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# Monograph

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# The ammonoids from the *Gattendorfia* Limestone of Gattendorf (Devonian–Carboniferous boundary; Upper Franconia, Germany)

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**Abstract.** The early Tournaisian (Early Carboniferous; Mississippian) ammonoids from the classical abandoned limestone quarry of Gattendorf (Upper Franconia) are revised, using the historical collections as well as so far undescribed material. The ammonoid assemblage is composed of prionoceratid ammonoids of the six genera *Mimimitoceras*, *Paragattendorfia*, *Stockumites*, *Acutimitoceras*, *Gattendorfia* and *Gattenpleura*, which indicate a stratigraphic position near the Devonian–Carboniferous boundary in the earliest Carboniferous. The new species *Stockumites hofensis* sp. nov. and *S. nonaginta* sp. nov. are described.

**Keywords.** Ammonoida, Early Carboniferous, Upper Franconia, taxonomy, stratigraphy.

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# Introduction

The geological outcrop of Gattendorf in Upper Franconia is one of the classic sites for Early Carboniferous ammonoids. It is the source of the name for the genus *Gattendorfia* and the *Gattendorfia* Stufe ammonoid zone used earlier in Central Europe and other regions. From Gattendorf, Münster (1839b) described "*Goniatites subinvolutus*" and "*Goniatites subbilobatus*", the first two Early Tournaisian ammonoid species ever established; the first of these subsequently became the type species of the genus *Gattendorfia* and was for a long time used as the index species for the beginning of the Carboniferous (Paeckelmann & Schindewolf 1937).

The Gattendorf outcrop played a key role in the exploration of the Devonian–Carboniferous boundary about 100 years ago. It was at the centre of a vigorous debate about the succession of ammonoid assemblages between O.H. Schindewolf, who examined the Gattendorf section in the course of his doctoral thesis (Schindewolf 1916, 1923), and H. Schmidt, who studied the time-equivalent successions in the Rhenish Mountains (Schmidt 1924) at about the same time. In their sometimes very polemical

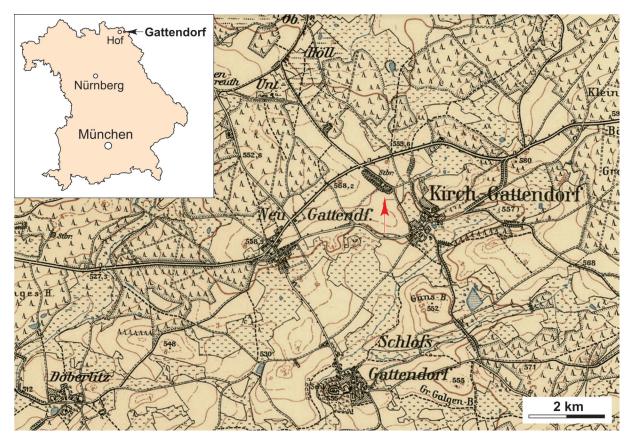
discussion, Schindewolf had the disadvantage that the outcrop he examined suffers from a stratigraphic gap that was unknown at that time. His erroneous conclusion that the *Gattendorfia* Stufe lies between the *Clymenia* Stufe and the *Wocklumeria* Stufe was corrected by him after subsequent intensive study of the Rhenish sections (Schindewolf 1926b).

Probably because of the stratigraphic gap, the Gattendorf outcrop was not intensively investigated in the following years. A situation that did not change towards the end of the 20<sup>th</sup> century, when possible GSSP candidates for the Devonian–Carboniferous boundary were examined in great detail.

The first monographic description of the Early Carboniferous ammonoid assemblage from Gattendorf is now 100 years old (Schindewolf 1923). Apart from a few isolated descriptions of individual specimens, no comprehensive revision of this assemblage has until now been undertaken. Here, we present a new description of the Early Carboniferous ammonoids from Gattendorf, so that they can be compared with assemblages of the same age from the Rhenish and Thuringian mountains.

# The former quarry outcrop of Gattendorf

The former limestone quarry of Gattendorf (with the central geographic coordinates: 52.32578° N, 12.00608° E) was located 400 m northwest from the Kirchgattendorf church and 7 km east from the city centre of Hof an der Saale (Fig. 1). The quarry was in operation as early as the 18<sup>th</sup> century for technical marble; Wirsing (1775: pl. 1 fig. 6) already illustrated an example with the description "Dunkelrother Marmor mit rothbraunen Wolken, und ins Helle spielenden Flecken". In Helfrecht (1797: 17) there is then a reference to fossils ("Versteinerungen von Seegewächsen und Seeconchylien") in the marble of Gattendorf.



**Fig. 1.** The geographic position of Gattendorf in Bavaria and the position of the abandoned Gattendorf quarry in the topographic map of 1930.

The first monographic work on fossils from Upper Franconia including some specimens from the Gattendorf quarry was carried out by Münster (1832, 1839a, 1839b, 1840, 1842, 1843), who described a series of mostly Late Devonian ammonoids, nautiloids, trilobites and other invertebrates. Subsequently, ammonoids from Gattendorf were mentioned and illustrated several times (e.g., Gümbel 1863; Frech 1902), but mostly these referred to material previously described by Münster.

Intensive work on the Gattendorf outcrop was only later carried out with the investigations of Schindewolf (1916, 1921, 1923), who described the entire section, which is 32 metres thick in total and extends from the base of the Famennian to the basal Early Carboniferous. The lower 25 metres are limestones with a mostly nodular and fibrous structure. Schindewolf distinguished 25 beds within the section, of which bed 21 provided ammonoids of the early Tournaisian. This bed should be between 25 and 55 cm thick and consists of shales with intercalated limestone nodules. Schindewolf (1916: 37) placed this bed in the "Stufe VI" (= *Wocklumeria* Stufe), but later (Schindewolf 1920: 116; 1923: 255) he renamed the "Stufe VI" as *Gattendorfia* Stufe and in the latter paper listed the following six ammonoid species (with revised identifications):

It is not easy to understand why Schindewolf combined this bed with the underlying bed 20, from which only clymeniids were listed, into the same stage. It must be said, however, that Schindewolf did not realise at the time that there is a large stratigraphic gap in the strata of the Devonian–Carboniferous boundary in the Gattendorf section. This gap between beds 20 and 21 spans at least the upper half of the former *Wocklumeria* Stufe, i.e., the interval characterised by species of the genera *Parawocklumeria* Schindewolf, 1926 and *Wocklumeria* Wedeking, 1918. A similar gap is also known from the Buschteich quarry near Schleiz in Thuringia (Girard *et al.* 2017).

In a later paper, Schindewolf (1924) added the new species *Paragattendorfia humilis*, *Gattendorfia ventroplana* and *Gattendorfia involuta* to the species list of bed 21 at Gattendorf; for the latter, however, he did not give a locality. In this work he once again underlined his wrong assumption that the *Gattendorfia* Stufe lies below the *Wocklumeria* Stufe and also proposed a "Stufe VII" (= *Wocklumeria* Stufe) as the youngest stratigraphic unit of the Late Devonian.

Two years later, Schindewolf (1926b) revised his view on the position of the *Wocklumeria* and *Gattendorfia* Stufen after more intensely studying some of the sections in the Rhenish Mountains. Meanwhile, he had abandoned his earlier idea (Schindewolf 1920) that there is a phylogenetic lineage from *Gattendorfia* to *Wocklumeria* when discovering that the latter is a clymeniid, not a goniatite. However, he did not share the opinion of Schmidt (1924, 1925) that the *Gattendorfia* Stufe should already be placed in the Carboniferous. This disagreement was later settled at the second International Carboniferous Congress at Heerlen (1935), when *Gattendorfia subinvoluta* was designated as the index fossil for the beginning of the Carboniferous (Paeckelmann & Schindewolf 1937).

Interestingly, this first intensive study interval of the Gattendorf section was also the last. In the following years, specimens of ammonoids were sometimes used for comparisons with material from other regions, but a comprehensive taxonomic revision of the ammonoid assemblages and their stratigraphic succession has, until now, not been carried out.

<sup>&</sup>quot;Postprolobites varicosus Schindewolf, 1923" = Mimimitoceras varicosum (Schindewolf, 1923)

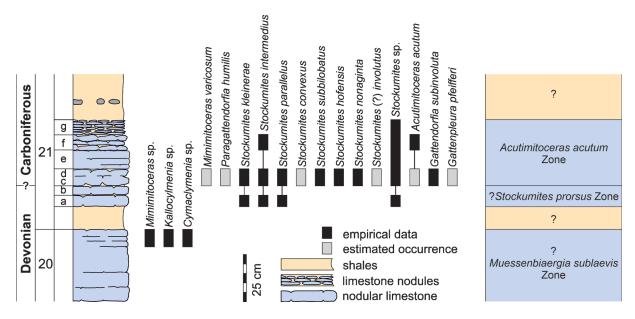
<sup>&</sup>quot;Imitoceras Gürichi (Frech, 1902)" = Stockumites hofensis sp. nov.

<sup>&</sup>quot;Imitoceras intermedium Schindewolf, 1923" = Stockumites intermedius (Schindewolf, 1923)

<sup>&</sup>quot;Imitoceras Denckmanni (Wedekind, 1918)" = Stockumites kleinerae (Korn, 1984)

<sup>&</sup>quot;Imitoceras acutum Schindewolf, 1923" = Acutimitoceras acutum (Schindewolf, 1923)

<sup>&</sup>quot;Gattendorfia subinvoluta (Münster, 1839)" = Gattendorfia subinvoluta (Münster, 1839)



**Fig. 2.** The stratigraphic section spanning the Devonian–Carboniferous boundary in the Gattendorf section and the occurrence of ammonoid species.

Unfortunately, the disused quarry began to be used for waste disposal in the 1970s. This led to almost complete backfilling, so that by 1989 only a small section, including the Devonian–Carboniferous boundary beds, remained exposed (Fig. 1). A detailed examination of the very limited accessible part of the section showed that bed 21 can be subdivided (Fig. 2) and that the sub-units do not contain a uniform ammonoid assemblage (Korn 1993). It can be assumed that the lower part of bed 21 (bed 21a) can be correlated with the "Stockum Limestone" of the Rhenish Mountains and thus has a position immediately at the Devonian–Carboniferous boundary. The higher beds, of which especially subunits 21c–d yielded particularly many ammonoid specimens, can be correlated with the base of the Hangenberg Limestone of Oberrödinghausen; encompassing a single ammonoid zone, the *Acutimitoceras acutum* Zone.

The uppermost part of the underlying bed 20 yielded poorly preserved specimens of *Mimimitoceras* Korn, 1988, *Cymaclymenia* Hyatt, 1884 and *Kalloclymenia* Wedekind, 1914; especially with the latter genus, the age of this horizon can be placed in the lower range of the traditional "*Wocklumeria* Stufe". This means that the stratigraphic gap encompasses the entire younger portion of the "*Wocklumeria* Stufe". In fact, the genera *Parawocklumeria* and *Wocklumeria* have never been reported from the Gattendorf outcrop. Here, we revise the ammonoids from the *Gattendorfia* Limestone, using the historical collections as well as so far undescribed collections.

# Material and methods

A total amount of about 350 specimens is available for study, but only 150 of these are sufficiently preserved and could be identified to the species level. The specimens range in size from a few millimetres to around 100 mm in conch diameter. All have been deformed to a lesser or greater extent by tectonic stress on the entire rock complex. This deformation particularly affected the body chambers of the larger specimens, while some of the phragmocones remained relatively unaffected. Because of the deformation, it was not possible to carry out precise measurements for many of the specimens; the shown values are partly interpolated.

Here, we describe the species based on the original type material and additional material collected by Denckmann in 1912, Schindewolf in 1934, Korn in 1989 and Weyer in 1995. This is to complement earlier

studies, particularly that of Schindewolf (1923), by figuring diagrams of the ontogenetic development of sectioned specimens and photographs of the best-preserved available specimens.

The description of the material largely follows the scheme and terminology, which was proposed by Korn (2010) and Klug *et al.* (2015) for Palaeozoic ammonoids (Fig. 3). The terminology of the suture line follows Korn *et al.* (2003); the principal sutural elements described here are therefore external (E), adventive (A), lateral (L), umbilical (U) and internal (I) lobes.

# Abbreviations used in the species descriptions

ah = apertural height dm = conch diameter IZR = imprint zone rate uw = umbilical width WER = whorl expansion rate

wh = whorl height ww = whorl width

# Abbreviations of the host institutions of the studied specimens

BGRB = Bundesanstalt für Geologie und Rohstoffe, Geowissenschaftliche Sammlungen Berlin

MB.C. = Cephalopod collection of the Museum für Naturkunde, Berlin

SMF = Senckenberg Museum, Frankfurt am Main

SNSB BSPG = Bayerische Staatssammlung für Paläontologie und Geologie, München

# **Results**

Order Goniatitida Hyatt, 1884 Suborder Tornoceratina Wedekind, 1914

# Superfamily Prionoceratoidea Hyatt, 1884

[nom. transl. Bogoslovsky (1971: 94), pro Prionocerae Hyatt, 1884; nom. correct. Kullmann (2009: 2), pro Prionocerataceae]

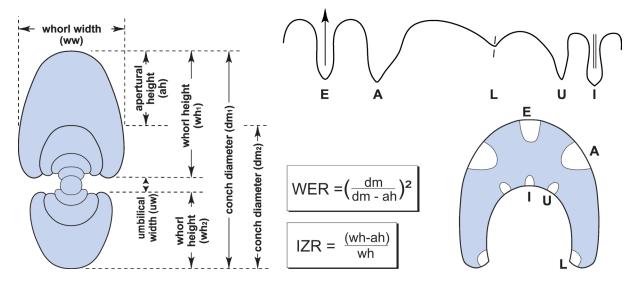


Fig. 3. The morphological terms used in the description of the ammonoid conchs and suture lines.

# **Diagnosis**

Superfamily of the suborder Tornoceratina with discoidal to globular, primarily involute conchs without coarse ornament. Many modifications of the conch shape during ontogeny and phylogeny; advanced forms may possess a wide umbilicus and may bear a coarse ornament. Basic suture line with the elements E A L I, development of supplementary external, adventive, lateral and umbilical lobes occur in various lineages. Ornament primarily with growth lines only; ribs are developed in some lineages. Growth lines have a convex course in the early forms, but there are trends toward biconvex growth lines in many lineages (after Korn & Klug 2002).

# **Included families**

Prionoceratidae Hyatt 1884; Cheiloceratidae Frech, 1897; Sporadoceratidae Miller & Furnish, 1957; Praeglyphioceratidae Ruzhencev, 1957; Maximitidae Ruzhencev, 1960; Gattendorfiidae Bartzsch & Weyer, 1987.

# Family Prionoceratidae Hyatt, 1884

[nom. correct. Bogoslovsky (1971: 180), pro Prionocerae Hyatt, 1884]

# **Diagnosis**

Family of the superfamily Prionoceratoidea with the sutural formula E A L U I or  $(E_1 E_m E_1) A L U I$  in some advanced forms; adventive lobe deep, V-shaped or lanceolate and pointed, only rarely blunt; the lateral lobe has a position on the umbilical seam. Conch in the juvenile stage usually subinvolute, in some lineages subevolute or evolute; adult stage usually involute, but subinvolute in some genera. Shell ornament with fine to coarse growth lines, mostly without ribs.

# **Included subfamilies**

Prionoceratinae Hyatt, 1884; Imitoceratinae Ruzhencev, 1950; Karagandoceratinae Librovitch, 1957; Voehringeritinae Bartzsch & Weyer, 1988; Acutimitoceratinae Korn, 1994; Balviinae Korn in Korn & Klug, 2002.

# Subfamily Prionoceratinae Hyatt, 1884

[nom. transl. Bartzsch & Weyer (1988a: 136), pro Prionocerae Hyatt, 1884]

# **Diagnosis**

Subfamily of the family Prionoceratidae with the sutural formula E A L U I, adventive lobe V-shaped or lanceolate, pointed. Conch in the juvenile stage usually subinvolute, rarely subevolute; adult stage involute or subinvolute. Coiling rate usually very low or low (WER = 1.40–1.75). Shell ornament with fine to coarse growth lines, without ribs.

# **Included genera**

Prionoceras Hyatt, 1884; Haugiceras Cossmann 1900 [synonym of Prionoceras]; Postprolobites Wedekind, 1913 [synonym of Prionoceras]; Paragattendorfia Schindewolf, 1924; Cunitoceras Weyer, 1972 [problematic genus]; Mimimitoceras Korn, 1988; Globimitoceras Korn, 1993; Rectimitoceras Becker 1996 [synonym of Mimimitoceras]; Kornia Ebbighausen & Bockwinkel, 2007.

# Morphology

Species of the subfamily Prionoceratinae are characterised by a simple conch geometry; the conch is discoidal and more often pachyconic to globular with a nearly closed or closed umbilicus and almost

always a very low or low coiling rate. This morphology is shared by the two main genera *Prionoceras* and *Mimimitoceras* (e.g., Korn *et al.* 2014, 2015). Another common feature of the two genera are the shell constrictions, which are present in all species at least in the early stage of ontogeny. Almost all species have a shell ornament consisting only of growth lines; these almost always have a convex course on the flank and form a broad, shallow ventral sinus.

The suture line also shows little variation. It consists of the basic elements E A L U I; the shape of the external and adventive lobe varies between species. Usually, species with a discoidal conch show a narrower, sometimes lanceolate external lobe, while in globular species it is often broader and V-shaped. A deviation from this rule, however, is *Globimitoceras* with a globular conch but with a very narrow external lobe.

# **Ontogeny**

The species of the subfamily underwent a comparatively simple ontogenetic development; this means that the morphology of juveniles and adults does not differ markedly. Conch allometry is usually weakly developed; the ontogenetic trajectories (Korn 2012) are often monophasic with a simple decrease of the ww/dm ratio, for example. These simple ontogenetic trajectories are mainly caused by the small width of the umbilicus in the juvenile stage. Therefore, the whorl profiles are rather similar at all growth stages and range from C-shaped to horseshoe-shaped. Only the trend towards more slender conchs that is present in most Palaeozoic ammonoids is evident.

# **Phylogeny**

The Prionoceratinae are the ancestral subfamily of the family Prionoceratidae and thus of all post Devonian ammonoids. While the prionoceratids of the Famennian formed only one previously known side branch, the subfamily Balviinae with its paedomorphic conchs (Korn 1992a, 1995a, 1995b) is distinguished by divergent morphologies. Several side branches formed in the earliest Carboniferous. The most successful of these is the subfamily Acutimitoceratinae, described in more detail below. Less successful side branches are the genera *Globimitoceras*, *Kornia* and *Paragattendorfia*, all of them restricted to the Early and Middle Tournaisian, but apparently extinct without descendants.

# Stratigraphic occurrence

The Prionoceratinae have its acme in the middle and late Famennian, where several taxa are used as index species (Korn *et al.* 2014, 2015) that complement the clymeniid-based zonation. According to current knowledge, the Prionoceratinae are one of the few ammonoid lineages that survived the Hangenberg Event at the Devonian–Carboniferous boundary (Korn 1986, 1993, 2000; Becker 1993; Kullmann 2000). In contrast to the "failed survivors", the cymaclymeniids, which survived the biocrisis with a few forms but became extinct shortly afterwards (Korn 1990; Korn *et al.* 2004), the evolution of the prionoceratids is, in contrast to the cymaclymeniids, not a "dead clade walking" (Jablonski 2002), but the evolution of a group with a very successful radiation in the Early Carboniferous. However, this successful radiation was caused by flourishing of the subfamily Acutimitoceratinae, while the genera of the Prionoceratinae have only a short stratigraphic range, apparently restricted to the early and middle Tournaisian. The late Tournaisian record of the problematic species *Cunitoceras schindewolfi* Weyer, 1972 in the Harz Mountains requires confirmation.

# Geographic occurrence

The Prionoceratinae are a subfamily with an almost global distribution in the Middle and Late Famennian; in the Early and Middle Tournaisian the distribution is significantly restricted. The most important occurrences in Europe are in the Rhenish Mountains (Vöhringer 1960; Korn 1994; Korn & Weyer 2003), Franconia (Schindewolf 1923; Korn 1994), Thuringia (Weyer 1977), questionably the Harz

Mountains (Schindewolf 1951), Silesia (Dzik 1997), the Carnic Alps (Korn 1992b) and the Montagne Noire (Becker & Weyer 2004; Korn & Feist 2007). Early Carboniferous species are also known from the Anti-Atlas (Bockwinkel & Ebbighausen 2006), the South Urals (Popov 1975), Guizhou (Ruan 1981), Karaganda (Librovitch 1940) and possibly Michigan (Winchell 1862; Miller & Garner 1955).

# Genus Mimimitoceras Korn, 1988

# Type species

Mimimitoceras trizonatum Korn, 1988; original designation.

# Diagnosis

Genus of the subfamily Prionoceratinae with discoidal to globular conchs; umbilicus in the early juvenile stage slightly opened in most of the species and usually rapidly closing during the early whorls. External lobe usually V-shaped in globular species and lanceolate in discoidal species. Shell constrictions accompanied by an apertural shell bulge in the early and middle growth stage, internal shell thickenings usually cause deep steinkern constrictions throughout ontogeny.

# **Included species**

Species lists including the Devonian species of the genus were published several times (Korn 1994; Korn & Klug 2002; Korn *et al.* 2015). The following Carboniferous species of *Mimimitoceras* are known from:

Central Europe (Schindewolf 1923; Korn 1992b, 1993; Korn & Weyer 2023): *Postprolobites varicosus* Schindewolf, 1923; *Mimimitoceras crestaverde* Korn, 1992; *Mimimitoceras hoennense* Korn, 1993; *Mimimitoceras perditum* Korn & Weyer, 2023.

North Africa (Bockwinkel & Ebbighausen 2006; Korn & Weyer 2023): *Mimimitoceras mina* Korn & Weyer, 2023.

## Remarks

*Mimimitoceras* was revised with the description of Devonian North African material by Korn *et al.* (2015). The genus occurs in late Famennian ammonoid assemblages with numerous species; only two species are known so far from the basal Carboniferous Hangenberg Limestone of the Rhenish Mountains.

Minimitoceras is easily distinguished from the other genera of the subfamily Prionoceratinae by the presence of a bulging radial ridge in front of the shell constrictions (Korn 1988). This bulge is usually not present throughout ontogeny; the shell constrictions may disappear in the adult stage. In some stratigraphically older species, such as M. lineare (Münster, 1839) from the Late Famennian Clymenia laevigata Zone, they may be restricted to the juvenile stage. Based on this very minor variation, which rather describes a difference between species, Becker (1996) proposed the genus Rectimitoceras.

# *Mimimitoceras varicosum* (Schindewolf, 1923) Fig. 4; Table 1

Postprolobites varicosus Schindewolf, 1923: 405, text-fig. 13b.

*Imitoceras varicosum* – Vöhringer 1960: 122, pl. 2 fig. 1c. — Weyer 1977: 170, pl. 2 fig. 2. — Bartzsch & Weyer 1982: 19.

Mimimitoceras varicosum – Korn 1994: 22, text-fig. 64e–f.

non Aganides varicosus - Schmidt 1925: 533, pl. 23 fig. 1.

non *Prionoceras varicosum* – Lange 1929: 60, pl. 1 figs 13, 13a. — Schindewolf 1952: 294, pl. 2 figs 3–4. — Petter 1959: 250, pl. 18 fig. 12, text-fig. 56k.

non Imitoceras varicosum – Vöhringer 1960: 122, pl. 2 fig. 1a-b, text-fig. 4.

non *Mimimitoceras varicosum* – Korn 1992a: 33; 1994: 22, text-figs 19a, c, 20c–d, 21f, 22c. — Becker 1996: 35. — Korn & Weyer 2003: text-fig. 14a. — Bockwinkel & Ebbighausen 2006: 94, text-figs 7a–b, 8.

# **Diagnosis**

Species of *Mimimitoceras* with thickly pachyconic and subinvolute conch at 20-30 mm dm (ww/dm=0.80-0.85). Whorl cross section depressed; coiling rate low (WER  $\sim 1.70$ ). Ornament with rather coarse and sharp, narrow-standing growth lines with weakly biconvex course. Prominent shell constrictions with biconvex course.

# **Material examined**

## Lectotype

GERMANY • Upper Franconia, old quarry 400 m north-west of Kirchgattendorf; bed 21 ("*Gattendorfia* Limestone"); Schindewolf 1916 Coll.; illustrated by Schindewolf (1923: text-fig. 13b), Vöhringer (1960: pl. 2 fig. 1c) and Korn (1994: text-fig. 64E), re-illustrated here in Fig. 4B; SMF Mbg.4706.

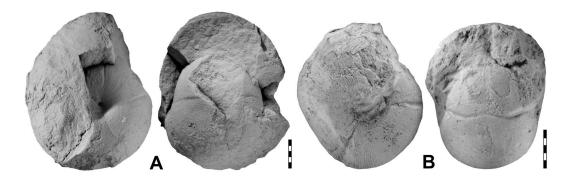
# **Paralectotype**

GERMANY • 1 specimen; Upper Franconia, old quarry 400 m north-west of Kirchgattendorf; bed 21 ("Gattendorfia Limestone"); Schindewolf 1916 Coll.; illustrated in Fig. 4A; SMF Mbg.7560.

# **Description**

Lectotype SMF.Mbg.4706 is a moderately well-preserved, weakly deformed specimen with 19 mm conch diameter, but offering a fairly good impression of the conch geometry and ornament (Fig. 4B). The conch is thickly pachyconic (ww/dm=0.83) with an obviously closed umbilicus. Flanks and venter form an almost semi-circular arch; the coiling rate is low (WER=1.68). The shell bears constrictions which, like the coarse growth lines, are weakly biconvex in their course; the lateral sinus is very shallow and the slightly deeper ventral sinus is rather narrow. On the flanks, they are accompanied by a barely visible shell bulge on the apertural side.

Paralectotype SMF.Mbg.7560 with 28 mm conch diameter is very similar to the holotype in conch shape and ornamentation (Fig. 4A). The course of the constrictions, which are less pronounced in this specimen, is almost linear.



**Fig. 4.** *Mimimitoceras varicosum* (Schindewolf, 1923) from Gattendorf, bed 21; both Schindewolf 1916 Coll. **A.** Specimen SMF Mbg.7560. **B.** Lectotype SMF Mbg.4706. Scale bar units=1 mm.

**Table 1.** Conch measurements, ratios and rates of *Mimimitoceras varicosum* (Schindewolf, 1923) from Gattendorf.

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
SMF Mbg.7560	27.9	22.4	14.9	1.2	6.7	0.80	1.50	0.04	1.73	0.55
SMF.Mbg.4706	19.2	16.0	10.8	0.3	4.4	0.83	1.48	0.02	1.68	0.59

### Remarks

The species name "Imitoceras varicosum" was used by Vöhringer (1960) for globular specimens from the Hangenberg Limestone of Oberrödinghausen; this view was also followed by subsequent researchers of assemblages of the same age (Korn 1994; Becker 1996; Korn & Weyer 2003). However, when reexamining the material from Gattendorf, it must be noted that material from the two localities differ; therefore, Korn & Weyer (2023) introduced the new species Mimimitoceras perditum for the material from the Rhenish Mountains. Mimimitoceras varicosum differs in the stouter conch from M. perditum (ww/dm ~ 0.80 in M. varicosum but ~ 0.70 in M. perditum). Mimimitoceras varicosum has biconvex growth lines with rather distinct lateral sinus, while M. perditum has finer growth lines with nearly straight course. Most probably, the type material of Mimimitoceras varicosum originates from the Acutimitoceras ucatum Zone (Korn & Weyer 2023), as younger strata of the Gattendorfia Stufe are not known from the Gattendorf locality. In contrast, M. perditum occurs not frequently in the upper part of the Hangenberg Limestone (Eocanites delicatus Zone).

Mimimitoceras varicosum is superficially similar to the co-occurring Stockumites kleinerae (Korn, 1984) in the stout conch with a ww/dm ratio of 0.80 at 20 mm diameter. However, M. varicosum has distinct shell constrictions at this stage, which are not present in S. kleinerae. In addition, the growth lines of M. varicosum are clearly biconvex but convex in S. kleinerae.

## Genus *Paragattendorfia* Schindewolf, 1924

# Type species

Paragattendorfia humilis Schindewolf, 1924; original designation.

## Diagnosis

Genus of the subfamily Prionoceratinae with a pachyconic to globular conch in the juvenile and adult stage. The umbilicus opens stepwise during ontogeny, the umbilical width ratio remains nearly constant throughout ontogeny. Shell with fine to lamellar, convex or straight growth lines. External lobe and adventive lobe V-shaped.

# **Genus composition**

Central Europe (Schindewolf 1924; Vöhringer 1960; Weyer 1972): *Paragattendorfia humilis* Schindewolf, 1924; *Imitoceras patens* Vöhringer, 1960; *Paragattendorfia sphaeroides* Weyer, 1972.

North Africa (Bockwinkel & Ebbighausen 2006): *Paragattendorfia aboussalamae* Bockwinkel & Ebbighausen, 2006.

Central Asia (Librovitch 1940): *Gattendorfia applanata* Librovitch, 1940; *Gattendorfia kazakhstanica* Librovitch, 1940; *Gattendorfia occlusa* Librovitch, 1940; *Gattendorfia reticulata* Librovitch, 1940.

South China (Ruan 1981): Imitoceras (Imitoceras) subpatens Ruan, 1981; Imitoceras (Imitoceras) globoidale Ruan, 1981.

### Remarks

Several species were placed in the genus *Paragattendorfia* since its revision by Weyer (1972). However, *Paragattendorfia* was a somewhat problematic genus. It was inadequately defined by Schindewolf (1924) and insufficiently characterised by the statement that "with a general similarity of shape to *Gattendorfia*, it only differs from the latter in that the lateral lobe lies on the seam and not next to it as in *Gattendorfia*". Furthermore, the inner lobe elements should be very narrow and deep; the growth lines should be linear without ventral sinus and constrictions were not seen.

With the redescription and diagnosis of the type species *P. humilis*, *Paragattendorfia* can be stabilised as a genus belonging to the subfamily Prionoceratinae because of the globular conch geometry, the low aperture throughout ontogeny and the rather simple ontogenetic pathways (Korn & Weyer 2023).

Paragattendorfia is unique among the prionoceratids of the Early Tournaisian in its stepwise opening of the umbilicus, meaning than the uw/dm trajectory is nearly isometric. In this respect, it can easily be separated from *Mimimitoceras*, which may have a similar morphology in distinct growth stages, but possesses an involute adult conch.

# Stratigraphic range

In the Rhenish Mountains, the two species *P. patens* and *P. sphaeroides* only occur in the higher part of the Hangenberg Limestone (*Pseudarietites westfalicus* Zone and *Eocanites delicatus* Zone). At Gattendorf, however, no ammonoids are known from beds higher than the *Acutimitoceras acutum* Zone, hence the genus has a duration throughout the "*Gattendorfia* Stufe". The species described from Kazakhstan (Librovitch 1940) have possibly a middle Tournaisian age.

# **Paragattendorfia humilis** Schindewolf, 1924 Fig. 5; Table 2

Paragattendorfia humilis Schindewolf, 1924: 105.

# **Diagnosis**

Species of *Paragattendorfia* with conchs reaching 40 mm diameter. Conch at 25 mm dm thickly pachyconic and subinvolute (ww/dm  $\sim$  0.75; uw/dm  $\sim$  0.18). Whorl profile at 25 mm dm moderately depressed (ww/wh  $\sim$  1.70); coiling rate low (WER  $\sim$  1.65). Venter broadly rounded, umbilical margin rounded. Growth lines lamellar, wide-standing, with convex course. Without constrictions on the shell surface.

# **Material examined**

# Lectotype

GERMANY • Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("Gattendorfia Limestone"); Schindewolf 1916 Coll.; MB.C.4691.

# Additional material

GERMANY • 1 specimen; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("*Gattendorfia* Limestone"); Schindewolf 1934 Coll.; illustrated in Fig. 5A; BGRB X13380.

# **Description**

Lectotype MB.C.4691 is not suitable for an illustration; it is a phragmocone fragment with about 8.5 mm whorl width. It allows almost only a view of a septal surface of a crescent-shaped whorl profile.

**Table 2.** Conch measurements, ratios and rates of *Paragattendorfia humilis* Schindewolf, 1924 from Gattendorf.

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
BGRB X13380	25.9	19.7	11.7	4.4	5.9	0.76	1.68	0.17	1.68	0.49
BGRB X13380	21.0	16.6	9.6	4.0	_	0.79	1.73	0.19	_	_

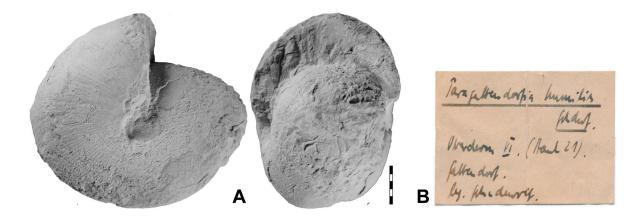
Specimen BGRB X13380 is a laterally distorted conch with 26 mm diameter (Fig. 5A), showing shell remains but no suture line. The conch is thickly pachyconic (ww/dm  $\sim 0.75$  and subinvolute (uw/dm  $\sim 0.17$ ) with low coiling rate (WER  $\sim 1.68$ ). The umbilical margin is rounded and the umbilical wall stands almost vertical to the symmetry plane. The flanks and venter are evenly broadly rounded. The shell bears unevenly distributed, lamellar growth lines, which are already slightly directed backwards on the inner flank and extend in a convex are across the flanks. They form a shallow sinus on the venter.

#### Remarks

Paragattendorfia humilis was very inadequately defined in the original description. Schindewolf (1924: 105) stated only that it "was recorded at Gattendorf as a rare companion of *Gattendorfia*" and that it is characterised by "a moderately wide umbilicus, very low whorls and a semilunate cross-section with a broadly convex external side". An illustration was not provided and he did not explain at what size stage this morphology should be present. The species definition is therefore almost useless because it can refer to a number of different earliest Tournaisian ammonoids.

Only two specimens are available. The lectotype proposed here is a fragment of a phragmocone, labelled by Schindewolf himself as "*Paragattendorfia humilis*" (Fig. 5B). It is rather clear that this specimen belonged to the type series. The second specimen is much better preserved, but it belongs to the collection assembled by Schindewolf as late as 1934.

Paragattendorfia humilis differs from the other species *P. patens* and *P. sphaeroides* from the Rhenish Mountains in the course of the growth lines, which is strongly convex in *P. humilis* but nearly linear in *P. patens* and *P. sphaeroides*. Both species have a wider umbilicus than *P. humilis*; the uw/dm ratio is about 0.30 in *P. patens* and 0.20 in *P. sphaeroides*, while below 0.20 in *P. humilis*.



**Fig. 5.** *Paragattendorfia humilis* Schindewolf, 1924 from Gattendorf, bed 21. **A.** Specimen BGRB X13380 (Schindewolf 1934 Coll.). **B.** Original label of lectotype MB.C.4691 (handwriting of Schindewolf). Scale bar units=1 mm.

# Subfamily Acutimitoceratinae Korn, 1994

# **Diagnosis**

Subfamily of the family Prionoceratidae with the sutural formula E A L U I; adventive lobe V-shaped or lanceolate, pointed. Conch in the juvenile stage subevolute or evolute; adult stage involute or subinvolute. Coiling rate usually moderately high or high (WER = 1.75–2.25) and rarely very high (up to 2.35). Shell ornament with fine to coarse growth lines, usually without ribs.

# **Subfamily composition**

The subfamily comprises six genera: *Acutimitoceras* Librovitch, 1957 (4 species); *Costimitoceras* Vöhringer, 1960 (3 species); *Sulcimitoceras* Kusina, 1985 (1 species); *Nicimitoceras* Korn, 1993 (7 species) and *Stockumites* Becker, 1996 (36 species).

# Morphology

In the adult stage, species of the subfamily Acutimitoceratinae are distinguished from those of the Prionoceratinae almost exclusively by the higher whorl expansion rate of the former. In the Acutimitoceratinae it is almost always above a value of 1.75 and in the Prionoceratinae below this value. In Acutimitoceratinae, adult conchs are almost always completely involute and range from thinly discoidal to globular; in contrast to the mostly stout conchs of the Prionoceratinae, however, discoidal conchs are more common than pachyconic or globular conchs in the Acutimitoceratinae. Oxyconic conchs occur independently in several evolutionary lineages.

Juvenile conchs of the Acutimitoceratinae show a very wide variation in their morphology, ranging from subinvolute to very evolute. Likewise, the length of the more widely umbilicate juvenile stage varies markedly between species.

The shell ornament consists of simple growth lines in almost all species, these growth lines are usually convex across the flank and form a sinus on the venter. Only some species show growth lines with a biconvex course. Spiral lines occur in *Costimitoceras* and, together with the growth lines, form a reticulate ornament. Some species possess shell constrictions, in others only radial internal shell thickenings are present. Some species have neither shell constrictions nor internal shell thickenings.

The suture line is simple and consists of the elements E A L U I. The external lobe is usually lanceolate with parallel flanks; in some cases, however, the external lobe may be narrow V-shaped or very weakly pouched. The adventive lobe is often V-shaped and varies in shape from symmetrical to moderately asymmetrical.

### **Ontogeny**

The ontogeny of the Acutimitoceratinae shows spectacular changes; differentiating it from all species of the Prionoceratinae. All acutimitoceratins show an early ontogenetic stage of variable length in which the juvenile whorls only slightly embrace the preceding one, resulting in a rather widely umbilicate or even serpenticonic juvenile conch shape. In the middle growth stage, the closure of the umbilicus begins by more or less wide overlap upon the preceding whorl. In most species, the umbilicus is closed by 10 mm conch diameter.

Ontogenetic changes in acutimitoceratin conch morphology can be illustrated in diagrams of ontogenetic trajectories (Korn 2012), which show the ontogenetic trajectory of the ww/dm ratio follows a strikingly triphasic course. The amplitude of change depends on the length of the widely umbilicate juvenile stage and the width of the conch in the middle growth stage. Species with stout conchs tend to show a more pronounced triphasic ontogeny than discoidal forms.

# **Phylogeny**

The Acutimitoceratinae are the dominant earliest Carboniferous ammonoid group immediately after the Hangenberg Event. The origin of the subfamily is most probably in the genus *Mimimitoceras* or related forms of which some developed rather evolute inner whorls already in the late Famennian (Korn *et al.* 2015). Although specimens of the subfamily Acutimitoceratinae are very abundant in all earliest Carboniferous ammonoid occurrences, there is no undoubted record older than the Hangenberg Event. This means that the phylogenetic origin of the entire group, which most probably gave rise to all post-Hangenberg ammonoids (except for a few failed survivors such as some clymeniids and species of *Mimimitoceras*), is still unknown.

The Acutimitoceratinae gave rise to at least two ammonoid clades, the subfamily Imitoceratinae and the family Gattendorfiidae. The first is characterised by a pouched external lobe and the second by an incompletely closed or open umbilicus in the adult stage. A possible third evolutionary lineage are the prolecanitids and with these all Mesozoic ammonoids.

# Stratigraphic occurrence

Species of the subfamily Acutimitoceratinae are present already in the lowermost beds deposited directly after the Hangenberg Event with morphologically advanced species, i.e., species with a widely involute juvenile conch (e.g., Korn 1984; Price & House 1984; Kusina 1985; House 1996; Korn *et al.* 2004). Investigations in the Oberrödinghausen section show that most of the species have a very short stratigraphic range. A wide distribution across several ammonoid zones, as considered possible by Vöhringer (1960), could not be confirmed by our new study and revision.

In contrast to the good stratigraphic control on early Tournaisian species, little is known about the subfamily's middle Tournaisian occurrences. Occurrences of possible members of the subfamily in Karaganda (Librovitch 1940) and the American Midcontinent (Miller & Collinson 1951) require confirmation.

# Geographic occurrence

The subfamily Acutimitoceratinae has a very wide geographic range. In practically all assemblages of early Tournaisian ammonoids, the species of this subfamily are the dominant elements. The following list provides an overview on the occurrences (and selected references) of the Acutimitoceratinae: Rhenish Mountains (Schmidt 1924, 1925; Vöhringer 1960; Korn 1981, 1984; Becker 1988; Korn 1992c, 1994; Korn *et al.* 1994; Becker 1996; Korn & Weyer 2003), Thuringia (Schindewolf 1952; Weyer 1976, 1977; Bartzsch & Weyer 1982, 1986), Upper Franconia (Schindewolf 1923; Korn 1994), Silesia (Tietze 1869, 1870; Weyer 1965; Dzik 1997), Carnic Alps (Korn 1992b), Montagne Noire (Becker & Weyer 2004; Korn & Feist 2007), Anti-Atlas (Korn 1999; Korn *et al.* 2004; Bockwinkel & Ebbighausen 2006; Ebbighausen & Korn 2007; Becker *et al.* 2013), Gourara in Algeria (Ebbighausen *et al.* 2004), South Urals (Balashova 1953; Barskov *et al.* 1984; Kusina 1985; Nikolaeva 2020), Karaganda (Librovitch 1940), Guizhou (Sun & Shen 1965; Ruan 1981; Sheng 1989), questionable also Missouri (Furnish & Manger 1973) and Illinois (Smith 1903; Miller & Collinson 1951).

#### Remarks

In the revision of the Treatise, Kullmann (2009) applied a very conservative concept with respect to the subdivision of the Early Carboniferous prionoceratid ammonoids; he did not accept the subfamilies Acutimitoceratinae, Imitoceratinae and Balviinae as valid. Instead, he merged the subfamily Acutimitoceratinae with the family Gattendorfiidae without accepting subfamilies. This means that two rather well-separable ammonoid groups were lumped: on one side the conservative clade with forms that close the umbilicus in the adult stage (e.g., *Acutimitoceras*, *Stockumites*, *Nicimitoceras*) and on the other

side those forms in which the umbilicus stays open in the adult stage (e.g., *Gattendorfia*, *Weyerella*). Furthermore, Kullmann (2009) also put the genera *Imitoceras* and *Irinoceras* in the Prionoceratidae, despite their close morphological similarity, in conch shape, ontogenetic development and suture line, with *Nicimitoceras*, which suggests instead a rather close phylogenetic relationship with that genus. As Bockwinkel & Ebbighausen (2006) showed in their study of Early Tournaisian assemblages from Morocco, early representatives of *Imitoceras* can easily be related to genera of the Acutimitoceratinae (e.g., *Nicimitoceras*). Thus, Kullman's (2009) concept of the family Prionoceratidae is most probably of a polyphyletic taxon.

# Genus Stockumites Becker, 1996

# Type species

Imitoceras intermedium Schindewolf, 1923, p. 333; original designation.

## Genus diagnosis

Genus of the subfamily Acutimitoceratinae with a discoidal to globular conch with low to high coiling rate (WER=1.70–2.10 and rarely up to 2.35); inner whorls subinvolute to very evolute to variable degree. Venter broadly or narrowly rounded. Ornament usually with convex or rarely with biconvex growth lines, shell surface with or without constrictions. Suture line with deep, lanceolate external lobe (as deep as the adventive lobe).

# **Genus composition**

Central Europe (Münster 1839b; Schindewolf 1923; Schmidt 1925; Vöhringer 1960; Korn 1984): Goniatites subbilobatus Münster, 1839; Imitoceras intermedium Schindewolf, 1923; ? Gattendorfia involuta Schindewolf, 1924; Aganides prorsus Schmidt, 1925; Imitoceras prorsum antecedens Vöhringer, 1960; Imitoceras prorsum convexum Vöhringer, 1960; Imitoceras depressum Vöhringer, 1960; Imitoceras liratum exile Vöhringer, 1960; Imitoceras liratum simile Vöhringer, 1960; Imitoceras undulatum Vöhringer, 1960; Acutimitoceras kleinerae Korn, 1984; Acutimitoceras procedens Korn, 1984; Acutimitoceras stockumense Korn, 1984; Stockumites parallelus Korn & Weyer, 2023; Stockumites voehringeri Korn & Weyer, 2023; Stockumites hofensis sp. nov.; Stockumites nonaginta sp. nov.

North Africa (Korn & Klug 2002; Ebbighausen et al. 2004; Bockwinkel & Ebbighausen 2006; Ebbighausen & Bockwinkel 2007): Acutimitoceras hilarum Korn in Korn & Klug, 2002; Acutimitoceras algeriense Ebbighausen, Bockwinkel, Korn & Weyer, 2004; Acutimitoceras sinulobatum Ebbighausen, Bockwinkel, Korn & Weyer, 2004; Acutimitoceras hollardi Bockwinkel & Ebbighausen, 2006; Acutimitoceras occidentale Bockwinkel & Ebbighausen, 2006; Acutimitoceras posterum Bockwinkel & Ebbighausen, 2006; Acutimitoceras endoserpens Ebbighausen & Bockwinkel, 2007; Acutimitoceras pentaconstrictum Ebbighausen & Bockwinkel, 2007; Acutimitoceras sarahae Ebbighausen & Bockwinkel, 2007; Stockumites marocensis Korn & Weyer, 2023.

South Urals (Barskov et al. 1984; Kusina 1985; Nikolaeva 2020): Acutimitoceras mugodzharense Kusina in Barskov et al., 1984; Acutimitoceras pulchrum Kusina, 1985; Acutimitoceras alabasense Nikolaeva, 2020; Acutimitoceras dzhanganense Nikolaeva, 2020.

Central Asia (Librovitch 1940): Imitoceras rotiforme Librovitch, 1940.

South China (Sun & Shen 1965; Ruan 1981): *Imitoceras inequalis* Sun & Shen, 1965; *Imitoceras sinense* Sun & Shen, 1965; *Imitoceras (Imitoceras) crassum* Ruan, 1981.

North America (questionable species) (Rowley 1895; Moore 1928): *Goniatites louisianensis* Rowley, 1895; *Aganides compressus* Moore, 1928.

### Remarks

Stockumites was introduced by Becker (1996) as a subgenus of Acutimitoceras to separate the species with rounded venter from the acute species (such as A. acutum and A. wangyuense). This difference alone would probably not justify two genera. However, a closer examination of the material from various regions (Rhenish Mountains, Upper Franconia, Thuringia, Guizhou) shows that the acute venter is not the only character that distinguishes Acutimitoceras from Stockumites. An additional distinguishing character is the attached keel, which gives the venter a galeate profile in cross-section in Acutimitoceras. Therefore, we define Acutimitoceras as possessing both these characters, while the genus Stockumites only has the rounded venter without an attached keel.

The Central European species of *Stockumites* can be classified into different categories based on their morphology:

- (1) Conch size: some of the species (*S. kleinerae*, *S. intermedius*, *S. voehringeri*, *S. subbilobatus*) attain a diameter of 70 mm; most of the others remain smaller (up to about 40–50 mm).
- (2) Adult conch shape: within the genus *Stockumites*, the general conch shape varies from thickly discoidal (most of the species) to thickly pachyconic (*S. kleinerae*, *S. depressus*).
- (3) Juvenile conch shape: in the juvenile stage, the conch shape varies between subinvolute (*S. depressus*) and evolute (*S. convexus*, *S. antecedens*). Within the genus, a temporal morphological trend from evolute to subinvolute can be observed; the umbilicus is particularly wide in the inner whorls of the stratigraphically older species.
- (4) Growth line strength: some species have lamellar growth lines (*S. intermedius*, *S. undulatus*) and others very fine or barely visible growth lines.
- (5) Growth line course: most species have convex growth lines, but these are weakly biconvex in *S. parallelus* and distinctly biconvex *in S. undulatus*.
- (6) Constrictions: some species (S. similis, S. exilis, S. parallelus) have shell constrictions, others (S. kleinerae, S. voehringeri, S. subbilobatus, S. convexus) have inner shell thickenings and still others (S. intermedius, S. depressus, S. undulatus, S. antecedens) have neither.

# **Stockumites kleinerae** (Korn, 1984) Figs 6–7; Table 3

Acutimitoceras kleinerae Korn, 1984: 74, pl. 1 figs 1-5, pl. 3 fig. 23, text-figs 4c-d, 5a.

*Acutimitoceras kleinerae* — Korn 1992b: 16, pl. 2 figs 4–5; 1994: 47, text-figs 36e, 38a–e, 40b, 44g–h, 45e, 48c–d, 56a–b, 57d–e. — Schoenlaub *et al.* 1992: pl. 5 figs 4–5. — Kullmann 2000: text-fig. 4h. — Korn & Klug 2002: 197, text-fig. 173a.

Stockumites kleinerae – Korn & Weyer 2023: 47, figs 29–30.

Imitoceras Denckmanni - Schindewolf 1923: 336, pl. 15 figs 5-6, text-fig. 4h.

Imitoceras substriatum – Vöhringer 1960: 128, pl. 3 fig. 1, text-fig. 9.

non Acutimitoceras kleinerae – Sheng 1989: 110, pl. 33 figs 3–5.

# **Diagnosis**

Species of *Stockumites* with a conch reaching 70 mm diameter. Conch at 5 mm dm pachyconic to globular, subinvolute to subevolute (ww/dm=0.60-0.90; uw/dm=0.20-0.40); at 15 mm dm pachyconic to globular, involute (ww/dm=0.80-0.90; uw/dm=0.05-0.15); at 30 mm dm thickly pachyconic, involute (ww/dm  $\sim 0.75$ ; uw/dm=0.00-0.05). Whorl profile at 30 mm dm weakly depressed

(ww/wh  $\sim$  1.35); coiling rate moderately high (WER  $\sim$  1.80). Venter very broadly rounded, umbilical margin broadly rounded. Growth lines fine to coarse, wide-standing, with convex course. Without constrictions on the shell surface; with weak internal shell thickenings. Suture line with narrow external lobe and narrowly V-shaped adventive lobe (from Korn & Weyer 2023).

# **Material examined**

## Holotype

GERMANY • Rhenish Mountains, forestry road cutting 900 m east of Stockum; Stockum Limestone (*Stockumites prorsus* Zone); Korn 1982 Coll.; illustrated by Korn (1984: pl. 1 fig. 3) and Korn (1994: text-fig. 38b); SMF 43001.

# **Paratypes**

GERMANY • 15 specimens; Rhenish Mountains, forestry road cutting, 900 m east of Stockum; Stockum Limestone; Korn 1982 Coll.; SMF 43002–SMF 43016 • 13 specimens; Rhenish Mountains, trench II, 950 m east of Stockum; Stockum Limestone; Korn 1982 Coll.; SMF 43017–SMF 43029 • 10 specimens; Rhenish Mountains, Müssenberg; Hangenberg Limestone, bed 3c; Korn 1980 Coll.; SMF 43030–SMF 43039.

## Additional material

GERMANY • 3 specimens; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("Gattendorfia Limestone"); Schindewolf 1916 Coll.; SMF Mbg.3108, SMF Mbg.7561–SMF Mbg.7562 • 1 specimen; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("Gattendorfia Limestone"); GZG. INV.141 • 4 specimens; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("Gattendorfia Limestone"); Schindewolf 1934 Coll.; BGRB X13381–BGRB X13383, BGRB unnumbered specimen • 1 specimen; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21a ("Gattendorfia Limestone"); Korn 1989 Coll.; MB.C.31261 • 2 specimens; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21c–d ("Gattendorfia Limestone"); Korn 1989 Coll.; MB.C.31262.1–MB.C.31262.2.

# **Description**

Specimen MBG3108 is a comparatively well-preserved, only slightly deformed conch with a diameter of 67 mm (Fig. 6A). It is thickly discoidal (ww/wh nearly 0.60) with an almost completely closed umbilicus. The whorl width slightly exceeds the whorl height (ww/wh = 1.04); the coiling rate is moderate (WER = 1.87). The whorl profile shows a very broadly rounded venter. It seems to be somewhat narrowed at the aperture, but this is apparently caused by deformation of the body chamber. The ornament consists of coarse growth lines with a convex course.

Specimens BGRB X13381 (Fig. 6C), BGRB X13382 (Fig. 6D) and BGRB X13383 (Fig. 6E) show similar conch morphologies between 18 and 32 mm conch diameter; only the ww/dm ratio decreases from 0.84 to 0.78.

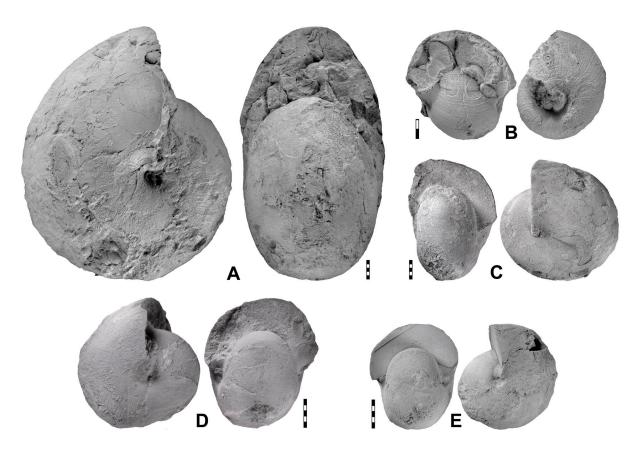
The small specimen GZG.INV.141 has a globular shape (ww/dm=0.86) with a slightly opened umbilicus (uw/dm=0.14) at 10 mm conch diameter (Fig. 6B). It shows coarse growth lines that curve forward on the flank and form a broad, flat ventral projection. A shallow shell constriction is present at a conch diameter of about 7 mm.

The cross sections of specimens MB.C.31261, SMF Mbg.7561, SMF Mbg.7562 and MB.C.31262.1 show the ontogenetic changes of the conch geometry from the innermost whorls up to a conch diameter of 34 mm (Fig. 7A–D). They show that the early juvenile evolute stage with a crescent-shaped whorl profile is present up to a conch diameter of about 5 mm. After this, rapid increase of the whorl width and stagnation of opening of the umbilicus leads to a pachyconic, subinvolute or involute conch with a C-shaped whorl profile already at 8 mm diameter.

**Table 3.** Conch measurements, ratios and rates of *Stockumites kleinerae* (Korn, 1984) from Gattendorf.

specimen	dm	ww	Wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
SMF Mbg.3108	67.3	39.7	38.3	1.4	18.1	0.59	1.04	0.02	1.87	0.53
MB.C.31261	33.7	25.0	21.1	1.3	8.8	0.74	1.18	0.04	1.83	0.58
BGRB X13381	32.1	25.0	17.5	1.5	7.8	0.78	1.43	0.05	1.74	0.56
BGRB X13382	23.1	20.1	13.6	1.0	5.6	0.87	1.47	0.04	1.75	0.59
MB.C.31262.1	27.9	22.7	14.4	2.3	6.2	0.81	1.58	0.08	1.65	0.57
SMF Mbg.7561	24.8	20.8	12.7	2.8	6.1	0.84	1.63	0.11	1.76	0.52
BGRB X13383	18.6	15.7	9.7	1.1	4.3	0.84	1.62	0.06	1.69	0.55
SMF Mbg.7562	14.5	11.3	7.3	2.0	3.1	0.78	1.56	0.14	1.63	0.57
GZG.INV.141	9.8	8.4	5.2	1.4	2.4	0.86	1.62	0.14	1.75	0.54

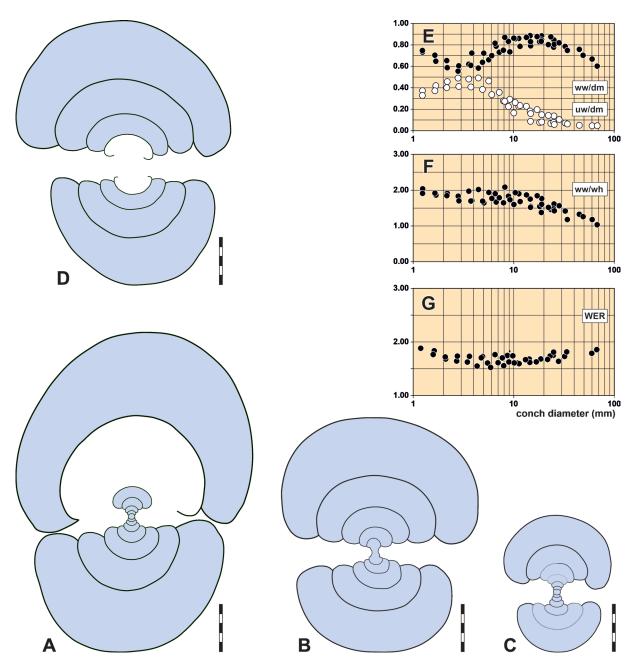
The growth trajectory of the ww/dm ratio shows a distinct triphasic ontogeny (Fig. 7E), while the ww/ wh trajectory is weakly biphasic with a nearly continuous decrease from a value of 2.00 at 1 mm conch diameter to 1.00 at 70 mm diameter (Fig. 7F). The coiling rate is rather low in all growth stages and exceeds a WER value of 1.80 only in the adult stage at about 60 mm conch diameter (Fig. 7G).



**Fig. 6.** *Stockumites kleinerae* (Korn, 1984) from Gattendorf, bed 21. **A.** Specimen SMF Mbg.3108 (Schindewolf 1916 Coll.). **B.** Specimen GZG.INV.141. **C.** Specimen BGRB X13381 (Schindewolf 1934 Coll.). **D.** Specimen BGRB X13382 (Schindewolf 1934 Coll.). **E.** Specimen BGRB X13383 (Schindewolf 1934 Coll.). Scale bar units=1 mm.

### Remarks

Stockumites kleinerae is, next to Mimimitoceras varicosum, the stoutest ammonoid species in the ammonoid assemblage from bed 21 of Gattendorf. However, both species can easily be distinguished by the presence (M. varicosum) or absence (S. kleinerae) of shell constrictions. S. kleinerae differs from S. intermedius by the coarser growth lines, which are dense and sharply formed in the adult stage of S. kleinerae, whereas in S. intermedius they are widely spaced and lamellar.



**Fig. 7.** Stockumites kleinerae (Korn, 1984) from Gattendorf. **A.** Cross section of specimen MB.C.31261 (Korn 1989 Coll.) from bed 21a. **B.** Cross section of specimen SMF Mbg.7561 (Schindewolf 1916 Coll.) from bed 21. **C.** Cross section of specimen SMF Mbg.7562 (Schindewolf 1916 Coll.) from bed 21. **D.** Cross section of specimen MB.C.31262.1 (Korn 1989 Coll.) from bed 21c–d. **E–G.** Ontogenetic development of the conch width index (ww/dm), umbilical width index (uw/dm), whorl width index (ww/wh) and whorl expansion rate (WER) of selected specimens. Scale bar units=1 mm.

# Stockumites intermedius (Schindewolf, 1923) Figs 8–9; Table 4

Imitoceras intermedium Schindewolf, 1923: 333, pl. 16 fig. 2, text-fig. 4f.

*Imitoceras intermedium* – Librovitch 1940: pl. 2 fig. 5a–b. — Vöhringer 1960: 131, pl. 3 figs 2, 7–8, text-fig. 11. — Furnish & Manger 1973: 20, text-fig. 2b, d. — Weyer 1977: 177, text-fig. 2.1. — House 1985: pl. 6.7.29, text-fig. 6.7.14b.

*Acutimitoceras intermedium* — Korn 1984: 75, pl. 3 figs 20–23, text-figs 4e, 5h–I; 1992b: 15, pl. 1 figs 22–27, 30, pl. 2 figs 2–3, 7–9, 15–16, 21–22, 26–27; 1992c: 178, pl. 1 figs 7–11; 1994: 47, text-figs 37a–c, 40c, 41a–e, 44a–c, 45a–c, 47b, 48a–b, 56d–f, 57b–c; 1999: 166, pl. 2 fig. 8. — Schönlaub *et al.* 1992: pl. 4 figs 22–27, 30, pl. 5 figs 2–3, 7–9, 15–16, 21–22, 26–27. — Korn *et al.* 1994: text-fig. 20b. — Belka *et al.* 1999: pl. 5 figs 7–8. — Kullmann 2000: text-fig. 4g. — Korn & Klug 2002: 197, text-fig. 173b. — Korn & Weyer 2003: pl. 2 figs 12–13. — Bockwinkel & Ebbighausen 2006: 97, text-figs 13–14. — Ebbighausen & Bockwinkel 2007: 131, text-figs 8f–g, 10, 12a–b. — Korn & Feist 2007: 106, text-fig. 6b–c, h.

Stockumites intermedius – Becker et al. 2002: pl. 2 figs 13–14. — Korn & Weyer 2023: 51, figs 7d, 31–34.

Aganides infracarbonicus - Schmidt 1924: 149, pl. 8 figs 1-2; 1929: 61, pl. 15 fig. 8.

non *Imitoceras intermedium* – Librovitch 1940: 138, pl. 35 figs 2–3. — Schindewolf 1952: 291, text-figs 4–6. — Balashova 1953: 198, pl. 12 figs 11–20. — Furnish & Manger 1973: 20, pl. 1 figs 11–15. non *Imitoceras (Imitoceras) intermedium* – Ruan 1981: 64, pl. 12 figs 1–6, 9–13, 17–28.

# **Diagnosis**

Species of *Stockumites* with a conch reaching 120 mm diameter. Conch at 5 mm dm thinly pachyconic, subinvolute to subevolute (ww/dm  $\sim$  0.70; uw/dm=0.20–0.40); at 15 mm dm thinly pachyconic, involute (ww/dm  $\sim$  0.65; uw/dm  $\sim$  0.00); at 30 mm dm thinly pachyconic, involute (ww/dm  $\sim$  0.65; uw/dm  $\sim$  0.00). Whorl profile at 30 mm dm weakly depressed (ww/wh = 1.10–1.20); coiling rate moderately high (WER=1.85–1.95). Venter broadly rounded, umbilical margin very broadly rounded. Growth lines lamellar, wide-standing, with convex course. Without constrictions on the shell surface; without internal shell thickenings. Suture line with narrowly lanceolate external lobe and narrowly V-shaped adventive lobe (from Korn & Weyer 2023).

# **Material examined**

## Lectotype

GERMANY • Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("*Gattendorfia* Limestone"); Schindewolf 1916 Coll.; illustrated by Schindewolf (1923: pl. 16 fig. 2), Librovitch (1940: pl. 2 fig. 5) and Korn (1994: text-fig. 56f); re-illustrated here in Fig. 8A; SMF Mbg.3111.

# **Paralectotypes**

GERMANY • 9 specimens; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("Gattendorfia Limestone"); Schindewolf 1916 Coll.; SMF Mbg.7563–SMF Mbg.7571.

# **Additional material**

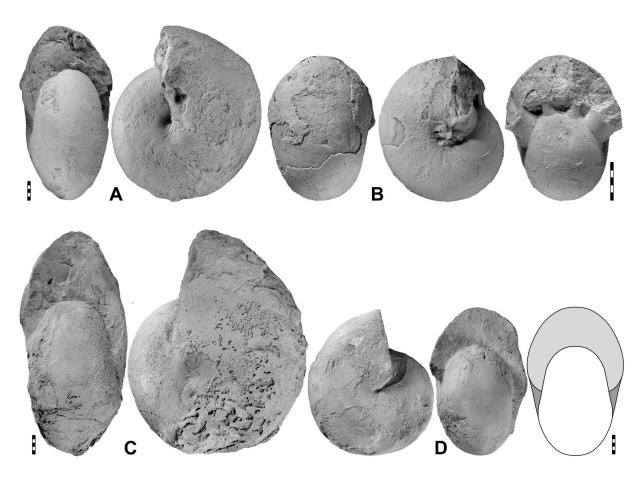
GERMANY • 31 specimens; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("Gattendorfia Limestone"); Schindewolf 1934 Coll.; BGRB X13384, BGRB unnumbered • 1 specimen; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("Gattendorfia Limestone"); Paul Coll.; BGRB unnumbered • 5 specimens; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21a ("Gattendorfia Limestone"); Korn 1989 Coll.; MB.C.31263.1–MB.C.31263.5 • 2 specimens; Upper

Franconia, 400 m north-west of Kirchgattendorf; bed 21c–d ("*Gattendorfia* Limestone"); Korn 1989 Coll.; MB.C.31264.1–MB.C.31264.2 • 1 specimen; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21f ("*Gattendorfia* Limestone"); Korn 1989 Coll.; MB.C.31265.

# **Description**

Lectotype SMF Mbg.3111 is a rather poorly preserved specimen with 46 mm conch diameter; the last half whorl is deformed and partly eroded (Fig. 8A). The penultimate half whorl appears to be only slightly deformed and allows the study of conch morphology and ornament. At 36 mm in diameter, the conch is thickly discoidal (ww/dm  $\sim$  0.60) with an almost closed umbilicus that is characterised by its very broadly rounded margin. The shell bears lamellar growth lines running in a convex arc across the flank and forming a broad, deep sinus on the venter (Fig. 9E).

Paralectotype SMF Mbg.7563 is a rather well-preserved specimen with 19 mm diameter (Fig. 8B). It is thickly pachyconic (ww/dm  $\sim 0.78$ ) with an almost closed umbilicus, a broadly rounded umbilical margin and a broadly rounded venter. The well-preserved shell ornament shows lamellar growth lines that are rursiradiate with a very weakly biconvex course across the flanks and a broad ventral sinus (Fig. 9C). The suture line has a lanceolate and deep external lobe, a broadly rounded ventrolateral saddle and a weakly asymmetrical adventive lobe (Fig. 9D).



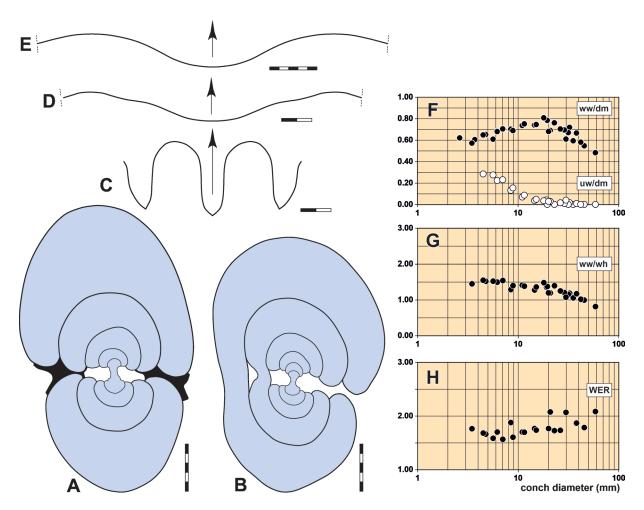
**Fig. 8.** *Stockumites intermedius* (Schindewolf, 1923) from Gattendorf. **A.** Lectotype SMF Mbg.3111 (Schindewolf 1916 Coll.) from bed 21. **B.** Paralectotype SMF Mbg.7563 (Schindewolf 1916 Coll.) from bed 21. **C.** Specimen BGRB X13384 (Schindewolf 1934 Coll.) from bed 21. **D.** Specimen MB.C.31263.1 (Korn 1989 Coll.) from bed 21a. Scale bar units=1 mm.

Specimens BGRB X13384 (60 mm dm; Fig. 8C) and MB.C.31263.1 (39 mm dm; Fig. 8D) have similar conch shapes to the lectotype. The only small difference is that specimen MB.C.31263.1 is stouter (ww/dm=0.67) than the lectotype.

The two cross sections SMF Mbg.7564 (Fig. 9A) and SMF Mbg.7565 (Fig. 9B) show deformed specimens. Although the morphometric data cannot be precisely extracted, they allow an insight into ontogenetic changes in the interval between 4 and 30 mm conch diameter. Due to the partly strong deformation of the body chambers, the values of the coiling rate are particularly problematic. However, the trajectories of the conch parameters ww/dm, uw/dm and ww/wh (Fig. 9F–G) agree quite well with the comparison sample from bed 6 of the Oberrödinghausen section.

#### Remarks

"Imitoceras intermedium" was established by Schindewolf (1923) for forms that occupy a morphological position between the slender form "Imitoceras Gürichi" (= S. hofensis sp. nov.) and the stout form



**Fig. 9.** Stockumites intermedius (Schindewolf, 1923) from Gattendorf, bed 21, all (Schindewolf 1916 Coll.). **A.** Cross section of specimen SMF Mbg.7564. **B.** Cross section of specimen SMF Mbg.7565. **C.** Suture line of paralectotype SMF Mbg.7563, at dm=16.7 mm, ww=12.9 mm, wh=8.3 mm. **D.** Growth line course of paralectotype SMF Mbg.7563, at dm=14.8 mm, ww=11.4 mm, wh=7.3 mm. **E.** Growth line course of lectotype SMF Mbg.3111, at ww=18.6 mm, wh=14.0 mm. **F–H.** Ontogenetic development of the conch width index (ww/dm), umbilical width index (uw/dm), whorl width index (ww/wh) and whorl expansion rate (WER) of selected specimens. Scale bar units=1 mm.

**Table 4.** Conch measurements, ratios and rates of *Stockumites intermedius* (Schindewolf, 1923) Gattendorf.

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
BGRB X13384	59.9	28.8	35.1	0.0	18.4	0.48	0.82	0.00	2.08	0.48
SMF Mbg.3111	46.2	25.2	25.1	0.0	11.6	0.55	1.00	0.00	1.78	0.54
MB.C.31263.1	38.7	25.7	21.8	0.3	10.4	0.67	1.18	0.01	1.87	0.52
SMF Mbg.7563	19.3	15.2	11.1	0.8	_	0.78	1.36	0.04	_	_

<sup>&</sup>quot;Imitoceras Denckmanni" (= Stockumites kleinerae) in their conch morphology, i.e., "rather thickly discoidal" shapes.

Stockumites intermedius differs from the simultaneously occurring species *S. kleinerae* by the more strongly compressed conch (ww/dm=0.60–0.65 in *S. intermedius*, but 0.75–0.80 in *S. kleinerae* at 30 mm dm). In addition, *S. intermedius* has lamellar growth lines, which are very coarse in *S. kleinerae* and are also visible on the inner surface of the shell.

# Stockumites subbilobatus (Münster, 1839)

Figs 10–12; Tables 5–6

Goniatites subbilobatus Münster, 1839: 21, pl. 17 fig. 1.

*Imitoceras subbilobatum* – Schindewolf 1952: 291. — Librovitch 1940: 13, pl. 1 fig. 4. — Weyer 1977: 177, text-fig. 2.2.

Acutimitoceras subbilobatum - Korn 1994: 51, text-fig. 56g.

non Sporadoceras subbilobatum – Frech 1897: 177g, text-fig. 3.

non *Imitoceras subbilobatum* – Librovitch 1940: 13, pl. 1 figs 1–3. — Balashova 1953: 191, pl. 11 figs 1–16. — Vöhringer 1960: 135, pl. 3 fig. 3, text-fig. 14.

non *Prionoceras* (*Imitoceras*) *subbilobatum* – Kullmann 1960: 528, pl. 7 fig. 5, text-fig. 16a. —Weyer 1965: 446, pl. 7 fig. 2.

non *Imitoceras* (*Imitoceras*) *subbilobatum* – Ruan 1981: 65, pl. 12 figs 14–16.

non *Acutimitoceras subbilobatum* — Barskov *et al.* 1984: pl. 1 figs 5–6, text-fig. 3. — Korn 1984: 76, pl. 2 figs 13–15, text-fig. 5e; 1992b: 15, pl. 1 figs 28–29, pl. 2 figs 13–14, 23–24; 1992c: 178, pl. 1 figs 2–3, pl. 2 figs 7–8; 1994: 51, text-figs 37d, 39, 42a–c, 44d–f, 47a, 50a, 53a–b, 58f. — Sheng 1989: 111, pl. 33 figs 1–2. — Schönlaub *et al.* 1992: 15, pl. 5 figs 28–29, pl. 6 figs 13–14, 23–24. — Kullmann 2000: text-fig. 4f. — Korn & Klug 2002: 197, text-fig. 173c, f. — Korn *et al.* 2003: 1125, text-fig. 3c. — Korn & Weyer 2003: pl. 2 figs 6–7, text-fig. 14d. — Bockwinkel & Ebbighausen 2006: 99, text-figs 15, 16a–d. — Korn & Feist 2007: 106 fig. 6a.

non *Imitoceras* (*Acutimitoceras*) *subbilobatum* – Kusina 1985: 43, pl. 3 fig. 5. — Bogoslovsky 1987: pl. 5 fig. 5, pl. 6 fig. 4.

non *Stockumites subbilobatus* – Becker *et al.* 2002: pl. 4 figs 6–7. — Becker & Weyer 2004: 18, text-fig. 3c.

# **Diagnosis**

Species of *Stockumites* with a conch reaching 70 mm diameter. Conch at 5 mm dm thickly discoidal and evolute (ww/dm  $\sim 0.50$ , uw/dm  $\sim 0.50$ ); at 15 mm dm thinly pachyconic, subinvolute (ww/dm  $\sim 0.65$ , uw/dm  $\sim 0.15$ ); at 30 mm dm thickly discoidal, involute (ww/dm  $\sim 0.55$ , uw/dm  $\sim 0.00$ ). Whorl profile

at 30 mm dm weakly compressed (ww/wh  $\sim$  0.90); coiling rate moderately high (WER  $\sim$  1.90). Venter rounded, umbilical margin rounded. Growth lines fine and lamellar, wide-standing, with convex course. Without constrictions on the shell surface; without internal shell thickenings. Suture line with lanceolate external lobe and narrowly V-shaped adventive lobe.

### **Material examined**

# Holotype

GERMANY • Upper Franconia, 400 m north-west of Kirchgattendorf; Münster Coll.; illustrated by Münster (1839b: pl. 17 fig. 1) and Korn (1994: text-fig. 56g); re-illustrated here in Fig. 10; SNSB BSPG AS VII 26.

#### Additional material

GERMANY • 31 specimens; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("Gattendorfia Limestone"); Schindewolf 1934 Coll.; BGRB X13385–BGRB X13391, BGRB unnumbered • 1 specimen; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21c–d ("Gattendorfia Limestone"); Korn 1989 Coll.; MB.C.31266.

# **Description**

Holotype SNSB BSPG AS VII 26 is a poorly preserved specimen with about 70 mm conch diameter (Fig. 10). About two thirds of the last whorl belong to the body chamber. Especially the last whorl is strongly distorted, which has led to a markedly deviating morphology of the body chamber. The penultimate half whorl is less affected by deformation and allows statements about the conch morphology. At 49 mm diameter the conch is thinly discoidal (ww/dm=0.44). The apparently little deformed phragmocone shows subparallel flanks, which converge rather slowly to the continuously rounded venter.

Specimen BGRB X13385 is a moderately preserved conch 41 mm in diameter (Fig. 11A); it is somewhat deformed and shows the surface of the shell on the outer and inner sides in addition to the conch shape. The conch is thickly discoidal (ww/dm=0.48) and almost completely involute. The umbilical margin is narrowly rounded; the flanks converge to the rather narrowly rounded venter. The shell bears fine, lamellar growth lines with a convex course. There are no constrictions on the shell surface or on the internal mould.



**Fig. 10.** Stockumites subbilobatus (Münster, 1839), holotype SNSB BSPG AS VII 26 (Münster Coll.) from Gattendorf. Scale bar units = 1 mm.

**Table 5.** Conch measurements, ratios and rates of *Stockumites subbilobatus* (Münster, 1839) from Gattendorf.

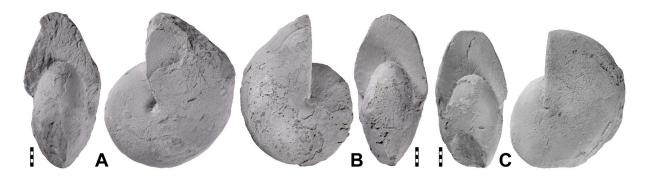
specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
SNSB BSPG AS VII 26	67.4		37.0	_	19.1	_	_	0.00	1.95	0.48
SNSB BSPG AS VII 26	48.8	21.3	28.5	0.0	_	0.44	0.75	0.00	_	_
BGRB X13390	53.9	22.7	32.2	0.7	14.0	0.42	0.70	0.01	1.82	0.57
BGRB X13385	41.0	19.7	22.9	0.5	11.6	0.48	0.86	0.01	1.94	0.49
BGRB X13388	40.8	19.7	23.8	0.6	11.9	0.48	0.83	0.02	1.99	0.50
BGRB X13386	40.0	19.4	22.6	0.5	11.3	0.48	0.86	0.01	1.94	0.50
BGRB X13391	37.4	17.2	22.1	0.4	10.1	0.46	0.78	0.01	1.88	0.54
BGRB X13387	36.2	18.6	19.5	0.4	_	0.51	0.95	0.01	_	_
BGRB X13389	32.0	15.1	19.0	0.3	8.8	0.47	0.79	0.01	1.91	0.53

Table 6. Conch ontogeny of Stockumites subbilobatus (Münster, 1839) from Gattendorf.

dm	conch shape	whorl cross section shape	whorl expansion
2 mm	thickly discoidal; evolute (ww/dm ~ 0.55; uw/dm ~ 0.45)	moderately depressed; moderately embracing (ww/wh $\sim$ 1.90; IZR $\sim$ 0.25)	low (WER ~ 1.65)
5 mm	thickly discoidal; evolute (ww/dm ~ 0.50; uw/dm ~ 0.50)	moderately depressed; strongly embracing (ww/wh $\sim 1.85$ ; IZR $\sim 0.35$ )	low (WER ~ 1.50)
15 mm	thinly pachyconic; subinvolute (ww/dm ~ 0.65; uw/dm ~ 0.15)	weakly depressed; very strongly embracing (ww/wh $\sim 1.25$ ; IZR $\sim 0.55$ )	moderate (WER ~ 1.80)
30 mm	thickly discoidal; involute (ww/dm ~ 0.50; uw/dm ~ 0.00)	weakly compressed; very strongly embracing (ww/wh $\sim 0.85$ ; IZR $\sim 0.50$ )	moderate (WER ~ 1.90)

The two specimens BGRB X13386 (40 mm dm; Fig. 11B) and BGRB X13387 (36 mm dm; Fig. 11C) hardly differ from specimen BGRB X13385 in conch morphology and ornamentation. Specimen BGRB X13389 shows the suture line, which possesses a narrow, lanceolate external lobe, a broadly rounded, slightly asymmetric ventrolateral saddle and a V-shaped adventive lobe (Fig. 12B).

The cross section of specimen BGRB X13388 allows the study of the conch geometry and its ontogeny up to a diameter of 41 mm (Fig. 12A). The ontogenetic changes are very conspicuous and characterised

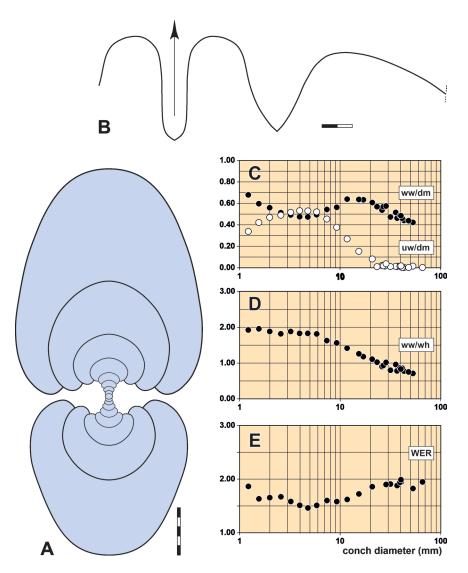


**Fig. 11.** Stockumites subbilobatus (Münster, 1839) from Gattendorf, bed 21, all Schindewolf 1934 Coll. **A.** Specimen BGRB X13385. **B.** Specimen BGRB X13386. **C.** Specimen BGRB X13387. Scale bar units=1 mm.

by the transition of a serpenticonic juvenile stage to a goniatitoid middle and adult stage. The conch is widely umbilicate (uw/dm > 0.50) with a kidney-shaped whorl profile up to about 6 mm diameter; thereafter the uw/dm ratio becomes rapidly smaller and already at 20 mm conch diameter the umbilicus is almost completely closed. At 20 mm diameter the conch is thinly pachyconic (ww/dm  $\sim 0.62$ ) with broadly rounded, nearly parallel flanks and a broadly rounded venter. The ontogenetic trajectories of the ww/dm and uw/dm ratios are markedly triphasic (Fig. 12C–E), but the phases of these two parameters are not synchronous.

### Remarks

Stockumites subbilobatus is a somewhat problematic species because the holotype is poorly preserved and therefore a comparison with other specimens, which are usually considerably smaller, is rather difficult. However, the apparently low number of species occurring in the Gattendorf section allows for



**Fig. 12.** *Stockumites subbilobatus* (Münster, 1839) from Gattendorf, bed 21. **A.** Cross section of specimen BGRB X13388 (Schindewolf 1934 Coll.). **B.** Suture line of specimen BGRB X13389 (Schindewolf 1934 Coll.), at ww=13.1 mm, wh=13.2 mm. **C–E.** Ontogenetic development of the conch width index (ww/dm), umbilical width index (uw/dm), whorl width index (ww/wh) and whorl expansion rate (WER) of selected specimens. Scale bar units=1 mm.

a discussion about the identity of this species. It had therefore to be determined which of the smaller specimens, some of which have been cross-sectioned, correspond most closely to the conch morphology of the holotype. We choose such specimens, which, at a conch diameter of about 30–50 mm, most resemble the undeformed part of the holotype.

The restriction of the species *S. subbilobatus* on the basis of the holotype and some other specimens from Gattendorf leads to an extensive modification of the synonymy list; most of the records previously considered to belong to this species have to be excluded.

These include first and foremost the specimens from the Rhenish Mountains, which can no longer be identified as *S. subbilobatus*, but these belong to at least two other species:

- (1) Specimens from the Stockum Limestone, its time-equivalent strata (*Stockumites prorsus* Zone) and the lower part of the Hangenberg Limestone (*Acutimitoceras ucatum* Zone): These specimens (e.g., Korn 1984, 1994) possess shell constrictions and a more strongly compressed conch; the ww/dm ratio is 0.45 at 30 mm conch diameter, in contrast to 0.50 in *S. subbilobatus*. This species is newly described by Korn & Weyer (2023) as *Stockumites parallelus*.
- (2) Specimens from the middle part of the Hangenberg Limestone (*Paprothites dorsoplanus* and *Pseudarietites westfalicus* zones). These specimens (e.g., Vöhringer 1960; Korn 1994) have internal shell thickenings and a stouter conch than *S. subbilobatus* (ww/dm=0.50–0.60). This species is newly redescribed by Korn & Weyer (2023) as *Stockumites voehringeri*.

Furthermore, many specimens have been placed in *S. subbilobatus* simply based on their slender conch shape (Librovitch 1940; Kullmann 1960; Ruan 1981; Barskov *et al.* 1984; Kusina 1985; Bogoslovsky 1987; Korn 1992b; Becker *et al.* 2002; Becker & Weyer 2004). These are listed here in the synonymy list; however, a discussion of all these forms is beyond the scope of this research.

Stockumites subbilobatus belongs to the species of the genus with a rather slender conch. Among the species known from Gattendorf, however, the conchs of S. parallelus and S. hofensis sp. nov. are even more slender; at 20 mm conch diameter, the ww/dm ratio is  $\sim 0.60$  in S. subbilobatus, but only about 0.50 in S. parallelus and S. hofensis. In addition, S. parallelus has shell constrictions and S. hofensis shows clearly convergent flanks.

Stockumites intermedius has a very similar ornament with widely spaced lamellar growth lines, but has a stouter conch (ww/dm=0.70–0.75 at 20 mm dm) and a very broadly rounded umbilical margin (narrowly rounded in *S. subbilobatus*).

A conch form similar to S. subbilobatus can be seen in S. hilarus. This species also has a rather slender conch (ww/dm  $\sim 0.60$ ) and a very widely umbilicate juvenile conch, but in contrast to S. subbilobatus it bears conspicuous constrictions.

# Stockumites parallelus Korn & Weyer, 2023 Figs 13–14; Tables 7–8

Imitoceras subbilobatum – Vöhringer, 1960: 135, text-fig. 14.

*Acutimitoceras subbilobatum* – Korn 1984: 76, pl. 2 figs 13–15, text-fig. 5e; 1992c: 178, pl. 1 figs 2–3, pl. 2 figs 7–8; 1994: 51, text-figs 37d, 39, 42a–c, 50a. — Kullmann 2000: text-fig. 4f. — Korn & Klug 2002: 197, text-fig. 173c, f. — Korn *et al.* 2003: 1125, text-fig. 3c. — Korn & Weyer 2003: pl. 2 figs 6–7, text-fig. 14d.

Stockumites parallelus – Korn & Weyer 2023: 57, figs 7f, 35. ? Aganides ornatissimus – Schmidt 1924: 149, pl. 8 figs 3–4.

# **Diagnosis**

Species of *Stockumites* with a conch reaching 70 mm diameter. Conch at 5 mm dm thinly pachyconic, subinvolute (ww/dm  $\sim$  0.65; uw/dm  $\sim$  0.20); at 15 mm dm thickly discoidal, involute (ww/dm  $\sim$  0.55; uw/dm  $\sim$  0.05); at 30 mm dm thickly discoidal, involute (ww/dm  $\sim$  0.50; uw/dm  $\sim$  0.00). Whorl profile at 30 mm dm weakly compressed (ww/wh  $\sim$  0.90); coiling rate moderately high (WER  $\sim$  1.90). Venter rounded, umbilical margin rounded, flanks subparallel. Growth lines fine, narrow-standing, with slightly biconvex course. Weak constrictions on the shell surface; coarse internal shell thickenings. Suture line with lanceolate external lobe and narrowly V-shaped adventive lobe (from Korn & Weyer 2023).

### **Material examined**

## Holotype

GERMANY • Rhenish Mountains, forestry road cutting 900 m east of Stockum; Stockum Limestone (*Stockumites prorsus* Zone); Korn 1982 Coll.; illustrated by Korn (1994: text-fig. 42a); SMF 43083.

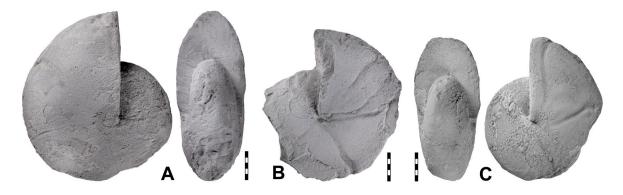
#### Additional material

GERMANY • 26 specimens; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("Gattendorfia Limestone"); Schindewolf 1934 Coll.; BGRB X13392–BGRB X13395, BGRB unnumbered • 1 specimen; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21a ("Gattendorfia Limestone"); Korn 1989 Coll.; MB.C.31267 • 1 specimen; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21c–d ("Gattendorfia Limestone"); Korn 1989 Coll.; MB.C.31268.

# **Description**

The three specimens shown here, MB.C.31267 (30 mm dm; Fig. 13A), BGRB X13392 (26 mm dm; Fig. 13B) and BGRB X13393 (25 mm dm; Fig. 13C), allow the study of the middle growth stage. The variation of the conch parameters is low; an ontogenetic trend towards a more slender conch is visible. At about 30 mm conch diameter, the conch is thinly discoidal (ww/dm=0.40–0.45) with a nearly completely closed umbilicus. All three show constrictions of the shell surface, which, however, become fainter with increasing size of the specimens. On the internal mould, the constrictions are considerably deeper because the shell constrictions are reinforced internally by thickening of the shell.

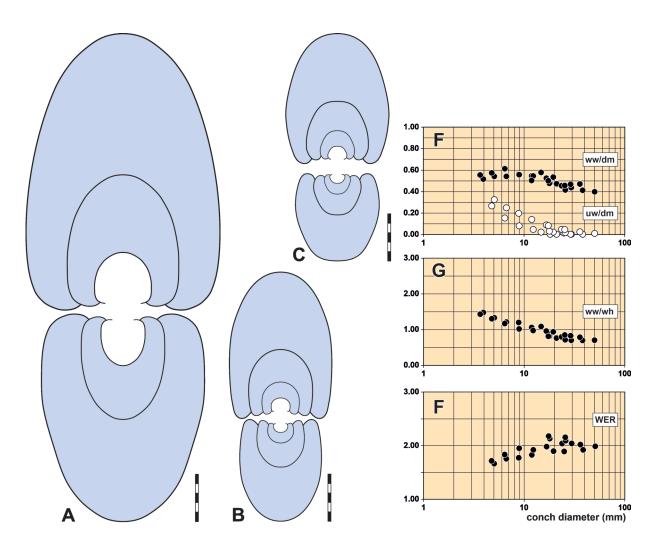
The cross sections of the three specimens MB.C.31268, BGRB X13394 and BGRB X13395 show very similar pictures (Fig. 14A–C). The innermost whorls are not preserved, but it can be assumed that they are evolute. The whorl profile is horseshoe-shaped at 6 mm, conch diameter and the widest part is on the inner half of the flank at some distance from the rather narrowly rounded umbilical margin. In the



**Fig. 13.** *Stockumites parallelus* Korn & Weyer, 2023 from Gattendorf. **A.** Specimen MB.C.31267 (Korn 1989 Coll.) from bed 21a. **B.** Specimen BGRB X13392 (Schindewolf 1934 Coll.) from bed 21. **C.** Specimen BGRB X13393 (Schindewolf 1934 Coll.) from bed 21. Scale bar units=1 mm.

**Table 7.** Conch measurements, ratios and rates of *Stockumites parallelus* Korn & Weyer, 2023 from Gattendorf.

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.31268	51.6	20.4	29.2	0.5	14.9	0.40	0.70	0.01	1.98	0.49
MB.C.31267	30.0	13.1	18.7	0.0	9.0	0.44	0.70	0.00	2.03	0.52
BGRB X13394	26.1	10.8	15.1	0.4	8.0	0.41	0.71	0.02	2.09	0.47
BGRB X13393	25.3	11.6	15.0	0.3	6.9	0.46	0.77	0.01	1.89	0.54
BGRB X13395	24.0	10.9	13.7	1.1	7.1	0.45	0.79	0.05	2.03	0.48



**Fig. 14.** *Stockumites parallelus* Korn & Weyer, 2023 from Gattendorf. **A.** Cross section of specimen MB.C.31268 (Korn 1989 Coll.) from bed 21c–d. **B.** Cross section of specimen BGRB X13394 (Schindewolf 1934 Coll.) from bed 21. **C.** Cross section of specimen BGRB X13395 (Schindewolf 1934 Coll.) from bed 21. **D**–**F.** Ontogenetic development of the conch width index (ww/dm), umbilical width index (uw/dm), whorl width index (ww/wh) and whorl expansion rate (WER) of selected specimens. Scale bar units=1 mm.

**Table 8.** Conch ontogeny of *Stockumites parallelus* Korn & Weyer, 2023 from Gattendorf.

dm	conch shape	whorl cross section shape	whorl expansion
5 mm	thickly discoidal; subinvolute (ww/dm $\sim 0.54$ ; uw/dm $\sim 0.28$ )	weakly depressed; moderately embracing (ww/wh $\sim 1.25$ ; IZR $\sim 0.30$ )	low (WER ~ 1.65)
15 mm	thickly discoidal; involute (ww/dm ~ 0.55; uw/dm ~ 0.10)	weakly depressed; very strongly embracing (ww/wh $\sim 1.05$ ; IZR $\sim 0.50$ )	moderate (WER ~ 1.95)
30 mm	thickly discoidal; involute (ww/dm ~ 0.45; uw/dm ~ 0.00)	weakly compressed; very strongly embracing (ww/wh $\sim$ 0.70; IZR $\sim$ 0.50)	Moderate to high (WER = 1.90–2.00)

ontogenetic interval between 4 and 52 mm conch diameter, the growth trajectories are rather simple. The ww/dm ratio decreases from about 0.55 to 0.40; at the same time the ww/wh ratio decreases from 1.50 to 0.65 (Fig. 14D).

#### Remarks

As can be seen from the synonymy list, specimens of the new species were often assigned to *Stockumites subbilobatus*. However, the holotype of *S. subbilobatus* has no constrictions and is stouter than *S. parallelus*. With a conch diameter of 30 mm, the width-to-diameter ratio is about 0.45 for *S. parallelus*, but about 0.50 for *S. subbilobatus*.

Stockumites parallelus has the most slender conch of the genus at Gattendorf; already at a diameter of 20 mm the ww/dm ratio is less than 0.50. Another criterion good for distinguishing *S. parallelus* from the other species of the assemblage are the conspicuous shell constrictions, which are furthermore reinforced on the inner side of the shell and therefore lead to very deep constrictions of the internal mould.

# *Stockumites convexus* (Vöhringer, 1960) Fig. 15; Table 9

Imitoceras prorsum convexum Vöhringer, 1960: 139, pl. 2 fig. 5, text-fig. 17.

*Imitoceras prorsum convexum* – Weyer 1977: 172, pl. 2 figs 8–9. *Acutimitoceras convexum* – Korn 1992b: 16, pl. 2 figs 17–18; 1994: 42, text-figs 49a–c, 50e, 52a, 54d, 56c. — Schönlaub *et al.* 1992: 16, pl. 5 figs 17–18. — Korn & Weyer 2003: 100, pl. 2 figs 1–2. *Stockumites convexus* – Becker & Weyer 2004: 18, text-fig. 3g. — Korn & Weyer 2023: 64, figs7e, 39–40.

### **Diagnosis**

Species of *Stockumites* with a conch reaching 40 mm diameter. Conch at 5 mm dm thickly discoidal to thinly pachyconic, subevolute to evolute (ww/dm=0.55–0.65; uw/dm=0.40–0.50); at 15 mm dm thickly discoidal, involute (ww/dm=0.45–0.55; uw/dm=0.05–0.10); at 25 mm dm thickly discoidal, involute (ww/dm=0.45–0.55; uw/dm  $\sim$  0.00). Whorl profile at 25 mm dm weakly compressed (ww/wh  $\sim$  0.90); coiling rate moderate to high (WER=1.90–2.10). Venter broadly rounded, umbilical margin broadly rounded. Growth lines coarse, wide-standing, with convex course. Weak constrictions on the shell surface; coarse internal shell thickenings. Suture line with lanceolate external lobe and V-shaped adventive lobe.

**Table 9.** Conch measurements, ratios and rates of *Stockumites convexus* (Vöhringer, 1960) from Gattendorf.

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
BGRB X13396	19.8	10.6	11.3	0.4	5.1	0.53	0.94	0.02	1.81	0.55

#### Material examined

# Holotype

GERMANY • Rhenish Mountains, Oberrödinghausen railway cutting; bed 6 (*Acutimitoceras acutum* Zone); Vöhringer Coll.; illustrated by Vöhringer (1960: pl. 2 fig. 6) and Korn (1994: text-fig. 49a), reillustrated here in Fig. 15A; GPIT-PV-63903.

#### Additional material

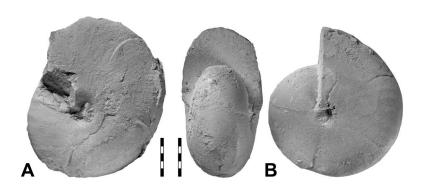
GERMANY • 1 specimen; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("*Gattendorfia* Limestone"); Schindewolf 1916 Coll.; SMF Mbg.7572 • 1 specimen; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("*Gattendorfia* Limestone"); Schindewolf 1934 Coll.; BGRB X13396.

# **Description**

Specimen BGRB X13396 is a fairly well preserved, only slightly distorted specimen with a diameter of 20 mm (Fig. 15B). It has been preserved almost entirely with the shell and therefore allows the ornament to be studied. The conch is thickly discoidal (ww/dm=0.53) with the umbilicus not completely closed. The whorl profile shows almost parallel, only slightly convergent flanks, a rounded umbilical margin and a continuously rounded venter. The coiling rate is comparatively low (WER=1.81). The shell bears convex, fine growth lines, which are somewhat stronger on the venter than on the flanks. In addition, the shell surface shows four constrictions spaced less than 90 degrees apart. They extend from the umbilical margin across the flanks and venter. The last of these constrictions, however, is restricted to the outer flank and the venter.

## Remarks

Stockumites convexus is one of the rare species in the assemblage from Gattendorf. It differs from most of the other species in its shell constrictions. Only *S. parallelus* also has shell constrictions, but has a more strongly compressed conch (ww/dm=0.50 at 20 mm dm) than *S. convexus* (ww/dm=0.55 at 20 mm dm). Furthermore, *S. convexus* has a slightly opened umbilicus at 20 mm conch diameter, whereas the umbilicus is completely closed in *S. parallelus*. But the most important is the course of the growth lines and constrictions: they are convex in *S. convexus* and slightly biconvex in *S. parallelus*.



**Fig. 15.** *Stockumites convexus* (Vöhringer, 1960) from Gattendorf, bed 21. **A.** Specimen SMF Mbg.7572 (Schindewolf 1916 Coll.). **B.** Specimen BGRB X13396 (Schindewolf 1934 Coll.). Scale bar units = 1 mm.

# Stockumites hofensis sp. nov.

urn:lsid:zoobank.org:act:0776DC38-0887-4CEB-98A7-99A3408F2F14 Figs 16–18; Tables 10–11

Imitoceras Gürichi – Schindewolf 1923: 331, pl. 15 fig. 1, pl. 16 fig. 1, text-fig. 4d.

# **Diagnosis**

Species of *Stockumites* with a conch reaching 90 mm diameter. Conch at 5 mm dm thickly discoidal, subinvolute (ww/dm  $\sim$  0.58, uw/dm  $\sim$  0.18); at 15 mm dm thickly discoidal, involute (ww/dm  $\sim$  0.55, uw/dm  $\sim$  0.02); at 30 mm dm thinly discoidal, involute (ww/dm  $\sim$  0.40, uw/dm  $\sim$  0.00). Whorl profile at 30 mm dm weakly compressed (ww/wh  $\sim$  0.65); coiling rate high (WER  $\sim$  2.05). Venter narrowly rounded, umbilical margin rounded. Growth lines fine, narrow-standing, with convex course. Without constrictions on the shell surface; without internal shell thickenings. Suture line with lanceolate external lobe and narrowly V-shaped adventive lobe.

## **Etymology**

After the city of Hof, seven kilometres west of the Gattendorf outcrop.

## **Material examined**

# Holotype

GERMANY • Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21c-d ("Gattendorfia Limestone"); Korn 1989 Coll.; illustrated in Fig. 16C; MB.C.31269.1.

# **Paratypes**

GERMANY • 6 specimens; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("*Gattendorfia* Limestone"); Schindewolf 1934 Coll.; BGRB X13397–BGRB X13402 • 15 specimens; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21c–d ("*Gattendorfia* Limestone"); Korn 1989 Coll.; MB.C.31269.2–16.

## Additional material examined

GERMANY • 55 specimens; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("Gattendorfia Limestone"); Schindewolf 1934 Coll.; BGRB unnumbered.

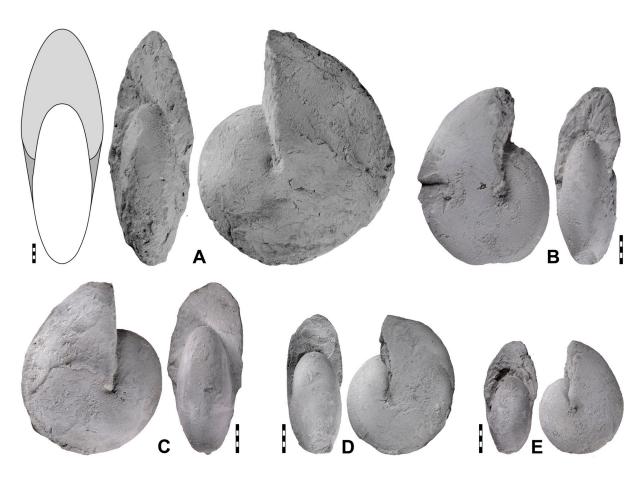
## **Description**

Specimen MB.C.31269.1 is selected as the holotype because it shows the suture line and the shell ornamentation in addition to the only slightly distorted conch shape (Fig. 16C); it was also taken at a well-documented stratigraphic position in the section. Therefore, it can best be taken as representative of the species. It has a diameter of 30 mm and is thinly discoidal (ww/dm=0.43) with a depressed whorl profile (ww/wh = 0.70). The conch is widest at the rounded umbilical margin, from where the somewhat flattened flanks converge to the narrowly rounded venter. The coiling rate is moderately high (WER=1.96). Some remains of the shell show very fine, lamellar-like, quite widely spaced growth lines with a convex course. The suture line has a narrow, lanceolate external lobe, a broadly rounded, nearly symmetric ventrolateral saddle and a V-shaped, symmetric adventive lobe (Fig. 17C).

The paratypes BGRB X13397, BGRB X13398, BGRB X13399 and BGRB X13400 (Fig. 16A–B, D–E) agree, in their conch proportions, broadly with the holotype; the intraspecific variation is quite small. However, it must be taken into account that the conch undergoes an ontogenetic change towards a more slender adult shape.

The cross sections of the paratypes MB.C.31269.2, MB.C.31269.3 and MB.C.31269.4 show rather similar ontogenetic developments of the conch geometry (Fig. 18A–C). The best preserved of these is specimen is MB.C.31269.3; it allows the study from the initial stage up to a diameter of 31 mm (Fig. 18B). The innermost whorls up to 2.5 mm conch diameter have a kidney-shaped profile; they embrace each other very little. After that, the whorls begin to increase in height and at a conch diameter of about 10 mm, they have a horseshoe-shaped profile. After that, more intensive growth in height leads to the formation of the characteristic adult stage with a compressed whorl profile; this is characterised by strongly convergent flanks and a slightly rounded venter.

The ontogenetic trajectories show a very simple biphasic or monophasic course (Fig. 18D–F). The ww/dm ratio remains constant between 1 mm and 10 mm conch diameter at a value of 0.60; in the later stage it decreases continuously down to a value of 0.35 at 70 mm diameter. The uw/dm ratio is high at 1.5 mm conch diameter (uw/dm=0.45) with continuous reduction thereafter. The umbilicus is almost closed already at a conch diameter of around 10 mm. The ww/wh trajectory is monophasic with a continuous decline from about 2.00 at 1 mm diameter to 0.60 at 70 mm diameter. In contrast, the evolution of the coiling rate is biphasic; a rapid ontogenetic increase means that the value of WER=2.00 is already reached at a conch diameter of 7 mm. After that, the value remains stable in the following ontogeny.



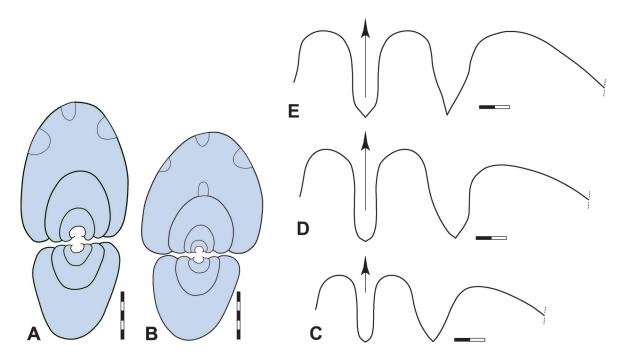
**Fig. 16.** *Stockumites hofensis* sp. nov. from Gattendorf. **A.** Paratype BGRB X13397 (Schindewolf 1934 Coll.) from bed 21. **B.** Paratype BGRB X13398 (Schindewolf 1934 Coll.) from bed 21. **C.** Holotype MB.C.31269.1 (Korn 1989 Coll.) from bed 21c–d. **D.** Paratype BGRB X13399 (Schindewolf 1934 Coll.) from bed 21. **E.** Paratype BGRB X13400 (Schindewolf 1934 Coll.) from bed 21. Scale bar units = 1 mm.

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
BGRB X13401	73.4	24.0	42.4	0.0	21.9	0.33	0.57	0.00	2.03	0.48
BGRB X13397	61.4	21.7	35.4	0.0	19.2	0.35	0.61	0.00	2.12	0.46
BGRB X13402	36.0	13.6	20.1	0.0	10.5	0.38	0.68	0.00	1.99	0.48
BGRB X13398	31.3	12.2	18.6	0.0	9.7	0.39	0.65	0.00	2.09	0.48
MB.C.31269.3	31.3	12.5	17.9	0.1	9.0	0.40	0.70	0.00	1.97	0.50
MB.C.31269.1	30.4	13.2	19.0	0.0	8.7	0.43	0.70	0.00	1.96	0.54
MB.C.31269.5	24.9	11.5	14.5	0.6	7.3	0.46	0.80	0.02	2.00	0.50
BGRB X13399	24.8	10.3	14.5	0.0	7.0	0.42	0.71	0.00	1.94	0.52
MB.C.31269.2	23.0	10.7	12.9	0.2	6.8	0.47	0.83	0.01	2.03	0.47
BGRB X13400	19.6	9.4	12.0	0.0	6.0	0.48	0.79	0.00	2.08	0.50

The suture lines show a slight variation in their course. While the external lobe is always deep and narrowly lanceolate, the V-shaped adventive lobe shows differently shaped flanks ranging from almost straight to sigmoidal (Fig. 17C–E).

### Remarks

Stockumites hofensis sp. nov. resembles S. nonaginta sp. nov.; both species are difficult to distinguish without knowledge of the suture line. This differs with regard to the adventive lobe, which is narrowly



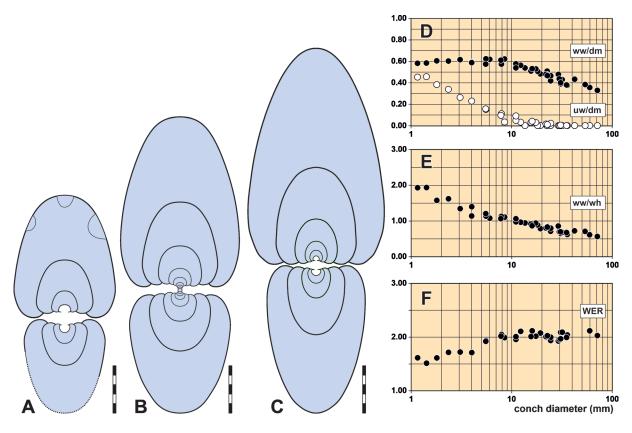
**Fig. 17.** *Stockumites hofensis* sp. nov. from Gattendorf. **A.** Cross section of paratype MB.C.31269.5 (Korn 1989 Coll.) from bed 21c–d. **B.** Cross section of paratype MB.C.31269.6 (Korn 1989 Coll.) from bed 21c–d. **C.** Suture line of holotype MB.C.31269.1 (Korn 1989 Coll.) from bed 21c–d, at ww=9.6 mm, wh=10.8 mm. **D.** Suture line of paratype BGRB X13398 (Schindewolf 1934 Coll.) from bed 21, at dm=28.8 mm, ww=11.4 mm, wh=15.1 mm. **E.** Suture line of paratype BGRB X13397 (Schindewolf 1934 Coll.) from bed 21, at ww=12.6 mm, wh=15.7 mm. Scale bar units=1 mm.

<b>Table 11. (</b>	Conch ontogeny	of Stockumites	hofensis sp.	nov. from	Gattendorf.

dm	conch shape	whorl cross section shape	whorl expansion
2 mm	thickly discoidal; subevolute	moderately depressed; strongly embracing	low
	$(ww/dm \sim 0.58; uw/dm \sim 0.35)$	$(ww/wh \sim 1.60; IZR \sim 0.40)$	$(WER \sim 1.65)$
5 mm	thickly discoidal; subinvolute	weakly depressed; very strongly embracing	moderate
	$(ww/dm \sim 0.58; uw/dm \sim 0.20)$	$(ww/wh \sim 1.25; IZR \sim 0.50)$	$(WER \sim 1.80)$
15 mm	thickly discoidal; involute	weakly compressed; very strongly embracing	high
	$(ww/dm \sim 0.50; uw/dm \sim 0.02)$	$(ww/wh \sim 0.90; IZR \sim 0.50)$	$(WER \sim 2.05)$
30 mm	thinly discoidal; involute	weakly compressed; very strongly embracing	high
	$(ww/dm \sim 0.40;  uw/dm \sim 0.00)$	$(ww/wh \sim 0.70; IZR \sim 0.50)$	$(WER \sim 2.00)$

V-shaped in *S. hofensis*, but wide V-shaped and almost rectangular in *S. nonaginta*. The whorl profile also shows some differences; in *S. hofensis* the conch is widest in close proximity to the umbilicus, while in *S. nonaginta* the widest point is some distance from the umbilicus on the inner flank.

Stockumites hofensis sp. nov. differs from *S. subbilobatus* by the more slender conch; at 30 mm dm the ww/dm ratio is about 0.42 in *S. hofensis* but more than 0.50 in *S. subbilobatus*. In addition, *S. subbilobatus* has lamellar growth lines in contrast to *S. hofensis* with very fine growth lines.



**Fig. 18.** *Stockumites hofensis* sp. nov. from Gattendorf, bed 21c–d. **A.** Cross section of paratype MB.C.31269.2 (Korn 1989 Coll.). **B.** Cross section of paratype MB.C.31269.3 (Korn 1989 Coll.). **C.** Cross section of paratype MB.C.31269.4 (Korn 1989 Coll.). **D–F.** Ontogenetic development of the conch width index (ww/dm), umbilical width index (uw/dm), whorl width index (ww/wh) and whorl expansion rate (WER) of selected specimens. Scale bar units=1 mm.

# Stockumites nonaginta sp. nov.

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Figs 19–20; Tables 12–13

## **Diagnosis**

Species of *Stockumites* with a conch reaching 70 mm diameter. Conch at 5 mm dm thinly pachyconic, subinvolute (ww/dm  $\sim$  0.70, uw/dm  $\sim$  0.16); at 15 mm dm thinly pachyconic, involute (ww/dm  $\sim$  0.65, uw/dm  $\sim$  0.00); at 30 mm dm thinly discoidal, involute (ww/dm  $\sim$  0.50, uw/dm  $\sim$  0.00). Whorl profile at 30 mm dm weakly compressed (ww/wh  $\sim$  0.85); coiling rate high (WER  $\sim$  2.05). Venter rounded, umbilical margin rounded. Growth lines very fine, narrow-standing, with convex course. Without constrictions on the shell surface; without internal shell thickenings. Suture line with lanceolate external lobe and widely V-shaped adventive lobe.

# **Etymology**

From the Latin 'nonaginta', meaning '90' and referring to the shape of the adventive lobe.

#### Material examined

# Holotype

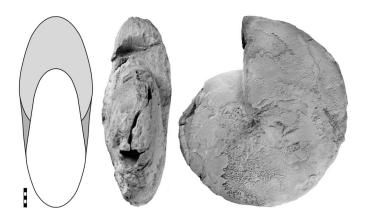
GERMANY • Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("Gattendorfia Limestone"); Schindewolf 1934 Coll.; illustrated in Fig. 19; BGRB X13403.

# **Paratypes**

GERMANY • 2 specimens; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21c-d ("Gattendorfia Limestone"); Korn 1989 Coll.; MB.C.31270.1–2.

# **Description**

Holotype BGRB X13403 is 51 mm in diameter (Fig. 19), which allows for the study of the conch morphology as well as areas of the shell surface and the suture line. The conch is thinly discoidal with an almost completely closed umbilicus (ww/dm=0.37; uw/dm=0.02). The whorl profile is compressed (ww/dm=0.67); it is widest on the inner flank at a short distance from the rounded umbilical margin. The flanks slowly converge towards the continuously rounded venter. It appears that the shell is completely smooth; small remnants of shell show only very faint growth lines. The suture line has a very narrow



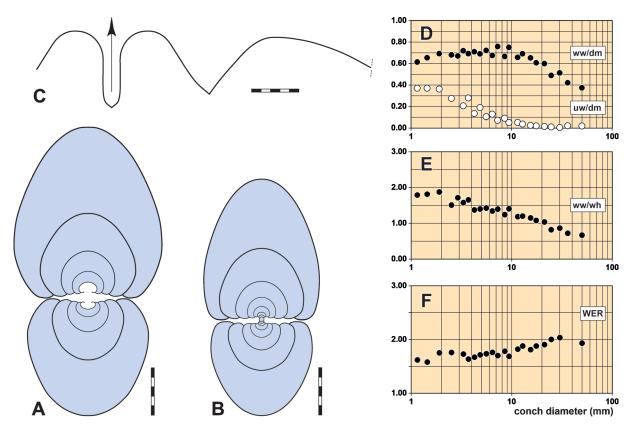
**Fig. 19.** *Stockumites nonaginta* sp. nov., holotype BGRB X13403 (Schindewolf 1934 Coll.) from Gattendorf, bed 21. Scale bar units=1 mm.

<b>Table 12.</b> Conch measurements	ratios and rates	of Stockumites no	<i>naginta</i> sp. no	ov from Gattendorf

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
BGRB X13403	50.9	18.9	28.3	0.9	14.3	0.37	0.67	0.02	1.93	0.49
MB.C.31270.2	30.4	15.6	18.0	0.1	9.1	0.51	0.86	0.00	2.04	0.49
MB.C.31270.1	25.0	12.2	14.8	0.2	7.3	0.49	0.82	0.01	2.00	0.51

and deep, parallel-sided external lobe, which continues into a broadly rounded ventrolateral saddle. The adventive lobe is almost right-angled V-shaped (Fig. 20C).

The two sectioned paratypes MB.C.31270.1 and MB.C.31270.2 show very similar conch proportions and virtually the same ontogenetic trajectories (Fig. 20A–B). The inner whorls are subevolute up to 2 mm conch diameter (the uw/dm reaches 0.36); then the umbilicus is slowly closed. The whorl profile is kidney-shaped to a conch diameter of 2 mm; thereafter it is C-shaped up to a conch diameter of 10 mm. With a diameter of 10 mm the conch flattens out and with a diameter of 30 mm the conch is thickly discoidal (ww/dm=0.50).



**Fig. 20.** *Stockumites nonaginta* sp. nov. from Gattendorf. **A.** Cross section of paratype MB.C.31270.1 (Korn 1989 Coll.) from bed 21c–d. **B.** Cross section of paratype MB.C.31270.2 (Korn 1989 Coll.) from bed 21c–d. **C.** Suture line of holotype BGRB X13403 (Schindewolf 1934 Coll.) from bed 21, at dm=47.5 mm, ww=18.7 mm, wh=26.0 mm. **D**–**F.** Ontogenetic development of the conch width index (ww/dm), umbilical width index (uw/dm), whorl width index (ww/wh) and whorl expansion rate (WER) of selected specimens. Scale bar units=1 mm.

**Table 13.** Conch ontogeny of *Stockumites nonaginta* sp. nov. from Gattendorf.

dm	conch shape	whorl cross section shape	whorl expansion
2 mm	thinly pachyconic; subevolute (ww/dm ~ 0.68; uw/dm ~ 0.35)	moderately depressed; strongly embracing (ww/wh ~ 1.80; IZR ~ 0.40)	low (WER ~ 1.70)
5 mm	thickly discoidal; subinvolute (ww/dm ~ 0.70; uw/dm ~ 0.15)	weakly depressed; very strongly embracing (ww/wh $\sim 1.45$ ; IZR $\sim 0.50$ )	low (WER ~ 1.70)
15 mm	thinly pachyconic; involute (ww/dm ~ 0.65; uw/dm ~ 0.02)	weakly depressed; very strongly embracing (ww/wh $\sim 1.15$ ; IZR $\sim 0.55$ )	moderate (WER ~ 1.85)
30 mm	thickly discoidal; involute (ww/dm $\sim$ 0.48; uw/dm $\sim$ 0.00)	weakly compressed; very strongly embracing (ww/wh $\sim$ 0.85; IZR $\sim$ 0.50)	high (WER ~ 2.05)

The growth trajectories of the cardinal conch parameters show different courses (Fig. 20D–F). A biphasic course can be seen in the ww/dm ratio. Between 1 and 10 mm conch diameter the ww/dm value increases slowly from 0.60 to 0.70; thereafter there is a continuous decrease to 0.50 at 30 mm dm. The course of the ww/wh trajectory is monophasic with a smooth decline from 2.00 at 1 mm dm to 0.85 at 30 mm.

#### Remarks

*Stockumites nonaginta* sp. nov. and *S. hofensis* sp. nov. are very similar species and can only be reliably distinguished by the suture line. While the adventive lobe of *S. nonaginta* is broadly V-shaped and almost rectangular, it is narrowly V-shaped in *S. hofensis*.

To distinguish the two species within the assemblage, the suture lines of several specimens were exposed. Unfortunately, this was not successful for all sectioned specimens, so that it is not entirely certain whether the suture lines of the two sectioned specimens actually correspond to the holotype.

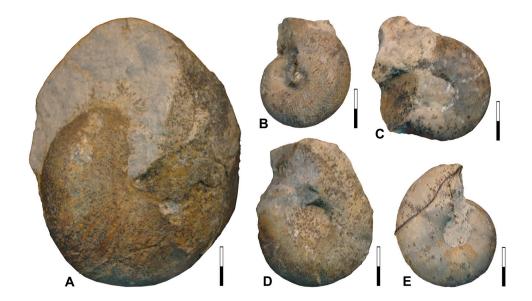
**Stockumites** sp. Fig. 21

#### Material examined

GERMANY • 5 specimens; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21a ("Gattendorfia Limestone"); Korn 1989 Coll.; MB.C.31271–MB.C.31275 • 180 specimens; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("Gattendorfia Limestone"); Schindewolf 1934 Coll.; BGRB unnumbered • 22 specimens; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21a ("Gattendorfia Limestone"); Korn 1989 Coll.; MB.C.31276.1–22 • 8 specimens; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21c–d ("Gattendorfia Limestone"); Korn 1989 Coll.; MB.C.3127.1–8 • 2 specimens; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21f ("Gattendorfia Limestone"); Korn 1989 Coll.; MB.C.31278.1–2 • 1 specimen; Upper Franconia, 400 m north-west of Kirchgattendorf; bed; Weyer 1995 Coll.; MB.C.31279 • 7 specimens; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21e; Weyer 1995 Coll.; MB.C.31280.1–7 • 2 specimens; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21e; Weyer 1995 Coll.; MB.C.31280.1–7 • 2 specimens; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21f; Weyer 1995 Coll.; MB.C.31281.1–2.

## **Description**

From the many specimens that cannot be determined more precisely, five small examples are shown here (Fig. 21), which show different juvenile morphologies. Specimens MB.C.31271 and MB.C.31272 (Fig. 21A–B) already have an almost completely involute conch in the early stage; both possess lamellar growth lines running with a concave arc across the flank. Constrictions are not present on either specimen.



**Fig. 21.** *Stockumites* sp., juvenile specimens (Korn 1989 Coll.) from Gattendorf, bed 21a. **A.** Specimen MB.C.31271. **B.** Specimen MB.C.31272. **C.** Specimen MB.C.31273. **D.** Specimen MB.C.31274. **E.** Specimen MB.C.31275. Scale bar units = 1 mm.

In contrast to the two previously described specimens, the three other specimens MB.C.31273—MB.C.31275 (Fig. 21C–E) show an open umbilicus with a conch diameter of 6 mm (uw/dm about 0.25). While specimenMB.C.31273 appears largely smooth, specimens MB.C.31274 and MB.C.31275 have quite strong growth lines that run along the flank with a concave arc and form a sinus on the venter. Both specimens have faint constrictions in the shell.

# Stockumites (?) involutus (Schindewolf, 1924) Fig. 22

Gattendorfia involuta Schindewolf, 1924: 105.

Gattendorfia involuta – Becker in Becker et al. 2021: 409.

non Gattendorfia involuta – Becker in Becker et al. 2021: 410, text-fig. 15.

### Material examined

## Lectotype

GERMANY • Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("Gattendorfia Limestone"); Schindewolf 1934 Coll.; illustrated in Fig. 22A; MB.C.31282.

## **Description**

Lectotype MB.C.31282 is a poorly preserved, incomplete specimen with a conch diameter of only 12 mm (Fig. 22A). A species diagnosis can thus not be given. The conch dimensions cannot be accurately determined, but it is clear that the conch is thickly discoidal and subinvolute (ww/dm=0.50; uw/dm=0.22). No shell is preserved and the internal mould shows several very shallow constrictions spaced 90 degrees apart.

#### Remarks

"Gattendorfia involuta" is a very problematic species; the name was not used for nearly hundred years. The type material, consisting only of one poorly preserved specimen, has never been described properly.

Becker (in Becker *et al.* 2021) was not aware of the type material of *Gattendorfia involuta*, and proposed a neotype for reviving the species. This was a specimen already figured by Vöhringer (1960) under the name *Gattendorfia tenuis*; it became the holotype of the species *G. schmidti* newly introduced by Korn & Weyer (2023). However, this neotype determination seriously complicated the problematic research history of this species. For this reason, it is necessary to review and discuss the research history of this species (from Korn & Weyer 2023):

Schindewolf (1926b: 92) explained that after writing his article on the ammonoid assemblages of Saalfeld (Schindewolf 1924), he had the opportunity to also study the Devonian–Carboniferous boundary section near Wocklum in the Rhenish Mountains in greater detail. During this visit he realised that the *Gattendorfia* Stufe is not older but younger than the *Wocklumeria* Stufe.

Schindewolf (1952: 297) discussed again his previously newly established third species "Gattendorfia involuta Schindewolf, 1924". In this discussion, he stated that this species had no valid name and that he would refer to it as the new species Gattendorfia tenuis. In this article, he described and illustrated a specimen of 73 mm diameter from Saalfeld as the type for that species. He also wrote that he had previously owned excellently preserved specimens from Oberrödinghausen in the Rhenish Mountains and Ebersdorf (Dzikowiec) in Silesia. A rather well-preserved specimen from Ebersdorf, collected by Schindewolf in 1918 and described as Gattendorfia tenuis by Weyer (1965: 447), belongs to G. schmidti described by Korn & Weyer (2023). From what has already been said above, it is clear that these specimens he mentioned did not belong to the type series.

Vöhringer (1960: 153) used the species name *G. tenuis* for specimens from Oberrödinghausen, which however belong to three different species. He presented a specimen with a diameter of 57 mm as a photograph and also cross sections of two other, smaller specimens. The assignment of his large specimen to *G. tenuis* is almost certainly in error, because it deviates considerably from the holotype in the direction of the constrictions. Nevertheless, this concept was accepted by Korn (1994, 2006).

Becker (in Becker *et al.* 2021: 409) saw the need to revive the hitherto unused species name "*Gattendorfia involuta* Schindewolf, 1924" and designated specimen GPIT-PV-63952, illustrated by Vöhringer (1960: pl. 5 fig. 6) as *G. tenuis*, as the neotype for "*G. involuta*". However, this procedure is to be criticised for several reasons:



**Fig. 22.** *Stockumites* (?) *involutus* (Schindewolf, 1924) from Gattendorf, bed 21. **A.** Specimen MB.C.31282 (Schindewolf Coll.). **B.** Original label of lectotype MB.C.31282 (handwriting by Schindewolf). Scale bar units = 1 mm.

- 1. The neotype does not come from the type region. The claim by Becker that Schindewolf possessed syntypes from Oberrödinghausen (and that this is one of the two type localities) is not correct (see above), since Schindewolf only carried out extensive studies in the Rhenish Mountains Devonian—Carboniferous boundary sections after writing his 1924 article.
- 2. With the determination of a neotype from another region, the species "*G. involuta*" would become a widespread species by definition, but not by empirical data.
- 3. The same is true for the stratigraphic range of the species. All ammonoid specimens from Gattendorf come from the lowest part of the *Gattendorfia* Limestone (*Acutimitoceras acutum* Zone), while the "neotype" comes from the highest bed of the *Gattendorfia* Limestone (*Eocanites delicatus* Zone). With the neotype proposal, *Gattendorfia involuta* would become a long-ranging species by definition, not by empirical data.
- 4. The determination of a neotype is unnecessary, because a specimen of "G. involuta" personally labelled by Schindewolf is present in the collection of the Museum für Naturkunde, Berlin; this specimen was probably taken by him when he moved from Marburg to Berlin in 1927.
- 5. The illustration of another supposedly "typical" specimen by Becker (in Becker *et al.* 2021: text-fig. 15) adds to the confusion. The poorly preserved specimen is from the basal bed of the Hangenberg Limestone, while the proposed neotype is from the highest bed of the unit. The specimen cannot be considered typical because it does not seem to have constrictions like the proposed neotype. Surprisingly, such differences in *G. subinvoluta* were attributed by Becker to "biogeographic separation through a narrow oceanic system".

Here, we describe the small lectotype to clarify the nomenclatural problems with this species. However, the lectotype is so poorly preserved that it is not diagnostic. It is not clear either to which genus the specimen belongs. The conch shape argues against an identification as *Gattendorfia*; it is more reminiscent of some species of the genus *Stockumites*, which only close the umbilicus at a late ontogenetic stage. Therefore, it cannot be clarified which relationships this problematic species has to other species. Apart from the poorly preserved lectotype, no other specimens are currently known; therefore, it is also not possible to make statements about the adult morphology of the species. The species must therefore be regarded as a problematic for the time being.

## Genus Acutimitoceras Librovitch, 1957

#### **Type species**

Imitoceras acutum Schindewolf, 1923, p. 333; original designation.

# Genus diagnosis

Genus of the Acutimitoceratinae with a discoidal, lenticular conch with low to high coiling rate (WER=1.70–2.20); inner whorls subevolute or evolute. Venter narrowly rounded or oxyconic with an attached ventral keel. Ornament with biconvex growth lines, shell with constrictions. Suture line with deep and broad, V-shaped external lobe (as deep as the adventive lobe).

## **Genus composition**

Central Europe (Schindewolf 1923; Korn & Weyer 2023): *Imitoceras acutum* (Schindewolf, 1923); *Acutimitoceras ucatum* Korn & Weyer, 2023; *Acutimitoceras paracutum* Korn & Weyer, 2023.

South China (Sun & Shen 1965): Imitoceras wangyuense Sun & Shen, 1965.

## Remarks

Acutimitoceras was established by Librovitch (1957) for prionoceratids with a sharpened venter. The genus was subsequently not considered further but was revived and broadened by Korn (1981, 1984) to include those early Tournaisian prionoceratid species that differ from the genus Mimimitoceras by more widely umbilicate inner whorls. However, this definition also includes species that are now placed in other genera (e.g., Stockumites, Nicimitoceras, Hasselbachia).

Acutimitoceras was then restricted to the oxyconic forms by Becker (1996), who established the subgenus Stockumites for those forms with a rounded venter throughout ontogeny. This concept was either not supported (e.g., Korn & Klug 2002; Korn & Weyer 2003; Korn 2006; Korn & Feist 2007) or accepted on the condition that Stockumites remains only a subgenus of Acutimitoceras (Kullmann 2009). However, a closer examination of the material from the various regions (Rhenish Mountains, Upper Franconia, Thuringia, Guizhou) shows that the acute venter is not the only character to distinguish Acutimitoceras from Stockumites (Korn & Weyer 2023). An additional good distinguishing character is the attached keel, which gives the external side a galeate profile in cross-section even when the venter is not acute. Therefore, Acutimitoceras is reduced here to the forms with these two characters and the genus Stockumites is accepted for the forms without an attached keel.

# Acutimitoceras acutum (Schindewolf, 1923) Figs 23–24; Tables 14–15

*Imitoceras acutum* Schindewolf, 1923: 338, pl. 15 figs 3–4. *Acutimitoceras acutum oxynotum* Bartzsch & Weyer, 1996: 96, text-figs 2–4.

*Imitoceras acutum* – Weyer 1976: 841, text-figs 1–3; 1977: 172, pl. 1 figs 5–6; 1979: pl. 1 fig. 3, pl. 3 fig. 7, pl. 5 fig. 13.

Acutimitoceras acutum – Bartzsch & Weyer 1986: pl. 2 fig. 4. — Korn 1994: 42, text-figs 56h, 57a; 2006: text-fig. 3a.

non Aganides acutus - Schmidt 1925: 534, pl. 19 fig. 5.

non Imitoceras acutum – Vöhringer 1960: 137, pl. 1 fig. 7, text-fig. 16.

non *Acutimitoceras acutum* – Korn 1992b: 15, pl. 1 figs 19–20; 1994: 42, text-figs 49j–k, 50b, 51a, 53c–d. — Schönlaub *et al.* 1992: pl. 4 figs 19–20.

non Acutimitoceras acutum acutum – Bartzsch & Weyer 1996: 95, text-fig. 1.

non Acutimitoceras (Acutimitoceras) acutum – Becker 1996: 36.

## **Diagnosis**

Species of *Acutimitoceras* with a thickly discoidal and subinvolute conch at 6 mm dm (ww/dm  $\sim$  0.52; uw/dm  $\sim$  0.25), thinly discoidal and involute conch at 12 mm dm (ww/dm  $\sim$  0.40; uw/dm  $\sim$  0.10) and thinly discoidal and involute conch at 24 mm dm (ww/dm  $\sim$  0.35; umbilicus closed). Whorl profile at 24 mm dm compressed (ww/wh  $\sim$  0.60); coiling rate high (WER  $\sim$  2.20). Venter subacute at 12 mm dm and acute at 20 mm dm. Fine growth lines with weakly biconvex course. Weak constrictions on the shell surface; they largely follow the course of the growth-lines.

### Material examined

#### Holotype

GERMANY • Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("Gattendorfia Limestone"); Schindewolf 1916 Coll.; illustrated by Schindewolf (1923: pl. 15 fig. 3), Korn (1994: text-fig. 56h) and Korn (2006: text-fig. 3a); re-illustrated here in Fig. 23A; SMF Mbg.3105.

## **Paralectotype**

GERMANY • Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("Gattendorfia Limestone"); Schindewolf 1916 Coll.; SMF Mbg.3106.

#### **Additional material**

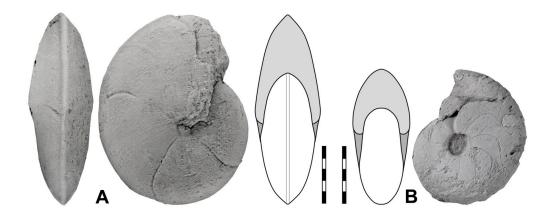
GERMANY • 1 specimen; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21f; Korn 1989 Coll.; MB.C.31283 • 1 specimen; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21d; Weyer 1995 Coll.; MB.C.31284.

## **Description**

Lectotype SMF Mbg.3105 is a rather well-preserved specimen 16.6 mm in diameter; it is fully covered with shell (Fig. 23A). Its conch shape is lenticular with an almost closed umbilicus (ww/dm=0.35; uw/dm=0.04) and a high coiling rate (WER=2.10). The whorl profile forms a narrow triangle; the flanks converge, beginning at the umbilical margin, slowly towards the venter but in the outer flank area, they converge more rapidly towards the raised ventral keel. The shell surface shows fine, convex growth lines which form a low ventrolateral projection and a deep V-shaped ventral sinus (Fig. 24C). Shell constrictions follow the course of the growth lines and are spaced at 90 degrees.

The smaller specimen MB.C.31283 shows the morphology of an intermediate growth stage with 11 mm conch diameter (Fig. 23B). The conch is thinly discoidal and subinvolute (ww/dm=0.42; uw/dm=0.16). It illustrates the transition from the early stage with a rounded venter to the older stage with an acute venter, showing a clear narrowing of the venter at a conch diameter of around 10 mm. The suture line has a V-shaped external lobe, a narrow, narrowly rounded ventrolateral saddle, and a large, asymmetrical adventive lobe with a convexly curved ventral flank and almost straight dorsal flank (Fig. 24B).

Paralectotype SMF.Mbg.3106 was sectioned already by Schindewolf; it shows a partially distorted cross-sectional image that did not hit the specimen perfectly in the centre (Fig. 24A). Nevertheless, the specimen gives a good overview of the ontogenetic changes from the evolving juvenile stage to the involute, disk-shaped adult stage with a sharpened venter.



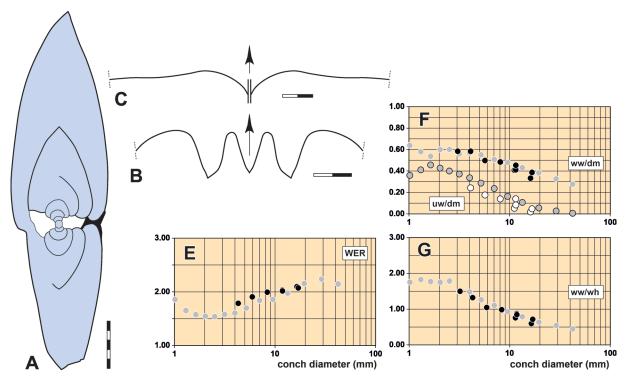
**Fig. 23.** Acutimitoceras acutum (Schindewolf, 1923) from Gattendorf. **A.** Lectotype SMF Mbg.3105 (Schindewolf 1916 Coll.) from bed 21. **B.** Specimen MB.C.31283 (Korn 1989 Coll.) from bed 21f. Scale bar units=1 mm.

**Table 14.** Conch measurements, ratios and rates of *Acutimitoceras acutum* (Schindewolf, 1923) from Gattendorf.

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
SMF.Mbg.3105	16.6	5.7	9.6	0.7	5.2	0.35	0.60	0.04	2.10	0.46
SMF.Mbg.3105	11.5	4.8	6.4	0.8	_	0.42	0.76	0.08	_	_
MB.C.31283	11.9	5.0	5.7	1.9	3.6	0.42	0.88	0.16	2.04	0.38

Table 15. Conch ontogeny of Acutimitoceras acutum (Schindewolf, 1923) from Gattendorf und Saalfeld.

dm	conch shape	whorl cross section shape	whorl expansion
2 mm	thickly discoidal; subevolute	moderately depressed; strongly embracing	low
	$(ww/dm \sim 0.58; uw/dm \sim 0.40)$	$(ww/wh \sim 1.75; IZR \sim 0.40)$	(WER ~ 1.55)
5 mm	thickly discoidal; subinvolute	weakly depressed; very strongly embracing	low
	$(ww/dm \sim 0.55;  uw/dm \sim 0.20)$	$(ww/wh \sim 1.25; IZR \sim 0.45)$	$(WER \sim 1.70)$
15 mm	thinly discoidal; involute	weakly compressed; very strongly embracing	high
	$(ww/dm \sim 0.40; uw/dm \sim 0.08)$	$(ww/wh \sim 0.65; IZR \sim 0.45)$	$(WER \sim 2.05)$
30 mm	extremely discoidal; involute	weakly compressed; very strongly embracing	high
	(ww/dm $\sim$ 0.30; uw/dm $\sim$ 0.00)	$(ww/wh \sim 0.55; IZR \sim 0.45)$	$(WER \sim 2.20)$



**Fig. 24.** *Acutimitoceras acutum* (Schindewolf, 1923) from Gattendorf. **A.** Cross section of paralectotype SMF Mbg.3106 (Schindewolf 1916 Coll.) from bed 21. **B.** Suture line of specimen MB.C.31283 (Korn 1989 Coll.) from bed 21f, at dm=11.5 mm, ww=4.8 mm, wh=5.5 mm. **C.** Growth line and constriction course in lectotype SMF.Mbg.3105 (Schindewolf 1916 Coll.) from bed 21, at dm=16.4 mm, ww=5.0 mm, wh=9.0 mm. **D**–**F.** Ontogenetic development of the conch width index (ww/dm), umbilical width index (uw/dm), whorl width index (ww/wh) and whorl expansion rate (WER) of selected specimens. Grey dots=specimen MB.C.1986 from the Pfaffenberg near Saalfeld, from Bartzsch & Weyer (1996). Scale bar units=1 mm.

#### Remarks

Bartzsch & Weyer (1996) introduced the subspecies *Acutimitoceras acutum oxynotum* to separate forms that later in ontogeny gain the character of an acute venter than in the nominate species. However, this comparison was done with the material from the Rhenish Mountains. The lectotype from Upper Franconia is obviously identical in shell geometry with the specimens from Thuringia. They also share the character of convergent flanks. For these reasons, *Acutimitoceras acutum oxynotum* must be regarded as a junior synonym of *A. acutum*.

Acutimitoceras ucatum from the Rhenish Mountains has convex flanks; the whorls are widest in some distance from the umbilicus (Korn & Weyer 2023). The growth lines have a weakly biconvex course in A. acutum, but show stronger undulation in A. ucatum. Acutimitoceras paracutum from the Rhenish Mountains has a similar conch morphology and ornament, but differs in having a much lower coiling rate (WER  $\sim 1.70$ ) in contrast to  $\sim 2.10$  in A. acutum).

Family Gattendorfiidae Bartzsch & Weyer, 1987

[nom. transl. Korn (1994: 69), ex Gattendorfiinae Bartzsch & Weyer, 1987]

## **Diagnosis**

Family of the superfamily Prionoceratoidea with the sutural formula E A L U I; external lobe lanceolate or slightly pouched; adventive lobe deep, V-shaped or lanceolate and pointed; the lateral lobe has a position on the umbilical wall. Conch in the juvenile stage subevolute or evolute; adult stage involute to evolute, but usually subinvolute. Shell ornament with fine to coarse growth lines, often with rursiradiate direction. Ribs occur in several independent lineages in varying morphology.

#### **Included subfamilies**

Gattendorfiinae Bartzsch & Weyer, 1987; Pseudarietitinae Bartzsch & Weyer, 1987.

## Remarks

In the Treatise revision, Kullmann (2009) expressed a view of the family Gattendorfiidae that is clearly different from previously published concepts (Bartzsch & Weyer 1987, 1988a; Korn 1994; Korn & Klug 2002). His scheme differs, on the one hand, in that the gattendorfiid and pseudarietitid clades are not considered as sister groups and, on the other hand, in that genera such as *Acutimitoceras* and *Stockumites* are also placed in the family Gattendorfiidae. The subfamily Acutimitoceratinae is treated there as a junior synonym of the family Gattendorfiidae.

Kullmann's (2009) definition of the family Gattendorfiidae both contains and creates some problems. It states that the family is characterised by a "shell surface with rursiradiate growth lines or ribbing"; however, this only applies to some representatives (*Gattendorfia*, *Zadelsdorfia*, *Weyerella*, *Gattenpleura*). This does not apply to those genera that we place in the subfamily Acutimitoceratinae. The biggest problem with this scheme, however, is that it cuts the evolutionary line from *Stockumites* to *Nicimitoceras* to *Imitoceras* and, with the placement of the latter genus in the family Prionoceratidae, this would make the family polyphyletic.

Subfamily Gattendorfiinae Bartzsch & Weyer, 1987

## **Diagnosis**

Subfamily of the family Gattendorfiidae with subevolute to evolute inner whorls, adult stage subinvolute to evolute. Ornament usually with coarse rursiradiate growth lines; in some species with radial folds but usually without sharp ribs.

## **Subfamily composition**

In total, about 75 species of the Gattendorfinae have been described so far. They belong to the genera: *Gattendorfia* Schindewolf, 1920 (10 species); *Kazakhstania* Librovitch, 1940 (9 species); *Zadelsdorfia* Weyer, 1972 (32 species); *Gattenpleura* Weyer, 1976 (3 species); *Hasselbachia* Korn & Weyer, 2003 (4 species) and *Weyerella* Bockwinkel & Ebbighausen, 2006 (17 species).

#### Remarks

### Morphology

The morphology within the subfamily Gattendorfiinae is very diverse and it is hardly possible to find a common character for all species. Such a character could possibly be the rursiradiate course of the growth lines.

All species of the subfamily share the character of widely umbilicate juvenile whorls; however, the umbilicus is almost never completely closed during ontogeny. Therefore, the morphology of the adult stage is highly variable and can range from serpenticonic (*Kazakhstania* and some species of *Gattendorfia*) to moderately umbilicate and molariform (*Weyerella*) to goniatitoid with a narrow umbilicus (*Zadelsdorfia*). Almost all species of the Gattendorfiinae have a low coiling rate (WER usually between 1.50 and 1.75 and only rarely higher).

The ornament often consists of rather coarse, mostly rursiradiate growth lines on the flank, which form a wide ventral sinus of varying depth. Spiral lines are rare (*Weyerella reticulum*) and ribs appear in *Gattenpleura* and some species of *Gattendorfia*. Species of the genera *Gattendorfia* and *Kazakhstania* often have shell constrictions; in *Hasselbachia* they are limited to the flanks as short notches.

#### **Ontogeny**

In the subfamily Gattendorfiinae, the complexity of ontogeny depends on the adult conch shape. While species with an almost serpenticonic adult stage show very simple ontogenetic trajectories, species with a goniatitoid adult stage (*Gattendorfia*, *Zadelsdorfia*, *Gattenpleura*, *Hasselbachia*) usually have very complex ontogenetic trajectories. This was demonstrated using the example of *Zadelsdorfia crassa* by Korn & Vöhringer (2004); in this species the trajectory of the ww/dm ratio is conspicuously triphasic. There is also a very marked change in whorl profiles during ontogeny; in *Z. crassa*, kidney-shaped, trapezoidal, circular, and horseshoe-shaped whorl profiles occur in succession.

#### **Phylogeny**

The origin of the subfamily Gattendorfinae (and the entire family Gattendorfidae) has not yet been satisfactorily clarified. This is at least partly owing to the fact that in the lowest part of the *Gattendorfia* Limestone several species of *Gattendorfia* (*G. subinvoluta*, *G. rhenana*, *G. immodica*) and *Gattenpleura* (*G. pfeifferi*) with quite complex morphology cryptically appear almost simultaneously. Two hypothesis may be discussed here:

- (1) An origin from the subfamily Prionoceratinae: Vöhringer (1960: 179) thought that it is possible that *Gattendorfia* could have originated from *Mimimitoceras varicosum* via *Kornia sphaeroidalis*. This assumption is mainly based on the interpretation that the presence of shell constrictions is an important character. This hypothesis could be strengthened by another argument not mentioned by Vöhringer the low coiling rate in the gattendorfiids. This hypothesis states that the main morphological novelty in the Gattendorfiinae is the widely umbilicate juvenile whorl.
- (2) An origin from the subfamily Acutimitoceratinae: this hypothesis was suggested by Korn (1986); the concept was taken over by Kullmann (2009) in the subdivision of the Prionoceratoidea. The hypothesis is based on the assumption that the evolute juvenile whorls are an important character and were passed

from *Stockumites* to *Gattendorfia*. This hypothesis could be supported by the fact that several species of *Gattendorfia* have rounded trapezoidal whorl profiles in the juvenile whorls similar to, for example, the stratigraphically early species *Stockumites hilarum*.

The intra-subfamily phylogenetic relationships also do not appear clear. The common character of the rursiradiate growth lines in almost all representatives of the Gattendorfiinae can be taken as evidence that it is at least a monophyletic unit. There may be several evolutionary lineages, (1) *Gattendorfia–Zadelsdorfia*, (2) *Gattendorfia–Kazakhstania*, (3) *Gattenpleura–Weyerella* and (4) *Gattenpleura–Hasselbachia*. This includes the hypothesis that *Weyerella* with the genuinely simple conch morphology and faint ornament is not the ancestor of the obviously much more complex *Gattenpleura*, but on the contrary is the descendent of *Gattenpleura* and characterised by simplification of conch and ornament. The origin of *Gattenpleura* remains unclear.

## Stratigraphic occurrence

Species of the subfamily Gattendorfiinae are known from strata of the Early and Middle Tournaisian. *Gattendorfia*, *Gattenpleura* and *Hasselbachia* are restricted to the Early Tournaisian, while *Zadelsdorfia*, *Weyerella* and *Kazakhstania* also extend from the Early Tournaisian into the Middle Tournaisian.

### Geographic occurrence

Species of the Gattendorfiinae are nearly global in distribution; they have been described from the Rhenish Mountains (Schmidt 1924, 1925; Vöhringer 1960; Korn 1994, 2006; Becker 1997; Korn & Weyer 2003; Korn & Vöhringer 2004; Becker et al. 2021), Thuringian Mountains (Schindewolf 1924, 1926a, 1952; Pfeiffer 1954; Weyer 1976, 1977; Bartzsch & Weyer 1982, 1986, 1987, 1988a, 1988b, 1996), Upper Franconia (Münster 1839b; Schindewolf 1923), Silesia (Weyer 1965; Dzik 1997), the Carnic Alps (Korn 1992b; Schönlaub et al. 1992), the Montagne Noire (Korn & Feist 2007). They are also known from Anti-Atlas (Korn et al. 2002; Bockwinkel & Ebbighausen 2006; Ebbighausen & Bockwinkel 2007), western Algeria (Conrad 1984; Ebbighausen et al. 2004), the South Urals (Popov 1975; Popov & Kusina 1997), Karaganda (Librovitch 1940) and Mongolia (Kusina & Lazarev 1994). In China they were described from Xinjiang (Sheng 1984; Ruan 1995), Tibet (Liang 1976) as well as Guizhou (Ruan 1981) and in the United States from Montana (Gordon 1986), New Mexico (Gordon 1986), Iowa (Furnish & Manger 1973), Indiana (Smith 1903; Gutschick & Treckman 1957), Kentucky (Work & Mason 2005, 2009), Michigan (Miller & Garner 1955), Missouri (Miller & Collinson 1951) and Ohio (Smith 1903; Manger 1971).

Genus Gattendorfia Schindewolf, 1920

# Type species

Goniatites subinvolutus Münster, 1839, p. 23; original designation.

# **Diagnosis**

Genus of the Gattendorfiinae with discoidal to pachyconic conchs with low to moderately high coiling rate (WER = 1.50–1.90); inner whorls subevolute to evolute, adult stage subevolute to evolute. Ornament with convex or slightly biconvex, rursiradiate growth lines, shell with or without constrictions. Suture line with deep, lanceolate external lobe; adventive lobe usually symmetric.

## **Genus composition**

Central Europe (Münster 1839b; Schindewolf 1924, 1952; Vöhringer 1960): *Goniatites subinvolutus* Münster, 1839; *Gattendorfia ventroplana* Schindewolf, 1924 [synonym of *Gattendorfia subinvoluta*]; *Gattendorfia tenuis* Schindewolf, 1952; *Gattendorfia costata* Vöhringer, 1960; *Gattendorfia rhenana* 

Korn & Weyer, 2023; *Gattendorfia bella* Korn & Weyer, 2023; *Gattendorfia valdevoluta* Korn & Weyer, 2023; *Gattendorfia schmidti* Korn & Weyer, 2023; *Gattendorfia corpulenta* Korn & Weyer, 2023; *Gattendorfia immodica* Korn & Weyer, 2023.

#### Remarks

Gattendorfia and Zadelsdorfia are closely related genera and it is not easy to separate them clearly. This is mainly because the ontogeny of many species is poorly known. Both genera contain species that have a more or less widely opened umbilicus even in the adult stage. The juvenile and preadult stages are usually evolute, while the uw/dm ratio can range between 0.20 and 0.50 in the adult stage among the species. The species of Gattendorfia and Zadelsdorfia can be subdivided into different groups with their characteristics such as conch shape (slender – stout), adult umbilical width (low – high), shape of the umbilical margin (rounded – subangular – angular), shell constrictions (absent – convex – concavoconvex) and growth lines (fine – lamellar). There is no obvious covariation of these characters. It is easiest to group the species according to the ww/dm and uw/dm ratios in the adult stage:

- (1) Forms with discoidal conch shape and moderately wide umbilicus in the adult stage: *G. subinvoluta*, *G. rhenana*, *G. schmidti*.
- (2) Forms with discoidal conch shape and wide umbilicus in the adult stage: G. bella, G. valdevoluta.
- (3) Forms with pachyconic conch shape and wide umbilicus in the adult stage: G. costata, G. immodica.
- (4) Forms with pachyconic to globular conch shape and moderately wide umbilicus in the adult stage: *Z. crassa*, *Z. oblita*.

The genus *Zadelsdorfia* was proposed by Weyer (1972) with the type species *Gattendorfia asiatica* Librovitch, 1940; it was introduced to include gattendorfiid ammonoids with a pouched external lobe. At the time it seemed to be restricted to the Middle Tournaisian, but in the meantime it has been demonstrated that Early Tournaisian species, among them *G. crassa* and several North African species, also possess a pouched external lobe (Korn 1994; Bockwinkel & Ebbighausen 2006; Ebbighausen & Bockwinkel 2007).

Korn & Feist (2007) regarded *Zadelsdorfia* as a junior synonym of *Gattendorfia*. However, it appears to be justified to separate the two genera on the basis of the shape of the external lobe (lanceolate in *Gattendorfia* but pouched in *Zadelsdorfia*) and the conch ontogeny (*Gattendorfia* has a widely umbilicate conch in adulthood, while in *Zadelsdorfia* the umbilicus is narrow in the adult stage). Furthermore, the adventive lobe tends to be asymmetric in *Zadelsdorfia*, while it is almost symmetric in *Gattendorfia*.

Bockwinkel & Ebbighausen (2006) separated the group of "Gattendorfia molaris" as an independent genus Weyerella. Gattendorfia differs from Weyerella primarily in the size of the conch, which in Gattendorfia reaches more than 50 mm diameter, while conchs of Weyerella usually do not exceed 25 mm. Another distinguishing feature is the width of the umbilicus in the juvenile stage; in Gattendorfia the umbilicus is very wide (> 0.55 of the diameter), whereas the uw/dm ratio in Weyerella only reaches a maximum of 0.50. According to Bockwinkel & Ebbighausen (2006), "Weyerella differs from typical Gattendorfia in the mode of umbilicus, closing with an overlap of the whorls over the preceding and in the platyconic conch shape of the adult conch."

*Gattendorfia subinvoluta* (Münster, 1839) Fig. 25; Table 16

Goniatites subinvolutus Münster, 1839: 23, pl. 17 fig. 2. Gattendorfia ventroplana Schindewolf, 1924: 105.

*Goniatites subinvolutus* – Gümbel 1862: 305, pl. 5 fig. 36. *Sporadoceras subinvolutum* – Frech 1902: 82, pl. 3 fig. 17.

*Gattendorfia subinvoluta* — Schindewolf 1923: 409, pl. 16 figs 9–10, text-fig. 14a–c; 1952: 295, text-fig. 15. — Schmidt 1929: 62, pl. 15 figs 12–13. — Librovitch 1940: pl. 3 fig. 5. — Miller & Collinson 1951: 467, pl. 69 fig. 18. — Pareyn 1961: 68, text-fig. 2a. — Bartzsch & Weyer 1982: 18, text-fig. 3. — Kullmann 1983: 234, text-fig. 2d. — Korn 1992b: pl. 1 figs 17–18, pl. 2 figs. 25, 28–29; 1994: 71, text-fig. 64a–c. — Schönlaub *et al.* 1992: pl. 4 figs 17–18, pl. 5 figs 25, 28–29.

non *Gattendorfia subinvoluta* — Schmidt 1924: 151, pl. 8 figs 7—8; 1925: 535, pl. 19 fig. 8. — Vöhringer 1960: 151, pl. 5 fig. 5, text-figs 26, 35. — Ruan 1981: 82, pl. 19 figs 20—22. — Korn 1994: 71, text-figs. 65a, 66a, 67c, 68c; 2006: text-fig. 3j. — Luppold *et al.* 1994: text-fig. 15b. — Korn & Feist 2007: 107, text-fig. 6e, g — Korn & Weyer 2003: 100, pl. 2 figs. 10—11, text-fig. 14g. — Kullmann 2009: text-fig. 3.1.

## **Diagnosis**

Species of *Gattendorfia* with a conch reaching 90 mm diameter. Conch at 80 mm dm thinly discoidal, subevolute (ww/dm  $\sim 0.40$ ; uw/dm  $\sim 0.40$ ). Whorl profile in the juvenile stage trapezoidal, at 80 mm dm weakly depressed (ww/wh  $\sim 1.10$ ); coiling rate low (WER  $\sim 1.70$ ). Venter broadly rounded, umbilical margin narrowly rounded. Growth lines lamellar, wide-standing, with convex course; with short ribs on the umbilical margin. Without constrictions on the shell surface; without internal shell thickenings.

#### Material examined

## Holotype

GERMANY • 1 specimen; Upper Franconia, 400 m north-west of Kirchgattendorf; Münster Coll.; illustrated by Münster (1839b: pl. 17 fig. 1) and Korn (1994: text-fig. 56g), re-illustrated here in Fig. 25A; SNSB BSPG AS VII 30.

## Additional material

GERMANY • 1 specimen; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("Gattendorfia Limestone"); Schindewolf 1916 Coll.; MBG 3118 • 1 specimen; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("Gattendorfia Limestone"); MB.C.8015 • 1 specimen; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21c-d ("Gattendorfia Limestone"); Korn 1989 Coll.; MB.C.31285 • 1 specimen; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("Gattendorfia Limestone"); Schindewolf 1916 Coll.; SMF Mbg.3119.

## **Description**

Holotype SNSB BSPG AS VII 30 is a rather poorly preserved specimen with 80 mm conch diameter; although it allows the study of the conch form; it is strongly weathered without preserved shell remains (Fig. 25A). The conch is thinly discoidal and subevolute (ww/dm=0.38; uw/dm=0.37) and it can be assumed from a view into the umbilicus that the penultimate whorl had a similar shape. No constrictions are visible on the internal mould.

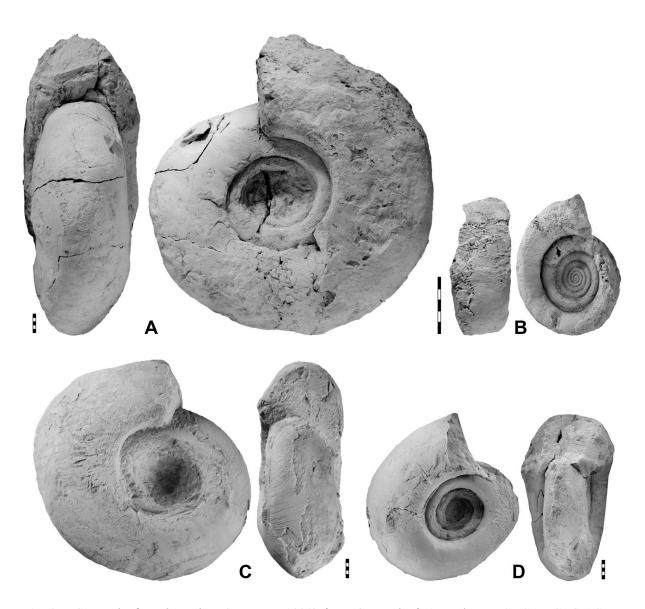
Specimen MB.C.8015 suffered from the very unprofessional earlier preparation in which the umbilicus and inner whorls were badly damaged (Fig. 25C). However, the specimen, which, at 60 mm conch diameter, has conch parameters very similar to the holotype, shows some areas of the shell surface with preserved ornament. This consists of lamellar, widely spaced growth lines extending with a backward direction across the flank and forming a broad, deep sinus on the venter. The specimen lacks constrictions.

Specimen SMF Mbg.3118 has a diameter of about 45 mm and is strongly deformed, especially near the aperture (Fig. 25D). It shows lamellar growth lines directed backwards on the flank.

The holotype of "G. ventroplana" (MBG3119) is a corroded specimen that has grown to 12 mm in diameter with seven whorls (Fig. 25B). The conch is serpenticonic and very evolute (uw/dm  $\sim 0.55$ ) with a broad, rounded-trapezoidal whorl profile (ww/wh  $\sim 1.70$ ). The venter is flattened and separated from the flanks and umbilical wall by a rounded shoulder. The specimen does not bear any shell remains. The internal form, however, has three moderately deep constrictions per whorl; these run rursiradiate immediately from the umbilicus and form a shallow ventral sinus. There are three of these constrictions on each of the last and penultimate whorls; they are spaced at intervals greater than 90 degrees.

#### Remarks

The name *Gattendorfia subinvoluta* has long been used to unite material with quite widely varying morphology. Vöhringer (1960) and subsequently Korn (1994) classified specimens from the lower



**Fig. 25.** *Gattendorfia subinvoluta* (Münster, 1839) from Gattendorf. **A.** Holotype SNSB BSPG AS VII 30 (Münster Coll.). **B.** Holotype of "*Gattendorfia ventroplana* Schindewolf, 1923" SMF Mbg.3119 (Schindewolf 1916 Coll.). **C.** Specimen MB.C.8015. **D.** Specimen SMF Mbg.3118 (Schindewolf 1916 Coll.). Scale bar units=1 mm.

**Table 16.** Conch measurements, ratios and rates of *Gattendorfia subinvoluta* (Münster, 1839) from Gattendorf

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
SNSB BSPG AS VII 30	80.2	30.3	27.3	30.0	19.1	0.38	1.11	0.37	1.72	0.30
SNSB BSPG AS VII 30	61.2	25.7	21.3	25.2	_	0.42	1.21	0.41	_	_
MB.C.8015	60.6	23.6	23.2	23.5	_	0.39	1.02	0.39	_	_
SMF Mbg.3118	44.7	26.6	18.0	16.4	12.6	0.60	1.48	0.37	1.94	0.30
SMF Mbg.3119	12.2	5.2	3.1	6.7	2.8	0.43	1.68	0.55	1.70	0.09
SMF Mbg.3119	9.1	4.3	2.0	5.4	_	0.47	2.09	0.59	_	_

part of the Hangenberg Limestone of Oberrödinghausen as *G. subinvoluta*; however, these are clearly distinguished from *G. subinvoluta* by their fine shell constrictions and the broader conch. They were described as the new species *G. rhenana* by Korn & Weyer (2023).

*Gattendorfia subinvoluta* can be easily distinguished from most of the other species of the genus by the absence of shell constrictions. Another species without constrictions is *G. costata*, but this species has a much broader, pachyconic conch.

The species of *Gattendorfia* described by Bockwinkel & Ebbighausen (2006) and Ebbighausen & Bockwinkel (2007) from the Anti-Atlas do not possess shell constrictions, however, all are considerably more narrowly umbilicate and have a wider adult conch.

Schindewolf (1923) initially regarded the single specimen MBG.3319 as inner whorls of *Gattendorfia subinvoluta*; a year later he named the new species *G. ventroplana*. Thereafter, the species was almost always regarded as a younger synonym of *G. subinvoluta* (Vöhringer 1960; Korn 1994). Unfortunately, the larger specimens of the species do not provide any insight into the inner whorls, so that it cannot be clarified completely whether the specimen of *G. ventroplana*, which is only 12 mm in size, is merely the juvenile stage of *G. subinvoluta*.

## Genus Gattenpleura Weyer, 1976

### Type species

Gattenpleura bartzschi Weyer, 1976, p. 846; original designation.

## **Diagnosis**

Genus of the Gattendorfiinae with a discoidal conch with low coiling rate (WER=1.50–1.75); inner whorls subevolute or evolute, adult stage subinvolute to subevolute. Whorl profile with a depression on the inner flank, umbilical margin raised. Ornament with convex or slightly biconvex, rursiradiate growth lines, shell with or without constrictions. Some species with shallow radial riblets. Suture line with deep, lanceolate or narrowly V-shaped external lobe (as deep as the adventive lobe).

#### **Genus composition**

Gattenpleura bartzschi Weyer, 1976; Gattenpleura pfeifferi Weyer, 1976; Gattendorfia concava Vöhringer, 1960.

## Remarks

*Gattenpleura* was established by Weyer (1976) for forms that differ from *Gattendorfia* in two characters, namely the dorsolateral groove and the presence of riblet-like, splitting radial folds on the shell. Here, we

change this original definition in such a way that the dorsolateral groove is regarded as a key distinguishing character from *Gattendorfia* and especially from *Weyerella*. This means that "*Gattendorfia concava*" is also assigned to *Gattenpleura*. Weyer (1976) had already pointed out the close relationship; according to this, "*Gattendorfia concava*" should be an almost direct ancestor of both "*Gattendorfia molaris*" and the two newly described species of *Gattenpleura*.

# Gattenpleura pfeifferi Weyer, 1976 Fig. 26; Table 17

Gattenpleura pfeifferi Weyer, 1976: 848, pl. 3 figs 1–7, text-figs 6–8.

Gattenpleura pfeifferi – Weyer 1979: pl. 5 fig. 12. — Bartzsch & Weyer 1988: 44, text-fig. 3, photo 5.

## **Diagnosis**

Species of *Gattenpleura* with thinly discoidal and involute conch at 30 mm dm (ww/dm  $\sim$  0.40; uw/dm  $\sim$  0.03). Whorl profile weakly depressed (ww/wh  $\sim$  0.75); coiling rate low (WER  $\sim$  1.60). Shallow lateral spiral groove, weak ribs with rursiradiate direction and convex course on the flank.

## **Material examined**

#### Holotype

GERMANY • Thuringia, Saalfeld-Obernitz, Pfaffenberg; bed 2 ("*Gattendorfia* Limestone"); Bartzsch Coll.; illustrated by Weyer (1976: pl. 3 figs 1–7); MB.C.764.1.

#### Additional material

GERMANY • 1 specimen; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("*Gattendorfia* Limestone"); Denckmann 1912 Coll.; MB.C.765 • 1 specimen; Upper Franconia, 400 m north-west of Kirchgattendorf; bed 21 ("*Gattendorfia* Limestone"); Schindewolf 1934 Coll.; BGRB X13404.

## **Description**

Specimen MB.C.765 is a somewhat deformed but otherwise relatively well-preserved conch with a diameter of 32 mm (Fig. 26A). It is thinly discoidal with an almost closed umbilicus (ww/dm=0.39; uw/dm=0.03) and has a low coiling rate (WER=1.61). The whorl profile shows an evenly rounded venter and almost parallel flanks with a shallow depression on the inner flank near the umbilicus caused by a shallow longitudinal groove. The umbilical margin is slightly raised.



**Fig. 26.** *Gattenpleura pfeifferi* Weyer, 1976 from Gattendorf, bed 21. **A.** Specimen MB.C.765 (Denckmann 1912 Coll.). **B.** Specimen BGRB X13404 (Schindewolf 1934 Coll.). Scale bar units=1 mm.

**Table 17.** Conch measurements, ratios and rates of *Gattenpleura pfeifferi* Weyer, 1976 from Gattendorf.

specimen	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
MB.C.765	32.2	12.7	17.1	1.1	6.8	0.39	0.74	0.03	1.61	0.60
MB.C.765	25.1	11.1	13.8	0.9	_	0.44	0.81	0.03	_	_
BGRB X13404	20.2	10.5	10.3	1.4	4.5	0.52	1.02	0.07	1.65	0.57

The ornament shows a change on the last whorl. Initially, only sharp growth lines are visible, but at about 24 mm conch diameter, flat, rounded plications appear, which become coarser on the second half of the last whorl. Their course is first radial from the umbilicus and they bend strongly backwards on the inner flank to form a rather narrow ventral sinus. On the venter the ribs are weaker than on the outer flank. Between the ribs and on the ribs stand sharp, dense growth lines.

The smaller specimen BGRB X13404 (Fig. 26B) is 20 mm in diameter and is stouter with a slightly wider umbilicus (ww/dm=0.52; uw/dm=0.07) than in specimen MB.C.765; however, this can be explained by ontogenetic changes. It also shows incipient radial plications and a weaker dorsolateral depression.

#### Remarks

Gattenpleura pfeifferi differs from G. bartzschi in the much narrower umbilicus (uw/dm  $\sim$  0.25) and less pronounced dorsolateral depression. The other similar species is Weyerella concava, which has a very similar conch form; however, this species has no ribs.

## Discussion

Gattendorf in Upper Franconia is the name-giving locality for the earliest Tournaisian (Early Carboniferous) *Gattendorfia* Stufe of the ammonoid stratigraphy used earlier in Germany, and the old abandoned marble quarry is one of the classic Carboniferous ammonoid sites.

The Gattendorf ammonoid assemblage is composed of prionoceratid ammonoids of the species *Mimimitoceras*, *Paragattendorfia*, *Stockumites*, *Acutimitoceras*, *Gattendorfia* and *Gattenpleura*. Except for *Stockumites* with seven or eight species in the assemblage, all genera are represented by only one species.

The new species *Stockumites hofensis* sp. nov. and *S. nonaginta* sp. nov. are described. The two problematic species "*Gattendorfia involuta*" and *Paragattendorfia humilis* are revised based on type material; while the first of these must remain problematic and is tentatively attributed to *Stockumites*, the second is described by a better-preserved specimen.

The composition speaks for a stratigraphic attribution to the Devonian–Carboniferous boundary and the earliest Carboniferous *Acutimitoceras acutum* Zone, but it is probable that the samples from Gattendorf also contain latest Devonian elements.

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