RESEARCH PAPER

Upper Frasnian Tornoceratidae (Ammonoidea) from the Sand Formation (Bergisch Gladbach-Paffrath Syncline, Rhenish Massif)

Till Söte[1] · Ralph Thomas Becker[1] · Karl Josef Herd[2] · Jürgen Bockwinkel[3]

Abstract

Excavations in the Sand district of Bergisch Gladbach (Rhenish Massif, Germany) yielded a rich ammonoid fauna of the upper Frasnian "*Archoceras*" *varicosum* Zone (Upper Devonian I-K, interval between the two Kellwasser levels). The previously unknown assemblages include six tornoceratid genera with 20 species, including seven new species (*Aulatornoceras steinhauseni* sp. nov., *Aul. frenklerae* sp. nov., *Aul. ventrosulcatum* sp. nov., *Crassotornoceras nudum* sp. nov., *Cr. hetzeneggeri* sp. nov., *Retrotornoceras juxi* sp. nov., *Tornoceras aequilobum* sp. nov.) and taxa described in open nomenclature. There are five associated gephuroceratid genera with nine species. The unexpectedly high genus- and species-level diversity at Sand, supported by statistical indices, is unprecedented compared to other contemporaneous ammonoid faunas. It highlights the currently fragmentary knowledge of top-Frasnian ammonoid faunas on a global scale. *Phoenixites frechi*, the dominant tornoceratid of hypoxic and organic-rich Kellwasser facies of Europe and North Africa, is completely missing at Sand. The local assemblage structure is analyzed statistically and interpreted in terms of palaeoecology. The occurrence of a new type of "Housean Pits", probably caused by parasitism, is found in nine species of five genera, mostly in tornoceratids. The Sand fauna indicates that the species origination rate in tornoceratids remained high after the Lower Kellwasser Event.

Keywords Ammonoidea · Goniatitida · Upper Devonian · Frasnian · Rhenish Massif · Kellwasser Crisis

Introduction

The upper Frasnian Kellwasser Crisis was a 1st order global extinction event (e.g., Raup and Sepkoski 1982; Schindler 1990; Racki 2005; De Vleeschouwer et al. 2017; Carmichael et al. 2019), which was especially severe in pelagic organism groups, and notably in ammonoids (e.g., Becker 1993a, b; Becker and House 1993, 1994). Whilst the order Agoniatida (suborder Gephuroceratina) was wiped out completely, five lineages of the Tornoceratidae (Goniatitida, Tornoceratina) survived. However, all groups apart from the genus *Phoenixites* (Falcitornoceratinae), the Tornoceratinae (*Tornoceras*,

Linguatornoceras, Crassotornoceras) and Aulatornoceratinae (*Aulatornoceras*), were affected to such an extent that they disappeared from the fossil record for at least five conodont zones (until the *Pa. glabra prima* Zone) and therefore representing Lazarus taxa (Flessa and Jablonski 1983; Jablonski 1986; Fara 2001; Schneider 2018).

Various authors claimed that the Kellwasser Crisis is better characterized by a significant reduction of speciation rates, rather than by elevated extinctions, leading indirectly to an absolute decrease in biodiversity (e.g., Bambach et al. 2004; Stigall 2012). In this context, the study of upper Frasnian goniatites, and especially of tornoceratids, becomes an important topic. The revision of old faunas and the description of new and partly rich assemblages enables to clarify aspects of regional and global diversity as well as the timing and patterns of extinctions, survival, and originations. Only detailed morphological comparisons can address the question of whether supposed representatives of upper Frasnian and lower Famennian taxa indeed belonged to single species or whether there was a morphological and taxonomic change in the intervening Lazarus phases.

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✉ Till Söte
  t_soet01@uni-muenster.de

[1] Institut für Geologie und Paläontologie, Westfälische Wilhelms-Universität Münster, Corrensstraße 24, 48149 Münster, Germany

[2] Am Gartenfeld 66, 51519 Odenthal-Holz, Germany

[3] Dechant-Feinstraße 22, 51375 Leverkusen, Germany

Within the Rhenish Massif, the Bergisch Gladbach-Paffrath Syncline is one of the classical areas for Devonian palaeontology and stratigraphy. It is long-known to the geological community, with earliest research dating back to the eighteenth century (Beuth 1776; Schröter 1777). However, even today substantial gaps of knowledge exist and require ongoing palaeontological research. One of these gaps is the long neglected goniatite fauna of the upper Frasnian Sand Formation. Some specimens have been briefly mentioned in the past but without any taxonomic investigation or documentation (e.g., Jux 1967). Mostly based on unpublished collections by KJH, HF, and HS, we present a comprehensive survey of the rich and unexpectedly diverse Sand ammonoid fauna, with a focus on the tornoceratids. The results of our study provide a first step towards an understanding of upper Frasnian tornoceratid diversity, extinction, and origination rates. Future steps will concentrate on further unpublished faunas from the eastern Rhenish Massif (e.g., Martenberg), the Eifel Mountains (Büdesheim), and Morocco (Dra Valley, Tafilalt/Maider regions, Meseta).

Abbreviations Ammonoids—"*Arch.*" = "*Archoceras*", *Aul.* = *Aulatornoceras*, *Cr.* = *Crassotornoceras*, *Crick.* = *Crickites*, *G.* = *Goniatites*, *Lob.* = *Lobotornoceras*, *Ling.* = *Linguatornoceras*, *M.* = *Manticoceras*, *Ph.* = *Phoenixites*, *Retro.* = *Retrotornoceras*, *Serra.* = *Serramanticoceras*, *Sphaero.* = *Sphaeromanticoceras*, *T.* = *Tornoceras*, UD = Upper Devonian, with the ammonoid zonal key of Becker and House (2000a); Conodonts—*A.* = *Ancyrognathus*, *Pa.* = *Palmatolepis*, *Po.* = *Polygnathus*.

Studied section

The investigated locality is situated at the Herkenrather Straße 70 in the Bergisch Gladbach-Sand district (topographic sheet 5009 Overath; GPS 50° 59′ 18.1″ N, 7° 09′ 40.9″ E). This area belongs to the Bergisch Gladbach-Paffrath Syncline and lies just E of the Rhine river. During short times in 2003, 2009, 2012 and 2013, excavations for the construction of a supermarket and for an enlargement of its parking lots opened several outcrops of the Sand Formation (Fig. 1). Weber et al. (2013) provided an overview of the fauna collected there. The younger excavations yielded most of the goniatite fauna investigated herein. There is no detailed section log since intensive tectonics (variable strike directions) hindered a simple stratigraphic correlation (Weber et al. 2013). Goniatites come from five of the six collecting sites named as Sand 1 to 5 and Sand A (Fig. 1). The occurrences of individual taxa at each spot are marked in Table 1. Based on the overall dip in the Bergisch Gladbach-Paffrath Syncline, the more northern collecting spot (Sand 4) should be slightly older than the middle and more southern spots (Sand 3A to 3C and Sand A). In autumn 2019, two laminated marly limestone beds from just S of Sand A were sampled for conodonts. Apart from isolated specimens of *Po. alatus*, *Pa. hassi*, and *A. triangularis*, the samples lacked conodonts. The associated microfauna is rich in entomozoid ostracods, including *Entomozoe* (*Nehdentomis*) *pseudorichterina*. However, there are no forms with concentric ornament that could provide a precise placing in the very detailed upper Frasnian entomozoid zonation. Additionally, the samples yielded orthoconic cephalopods and some juvenile ammonoids.

Rare goniatites of the Sand Formation occur at six other localities: (1) The type locality of the formation at forested streams between Halfen-Dombach and Plätz, ca. 700 m W of the Herkenrather Straße 70. (2) E of Breite, at a forested stream ca. 1.3 km E of the Herkenrather Straße 70. (3) SW of Wesselsteinbach, at forested streams between Sand and Herkenrath. (4) At the escarpment of the Lerbach brook W of Kaltenbroich and ca. 800 m SSE of the Herkenrather Straße 70. (5) At the former construction site at Herkenrather Straße 59–61, directly opposite of Herkenrather Straße 70. (6) At the base of the Kreishaus section ca. 2.4 km SW of the Herkenrather Straße 70.

The only currently accessible collecting spot is locality 4 at the Lerbach brook. Isolated specimens that cannot be placed in the new succession are listed in Table 1 in the "+" column.

Research history

Fliegel (1923: 379) was the first to recognize a separate "Mergelschiefer-Stufe" on top of the Hombach Formation, a unit which is roughly correlatable with the Sand Formation. The term "Sander Schichten" was coined much later by Jux and Groos (1967) for sandy and marly shales, including 5–10 m thick, black, bituminous, calcareous "Kellwasser shales" at the top. In the same year, Jux (1967) described the dendroid graptolite *?Palaeodictyota montana* (see Hartkopf-Fröder and Weber 2016 for a paratype) from the Sand Formation and mentioned the occurrence of several goniatites belonging to *Tornoceras* and *Manticoceras*. Despite a focus on the overlying, lower Famennian Knoppenbissen Formation, Jux and Krath (1974) noticed several fossil groups (e.g., tentaculitoids, ostracods, goniatites, bivalves, and crinoids) and bitumen-bearing calcareous geodes in the Sand Formation. In the annotations to the geological map of sheet Overath, Jux (1982) provided a useful overview of the latter. Jux (1984) focused on acritarch communities in the Bergisch Gladbach area and recognized a diversity peak (more than 40 species) in the Sand Formation. Amirie (1984, 1989) also reported acritarch populations, dominated by baltisphaerids. Queins (1988) studied tentaculitoids and
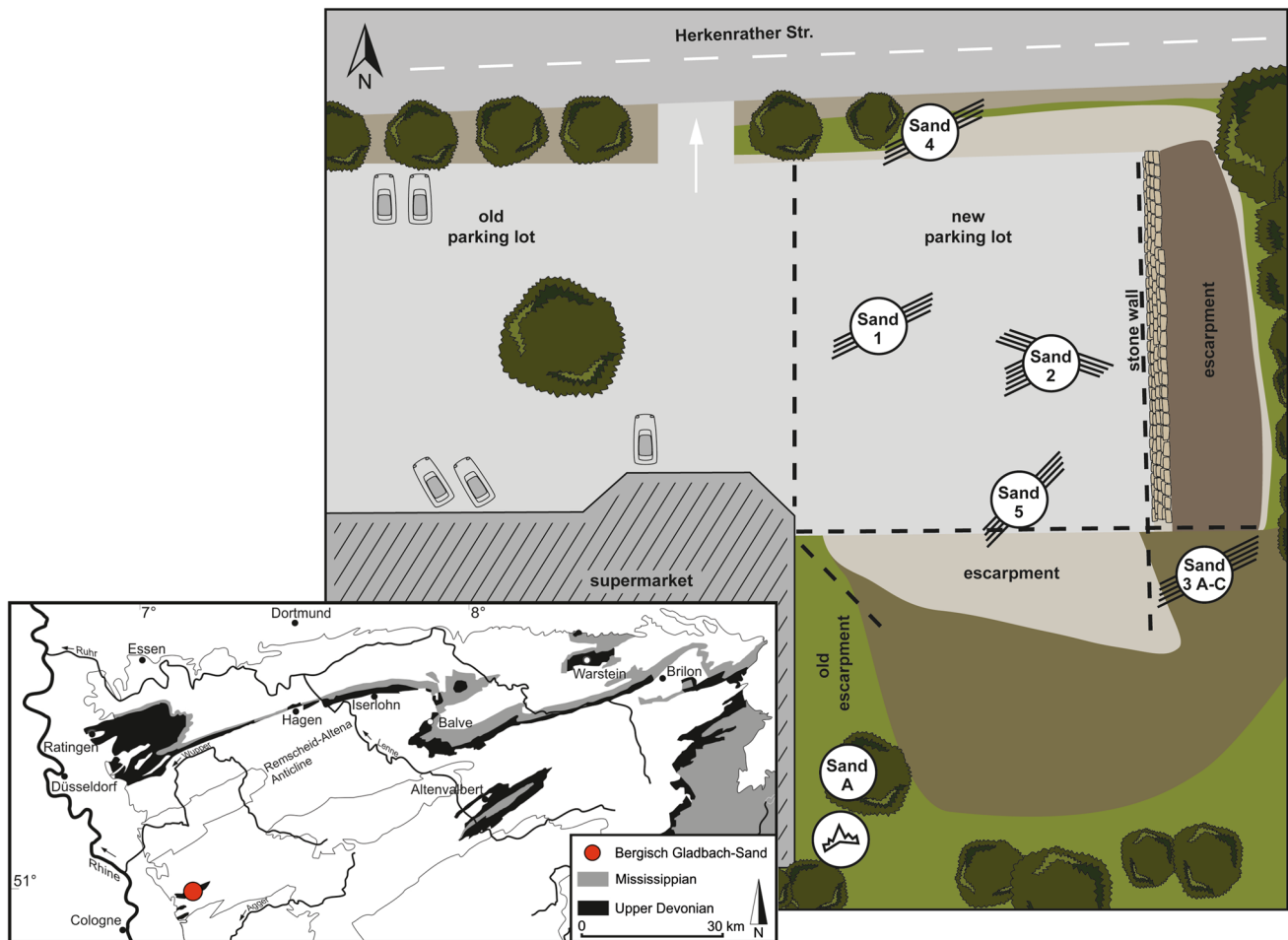
Fig. 1 Collecting spots of goniatites and conodont samples in the Sand Formation of Bergisch Gladbach-Sand (Herkenrather Straße 70: small-scale map of the supermarket and new parking lots) in the frame of the geological map of the northern Rhenish Massif. The general dip of the Bergisch Gladbach-Paffrath Syncline is to the SSE, with the oldest collecting spots in the NNW

Kleinebrinker (1992) conodonts and the coalification of the Devonian of Bergisch Gladbach. An unpublished field trip guidebook by Jux (1991) also describes the Sand Formation and includes a correlation with the top-Frasnian Upper Kellwasser beds. Three summaries of the Sand Formation and of the Bergisch Gladbach-Paffrath Syncline, in general, were published by Hartkopf-Fröder et al. (2004), Jux (2008), and Ribbert (2012). Hartkopf-Fröder et al. (2004) provided a regional geological map. Korn et al. (2013) described goniatites from Büdesheim (Eifel) but also mentioned one specimen of "*Archoceras*" from Sand (leg. KJH; specimen MB.C.29344). Most recently, Hartkopf-Fröder and Weber (2016) outlined the palaeogeographical and facies evolution of the Bergisch Gladbach-Paffrath Syncline, which included data on the Sand Formation.

Stratigraphy and facies

According to Piecha (2004), the approximately 30 m thick Sand Formation ranges from the *Pa. jamieae* to the upper *Pa. linguiformis* Zone. The conodont evidence is, however, weak. Kleinebrinker (1992) recorded *Pa. foliacea, Pa. gigas*, and the long-ranging *Po. webbi*. The first species enters high in the *Pa. feisti* Zone (upper MN Zone 11 sensu Klapper 1989) and ranges to the base of the *Pa. bogartensis* Zone (basal MN Zone 13a, Klapper and Kirchgasser 2016). The second refers to a junior synonym of *Pa. winchelli* (or *Pa. subrecta*), which ranges from the base of the *Pa. winchelli* Zone (base MN 12 Zone) right to the Frasnian–Famennian boundary. Our new samples add *Pa. hassi, A. triangularis,* and *Po. alatus* to the conodont faunal list. The first ranges from higher parts of the middle to the top of the Frasnian, the second characterizes

Table 1 Species list of the 11 goniatite genera and 30 species recorded so far from Bergisch Gladbach-Sand (with references to figured representatives of taxa that are not treated in the systematic chapter) and occurrences of taxa at the individual collecting spots

Tornoceratoidea	4	1	2	3	3A	3B	3C	A	+	Σ
Aulatornoceras auris (Quenstedt, 1846)	–	5	–	–	–	–	–	1	–	6
Aulatornoceras constrictum (Steininger, 1849)	–	–	–	–	–	–	–	6	–	6
Aulatornoceras aff. *constrictum* (Steininger, 1849)	–	1	–	–	–	–	–	–	–	1
Aulatornoceras eifliense (Steininger, 1849)	–	–	–	1	–	–	–	4	3	8
Aulatornoceras steinhauseni sp. nov.	–	4	–	–	–	–	–	–	–	4
Aulatornoceras frenklerae sp. nov.	1	–	–	–	–	2	–	1	–	4
Aulatornoceras ventrosulcatum sp. nov.	–	1	–	–	–	–	–	–	1	2
Aulatornoceras aff. *ventrosulcatum*	–	1	–	–	–	–	–	–	–	1
Aulatornoceras sp.	–	1	–	–	–	–	–	1	–	2
Crassotornoceras crassum (Matern, 1931a)	2	–	–	1	–	1	–	8	–	12
Crassotornoceras belgicum (Matern, 1931b)	–	–	–	–	1	–	1	5	2	9
Crassotornoceras aff. *belgicum* (Matern, 1931b)	–	–	–	–	–	–	–	1	–	1
Crassotornoceras nudum sp. nov.	1	–	–	–	–	–	–	3	–	4
Crassotornoceras hetzeneggeri sp. nov.	–	–	–	1	–	–	–	3	–	4
Crassotornoceras sp.	–	1	–	1	1	–	–	4	1	8
Linguatornoceras cf. *clausum* (Glenister, 1958)	1	–	–	1	–	–	–	1	–	3
Linguatornoceras linguum (Sandberger and Sandberger, 1851)	4	–	–	1	–	–	–	7	–	12
Linguatornoceras sp. 1 (Sandberger and Sandberger, 1851)								1	–	1
Lobotornoceras ausavense (Steininger, 1849)	–	–	–	2	–	–	–	1	–	3
Retrotornoceras juxi sp. nov.	1	–	–	–	–	–	–	–	–	1
Tornoceras holwilli (House, 2002)	–	–	–	3	2	2	1	3	–	11
Tornoceras aequilobum sp. nov.	2	–	–	1	–	–	–	3	–	6
Tornoceras sp.	–	–	–	1	–	1	–	–	–	2

Gephuroceratoidea	4	1	2	3	3A	3B	3C	A	+	Σ
"*Archoceras*" *varicosum* (Drevermann, 1901) (Fig. 2n, cf. Fig. 2o-p)	1	–	–	–	1	3	–	8	–	13
"*Archoceras*" sp.	–	–	–	1	1	–	–	1	–	3
Clauseniceras sp. 1 (Figs. 2q, 3a)	–	–	–	–	–	–	–	3	–	3
Manticoceras aff. *lamed* (Sandberger and Sandberger, 1851) (Fig. 3b–c)	1	–	–	–	–	5	–	6	–	12
Manticoceras cordatum (Sandberger and Sandberger, 1851) (Fig. 3d–f)	–	–	2	6	10	3	–	4	–	25
Manticoceras drevermanni Wedekind, 1913 (Fig. 3g–h)	–	–	–	–	–	–	–	–	3	3
Manticoceras sp.	2	–	–	1	7	1	–	2	1	14
Serramanticoceras serratum (Steininger, 1849) (Fig. 3l–o)	–	–	1	5	6	11	–	2	–	25
Serramanticoceras cf. *obliquesulcatum* (Clausen, 1969) (Fig. 3p)	–	–	–	–	–	1	–	–	–	1
Serramanticoceras sp.	–	–	–	1	1	1	–	–	–	3
Sphaeromanticoceras affine (Steininger, 1849) (Fig. 3i)	–	–	–	2	3	3	1	3	–	12
Sphaeromanticoceras orbiculum (Beyrich, 1837) (Fig. 3j–k)	1	–	–	3	–	3	–	–	–	7
Sphaeromanticoceras sp.	1	–	–	–	2	3	–	2	–	8

all of the upper Frasnian, and the third ranges through the complete Frasnian (e.g., Klapper 1997). Therefore, the new samples do not constrain the age of the formation and of our goniatite faunas to a discrete conodont zone. It is well possible that the Sand Formation includes all of the upper Frasnian (sensu Becker and House 1999) since the underlying Hombach Formation lacks any upper Frasnian conodonts or goniatites (Hartkopf-Fröder and Weber 2016).

The lower half of the Sand Formation differs from the underlying strata by the lack of regularly occurring limestone beds. These are replaced by greyish to brownish shales and marls including some concretionary limestone layers (Hartkopf-Fröder et al. 2004). Prominent black calcareous shales and laminated marly horizons mark the upper Sand Formation and represent the Upper Kellwasser beds (Jux and Groos 1967). The macrofauna of the Sand Formation is not abundant but diverse. It consists of inarticulate (lingulids) and articulate brachiopods, goniatites (including anaptychi), tentaculitoids (homoctenids and dacryoconarids), ostracods (mostly entomozoaceans), orthoconic cephalopods, gastropods, bivalves ("*Buchiola*" and *Guerichia*), crinoids, dendroid graptolites, trilobites, rare wood remains, and even deep-water rugose corals (e.g., Jux 2008; Weber et al. 2013). Although microfossils have been neglected, many groups are known, such as ostracods, conodonts, acritarchs, other palynomorphs, sponge spicules, and radiolarians (e.g., Jux 2008; Weber et al. 2013). Ammonoids and other molluscs are preserved as small-sized pyritic moulds, which changed during diagenesis into iron oxides, leading to a wide range of brown to bluish secondary colors. The best-preserved specimens are characterized by surrounding, white crystalline seams that have to be removed by mechanical preparation. Most levels are rich in anaptychi with preserved organic films, while large-sized goniatites are almost lacking. As an exception, there was a large fragmentary, calcareous *Manticoceras* body chamber, in which many smaller, juvenile goniatites were washed in.

In agreement with Kleinebrinker (1992), the environment during the deposition of the Sand Formation was a quiet, distal, outer shelf basin with poor ventilation. Oxygen levels were sufficient to support at least episodically the settlement of a restricted deep-water benthos assemblage. There is no evidence of any photic zone faunal elements or of storm deposition.

Based on the presence of its index species at the most northern, supposedly oldest collecting spot (Sand 4), the complete Sand goniatite fauna is assigned to the "*Archoceras*" *varicosum* Zone (Fig. 4; UD I-K sensu Becker and House 1993, 1994, 2000a). This zone starts with the Lower Kellwasser level (Fig. 4; top *Pa. winchelli* Zone or MN Zone 12, Becker et al. 1993) and ranges to a level in the lower part of the *Pa. bogartensis* Zone (lower MN Zone 13a). There is no evidence for early *Crickites* species at Sand, which define the lower part of UD I-L (*Crickites* genozone, see Fig. 4). However, *Crick. holzapfeli*, the index species of UD I-L$_2$, has been reported from the Upper Kellwasser level at the top of the Sand Formation (Jux and Krath 1974), from well above our collecting level and far from localities in Sand (Kreishaus section; see spot 6 of the other localities listed above). Based on the association with *M. drevermanni*, older collections from the Sand Formation are also assigned to the

upper Frasnian. The type-level of *M. drevermanni* is in the Upper Kellwasser Limestone of Bicken (Wedekind 1913) but relatives enter elsewhere much earlier (UD I-I in the Canning Basin, Becker and House 2009).

Ammonoid diversity and palaeoecology

The Sand goniatite fauna is characterized by a high alpha diversity (local species richness), which, on a global scale, is only rivalled by the so far incompletely documented Büdesheim Shale faunas (e.g., Clausen 1969; Korn et al. 2013). The eutrophic facies at Sand sustained an unusually diverse population, which was obviously only partially affected by the hypoxic bottom conditions. This resembles goniatite faunas from lower Famennian hypoxic goniatite shales, such as the overlying Knoppenbissen Formation (Jux and Krath 1974; Weber 2016) or from the famous Nehden Goniatite Shale of the eastern Sauerland (Becker 1993a; Becker et al. 2016).

The total number of Sand ammonoid specimens identified at the genus level is 240 and 200 at the species level. The assemblage structure is relatively evenly distributed between members of the Tornoceratoidea (46.25%) and Gephuroceratoidea (53.75%). This differs significantly from upper Frasnian oxic cephalopod limestones, where Gephuroceratoidea are much more dominant (e.g., Rhenish Massif: Wedekind 1913; Matern 1931a; House and Ziegler 1977; Montagne Noire: Becker and House 1994; Timan: Bogoslovskiy 1969; Becker et al. 2000; Rudnyi Altai: Bogoslovskiy 1969; Western Australia: Becker and House 2009). Based on the number of specimens assigned at the species level (not corrected) and on an approach of relative abundance (corrected), which includes statistical projections of specimens allocated to genera only, we calculated the Shannon diversity index (H), the Pilou's evenness (J), and the Simpson diversity index (D).

The Shannon diversity index (H) is given by the following formula (Shannon 1948; Spellerberg and Fedor 2003):

$$H = - \sum_{i=1}^{s} p_i \times \ln p_i,$$

with $p_i = \dfrac{n_i}{n}$.

For the complete Sand fauna, H varies only slightly between 3.00 (not corrected) and 2.97 (corrected), with $H_{max} = \ln(s) = 3.37$, $s =$ number of species, and $n =$ number of specimens.

The typical value of H ranges between 1.5 and 3.5 and is rarely greater than 4. Due to our alpha diversity of 29 taxa, our value of H can not exceed 3.37. However, H is
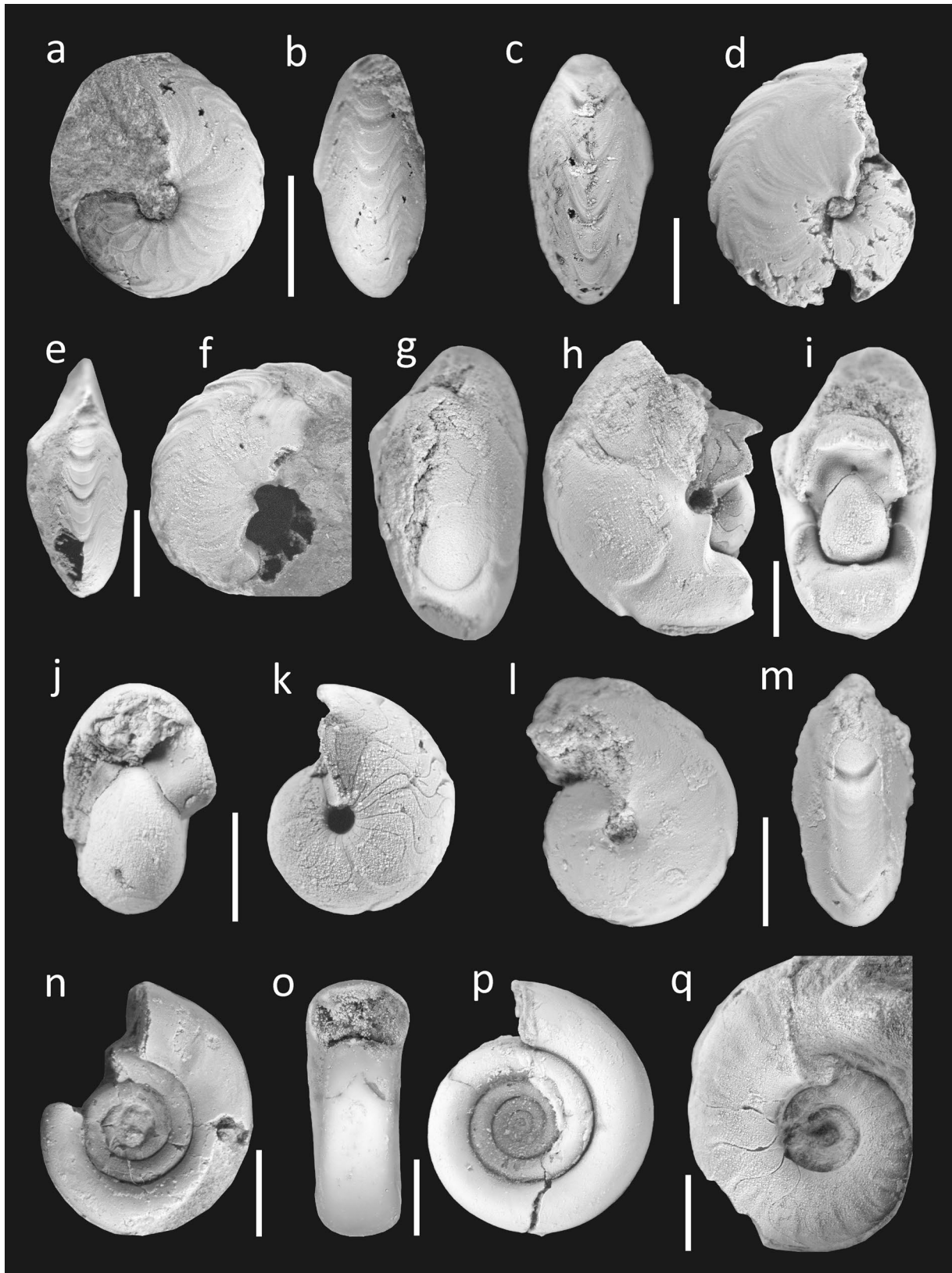
◀**Fig. 2** Tornoceratidae and Gephuroceratoidea from the upper Frasnian Sand Formation (scale bar 2 mm). **a, b** *Aulatornoceras steinhauseni* sp. nov., paratype MB.C.29356.4, showing the bundled growth ornament with high ventrolateral projection without a spiral furrow and the ventral band; lateral and ventral views, Sand 1, ×11, **c, d** *Aul. steinhauseni* sp. nov., holotype MB.C.29356.1, subadult specimen with typical growth lirae, V-shaped ventral varices, and incipient ventrolateral furrows; ventral and lateral views, Sand 1, ×8, **e, f** *Aul. steinhauseni* sp. nov., paratype MB.C.29356.3, showing the typical ornament without ventrolateral furrows; ventral and lateral views, Sand 1, ×8, **g–i** *Aul. frenklerae* sp. nov., holotype MB.C.29359, showing the typical varices, lateral and inner suture, and the late onset of incipient ventrolateral furrows; ventral, lateral and oral views, Sand A, ×7, **j, k** *Aul. frenklerae* sp. nov., paratype MB.C.29358, juvenile specimen with V-shaped A-lobe and varices, still lacking ventrolateral furrows; oral and lateral views, Sand 4, ×10, **l, m** *Aul. ventrosulcatum* sp. nov., holotype MB.C.29360, showing the typical high whorl height, shallow ventrolateral furrows, ventrally restricted varices, and weak ventral band; lateral and ventral views, Dombach-Sander-Straße, ×10, **n** "*Archoceras*" *varicosum* (Drevermann, 1901), MB.C.29345, typical specimen with varices; lateral view, Sand A, ×8, **o, p** "*Arch.*" cf. *varicosum* (Drevermann, 1901), MB.C.29344, with characteristic, simple suture but without varices; oral and lateral views, Sand A, ×7, **q** *Clauseniceras* sp. 1, MB.C.29364.1, juvenile of a new species with regular, weak, subconvex lateral ribbing and suture with subsymmetric flank saddle; lateral view, Sand A, ×7

badly usable to compare the biodiversity of different faunas, because the value of *H* does not differ between a fauna with many species and uneven distribution or less species with a more even distribution.

Therefore, the Pilou's eveness (*J*) is preferred here and better usable for comparison of different faunas. Generally, *J* describes the mass of uniform distribution between species in a given sample. It can range between 0 and 1, where 0 is the maximum uneven distribution and 1 the maximum uniform distribution. It is denoted by $J = H/H_{max}$. For the Sand goniatite fauna, it ranges between 0.89 (not corrected) and 0.88 (corrected). This is an extraordinarily high value for *J*, proving both a high ammonoid biodiversity and numerical equality of the palaeocommunity. Typically, unequal faunas with a few dominant species and a high number of rare forms are more common.

The Simpson diversity index (*D*) is given by Simpson (1949):

$$D = 1 - \sum_{i=1}^{s} \frac{n_i(n_i - 1)}{n(n - 1)}.$$

In both approaches (not corrected and corrected), *D* is around 0.94. As a measurement of biodiversity, it refers to the probability that two randomly chosen specimens from a given sample do not belong to the same species with *D* ranging between 0 and 1. For a given species richness, *D* increases as equitability increases. With a value of 0.94, the

Simpson diversity index (*D*) is exceedingly high and further underlines the high ammonoid biodiversity of the intra-Kellwasser fauna (UD I-K) of the Sand Formation.

There is so far no literature on upper Frasnian ammonoids that provides similar quantitative assemblage data and calculations that could be used for statistical comparisons. Currently, we can only compare simple species counts (alpha diversities) from known localities of the same age (UD I-K), especially, where there is evidence for intensive collecting, partly over many decades:

- Seßacker, Trench II (southern Rhenish Massif, Germany); Matern (1931a): 15 species (5 tornoceratids), Lower Kellwasser Limestone and overlying cephalopod limestones
- Alter Tal (Harz Mountains, Germany); Fuhrmann (1954): 9 species (2 tornoceratids), limestones above the Lower Kellwasser Limestone
- Waterside Cove (Cornwall, U.K.); House (2002): 19 species (9 tornoceratids), goniatite shale
- Coumiac (Montagne Noire, France); Becker and House (1994): 5 or 6 species (2 tornoceratids), Lower Kellwasser Limestone and overlying cephalopod limestones
- Oued Mzerreb (Dra Valley, Morocco); Becker et al. (2004): 2 species (0 tornoceratids), Lower Kellwasser Limestone equivalent
- Płucki (Holy Cross Mountains, Poland); Dzik (2002): 4 species (2 tornoceratids), Lower Kellwasser Limestone equivalent
- Lower Hannover Shale (New York State, USA); Miller (1938), House and Kirchgasser (2008) and new collections: 5 species (3 tornoceratids), goniatite shale
- Delphi (Indiana, USA); Miller (1938) and House and Kirchgasser (2008): 3 species (0 tornoceratids), goniatite shale

The much higher total diversity in the Sand Formation may partly reflect a larger sample size than in some of these sections. Furthermore, we use specimens from different collecting spots and not only from one single bed, which can cause an overestimation of the biodiversity. Other aspects such as potential undetected sexual dimorphism, which was, however, never verified for palaeozoic ammonoids, have to be taken into account, but can not be addressed within this study. It is, therefore, necessary to collect more quantitative data from other contemporaneous localities. These can be subject to more detailed statistical treatments, which consider sample size differences relative to variable local assemblage structures.
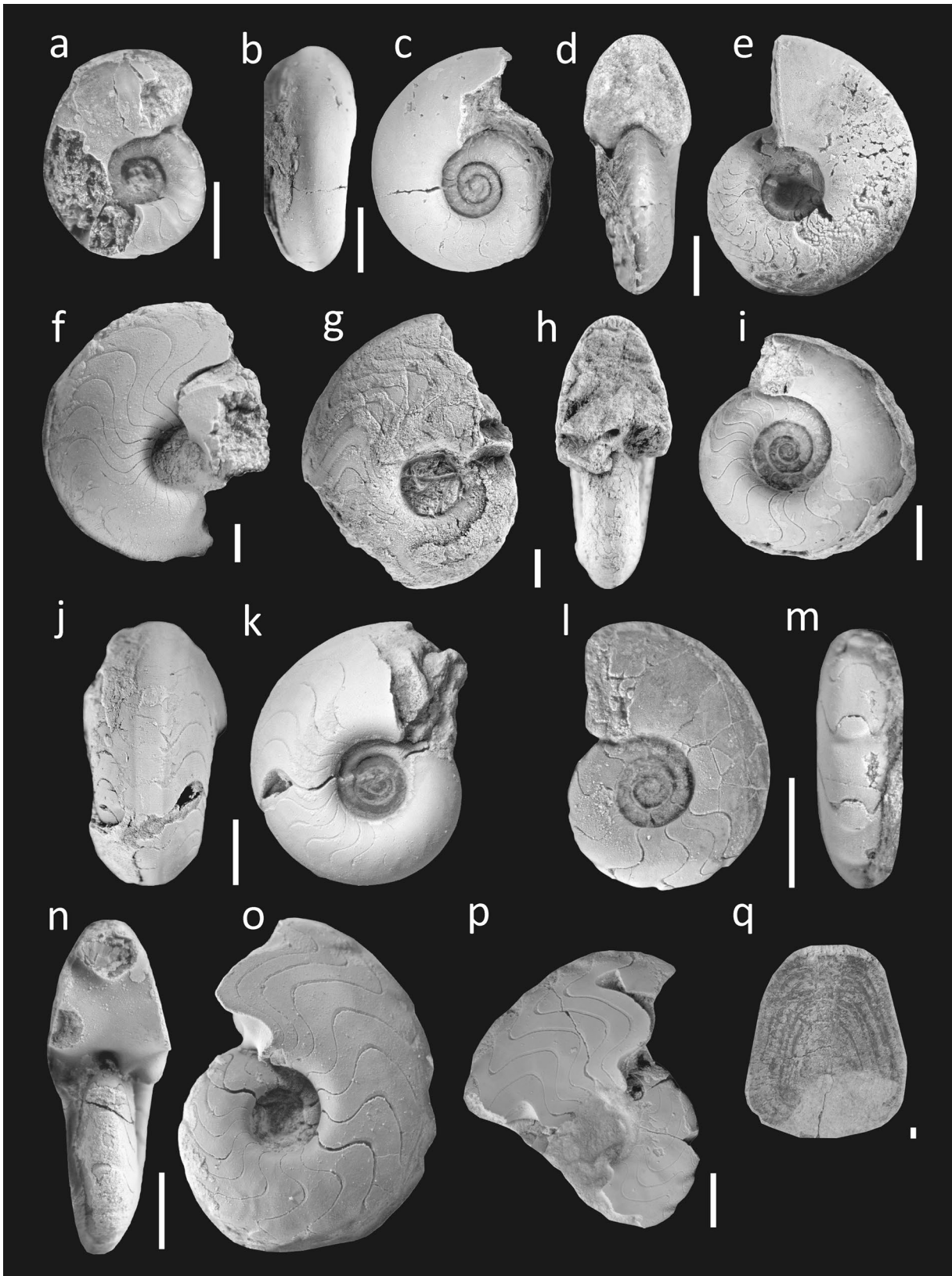
◄**Fig. 3** Examples of Gephuroceratidae from the upper Frasnian Sand Formation (scale bar 2 mm). **a** *Clauseniceras* sp. 1, MB.C.29364.2, juvenile specimen showing radial flank ribbing and typical sutures; lateral view, Sand A, ×7, **b**, **c** *Manticoceras* aff. *lamed* (Sandberger and Sandberger, 1850/51), MB.C.29389, juvenile with visible protoconch and slender cross-section; ventral and lateral views, Sand 4, ×6, **d**, **e** *M. cordatum* (Sandberger and Sandberger, 1850/51), MB.C.29391, showing the suture and tegoid whorl form; ventral and lateral views, Sand A, ×5.5, **f** *M. cordatum* (G. & F. Sandberger, 1850/51), MB.C.29390, typical specimen showing the suture with a pronounced dorsolateral saddle; lateral view, Sand 3A, ×3.5, **g–h** *M. drevermanni* Wedekind, 1913, MB.C.29392, with pointed umbilical lobe and triangular flank saddle as typical for the species; lateral and ventral views, Dombach-Sander-Straße, ×3.5, **i** *Sphaeromanticoceras affine* (Steininger, 1949), MB.C.29397, juvenile with Ritzstreifung on the mould; lateral view, Sand 3C, ×5, **j**, **k** *Sphaero. orbiculum* (Beyrich, 1837), MB.C.29398, juvenile with Ritzstreifung and keeled venter as typical for the genus; ventral and lateral, Sand 3, ×6, **l**, **m** *Serramanticoceras serratum* (Steininger, 1849), MB.C.29395, small specimen with still rounded venter and characteristic ventral varices; lateral and ventral views, Sand 3A, ×10, **n**, **o** *Serra. serratum* (Steininger, 1849), MB.C.29396, with semi-trapezoidal whorl cross section and typical suture; oral and lateral views, Sand 3B, ×6, **p** *Serra.* cf. *obliquesulcatum* (Clausen, 1969), MB.C.29394, with ventral varices extending in the early part of the last whorl onto the flanks; lateral view Sand 3, ×5, **k** Anaptychid jaw, specimen Sand3_AnaCH03, squashed, isolated lower jaw with central fractures and concentric, lamellose growth lirae; Sand 3, ×1

Interestingly, both the Tornoceratoidea and Gephuroceratoidea independently developed in UD I-K new genera (*Retrotornoceras* and "*Archoceras*") with a characteristic, simplified suture. This new feature is possibly an adaptation to ecological changes (high-productivity regime, dysoxic/anoxic conditions) due to the Lower Kellwasser Event. Simple sutures mean a reduced pellicle surface within the chambers and, therefore, probably a less efficient osmotic pump and slow vertical mobility (Mutvei 1967; Klug and Hoffmann 2015). Conveniently, the genus *Beloceras,* with its complicated, extremely multilobate sutures, is generally rare in hypoxic facies and is actually completely missing in the Sand Formation. However, "*Archoceras*" (6.6% in total, 12% of Sand Gephuroceratoidea) and *Retrotornoceras* (0.4% in total, 1% of Sand Tornoceratoidea) represent only minorities in terms of abundance (Fig. 5). Typical for a stratigraphic position above the Lower Kellwasser level is the absence at Sand of members of the Acanthoclymeniidae, oxyconic Virginoceratinae, and of Maternoceratinae (see Becker and House 1993). However, it is remarkable that the Sand fauna apparently lacks *Delphiceras*, which is a characteristic genus of hypoxic strata of UD I-K in North America, southern Morocco, the Ardennes, SW England, and the Eifel Mountains (Gatley 1983; Becker and House 1993, 2000a; House 2002; new collections).

Another intriguing palaeoecological aspect is the apparent local absence of *Ph. frechi* and of any other species of this long-ranging genus. In the upper Frasnian, it was widespread and very common in the black Kellwasser Limestone facies, especially of more shallow, hypoxic, pelagic carbonate platforms (e.g., of southern Morocco), where its streamlined, strongly compressed shell enabled it to cope with currents and storms. Though *Ph. frechi* was not the only survivor of the Upper Kellwasser Event, it represents the only species blooming enormously directly after the Frasnian–Famennian boundary (Becker 1993a, b). Therefore, it was a typical "disaster taxon" (Fischer and Arthur 1977; Harries et al. 1996). Only after the extinction (gephuroceratids) and disappearance (Aulatornoceratinae and Tornoceratinae) of other ammonoid taxa, it spread opportunistically to the post-crisis (basal Famennian) calm goniatite shale facies, for example of the Montagne Noire (Col du Puech de la Suque, Becker 1993a).

The high alpha diversity of Sand ammonoids and the high amount of new taxa shed new light on the discussion, whether the global Kellwasser Crisis does represent a major mass extinction or just a time of reduced speciation. Our new results indicate a continuing, high speciation rate in tornoceratids with and after the Lower Kellwasser Event

Stage	Formation		Ammonoid genozone	Key
Famennian	?			
	Knoppenbissen Formation (lower part)		*Praemeroceras*	UD II-E
			Paratorleyoceras	UD II-D
			Cheiloceras	UD II-C
			Compactoceras	UD II-B
			Phoenixites	UD II-A
Frasnian	Upper Kellwasser Horizon Lower		*Crickites*	UD I-L
			"*Archoceras*"	UD I-K
	Sand Formation		*Neomanticoceras*	UD I-J
			Playfordites	UD I-I
	Hombach Formation		*Beloceras*	UD I-H
	Tonschiefer Formation		*Mesobeloceras*	UD I-G

Fig. 4 Stratigraphy of the Bergisch Gladbach-Paffrath Syncline

Fig. 5 Bar plots showing the relative ammonoid abundance at genus level. **a** Relative abundance of Tornoceratoidea genera, **b** Relative abundance of Gephuroceratoidea genera
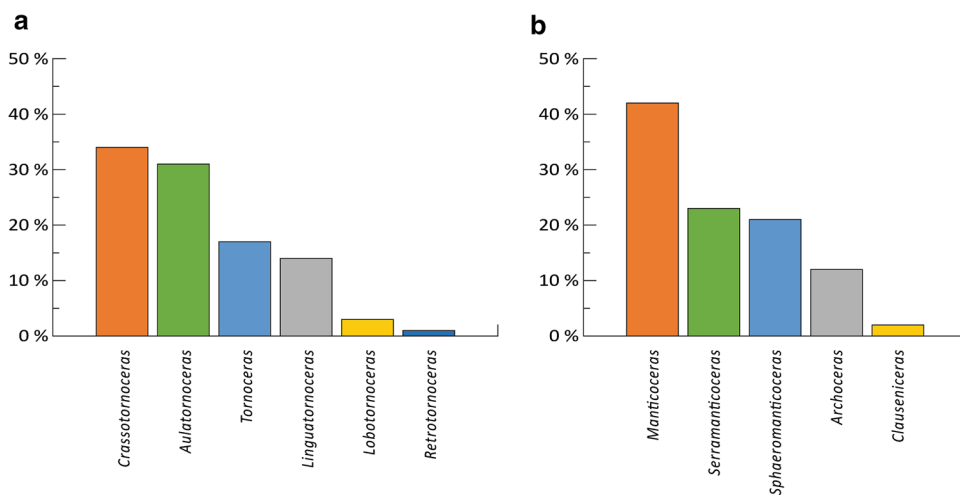
(within UD I-K). This will be further substantiated by comparisons with pre-Kellwasser faunas and with unpublished collections from other regions. The revision of Upper Kellwasser faunas (UD I-L) will eventually provide precision concerning the timing and rates of terminal Frasnian extinctions.

Internal parasitism of ammonoids

Representative specimens of five genera (*Aulatornoceras*, *Crassotornoceras*, *Linguatornoceras*, *Tornoceras* and *Clauseniceras*) of both ammonoid superfamilies display a new type of "Housean Pits" on their steinkerns. "Housean Pits" were first described by House (1960) and denote more or less regularly distributed pits on internal moulds. They occur as a result of internal parasitism (probably by trematodes), which resulted in a subsequent local thickening of the inner shell wall (De Baets et al. 2011). Most occurrences are found in Emsian and Eifelian anarcestid ammonoids, the superfamily which includes the ancestors of both the Tornoceratoidea and Gephuroceratoidea. "Housean Pits" on tornoceratids (Aulatornoceratinae) have so far only been shortly mentioned by De Baets et al. (2015). We present the first observation of "Housean Pits" on gephuroceratid ammonoids (specimen MB.C.29364.3, Pit type 6). A very rare case of "Housean Pits" has been documented in sporadoceratids from the middle Famennian of Poland (Rakocinski 2012). This group derived via the Cheiloceratoidea from tornoceratids (e.g., Becker 1993a). Furthermore, isolated blister pearls are known in Jurassic ammonoids from Germany (Keupp 1986) and blister pearl clusters are known for instance from Silurian nautiloids (Stridsberg and Turek 1997; Manda and Turek 2009; Turek and Manda 2010).

The "Housean Pits" from Bergisch Gladbach-Sand are exclusively circular and occur on the flanks in two ways.

Rarely, they appear as a few pairs (e.g., MB.C.29406.1, Fig. 6g–h), slightly resembling Pit type 4 (Opitzian pits) sensu De Baets et al. (2011) and De Baets et al. (2013). However, in the case of our *T. aequilobum* sp. nov., the paired pits are neither connected nor were they formed at the aperture. Most of the pits in Bergisch Gladbach-Sand ammonoids are more or less spirally arranged, isolated circular pits on the flanks (e.g., MB.C.29413, Fig. 6l–n). We propose a new Pit type 6 extending the nomenclature of De Baets et al. (2011). They differ from Pit type 3 by occurring not only at the end of the body chamber, with more pits per whorl, and from Pit type 2 by being larger, occurring in smaller numbers, and only in a single undulating flank row. At specimen MB.C.29413 (Fig. 6l–n) the new Pit type 6 is not formed at the end of the body chamber but at least 170° away from the last suture. Because it is not clear whether the pits occur at the aperture and since there is no observable effect on shell growth, Type 6 pits are still considered as "Housean Pits" and not as "Opitzian Pits".

The following summary extends the original scheme by De Baets et al. (2011, 2015):

- Pit type 1 (Housean Pits): fairly large oval pits, which are lengthened in a longitudinal direction, predominately ordered in large spiral rows and often paired.
- Pit type 2 (Housean Pits): multiple, small pits, arranged in more or less radial rows or more chaotically.
- Pit type 3 (Housean Pits): rare circular pits with a central deepening.
- Pit type 4 (Opitzian Pits): flat, large, radially arranged, paired pits formed at the front of the body chamber and locally affecting shell growth at the aperture.
- Pit type 5: kidney-shaped pits in the middle of the venter usually at the most posterior points of the hyponomic sinus of their growth lines. Pit type 5 is probably not

formed due to parasitism (see discussion in De Baets et al. 2015).

- Pit type 6 (Housean Pits, new): multiple, medium-sized pits, arranged in a more or less radial row, and partially formed in the middle of the body chamber without affecting the shell growth at the aperture.

The "Housean Pits" occurring on five different genera of goniatites from the upper Frasnian of Bergisch Gladbach-Sand confirm the discovery of Rakocinski (2012) that ammonoid parasitism was not only a common phenomenon in the Lower and Middle Devonian, but also a recurrent palaeopathological feature in Upper Devonian anarcestid descendents.

Systematics

The ammonoids were described using the morphological key of Korn (2010). For conch dimensions and morphological terminology see Fig. 7. Concerning the open nomenclature, we follow Bengtson (1988). Although most of the Sand tornoceratids are small in size, the large majority of specimens display all morphological features required for reliable identification and for the introduction of new taxa. Whilst members of the Tornoceratinae may reach moderate size (50–100 mm dm), *Crassotornoceras, Aulatornoceras*, and *Retrotornoceras* are very small genera that hardly reach 20 mm dm, not only in hypoxic goniatite shale facies but also in oxic cephalopod limestones, where environmental conditions should have been optimal.

The Tornoceratidae and all figured Gephuroceratoidea are housed in the Museum für Naturkunde Berlin, with the catalogue numbers MB.C.29344 to MB.C.29413 and MB.C.29434 to MB.C.29435. The remaining Gephuroceratoidea are currently deposited at the Institute of Palaeontology and Geology of the University of Münster. The anaptychids, including the illustrated specimen, are currently stored by KJH.

Institutional abbreviations. WWU—University of Münster, Münster, Germany; OUM—Oxford University Museum, Oxford, UK; MB—Museum für Naturkunde Berlin, Berlin, Germany; SMF—Senckenberg Museum, Frankfurt a.M., Germany; MRHN—Royal Belgian Institute of Natural Sciences, Brussels, Belgium; SedgM—Sedgwick Museum of Earth Sciences, Cambridge, UK; MWNH—Museum Wiesbaden, Wiesbaden, Germany.

Order **Goniatitida** Hyatt, 1884
Family **Tornoceratidae** Wedekind, 1910
Subfamily **Tornoceratinae** Wedekind, 1910

Genus *Tornoceras* Hyatt, 1884

Tornoceras holwilli (House, 2002), emended
Figures 6a–e, 8a–b, 9a; Tables 1, 2

e.p.	1895	*Tornoceras simplex* Mut. *ovata* Münster—Holzapfel: 99–100 [non fig. 6 = *Ling. linguum*]
e.p.	1897	*Tornoceras simplex*—Frech, pl. 32a, fig. 11 [only]
?	1902	*Tornoceras simplex* mut. *ovata*—Frech: 47, pl. III, figs. 21a–b
?	1965	*Tornoceras (Linguatornoceras)* aff. *linguum*—House: 112–113, fig. 13E, pl. 9, figs. 82–83
v	2000	*Tornoceras typum*—Becker et al.: 73, 75, 90–92, fig. 7D, pl. 2, figs. 7–8
	2002	*Linguatornoceras* "*ovatum*" Frech—House: 275, figs. 3D–E
*	2002	*Linguatornoceras holwilli*—House: 275, fig. 3L, pl. 3, figs. I–J
e.p.	2002	*Linguatornoceras* sp. —Dzik: figs. 56Q–U [non figs. 54 N–S, partly = *Ph. frechi*]
?e.p.	2008	*Linguatornoceras* aff. *linguum*—House and Kirchgasser: 167–168, text-figs. 56A–C, 56E–F (repeated from House 2002), pl. 27, fig. 12, pl. 33, figs. 7–8 [?non text-fig. 56D, pl. 33, figs. 1–2, 5–6]
e.p.	2008	*Linguatornoceras linguum*—House and Kirchgasser: pl. 27, fig. 14 [non pl. 27, fig. 13 = *L. clausum*]

Holotype. OUM D224 (Oxford University Museum, Oxford).

Material. MB.C.29399.1, MB.C.29399.2, MB.C.29399.3, MB.C.29400.1, MB.C.29400.2, MB.C.29401.1, MB.C.29401.2, MB.C.29402, MB.C.29403.1, MB.C.29403.2, MB.C.29403.3.

Type locality. Waterside Cove, South Devon.

Type level. Saltern Cove Goniatite Bed, upper Frasnian, UD I-K/L.

Diagnosis (emended). See House (2002: 275), adding as distinctive features a narrow, asymmetrically rounded, deep A-lobe and an arched, moderately wide ventrolateral saddle, which height is 50–80% of the height of the dorsolateral saddle.

Description. The Sand material contains 11 small, well-preserved specimens displaying the conch form, sutures, and ornament. Conch shape in intermediate stages thickly discoidal (ww/dm 0.50 at 10 mm dm), with rounded flanks, becoming subsequently thinly discoidal (ww/dm 0.47 just after 10 mm dm) and weakly compressed (ww/wh 0.80–0.95 at 9–12 mm dm). All specimens are involute and the WER is increasing from moderate (1.75–1.85 at 3.50 mm dm) to very high (2.50 at 16 mm dm). Specimen MB.C.29402 is a juvenile of 6.2 mm dm with a broad, gently ascending dorsolateral saddle, markedly asymmetric, rounded A-lobe,
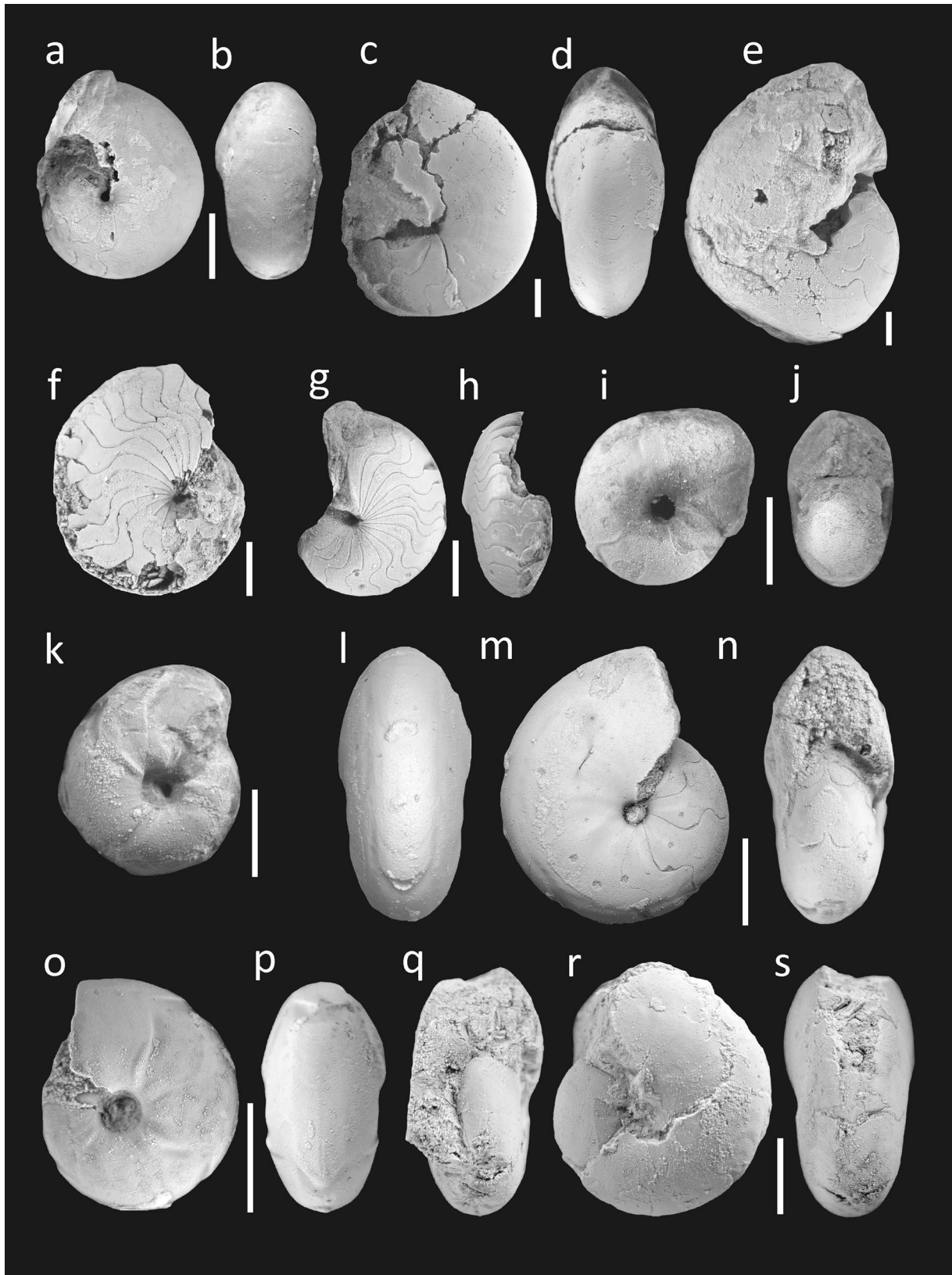
◀**Fig. 6** Tornoceratinae from the upper Frasnian Sand Formation (scale bar 2 mm). **a**, **b** *Tornoceras holwilli* (House, 2002), MB.C.29402, showing the wide ventral sinus of the growth lines and the relatively narrow, slightly asymmetric A-lobe, which is intermediate towards *Linguatornoceras*; lateral and ventral views, Sand 3C, ×5, **c**, **d** *T. holwilli* (House, 2002), MB.C.29399.3, showing the smooth rounded flank, and asymmetric A-lobe; lateral and ventral views, Sand 3, ×3.5, **e** *T. holwilli* (House, 2002), MB.C.29401.1, subadult with narrow, asymmetric A-lobe; lateral view, Sand 3B, ×3, **f** *T. aequilobum* sp. nov., paratype MB.C.29406.3, partly squashed specimen with dense septal spacing, showing the wide A-lobe and low ventrolateral saddle; lateral view, Sand A, ×5, **g**, **h** *T. aequilobum* sp. nov., holotype MB.C.29406.1, showing the shallow, symmetric A-lobe of closely spaced septa as well as some irregular "Housean Pits"; lateral and ventral views, Sand A, ×5, **i**, **j** *Crassotornoceras crassum* (Matern, 1931a), MB.C.29370, juvenile with pachyconic conch displaying weak varices and a typical suture with a low ventrolateral saddle; lateral and oral views, Sand 3B, ×8, **k** *Cr. crassum* (Matern, 1931a), MB.C.29372.2, displaying marked, concavo-convex varices, slightly intermediate towards *Cr. belgicum* due to a rib associated with the last varix; lateral view, Sand A, ×8, **l–n** *Cr.* aff. *belgicum* (Matern, 1931b), MB.C.29413, displaying weak lateral ribbing, ventral varices, incipient ventrolateral furrows, *Crassotornoceras*-type sutures, and "Housean Pits"; lateral and ventral views, Sand A, ×8, **o**, **p** *Cr. belgicum* (Matern, 1931b), MB.C.29365.1, with typical varices and associated lateral ribbing; lateral and ventral views, Dombach-Sander-Straße, ×10, **q–s** *Cr. nudum* sp. nov., holotype MB.C.29373.1, with a typical *Crassotornoceras*-type suture but lacking varices or ribbing; ventral, lateral and ventral views, Sand A, ×7

and strongly asymmetric ventrolateral saddle (Fig. 8b). It possesses a closed umbilicus (uw/dm 0.05), short and well-rounded umbilical wall, and gently rounded flanks (Fig. 6a–b). Growth lines of MB.C.29399.3 (at 4.6 mm wh) are characterized by a low dorsolateral projection, wide, ascending lateral sinus, marked, narrow ventrolateral projection, and a wide, moderately deep, rounded ventral sinus (Fig. 9a). A larger specimen (MB.C.29401.1, 16 mm dm) displays an asymmetrically rounded A-lobe and broad ventrolateral saddle that is slightly lower than the dorsolateral saddle (Figs. 6e, 8a). Specimen MB.C.29401.2 differs by a slightly wider A-lobe. Impressions of the fine biconvex growth lines with a wide ventral sinus are also preserved in MB.C.29399.3 (Fig. 6d). The cross-section is tegoid, with rounded flanks.

Remarks. In the early literature on Devonian ammonoids, our form would have been listed as *T. simplex* (Buch, 1832), which, however, was originally shown to possess a markedly open umbilicus (for discussion see House 1965: 112, and Becker 1993a). The age of this form, currently a nom. dub., is unclear; it could well represent an Eifelian taxon. Holzapfel (1895) recognized several *T. simplex* variants ("mutants"), whose names are available as subspecies or species. Specimens with a variably narrow A-lobe and arched ventrolateral saddle were included in his "Mut. *ovata* Münster". The latter name refers to the much larger Famennian *G. ovatus* Münster, 1832, another nom. dub. of unresolved

taxonomic affinities (for discussion see Becker 1993a: 277). Reading Holzapfel's (1895) description, it becomes clear that he combined under the same name a range of very different tornoceratids, including *Linguatornoceras* species.

Frech (1902) followed Holzapfel's taxonomic concept and applied it to Büdesheim *Tornoceras*. But he illustrated under the name "*Tornoceras simplex* mut. *ovata*" a suture with an unusually small and narrow ventrolateral saddle that is not typical for the most common Büdesheim form. When House (1965) introduced the subgenus *Linguatornoceras*, he included the common Büdesheim species and similar North American specimens as *T.* (*Ling.*) aff. *linguum*. The latter is intermediate between *Tornoceras* and *Linguatornoceras* and we restrict *Linguatornoceras* to species with an at least subparallel-sided A-lobe.

House (1963, 1965, 2002) emphasized that the Büdesheim form occurs also at Waterside Cove in South Devon. He assigned a few specimens characterized by incomplete preservation of the E-lobe, probably caused by an episodic siphuncle shift, to a new species, *Ling. holwilli*. In all other aspects, it is identical with his *Ling.* aff. *linguum* or *Ling.* "*ovatum*" Frech. Since we are not convinced about the taxonomic significance of the episodically incomplete E-lobe, *holwilli* seems to be the available name for the common *Tornoceras* species of Sand. Specimens with narrower and smaller ventrolateral saddle (Frech 1902; House 1965; House and Kirchgasser 2008) are assigned with an uncertainty: these could represent intraspecific variants. We exclude specimens with a much lower ventrolateral saddle (< 50% of height of dorsolateral saddle; e.g., *T.* cf. *typum* in Becker and House 1994; House and Kirchgasser 2008). They are intermediate towards *T. contractum* Glenister, 1958.

Tornoceras holwilli is closely related to *T. typum* (Sandberger and Sandberger, 1851), which differs in the mature flattening of its converging flanks, lower WER (ca. 2.00), a high relief of the suture, and a less arched ventrolateral saddle. Despite many references in the literature, including old quotations of "*T. simplex*", *T. typum* is poorly known apart from its lectotype from Oberscheld (Rhenish Massif). A revision based on the morphometry of topotypes will have to specify the *holwilli-typum* relationships. The Givetian/Frasnian North American *T. uniangulare–T. iowaense* Group differs from *T. holwilli* in their narrower ventrolateral saddle with an obliquely ascending lateral pronge. Rhenish upper Givetian *Tornoceras*, including *T. wunderlichi* Bockwinkel and Korn (2015), belong to the *T. contractum* Group with a low ventrolateral saddle (see Bockwinkel et al. 2013 and Bockwinkel and Korn 2017). The top-lower Frasnian *Domanikoceras timidum* Becker and House in Becker et al. (2000) is thicker and lacks a lateral sinus of the growth lines.

Stratigraphic range. Lower Frasnian of the Timan (Becker et al. 2000, upper UD I-D) to the upper Frasnian of South Devon (House 2002, UD I-K/L).

Tornoceras aequilobum sp. nov.
Figures 6f–h, 8c–d; Tables 1, 2

Etymology. Named after the subsymmetrically rounded A-lobe.

Holotype. MB.C.29406.1 (Museum für Naturkunde Berlin).

Paratypes. MB.C.29404.1, MB.C.29404.2, MB.C.29405, MB.C.29406.2, and MB.C.29406.3.

Type locality. Loc. Sand A, construction site at the Herkenrather Straße 70 of Bergisch Gladbach-Sand.

Type level. Sand Formation, upper Frasnian, UD I-K.

Diagnosis. Conch thinly discoidal (ww/dm 0.45–0.55 at 6–8 mm dm), weakly compressed (ww/wh 0.80–0.95 at 6–8 mm dm), with slightly flattened flanks and high to very high whorl expansion rate (WER ca. 2.40–2.50). Conch always involute (uw/dm 0.05) and smooth. Suture with a wide, asymmetric and low dorsolateral saddle, moderately shallow, subsymmetric, widely rounded A-lobe, low, asymmetrically rounded ventrolateral saddle with almost the same height as the dorsolateral saddle, and small, very narrow, short E-lobe; septal spacing characteristically dense (ca. 20 sutures per whorl).

Description. The Sand specimens range in size between 3.5 to 8.4 mm dm. Holotype MB.C.29406.1 is still attached to its rock matrix and is a late juvenile with 6.6 mm dm, but it is the best-preserved specimen. It displays dense septal spacing, the typical, broad, subsymmetric, rounded A-lobe, a thinly discoidal involute conch (ww/dm 0.45, uw/dm 0.05), and a moderately wide, gently rounded venter. The umbilical wall is rounded in the partially crushed paratype MB.C.29406.3. The internal suture and the growth lines are not preserved. There are no furrows or ribbing. All specimens have dense septal spacing in common (e.g., Fig. 6f–h). In the juvenile paratype MB.C.29404.1, it is already developed at 3.5 mm dm.

Remarks. The species differs from most other named *Tornoceras* species by the wide, almost symmetrically rounded A-lobe, low relief of suture, and dense septal crowding. The septal crowding being already developed on juveniles is ruling out maturity as a potential reason. While it is observed on each specimen of *T. aequilobum* sp. nov., it has to be considered that ecological stress can support dense septal crowding. Holzapfel (1895) identified lower/middle Frasnian specimens from many different localities with a subsymmetric saddle and A-lobe, but with higher relief of the suture, as "*T. simplex* Mut. *angustelobata*". Only a suture was illustrated. In the absence of any figured type-material, this taxon is currently a nom. dub. More material of *T. aequilobum* sp. nov. is available from Büdesheim (Eifel) and Boudouda (Morrocan Meseta).

Stratigraphic range. Currently restricted to the upper Frasnian (UD I-I/J to UD I-K).

Genus ***Crassotornoceras*** House and Price, 1985

Crassotornoceras crassum (Matern, 1931a), emended
Figures 6i–k, 8e, 9b; Tables 1, 2, 3, 4

v *	1931a	*Tornoceras ausavense crassum* Matern: 27, pl. 3, fig. 14a–b
	1931b	*Tornoceras ausavense crassum*—Matern: 9
	1936	*Tornoceras ausavense crassum*—Maillieux: 56–57
	1958	*Tornoceras (Tornoceras) crassum*—House: pl. 19, fig. 1
v	1985	*Crassotornoceras crassum*—House and Price: 165–168, figs. 3A, 3B, 3D, 4, pl. 16, figs. 4, 8–11
v	1993a	*Crassotornoceras crassum*—Becker: 185, figs. 68d, I, pl. 3, figs. 18–19
	2002	*Crassotornoceras crassum*—Korn and Klug: 155, figs. 144G, N
cf.	2008	*Crassotornoceras* aff. *crassum*—House and Kirchgasser: 168–169, text-figs. 53E–F, pl. 33, figs. 9–20, tab. 27
v	2016	*Crassotornoceras crassum*—Becker et al.: 183

Holotype. SMF XI 342a (Senckenberg Museum, Frankfurt a.M.).

Material. MB.C.29369, MB.C.29370, MB.C.29371.1, MB.C.29371.2, MB.C.29372.1, MB.C.29372.2, MB.C.29372.3, MB.C.29372.4, MB.C.29372.5, MB.C.29372.6, MB.C.29372.7, MB.C.29372.8.

Type locality. Büdesheim, Eifel.

Type level. Büdesheim Goniatite Shale, upper Frasnian, UD I-I/J.

Diagnosis (emended). Very small-sized; earliest post-embryonic stages until ca. 3 mm dm cadiconic, moderately depressed (ww/wh ca. 1.50 at 2.5 mm dm), with open umbilicus (uw/dm ca. 0.25 at 2.5 mm dm) and moderate WER (1.75 at 2.5 mm dm); at ca. 7 mm thickly discoidal (ww/dm slightly decreasing to 0.50), weakly depressed (ww/wh down to 1.10), subinvolute (uw/dm 0.15), and with slightly

increasing WER (ca. 1.80); with 3–5 prominent, biconvex varices per whorl, which follow the undulose, strongly biconvex growth lines characterized by a low dorsolateral salient, widely rounded, asymmetric lateral sinus, high ventrolateral projection, and broadly rounded ventral sinus. Suture with an asymmetrically arched, wide dorsolateral saddle, small, narrowly rounded A-lobe, ventrolateral saddle that is much lower than the dorsolateral saddle, and small, narrow, short E-lobe.

Description. Conch diameters of the Sand specimens range between 3 mm (MB.C.29371.2) and 6.5 mm (MB.C.29372.3). The material is relatively consistent in its morphology, which suggests small intraspecific variability. Specimen MB.C.29370 is a representative juvenile (3.95 mm dm) that displays regular, strongly biconvex varices with a high ventrolateral projection, an open umbilicus (uw/dm 0.16), and a thinly pachyconic (ww/dm 0.61), weakly depressed (ww/wh 1.28) conch form with the narrowly rounded umbilical wall, smoothly rounded flanks and venter (Fig. 6i–j). It displays the typical suture with a wide dorsolateral saddle and small A-lobe (Figs. 6i, 8e). The body chamber is at least 350° long, occupying originally a complete whorl. Rather undulose biconvex growth lines can be observed near the aperture in specimen MB.C.29372.2 (Fig. 9b). They follow in general the course of the varices (Fig. 6k), with a very low dorsolateral projection, widely rounded, ascending lateral sinus, a very high, subtriangular ventrolateral projection, and wide ventral sinus.

Remarks. Crasstornoceras crassum is one of just a few ammonoid species, which survived the Kellwasser Crisis. Lower Famennian specimens (Be1061 and Be703 sensu Becker 1993a) from the eastern Rhenish Massif are identical in terms of conch morphology, suture and growth lines compared to upper Frasnian material. The species is easy to distinguish from associated *Cr. belgicum* by the lack of flank ribs. The contemporaneous *Cr. anissi* House and Price, 1985 from South Devon differs by its higher number of varices, which have a low ventrolateral projection. Specimens from the Point Breeze Goniatite Bed of the Angola Shale of New York (UD I-I/J) identified by House and Kirchgasser (2008) as *Cr.* aff. *crassum* also develop a higher number of varices per whorl during ontogeny, but with a very prominent, strong ventrolateral projection.

Stratigraphic range. Ranges from the upper Frasnian (UD I-J) to the lower Famennian (UD II-C).

Crassotornoceras belgicum (Matern, 1931b), emended
Figures 6o–p, 8g, 9c; Tables 1, 2, 4, 5

*	1931b	*Tornoceras belgicum* Matern: 9–11, fig. 2
	1936	*Tornoceras belgicum*—Maillieux: 57, fig. 2
aff.	1958	*Tornoceras* (?*Aulatornoceras*) aff. *belgicum*—House: 190–191, pl. 21, figs. 6, 7, 11
v	1985	*Crassotornoceras belgicum*—House and Price: 169, text-fig. 3C, pl. 16, figs. 1–3 [re-illustration of holotype]
	2002	*Crassotornoceras belgicum*—Korn and Klug: 155
non	2002	*Aulatornoceras belgicum*—Dzik: figs. 52B–C, 53P–R, 54I–M, 56N–P [= *Aul.* cf. *constrictum*]

Holotype. MRHN, unnumbered (Royal Belgian Institute of Natural Sciences, Brussels).

Material. MB.C.29365.1, MB.C.29365.2, MB.C.29366, MB.C.29367, MB.C.29368.1, MB.C.29368.2, MB.C.29368.3, MB.C.29368.4, MB.C.29368.5.

Type locality. Quarry behind the church at Boussu en Fagne, Belgium.

Type level. Upper Matagne Shale (F3b), upper Frasnian, UD I-L.

Diagnosis (emended). Very small-sized; conch well-rounded, changing from thinly pachyconic (ww/dm 0.65), weakly depressed (ww/wh ca. 1.20), with moderate to high WER (1.90–2.05), and open umbilicus (uw/dm 0.15) at 3–4 mm dm to thickly discoidal (ww/dm 0.45), weakly compressed (ww/wh 0.90–1.00), with high WER (2.00–2.10) and narrow umbilicus (uw/dm 0.10) at 6.5 mm dm; per whorl with 3–4, widely-spaced, strongly biconvex varices and around six parallel, prominent ribs on the flank. Suture with wide, asymmetric highly arched dorsolateral saddle, small, narrowly rounded, slightly asymmetric A-lobe, small, low, rounded ventrolateral saddle, and small, short E-lobe.

Description. The Sand material demonstrates that the conch shape is shifting during ontogeny from thinly pachyconic (ww/dm 0.64 in MB.C.29368.2) in juveniles to thickly discoidal (ww/dm < 0.60). MB.C.29365.1 (4.3 mm dm, Fig. 6o–p) resembles the Belgium holotype with respect to conch size, the small, open umbilicus (uw/dm 0.16) with short, rounded wall, ribbing on the flanks, and the strictly biconvex varices. However, it is slightly thinner and the ribs do not reach the ventrolateral projection. Around 270° of the body chamber is preserved. Growth lines show a very low dorsolateral salient, wide, ascending lateral sinus, a very narrow, strong ventrolateral projection, and a wide, moderately deep ventral sinus (Fig. 9c). Even juvenile specimens of only 3.2 mm dm, such as MB.C.29368.2, display the typical sutures and regular ribs. MB.C.29365.1 displays
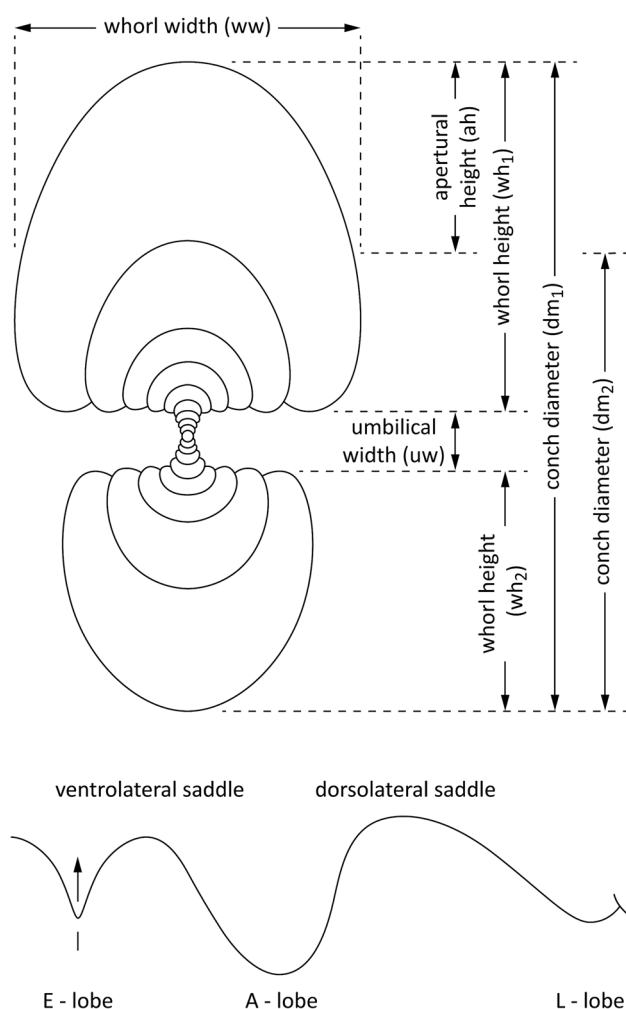
Fig. 7 Measured conch dimensions applying the morphological key of Korn (2010) and terminology of a typical tornoceratid suture

the suture with an arched dorsolateral saddle, small rounded A-lobe, and a ventrolateral saddle that is much lower than the dorsolateral saddle (Fig. 8g).

Remarks. The species is easy to distinguish from all other crassotornoceratids due to its prominent ribs.

Stratigraphic range. Restricted to the upper Frasnian (UD I-K/L).

Crassotornoceras aff. **belgicum** (Matern, 1931b)
Figures 6l–n, 8f; Tables 1, 2, 4

Material. MB.C.29413.

Description. Specimen MB.C.29413 has an ovoid, thinly discoidal conch shape (ww/dm 0.45 at 6.3 mm dm) with a very narrow umbilicus (uw/dm 0.07), fast-expanding

whorls (WER 2.38), widely-spaced, deeply rounded ventral varices (Fig. 6l, n), and seven weak, straight ribs on the inner flanks (Fig. 5m). There is a faint ventrolateral furrow. It also displays more or less regularly distributed "Housean Pits" (Pit type 6, Fig. 6m). The suture possesses a highly arched, asymmetrically rounded dorsolateral saddle, an asymmetric, narrowly rounded A-lobe, and a small, low ventrolateral saddle (Fig. 8f).

Remarks. This currently unique specimen differs from *Cr. belgicum* in its more compressed conch, the absence of lateral varices, and the presence of an incipient ventrolateral furrow, which is normally typical for *Aulatornoceras*. For example, *Aul. ventrosulcatum* sp. nov. (see below) lacks ribs on the flanks, is wider umbilicate, and displays a weak ventral band, as typical for the genus. Since the latter is absent in MB.C.29413, it conforms neither with *Aulatornoceras*, nor with typical *Crassotornoceras*. Because we have only one specimen, we place it in open nomenclature until further material becomes available.

Stratigraphic range. Restricted to the upper Frasnian (UD I-K).

Crassotornoceras nudum sp. nov.
Figures 6q–s, 8h, 10; Tables 1, 2, 4

Etymology. From the latin *nudus* = naked, due to the lack of any ornamentation on flanks and venter.

Holotype. MB.C.29373.1 (Museum für Naturkunde Berlin).

Paratypes. MB.C.29374, MB.C.29373.2, MB.C.29373.3.

Type locality. Sand A, construction site at the Herkenrather Straße 70 of Bergisch Gladbach-Sand.

Type level. Sand Formation, upper Frasnian, UD I-K.

Diagnosis. Very small-sized; conch at 5.0 to 6.5 mm dm thickly discoidal (ww/dm 0.47–0.49), weakly compressed (ww/wh 0.90–1.00), involute (uw/dm 0.10–0.15), with high whorl expansion rate (WER 2.00–2.10), and well-rounded venter; no varices. Suture with an arched, wide dorsolateral saddle, narrow, subsymmetric A-lobe, ventrolateral saddle that is markedly lower than the dorsolateral saddle, and a small, short, divergent, pointed E-lobe.

Description. The holotype has a conch diameter of 6.45 mm and preserves a short part of the body chamber (ca. 50°). Its flanks and venter are smoothly rounded (Fig. 6s). Despite some incrustation (Fig. 6r), it is clear that the umbilicus is small and open. There is a typical crassotornoceratid-type
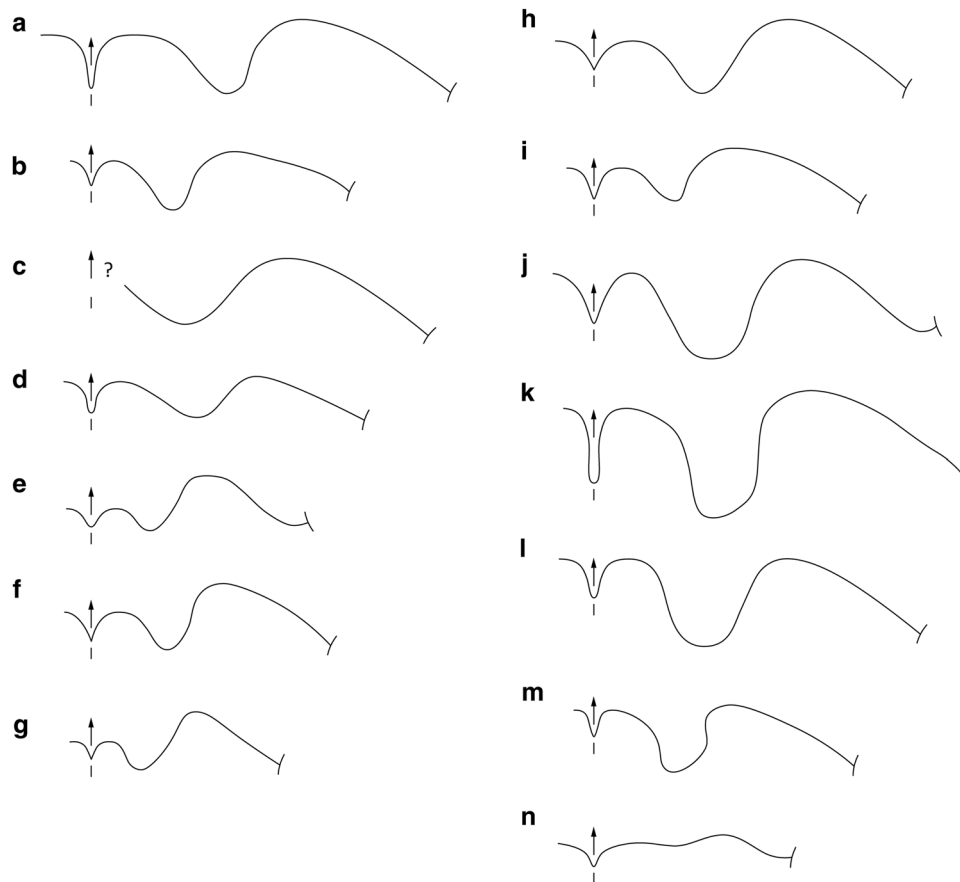
Fig. 8 Sutures of Tornoceratinae from Bergisch Gladbach-Sand. **a** *Tornoceras holwilli* (House, 2002), MB.C.29401.1, Sand 3B, at 5.10 mm wh, **b** *T. holwilli* (House, 2002), MB.C.29402, Sand 3C, at 2.32 mm wh, **c** *T. aequilobum* sp. nov., paratype MB.C.29406.3, Sand A, at 4.71 mm wh, **d** *T. aequilobum* sp. nov., holotype MB.C.29406.1, Sand A, at 2.75 mm wh, **e** *Crassotornoceras crassum* (Matern, 1931a), MB.C.29370, Sand 3B, at 1.35 mm wh, **f** *Cr.* aff. *belgicum* (Matern, 1931b), MB.C.29413, Sand A, at 1.90 mm wh, **g** *Cr. belgicum* (Matern, 1931b), MB.C.29365.1, Dombach-Sander-Straße, at 1.15 mm wh, **h** *Cr. nudum* sp. nov., holotype MB.C.29373.1, Sand A, at 2.86 mm wh, **i** *Cr. hetzeneggeri* sp. nov., holotype MB.C.29375, Sand 3, at 2.25 mm wh, **j** *Lobotornoceras ausavense* (Steininger, 1849), MB.C.29388.1, Sand 3, at 3.50 mm wh, **k** *Linguatornoceras* cf. *clausum* (Glenister, 1958), MB.C.29381, Sand 3, at 9.20 mm wh, **l** *Ling. linguum* (Sandberger and Sandberger, 1850/51), MB.C.29386.2, Sand A, at 3.50 mm wh, **m** *Ling.* sp. 1, MB.C.29387, Sand A, at 2.25 mm wh, **n** *Retrotornoceras juxi* sp. nov., holotype MB.C.29393, Sand 4, at 1.30 mm wh

suture with an arched, relatively high dorsolateral saddle, moderately wide, subsymmetric A-lobe, and low, well-rounded ventrolateral saddle (Fig. 8h). None of the types possesses varices or flank riblets. Paratype MB.C.29374 is a juvenile with open umbilicus. Its sutural relief is slightly shallower than in the holotype, suggesting some ontogenetic change. Growth lines are not preserved in any specimen.

Remarks. The suture resembles other species of *Crassotornoceras*. However, the species is unique within the genus due to the lack of ribbing and varices. In this respect, it is intermediate between *Crassotornoceras* and *Tornoceras*, in which the umbilicus closes during early stages, during or just after the second whorl (e.g., Miller 1938; House 1965). *Crassotornoceras hetzeneggeri* sp. nov. displays weak ribs,

and is more rotund, with higher whorl widths (Fig. 10). More material of *Cr. nudum* sp. nov. is available from Büdesheim (Eifel).

Stratigraphic range. Currently restricted to the upper Frasnian (UD I-I/J to UD I-K).

Crassotornoceras hetzeneggeri sp. nov.
Figures 8i, 9d, 10, 11a–b; Tables 1, 2, 4

Etymology. Named after the owner of the local supermarket, Markus Hetzenegger (Bergisch Gladbach), who was always very supportive for the fossil collecting.

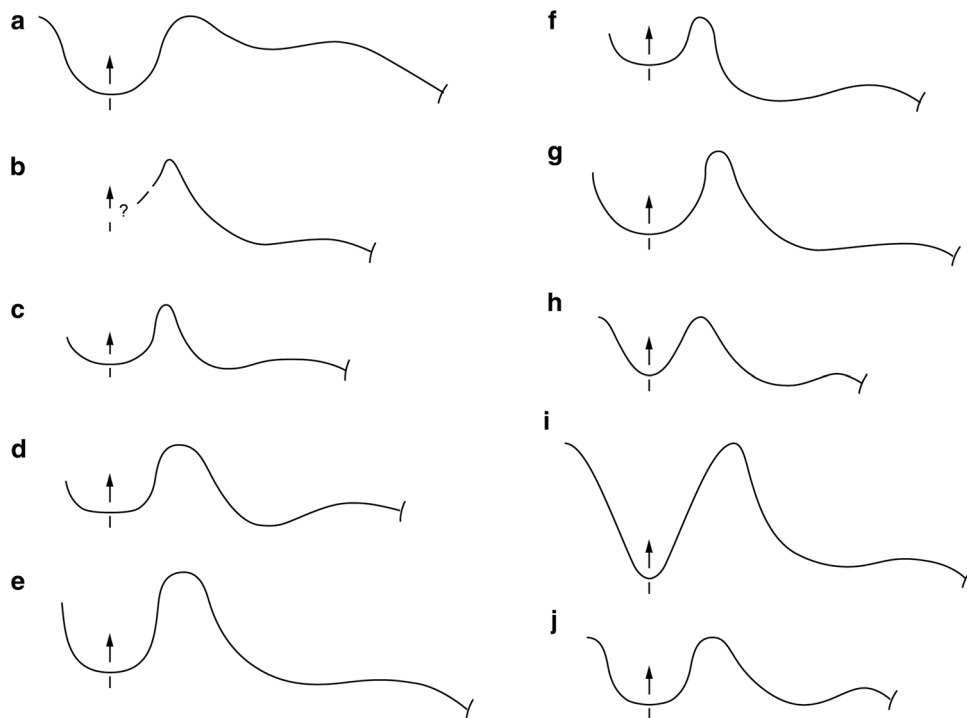*Holotype*. MB.C.29375 (Museum für Naturkunde Berlin).

Fig. 9 Growth lines of Tornoceratidae from Bergisch Gladbach-Sand. **a** *Tornoceras holwilli* (House, 2002), MB.C.29399.3, Sand 3, at 4.60 mm wh, **b** *Crassotornoceras crassum* (Matern, 1931a), MB.C.29372.2, Sand A, at 2.30 mm wh, **c** *Cr. belgicum* (Matern, 1931b), MB.C.29365.1, Dombach-Sander-Straße at 1.90 mm wh, **d** *Cr. hetzeneggeri* sp. nov., holotype MB.C.29375, Sand 3, at 3.20 mm wh, **e** *Aulatornoceras auris* (Quenstedt, 1846), MB.C.29346.5, Sand 1, at 6.50 mm wh, f *Aul. constrictum* (Steininger, 1849), MB.C.29349.1, Sand A, at 3.20 mm wh, **g** *Aul. eifliense* (Steininger, 1849), MB.C.29353.1, Sand A, at 2.90 mm wh, **h** *Aul.* aff. *ventrosulcatum*, specimen MB.C.29354, Sand 1, at 1.40 mm wh, **i** *Aul. steinhauseni* sp. nov., holotype MB.C.29356.1, Sand 1, at 3.15 mm wh, **j** *Aul. ventrosulcatum* sp. nov., holotype MB.C.29360, Dombach-Sander-Straße, at 2.00 mm wh

Paratypes. MB.C.29434.1, MB.C.29434.2, MB.C.29434.3.

Type locality. Sand 3, construction site at the Herkenrather Straße 70 of Bergisch Gladbach-Sand.

Type level. Sand Formation, upper Frasnian, UD I-K.

Diagnosis. Very small-sized; conch at 6 mm dm thinly pachyconic (ww/dm ca. 0.60), weakly depressed (ww/wh 1.05–1.35), involute (uw/dm 0.08), with high whorl expansion rate (WER 2.00–2.10); faint, undulose ribbing near the umbilicus, no varices, growth lines biconvex, with a tongue-shaped, high ventrolateral projection, and deep, wide ventral sinus. Suture with a wide, arched, moderately high, asymmetric dorsolateral saddle, a narrow, small, asymmetrically rounded A-lobe, small ventrolateral saddle that is much lower than the dorsolateral saddle, and narrowly V-shaped, short E-lobe.

Description. The holotype shows a well-rounded, thickly discoidal conch shape at 6.45 mm dm. The umbilicus is small but open (uw/dm 0.08), with a short, steeply rounded umbilical margin. The flanks are slightly converging towards the rounded venter (Fig. 11b), lacking any edges or spiral furrows. There are very weak, undulose ribs on the inner flanks (Fig. 11a). The strongly biconvex, undulose growth lines possess a very low dorsolateral salient, a moderately wide sinus on the flanks, a high ventrolateral projection, and a moderately deep ventral sinus (Fig. 9d). The suture is typical for *Crassotornoceras*, with a very broad, asymmetrically arched but not very high dorsolateral saddle, small, asymmetric A-lobe characterized by a steeper lateral than ventral limb, and a short, slightly asymmetric ventrolateral saddle that reaches more than 50% of the height of the dorsolateral saddle. The inner suture is not accessible.

Remarks. The new species differs from *Cr. nudum* sp. nov. in its more rotund, thicker conch form at comparable size, weak ribs, and lower WER in juveniles (Fig. 10). All other crassotornoceratids possess varices on the inner moulds. Apart from its closed umbilicus, *T. holwilli* differs at the same size in a slightly higher dorsolateral saddle and a lower ventrolateral projection of the growth lines. More material of *Cr. hetzeneggeri* sp. nov. is available from Büdesheim (Eifel).

Table 2 Conch dimensions of Bergisch Gladbach-Sand Tornoceratinae [in mm]

specimen	dm	wh	ah	ww	uw	ww/wh	uw/dm	ww/dm	WER	IZR
Tornoceras holwilli (House, 2002) from the Sand Formation										
MB.C.29404.1	3.28	1.70	0.85	–	0.40	–	0.12	–	1.82	0.50
MB.C.29402	6.20	3.52	–	3.12	0.28	0.89	0.05	0.50	–	–
MB.C.29403.1	8.70	4.85	–	4.10	–	0.85	–	0.47	–	–
MB.C.29403.3	9.30	5.20	–	4.35	0.50	0.84	0.05	0.47	–	–
MB.C.29399.3	12.00	6.50	–	5.90	0.50	0.91	0.04	0.49	–	–
MB.C.29401.1	16.00	9.00	5.90	–	–	–	–	–	2.51	0.34
Tornoceras aequilobum sp. nov. from the Sand Formation										
MB.C.29406.1	6.60	3.66	–	3.00	0.30	0.82	0.05	0.45	–	–
MB.C.29405	7.87	4.50	–	4.05	0.30	0.90	0.04	0.51	–	–
MB.C.29406.3	8.40	4.80	–	–	0.35	–	0.04	–	–	–
Crassotornoceras crassum (Matern, 1931b) from the Sand Formation										
MB.C.29370	3.95	1.87	–	2.40	0.65	1.28	0.16	0.61	–	–
MB.C.29369	4.10	2.14	–	2.45	0.65	1.14	0.16	0.60	–	–
MB.C.29372.3	6.56	–	1.60	3.05	1.00	–	0.15	0.46	1.75	–
Crassotornoceras belgicum (Matern, 1931a) from the Sand Formation										
MB.C.29368.2	3.19	1.73	–	2.05	0.41	1.18	0.13	0.64	–	–
MB.C.29368.4	3.59	1.70	1.00	2.08	0.35	1.22	0.10	0.58	1.92	0.26
MB.C.29365.2	3.75	1.85	1.10	2.20	0.60	1.19	0.16	0.59	2.00	0.30
MB.C.29368.5	3.80	1.95	1.15	2.25	0.60	1.15	0.16	0.59	2.06	0.31
MB.C.29365.1	4.30	2.06	1.25	2.27	0.70	1.10	0.16	0.53	1.99	0.39
MB.C.29368.3	4.52	2.35	1.40	2.75	0.40	1.17	0.09	0.61	2.10	0.40
MB.C.29368.1	6.46	3.18	1.95	–	0.58	–	0.09	–	2.05	0.39
Crassotornoceras aff. *belgicum* (Matern, 1931a) from the Sand Formation										
MB.C.29413	6.30	3.45	2.22	2.83	0.44	0.82	0.07	0.45	2.38	0.36
Crassotornoceras nudum sp. nov. from the Sand Formation										
MB.C.29373.2	4.87	2.32	–	2.41	0.65	1.04	0.13	0.49	–	–
MB.C.29373.1	6.45	3.10	2.00	3.00	0.90	0.97	0.14	0.47	2.10	0.31
Crassotornoceras hetzeneggeri sp. nov. from the Sand Formation										
MB.C.29434.1	5.57	2.57	1.60	3.50	0.45	1.36	0.08	0.63	1.97	0.38
MB.C.29375	6.45	3.46	2.00	3.55	0.50	1.03	0.08	0.55	2.10	0.42
Lobotornoceras ausavense (Steininger, 1849) from the Sand Formation										
MB.C.29388.1	7.78	4.50	2.85	3.40	0.35	0.76	0.04	0.44	2.49	0.37
MB.C.29388.2	8.40	5.00	2.90	3.45	0.25	0.69	0.03	0.41	2.33	0.42
Linguatornoceras cf. *clausum* (Glenister, 1958) from the Sand Formation										
MB.C.29383	7.13	4.00	–	–	0.50	–	0.07	–	–	–
MB.C.29381	16.50	10.30	6.40	10.00	1.00	0.97	0.06	0.61	2.67	0.38
Linguatornoceras linguum (G. & F. Sandberger 1850/56) from the Sand Formation										
MB.C.29384.2	5.60	3.00	–	3.30	0.50	1.10	0.09	0.59	–	–
MB.C.29386.2	7.85	4.61	–	4.00	0.25	0.87	0.03	0.51	–	–
MB.C.29386.4	9.10	5.37	3.20	5.10	0.30	0.95	0.03	0.56	2.38	0.40
MB.C.29385	10.00	6.00	–	4.50	0.30	0.75	0.03	0.45	–	–
Linguatornoceras sp. 1 from the Sand Formation										
MB.C.29387	5.40	2.30	1.50	2.25	0.40	0.98	0.07	0.42	1.92	0.35

Stratigraphic range. Currently restricted to the upper Frasnian (UD I-I/J to UD I-K).

Genus *Lobotornoceras* Schindewolf, 1936

Lobotornoceras ausavense (Steininger, 1849), emended
Figures 8j, 11c–f; Tables 1, 2

*	1849	*Goniatites Ausavensis* Steininger: 27
	1853	*Goniatites Ausavensis*—Steininger: 43, pl. 1, figs. 6, 6a, 7, 7a
v	1897	*Tornoceras Ausavense*—Foord and Crick: 106–107
	1902	*Tornoceras ausavense*—Frech: 48, figs. 11a, d
v	1931a	*Tornoceras ausavense ausavense*—Matern: 26–27, pl. 3, figs. 13a–b [further synonymy]
	1936	*Lobotornoceras ausavense*—Schindewolf: 690, fig. 1
	1978	*Lobotornoceras ausavense*—House: pl. 9, figs. 8, 14 [neotype]
v	2000b	*Lobotornoceras ausavense*—Becker and House: 33
	2002	*Lobotornoceras ausavense*—Korn and Klug: 158, fig. 144R
	2008	*Lobotornoceras ausavense*—House and Kirchgasser: text-figs. 58C, F
v	2018	*Lobotornoceras ausavense*—Becker et al.: 176

Neotype. SedgM H9932 (Sedgwick Museum of Earth Sciences, Cambridge), designated by House (1978).

Material. MB.C.29388.1, MB.C.29388.2, MB.C.29435.

Type locality. 250 m SSE of the Büdesheim Church, Eifel.

Type level. Büdesheim Goniatite Shale, upper Frasnian, UD I-I/J.

Diagnosis (emended). Small-sized; conch thinly discoidal and weakly compressed (ww/dm 0.40–0.45 and ww/wh 0.70 at 8 mm dm), involute (uw/dm < 0.10), with very high whorl expansion rate (WER 2.30–2.50 at 8 mm dm), with flattened flanks, narrowly rounded venter, and 4–6 weakly biconvex, later prorsiradiate and nearly convex varices per whorl that begin on the inner flanks and are strongest on the venter. Suture with moderately deep and wide, rounded, slightly divergent I-lobe, shallow and wide, internal L_i-lobe, small, low saddle at the umbilical seam, small, asymmetrically rounded L_e-lobe just outside the umbilicus, asymmetrically arched, high dorsolateral saddle, subsymmetric, moderately wide, well rounded A-lobe, high, narrow, asymmetrically rounded ventrolateral saddle, and small, narrow, short E-lobe.

Description. MB.C.29388.1 and MB.C.29388.2 display the L_e-lobe just outside the umbilicus as typical for *Lobotornoceras* (Figs. 8j, 11d–e). In the last septum of MB.C.29388.1, the L_e-lobe is deeper and closer to the umbilicus than the internal L_i-lobe (Fig. 11d). The secondary saddle dividing the L-lobe is, therefore, asymmetric, and thus not as in the illustration of Schindewolf (1936, compare his fig. 1). It is more symmetric in the second specimen, which fully displays the inner suture on the last septal face (Fig. 11f). There is no change of sutures between 4.5 and 8.3 mm dm. MB.C.29388.1 possesses a first biconvex varix with a shallow lateral sinus and subsequent subconvex and prorsiradiate varices (Fig. 11d). In MB.C.29435, the varices are rather weak. The cross-section is always weakly tegoid, with maximum ww on the inner flanks, and with a narrowly rounded venter. The umbilicus of the moulds is punctiform (uw/dm 0.03–0.04) and was probably sealed by shell.

Remarks. Matern (1931a) mentioned that biconvex varices following the growth lines occur only at later ontogenetic stages (ca 16 mm dm) but the neotype has four marked, weakly biconvex varices on the half whorl before ca. 9 mm dm (from ca. 3.5 mm wh on). Specimens from Sand possess only subconvex varices except for the first in MB.C.29388.1. The Sand representatives are identical with the type material from Büdesheim. The older *Lob. hassoni* House, 1978 lacks varices, whilst the Russian *Lob. strangulatum* (Keyserling, 1844) is characterized by sutures with a

Table 3 Conch ontogeny of *Crassotornoceras crassum* (Matern, 1931b)

dm	Conch shape	Whorl cross-section shape	Whorl expansion
2.5 mm	Thinly pachyconic; subinvolute (ww/dm ~ 0.70; uw/dm = 0.25)	Moderately depressed; – (ww/wh ~ 1.50; –)	Moderate (WER ~ 1.75)
4 mm	Thinly pachyconic; subinvolute (ww/dm ~ 0.60; uw/dm = 0.15)	Weakly depressed; strongly embracing (ww/wh ~ 1.15–1.30; IZR ~ 0.40)	Moderate (WER ~ 1.85–1.95)
7 mm	Thickly discoidal; subinvolute (ww/dm ~ 0.45–0.60; uw/dm = 0.15)	Weakly depressed; very strongly embracing (ww/wh ~ 1.10; IZR ~ 0.50)	Moderate (WER ~ 1.75–1.90)

strongly asymmetric A-lobe and ventrolateral saddle (see Becker et al. 2000).

Stratigraphic range. Within the upper Frasnian, the Sand specimens extend the range of the species from UD I-I/J (Büdesheim; Tafilalt, Becker and House 2000b; Becker et al. 2018) to UD I-K. Close relatives (*Lob. ausavense* n. ssp. of Becker et al. 2004) occur, however, even earlier, in the upper part of the middle Frasnian (UD I-H).

Genus *Linguatornoceras* House, 1965

Linguatornoceras cf. *clausum* (Glenister, 1958), emended
Figures 8k, 11g–h; Tables 1, 2

*	1958	*Tornoceras* (*Tornoceras*) *clausum* Glenister: 92–93, text-fig. 16A, C, pl. 15, figs. 7–9
v non	2000	*Linguatornoceras* aff. *clausum*—Becker et al.: 75, 77, 91, 93, fig. 7E (not 7D as stated in fig. caption), pl. 2, figs. 9–10
v	2000	*Linguatornoceras clausum*—Becker et al.: 78, 79, 80, 93, 94, 96, 97, fig. 7F (not 7E as stated in fig. caption)
	2002	*Linguatornoceras clausum*—Korn and Klug: 158, figs. 144C, P
non	2002	*Linguatornoceras* sp. aff. *L. clausum*—Dzik: figs. 53K–N [=compressed *Tornoceras*]
cf.	2006	*Linguatornoceras* aff. *clausum*—Woroncowa-Marcinowska: 135–137, figs. 29A, 32A–B
e.p.	2008	*Linguatornoceras linguum*—House and Kirchgasser: 167, pl. 27, fig. 13 [non fig. 14 = *T. holwilli*]

Holotype. 1756 (Geoscience Australia, formerly BMR, Canberra).

Material. MB.C.29381, MB.C.29382, MB.C.29383.

Type locality. Section RS 190, McWhae Ridge area, SE of Bugle Gap, Canning Basin of Western Australia.

Type level. Virgin Hills Formation, upper Frasnian. Glenister (1958) noted its co-occurrence with *Ponticeras retorquatum*, which enters at the base of UD I-J (Becker et al. 1993; Becker and House 2009).

Diagnosis (emended). Small-sized (up to ca. 50 mm dm); earliest stages until ca. 3 mm dm cadiconic, with ww/dm decreasing from 0.80 to 0.70, ww/wh decreasing from 2.50 to 1.60, low whorl expansion rate (WER 1.60–1.70), and uw/dm reaching 0.20; after the third whorl gradually weakly depressed (until 6 mm dm) to increasingly compressed (ww/wh down to 0.80–1.10), thinly pachyconic, with umbilicus completely closing after the third whorl, at 20 mm dm extremely high, slightly tegoid conch (WER 2.50–2.70),

weakly compressed (ww/wh 0.70–0.90), with rounded umbilical wall, highest whorl width in the midflank area, and weakly rounded venter. Growth lirae strongly biconvex, with a wide lateral sinus, broad and high ventrolateral projection, and a deep, moderately wide, U-shaped ventral sinus. Suture with a moderately broad, asymmetrically arched, high dorsolateral saddle, deep, lingulate, markedly outwards curved A-lobe, high, asymmetric, obliquely rounded ventrolateral saddle with the same height as dorsolateral saddle, and a subparallel, narrow, short E-lobe.

Description. MB.C.29381 is the best-preserved specimen among the Sand material and fully septate at 16.5 mm dm (Fig. 11g–h). In general, it resembles the larger Canning Basin types, especially in terms of sutures (Fig. 8k), whorl height (WER 2.67), and cross-section. However, it is somewhat more rotund, with a ww/wh of 0.97, whilst the figured cross-section of Canning Basin paratype 1757 (Glenister 1958) suggests a rate of only 0.75–0.80 at ca. the same size. A similar suture as in the types is visible on MB.C.29382 at only 4.6 mm dm. In contrast, MB.C.29383 is a partially preserved internal mould, which differs in a slightly shorter A-lobe. However, it is still deeper than the A-lobe of *Tornoceras* and slightly asymmetrical. All specimens are strictly involute, have rounded and slightly converging flanks, a rounded venter, and lack ventrolateral furrows. "Housean Pits" are preserved in MB.C.29383.

Remarks. The emended diagnosis employs the paratype cross-section of Glenister (1958). However, the intraspecific variability of the Canning Basin species has not yet been established and it is not clear whether there are possibly morphometric changes from zone to zone within the upper Frasnian. Due to the whorl width difference between our Sand specimens and the sectioned Australian paratype, we assign our material with a cf. to *Ling. clausum*. In *Ling. linguum*, the A-lobe is more symmetric. In *Ling. yudinae* it is very similar as in *Ling. clausum* but the species is characterized by a narrow ventrolateral furrow and dense ventral varices. Varices characterize also the poorly known *Ling. restrictum* (Eichwald, 1851). Based on the re-examination of its holotype, *Ling. nummularium* (Roemer, 1843) is much more compressed. All named Famennian linguatornoceratids possess a hook-shaped, subangular A-lobe. The middle Frasnian *Ling.* aff. *clausum* sensu Becker et al. (2000) and Becker and House (2009) combines *Ling. linguum*-type sutures with a rounded, tegoid cross-section; this form is intermediate between *T. holwilli* and *Ling. clausum*.

Table 4 Adult characteristics of species within the genus *Crassotornoceras*

Species	Cross-section	Size of umbilicus	Ribs	Varices	Furrows
anissi	Weakly depressed	Open	None	6–8 p. wh.	None
belgicum	Weakly compressed	Open	Lateral	3–5 p. wh.	None
aff. *belgicum*	Weakly compressed	Punctiform	Lateral	3–5 p. wh.	Weak
crassum	Weakly depressed	Open	None	3–5 p. wh.	None
hetzeneggeri sp. nov.	Weakly depressed	Punctiform	Weak, lateral	None	None
isolatum	Weakly depressed	Open	Lateral	None	None
nitidum	Weakly depressed	Open	None	3–5 p. wh., ventral	None
nudum sp. nov.	Weakly compressed	Punctiform	None	None	None

Table 5 Conch ontogeny of *Crassotornoceras belgicum* (Matern, 1931b)

dm	Conch shape	Whorl cross-section shape	Whorl expansion
3 mm	Thinly pachyconic; subinvolute (ww/dm ~ 0.65; uw/dm = 0.15–0.20)	Weakly depressed; moderately embracing (ww/wh ~ 1.10–1.30; IZR ~ 0.30)	Moderate (WER ~ 1.90–1.95)
6.5 mm	Thinly discoidal; involute (ww/dm ~ 0.45; uw/dm = 0.10–0.15)	Weakly compressed; strongly embracing (ww/wh ~ 0.90–1.00; IZR ~ 0.40)	High (WER ~ 2.00–2.10)

Stratigraphic range. In the Canning Basin type-region, the species enters at the base and ranges almost to the top of the upper Frasnian (UD I-I$_1$ to I-L$_1$). The same lower range is observed in the Timan (Becker et al. 2000). Unpublished material from the lower Famennian of the Cox Quarry in Bergisch Gladbach and from Nehden (both UD II-D) suggests that *Ling. clausum* or close relatives belonged to the few survivors of the global Kellwasser Crisis, but with a Lazarus Phase for the first six Famennian conodont zones (UD II-A to C).

Linguatornoceras linguum (Sandberger and Sandberger, 1851/52), emended
Figures 8l; 11i, j; Tables 1, 2

v * 1851/52 *Goniatites retrorsus* var. *lingua* Sandberger and Sandberger 1851: pl. 10, figs. 20–21; 1852: 109

e.p. 1895 *Tornoceras simplex* Mut. *ovata* Münster—Holzapfel: fig. 6 [only]

v 1908 *Goniatites retrorsus var. lingua*—Schöndorf: 47 [lectotype]

non 1965 *Tornoceras* (*Linguatornoceras*) aff. *linguum*—House: 112–113, fig. 13E, pl. 9, figs. 82–83 [=*T. holwilli*]

v 1993a *Linguatornoceras linguum*—Becker: 188, figs. 69a, 70d, pl. 3, figs. 13–14 [lectotype]

e.p. 2002 *Linguatornoceras lingua*—Korn and Klug: 158, [non figs. 144E, H = *L. haugi*]

non 2008 *Linguatornoceras* aff. *linguum*—House and Kirchgasser: 167–168, text-figs. 56A–F, pl. 27, fig. 12, pl. 33, figs. 1–2, 5–8. tab. 26 [=*T. holwilli* and relatives]

non 2008 *Linguatornoceras linguum*—House and Kirchgasser: 167, pl. 27, figs. 13–14 [fig. 13 = *Ling. clausum*, fig. 14 = *T. holwilli*]

Lectotype. MWNH-PA-SDB-55 (Museum Wiesbaden, Wiesbaden), designated by Becker (1993a).

Material. MB.C.29384.1, MB.C.29384.2, MB.C.29384.3, MB.C.29384.4, MB.C.29385, MB.C.29386.1, MB.C.29386.2, MB.C.29386.3, MB.C.29386.4, MB.C.29386.5, MB.C.29386.6, MB.C.29386.7.

Type locality. Büdesheim, Eifel.

Type level. Büdesheim Goniatite Shale, upper Frasnian, UD I-I/J.

Diagnosis (emended). Small-sized; conch changing from thinly pachyconic and weakly depressed (ww/dm 0.65 and ww/wh 1.10 at 4 mm dm) gradually to thinly discoidal and increasingly compressed (ww/dm 0.40 and ww/wh 0.70 at 25 mm dm), with flattened, slightly converging flanks and a slender, rounded venter, and very high (WER 2.40 at 9 mm dm) to high (WER 2.10 at 25 mm dm) whorl expansion
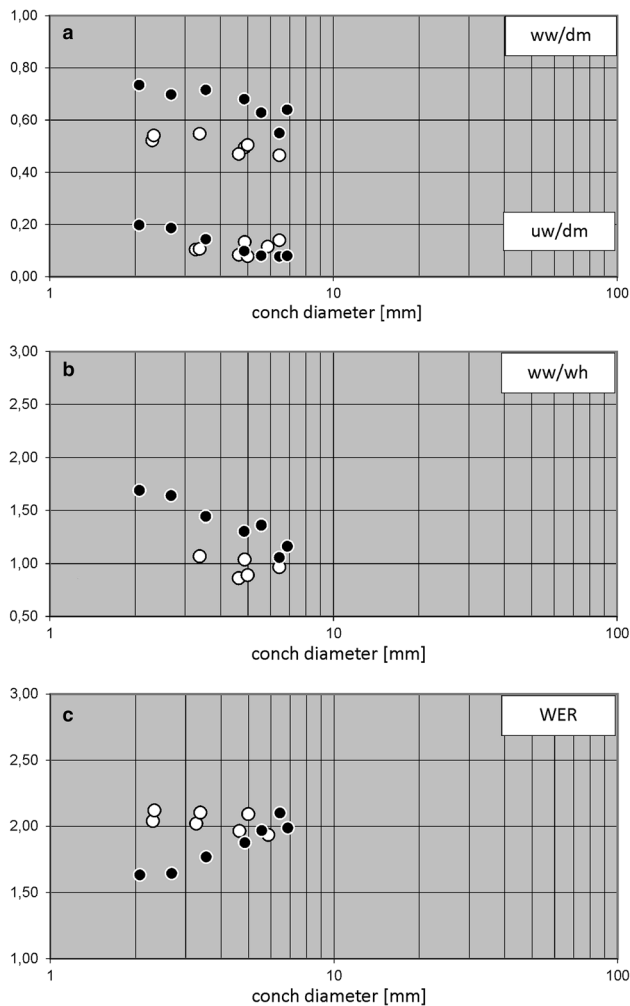
Fig. 10 Conch ontogeny of *Crassotornoceras nudum* sp. nov. (white circles) and *Cr. hetzeneggeri* sp. nov. (black circles). **a** conch width index (ww/dm) and umbilical width index (uw/dm), **b** whorl width index (ww/wh), **c** whorl expansion rate (WER)

rate; umbilicus probably closed at maturity (uw/dm < 0.05) and no varices. Growth lines biconvex, with a broadly rounded lateral sinus, narrow, high ventrolateral projection, and relatively narrow ventral sinus. Suture with a broad, asymmetrically arched dorsolateral saddle, subsymmetric, deep, lingulate A-lobe, narrow, high, asymmetrically rounded ventrolateral saddle, and small, short, and narrow E-lobe.

Description. The Sand specimens range in size between 5.6 mm (MB.C.29384.2) and ca. 25 mm diameter (fragmentary MB.C.29386.5), the same size as the lectotype (Becker 1993a). Despite its limited preservation, MB.C.29386.5 can confirm that the species becomes thinly discoidal towards maturity. The best preserved specimens are MB.C.29386.2 (Fig. 11i–j) and MB.C.29386.4. The first is fully septate at 7.85 mm dm and shows a deep, moderately wide,

symmetrically rounded, lingulate A-lobe and a slightly divergent, short, narrow E-lobe (Fig. 8l). Its umbilical margin is very short, from where the flanks converge towards a moderately narrow venter with rounded edges. MB.C.29386.4 is somewhat thicker (Table 2) and fully preserved at 9.1 mm dm. The body chamber occupies at least 180°. Partly, it displays the inner suture with a deep, narrowly rounded I-lobe. "Housean Pits" are preserved in MB.C.29386.3. Growth lines could not be observed on any specimen.

Remarks. Ontogenetic changes and intraspecific variability of the Büdesheim type population is part of ongoing research. In the Büdesheim lectotype, the A-lobe is somewhat narrower than in our specimens and slightly asymmetric whilst the ventrolateral saddle becomes as high as the dorsolateral saddle; this may reflect size differences and variability. *Linguatornoceras* aff. *linguum* sensu House (1965) and House and Kirchgasser (2008) lack a true lingulate A-lobe and are related to *T. holwilli*. In the middle Frasnian, Russian *Ling.* aff. *clausum* sensu Becker et al. (2000) the flanks are better rounded than in *Ling. linguum* and the ventrolateral saddle is slightly lower.

Stratigraphic range. UD I-I/J of Büdesheim to UD I-K of Sand, possibly ranging to the Frasnian top (UD I-L).

***Linguatornoceras* sp. 1**
Figures 8m, 11k–l; Tables 1, 2

Material. MB.C.29387.

Description. The fully septate specimen MB.C.29387 is a well-preserved internal mould of 5.4 mm in diameter that shows shell form and sutures. The umbilicus is punctiform (uw/dm 0.07, Fig. 11k), with a very short, rounded umbilical wall. The conch is thinly discoidal and weakly compressed (ww/dm 0.42 and ww/wh 0.98), with a maximum whorl width on the inner flanks, converging from there with gentle curvature towards the slightly edged venter (Fig. 11l). The whorl expansion rate is moderate (WER 1.92). There are no ribs, varices or impressed growth lines. The suture is distinctive because of the moderately wide, asymmetrically rounded A-lobe and the ventrolateral saddle that remains slightly lower than the strongly asymmetric, broad dorsolateral saddle. The sutural relief is moderate and the septal spacing of the last three sutures is reduced. Only a short part of the body chamber is preserved.

Remarks. The dense spacing of the last three sutures reflects slowed growth despite the small size, probably due to the onset of unfavourable environmental conditions (Davis et al. 1996; Kraft et al. 2008; Klug et al. 2015). Noteworthy are
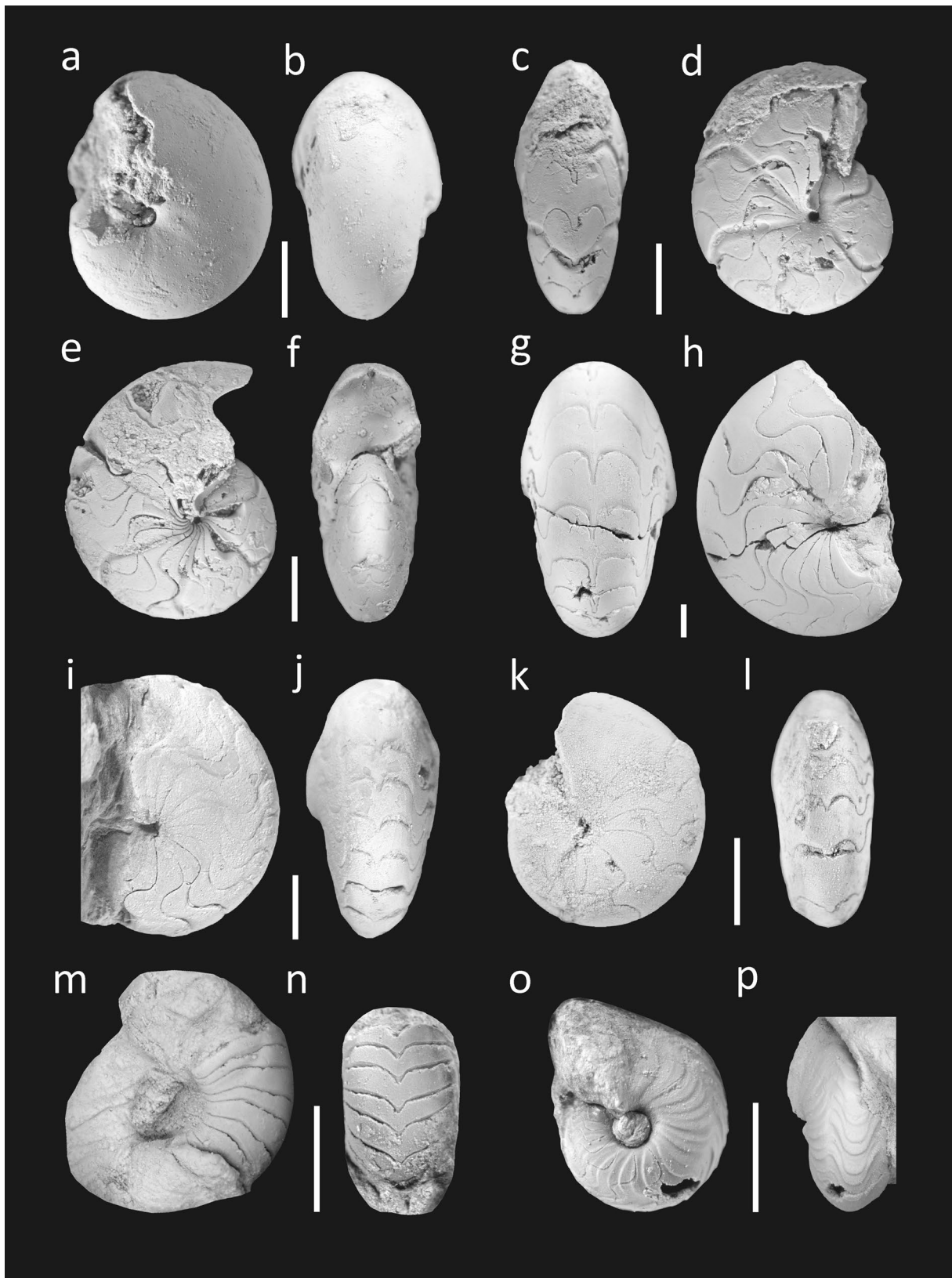
◄**Fig. 11** Tornoceratidae from the upper Frasnian Sand Formation (scale bar 2 mm). **a**, **b** *Crassotornoceras hetzeneggeri* sp. nov., holotype MB.C.29375, showing the punctiform umbilicus, a well-rounded, pachyconic conch form, incipient dorsolateral ribbing, and traces of growth ornament with high ventrolateral projection; lateral and ventral views, Sand 3, ×7, **c**, **d** *Lobotornoceras ausavense* (Steininger, 1849), MB.C.29388.1, displaying five weakly biconvex to subconvex varices, an asymmetric subdivision of the L-lobe at the umbilical seam, and deep, symmetrical A-lobe; ventral and lateral views, Sand 3, ×6.5, **e**, **f** *Lob. ausavense* (Steininger, 1849), MB.C.29388.2, showing a symmetric subdivision of the L-lobe at the umbilical seam and the deep I-lobe; lateral and ventral views, Sand 3, ×6, **g**, **h** *Linguatornoceras* cf. *clausum* (Glenister, 1958), MB.C.29381, relatively thick specimen displaying the deep, asymmetrically lingulate A-lobe; ventral and lateral views, Sand 3, ×3, **i**, **j** *Ling. linguum* (Sandberger and Sandberger, 1850/51), MB.C.29386.2, weakly compressed mould with flattened flank and deep, lingulate A-lobe; lateral and ventral views, Sand A, ×6, **k**, **l** *Ling.* sp. 1, MB.C.29387, with slightly edged venter and asymmetrical A-lobe; lateral and ventral views, Sand A, ×8, **m**, **n** *Retrotornoceras juxi* sp. nov., holotype MB.C.29393, with open umbilicus and simple suture lacking an A-lobe; lateral and ventral views, Sand 4, ×11, **o**, **p** *Aulatornoceras auris* (Quenstedt, 1846), MB.C.29346.4, with characteristic ventral festoons following the lateral growth line bundles; lateral and ventral views, Sand 1, ×10

"Housean Pits", which occur on both sides on the mid- and outer flanks. *Linguatornoceras* sp. 1 belongs to the group of early linguatornoceratids that lack varices, such as *Ling. linguum, Ling.* aff. *clausum*, and *Ling. clausum*. All three taxa are thicker at the same size (ww/dm > 0.50), still slightly depressed, and lack subangular ventral edges. The asymmetric shape of the A-lobe resembles *Ling. clausum* but the ventrolateral saddle is lower, which, however, could be a juvenile feature. In *T. holwilli* and the closely related *T. typum*, which shares with *Ling.* sp. 1 the flattened flanks, the A-lobe is more rounded and divergent, not lingulate. We prefer to put this species in open nomenclature, because only one specimen with signs of ecological stress ist available. More and better-preserved material from the Büdesheim locality is available.

Stratigraphic range. Restricted to the upper Frasnian (UD I-K).

Genus ***Retrotornoceras*** House, 2002

Retrotornoceras juxi sp. nov.
Figures 8n, 11m–n; Tables 1, 6

Etymology. After the late Prof. Ulrich Jux (Bergisch Gladbach, University of Cologne), who contributed during his lifetime a considerable amount to the knowledge of the Sand Formation.

Holotype. MB.C.29393 (Museum für Naturkunde Berlin).

Type locality. Sand 4, construction site at the Herkenrather Straße 70 of Bergisch Gladbach-Sand.

Type level. Sand Formation, upper Frasnian, UD I-K.

Diagnosis. Very small-sized; conch at ca. 5 mm dm subinvolute (uw/dm 0.28), discoidal (ww/dm 0.45), weakly depressed (ww/wh 1.25), with rounded inner flanks and broad, gently rounded venter; indistinctive, concave flank varices. Suture simplified, with a shallow, widely rounded, dorsolateral L-lobe, low, broadly rounded dorsolateral saddle, an incipient, wide (reduced) A-lobe descending obliquely towards the small, narrow, V-shaped E-lobe.

Description. The holotype is a small, incomplete, fully septate internal mould representing ca. a half whorl. Its simple suture is very distinctive (Figs. 8n, 11m–n) and characterized by a L-lobe extending considerably on the rounded umbilical wall. The A-lobe is very wide and extremely shallow in the first septa and completely reduced in later ones. The small E-lobe is pointed and divergent. Growth lines could not be observed. A shallow, concave flank varix occurs at the end of the preserved phragmocone (Fig. 11m).

Remarks. Despite its incomplete preservation, the morphology of our new form is very distinctive and unlike as in any other described Frasnian goniatite. The reduced A-lobe and general conch shape leads to an assignment to *Retrotornoceras*, a rare form that was previously only described from SW England (House 2002). The British *Retro. alobatum* is more slender and weakly compressed at 6 mm dm (ww/wh 0.81) and possesses a smaller umbilicus (uw/dm 0.15). Furthermore, its sutures seem to be even more reduced. Paratype NHM C18451 of *Retro. alobatum* (House 2002: pl. 3, fig. D) shows a dorsolateral L-lobe, as in our *Retro. juxi* sp. nov., but unlike as in the drawing of the holotype suture.

Stratigraphic range. Restricted to the upper Frasnian (UD I-K).

Subfamily **Aulatornoceratinae** Becker, 1993a (nom. transl. Korn and Klug 2002)

Genus ***Aulatornoceras*** Schindewolf, 1922

Remarks. Within *Aulatornoceras*, there are several species groups (see discussion in House and Kirchgasser, 2008), which need to be re-fined: In the *Aul. auris* Group, including also *Aul. paucistriatum* (D'Archiac and De Verneuil, 1842), *Aul. rhysum* (Clarke, 1898), *Aul. bickense* (Wedekind, 1918), *Aul. constrictum* (Steininger, 1849), *Aul. serriense* Becker, 1993a, *Aul. steinhauseni* sp. nov., *Aul. frenklerae* sp. nov. and *Aul. tumidum* House, 2002, the A-lobe is mostly lingulate, the ventral band often strong, and WER

Table 6 Conch dimensions of Bergisch Gladbach-Sand Tornoceratidae [in mm]

Specimen	dm	wh	ah	ww	uw	ww/wh	uw/dm	ww/dm	WER	IZR
Retrotornoceras juxi sp. nov. from the Sand Formation										
MB.C.29393	4.80	1.73	–	2.14	1.35	1.24	0.28	0.45	–	–
Aulatornoceras auris (Quenstedt, 1846) from the Sand Formation										
MB.C.29346.1	3.41	1.74	–	–	0.53	–	0.16	–	–	–
MB.C.29346.4	3.55	1.73	1.00	–	0.70	–	0.20	–	1.94	0.35
MB.C.29346.3	4.63	2.40	–	–	0.72	–	0.16	–	–	–
MB.C.29346.5	13.60	7.10	–	5.40	2.25	0.76	0.17	0.40	–	–
Aulatornoceras constrictum (Steininger, 1849) from the Sand Formation										
MB.C.29349.2	2.35	1.20	–	1.60	0.45	1.33	0.19	0.68	–	0.38
MB.C.29348.1	5.39	2.37	–	3.10	1.20	1.31	0.22	0.58	–	–
MB.C.29348.2	6.80	3.09	–	3.85	1.46	1.25	0.21	0.57	–	–
MB.C.29349.1	7.06	3.34	2.00	3.00	1.26	0.90	0.18	0.42	1.95	0.40
Aulatornoceras aff. *constrictum* (Steininger, 1849) from the Sand Formation										
MB.C.29355	3.10	1.45	0.93	1.70	0.52	1.17	0.17	0.55	2.05	0.36
Aulatornoceras eifliense (Steininger, 1849) from the Sand Formation										
MB.C.29351.1	5.33	3.05	1.75	2.70	0.30	0.89	0.06	0.51	2.22	0.43
MB.C.29351.2	6.00	3.45	2.20	3.10	0.40	0.90	0.07	0.52	2.49	0.36
Aulatornoceras steinhauseni sp. nov. from the Sand Formation										
MB.C.29356.4	3.77	2.00	–	1.85	0.60	0.93	0.16	0.49	–	–
MB.C.29356.2	5.21	2.80	–	–	0.77	–	0.15	–	–	–
MB.C.29356.3	5.67	3.00	–	2.50	0.60	0.83	0.11	0.44	–	–
MB.C.29356.1	5.83	3.24	2.00	3.00	0.60	0.93	0.10	0.51	2.32	0.38
Aulatornoceras frenklerae sp. nov. from the Sand Formation										
MB.C.29359 (internal)	3.80	2.20	1.25	2.62	0.55	1.19	0.14	0.69	2.22	0.43
MB.C.29357.2	4.00	2.00	–	–	0.40	–	0.10	–	–	–
MB.C.29359 (external)	7.71	3.87	1.90	4.20	0.80	1.09	0.10	0.54	1.76	0.51
Aulatornoceras ventrosulcatum sp. nov. from the Sand Formation										
MB.C.29360	4.05	2.10	1.32	2.20	0.60	1.05	0.15	0.54	2.20	0.37
Aulatornoceras aff. *ventrosulcatum* from the Sand Formation										
MB.C.29354	3.00	1.50	0.85	1.80	0.60	1.20	0.20	0.60	1.95	0.43

moderately high to high. The very poorly known *G. discus* Roemer, 1850 (re-named as *G. simile* by Giebel 1852 due to homonymy with a Carboniferous species) and *G. ammonitoides* Trenkner, 1867 may belong here, too (see discussion in Clarke, 1884). In the *Aul. eifliense* Group, including also *Aul. posterior* Becker, 1993a, *Aul. schurbuschense* Becker in Becker et al. (2016), and *Aul. ventrosulcatum* sp. nov. the umbilicus is narrower, the A-lobe also lingulate, the ventral band often weak, and WER high to extremely high. In advanced Famennian species, such as *Aul. lepiferum* Becker, 1993a and *Aul. compressum* (Grüneberg, 1925), the A-lobe is deep and wide, transitional towards *Polonoceras*. Some of the Sand specimens put in open nomenclature (*Aul.* aff. *constrictum*, *Aul.* aff. *ventrosulcatum*) could belong to a fourth, probably more ancestral group characterized by a wide A-lobe and low relief of the suture.

Aulatornoceras auris (Quenstedt, 1846), emended
Figures 9e, 11o–p, 12a–b, 13a–b; Tables 1, 6, 7

|		
*	1846	*Goniatites auris* Quenstedt: 64, pl. 3, figs. 7a–c
	1958	*Tornoceras* (*Aulatornoceras*) *auris auris*—House: 181–183, pl. 20, figs. 1–2, 4, 6–8; pl. 22, fig. 4 [further synonymy there]
v	1985	*Aulatornoceras auris*—House and Price: pl. 16, figs. 5–7; pl. 17, figs. 1–7. [pl. 17, figs. 1–4 = neotype]
v cf.	2000	*Aulatornoceras* cf. *auris*—Becker et al.: 78, fig. 4
cf.	2002	*Aulatornoceras* cf. *auris*—Dzik: fig. 51D
	2002	*Aulatornoceras auris*—Korn and Klug: 161, fig. 149A
e.p.	2002	*Aulatornoceras auris*—House: 276, figs. 3A–B, pl. 3, figs. B, C [fig. 3C = *Aul.* cf. *auris*]
	2008	*Aulatornoceras auris*—House and Kirchgasser: 176, text-fig. 60G, pl. 31, figs. 2–3
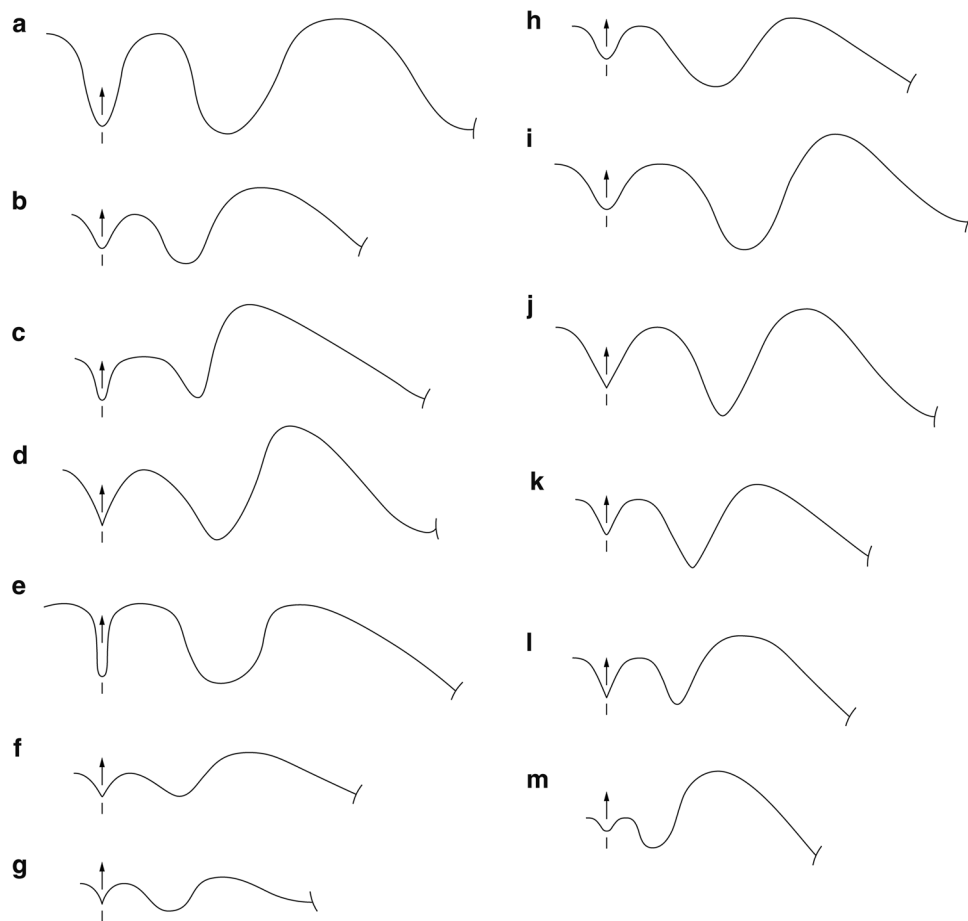
Fig. 12 Sutures of Aulatornoceratinae from Bergisch Gladbach-Sand. **a** *Aulatornoceras auris* (Quenstedt, 1846), MB.C.29346.5, Sand 1, at 4.00 mm wh, **b** *Aul. auris* (Quenstedt, 1846), MB.C.29346.4, Sand 1, at 1.10 mm wh, **c** *Aul. constrictum* (Steininger, 1849), MB.C.29348.2, Sand A, at 2.05 mm wh, **d** *Aul. constrictum* (Steininger, 1849), MB.C.29349.1, Sand A, at 2.14 mm wh, **e** *Aul. eifliense* (Steininger, 1849), MB.C.29353.1, Sand A, at 2.31 mm wh, **f** *Aul.* aff. *ventrosulcatum*, specimen MB.C.29354, Sand 1, at 1.05 mm wh, **g** *Aul.* aff. *constrictum* (Steininger, 1849), specimen MB.C.29355, Sand 1, at 0.80 mm wh, **h** *Aul. steinhauseni* sp. nov., holotype MB.C.29356.1, Sand 1, at 1.70 mm wh, **i** *Aul. frenklerae* sp. nov., holotype MB.C.29359, Sand A, at 2.90 mm wh, **j** *Aul. frenklerae* sp. nov., holotype MB.C.29359, Sand A, at 2.10 mm wh, **k** *Aul. frenklerae* sp. nov., paratype MB.C.29358, Sand 4, at 1.32 mm wh, **l** *Aul. frenklerae* sp. nov., holotype MB.C.29359, Sand A, at 1.25 mm wh, **m** *Aul. ventrosulcatum* sp. nov., holotype MB.C.29360, Dombach-Sander-Straße, at 0.90 mm wh

Table 7 Conch ontogeny of *Aulatornoceras auris* (Quenstedt, 1846)

dm	Conch shape	Whorl cross-section shape	Whorl expansion
2.5 mm	Thinly pachyconic; subinvolute (ww/dm ~ 0.65; uw/dm = 0.20–0.25)	Moderately depressed; strongly embracing (ww/wh ~ 1.60; IZR ~ 0.35)	Moderate (WER ~ 1.80)
10 mm	Thickly discoidal; subinvolute (ww/dm ~ 0.50; uw/dm = 0.15–0.20)	Weakly depressed; strongly embracing (ww/wh ~ 1.00–1.20; IZR ~ 0.35–0.40)	Moderate (WER ~ 1.75–1.85)
16 mm	Thinly discoidal; subinvolute (ww/dm ~ 0.40–0.45; uw/dm = 0.15)	Weakly compressed;– (ww/wh ~ 0.75–0.80; –)	Moderate (WER ~ 1.85)

Neotype. SedgM H9943 (Sedgwick Museum of Earth Sciences, Cambridge), designated by House and Price (1985).

Material. MB.C.29346.1, MB.C.29346.2, MB.C.29346.3, MB.C.29346.4, MB.C.29346.5, MB.C.29347.

Table 8 Conch ontogeny of *Aulatornoceras constrictum* (Steininger, 1849)

dm	Conch shape	Whorl cross-section shape	Whorl expansion
2.5 mm	Thinly pachyconic; subinvolute (ww/dm ~ 0.70; uw/dm = 0.20)	Weakly depressed; moderately embracing (ww/wh ~ 1.45; IZR ~ 0.25)	Moderate (WER ~ 1.85)
7 mm	Thinly discoidal; subinvolute (ww/dm ~ 0.40–0.50; uw/dm = 0.15)	Weakly compressed; strongly embracing (ww/wh ~ 0.90–1.00; IZR ~ 0.40)	Moderate (WER ~ 1.95)

Type locality. Büdesheim, Eifel.

Type level. Büdesheim Goniatite Shale, upper Frasnian, UD I-I/J.

Diagnosis (emended). Very small-sized; early stages thinly pachyconic and moderately depressed (ww/dm 0.65 and ww/wh 1.60 at 2.5 mm dm), becoming gradually thinly discoidal and weakly compressed (ww/dm 0.40–0.45 and ww/wh 0.75–0.80 at 16 mm dm), subinvolute (uw/dm 0.15–0.25 between 5 and 15 mm dm), relatively constant whorl expansion rates (WER 1.75–1.95), with short, rounded umbilical wall, gently rounded flanks, and flattened venter, bordered at maturity by ventrolateral edges; no varices. Strongly biconvex, bundled growth lines with low and broad dorsolateral salient, wide lateral sinus, very prominent, narrow ventrolateral projection lying in a spiral furrow, and a deep, U-shaped ventral sinus. The lateral bundles continue on the venter as festoons of a marked ventral band; bundle density and festoon numbers increase with growth. Suture with a broad, asymmetrically ascending dorsolateral saddle, deep and narrow, lingulate, slightly asymmetric A-lobe, moderately broad, asymmetrically rounded ventrolateral saddle that remains slightly lower than the dorsolateral saddle, and very narrow, slightly divergent E-lobe.

Description. MB.C.29346.5 is the largest representative from Sand reaching 13.6 mm dm, which is larger than the neotype (9 mm dm) but smaller than an incomplete topotype figured by House and Price (1985: pl. 17, figs. 5–7, 19–20 mm dm). Our specimens display the characteristic, strongly biconvex, bundled growth lines with broad lateral sinus, very high, tongue-shaped ventrolateral projection, and deep, moderately wide ventral sinus (Figs. 9e, 12a–b). In MB.C.29346.5, the ventral festoons are weaker and more closely spaced than in the neotype, resembling the ornament of the mentioned larger topotype. There are three finer lirae between the main lirae marking individual chapters of the ventral band. Other, smaller specimens display variably similar (MB.C.29347) or stronger bundles and festoons (MB.C.29346.4, Fig. 11o–p). In general, the ornament tends to get finer with growth. There is a limited intraspecific variation of umbilical width, where MB.C.29346.5 is a typical specimen (uw/dm 0.17), while the umbilicus of MB.C.29346.4 is slightly wider at a smaller size (uw/dm

0.20). The comparison of juvenile (MB.C.29346.4, Fig. 12b) and adult (MB.C.29346.5, Fig. 12a) sutures show that the ventrolateral saddle rises during ontogeny, but without reaching the height of the dorsolateral saddle.

Remarks. Aulatornoceras auris is defined by the lack of true varices. In the neotype of House and Price (1985), the strong flank bundles and festoons produce 12 shallow depressions per whorl that slightly resemble varices. But this type of ornament is different from the much more widely-spaced regular varices on the mould of the otherwise similar *Aul. constrictum* and of the much thicker *Aul. tumidum*. Some specimens of *Aul. auris* from Büdesheim suggest, that the umbilicus can be more open in juvenile stages (uw/dm up to 0.30). *Aulatornoceras paucistriatum* is even more evolute (uw/dm > 0.30). The North American *Aul. rhysum* is very close, if not conspecific with *Aul. auris*, and displays even stronger flank bundles and ventral festoons.

Stratigraphic range. So far restricted to the upper Frasnian (UD I-I to UD I-L).

Aulatornoceras constrictum (Steininger, 1849)
Figures 9f, 12c–d, 13c–j; Tables 1, 6, 8

*   1849   *Goniatites constrictus* Steininger: 27

      1853   *Goniatites constrictus*—Steininger: 43, pl. 1, fig. 9

      1902   *Tornoceras constrictum*—Frech: 49, figs. 11b–c

      1918   *Tornoceras constrictum*—Wedekind: 136

non 1925   *Tornoceras (Aulatornoceras) ?constrictum*—Grüneberg: 67, pl. 1, fig. 11 [= juvenile *Ling. guestphalicum*]

v cf. 2000   *Aulatornoceras bickense*—Becker et al.: fig. 9F; pl. 4, figs. 7–8

cf.   2002   *Aulatornoceras belgicum*—Dzik: figs. 52B–C, 53P–R, 54I–M, 56N–P

cf.   2002   *Aulatornoceras bickense*—House: 276, pl. 2, figs. M–N

Type. The Steininger Collection has been lost. A neotype from Büdesheim is required.

Material. MB.C.29348.1, MB.C.29348.2, MB.C.29349.1, MB.C.29349.2, MB.C.29349.3, MB.C.29349.4.

Type locality. Büdesheim, Eifel.

Type level. Büdesheim Goniatite Shale, upper Frasnian, UD I-I/J.

Diagnosis. see Steininger (1849).

Description. The early juvenile MB.C.29349.2 is weakly pachyconic, weakly depressed (ww/dm ca. 0.70 and ww/wh ca. 1.35 at 2.35 mm dm), and subinvolute (uw/dm 0.19). An ontogenetic change of the conch is expressed by MB.C.29349.1 (Fig. 13g–h), which has a subevolute (uw/dm 0.18 at 7 mm dm), weakly compressed (ww/wh 0.90), discoidal (ww/dm 0.42) conch with a short umbilical wall, gently rounded flanks, and moderately wide, slightly edged venter. It displays four distinctive varices on the last whorl, which follow the biconvex growth lines characterized by a high and very narrow ventrolateral projection lying in a moderately developed ventrolateral furrow. The ventral sinus is U-shaped, with a relatively flat base, and not as deep as the lateral sinus (Fig. 9f). The last whorl is mostly (ca. 280°) occupied by the body chamber; the specimen was mesodomic. The suture (Fig. 12d) contains a L-lobe extending onto the umbilical wall, a broad, very highly arched, asymmetrically rounded dorsolateral saddle, a deep, slightly asymmetric and rounded-subtriangular A-lobe, a curved, moderately broad ventrolateral saddle that reaches roughly 2/3 of the height of the dorsolateral saddle, and a divergent, V-shaped E-lobe. MB.C.29349.4 (Fig. 13i–j) differs from typical specimens by its rather chevron-shaped varices on the venter. Its cross-section is tegoid, the umbilicus more punctiform, but the weakly compressed, discoidal conch (ww/dm 0.50 at ca. 6 mm dm) fits into the ontogenetic trend. Both specimens, MB.C.29348.1 (Fig. 13c–d) and MB.C.29348.2 (Fig. 13e–f), represent slightly thicker variants of *Aul. constrictum* (see Table 6).

Remarks. The original illustration by Steininger (1853) showed a strongly involute, ca. 11.5 mm large goniatite from Büdesheim with slightly compressed, tegoid cross-section, high whorl expansion rate (WER 2.00), and three marked, biconvex varices on the last whorl. The illustration by Frech (1902) agrees in terms of whorl expansion rate, varices, and sutures. A correct understanding and emended diagnosis of *Aul. constrictum* depends on a future neotype. Until this neotype and a new type for *Aul. bickense* are selected, both species can not be distinguished properly. The small, lower Famennian *Aul. schurbuschense* (*Aul. auriforme* in Becker 1993a) differs in a very small (punctiform) umbilicus, lamellose ornament, weaker ventrolateral furrows, irregular spacing of the varices, and even smaller, lower ventrolateral saddle.

Stratigraphic range. Currently restricted to the upper Frasnian (UD I-I/J to UD I-K).

Aulatornoceras* aff. *constrictum (Steininger, 1849)
Figures 12g, 13p–q; Tables 1, 6

Material. MB.C.29355.

Description. The only available specimen MB.C.29355 possesses a thickly discoidal and weakly depressed conch (ww/dm 0.55 and ww/wh 1.17 at ca. 3 mm dm). It is subinvolute (uw/dm 0.17) and the whorl expansion rate is high (WER 2.05). The small specimen shows a tegoid whorl form with a maximum whorl width on the dorsolateral part of the flanks near the short, rounded umbilicall wall. Its body chamber occupies at least 190° (Fig. 13p–q). The rounded venter is bordered by ventrolateral double furrows, with weak U-shaped varices forming a weak ventral band displaying several intercalated growth lirae on each field (Fig. 13q). Impressions of the growth lines could not be observed on the internal mould. The suture is only moderately well preserved (Fig. 13p) and has a generally low relief, a dorsolaterally extended L-lobe, a low, broadly rounded dorsolateral saddle, a moderately wide and shallow, subsymmetric A-lobe, a small and low ventrolateral saddle, and a short, pointed, divergent E-lobe (Fig. 12g).

Remarks. The specimen differs from the closely related *Aul. constrictum* and *Aul.* aff. *ventrosulcatum* by its characteristic ventrolateral double furrows. Furthermore, no other aulatornoceratid possesses similar sutures even at juvenile stages. We prefer to put it in open nomenclature until more material allows to better characterize this probably new species.

Stratigraphic range. Restricted to the upper Frasnian (UD I-K).

Aulatornoceras eifliense (Steininger, 1849), emended
Figures 9g, 10e, 13k–m; Tables 1, 6, 9

*	1849	*Goniatites eifliensis* Steininger: 27
e.p.	1853	*Goniatites eifliensis*—Steininger: pl. 1, figs. 2, 2a [non pl. 1, figs. 3, 3a = *Aul.* cf. *auris*; see Foord and Crick 1897, Wedekind 1918, and Becker 1993a]
v e.p.	1850/51	*Goniatites retrorsus* var. *undulatus*—Sandberger and Sandberger: 103, 109, pl. 10, figs. 19a–c [neotype; ?pl. 10, fig. 18, non pl. 10, fig. 17, 17a = lectotype of *Truyolsoceras sandbergeri*, non pl. 10a = *?Falcitornoceras korni*]
e.p.	1902	*Tornoceras undulatus*—Frech: 49, figs. 12a, b [only]
v	1908	*Goniatites retrorsus var. undulatus*—Schöndorf: 47 [neotype]
	1918	*Tornoceras eifliense*—Wedekind: 137
	1993	*Aulatornoceras eifliense*—House and Kirchgasser: 276

Table 9 Conch ontogeny of *Aulatornoceras eifliense* (Steininger, 1849)

dm	Conch shape	Whorl cross-section shape	Whorl expansion
5.5 mm	Thickly discoidal; involute (ww/dm ~ 0.50; uw/dm = 0.05–0.10)	Weakly compressed; strongly embracing (ww/wh ~ 0.80–1.00; IZR ~ 0.35–0.45)	Very high (WER ~ 2.30–2.50)
8 mm	Thickly discoidal; involute (ww/dm ~ 0.55–0.60; uw/dm ~ 0.10)	Weakly compressed; strongly embracing (ww/wh ~ 0.80–0.90; IZR ~ 0.35)	Very high (WER ~ 2.45–2.50)

Table 10 Conch ontogeny of *Aulatornoceras steinhauseni* sp. nov.

dm	Conch shape	Whorl cross-section shape	Whorl expansion
4 mm	Thickly discoidal; subinvolute (ww/dm ~ 0.50; uw/dm = 0.15)	Weakly compressed;– (ww/wh ~ 0.95; –)	–
6 mm	Thinly discoidal; involute (ww/dm ~ 0.45; uw/dm = 0.10)	Weakly compressed; strongly embracing (ww/wh ~ 0.85; IZR ~ 0.40)	Very high (WER ~ 2.30)

v   1993a   *Aulatornoceras eifliense eifliense*—Becker: 216, pl. 9, figs. 4–6 [neotype]

2008   *Aulatornoceras eifliense*—House and Kirchgasser: 176–177, pl. 31, figs. 7–13, 16–20; tab. 31

Neotype. MWNH-PA-SDB-54 (Museum Wiesbaden, Wiesbaden), selected by Becker (1993a).

Material. MB.C.29350, MB.C.29351.1, MB.C.29351.2, MB.C.29352, MB.C.29353.1, MB.C.29353.2, MB.C.29353.3, MB.C.29353.4.

Type locality. Büdesheim, Eifel.

Type level. Büdesheim Goniatite Shale, upper Frasnian, UD I-I/J.

Diagnosis (emended). Small-sized; median stages (5–6 mm dm) thickly discoidal (ww/dm 0.50–0.55), weakly compressed (ww/wh ca. 0.90), involute (uw/dm ca. 0.07), with high whorls (WER 2.25–2.50), towards maturity increasingly compressed, thickly discoidal (ww/wh 0.70–0.75 and ww/dm ca. 0.45 at ca. 19 mm dm), with punctiform umbilicus, and very high whorls (WER ca. 2.50), tegoid cross-section (max. ww near the short, rounded umbilical wall), with weakly rounded venter bordered by canaliculate, narrow, ventrolateral furrows forming a minor, outer spiral ridge; no varices. Growth lines strongly biconvex, with short and low dorsolateral salient, wide lateral sinus, narrow and very high ventrolateral projection, and deep, U-shaped, moderately wide ventral sinus. Suture with an asymmetric, broad, highly arched dorsolateral saddle, deep, symmetrically rounded, lingulate A-lobe, high and slender ventrolateral saddle, and deep, narrowly rounded E-lobe.

Description. All sand specimens share a very high whorl expansion rate (WER 2.20–2.50) as well as a thickly discoidal and involute conch shape. Based on the comparison with the Büdesheim neotype, it seems that WER rates increase with growth whilst the umbilicus becomes extremely narrow. MB.C.29351.1 (Fig. 13k–m) closely resembles the neotype. As shown in Fig. 13l, its body chamber exceeds 220° (ca. 270° in the neotype). Growth lines are dense, weakly bundled (undulose) and display a high and narrow ventrolateral projection and broad, U-shaped ventral sinus (Fig. 9g). There is no marked ventral band; the ventral growth lirae are relatively closely spaced. The suture of MB.C.29353.1 (Fig. 11e) displays a broad, highly arched dorsolateral saddle, a subsymmetric, deeply rounded A-lobe, and a relatively narrow ventrolateral saddle, which reaches the height of the dorsolateral saddle. All Sand specimens show a very narrow and deep, scarcely rounded E-lobe, as in the neotype.

Remarks. The Sand specimens are very close to the neotype from Büdesheim. *Aulatornoceras eifliense* is part of a separate lineage within *Aulatornoceras* defined by high apertures and small umbilici (Becker 1993a). This lineage seems to have survived the Frasnian-Famennian boundary in parallel with the *Aul. auris* Group, giving rise in the lower Famennian to *Aul. posterior*.

Stratigraphic range. Ranges from the middle Frasnian (UD I-F) to upper Frasnian (UD I-K); but probably survived the Frasnian-Famennian boundary.

Aulatornoceras steinhauseni sp. nov.
Figures 2a–f, 9i, 12h; Tables 1, 6, 10

Etymology. After Harald Steinhausen (Cologne), for collecting some of the specimens of this publication and for his long, dedicated work in the regional palaeontological community.

Holotype. MB.C.29356.1 (Museum für Naturkunde Berlin).

Paratypes. MB.C.29356.2, MB.C.29356.3, MB.C.29356.4.

Type locality. Sand 1, construction site at the Herkenrather Straße 70 of Bergisch Gladbach-Sand.

Type level. Sand Formation, upper Frasnian, UD I-K.

Diagnosis. Very small-sized; conch changing between ca. 4–6 mm dm from thickly (ww/dm 0.50) to thinly discoidal (ww/dm 0.45), becoming increasingly compressed (from ww/wh 0.95 down to 0.85), more involute (uw/dm from 0.15 down to 0.10), always with strongly tegoid cross-section, very high whorls (WER ca. 2.30), and narrowly rounded venter bordered by weak to only incipient ventrolateral furrows. Strongly biconvex, undulose or bundled growth lines with short and low dorsolateral salient, wide lateral sinus, very high, narrow, subtriangular ventrolateral projection, and very deep, divergent, nearly V-shaped ventral sinus lying in a ventral band demarcated by fine lirae and prominent ventral varices that follow the course of the growth lines. Suture with a broad, asymmetrically arched dorsolateral saddle, moderately wide, asymmetrically rounded A-lobe, a moderately narrow, asymmetrically rounded ventrolateral saddle that is lower than the dorsolateral saddle, and short, divergent E-lobe.

Description. Holotype MB.C.29356.1 (Figs. 2c–d, 12h) is an internal mould of ca. 6 mm dm that shows the suture, the typical tegoid cross-section, the narrow umbilicus (uw/dm 0.10) bordered by a short, rounded umbilical wall, and the ventrolateral furrow that become only distinctive on the body chamber, which occupies ca. the last half whorl. It shows well the characteristic, bundled, strongly biconvex growth lines with the high ventrolateral projection and deep, divergent, near V-shaped ventral sinus. There are seven, more or less equally spaced, also V-shaped ventral varices on the body chamber, which define festoons of the ventral band that correspond strictly to the lateral growth line bundles. Each festoon bears one or two, widely spaced, fine growth lirae. The suture is characterized by a moderately broad dorsolateral saddle that ascends obliquely from the umbilicus, a relatively wide and asymmetric, *Tornoceras*-type A-lobe, and the ventrolateral saddle that remains lower than the dorsolateral saddle during ontogeny.

On paratype MB.C.29356.4 (Fig. 2a–b), the lateral growth line bundles resemble those of *Aul. auris* but on the venter they are divergent, again with ca. two distinctive and widely spaced growth lirae per festoon. The ventrolateral projections do not lie in a distinctive furrow. The uw/dm ratio of 0.16 at ca. 3.8 mm dm suggests that the umbilicus does not open with growth in the species, resulting in decreasing relative proportions. Sutures are similar as in the holotype, again with a relatively wide A-lobe and low, asymmetric, obliquely rising ventrolateral saddle. Paratypes MB.C.29356.2 and MB.C.29356.3 (Fig. 2e–f) are similar to each other, display the typical suture, and, in constrast to larger specimens, both lack ventrolateral furrows at a small size. All specimens share isolated ventral growth lirae sitting in variably positions of a longer festoon (Fig. 2b–c, e).

Remarks. In terms of ornament, some variants of *Aul. auris* resemble *Aulatornoceras steinhauseni* sp. nov. (Fig. 11o–p) but these lack ventral varices and posses a narrower, lingulate A-lobe. The lower Famennian *Aul. lepiferum* can be easily distinguished by its tabulate venter with ventral edges and sutures with a higher, narrow ventrolateral saddle. *Aulatornoceras ventrosulcatum* sp. nov. lacks a prominent festoon-like ornament and the varices of *Aul. constrictum* reach the umbilicus.

Stratigraphic range. Restricted to the upper Frasnian (UD I-K).

Aulatornoceras frenklerae sp. nov.
Figures 2g–k, 12i–l; Tables 1, 6, 11

Etymology. Named after Helga Frenkler (Odenthal) for collecting and providing some of the specimens of this publication and for her ongoing contributions to the regional palaeontological community.

Holotype. MB.C.29359 (Museum für Naturkunde Berlin).

Paratypes. MB.C.29357.1, MB.C.29357.2, MB.C.29358.

Type locality. Sand 1, construction site at the Herkenrather Straße 70 of Bergisch Gladbach-Sand.

Type level. Sand Formation, upper Frasnian, UD I-K.

Diagnosis. Very small-sized; conch changing between ca. 4 and 8 mm dm from thinly pachyconic (ww/dm 0.65–0.70) to thickly discoidal (ww/dm 0.50–0.55), becoming gradually less depressed (from ww/wh 1.15–1.20 down to 1.05–1.10), always involute (uw/dm 0.10), with decreasing whorl expansion rates (WER 2.20 down to 1.80), well-rounded flanks and venter, developing only late in ontogeny incipient ventrolateral furrows; with widely spaced, strongly biconvex varices on the flanks and venter and weak ventral band. Suture with a deep, pointed I-lobe, rounded L-lobe
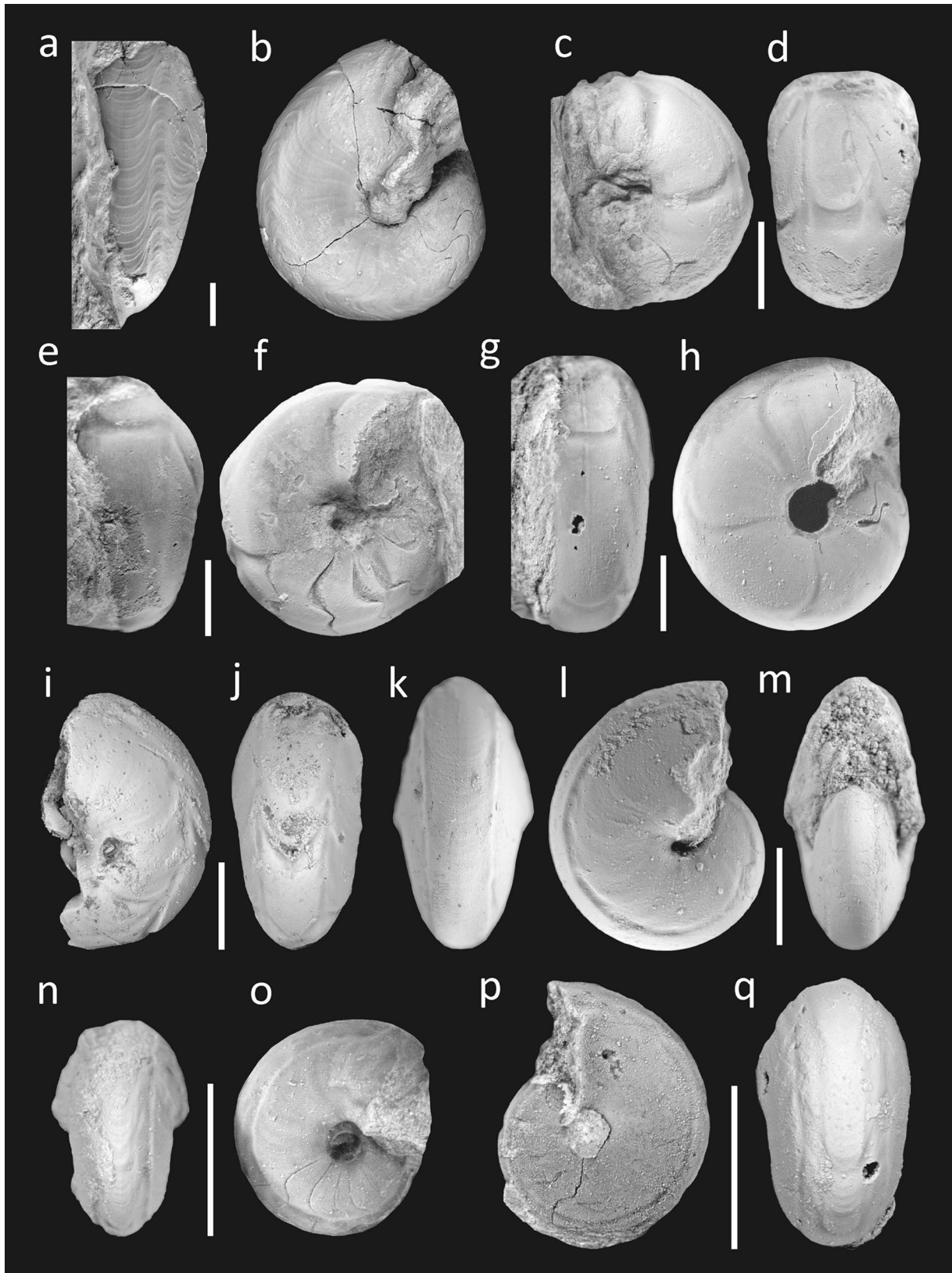
◀**Fig. 13** Aulatornoceratinae from the upper Frasnian Sand Formation (scale bar 2 mm). **a**, **b** *Aulatornoceras auris* (Quenstedt, 1846), MB.C.29346.5, subadult specimen displaying typical sutures, a ventrolateral groove and strongly biconvex growth lirae forming a ventral band; ventral and lateral views, Sand 1,×4, **c**, **d** *Aul. constrictum* (Steininger, 1849), MB.C.29348.1, small specimen showing ventrolateral furrows and regular, strongly biconvex varices; lateral and ventral views, Sand A,×8, **e**, **f** *Aul. constrictum* (Steininger, 1849), MB.C.29348.2, showing the varices and suture with a small ventrolateral saddle; ventral and lateral, Sand A,×7, **g**, **h** *Aul. constrictum* (Steininger, 1849), MB.C.29349.1, discoidal conch showing four varices and typical sutures; ventral and lateral views, Sand A,×7, **i**, **j** *Aul. constrictum* (Steininger, 1849), MB.C.29349.4, with regular varices, which are slightly more V-shaped on the venter than in typical specimens; lateral and ventral views, Sand A,×8, **k–m** *Aul. eifliense* (Steininger, 1849), MB.C.29351.1, typical specimen with high aperture, canaliculate ventrolateral grooves, and very weak ventral band; ventral, lateral and ventral views, Dombach-Sander-Straße,×9, **n**, **o** *Aul.* aff. *ventrosulcatum*, specimen MB.C.29354, juvenile specimen with extremely prominent ventrolateral grooves, undulose ventral band, and very broad dorsolateral saddle; ventral and lateral views, Sand 1,×15, **p**, **q** *Aul.* aff. *constrictum* (Steininger, 1849), specimen MB.C.29355, displaying ventrolateral double furrows and an undulose ventral band; lateral and ventral views, Sand 1,×15

extending dorsolaterally, very high, asymmetrically arched dorsolateral saddle that has a steeper mid-flank limb, deep, rounded V-shaped A-lobe, a moderately broad, subsymmetric ventrolateral saddle that remains lower than the dorsolateral saddle throughout ontogeny, and a relatively wide, short, V-shaped E-lobe.

Description. In the secondarily fragmented holotype (Fig. 2g–i), the body chamber occupies at least 180°. The thickly tegoid, involute conch is rounded, with incipient spiral depressions creating a rounded ventral edge originating on the body chamber but lacking on the visible inner whorl. There are four, markedly biconvex varices per whorl that weaken briefly at the apex of their narrow ventrolateral projection. The ventral sinus is wide, deep, and U-shaped. The same juvenile conch form as in the holotype is seen in paratype MB.C.29358 (Fig. 2j–k), which possesses a slightly open umbilicus, shallow varices, and a rather rounded venter without any furrows.

Figure 12i–l depicts the simple suture ontogeny based on the holotype and paratype MB.C.29358. Apart from a general increase of the suture relief, a slight dorsolateral widening of the L-lobe, a narrowing of the apex of the pronounced dorsolateral saddle, and a somewhat better rounding of the A-lobe, there is no change between 1.25 and ca. 3 mm wh. The ventrolateral saddle never reaches the height of the dorsolateral saddle during ontogeny. The development of the suture suggests that even very small specimens display already the characteristics required for species identifications.

Remarks. Based on the ontogenetically decreasing WER ratios, *Aul. frenklerae* sp. nov. may be assigned to the *Aul. auris* Group, where it is isolated due to the hardly developed ventrolateral furrows. At the same size, *Aul. bickense* is also stouter and subinvolute. In small *Aul. constrictum*, the A-lobe is less subtriangular and the ventrolateral furrows are well developed (e.g., Fig. 13i–j). Juvenile conchs of *Aul. frenklerae* sp. nov. could be mistaken for juvenile linguatornoceratids with varices (Fig. 2j–k). Among Frasnian *Linguatornoceras*, only the very poorly known *Ling. restrictum* possesses lateral varices but also a very deep, parallel-sided, tongue-shaped A-lobe, and higher whorls (WER ca. 2.40). The suture clearly differentiates our new species from *Crassotornoceras* and *Tornoceras*.

Stratigraphic range. So far only known from the upper Frasnian (UD I-K).

Aulatornoceras ventrosulcatum sp. nov.
Figures 2l–m, 9j, 12m; Tables 1, 6

Etymology. After the varices ("mould sulci") that are restricted to the venter.

Holotype. MB.C.29360 (Museum für Naturkunde Berlin).

Paratype. MB.C.29361.

Type locality. Dombach-Sander-Straße, Bergisch Gladbach-Sand.

Type level. Sand Formation, upper Frasnian, UD I-K.

Diagnosis. Very small-sized; conch thickly discoidal and weakly depressed (ww/dm 0.55 and ww/wh 1.05 at 4 mm dm), subinvolute (uw/dm 0.15), with high whorl expansion rate (WER 2.20), tegoid, with smooth, gently rounded flanks, and narrowly rounded venter bordered by ventrolateral furrows. Growth lines strongly biconvex, with short and low dorsolateral salient, wide lateral sinus, high, narrow ventrolateral projection, and an incipient ventral band indicated by undulose, U-shaped ventral growth lines; with widely spaced, prominent U-shaped varices that are restricted to the venter. Suture with a broad, asymmetric, strongly arched dorsolateral saddle, a small, deep, slightly asymmetrically rounded, lingulate A-lobe, a very small and low ventrolateral saddle, and a short, rounded, divergent E-lobe.

Description. Holotype MB.C.29360 (Figs. 2l–m, 12m) is a well preserved internal mould of ca. 4 mm dm. The involute and thickly discoidal conch is markedly tegoid, with a very short, rounded umbilical wall, maximum whorl width low on the very high whorl, and narrowly rounded venter marked by

Table 11 Conch ontogeny of *Aulatornoceras frenklerae* sp. nov.

dm	Conch shape	Whorl cross-section shape	Whorl expansion
4 mm	Thinly pachyconic; involute (ww/dm ~ 0.65–0.70; uw/dm = 0.10)	Weakly depressed; strongly embracing (ww/wh ~ 1.15–1.20; IZR ~ 0.45)	High (WER-2.20)
8 mm	Thickly discoidal; involute (ww/dm ~ 0.50–0.55; uw/dm = 0.10)	Weakly depressed; very strongly embracing (ww/wh ~ 1.05–1.10; IZR ~ 0.55)	Moderate (WER ~ 1.80)

deep, U-shaped varices (four per whorl). Ventrolateral furrows are narrow and moderately distinctive. The strongly biconvex growth lines are typical for aulatornoceratids, with a high, narrow ventrolateral projection and broadly U-shaped ventral sinus. A ventral band is weakly indicated by undulose impressions of bundled growth lines (Fig. 2m). The course of the suture, especially the very small size of the ventrolateral saddle, are distinctive, and of *Crassotornoceras*-type.

Remarks. *Aulatornoceras ventrosulcatum* sp. nov. differs from the related *Aul. constrictum* and lower Famennian *Aul. schurbuschense* by its only ventral varices. It differs from associated *Crassotornoceras* species, such as *Cr. belgicum* and *Cr. crassum*, by the ventrally restricted varices and the well-developed ventrolateral furrows.

Stratigraphic range. Restricted to the upper Frasnian (UD I-K).

Aulatornoceras aff. *ventrosulcatum*
Figures 9h, 12f, 13n–o; Tables 1, 6

Material. MB.C.29354.

Description. The juvenile specimen MB.C.29413 (Fig. 13n–o) is thinly pachyconic and weakly depressed (ww/dm ca. 0.60 and ww/wh 1.20 at 3 mm dm), subinvolute (uw/dm 0.20), and possesses a moderate whorl expansion rate (WER 1.95). The flanks and the venter are well-rounded, and the venter is bordered by distinctive canaliculate ventrolateral furrows with incipient spiral ridges (Fig. 13n). Weak varices are indicated on the venter only. Strongly biconvex growth line impressions are slightly visible on the flanks, followed by a characteristic, high ventrolateral projection, which peak lies directly inside the spiral furrow (Fig. 9h). The weak ventral band consists of undulose, slightly prominent growth line bundles, with two or three indistinctive lirae within one field (Fig. 13n). Sutures possess a generally low relief, a broadly rounded, asymmetric dorsolateral saddle embracing all of the flank until the ventrolateral furrows, a widely rounded, shallow A-lobe, a low, moderately broad, rounded ventrolateral saddle, and a small, pointed, divergent E-lobe (Fig. 12f).

Remarks. The species differs from all other aulatornoceratids by the very prominent ventrolateral furrows and its characteristic suture with a low relief, especially with the wide, non-lingulate A-lobe. Being only a juvenile specimen, the suture may change during later ontogeny but it differs markedly compared to juveniles of other Sand aulatornoceratids. MB.C.29354 resembles *Aul. ventrosulcatum* sp. nov. in terms of the weak ventral varices. We decided to put the species in open nomenclature until more material becomes available.

Stratigraphic range. Restricted to the upper Frasnian (UD I-K) (Fig. 3).

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