RESEARCH PAPER

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

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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 goniatitids, 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.
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. Future steps will concentrate on further unpublished localities (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. 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. = Serramantico-ceras, Sphaero. = Sphaeromantico-ceras, T. = Tornoceras, UD = Upper Devonian, with the ammonoid zonal key of Becker and House (2000a); Conodonts—A. = Ancyrognathus, Pa. = Palmatolepis, Po. = Polynathus.

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 Kreishauss 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 ?Palaeodicryota 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 bivalve-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
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...
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).

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 |
|-----------------|---|---|---|---|----|----|----|---|---|---|
| Aculatornoceras aurus (Quenstedt, 1846) | – | 5 | – | – | – | – | – | 1 | – | 6 |
| Aculatornoceras constrictum (Steininger, 1849) | – | – | – | – | – | – | – | 6 | – | 6 |
| Aculatornoceras aff. constrictum (Steininger, 1849) | – | 1 | – | – | – | – | – | – | – | 1 |
| Aculatornoceras eifliense (Steininger, 1849) | – | – | 1 | – | – | – | – | 4 | 3 | 8 |
| Aculatornoceras steinhauxeni sp. nov. | – | 4 | – | – | – | – | – | – | – | 4 |
| Aculatornoceras frenklerae sp. nov. | 1 | – | – | – | 2 | – | 1 | – | 4 |
| Aculatornoceras ventrosulcatum sp. nov. | – | 1 | – | – | – | – | – | 1 | 2 |
| Aculatornoceras aff. ventrosulcatum | – | 1 | – | – | – | – | – | – | 1 |
| Aculatornoceras 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 | – | – | – | 4 | 3 | 8 |
| Crassotornoceras sp. | – | 1 | – | 1 | – | – | 2 | – | 1 | 4 |
| Linguatornoceras cf. clausum (Glenister, 1958) | 1 | – | – | 1 | – | – | 1 | 3 | – | 4 |
| Linguatornoceras lingaum (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 justi 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 | – | – | – | 2 | – | 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. lamel (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 |
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-Feßler 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 anaptychii), tentaculitoids (homoeocerids and dacryonceratids), 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 Manticoeras 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 “Archo- ceras” 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 genzone, see Fig. 4). However, Crick. holzapfeli, the index species of UD I-L, 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 rivaled by the so far incompletely documented Budesheim 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 Gephyroceroidea (53.75%). This differs significantly from upper Frasnian oxic cephalopod limestones, where Gephyroceroidea 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 \(p_i = \frac{n_i}{n}\).

For the complete Sand fauna, \((H)\) varies only slightly between 3.00 (not corrected) and 2.97 (corrected), with \(H_{\text{max}} = \ln(s) = 3.37\), \(s = \text{number of species}\), and \(n = \text{number of specimens}\). 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 \((H)\) cannot exceed 3.37. However, \((H)\) is
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
- Plucki (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 cannot 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.
and very common in the black Kellwasser Limestone facies, long-ranging genus. In the upper Frasnian, it was widespread and of any other species of this local absence of Ph. frechi 2002; new collections).

...sandstones (Gatley 1983; Becker and House 1993, 2000a; House 1993). However, it is remarkable that the Sand fauna apparently lacks Archoceras, 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 (Aulotornoceratinae and Tornoceratinae) of other ammonoid taxa, it spread opportunistically to the post-crisis (basal Famennian) calm goniatiid 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.
(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. “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 sporo-
doceratids 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 hypnomic 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 goniatities 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 descendants.

**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. 1–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,
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. 6c, 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.

Freh (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 (Freh 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 Oberschled (Rhenish Massif). A revision based on the morphology of topotypes will have to specify the holwilli-typum relationships. The Givetian/ Frasnian North American T. uniangularis–T. iowaense Group differs from T. holwilli in their narrower ventrolateral saddle with an obliquely ascending lateral pronge. Rhenish upper Givetian Tornoceras, including T. wunderlichii 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)_—House: pl. 19, fig. 1

1985 _Crassotornoceras crassum_—House and Price: 165–168, figs. 3A, 3B, 3D, 4, pl. 16, figs. 4, 8–11

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 postembryonic 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.

**Remarks.** Crassotornoceras 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-II) 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

**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...
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...
Upper Frasnian Tornoceratidae (Ammonoidea) from the Sand Formation, Rhenish Massif, Germany

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, 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).
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  | 3.18  | 1.95 | – | 0.58 | – | 0.09 | – | 2.05 | 0.39 |
| **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

![Image]

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 L₄-lobe, small, low saddle at the umbilical seam, small, asymmetrically rounded Lₑ-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 Lₑ-lobe just outside the umbilicus as typical for *Lobotornoceras* (Figs. 8j, 11d–e). In the last septum of MB.C.29388.1, the Lₑ-lobe is deeper and closer to the umbilicus than the internal L₄-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

| dm    | Conch shape                       | Whorl cross-section shape       | Whorl expansion |
|-------|-----------------------------------|---------------------------------|-----------------|
| 2.5 mm| Thinly pachyconic; subinvolute    | Moderately depressed; –         | Moderate        |
|       | (ww/dm = 0.70; uw/dm = 0.25)      | (ww/wh = 1.50; –)               | (WER = 1.75)    |
| 4 mm  | Thinly pachyconic; subinvolute    | Weakly depressed; strongly embracing | Moderate        |
|       | (ww/dm = 0.60; uw/dm = 0.15)      | (ww/wh = 1.15–1.30; IZR = 0.40) | (WER = 1.85–1.95) |
| 7 mm  | Thickly discoidal; subinvolute    | Weakly depressed; very strongly embracing | Moderate        |
|       | (ww/dm = 0.45–0.60; uw/dm = 0.15) | (ww/wh = 1.10; IZR = 0.50)      | (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 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
\* v non 2002 Linguatornoceras sp. aff. L. clausum—Dzik: figs. 53K–N [= compressed Tornoceras]
\* cf. 2006 Linguatornoceras aff. clausum—Woroncowa-Marci- nowska: 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, linguate, 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.
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-I1 to I-L1). 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

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

**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 Frasian, UD I-I/I.

**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
Upper Frasnian Tornoceratidae (Ammonoidea) from the Sand Formation, Rhenish Massif, Germany

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
**Retrotornoceras juxi** sp. nov.

### Figures

- **8n**: A specimen of *Retrotornoceras juxi* sp. nov., 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 × 6.
- **10f**: A specimen of *Retrotornoceras juxi* sp. nov., showing a symmetric subdivision of the L-lobe at the umbilical seam and the deep I-lobe; ventral and lateral views, Sand 3 × 3.

### 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).

### Remarks

Within *Aulotornoceras*, 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. paucistratium* (D’Arcia and De Verneuil, 1842), *Aul. rhysum* (Clarke, 1898), *Aul. bickense* (Wedekind, 1918), *Aul. constrictum* (Steininger, 1849), *Aul. serriense* Becker, 1993a, *Aul. steinhauensi* sp. nov., *Aul. frenkerae* sp. nov. and *Aul. tumidum* House, 2002, the A-lobe is mostly lingulate, the ventral band often strong, and WER.
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.

### 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 |
|-----------------------------------------------|-----|-----|-----|-----|-----|--------|--------|--------|-----|-----|
| *Rettorotornoceras 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* (Steiningier, 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* (Steiningier, 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 frenkleri* 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|

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

*a* 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]

1985 *Aulatornoceras auris*—House and Price: pl. 16, figs. 5–7; pl. 17, figs. 1–7. [pl. 17, figs. 1–4 = neotype]

1992 *Aulatornoceras cf. auris*—Becker et al.: 78, fig. 4

2002 *Aulatornoceras cf. auris*—Dzik: fig. 51D

2002 *Aulatornoceras auris*—Korn and Klug: 161, fig. 149A

2008 *Aulatornoceras auris*—House and Kirchgasser: 176, text-fig. 60G, pl. 31, figs. 2–3

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Upper Frasnian Tornoceratidae (Ammonoidea) from the Sand Formation, Rhenish Massif, Germany

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.
**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 uw/dm ~ 0.20; 2.5 mm dm), becoming gradually thinly discoidal and weakly compressed (ww/dm ~ 0.40–0.80 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 chambers 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.

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| 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 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 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).

*Aulotornoceras 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 umbilical 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 aulotornoceratid 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 Goniatiies eifliensis—Steininger: 27
e.p. 1853 Goniatiies 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 Goniatiies 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 Truyolsioceras sandbergeri, non pl. 10a = *Falcitornoceras korni*]
e.p. 1902 Tornoceras undulatus—Frech: 49, figs. 12a, b [only]
v 1908 Goniatiies retrorsus var. undulatus—Schönndorf: 47 [neotype]
1918 Tornoceras eifliense—Wedekind: 137
1993 Aulatornoceras eifliense—House and Kirchgasser: 276

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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 increasing 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 canalicate, 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, 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 contrast 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 Aulotornoceras steinhauseneni sp. nov. (Fig. 11o–p) but these lack ventral varices and posses a narrower, linguately 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. Aulotornoceras 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).

**Aulotornoceras 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 thickly pachyconic (ww/dm 0.65–0.70) to thinly 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.
Upper Frasnian Tornoceratidae (Ammonoidea) from the Sand Formation, Rhenish Massif, Germany

**Fig. 13** Aulotornoceratinae from the upper Frasnian Sand Formation (scale bar 2 mm). a, b Aulotornoceras auris (Quenstedt, 1846), MB.C.29346.5, subadult specimen displaying typical sutures, a ventrolateral groove and strongly biconvex growth lines forming a ventral band; ventral and lateral views, Sand 1, × 15, 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. eiffiense (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, subsymmetrical 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 Cras-sotornoceras and Tornoceras.

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

**Aulotornoceras 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 vental 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...
deep, U-shaped varices (four per whorl). Ventrolateral furrows are narrow and moderately distinctive. The strongly biconvex growth lines are typical for aulotornoceratids, 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 aulotornoceratids 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 aulotornoceratids. 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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