameters of *Beneckeia buchi* (Alberti, 1834), Jena and Rüdersdorf Fm. from Rüdersdorf. A – NHMS-WT2894. B – NHMS-WT2906. C – NHMS-WT2904. D – NHMS-WT2892. E – Ontogenetic development of the umbilical width (Tab. 1). F – Ontogenetic development of the whorl expansion rate (Tab. 1).

auxiliary lobes is a subsequent interpretation and not justified by the original description (e.g. Schmidt 1928, Parnes 1962). *B. wogauana* in Schmidt (1928, p. 289, fig. 797), reproduced in Arkell *et al.* (1957, p. L143, fig. 173.14), is the original of *B. buchi* in Dunker (1851, pl. 42, fig. 3). All figured specimens related to the species fall into the variation of *B. buchi*, why we regard *B. wogauana* as a synonym of *B. buchi*.

Beneckeia wogauana mut. *Posterior* was introduced by Fritsch (1902) for large specimens from the Lower Wellenkalk Member below the Oolithbank Member (Jena Formation). Fritsch (1902) describes these specimens as large conchs with diameters from 7 to 10 cm, which falls into the normal size range of *B. buchi*. *Beneckeia* sp. cf. *B. wogauana* *posterior* Fritsch as figured in Parnes (1986) is, at first sight, indistinguishable from the Cenomanian (Upper Cretaceous) *Neolobites vibrayeanus* (d'Orbigny, 1841) as figured in Wiese & Schulze (2005, p. 934, fig. 4c) based on its ribbing. However, its suture line (Parnes 1986, pl. 23, fig. 4) characterizes the specimen as *Beneckeia*. The lower number of auxilliary lobes distinguishes it from

B. levantina, and it may best be interpreted as *B. buchi*. This would be the first record of the species outside the Germanic Basin.

Beneckeia denticulata Fritsch, 1902 from the *Myophoria* Beds of Jena (Thuringia) shows a serration in the main lateral lobe as in our specimens NHMS-WT2902 and MPRC41. This is a rare feature in *B. buchi*, why we consider *B. denticulata* as a synonym of *B. buchi*.

From *B. tenuis*, *B. buchi* differs by the higher number of auxilliary lobes (*B. tenuis*: 4, *B. buchi* 6). In *B. tenuis*, lobes and saddles are markedly shallower and broader, and E is located deeper on the flank as it is in *B. buchi*.

Occurrence. – The oldest specimen (NHMS-WT2908) from Rüdersdorf was collected 10 m and NHMS-WT2911 ca. 14 m above the base of the *Myophoria* Beds, where *B. buchi* is still very rare. Judging from the lithostratigraphic subdivision of the Germanic Basin as repeatedly presented by, e.g. Szulc (2000) or Hagdorn & Simon (2020, p. 436, fig. 1), the earliest *B. buchi* occur, therefore, in the terminal Buntsandstein. Of the same age

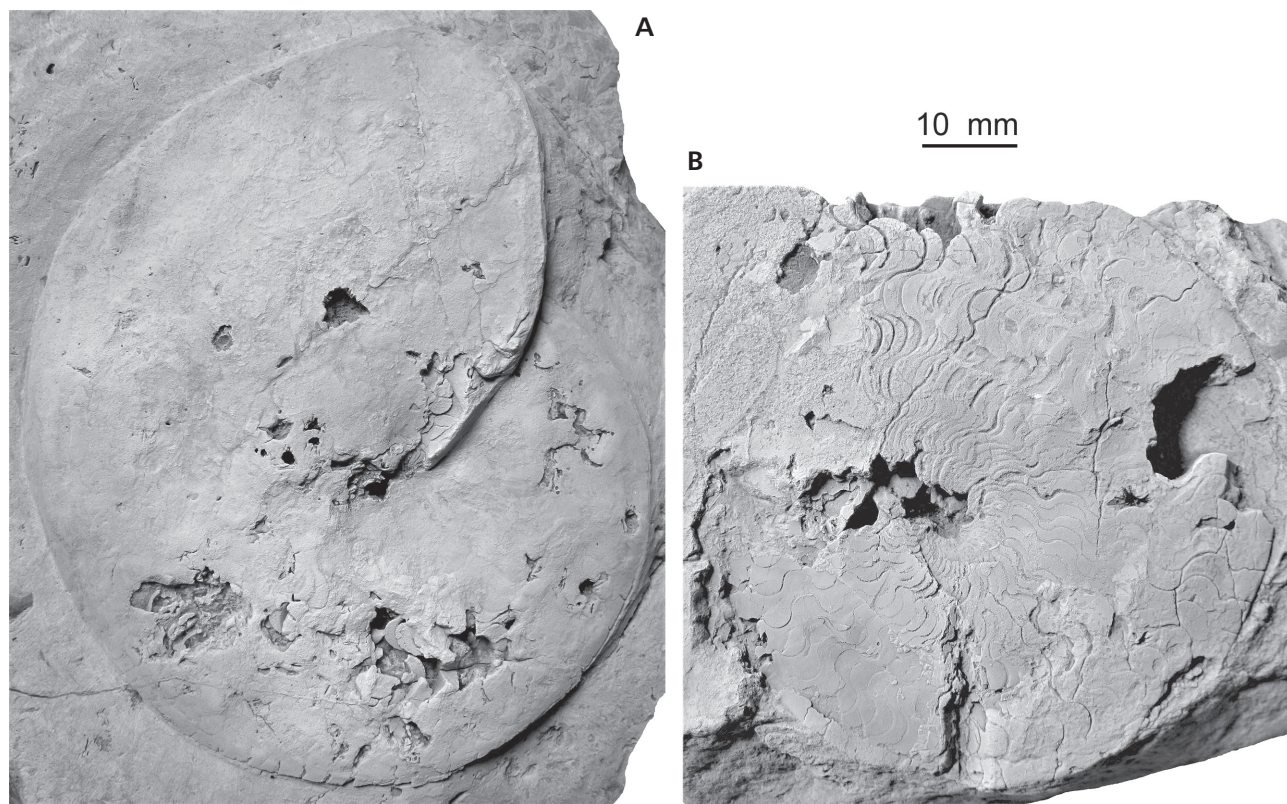


Figure 11. *Beneckeia tenuis* (von Seebach, 1857) from the “*tenuis* bank”, Röt Fm. (Upper Buntsandstein), of Jena-Drackendorf (Thuringia), coll. TB. A – oxyconic conch with sharp keel, adult specimen with narrow umbilicus and typical sickle-shaped aperture. B – specimen with lobes and saddles, characteristically markedly shallower and broader than in *B. buchi*.

is the *Beneckeia* figured by Niedźwiedzki *et al.* (2021) from the Lower Gogolin Beds in Muschelkalk facies of Poland, which correlate stratigraphically with the Upper Buntsandstein (Hagdorn & Simon 2020, p. 436, fig. 1). With the onset of the Jena Formation (base unit B, Lower Wellenkalk Member), *B. buchi* becomes more frequent. An abundance peak occurs in units E and F in the higher part of the Lower Wellenkalk Member in Rüdersdorf. This peak occurrence in the approximate stratigraphic position is well recorded from other parts of the Germanic Basin (Murr 1957 with further references), and a *Beneckeia* layer from this interval was described from Hesse and Lower Saxony (*Beneckeia-Schichten*: Schulz 1972, *Beneckeia buchi*-Lage: Look 1985). A rare mass accumulation of *B. buchi* with more than 30 specimens on bedding planes was reported by Schaumberg (1995), and a plate with more than 30 specimens comes from the base of Unit B of Rüdersdorf (NHMS-WT3107). The youngest specimen from Rüdersdorf (NHMS-WT2906) comes from 3 m below the top of the lower Oolithbank (unit G). From Hesse, Baumgarte & Schulz (1986) report a specimen from the same level and from the Lower Oolithbank. Picard (1888) reports numerous specimens from the Lower and Upper Oolithbank (Oolithbank Member). From the Jena area, R. Wagner (1897) and E. Wagner (1921) recorded

a peak occurrence of small specimens just above the top of the Oolithbank Member (e.g. Müller 1994, p. 239, fig. 268) and the last occurrence of *B. buchi* ca. 6 m above the top of the Oolithbank Member. Unfigured occurrences from the Terebratelbank of Thuringia (Picard 1899) are doubtful. This would suggest a range of *B. buchi* from the *Myophoria* Beds to the lowermost Middle Wellenkalk Member of the Jena Formation, where it has a short overlap with “*C.*” *antecedens* (see below). The *buchi* Marls from southern Germany (Schmidt 1907a; Freudenstadt Formation: Hagdorn *et al.* 2020, p. 452, fig. 1) equate stratigraphically approximately with the higher part of the Oolithbank Member (H. Hagdorn personal communication). A distribution of *B. buchi* throughout the Lower Muschelkalk (e.g. Steiner 1986, Urlichs 1999) lacks evidence.

The palaeobiogeographic distribution of *B. buchi* in Germany was mapped in Murr (1957, pp. 38, 39, fig. 10). It occurs also in the Netherlands (Vossenfeld Formation; Dertien 1972, Dertien & Dertien-te Voortwis 1975, Tjalckens 1975). From Poland, one specimen was described by Kaim & Niedźwiedzki (1999) from the lower Gogolin Formation, and some records exist from the upper Gogolin Formation (Noetling 1880, Rassmuss 1914, Assmann 1937, Kowal-Linka 2008). The scarcity of *B. buchi* in the

Gogolin Formation and its absence in the Górażdze Beds, the correlative of the Oolithbank Member (see Szulc *et al.* 2015) is in conflict with its supposed immigration into the Germanic Basin *via* the Upper Silesian or Carpathian gates (Urlichs & Mundlos 1985).

Family Balatonitidae Spath, 1951

Genus *Balatonites* Mojsisovics, 1879

Type species. – *Trachyceras balatonicum* Mojsisovics, 1873, p. 190 (see Spath 1951).

Remarks. – In a small note, Mojsisovics (1872, p. 190) introduced *Ammonites Balatonicus* as a nomen nudum. Hyatt & Smith (1905, p. 166), selecting a type species, referred to this paper and to “Abhandl. K.-k. geol. Reichsanstalt, Wien, vol. 10, p. 78, pl. 4, figs 2–6; pl. 30, fig. 20”, which is Mojsisovics (1882). Because the species became first valid with its description and figuring as *Trachyceras balatonicum* in Mojsisovics (1873, p. 426, pl. 13, figs 3, 4) (see also Vörös 2003b), *T. balatonicum* Mojsisovics, 1873 is available as type species for *Balatonites* (Spath 1951).

Excessive splitting in early works (*e.g.* Arthaber 1896, Rassmuss 1914) conveyed an impression that the number of *Balatonites* species almost equates the number of available specimens, and some 40 species of *Balatonites* were erected (*vide* Shigeta *et al.* 2010). The numerous *Balatonites* species of Arthaber (1896) from Hungary and Austria (*B. armiger*, *B. bullatus*, *B. corvini*, *B. diffissus*, *B. egregius*, *B. galataeae*, *B. haueri*, *B. jovis*, *B. jubilans*, *B. peleus*, *B. scylla*, *B. stenodiscus*, *B. variesellatus*) can be reduced to *B. egregius* Arthaber, 1896 as shown by Hohenegger & Tatzreiter (1992) based on statistical analyses. In need of revision are also the *Balatonites* records from the Germanic Basin (*a.o.* Rassmuss 1914, Assmann 1937), including *B. ottonis*, *B. trinodosus* (Hauer, 1892), *B. jovis* Arthaber, 1896, *B. doris* Arthaber, 1896, *B. egregius* Arthaber, 1896, *B. stenodiscus* Arthaber, 1896, *B. constrictus* Arthaber, 1896, *B. spinosus* Picard, 1899, *B. macer* Fritsch, 1902, *B. beyrichi* Frech, 1903–1908, *B. quaternonodatus* Rassmuss, 1914, *B. zimmeri* Rassmuss, 1914, *B. zimmermanni* Rassmuss, 1914, *B. cf. corvini*, *B. nobilis* Assmann, 1937 and *B. rothei* Wunsch, 1960. Some of these species will be commented on below in the context of the description of *B. ottonis*.

Occurrence. – *Balatonites* is recorded from Austria, Germany, Hungary, Israel, Poland, USA (Nevada), Russia (southern Primorye), northern Japan, China (Yunnan), Thailand and Vietnam. It ranges from the Bithynian into the Pelsonian (Anisian, Middle Triassic). In the Germanic Basin, *Balatonites* occurs in great numbers especially in Lower Silesia, Poland (Raciborowice), where hundreds of

specimens were collected over the years (Noetling 1880, Rassmuss 1914, Holdefleiß 1915, Assmann 1926, Kaim & Niedźwiedzki 1999). Towards the west, into the central Germanic Basin, *Balatonites* is extremely scarce, and only few specimens are recorded from Thuringia (Picard 1899, Wunsch 1960), Hesse (Kramm *et al.* 2020a) and Saxony-Anhalt (this work). *Ceratites cf. andersshanus* of Schmidt (1907a, pl. 2, fig. 9) from the Freudenstadt Formation of southern Germany may represent also a *Balatonites* (see below).

Balatonites ottonis (Buch, 1849)

Figures 12, 13; Tables 2, 5

- 1849 *Ammonites Ottonis*; Buch, pp. 18, 19; pl. 4, figs 4–6.
- 1867 *Ammonites Ottonis*, L. v. Buch. – Beyrich, pp. 110, 111; pl. 4, fig. 1.
- ? 1880 *Ammonites (Ceratites) Ottonis* Buch. – Noetling, pl. 14, fig. 12, 12a.
- 1882 *Balatonites cf. Ottonis* (v. Buch). – Mojsisovics, p. 78; pl. 5, fig. 1; pl. 6, fig. 1.
- 1903–1908 *Balatonites Ottonis* – Frech, p. 27, unnumbered fig. 1a, b; p. 40, unnumbered fig. 1a, b.
- 1903–1908 *Balatonites Ottonis* L. v. B. em. – Frech, pl. 1, fig. 5a, b.
- 1914 *Balatonites Ottonis* L. v. Buch sp. – Rassmuss, pp. 287–289.
- 1914 *Balatonites Zimmeri* nov. spec.; Rassmuss, p. 292; pl. 3, figs 1, 3.
- 1928 *Balatonites Ottonis* v. Buch sp. – Schmidt, p. 290, fig. 801.
- 1928 *Balatonites Zimmeri* Rassm. – Schmidt, p. 292, fig. 806.
- 1952 *Balatonites ottonis* v. Buch. – Hardt, p. 103, fig. 54.
- 1959 *Balatonites rothei* Wunsch. – Rothe, p. 67, fig. 3.
- 1960 *Balatonites rothei* H. sp. – Wunsch, pp. 329–336; pl. 22, figs 1–3.
- non 1988 *Balatonites aff. ottonis* (Buch). – Fantini Sestini, pl. 11, fig. 4.
- 1990 *Balatonites zimmeri* Rassmuss. – Dzik, pl. 14, fig. 3a, b.
- 1990 *Balatonites ottonis* (von Buch, 1849). – Dzik, pl. 15, figs 1, 2.
- 1999 *Balatonites ottonis* (Buch 1849). – Brack *et al.*, p. 862, fig. 6c.
- 1999 *Balatonites* of the *ottonis*-group. – Brack *et al.*, p. 862, fig. 6d (non e, f).
- 1999 *Balatonites ottonis* (Buch, 1849). – Kaim & Niedźwiedzki, p. 108, pl. 11, figs a, b.
- 1999 *Balatonites zimmeri*. – Urlichs, p. 345, fig. 6.
- 2003b *Balatonites cf. ottonis* (Buch, 1849). – Vörös, pp. 84, 85, pls a–i, fig. 15.
- 2004 *Balatonites*. – Hagdorn, p. 35, fig. 83.
- 2020a *Balatonites ottonis* – Hagdorn, p. 248, fig. 1f.
- 2020a *Balatonites ottonis* (v. Buch, 1849). – Hagdorn, p. 249.

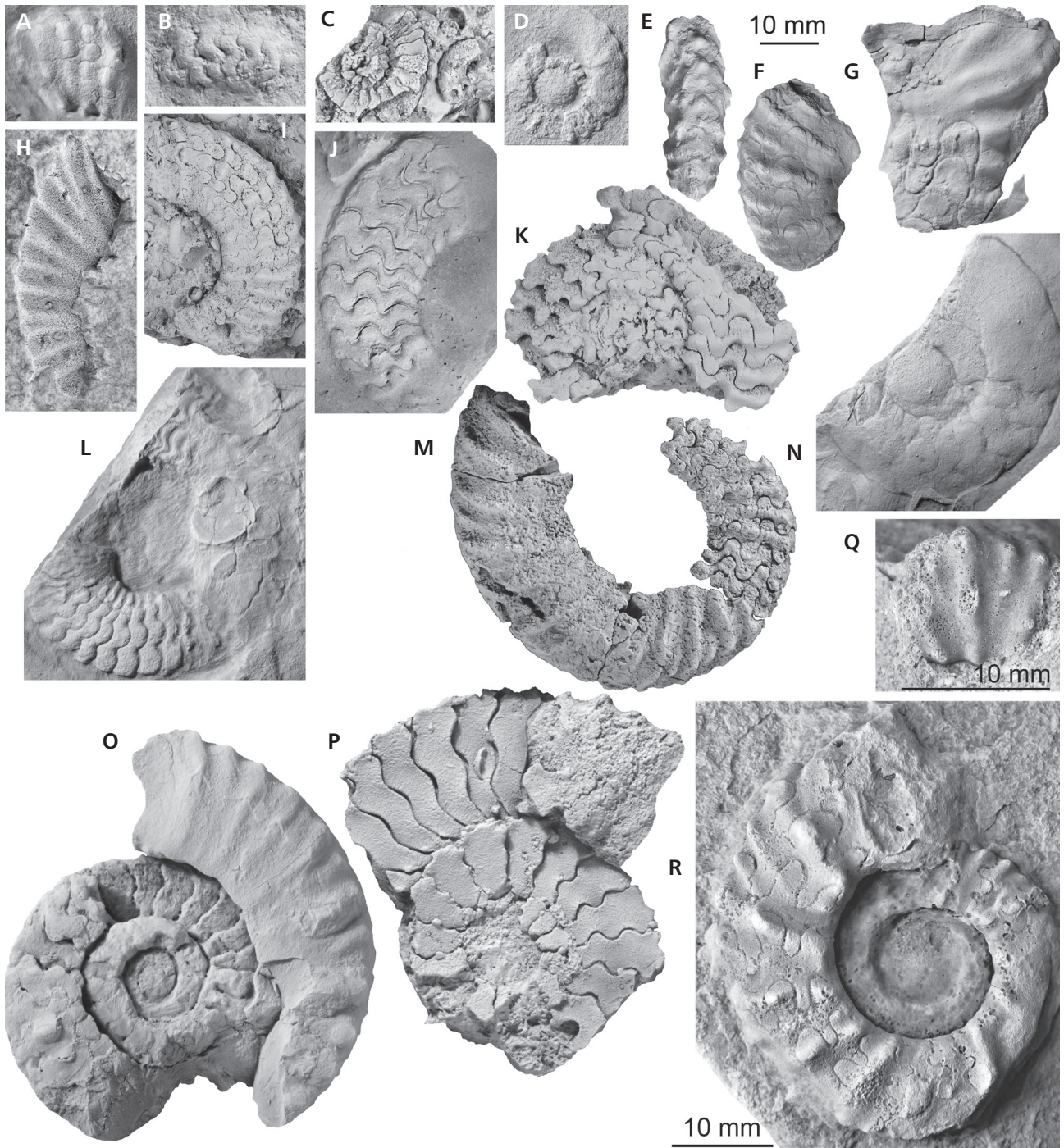


Figure 12. *Balatonites ottonis* (Buch, 1849), Jena and Rüdersdorf Fm. from Rüdersdorf, Jena Fm. from Hecklingen/Saxony Anhalt. A – NHMS-WT2887, fragment, upper part of unit D. B – NHMS-WT2886, fragment, upper part of unit D, together with NHMS-WT2887 oldest known specimens from Rüdersdorf. C – NHMS-WT2890, poorly preserved phragmocone of juvenile from a layer with *N. strombecki* (Griepenkerl, 1860) and *B. buchi* (Alberti, 1834), probably upper part of unit D or base of unit E. D – NHMS-WT2903, juvenile specimen, unit F. E, F – MPRC20, fragment of phragmocone, unit E or F. G – NHMS-WT2910, fragment, unit F. H – X13019, cast of a fragment, unit E or F. I – X7807, fragment of phragmocone (original Hardt 1952, p. 103, fig. 54.), unit E or F. J – MPRC18, fragment of phragmocone with ‘double sutures’, unit E or F. K – X13020, incomplete phragmocone, unit E or F. L – NHMS-WT2909, fragment of phragmocone, unit E. M – X13021, incomplete specimen, unit E or F. N – MPRC19, specimen from the uppermost part of the Oolithbank Member, youngest well-labelled record of the species from the Germanic Basin, uppermost unit G. O – NHMS-WT2889, probably the most complete specimen, unit E. P – NHMS-WT2883, fragment of phragmocone, unit F. Q – fragment of body chamber (?), Oolithbank Member of Hecklingen, Saxony-Anhalt (coll. JW), R – juvenile specimen, Oolithbank Member of Hecklingen, Saxony-Anhalt (coll. JW).

Type. – Holotype by monotypy is the original of Buch (1849, pl. 4, figs 4–6), which survived in the collection of the Museum für Naturkunde Berlin (MB.C. 438). It comes from the Muschelkalk near Siedlec (Schedlitz) (Upper Silesia, Poland), but detailed locality information is missing. The holotype was refigured in Dzik (1990, pl. 15, fig. 1), and a cast is figured in Brack *et al.* (1999, p. 862, fig. 6c).

Material. – 18 specimens (NHMS-WT2882, NHMS-WT2883, NHMS-WT2886, NHMS-WT2887, NHMS-WT2889, NHMS-WT2890, NHMS-WT2903, NHMS-WT2909, NHMS-WT2910, MPRC18 – MPRC20, X7807, X13019 – X13021, 2 specimens JW collection, unregistered).

Description. – Most specimens are poorly preserved and incomplete. However, they convey a good idea about the ontogeny of *B. ottonis* except of earliest growth stages. *B. ottonis* is a very evolute species with a shallow umbilicus, round umbilical shoulders and three rows of tubercles (umbilical, lateral, ventrolateral) plus a ventral row, in which ribbing dominates over tuberculation. NHMS-WT2903 (Fig. 12D) is the smallest but corroded specimen (dm ca. 19 mm). Worn ribs, arising at the shoulder of a wide umbilicus or slightly above, appear to have been simple and terminate in a ventrolateral clavus. Equally small is the corroded specimen NHMS-WT2909 (Fig. 12L), which however, shows with a wh/dm ratio of 0.3 the wide umbilicus already in juveniles. The fully septate specimen X7807 (original of Hardt 1952, p. 103, fig. 54; dm ca. 50 mm; Fig. 12I) has a wide umbilicus with a gently rounded shoulder, from where slightly prorsiradiate ribs arise from weak or stronger (e.g. NHMS-WT2890, Fig. 12C) umbilical tubercles. Secondaries can intercalate apparently irregularly just above the umbilical shoulder but also mid-flank. Ribs broaden towards the upper flank, and ca. 17 ribs per half whorl reach the ventrolateral shoulder to terminate in a row of slightly clavate umbilicolateral tubercles. Just above mid-flank, weak lateral tubercles are rather felt than seen. The same growth stage is represented by MPRC18 (Fig. 12J) and the septate part in X13021 (Fig. 12M). MPRC20 (Fig. 12E, F) represents a terminal phragmocone/begin body chamber and shows a chevron-like adapertural projection of the ribs, crossing the venter in unequal strength and linking to a ventral tubercle. At the beginning of the body chamber, a change of ornament can be observed in NHMS-WT2889 and X13021 (Fig. 12M, O). Ribbing becomes less dense and secondaries arise mainly above mid-flank to upper flank position. Lateral tubercles shift in a position in the upper third of the flanks and become strong, bullate and are fused with the ribs to form a collar-like swelling. Although some secondaries

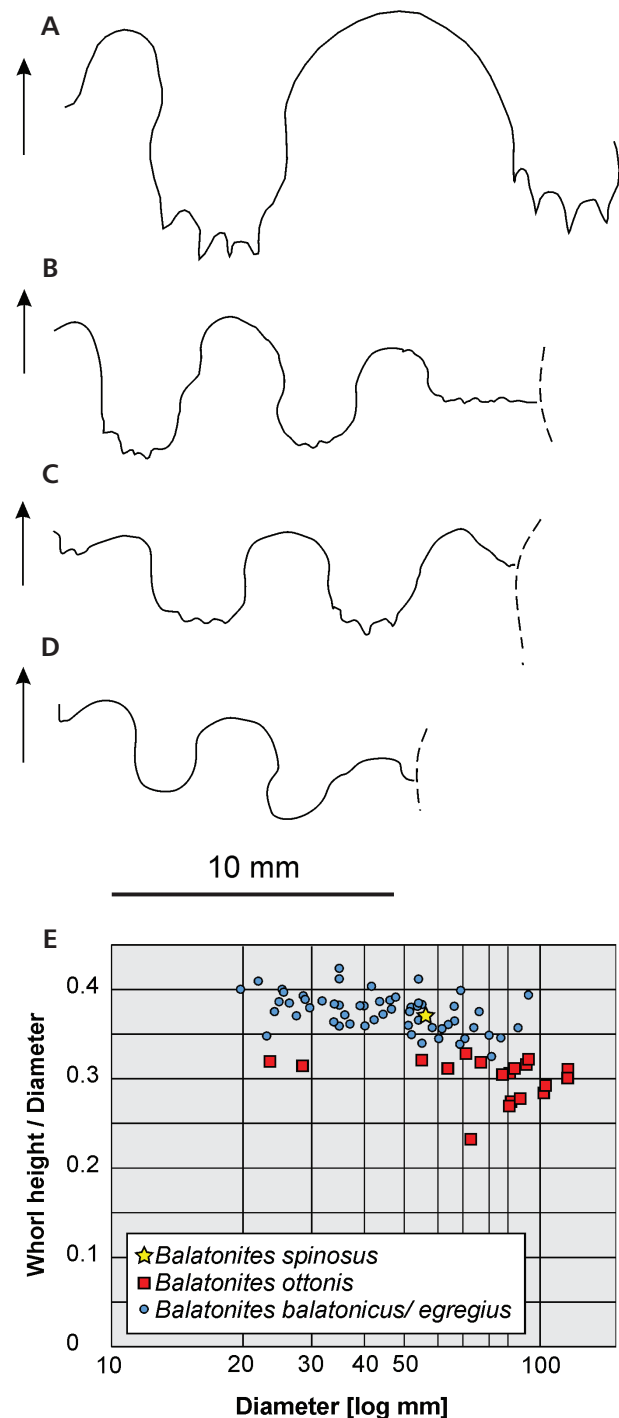


Figure 13. Sutures and measurements of *Balatonites ottonis* (Buch, 1849), Jena and Rüdersdorf Fm. from Rüdersdorf. A – MPRC20 with well developed lobal serrations. B – X7807 (original of Hardt 1952, p. 103, fig. 54). C – X13020. D – NHMS-WT2910. E – Ontogenetic development of the whorl height/ diameter ratio (Tab. 5).

still arise above the umbilical shoulder, they are faint and indistinct but become strong at the lateral tubercles, from where all ribs flex now gently forward (NHMS-WT2889, Fig. 12O).

Tab. 2. Conch parameters in mm and ratios of *Balatonites ottonis*.

Specimen	dm	bcl	ah	wh	uw	ww _{min}	ww _{max}	uw/dm	wh/dm	WER	IZR
NHMS-WT2889	67	105	20	22?	4.0?			0.06?	0.33?	2.85	0.09?
NHMS-WT2903	19	21?	5?	5?					0.27?	2.71?	
X13021	85	122	23	26?					0.31?	2.74	0.12?
MPRC20						0.6	0.9				

Whorl section appears to be compressed oval in intercostal and subrectangular to subpentagonal in costal section. Few measurements indicate a wh/dm ratio below 0.328 (Tab. 2).

The suture is ceratitic. Lobes and saddles are well-rounded. Usually, the opening of a lobe is not broader than its base (e.g. X7807, MPRC20, Fig. 13A, B), but occasionally, they can be slightly widened (e.g. X13020, X13021; Fig. 12K, M). The lobes vary in depth (e.g. NHMS-WT2910, MPRC20, NHMS-WT2887, X13021; Figs 12A, G, M; 13A), and the L lobe is somewhat larger and deeper than the neighbouring U lobe. Further U lobes are hardly discernible because the sutural corrugation fades out (e.g. X7807). The saddles are equally well rounded. The saddle on the middle of the flank is slightly larger than the others (X7807; Fig. 13B). Overall, the variation of the sutures is very low.

Discussion. – Our material from Rüdersdorf, in particular specimen NHMS-WT2889 (Fig. 12O), fits well the ornamentation of the holotype. The largest specimen from Rüdersdorf, X13021 (Fig. 12M), is possible an incomplete adult and has an estimated maximum dm of ca. 90 mm (see also NHMS-WT2889; Fig. 12O). We see no fundamental difference to the only almost complete adult (?) specimen figured of Frech (1903–1908), refigured by Kaim & Niedźwiedzki (1999, p. 108, pl. 11, figs a, b), which shows (similar to NHMS-WT2889) a body chamber of ca. 200° in spiral length at a size of ca. 108 mm. *B. zimmeri* Rassmus 1914, included into *B. ottonis* (see below), reaches a size of 116 mm and shows a progressive weakening of ventral sculpture, resulting in a broadly rounded venter.

Remarkable is the wh/dm ratio in *B. ottonis* or the *ottonis*-group, respectively, which is lower than 0.328 also in juvenile specimens. It is distinct from the group of *B. balatonicus*, *B. egregius* and *B. gemmatus*, which occupy a field with values between 0.338 and 0.424 (Fig. 13E). Thus, even poorly preserved specimens from Rüdersdorf (e.g. NHMS-WT2909, Fig. 12L; MPRC19, Fig. 12N) can be attributed to *B. ottonis*, because the wh/dm ratio deviates from all contemporaneous ammonoids. Adult *B. balatonicus* can also develop evolute stage as seen in Hohenegger & Tatzreiter (1992, fig. 19. 3). How-

ever, these differ from *B. ottonis* by a different mode of ribbing, showing bullate umbilicolateral swelling and looped ribs arising at the lateral tubercle.

The wh/dm ratio and the overall mode of ornamentation of *B. zimmeri* Rassmus, 1914 and *B. rothei* Wunsch, 1960 falls into the variation of *B. ottonis* and the species are regarded as synonyms. *Balatonites ottonis* can readily be distinguished from other species of *Balatonites* by i) its lower wh/dm ratio (Fig. 13E), ii) its much stronger ribbing and the lower number of ribs in later growth stages, iii) the weakening of ribbing in the lower parts of the flank in adult specimens, iv) the position of the lateral tubercles in the uppermost part of the flank in adult specimens and not in a close to mid-flank position, v) the occurrence of strong to spinose lateral tuberculation and vi) the dominance of ribbing over tuberculation. Within this context, we exclude the specimens of Brack *et al.* (1999, p. 862, fig. 6e, f) from *B. ottonis* due to its higher involution, weaker ornamentation, denser ribbing and well developed tuberculation with the lateral tubercle in a mid-flank position. Apart from *B. balatonicus* and *B. egregius*, well distinguishable by means of statistics (Hohenegger & Tatzreiter 1992), *B. ottonis* emerges as a third, well-recognizable species (comp. Vörös 2003b).

Some *Balatonites* of the *ottonis*-group as interpreted by Brack *et al.* (1999, p. 862, fig. 6a) show an atypical strong mode of ribbing without reduction of secondaries, but seemingly a comparable involution. This relates also to *B. aff. ottonis* of Fantini Sestini (1988) and *B. cf. ottonis* in Arthaber (1914, pl. 12, fig. 7): They show strong rectiradiate primary ribs arising at the umbilical shoulder and crossing the venter without the adapertural projection as in *B. ottonis*. Though, they seem to be comparably evolute. We tentatively exclude these specimens from *B. ottonis* and question, whether this could be a yet undescribed species of *Balatonites*. This relates also to *Ceratites cf. sondershusanus* figured by Schmidt (1907a, pl. 2, fig. 9), which we also include into this group. *A. (C.) ottonis* of Noetling (1880) may be a fragment of a *Balatonites*, but due to the idealized figure, we cannot relate it neither to *B. ottonis* nor any other species of *Balatonites* with confidence.

Occurrence. – At Rüdersdorf, *B. ottonis* ranges from the upper part of the unit D (NHMS-WT2886, NHMS-WT2887;

Lower Wellenkalk Member, *ca.* 15 to 18 m below the Oolithbank Member) to the uppermost part of the Oolithbank Member (MPRC19, uppermost unit G) with an abundance maximum in units E and F (NHMS-WT2883, NHMS-WT2889, NHMS-WT2890, NHMS-WT2903, NHMS-WT2909, NHMS-WT2910). There exist two records from the Oolithbank Member of Hecklingen, Saxony-Anhalt, Germany (collection J. Wiedenbeck, Hoym; Fig. 12Q, R). From the Fulda area (Hesse, Germany), two additional finds are reported (Kramm *et al.* 2020a, p. 744). Our find from the uppermost part of the Oolithbank Member (MPRC19) is the youngest well-labelled record of the species from the Germanic Basin. In the correlative beds of Poland, the Gogolin Beds, *B. ottonis* is part of a diversified *Balatonites* fauna without *B. balatonicus* (*e.g.* Rassmuss 1914), coming possibly from a single horizon or level in the upper Gogolin Beds (Kaim & Niedźwiedzki 1999). A comparable succession is observed in Hungary (Vörös 2003a). Further records exist from Austria and Italy (Mojsisovics 1888, Brack *et al.* 1999). In the Balaton area, *B. ottonis* seems to range into the lowermost *balatonicus* Subzone of the *balatonicus* Zone. This gives an upper Bithynian to lower Pelsonian age for *B. ottonis*.

***Balatonites balatonicus* (Mojsisovics, 1873)**

Figure 14; Tables 3, 5

- 1867 *Ammonites Ottonis* Buch. – Beyrich, pl. 4, fig. 2.
 1873 *Trachyceras Balatonicum* E. v. Mojsisovics.; Mojsisovics, pl. 13, fig. 3 only.
 1882 *Balatonites balatonicus* E. v. Mojsisovics. – Mojsisovics, pl. 4, fig. 2.
 ? 1882 *Balatonites balatonicus* E. v. Mojsisovics. – Mojsisovics, pl. 4, figs 4–6.
 1903–1908 *Balatonites ottonis* Leopold von Buch mut nov *Beyrichi*. – Frech, pl. 1, fig. 3.
 1912 *Balatonites balatonicus* Mojs. – Arthaber, pl. 2, fig. 7.
 1937 *Balatonites nobilis*. – Assmann, pl. 22, fig. 5.
 1938 *Balatonites nobilis* Assm. – Schmidt, p. 42, fig. 808a.
 1958 *Balatonites balatonicus* (Mojsisovics). – Popov, pl. 10, fig. 3.
 non 1975 *Balatonites* sp. aff. *B. balatonicus* (Mojs.). – Parnes, pl. 4, figs 8–10.
 non 1986 *Balatonites* sp. aff. *B. balatonicus* (Mojsisovics). – Parnes, pl. 4, fig. 13.
 1987 *Balatonites balatonicus* (Mojsisovics). – Vörös, pl. 1, figs 1, 2.
 1991 *Balatonites balatonicus* (Mojsisovics, 1873). – Tatzreiter & Vörös, pl. 1, fig. 3.
 1992 *Balatonites balatonicus* (Mojsisovics, 1873). – Hohe-negger & Tatzreiter, p. 813, fig. 18.1–3, 18.9–13, fig. 19.7–11, 16, 17.

2003b *Balatonites balatonicus* (Mojsisovics, 1873). – Vörös, pls a–1, figs 16–18; pls a–2, figs 2a, b, 3a, b; pls a–3, figs 2a, b, 3a, b, 4, 5; pls a–4, figs 1, 2a, b, 3, 4a, b; figs a–14, a–15, a–16, with additional synonymy.

Type. – In his original description, Mojsisovics (1873) designated no holotype. Writing about the tuberculation in larger and smaller specimens and figuring two specimens on his plate 13, figures 3 and 4, it is clear that a suite of specimens was available to him. Consequently, Assereto (1966) designated the original of *Trachyceras Balatonicum* Mojsisovics, 1873, pl. 13, fig. 3a, b as the lectotype. It was refigured by, *e.g.* Mojsisovics (1882, pl. 4, fig. 2a, b), Popov (1958, pl. 10, fig. 3) and Vörös (2003b, pls a–4, fig. 1) and is housed in the Geological Institute of Hungary, Budapest (reg. no. GIH T.349). Vörös (2003b), including the specimen from figure 4 into *B. egregius* morphotype *jovis*, referred to the remaining specimen on figure 3 as the holotype. As no monotypy exists, the holotype could only have been designated by the original author himself and the designation of the lectotype by Assereto (1966) is valid.

Material. – One specimen (X13018), which is the original of Beyrich (1867, pl. 4, fig. 2) from Rüdersdorf. It is an imprint (Fig. 14C), and Fig. 14A bases on a historical cast (X13355), which may or may not be contemporaneous. This specimen is the holotype by monotypy of *Balatonites beyrichi* Frech, 1903–1908. Beyrich (1867) gave Lower Muschelkalk as provenance, Frech (1903–1908) specified it and gave Schaumkalk as the find interval, which then should be – within our stratigraphic framework – unit H or higher.

Description. – The cast shows remnants of the last whorl (Fig. 14) and we estimate a size of *ca.* 60 mm. The wide umbilicus (wh/dm ratio *ca.* 0.385) has a subacute umbilical shoulder and a steep, slightly outward inclined umbilical wall. In the earliest whorl visible, still widely spaced rectiradiate primary ribs (*ca.* 6/half whorl), becoming broader towards the venter, arise from a pronounced tubercle at the umbilical shoulder and link to a lateral tubercle in the upper third of the flank. One to two secondaries, arising in a mid-flank position, intercalate irregularly and show weak lateral tubercles. Ribs are smoothly rounded. With increasing size, primary ribs become more dense (*ca.* 10 ribs/half whorl), and a row of inner lateral tubercles starts to develop in the lower third

Table 3. Conch parameters in mm and ratios of *Balatonites balatonicus*.

Specimen	dm	wh	wh/dm
X13018	60?	22?	0.385?

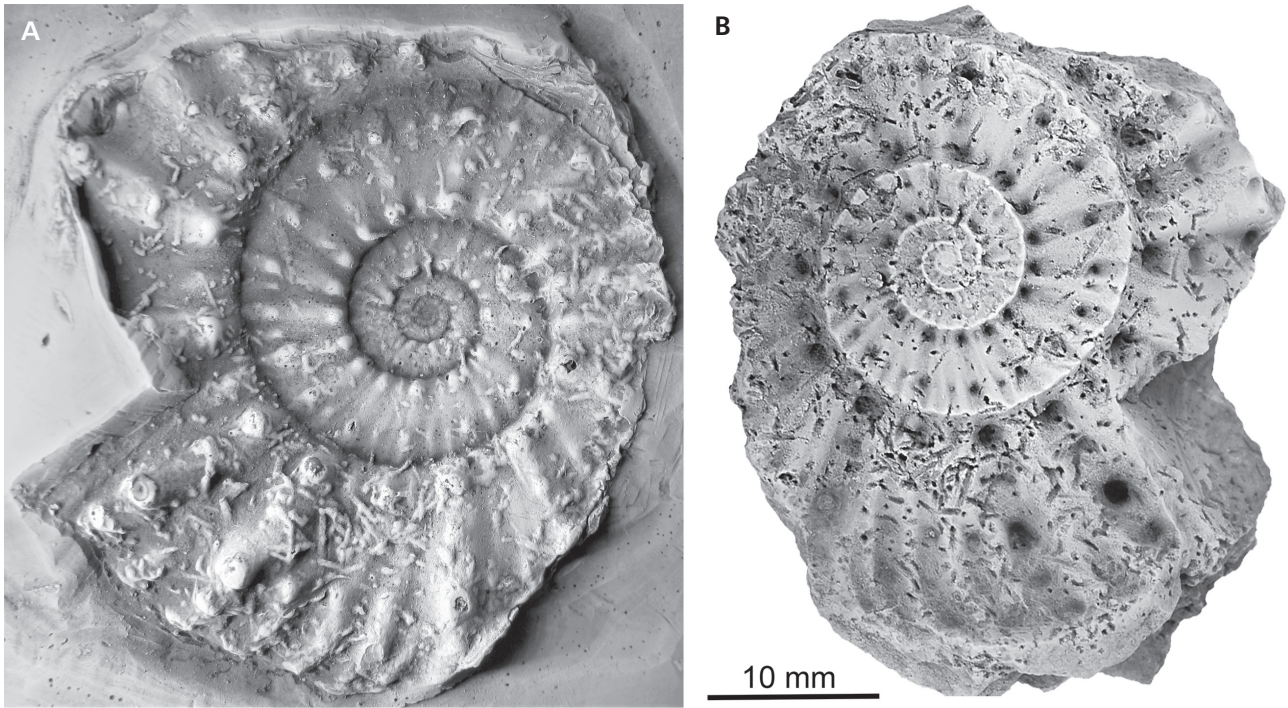


Figure 14. *Balatonites balatonicus* (Mojsisovics, 1873), Rüdersdorf Fm. from Rüdersdorf. A – X13355, historical cast. B – X13018, original of Beyrich (1867, pl. 4, fig. 2) and holotype by monotypy of *Balatonites beyrichi* Frech, 1903–1908, pl. 1, fig. 3. Unit H or higher.

of the flank. Rarely, weak secondaries arise from likewise weak umbilicolateral tubercles. In the last half whorl preserved, the umbilical wall becomes rounder, main ribbing can become very distant and up to three secondaries are intercalated, arising around the outer, slightly bullate lateral tubercles, which become very prominent at that point. Where visible, a rib links from the outer lateral to a ventrolateral tubercle.

The whorls section is difficult to assess in this cast but it seems that it was depressed oval with largest thickness around the outer lateral tubercles in intercostal and sub-pentagonal in costal section.

Discussion. – The coarse ribbing of this specimen, its overall style (spacing, secondaries) and conch dimensions differs from all contemporaneous species of *Balatonites*, except of *B. balatonicus*. There exists a good accordance with *B. balatonicus* figured in the literature (e.g. Tatzreiter & Vörös 1991; Vörös 1987, 2003b) and also with the lectotype. However, the position of the lateral tubercles in a high upflank position of the trituberculated stage and a change towards a persistent quatrituberculated stage (umbilical, inner lateral, outer lateral, ventrolateral tubercles) is not mirrored by any of the figured material. Vörös (2003b, p. 87) stated that “one to four accessory tubercles may appear irregularly on the ribs of the flanks...”, which relates to our specimen to some extent. A similar “surplus” of tubercles occurs in the holotype

of *Balatonites nobilis* Assmann, 1937, which bases on a cast of an imprint. Except of tuberculation, it shows good accordance with *B. balatonicus* in Tatzreiter & Vörös (1991, pl. 1, fig. 3), why we tentatively include into *B. balatonicus*. Whether or not this mode of tuberculation is expression of a regional *B. balatonicus* population cannot be discussed based on two specimens. It would, however, be interesting to test and document the material from the Balaton Highlands for this feature.

Balatonites sp. aff. *B. balatonicus* of Parnes (1975, 1986) shows a balatonitid venter and a rectiradiate strong ribbing, with apparently regularly intercalated secondaries. This mode of ribbing is not in agreement with *B. balatonicus* but similar to *B. egregius* in Hohenegger & Tatzreiter (1992, p. 812, fig. 18.12). If this was the case, the *Balatonites* fauna from Israel is stratigraphically best re-interpreted to represent a terminal Bithynian age (see above).

Occurrence. – *Balatonites balatonicus* occurs in the Pelsonian *balatonicus* to *zoldianus* Subzones of the *balatonicus* Zone in the Balaton Highland, encompassing the *balatonicus* Zone (Vörös 2003a, Jenks et al. 2015). The find from the Schaumkalk of Rüdersdorf comes at least from the *balatonicus* Subzone. Palaeobiogeographically, it occurs in Hungary, Austria, the West Carpathian area, the Dinarides and Turkey (fide Vörös 2003b). Our find is the first record of the species from the Germanic Basin of Germany.

***Balatonites egregius* (Arthaber, 1896)**

Figure 15; Tables 4, 5

- 1873 *Trachyceras Balatonicum*. – E. v. Mojsisovics, pl. 13, fig. 4.
- 1882 *Balatonites balatonicus* E. v. Mojsisovics. – Mojsisovics, pl. 4, fig. 3.
- ? 1882 *Balatonites Zitteli* E. v. Mojsisovics. – Mojsisovics, pp. 80, 81; pl. 5, fig. 2.
- 1896 *Balatonites egregius* Arth.; Arthaber, pp. 201–204; pl. 23, figs 2–4.
- 1896 *Balatonites egregius* Arth. var. *mirus*; Arthaber, pp. 204, 205; pl. 23, fig. 5.
- 1896 *Balatonites armiger* Arth.; Arthaber, pp. 205–206; pl. 23, figs 6–8.
- 1896 *Balatonites diffissus* Arth.; Arthaber, pp. 207, 208; pl. 23, fig. 9.
- 1896 *Balatonites variesellatus* Arth.; Arthaber, pp. 208, 209; pl. 24, fig. 1.
- 1896 *Balatonites stenodiscus* Arth.; Arthaber, pp. 209, 210; pl. 24, fig. 2.
- 1896 *Balatonites Haueri* Arth.; Arthaber, pp. 211, 212; pl. 24, fig. 3.
- 1896 *Balatonites Jovis* Arth.; Arthaber, pp. 212, 213; pl. 24, fig. 4.
- 1896 *Balatonites Doris* Arth.; Arthaber, pp. 213, 214; pl. 24, fig. 5.
- 1896 *Balatonites Galateae* Arth.; Arthaber, pp. 214–216; pl. 24, figs 6–8, pl. 25, fig. 1.
- 1896 *Balatonites jubilans* Arth.; Arthaber, pp. 216, 217; pl. 25, fig. 2, pl. 26, fig. 6.
- 1896 *Balatonites Seylla* Arth.; Arthaber, p. 218; pl. 25, figs 3, 4.
- 1896 *Balatonites Peleus* Arth.; Arthaber, p. 219; pl. 25, fig. 5.
- 1896 *Balatonites bullatus* Arth.; Arthaber, p. 220; pl. 25, fig. 6.
- 1896 *Balatonites Corvini* Arth.; Arthaber, pp. 222, 223; pl. 25, figs 7, 8.
- 1896 *Balatonites lineatus* var. *confertus* Arth.; Arthaber, pp. 221, 222; pl. 26, fig. 5.
- 1903–1908 *Balatonites Jovis* v. Arth. – Frech, p. 27, unnumbered fig., fig. 2, p. 40, unnumbered fig., fig. 2.
- 1906 *Balatonites lineatus* Arth. – Arthaber, pl. 35, fig. 18.
- 1914 *Balatonites* spec. ex aff. *trinodosi* Fr. v. Hauer. – Kraus, pl. 3, fig. 7.
- 1914 *Balatonites quarternondatus* n. sp.; Rassmuss, pl. 2, fig. 1.
- 1914 *Balatonites* n. sp. undet. – Rassmuss, pl. 2, fig. 2.
- 1914 *Balatonites constrictus* v. Arth. – Rassmuss, pl. 2, figs 3, 4.
- 1914 *Balatonites Zimmermanni* n. sp.; Rassmuss, pl. 3, fig. 2.
- 1914 *Balatonites* aff. *trinodosus* v. Hauer n. sp. – Rassmuss, pl. 3, fig. 4.
- 1914 *Balatonites* cf. *lineatus* v. Arth. – Rassmuss, pl. 4, fig. 1.
- 1914 *Balatonites stenodiscus* v. Arth. – Rassmuss, pl. 4, fig. 2.
- 1914 *Balatonites Doris* v. Arth. – Rassmuss, pl. 4, fig. 3.
- 1914 *Balatonites egregius* v. Arth. – Rassmuss, pl. 4, fig. 4.
- 1991 *Balatonites egregius* Arthaber, 1896. – Tatzreiter & Vörös, pl. 1, figs 1, 2, 4–7.
- 1991 *Balatonites egregius* (= AZ3, NHMB. “*jovis*”) Arthaber, 1896. – Tatzreiter & Vörös, pl. 1, fig. 8.
- 1992 *Balatonites egregius* Arthaber, 1896. – Hohenegger & Tatzreiter, p. 812, fig. 18.4–8, 14–17, p. 814, fig. 19.1–6, 12–15.
- 2003b *Balatonites egregius* Arthaber, 1896, morphotype *jovis*. – Vörös, pls a–5, figs 7a, b, 8–11.
- 2020a *Balatonites egregius*. – Hagdorn, p. 248, fig. 1g.

Type. – Not being aware of any earlier designation, we designate the original of Arthaber (1896, pl. 23, fig. 3) from the Rahnbauerkogel, Austria, as lectotype. The dominance of a *B. egregius* fauna without *B. balatonicus* plus the co-occurrence of *Noetlingites strombecki* (see below) suggests a terminal Bithynian (Middle Anisian) age for the lectotype.

Material. – The imprint of one specimen (X13022) and its historical cast (X13356).

Description. – X13022 (dm ca. 100 mm; Fig. 15) is strongly compressed and highly oval in intercostal and subpentagonal in costal section. Coiling is moderately evolute (wh/dm 0.394). Where well preserved, the umbilical shoulder is sharp and the umbilical wall is vertical. From the umbilical wall, somewhat irregularly spaced, markedly prorsiradiate primary ribs arise, ca. 15–17/half whorl, wearing small umbilicolateral tubercles, which can be slightly bullate. Above mid-flank, a row of sometimes weakly bullate lateral tubercles occurs, from where ribbing links to a ventrolateral tubercle. Secondaries intercalate irregularly in various positions between the inner third of the flank and around the lateral tubercles. Starting below these, the secondaries can wear also (weaker) lateral and have always ventrolateral tubercles. With increasing size, the umbilical tubercles seem to become a bit bullate, while the lateral tubercles strengthen. At the onset of the last preserved whorl, broad shallow, slightly adaperturally projecting ribs link from the ventrolateral tubercles to a ventral clavus. Adaperturally, these ribs become rapidly weaker as do the ventrolateral clavi. Although poorly preserved, the terminal parts of the preserved whorls show a blunt and smoothly rounded venter.

Discussion. – A bewildering morphological variability stimulated Arthaber (1896) to erect a considerable number

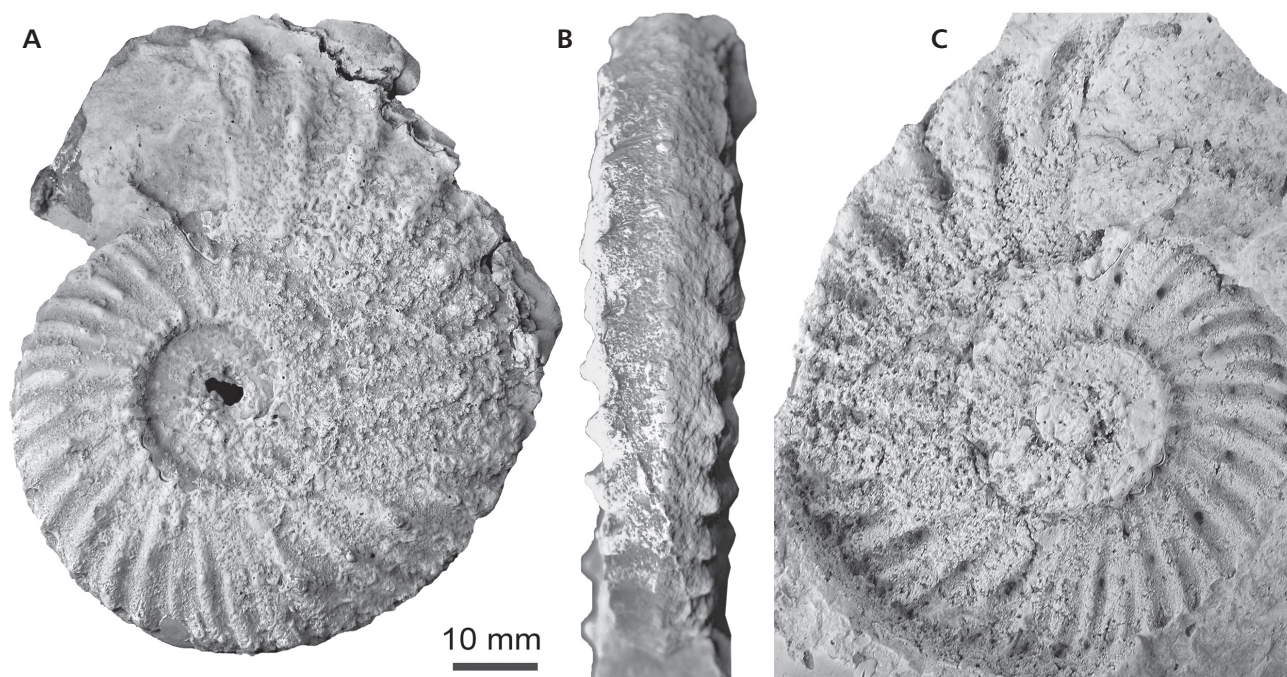


Figure 15. *Balatonites egregius* (Arthaber, 1896), Rüdersdorf Fm. from Rüdersdorf. A, B – X13356, historical cast. A – right side. B – venter. C – X13022, external mould of the same specimen. Above unit G.

Table 4. Conch parameters in mm and ratios of *Balatonites egregius*.

Specimen	dm	ah	wh	wh/dm	WER	IZR
X13022	98	25	28?	0.29?	2.68	0.11?

of *Balatonites* species, which, however, were condensed by Hohenegger & Tatzreiter (1992) to *Balatonites egregius* with statistic methods (see above). In fact, it almost appears that each specimen figured in the literature is different from another, impressively documenting a tremendous degree of innerspecific variability. The mode of ribbing, tuberculation and conch dimensions of X13022 can easily be placed within this variable species. Lacking the typical fine and irregular ribbing as observed in *B. egregius jovis* Arthaber, 1896 (see discussion in Vörös 2003b), our specimen is best regarded as *B. egregius sensu stricto*.

In our view, there is the possibility that *Balatonites zitteli* Mojsisovics, 1882 falls into the variability of *B. egregius*, in which case the specific name *zitteli* has priority over *egregius*. More material related to *B. zitteli* needs to be studied to resolve this. Vörös (2003b) preferred to include the species into *B. balatonicus* [*Balatonites balatonicus* (Mojsisovics, 1873) morphotype *zitteli*].

Occurrence. – Our specimen was labelled “Wellenkalk b”, which suggest an interval above unit G (*balatonicus* Zone). For geographic distribution see Vörös (2003b).

Family Ceratitidae Mojsisovics, 1879

Subfamily Bulogitinae Mietto & Manfrin, 2005 in Manfrin *et al.* (2005)

Genus *Bulogites* Arthaber, 1912

Type species. – *Ceratites multinodosus* Hauer, 1892, pl. 3, fig. 1, by original designation of Arthaber (1912, p. 342).

Bulogites zoldianus (Mojsisovics, 1882)

Figure 16, Table 5

- 1882 *Ceratites zoldianus*; E. v. Mojsisovics, pl. 10, figs 5, 6.
- 1963 *Bulogites zoldianus* (Mojsisovics). – Assereto, p. 113, pl. 6, fig 3 (with synonymies).
- 1969 *Bulogites* aff. *zoldianus* (Mojsisovics). – Gaetani, p. 545, pl. 36, figs 8–10.
- 2003b *Bulogites zoldianus* (Mojsisovics, 1882). – Vörös, pls a–6, fig. 1a–c; fig. a-17 (with additional synonymies).

Type. – Lectotype of *B. zoldianus* is *Ceratites zoldianus* Mojsisovics, 1882, pl. 10, fig. 6, from Dont in the Val di Zoldo (Italy), designated by Gaetani (1969) and refigured

Table 5. Conch parameters in mm and ratios of *Balatonites* used for Fig. 13.

Reference	Page/fig.	Species	dm	wh	wh/dm	Reference	Page/fig.	Species	dm	wh	wh/dm
Vörös (2003b)	p. 86	<i>balatonicus</i>	76.00	26.50	0.349	Vörös (2003b)	p. 86	<i>b. morph. zitteli</i>	25.20	10.00	0.397
idem	idem	<i>balatonicus</i>	72.00	27.00	0.375	idem	idem	<i>b. morph. zitteli</i>	24.60	9.50	0.386
idem	idem	<i>balatonicus</i>	65.00	22.00	0.338	idem	idem	<i>egregius</i>	88.80	31.70	0.357
idem	idem	<i>balatonicus</i>	63.10	23.00	0.365	idem	idem	<i>egregius</i>	53.00	20.30	0.383
idem	idem	<i>balatonicus</i>	63.00	24.00	0.381	idem	idem	<i>egregius</i>	51.70	19.70	0.381
idem	idem	<i>balatonicus</i>	61.00	22.00	0.361	idem	idem	<i>egregius</i>	44.60	17.30	0.388
idem	idem	<i>balatonicus</i>	59.00	21.00	0.356	idem	idem	<i>gemmatus</i>	52.00	21.40	0.412
idem	idem	<i>balatonicus</i>	56.00	20.00	0.357	idem	idem	<i>gemmatus</i>	40.40	16.30	0.403
idem	idem	<i>balatonicus</i>	52.00	20.00	0.385	Hohenegger & Tatzreiter (1992)	fig. 18, 2	<i>balatonicus</i>	70.00	25.00	0.357
idem	idem	<i>balatonicus</i>	50.00	19.00	0.380	idem	fig. 18, 4	<i>egregius</i>	53.00	18.00	0.340
idem	idem	<i>balatonicus</i>	49.60	18.60	0.375	idem	fig. 18, 8	<i>egregius</i>	58.00	20.00	0.345
idem	idem	<i>balatonicus</i>	49.20	17.70	0.360	idem	fig. 18, 14	<i>egregius</i>	54.00	20.00	0.370
idem	idem	<i>balatonicus</i>	45.00	17.00	0.378	idem	fig. 18, 16	<i>egregius</i>	77.00	25.00	0.325
idem	idem	<i>balatonicus</i>	43.00	16.00	0.372	idem	fig. 18, 12	<i>balatonicus</i>	46.00	18.00	0.391
idem	idem	<i>balatonicus</i>	43.00	16.00	0.372	idem	fig. 19, 16	<i>balatonicus</i>	52.00	19.00	0.365
idem	idem	<i>balatonicus</i>	41.00	15.00	0.366	X13018	Fig. 14B	<i>balatonicus</i>	52.00	20.00	0.385
idem	idem	<i>balatonicus</i>	39.00	14.00	0.359	X13022	Fig. 15C	<i>egregius</i>	94.00	37.00	0.394
idem	idem	<i>balatonicus</i>	38.80	14.80	0.381	NHMS-WT2889	Fig. 12O	<i>ottonis</i>	67.00	22.00	0.328
idem	idem	<i>balatonicus</i>	38.00	14.50	0.382	NHMS-WT2909	Fig. 12L	<i>ottonis</i>	61.00	19.00	0.311
idem	idem	<i>balatonicus</i>	36.00	13.00	0.361	X13021	Fig. 12M	<i>ottonis</i>	85.00	26.00	0.306
idem	idem	<i>balatonicus</i>	35.00	13.00	0.371	MPR C19	Fig. 12N	<i>ottonis</i>	53.00	17.00	0.321
idem	idem	<i>balatonicus</i>	34.00	14.00	0.412	NHMS-WT 2890	Fig. 12C	<i>ottonis</i>	23.50	7.50	0.319
idem	idem	<i>balatonicus</i>	34.00	13.00	0.382	NHMS-WT 2903	Fig. 12D	<i>ottonis</i>	28.00	8.80	0.314
idem	idem	<i>balatonicus</i>	34.00	12.20	0.359	Mojsisovics (1882)	p. 78	<i>ottonis</i>	102.00	29.00	0.284
idem	idem	<i>balatonicus</i>	33.10	12.70	0.384	Frech (1906)	pl 1, fig. 20	<i>ottonis</i>	82.00	25.00	0.305
idem	idem	<i>balatonicus</i>	33.00	12.00	0.364	Vörös (2003b)	p. 84	cf. <i>ottonis</i>	81.00	28.00	0.346
idem	idem	<i>balatonicus</i>	31.00	12.00	0.387	Wunsch (1960)	pl. 22	<i>rothei</i>	85.00	23.00	0.271
idem	idem	<i>balatonicus</i>	29.00	11.00	0.379	Picard (1899)	pl. 16, figs 1–3	<i>spinosus</i>	54.00	20.00	0.370
idem	idem	<i>balatonicus</i>	28.00	11.00	0.393	Rassmuss (1914)	pl. 3, fig. 1	<i>zimmeri</i>	116.00	35.00	0.302
idem	idem	<i>balatonicus</i>	27.00	10.00	0.370	idem	pl. 3, fig. 3	<i>zimmeri</i>	90.00	25.00	0.278
idem	idem	<i>balatonicus</i>	26.00	10.00	0.385	idem	pl. 4, fig. 2	<i>stenodiscus</i>	87.00	27.00	0.310
idem	idem	<i>balatonicus</i>	25.00	10.00	0.400	Dzik (1990)	pl. 15, fig. 1	<i>ottonis</i>	69.00	16.00	0.232
idem	idem	<i>balatonicus</i>	24.00	9.00	0.375	idem	pl. 15, fig. 2	<i>ottonis</i>	103.00	30.00	0.291
idem	idem	<i>balatonicus</i>	23.00	8.00	0.348	idem	pl. 14, fig. 3	<i>zimmeri</i>	116.00	36.00	0.310
idem	idem	<i>balatonicus</i>	22.00	9.00	0.409	Brack <i>et al.</i> (1999)	fig. 6a, b	<i>ottonis</i> -group	93.90	30.10	0.321
idem	idem	<i>balatonicus</i>	20.00	8.00	0.400	idem	fig. 6c	<i>ottonis</i> -group	93.00	29.40	0.316
idem	p. 88	<i>b. morph. zitteli</i>	66.70	23.00	0.345	idem	fig. 6c	<i>ottonis</i> -group	72.60	23.10	0.318
idem	idem	<i>b. morph. zitteli</i>	65.20	26.00	0.399	idem	fig. 6d	<i>ottonis</i> -group	86.00	23.60	0.274
idem	idem	<i>b. morph. zitteli</i>	50.10	17.50	0.349						
idem	idem	<i>b. morph. zitteli</i>	42.20	16.30	0.386						
idem	idem	<i>b. morph. zitteli</i>	34.00	14.40	0.424						
idem	idem	<i>b. morph. zitteli</i>	28.30	11.00	0.389						

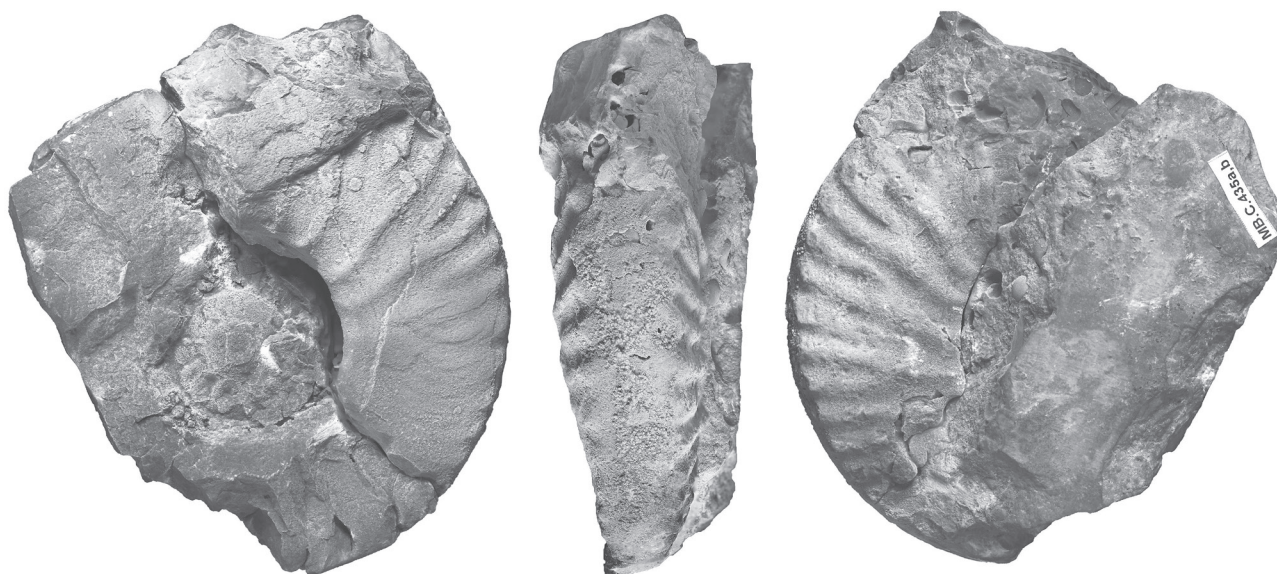


Figure 16. *Bulogites zoldianus* (Mojsisovics, 1882), higher part of Rüdersdorf Fm. from Rüdersdorf. Specimen MB.C. 435 from the historical Beyrich collection. Left: right side. Center: venter. Right: left side.

by Assereto (1963, pl. 6, fig. 3), therein erroneously referred to as holotype.

Material. – 1 specimen (MB.C. 435; Fig. 16) from the historical Beyrich collection.

Description. – The specimen shows the poorly preserved remnants of the septate phragmocone and the bodychamber, which covers a half whorl. Coiling is moderately evolute. The body chamber is high subtrapezoidal in costal section with largest thickness at the rounded umbilical shoulder. The umbilical wall is inclined inwards; the umbilicus is deep. Seven strong, slightly curved prorsiradiate ribs per third whorl on the body chamber (estimated 10 ribs per half whorl) arise from broad umbilicolateral bullae and link to weakly developed lateral bullae, situated below mid-flank, where bifurcation or the appearance of intercalatories start. Ribs become broader toward the slightly clavate ventrolateral tubercles. Between the lateral and ventrolateral tubercles, weak bullae can occur, suggesting a fourth row of tubercles. Ribbing fades at the ventrolateral row of tubercles, and the gently rounded venter remains smooth and unsculptured.

Discussion. – On an old label, written by Beyrich personally, he indicates that the specimen was found in 1854. He identified it as “*Ammonites Ottonis* L v. B.”, but a further label bears a statement of Mojsisovics from 1877: “nov. sp, verwandt mit den alpinen Formen Tr. Zoldianum und gosaviente” [“nov. sp., related to the alpine forms Tr. Zoldianum and gosaviente”]. Mojsisovics (1882, p. 39) again commented, referring to *B. zoldianus*

Mojsisovics 1882, that it is “eine nahe verwandte, noch nicht beschriebene Form” [“a closely related yet undescribed form”]. Judging, however, from the limited photographic documentation of the genus, our specimen seems to be virtually identical in all respects of ornament with *B. zoldianus* as figured by Mojsisovics (1882). *B. gosavienses* seems to have a much finer ribbing.

Occurrence. – In the Germanic Basin, *Bulogites* is rare. From Sondershausen (Thuringia, Germany), Picard (1892) described *Bulogites sonderhusanus*, which is possibly closely related to or synonymous with *B. multinodosus* (Spath 1934). *Ceratites* cf. *sonderhusanus* Picard, referred to as *Bulogites?* *sonderhusanus* by Wannenmacher & Stappenbeck (2012) (see also Urlichs & Mundlos 1985, fig. 2), was figured by Schmidt (1907a, pl. 2, fig. 9) from the “Rauhe Dolomite” (Freudenstadt Formation, Baden-Württemberg, Germany; see section in Schmidt 1907a, fig. 1). This suggests a stratigraphic level below the Oolithbank Member, which is not in accordance with the stratigraphic limitation of *Bulogites* to the terminal Pelsonian. We interpret the specimen as a *Balatonites* (see above). Further records exist from the Silesian Muschelkalk in the form of *B. zoldianus* (Mojsisovics, 1878) (e.g. Assmann 1926, 1937) (see Hagdorn 2020a).

Family Ceratitidae Mojsisovics, 1879

Genus uncertain

Comments. – Kozur (1974) used “*Ceratites*” *antecedens* and, using quotation marks, expressing his view that the

Table 6. Conch parameters in mm and ratios of *Bulogites zoldianus*.

Specimen	dm	wh	wh/dm
MB.C 435	90	30?	0.33?

antecedens group consists of a number of genera and species. After *Serpianites* Rieber 1973 was introduced for a group of bituberculated ceratitic Ammonoida, Urlichs & Mundlos (1985) addressed “*Ceratites*” *antecedens* as *Serpianites antecedens*, a procedure accepted by most works since then. We are less sure. Rieber (1973) gave a late Anisian to early Ladinian age for the genus, and – knowing the taxa from the Germanic Basin – he did not include “*C.*” *antecedens* into this group. The lack of a suture line in the type species of *Serpianites*, *S. serpiensis* (Airaghi, 1912), prevents a differential diagnosis with genera uniting similar morphologies. Morphologically, the type species of *Serpianites* deviates significantly from “*C.*” *antecedens* by the presence of a keel even at the beginning of the adult body chamber. We therefore exclude the species from *Serpianites*. This introduces the next problem, because, with the present material, we cannot assign “*C.*” *antecedens* to any contemporaneous, morphologically similar genera such as *Paraceratites* Hyatt 1900 (e.g. *P. trinodosus*) or *Schreyerites* (e.g. *S. binodosus*). *Paraceratites* with *P. elegans* Mojsisovics, 1882 as type species was introduced by Hyatt (1900) without a diagnosis. Following the diagnosis given in Arkell *et al.* (1957, p. L151: “...with a subcarinate venter; typically trituberculate with ribs that may become feebly, saddles less entire than in *Ceratites*”) and taking the type species as a template, the lack of a subcarinate venter, entire saddles and the lower number of saddles excludes “*C.*” *antecedens* from *Paraceratites*. *Schreyerites* Tatzreiter & Balini (1993) contains “involute ceratitids showing subtrapezoidal to subrectangular whorl sections and ornamentation represented by radial ribs and three series of nodes in umbilical, lateral and ventrolateral position. The suture line represents the most distinguishing feature of the genus and consists of five denticulated saddles on the lateral side” (Tatzreiter & Balini 1993, p. 1). Clearly, this cannot be related to “*C.*” *antecedens*, which shows only three non-denticulated saddles (Schmidt 1935, p. 295, fig. 811) and two rows of tubercles. Whether or not “*C.*” *antecedens* deserves an own genus cannot be answered currently due to the scarce documentation of the taxon. We, therefore, continue to use “*Ceratites*” *antecedens* to express the uncertain generic assignment within the Ceratitidae. Why Urlichs (2021) included “*C.*” *antecedens* into *Bulogites* remains enigmatic. This assignment is not in accordance with its morphology, suture line and the stratigraphic range of *Bulogites*.

“*Ceratites*” *antecedens* (Beyrich, 1858)

Figures 17, 18; Table 7

- 1858 *Ammonites antecedens*, H. sp.; Beyrich, pp. 211–214; pl. 4, fig. 4.
- *1867 *Ammonites antecedens*. – Beyrich, pp. 112, 113; pl. 4, fig. 3a, b.
- 1880 *Ceratites antecedens* BEYR. – Eck, pp. 36–38.
- ? 1882 *Ceratites antecedens* Beyr. – Fritsch, p. 19.
- 1885 *Ceratites antecedens* Beyr. – Eck, pp. 466–469.
- 1888 *Ceratites* nov. f. indet. – Wagner, pp. 35–38; pl. 5, fig. 1.
- 1889 *Ceratites antecedens* Beyrich. – Picard, pp. 635–637; pl. 26, figs 1–5.
- 1889 *Ceratites trinodosus* v. Mojs. – Jäkel, pp. 19–31; pl. 1, fig. 1a, b.
- 1891 *Ceratites antecedens* Beyr. – Eck, pp. 734, 735.
- ? 1902 *Ceratites* sp. – Fritsch, pp. 67, 68; pl. 4, fig. 6.
- 1903–1908 *Ceratites antecedens* Beyrich. – Frech, pl. 1, fig. 2a, b.
- 1907a *Ceratites antecedens* Beyrich. – Schmidt, pp. 89–95; pl. 2, figs 4–8.
- 1907b *Ceratites antecedens* Beyr. – Schmidt, pp. 528–533, figs 1–3.
- 1928 *Ceratites antecedens* Beyr. – Schmidt, pp. 294, 295, 811.
- 1935 *Ceratites antecedens* Beyrich. – Schmidt, pp. 198–212; pl. 13, figs 1–3, 5–8.
- 1951 *Ceratites antecedens* Beyr. – Rothe, pp. 67–69; pl. 9, figs 1–3.
- 1955 *Ceratites antecedens* Beyrich. – Claus, p. 39; pl. 2, fig. 7.
- 1974 “*Ceratites*” *antecedens*. – Kozur, pp. 10–15.
- 1985 *Serpianites antecedens*. – Urlichs & Mundlos, pp. 227, 228; fig. 5.
- 1986 *Serpianites antecedens* (Beyrich). – Baumgarte & Schulz, pp. 88–90, fig. 4.
- 1999 “*Ceratites*” *antecedens*. – Urlichs, pp. 346, 347; fig. 7.
- 2012 *Serpianites antecedens* (Beyrich). – Wannenmacher & Stappenbeck, p. 228, fig. 14.
- 2014 *Serpianites antecedens*. – Müller *et al.*, fig. 27, 1a–d.
- 2020a “*Ceratites*” *antecedens* Beyrich, 1858. – Hagdorn, pp. 251, 252; fig. 2a–c.
- 2021 *Bulogites antecedens* (Beyrich). – Urlichs, p. 275, fig. 5.

Type. – Holotype by monotypy is the original of Beyrich (1858), of which only a section and a suture line were figured (1858, pl. 4, fig. 4). The specimen survived in the collection of the Naturkundemuseum Berlin (MB.C. 436), and, judging from the historical labels, there can be no doubt that the present specimen is, in fact, the original. It is shown in Figure 17G. It is stated that the holotype was probably from Thuringia (“wahrscheinlich aus Thüringen”), but any details are missing.

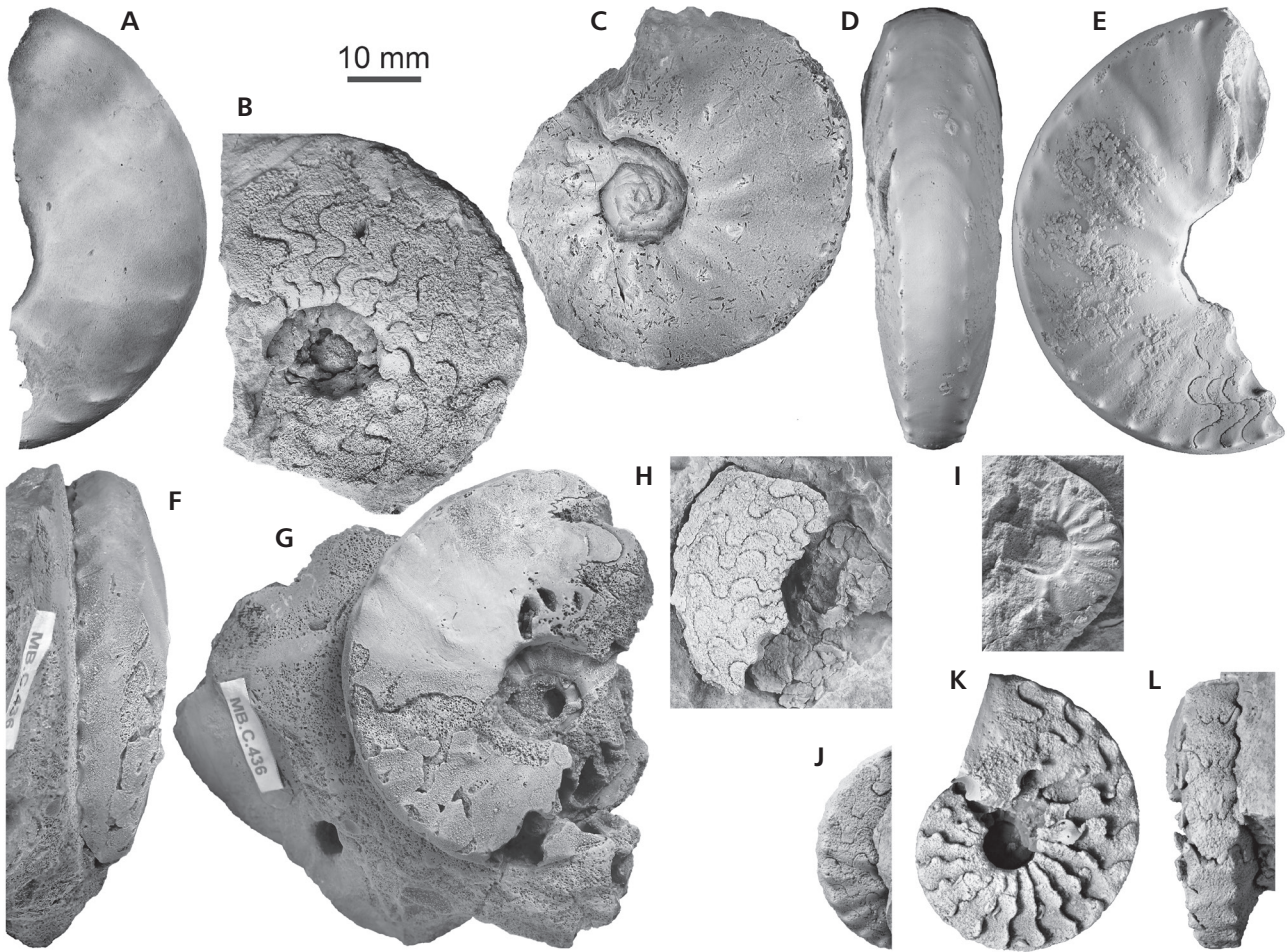


Figure 17. “*Ceratites*” *antecessors* (Beyrich, 1858), Rüdersdorf Fm. from Rüdersdorf. A – X13353, poorly preserved body chamber. B – X13026, phragmocone, unit I. C – X6109, original of Frech (1903–1908, pl. 1, fig. 2a) and probably a type of Beyrich from 1867 (?). D, E – X13024, body chamber with last chambers of the phragmocone, well preserved suture and the typical “treppenförmige Nabeltrichter” (‘stair-shaped umbilical funnel’, referring to the angular shape). F, G – MB.C. 436, the holotype of Beyrich (1858, pp. 211–214; pl. 4, fig. 4.) of unknown origin. H – X13354, part of phragmocone, Unit I. I – X13025, probably part of inner whorl or juvenile specimen, unit I. J, K, L – NHMS-WT2912, only specimen collected more or less *in situ*, upper part of unit I (Zwenger & Koszinski 2009, p. 46).

Material. – 8 specimens (MB.C. 436, X6109, X13024–X13026, X13353, X13354, NHMS-WT2912).

Description. – “*C.*” *antecessors* is moderately evolute, with a deep umbilicus and rounded umbilical shoulders (e.g. X13026, Fig. 17A; X6109, Fig. 17C). Specimen X13025 (Fig. 17I) is the smallest specimen (dm 25 mm) available. Broad, straight rectiradiate primary ribs arise at the umbilical shoulder, and in the lower third of the flank, secondaries intercalate irregularly. A row of rounded/slightly bullate inner lateral tubercles and a row of clavate ventrolateral tubercles exist. The venter is broadly rounded. With increasing size (NHMS-WT2912, dm 39 mm, Fig. 17J–L), ribbing becomes stronger, and shallow, and broad ribs transverse the venter, linking the ventrolateral clavi. Specimens X13026 (Fig. 17B) and X13354 (Fig. 17H) are even larger, but do not provide,

due to the poor preservation, additional data. X6109 (dm 60 mm, Fig. 17C), the original of Frech (1903–1908, pl. 1, fig. 2), remains moderately involute (uw/dm 0.17) and exhibits a subangular outline of the umbilicus, which reflects the “treppenförmigen Nabeltrichter” of Schmidt (1935) (“staircase-shaped umbilical funnel”). It is this feature, which was also well-documented by Beyrich (1867, pl. 4, fig. 3), and we believe that X6109 could be the original of Beyrich (1867, pl. 4, fig. 3).

Specimen X13024 (Fig. 17D, E) is a body chamber at an approximate diameter of 55 mm. The umbilicus displays also the “treppenförmigen Nabeltrichter”. The bituberculated stage disappeared, as in the bodychamber of X13353 (Fig. 17A), and only the ventrolateral clavi, progressively weakening, persist. Ribs become narrowly spaced at the begin of the body chamber but become more distant towards the aperture to form broad, slightly

Table 7. Conch parameters in mm and ratios of “*Ceratites*” *antecedens*.

Specimen	dm	bcl	ah	wh	uw	ww _{min}	ww _{max}	uw/dm	wh/dm	WER	IZR
NHMS-WT2912	45				5			0.1			
X6109	60		14?	20?	10			0.17	0.3?	1.2?	0.3?
X13024	63	95?	12?	25?	14?	8	20?	0.2	0.4?	1.2?	0.5?
X13025	25	30?			7?			0.3?			
X13026					12?						
X13353	60	95?	12?	25?	14?	8	20?	0.2	0.4?	1.2?	0.5?

flexuous swelling but fading in the inner part of the flank (X13024, Fig. 17D, E). A slightly lirate ornament might have been present. At that stage, the venter is almost smooth, but an adaperturally projecting constriction-like depression occurs. X13353 (Fig. 17A) shows even more reduction of ornament and a poorly sculptured flank. Only few distant ribs are still visible, and the ventrolateral clavi shifted down the umbilical shoulder to form comma-like, strongly prorsiradiate tubercles. These tubercles disappear almost completely on the terminal body chamber to leave an almost unsculptured surface except faint remnants of 3–4 shallow ribs.

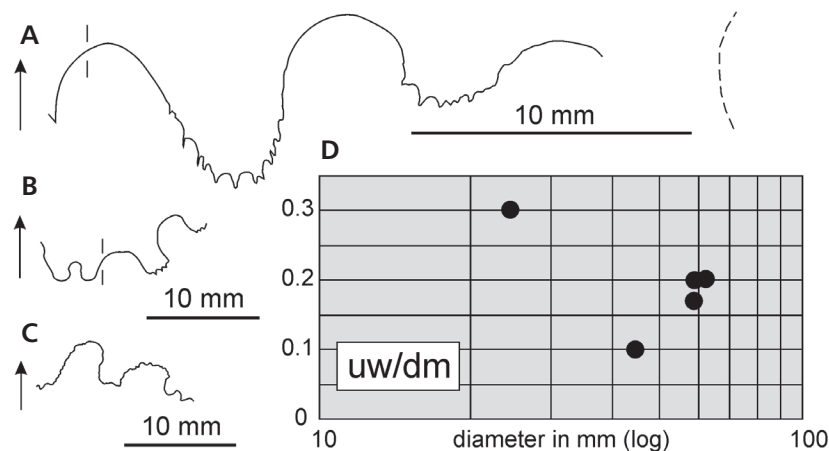
The sutures consist of a narrow and deep L, and two succeeding, small lobes become progressively shallower and smaller, of which half of the inner lobe is located on the umbilical shoulder. These are separated by two broad but shallow lateral auxilliary saddles (Fig. 18). The lobes are serrated although the denticulation of L can creep up more than half way up to the summit of the saddles (Fig. 18). The saddles are smooth and rounded.

Discussion. – In the original, detailed description of *Ammonites antecedens*, the holotype was not figured, but a cross-section and details of the suture line were presented (Beyrich 1858, pl. 4, fig. 4). We figure the holotype for the first time (Fig. 17F, G). It is a fully septate but incomplete specimen with a dm of ca. 55 mm and an umbilical width of 12 mm. The whorl section is trapezoidal with largest thickness at the umbilical shoulders. The umbilical shoulder is narrowly arched, leading into a steep, outward directed, straight or slightly rounded, broad wall of a comparatively deep umbilicus. Early whorls show primary ribs arising in the umbilical areas, while the last preserved whorl shows already reduction of ornament with sparse, shallow and broad ribbing arising in the lower third of the flank, bifurcation at/around an inner lateral tubercle and small ventrolateral clavi. The venter forms a broad bulge, crossed by few ribs, forming irregular, adaperturally directed chevrons. The holotype shows good accordance with the specimens figured by Beyrich (1867, pl. 4, fig. 3) and Jäkel (1889, pl. 1, fig. 1a), the latter described as *Ceratites trinodosus* but

included into “*C.*” *antecedens* already by Schmidt (1928). The species was described in detail by, e.g. Wagner (1922) and Schmidt (1907b), and it shows a considerable morphological variability. This was recognized and discussed by Schmidt (1935), and we follow Schmidt (1935) to understand “*C.*” *antecedens* as a variable species (contrasting Rothe 1951). Particularly characteristic is the unique suture line (e.g. Beyrich 1858, Schmidt 1935), which enables a safe identification of the species. This likewise is an argument against the splitting of “*C.*” *antecedens* into several genera as suspected by Kozur (1974). Our material falls into the variation as expressed by the few figured specimens. Whether “*C.*” *antecedens* represents more than one species, cannot be discussed with the scarce material figured in the literature: So far, only a bit more than a dozen specimens were figured.

Occurrence. – From the Oolithbank Member, Fritsch (1882) mentioned a specimen of “*C.*” *antecedens*, later figured by Fritsch (1902) as *Ceratites* sp. From Lieskau near Halle, Rothe (1951) recorded a specimen collected loose from the talus of quarry wall, allegedly exposing the Lower Wellenkalk Member and the Oolithbank Member (Rothe 1951), but it could have come also from the beds immediately overlying the Oolithbank Member. The oldest well-labelled specimen of the Jena Formation comes from the lowermost Middle Wellenkalk Member of Jena (Thuringia), ca. 1 m above the top of the Oolithbank Member (Wagner 1922). From Bad Kösen (Thuringia), a specimen was collected 2 m above the top of the Oolithbank Member (NHMS-WT3076). An abundance peak is reported to occur 1–3 m above the Oolithbank Member in the lower Middle Wellenkalk Member (Wagner 1922). A single specimen from northern Hesse was collected 5–6 m above the Oolithbank Member (Baumgarte & Schulz, 1986). Records exist up to the Terebratelbank Member and slightly above in Thuringia (Wagner 1888, 1922; Picard 1889). This stratigraphic position equates with the south German occurrences in the Freudenstadt Formation (Eck 1885, Schmidt 1907a, b, 1935). All specimens from Rüdersdorf come from the unit I of the Rüdersdorf Formation, corresponding to the equivalent

Figure 18. Sutures and conch parameters of “*Ceratites*” *antecedens* (Beyrich, 1858), Rüdersdorf Fm. from Rüdersdorf. A – X13024. B – NHMS-WT2912. C – X13353. D – ontogenetic development of the umbilical width/ diameter ratio (Tab. 5).



of the Middle Wellenkalk Member, the Terebratelbank Member and parts of the Upper Wellenkalk Member of the Jena Formation (Zwenger & Koszinski 2009, p. 37, fig. 10). The latter authors report a specimen from the higher part of Unit I (NHMS-WT2912, Fig. 17J–L), but it was collected loose. Assignments to the Terebratelbank Member of some of the Rüdersdorf material in the collection of the Bundesanstalt für Geowissenschaften und Rohstoffe Berlin are later designations on the labels, possibly based on theoretical assumptions (Zwenger & Koszinski 2009) and are doubtful. We speculate that it is easily possible that the Rüdersdorf material comes from the same stratigraphic level like the Thuringian and south German occurrences. There is no evidence that the Rüdersdorf material is younger, like suggested by, e.g. Hagdorn (2020a). In conclusion, it appears that “*C.*” *antecedens* ranges throughout the Middle Wellenkalk and Terebratelbank Member into the lowermost Upper Wellenkalk Member. A range into the Schaumkalkbank Member (Urlichs & Mundlos 1985) cannot be confirmed. Following Kozur (1974), we use “*C.*” *antecedens* as the marker for the base of the Pelsonian in the Germanic Basin.

The maximum abundance of “*C.*” *antecedens* in the Freudenstadt Formation of Baden-Württemberg, progressively decreasing finds towards Thuringia, Saxony-Anhalt, Lower Saxony and Rüdersdorf, and lacking records in the Polish parts of the Germanic Basin suggest an immigration of “*C.*” *antecedens* through the Burgundian Gate, as already earlier suggested by Frank (1931).

Family Hungaritidae Waagen, 1895

Genus *Noetlingites* Hyatt, 1900

Type species. – Type species of *Noetlingites* is *Ammonites Strombecki* Griepenkerl, 1860, originally designated by Hyatt (1900).

Noetlingites strombecki (Griepenkerl, 1860)

Figures 19–21, Table 8

- 1860 *Ammonites Strombecki*; Griepenkerl, pp. 161–167; pl. 7, figs 1–3.
- 1880 *Ammonites* (*Cer.*) *Strombecki* Griep. – Noetling, pp. 333, 334.
- 1882 *Hungarites Strombecki* (Griepenkerl). – Mojsisovics, p. 221; pl. 61, fig. 8.
- 1902 *Hungarites Strombeckii* Griepenkerl sp. – Fritsch, pp. 53–55; pl. 3, fig. 8.
- 1903–1908 *Hungarites Strombecki* Griep. sp. – Frech, pl. 1, fig. 8a–c.
- 1915 *Hungarites Strombecki* Griepenk. – Holdefleiß, p. 20.
- 1928 *Hungarites Strombecki* Griepenkerl sp. – Schmidt, pp. 289–290, fig. 800.
- 1932 *Hungarites Strombecki* Griep. – Claus, pp. 40–43.
- 1951 *Noetlingites strombecki* Griepenkerl. – Spath, p. 18.
- 1952 *Hungarites strombecki* Griep. – Hardt, pp. 98, 99; fig. 53.
- 1955 *Hungarites strombecki* Griepenkerl. – Claus, p. 38; pl. 2, fig. 3a, b.
- 1959 *Hungarites strombecki* Griepenk. – Rothe, p. 66, fig. 2
- 1960 *Hungarites strombecki* (Griep.) – Müller, p. 171, fig. 242.
- 1965 *Hungarites strombecki* (Griep.) – Müller, p. 197, fig. 267.
- 1977 *Hungarites strombecki* Griepenkerl. – Kelber, pp. 145–149, figs 1–3.
- 1981 *Hungarites strombecki* (Griep.) – Müller, p. 225, fig. 287a.
- 1994 *Hungarites strombecki* (Griep.) – Müller, p. 250, fig. 286.
- 1999 *Noetlingites strombecki*. – Urlichs, p. 344, fig. 3.
- 2001 *Noetlingites strombecki* (Griepenkerl 1860). – Tatzreiter, pp. 143–162, figs 9, 10; tab. 1.
- ? 2018 *Noetlingites* sp. – Mietto, Manfrin & Rigo, p. 230, fig. 5.

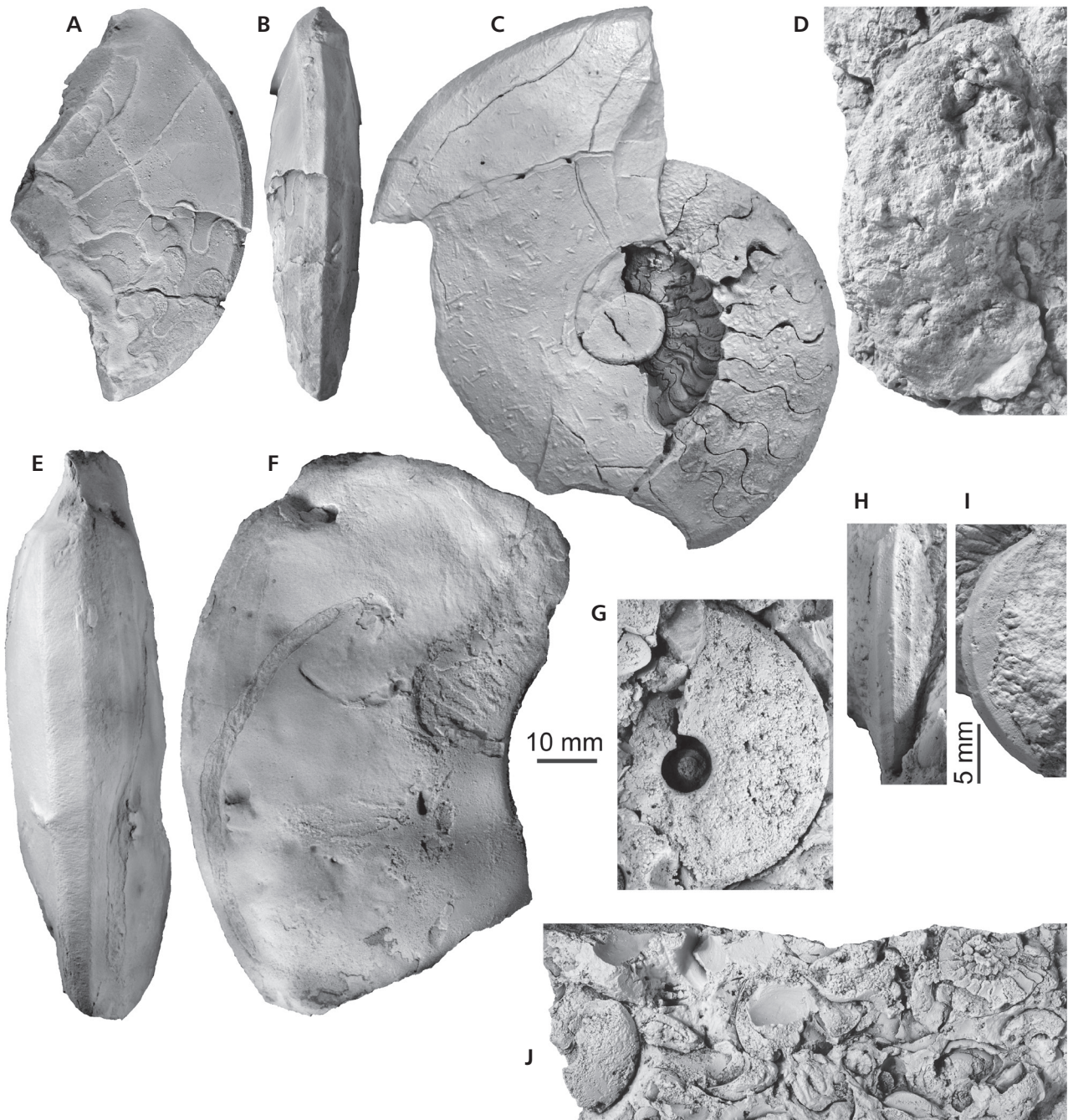


Figure 19. *Noetlingites strombecki* (Griepenkerl, 1860), Jena Fm. from Rüdersdorf. A, B – MPRC47, fragment with the typical distinctly demarcated keel, view from lateral and ventral, unit D or E. C – NHMS-WT2885, more or less adult specimen with “double sutures” (by pressure solution), unit D or E. D – NHMS-WT2884, fragment of body chamber, oldest known specimen from Rüdersdorf, middle to upper part of unit D. E, F – NHMS-WT2907, incomplete body chamber of probably adult specimen, unit E. G – MPRC45, preadult specimen with poorly preserved ribs. Specimen comes from same layer as NHMS-WT2890, probably upper part of unit D or base of unit E. H, I – X13023, juvenile specimen with well developed keel, view from lateral and ventral, probably unit E. J – NHMS-WT2890, contains two body chamber fragments of juvenile specimens with more or less developed keel (far left and far right on the plate), plate comes from same layer as MPRC45.

- 2019 *Hungarites strombecki*. – Gümbel, p. 44, fig. 34a, b.
 2019 *Noetlingites strombecki*. – Gümbel, p. 48, fig. 37e.
 2020a *Noetlingites strombecki* Griepenkerl (1860). – Hagdorn, p. 248, fig. 1d; p. 254.

Type. – Holotype by monotypy is the original of Griepenkerl (1860, pl. 7, figs 1–3) from a train cut near Neuwallmoden (Lower Saxony). Schmidt (1928, p. 290, fig. 800) refigured the specimen and gave the Technische Hochschule

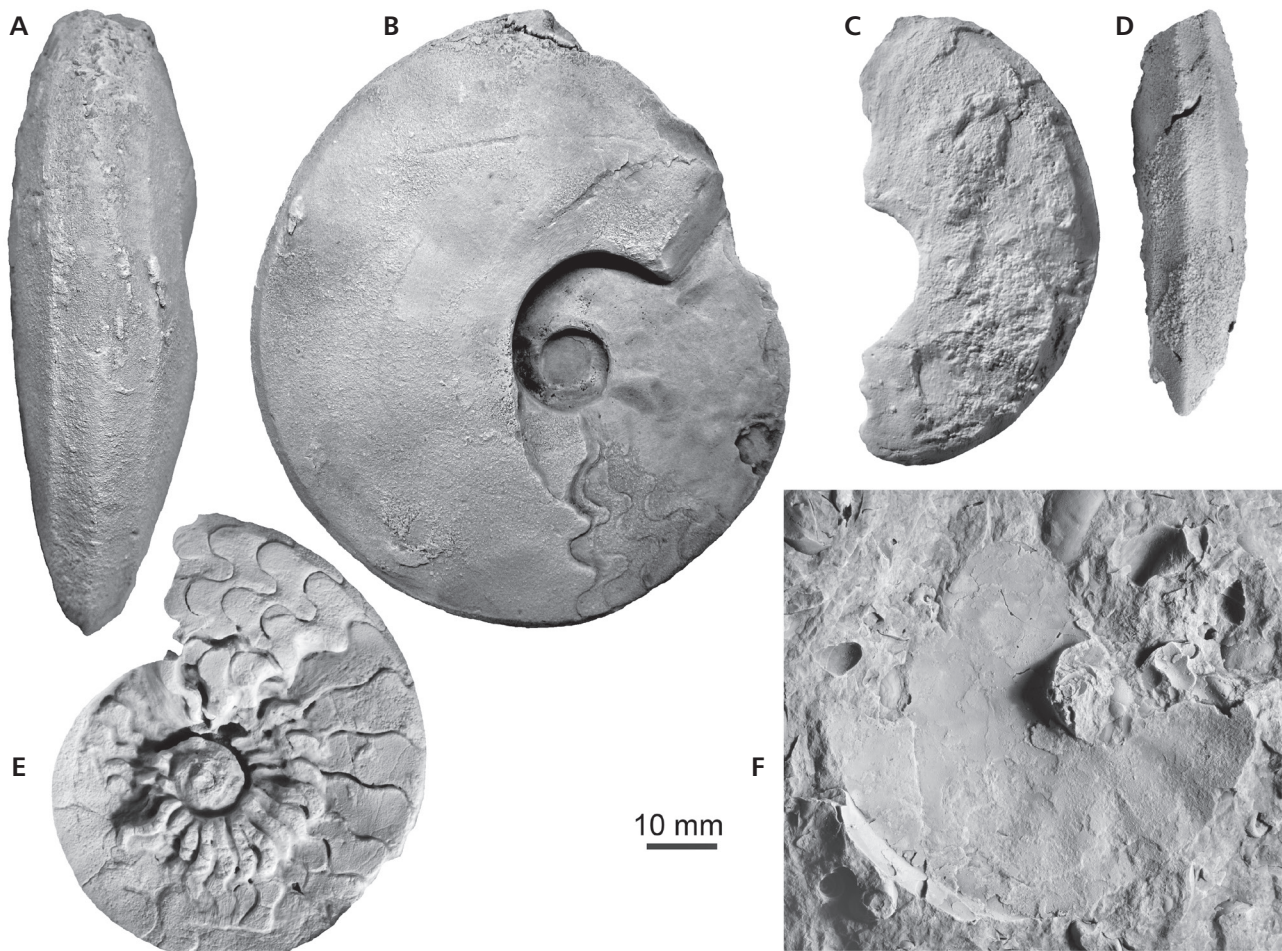


Figure 20. *Noetlingites strombecki* (Griepenkerl, 1860), Jena Fm. from Rüdersdorf. A, B – probably adult specimen with broad, shallow depressions and bulges on the body chamber, unit E (coll. FS). C – NHMS-WT2881, poorly preserved body chamber, uppermost unit D. D – NHMS-WT2905, fragment of body chamber with well-developed keel, uppermost unit D or base of unit E. E – NHMS-WT2888, phragmocone of adult specimen, comes from the same layer as specimen NHMS-WT2907, unit E. F – MPRC46, imprint of preadult specimen with well-developed ribs, uppermost unit D or base of unit E.

Braunschweig as depository. We have not yet been able to trace the specimen.

Material. – 13 specimens (X13023, MPRC45–MPRC47, NHMS-WT2881, NHMS-WT2884, NHMS-WT2885, NHMS-WT2888, NHMS-WT2890: two specimens, NHMS-WT2905, NHMS-WT2907, 1 specimen FS collection, unregistered). All are composite moulds or simple internal moulds.

Description. – Our material comprises mainly fragments of middle and late growth stages, but without evidence of adult modifications (measurements and ratios in Tab. 8). Protoconch, ammonitella, hatchlings or early juveniles/neoconchs are unknown. The smallest juvenile available (NHMS-WT2890, Fig. 19J) is an 8 mm large fragment of a poorly preserved body chamber. A well-developed keel is visible at that size, and the whorl section is compressed.

Specimen X13023 (Fig. 19H, I) shows a tricarinate venter with an elevated siphonal and two lower ventrolateral keels, separated by well-developed grooves. This feature is also seen in MPRC45 (Fig. 19G) at a size of 45 mm, but with increase size, the venter becomes progressively (sub-)fastigate. Whorl section is compressed oval with largest thickness around the lower third of the flank. MPRC45 (Fig. 19G) and NHMS-WT2885 (Fig. 19C) convey an impression of the umbilical area, showing a small umbilicus with a narrowly arched wall. Small juveniles show no ornament, but in the imprint MPRC46 (dm 55 mm, Fig. 20F), traces of 4 broad, widely spaced ribs are visible, which arise in the umbilicus and become thicker towards the venter. Adults start to develop broad, shallow depressions and bulges on the body chamber, partly visible in NHMS-WT2907 (Fig. 20E). It is ideally developed in an unregistered adult (coll. FS) with sutural crowding (dm 115 mm, Fig. 20A, B), which shows broad

Table 8. Conch parameters in mm and ratios of *Noetlingites strombecki*.

Specimen	dm	bcl	ah	wh	uw	uw/dm	wh/dm	WER	IZR
MPRC45	47	78	13?	22	8	0.17	0.47	1.91?	0.41?
NHMS-WT2885	85	140	23	35	10?	0.12?	0.41	1.88	0.34
NHMS-WT2881	68	100		25?			0.37?		
NHMS-WT2884	65	95?		35	12	0.18	0.54		
FS collection	113								

bulges in the lower third of the flank and two progressively deepening depressions, expression of maturity.

The sutures are ceratitic with serrated lobes, although the serration is eroded in our specimens. Complimentary descriptions can be found in Kelber (1977) as also mentioned below. E is small and subdivided by a small ventral saddle, and L is larger. Two visible U are somewhat smaller than L. The saddles are rounded and wider than the lobes, in some cases twice as wide.

Discussion: – Hyatt (1900) erected the genus *Noetlingites* with *Ammonites Strombecki* Griepenkerl, 1860 as the type species without further explanation, description or discussion. Diener (1916) criticized this procedure, and in his catalogue (Diener 1915), *Noetlingites* was synonymized with *Hungarites*. Although morphologically similar to *Hungarites* by the development of an almost fastigate to subplanulate venter with a keel, Spath (1951) and Arkell *et al.* (1957) mention the lack of a ventral saddle in E as observed in *Hungarites*: “Like *Hungarites* but venter fastigate throughout. Suture without median saddle in ventral lobe, 3 lateral lobes, broadly rounded saddles.” (Arkell *et al.* 1957, p. L156). This statement is incorrect. The type species of *Noetlingites* has a well-developed ventral saddle in E (Griepenkerl 1860, pl. 7, fig. 3), as also shown in the specimen of Tatzreiter (2001, p. 160, fig. 10b) and visible in our material (Fig. 21B). The characteristic suture line of *Noetlingites* shows, in fact, three lateral, narrow lobes and broadly rounded saddles (Kelber 1977, p. 148, fig. 3; Tatzreiter 2001, p. 160, fig. 10). However, in the type species of *Hungarites*, *Hungarites mojsisovicsi* (Roth, 1871), the suture line is more complex than in *Noetlingites* and shows at least four lateral lobal elements (Vörös 2018, p. 118, fig. 68), like in other species of *Hungarites* (Vörös 2018). This justifies a separation of the both genera (*e.g.* Tozer 1981). Furthermore, *Noetlingites* (Middle Anisian, Bithynian) is stratigraphically separated from *Hungarites* (terminal Anisian to Ladinian), making the first a potential precursor of the latter.

Our material does not supplement much to the knowledge of the species. Septal crowding suggests that adults reach sizes between *ca.* 83 mm (Kelber 1977) and 120 mm

(Schmidt 1928) to 130 mm (Tatzreiter 2001, p. 159, fig. 9), the latter exhibiting the body chamber modifications of the terminal growth stage like our specimen in Fig. 20A, B. Accordingly, our specimens NHMS-WT2885 (Fig. 19C, dm 100 mm) and NHMS-WT2907 (Fig. 19E, F) with a body chamber height of *ca.* 50 mm represent also most likely adults. *Noetlingites strombecki* is a morphologically stable species, and there occurs little morphological variations. This relates also to the suture line.

Pronoetlingites arifensis (Parnes 1962) from the terminal Bithynian of Israel (stratigraphically re-interpreted; see above) shows the same suture line with three lateral lobes like in *N. strombecki* (Parnes 1962, pl. 7, fig. 6). In addition, broad ribbing occurs in both species (comp. Fig. 20F), and the species are very closely related if not conspecific.

Occurrence. – *N. strombecki* is widely distributed in the Jena Formation of the Germanic Basin (Griepenkerl 1860, Fritsch 1902, Hardt 1952, Kozur 1974, Kelber 1977, Urlichs & Mundlos 1985), as well as in the Freudenstadt Formation of southern Germany (“Mergelige Schichten”, Schmidt 1907a, Urlichs & Mundlos 1985, Hagdorn & Nitsch 2009; see map in Kelber 1977, p. 146, fig. 1). Although often lacking precise stratigraphic locations, almost all finds appear to be restricted to the Lower Wellenkalk Member in the Germanic Basin (*e.g.* Fritsch 1902, Rassmuss 1914, Claus 1955, Kelber 1977,

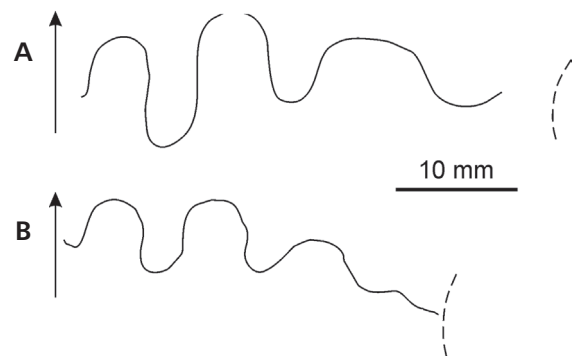


Figure 21. Sutures of *Noetlingites strombecki* (Griepenkerl, 1860), Jena Fm. from Rüdersdorf. A – MPRC47. B – NHMS-WT2888.

Urlichs & Mundlos 1985, Urlichs 1999) and, therefore, to the Bithynian. The occurrences in Rüdersdorf fit the stratigraphic distribution: *N. strombecki* occurs first in the Lower Wellenkalk Member (unit D, 18–20 m below the base of the Rüdersdorf Formation: NHMS-WT2884) and it ranges into the uppermost unit D to E (MPRC45–47, NHMS-WT2881, NHMS-WT2888, NHMS-WT2890, NHMS-WT2905, NHMS-WT2907), which is still within the Lower Wellenkalk Member. There appears to be an abundance maximum of *N. strombecki* below the Oolithbank Member (Fritsch 1902, Urlichs & Mundlos 1985) and in the middle part of the slightly older dolomites of the “Mergeligen Schichten” of the Freudenstadt Formation (Schmidt 1907a). Raab (former chemist in Rüdersdorf around 1900) labelled fossils in his collection with “*Hungarites-Beneckeia-Zone*”, which likely refers to the ‘E-Horizont’ (unit E). This reflects the abundance peak in that interval below the Oolithbank, which likely corresponds to the phase of greatest geographic distribution in the Germanic Basin as already suspected by Fritsch (1902). It is doubtful whether the specimen of Griepenkerl was really extracted from directly above the Röt as suggested by Claus (1932). Finds from Poland come from the Upper Gogolin Beds (Eck 1865, Noetling 1880, Assmann 1937), which correlate lithostratigraphically with the upper part of the Lower Wellenkalk Member, and a single specimen was recorded from the Lower Gogolin Beds (Eck 1865), which appears questionable. All these records are Bithynian in age, which is also true for the only Alpine record (Rahnbauerkogel, Styria, Austria: Tatzreiter 2001).

Mietto *et al.* (2018) figured a specimen from the upper Pelsonian *zoldianus* Subzone of the Alps as *Noetlingites*. A further possible specimen from the Balaton area (Hungary) comes from the lower *balatonicus* Zone (Vörös 2003b). It, therefore, appears that the genus is possibly not restricted to the Bithynian.

Superfamily Ptychitoidea Mojsisovics, 1882

Family Ptychitidae Mojsisovics, 1882

Genus *Discoptychites* Diener, 1916

Type species. – *Ammonites megalodiscus* Beyrich, 1867, originally designated by Diener (1916, p. 101).

Discoptychites dux (Giebel, 1853)

Figures 22–24, Table 9

- 1853 *Ammonites dux* H. sp.; Giebel, pp. 341–345; pl. 9.
- 1854 *Ammonites dux* Giebel. – Beyrich, pp. 513, 514; unnumb. fig.
- 1858 *Ammonites dux*. – Beyrich, pp. 208–211; pl. 4, figs 1–3.

- 1867 *Ammonites Dux* Gieb. – Beyrich, pp. 130–132; pl. 5, figs 1–3.
- 1882 *Ptychites dux* (Giebel). – Mojsisovics, p. 252.
- 1882 *Ptychites Suttneri*. – E. v. Mojsisovics, pp. 251, 252; pl. 74, figs 1–4, pl. 75, figs 2, 3.
- 1902 *Ptychites Beyrichii* Fr. – Fritsch, pl. 4, figs 3, 7–10, 12, 13; pl. 5, fig. 1.
- 1902 *Ptychites dux* Gieb. – Fritsch, pl. 5, fig. 2.
- 1903–1908 *Ptychites dux* (Gieb.). – Frech, pl. 1, fig. 1a, b.
- ? 1915 *Ptychites dux* Gieb. – Wurm, pp. 444–447, fig. 3a, b; pl. 36, figs 1–3.
- 1921 *Ptychites dux* Beyr. Gieb. – Claus, pp. 120–125, figs 1–6a.
- 1927 *Ptychites dux* Gieb. – Walther, pl. 9, fig. 61.
- 1928 *Ptychites Beyrichi* Fritsch. – Schmidt, p. 309, fig. 847.
- 1928 *Ptychites dux* Giebel sp. – Schmidt, p. 309, fig. 848.
- 1937 *Ptychites* sp. – Assmann, p. 105; pl. 22, fig. 4.
- 1955 *Ptychites beyrichi* v. Fritsch. – Claus, p. 40; pl. 3, fig. 1.
- 1955 *Ptychites dux* Giebel. – Claus, p. 40; pl. 3, fig. 2a, b.
- 1959 *Ptychites dux* Giebel. – Rothe, pp. 66, 67, fig. 1.
- 1965 *Ptychites dux* (Giebel). – Müller, p. 204, fig. 281.
- 1981 *Ptychites dux* (Giebel) – Müller, p. 233, fig. 301.
- 1994 *Ptychites dux* (Giebel) – Müller, p. 259, fig. 301.
- 1999 *Discoptychites* cf. *dux* (Giebel, 1853). – Kaim & Niedźwiedzki, p. 102, fig. 6a–f; p. 103, fig. 7a–d.
- ? 1999 *Discoptychites* sp. – Urlichs in Hauschke & Wilde, p. 346, fig. 8.
- 2001 *Discoptychites dux*. – Hagdorn, p. 66, unnumb. fig., p. 68, fig. a.
- 2020a *Discoptychites dux*. – Hagdorn, p. 253, fig. 3c.
- 2020 *Discoptychites dux*. – Kramm, Röhling & Hagdorn, p. 714, fig. 4c.

Type. – Holotype by monotypy is the original of Giebel (1853, pl. 9) from the Muschelkalk of Schraplau (Saxony-Anhalt, Germany). Kaim & Niedźwiedzki (1999) and Zwenger & Koszinski (2009) stated that it derives from the Schaumkalkbank Member. However, Giebel (1853) gave no precise location, and Picard (1923), describing the Muschelkalk from the find area Schraplau, clearly stated that the find horizon is unknown.

Material. – 13 specimens (MB.C. 1151, MB.C. 1153, X13027–X13031, X13057, BT51834–36, BT51834–43, BT51834–44, BT51995–27, NHMS-WT2984).

Description. – *Discoptychites dux* (Giebel, 1853) is very involute with a small umbilicus throughout ontogeny (for ratios and measurements, see Tab. 9) with a narrowly arched shoulder and steep flanks. Juveniles are somewhat subovoid and have a broadly rounded venter (X13029, Fig. 22F, G, size *ca.* 50 mm). Faint, broad rectiradiate ribs are rather felt than seen in this stage. Broad rectiradiate ribs, *ca.* in 10 per half whorl, occur at a size of *ca.* 80 mm,

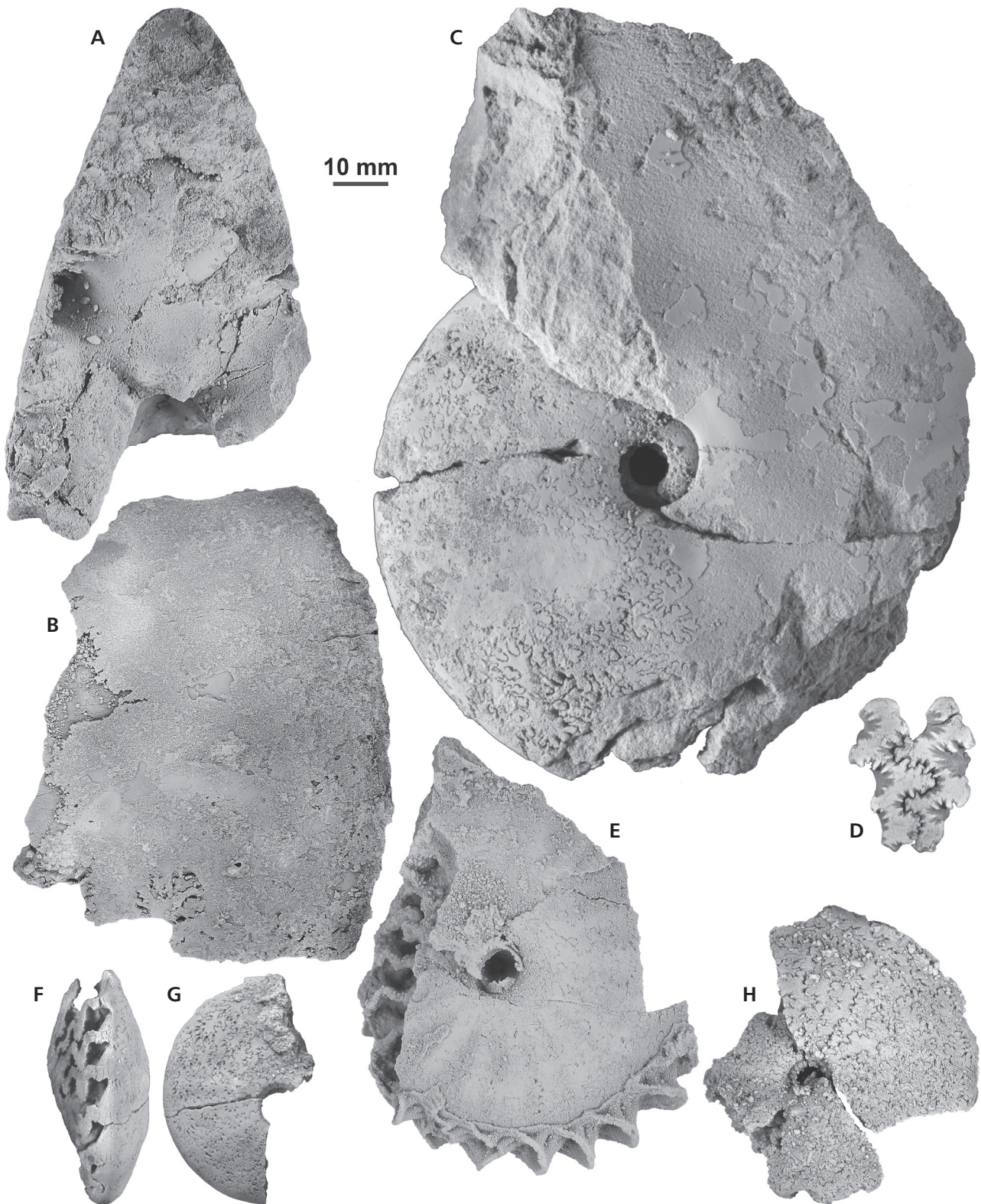
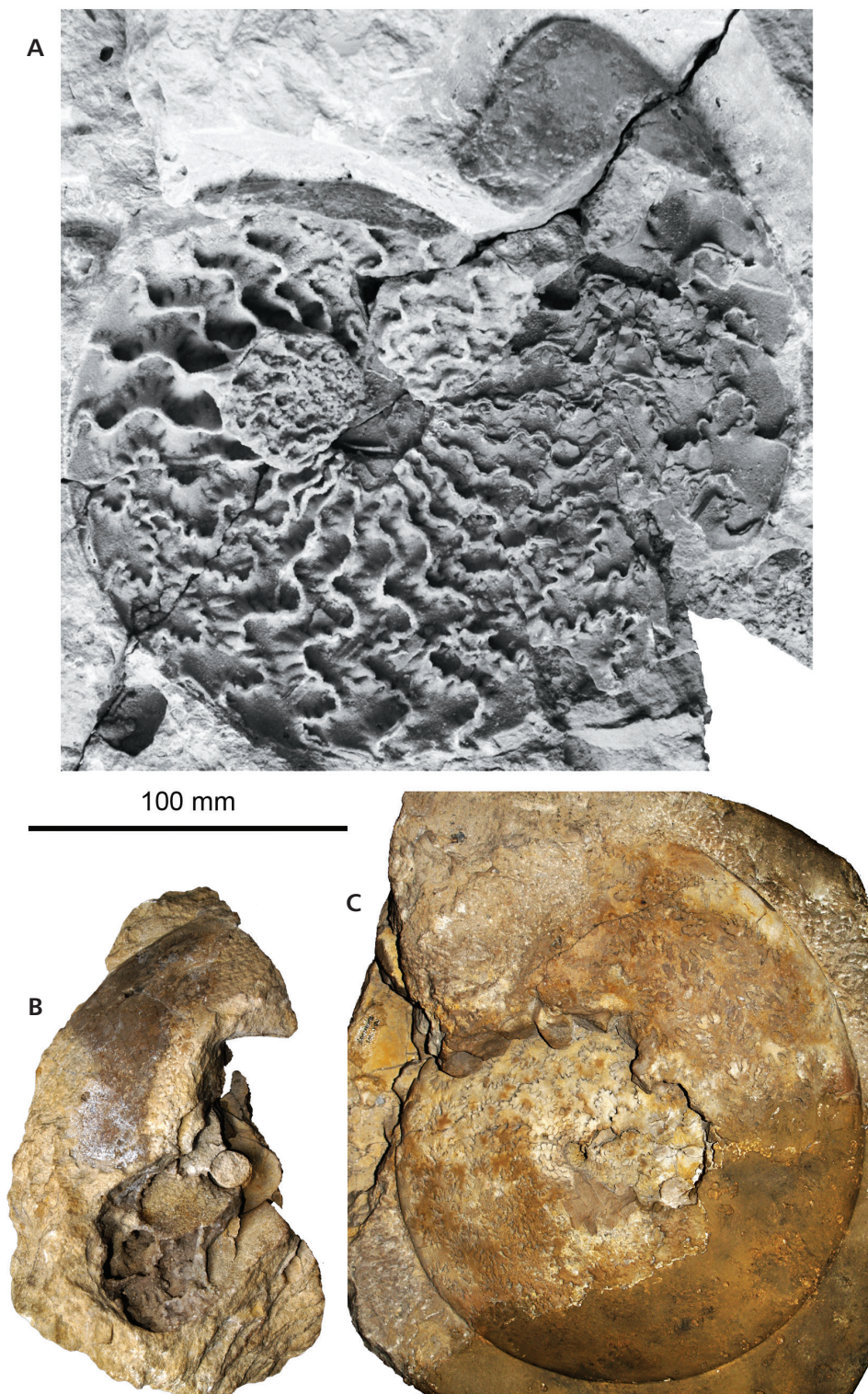


Figure 22. *Discoptychites dux* (Giebel, 1853), Rüdersdorf Fm. from Rüdersdorf. A, B – X13027, fragment of bodychamber with part of last chamber of the phragmocone, unit I. C – X13030, the most complete specimen from Rüdersdorf, unit I. D – X13031, fragment of chambers with well preserved suture, higher part of Rüdersdorf Fm. E – X13028, part of inner whorl, unit I. F, G – X13029, part of juvenile phragmocone, view on dorsal and ventral, unit I. H – X13057, phragmocone of a probably juvenile specimen, unit I.

Figure 23. The largest specimens of *Discoptychites dux* (Giebel, 1853), Rüdersdorf Fm. from Rüdersdorf. A – NHMS-WT2984, phragmocone with the rear end of the body chamber of probably adult specimen, higher part of unit I. B – MB.C. 1153, fragment, maybe mentioned by Beyrich (1858), unit I. C – MB.C. 1151, phragmocone that was artificially completed, probably a specimen mentioned by Beyrich too in the 19th century, unit I.

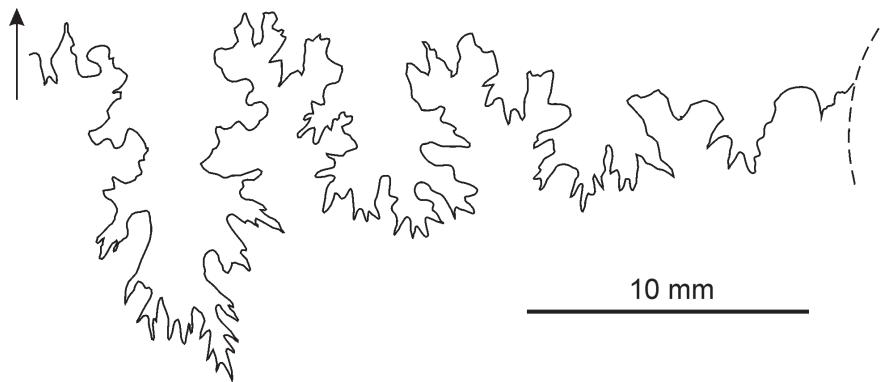


which start at the umbilical shoulder or in the lower third of the flank and disappear below the venter, resulting in a smooth, unsculptured venter (X13028, Fig. 22E). Subadult and mature specimens (X13030, Fig. 22C) lack ornament and remain very involute, showing a narrowly arched venter and a subtriangular more compressed

than depressed whorl section (X13030, 160 mm, Fig. 22C). In this specimen, the body chamber occupies half a whorl, but it is incomplete. The largest specimen available to us (NHMS-WT2984, dm 250 mm, Fig. 23A) is a phragmocone with the rear end of the body chamber preserved. The ammonitic suture with three lateral

Table 9. Conch parameters in mm and ratios of *Discoptychites dux*.

Specimen	dm	bcl	ah	wh	uw	ww _{min}	ww _{max}	uw/dm	wh/dm	WER	IZR
NHMS-WT2984	250?		100?	170?					0.7?	1.7?	0.4?
X13027						20?	70?				
X13028					8?						
X13029					8?	10?	16?				
X13030	180	25?			10?	10?		0.06?			

**Figure 24.** Suture of *Discoptychites dux* (Giebel, 1853), Rüdersdorf Fm. from Rüdersdorf, X13029.

lobes has deeply incised elements (Fig. 24). It has been documented in sufficient detail by Kaim & Niedźwiedzki (1999).

Discussion. – Overweg (1849) recorded the find of an ammonoid with entirely serrated suture line without a figure and without giving a name to the specimen. This is the earliest record of *D. dux* from Rüdersdorf. Giebel (1853) discussed this specimen briefly and erected *Ammonites dux* based on a specimen from Schraplau. One year later, Beyrich (1854) presented a figure of the Overweg specimen, clearly confirming its identity as *D. dux*. Although a number of specimens were mentioned from Rüdersdorf (Brahl 1854; Beyrich 1854, 1859b), most of the historical specimens appear to be lost. MB.C. 1153 (Fig. 23B) could be a fragment mentioned by Beyrich (1858) like MB.C. 1151 (Fig. 23C) a phragmocone that was artificially completed. However, the material from Rüdersdorf in conjunction with published records (e.g. Fritsch 1902, Claus 1921, Assmann 1937, Kaim & Niedźwiedzki 1999) provides sufficient information about the ontogeny of *D. dux*, although the earliest whorls remain unknown. The material from Germany and Poland shows morphologically no difference to the Pelsonian to Illyrian *D. suttneri* Mojsisovics, 1882, a Tethyan taxon. We therefore feel that the latter is a synonym of the first, which was tentatively discussed already by Kaim & Niedźwiedzki (1999). Mojsisovics (1882) himself recognized the large similarity between the two species

but consulted differences in the suture line as an argument to keep the species separate. However, a compilation of suture lines from *D. suttneri* and *D. dux* (Kaim & Niedźwiedzki 1999, p. 104, fig. 8) show that they are indistinguishable, which is a further argument to see *D. suttneri* as a junior synonym of *D. dux*.

Ptychites Beyrichii Fritsch, 1902 was introduced for forms with a narrower umbilicus, but, following Claus (1921) and Kaim & Niedźwiedzki (1999), we see this merely as a morphological variation of *D. dux*. *Discoptychites dux* of Wurm (1915), interpreted as *Ptychites beyrichi* by Schmidt (1928) and refigured by Urlichs (1999) as *Discoptychites* sp., is much more compressed with a narrowly arched but not acute venter and a somewhat larger umbilicus than in typical *D. dux*. We therefore tend to relate this specimen to *D. megalodiscus* Beyrich, 1867. As can be seen in Mojsisovics (1882, pl. 78, figs 1, 2), juveniles of *D. megalodiscus* have an almost triangular whorl section with largest whorl breadth at the umbilical shoulder and a sharp venter. This and the much more compressed whorls in adult specimens (Mojsisovics 1882, pl. 77) clearly separate *D. megalodiscus* from *D. dux*, although the suture lines are very similar (e.g. Beyrich 1867, pl. 2 fig. 3; Wurm 1915). The acute venter in the holotype of *Ammonites megalodiscus* Beyrich 1867, pl. 2, seems to be an artefact, because a narrowly rounded venter for adult specimens is described by Beyrich (1867).

Discoptychites dux was included into *Parapinacoceras* by Kozur (1974) and Urlichs & Mundlos (1985, p. 223,

fig. 2), a view, which is not compatible with the fundamentally different sutures of the both genera (Rein & Werneburg 2010, p. 90, fig. 2).

Occurrence. – In Rüdersdorf, no specimens were collected *in situ*. However, based on the lithology of the matrix, all available specimens derive most probably from unit I (Middle to Upper Wellenkalk Member). Of the same age are some records from Poland (Assmann 1937, Kaim & Niedźwiedzki 1999). A single specimen (MHI 2174) is recorded from the Terebratelbank Member of the Elm near Braunschweig (Lower Saxony, N Germany). From the Jena area (Thuringia), few records exist from the Schaumkalkbank Member (Zimmermann 1890, Claus 1921), and an unpublished specimen (NHMS-WT3073) derives probably from the Middle or Upper Wellenkalk Member. Tens of specimens come from the Schaumkalkbank Member of Freyburg/Unstrut (Saxony-Anhalt) (e.g. Fritsch 1902, Rothe 1959). Thus, *D. dux* crosses the Pelsonian/Illyrian boundary, and its stratigraphic value is poor.

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