

Upper Frasnian ammonoids and gastropods from Boudouda (Benahmed region, Moroccan Meseta)

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Fig. 1: Limonitized and squashed *Serramanticoceras* on the upper surface of the dark-grey, laminated paper shale of Bed 9 at Boudouda, photographed in lifetime orientation.

Abstract. The upper Frasnian of the Boudouda Formation of the Benahmed region yielded a diverse, originally pyritized (secondarily limonitized) ammonoid fauna that resembles assemblages from contemporaneous goniatite shales of the Rhenish Massif (Germany: Büdesheim Formation). There are nine species each of the Tornoceratidae and Gephuroceratoidea (Gephuroceratidae and Ponticeratidae). New endemic taxa are *Crassotornoceras boudoudense* n. sp., *Costornoceras multiseptatum* n. gen. n. sp., which both fall in the Crassotornoceratinae n. subfam., and *Costamanticoceras hybris* n. sp. *Tornoceras* aff. *contractum* and *Trimanticoceras* n. sp. (based on fragments) are left in open nomenclature. Eight more species are recorded for the first time from North Africa, *Aulatorenceras auris* and *Lobotornoceras ausavense* are illustrated for the first time from Morocco. Associated are three bactritid species, bivalves, brachiopods, and the small gastropod *Goniphilus delicatulus* n. gen. n. sp. Based on *Aulatorenceras auris*, *Lobotornoceras ausavensis*, “*Ponticeras*” *prumiense*, and *Manticoceras carinatum*, the ammonoid succession falls in the lower (pre-Kellwasser) part of the upper Frasnian (UD I-I and I-J). The local absence of Beloceratidae was controlled by the hypoxic facies. At species level, the fauna includes 2/3 common taxa with the distant Büdesheim region, while the similarity with the closer and contemporaneous Anti-Atlas faunas (Tafilalt, Maïder, and Dra Valley) is only 1/3. The insufficiently known upper Frasnian goniatite faunas of other Meseta regions are also different. This unusual pattern can be explained to a large extent by biofacies differences but the lack of Frasnian outcrops in the southern Meseta is also well-known. There may have been a palaeobiogeographic barrier caused by strong Eovariscan block faulting and uplift that started in the middle/upper Givetian. It was obviously biogeographically more relevant than the wide, structurally complex western Prototethys (Variscan Sea) between the Meseta and Rhenohercynian Zone.

1. Introduction

TERMIER & TERMIER (1951a, 1951b) noted the presence of Frasnian shales with manticoceratids at Boudouda NW of Benahmed. This initiated a thorough field survey, section logging and bed-by-bed collecting of ammonoids and associated fauna, such as bactritids, bivalves, gastropods, and brachiopods. The original preservation was pyritic; deep humid weathering led to oxidation and limonitization (Fig. 1).

For the locality position, section description, conodont faunas and microfacies proving a calm environment see the general Benahmed chapter. The upper Frasnian goniatite shale facies is unique for the Moroccan Meseta and for all of North Africa. In terms of sediment and overall faunal composition, the famous Büdesheim Goniatite Shale (Büdesheim Formation) of the Eifel Mountains of Germany (e.g., CLAUSEN 1968, 1969) is most similar. Distinctive is the richness and diversity of tornoceratids, as it is also known from the slightly younger Sand Formation of the Rhenish Massif (SÖTE et al. 2021). In the Moroccan Meseta, upper Frasnian ammonoids, mostly manticoceratids, occur in condensed cephalopod limestones of the Oued Cherrat (BECKER et al. 2020a) and in the Mrirt-Azrou Nappe (BECKER et al. 2020b). Very few limonitic gephuoceratids were collected from an extremely condensed shale unit of the Middle Atlas basement at Immouzer-du-Kandar (ABOUSSALAM et al. 2020). In the eastern Anti-Atlas, Kellwasser-type, organic-rich limestones commence with the basal upper Frasnian *semichatovae* Transgression (e.g., WENDT & BELKA 1991; BECKER et al. 2018b). Undescribed, originally pyritic faunas occur in intercalated marls of the Tafilalt Basin but are younger than the Boudouda fauna (see below). This is also true for the hematitic fauna of the *Carinoceras* Beds of Oued Mzerreb in the eastern Dra

Valley (BECKER et al. 2004a), which is dominated by oxyconic gephuoceratids.

This contribution aims to document the Frasnian goniatite faunas from Boudouda, their age, and palaeobiogeography. There is a focus on the Tornoceratidae, which are currently subject to vigorous revision (e.g., SÖTE et al. 2021). Identifications of the Gephyuroceratidae and Ponticeratidae have to remain somewhat arbitrary until the type material of long-established taxa is revised, too. The local bed-by-bed record of all species is given in Tab. 1, with their ranges plotted against the lithological log in Fig. 2. The complete ammonoid fauna is as follows:

Tornoceras aequilobum SÖTE, BECKER, HERD & BOCKWINKEL, 2021 (Figs. 3a-b)

Tornoceras aff. *contractum* GLENISTER, 1958 (Figs. 3c-d)

Lobotornoceras ausavense (STEININGER, 1849) (Figs. 3i-j)

Lobotornoceras hassoni HOUSE, 1978 (Figs. 3k-l)

Crassotornoceras hetzeneggeri SÖTE, BECKER, HERD & BOCKWINKEL, 2021 (Figs. 3g-h)

Crassotornoceras boudoudense n. sp. (Figs. 3e-f)

Costornoceras multiseptatum n. gen. n. sp. (Figs. 3m-p)

Aulatornoceras auris (QUENSTEDT, 1846) (Figs. 4a-b)

Aulatornoceras constrictum (STEININGER, 1849) (Figs. 4c-d)

Manticoceras carinatum (BEYRICH, 1837) (Figs. 4e-f)

Manticoceras cordatum (SANDBERGER & SANDBERGER, 1851) (Figs. 4g-h) (?= *M. intumescens* of TERMIER & TERMIER 1951b)

Sphaeromanticoceras orbiculum (BEYRICH, 1837) (Figs. 4i-j)

Sphaeromanticoceras affine (STEININGER, 1849) (Figs. 4k-l)

Serramanticoceras serratum (STEININGER, 1849) (Figs. 5c-d)

Trimanticoceras n. sp. (Figs. 5a-b)

Costamanticoceras hybris n. sp. (Figs. 4m-n)

"*Ponticeras*" *prumiense* (STEININGER, 1853) (Figs. 5e-f) and *Ponticeras* sp.

Family Tornoceratidae	2a	3a	4a	5a	6a	8a	9a	13a	14a	15a	16a	17a	18a	19a	20a	21a	23a	25	+
<i>Aulotornoceras auris</i>	1	-	-	-	-	-	-	1	-	1	-	3	-	-	-	-	-	-	2
<i>Aulotornoceras constrictum</i>	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	2	-	1	2
<i>Aulotornoceras</i> sp.	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
<i>Costornoceras multiseptatum</i> n. gen. n. sp.	-	-	1	-	-	-	-	1	-	1	-	2	-	-	1	1	-	-	-
<i>Crassotornoceras hetzeneggeri</i>	-	-	-	-	-	-	1	-	-	2	-	-	-	-	-	-	-	-	1
<i>Crassotornoceras boudoudense</i> n. sp.	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1
<i>Crassotornoceras</i> sp.	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
<i>Lobotornoceras ausavense</i>	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Lobotornoceras hassoni</i>	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	1	2
<i>Tornoceras aequilobum</i>	-	1	-	-	-	-	-	3	1	2	1	1	-	1	-	-	1	-	3
<i>Tornoceras</i> aff. <i>contractum</i>	-	-	-	-	-	-	1	-	2	4	1	-	-	-	1	-	-	-	3
<i>Tornoceras</i> sp.	-	-	-	-	1	-	-	4	-	2	1	-	-	-	-	-	-	-	-
Family Gephuroceratidae																			
<i>Costamanticoceras</i> n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
<i>Manticoceras cordatum</i>	-	-	2	-	-	-	-	4	-	1	-	2	-	-	1	-	-	2	-
<i>Manticoceras carinatum</i>	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-	-	3	-	2
<i>Manticoceras</i> sp.	-	-	-	2	-	-	-	-	-	-	-	-	1	-	-	-	-	1	1
<i>Serramanticoceras serratum</i>	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Sphaeromanticoceras affine</i>	-	1	1	1	1	2	-	-	-	3	-	1	-	-	1	-	1	-	1
<i>Sphaeromanticoceras orbiculum</i>	3	-	-	-	-	-	-	-	-	1	1	3	-	-	3	-	-	-	1
<i>Trimanticoceras</i> n. sp.	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-
Family Ponticeratidae																			
" <i>Ponticeras</i> " <i>prumiense</i>	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-
<i>Ponticeras</i> sp.	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-

Tab. 1: Local Frasnian ammonoid occurrences at Boudouda.

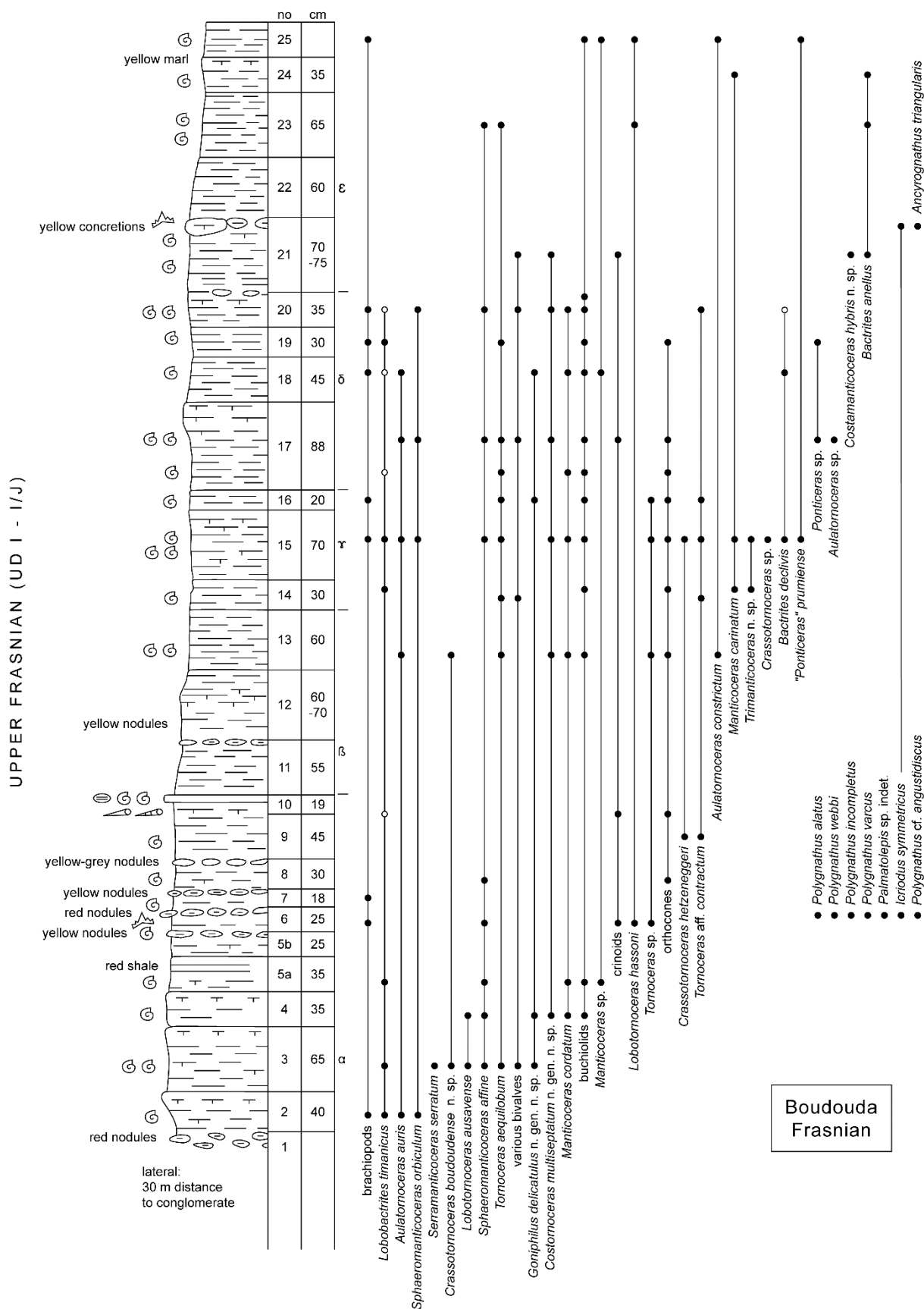


Fig. 2: Stratigraphic ranges of ammonoids, conodonts, and associated fauna in the upper Frasnian of Boudouda.

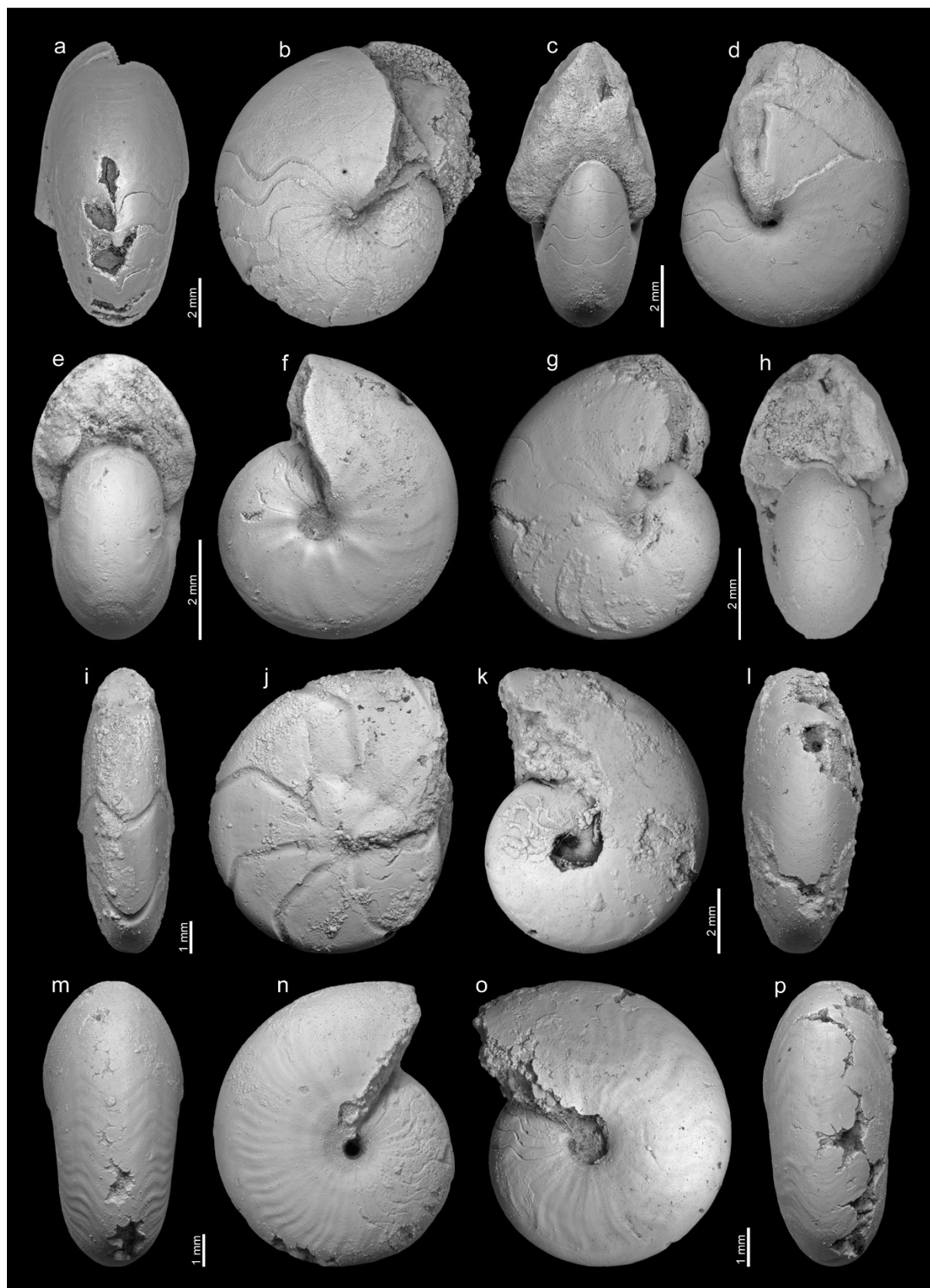


Fig. 3: Upper Frasnian ammonoids from Boudouda. **a-b.** *Tornoceras aequilobum*, GMM B6C.54-122, Bed 16a; **c-d.** *T. aff. contractum*, GMM B6C.54-132, Bed 15a; **e-f.** *Crassotornoceras boudoudense* n. sp., holotype GMM B6C.54-46, Bed 3a; **g-h.** *Crasso. hetzeneggeri*, GMM B6C.54-49, Bed 9a; **i-j.** *Lobotornoceras ausavense*, GMM B6C.54-60, loose; **k-l.** *Lobo. hassoni*, GMM B6C.54-61, Bed 6a; **m-p.** *Costornoceras multiseptatum* n. gen. n. sp., m-n. holotype GMM B6C.54-35, Bed 4a, o-p. paratype GMM B6C.54-42, loose.

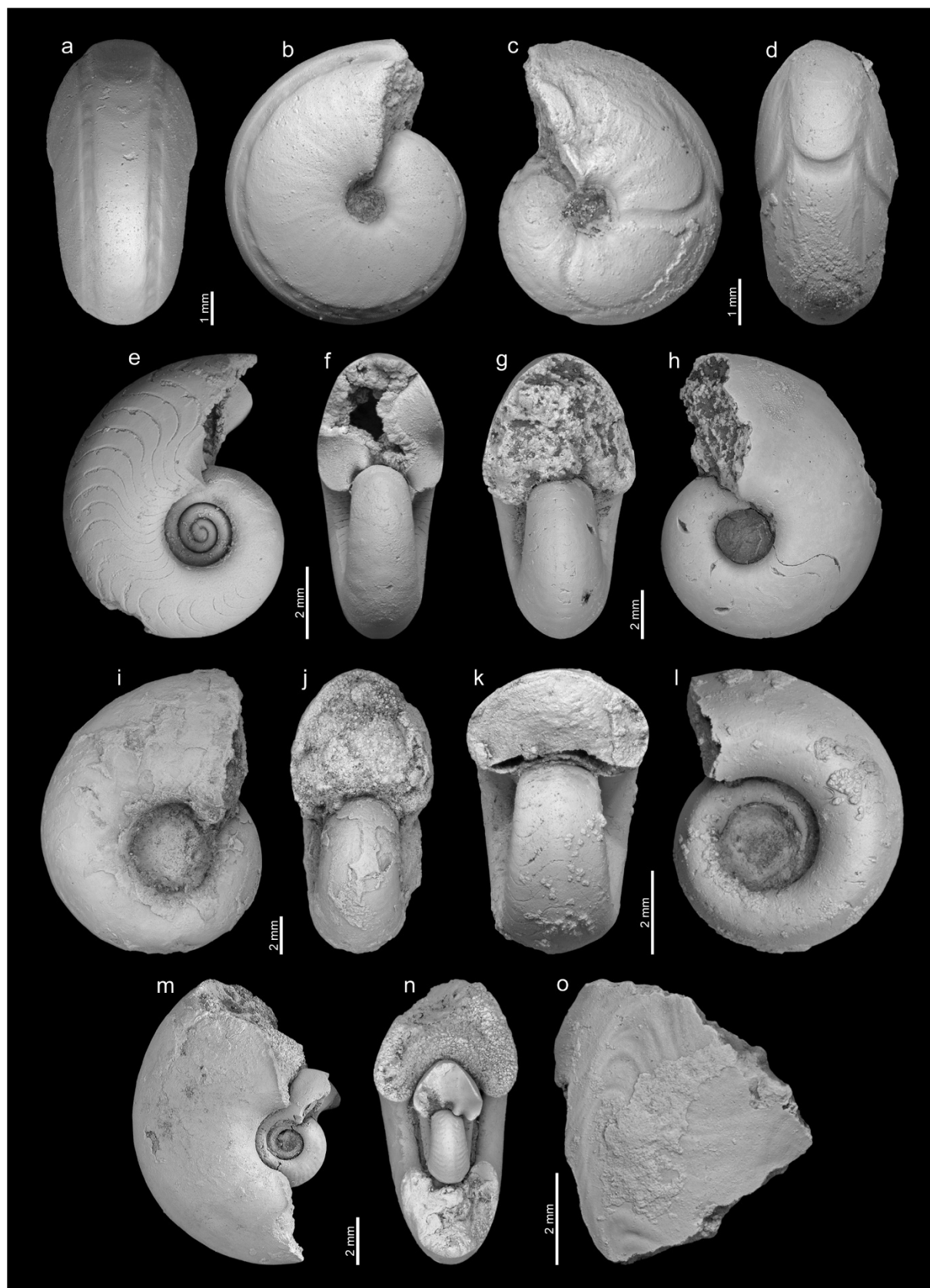


Fig. 4: Upper Frasnian ammonoids from Boudouda. **a-b.** *Aulatoceras auris*, GMM B6C.54-7, Bed 17a; **c-d.** *Aul. constrictum*, GMM B6C.54-13, Bed 21a; **e-f.** *Manticoceras carinatum*, GMM B6C.54-68, Bed 23a; **g-h.** *M. cordatum*, GMM B6C.54-76, Bed 25; **i-j.** *Sphaeromanticoceras orbiculum*, GMM B6C.54-110, Bed 16a; **k-l.** *Sph. affine*, GMM B6C.54-104, Bed 23a; **m-n.** *Costamanticoceras hybris* n. sp., holotype GMM B6C.54-34, Bed 21a; **o.** *Aulatoceras* sp., GMM B6C.54-3, Bed 17a.

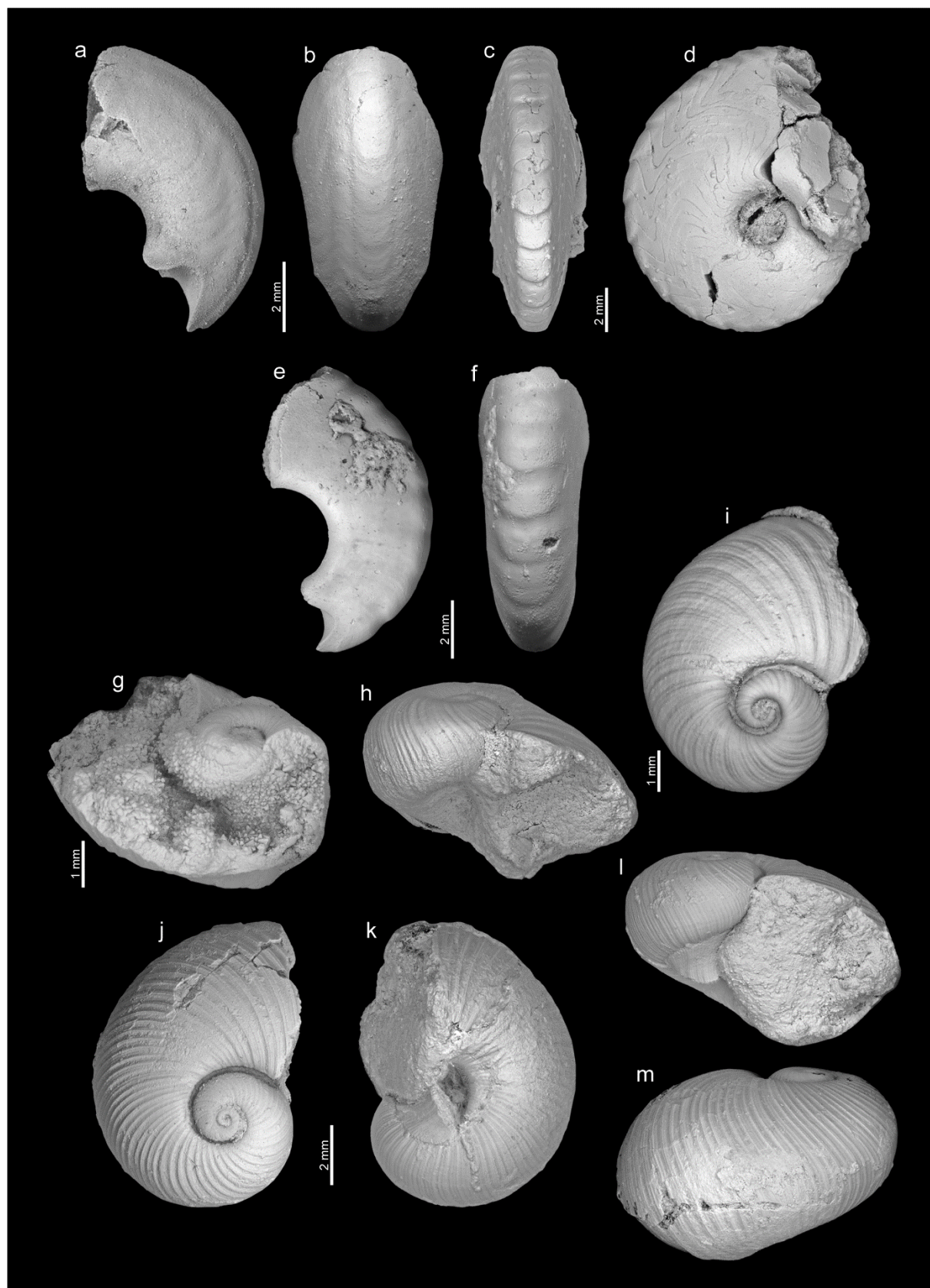


Fig. 5: Upper Frasnian ammonoids and gastropod from Boudouda and gastropods from Büdesheim. **a-b.** *Trimanticoceras* n. sp., GMM B6C.54-152, Bed 14a; **c-d.** *Serramanticoceras serratum*, GMM B6C.54-92, loose; **e-f.** “*Ponticeras*” *prumiense*, GMM B6C.54-2, Bed 25; **g-i.** *Goniphilus ausavensis* n. gen., Büdesheim, g. topotype GMM B6B.11-7, h-i. topotype and potential neotype GMM B6B.11-6, showing the inserted first whorl; **j-m.** *G. delicatulus* n. gen. n. sp., showing the typical inner whorl form, holotype GMM B6B.11-1, Bed 18a.

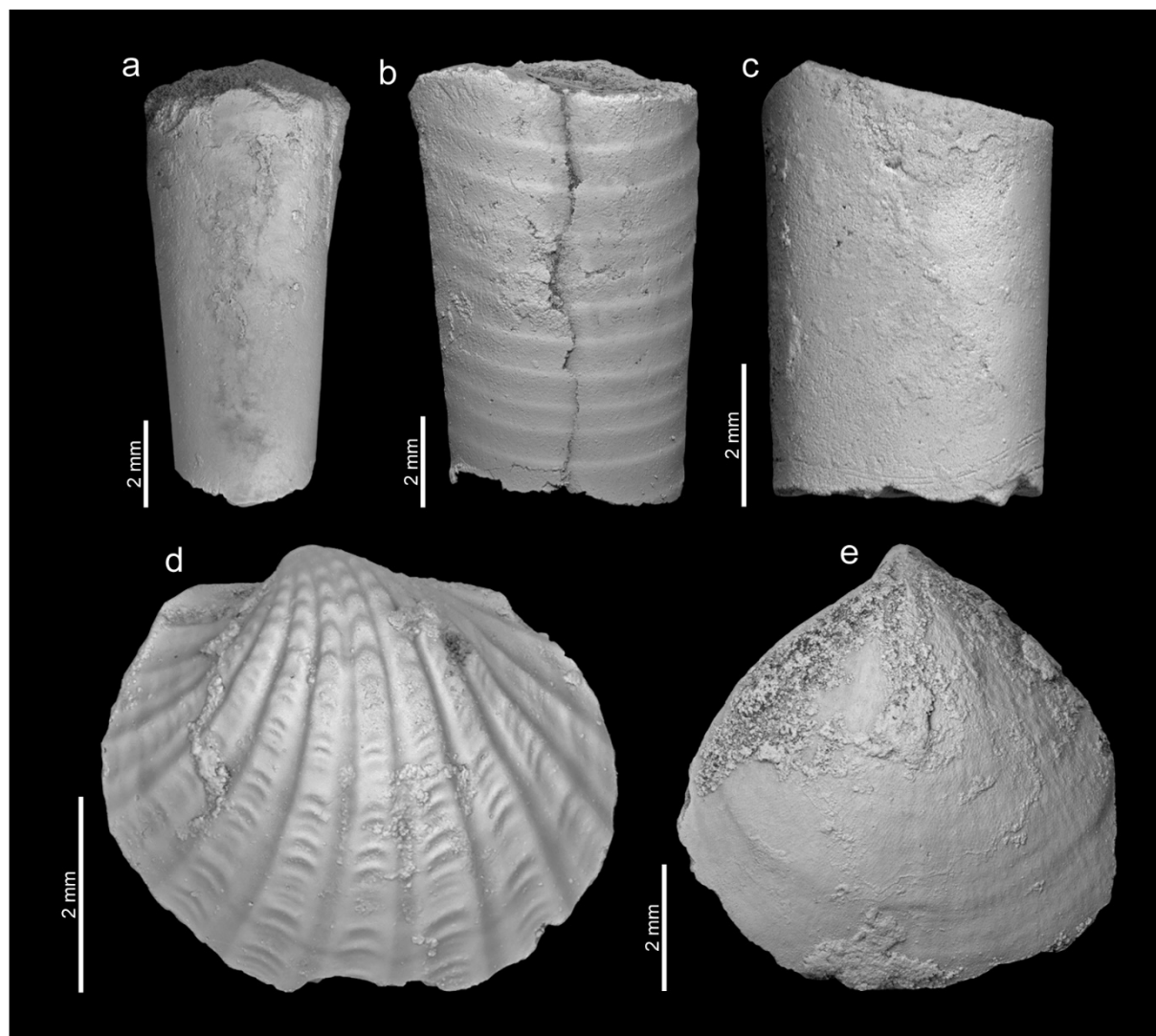


Fig. 6: Associated fauna from the Bououda Formation. **a.** *Bactrites declivis*, GMM B6C.54-27, Bed 18a; **b.** *Bac. annellus*, GMM B6C.54-21, loose; **c.** *Lobobactrites timanicus*, GMM B6C.54-56, Bed 19a; **d.** *Glyptohallicardia palmata*, GMM B6A.37-1, Bed 5a; **e.** ?athyridid, GMM B5B.16-1, Bed 2a.

Among the orthoconic cephalopods, there are three species of bactritids, which also closely resemble species known from Büdesheim (see CLAUSEN 1968):

Bactrites anellus CLAUSEN, 1968 (Fig. 6b)

Bactrites declivis CLAUSEN, 1968 (Fig. 6a)

Lobobactrites timanicus SCHINDEWOLF, 1933 (Fig. 6c)

A typical faunal element of hypoxic (pyritic) goniatite shales are buchiolid bivalves, which were monographed by GRIMM (1998). At least some of our

Boudouda specimens (Fig. 6d) belong to *Glyptohallicardia palmata* (GOLDFUSS, 1837), one of the most widespread Frasnian buchiolids, which occurs also at Büdesheim. A small-sized gastropod closely resembles the poorly known *Natica ausavensis* STEININGER, 1853 from Büdesheim (Figs. 5g-i) but is not conspecific. Due to the constant association of similar forms with goniatites, it is here described as *Goniphilus delicatulus* n. gen. n. sp. (Figs. 5j-m).

2. Biostratigraphic age

The Frasnian ammonoid zonation was refined by BECKER et al. (1993), who introduced a subdivision of the Upper Devonian I (UD I) into twelve zones (I-A to I-L), with regionally different subzones. Following the proposed substage definition by ZIEGLER & SANDBERG (1997: *semichatovae* Transgression), the upper Frasnian begins with UD I-I, not with the Lower Kellwasser faunas, as in the traditional definition of the Upper Adorf-Stufe sensu WEDEKIND (1913a). The *semichatovae* Transgression is characterized by a significant ammonoid radiation and migrations. Typical is a proliferation in genera, such as *Serramanticoceras*, *Playfordites*, *Trimanticoceras*, *Costamanticoceras*, *Stilleoceras* (an objective senior synonym of *Maternoceras* HOUSE & ZIEGLER, 1977; see BECKER 2018), *Ponticeras*, and the *Manticoceras latisellatum* Group, characterized by species with widely rounded flank saddles. Since BECKER & HOUSE (2009, p. 420) mentioned undescribed new *Playfordites* and *Costamanticoceras* from the middle Frasnian *Mesobeloceras* Zone of Australia, it seems that *Serramanticoceras* is internationally the most suitable genus to define UD I-I, which revives the original concept of BECKER et al. (1993).

Apart from *Stilleoceras* and *Playfordites*, the mentioned upper Frasnian genera are present at Boudouda. An important index species for UD I-I is *Aulatornoceras auris*, which occurs in Bed 2, and which enters also in the basal upper Frasnian of Germany (UD I/J, type-level at Büdesheim, Eifel Mountains; Martenberg, eastern Rhenish Massif), in southern France (BECKER & HOUSE 1994a), Western Australia (BECKER & HOUSE 2009) and in the Timan of northern Russia (BECKER et al. 2000). At Boudouda, Beds 2a to top 13a are assigned to a local *Aul. auris-Serr.*

serratum Zone representing division UD I-I. *Lobotornoceras ausavense*, which begins in Bed 3a, is also a typical UD I-I/J species at Büdesheim and in the Dra Valley of southern Morocco (BECKER et al. 2004a). However, closely related forms appear already in the middle Frasnian of the Timan and Dra Valley (BECKER et al. 2000, 2004a). Lobotornoceratids without varices were previously only known from the upper Givetian to middle Frasnian of North America and the Anti-Atlas (HOUSE 1978; HOUSE & KIRCHGASSER 2008; BECKER et al. 2004a; BOCKWINKEL et al. 2013). The Boudouda specimens, which cannot be distinguished from the lower Frasnian *Lobo. hassoni* of West Virginia, mean a considerable upper range extension. *Sphaeromanticoceras* enters high in the middle Frasnian of Australia (BECKER et al. 1993; BECKER & HOUSE 1993) but is very common in the UD I-I/J of Büdesheim.

The international separation of zones UD I-I and I-J is hampered by strong regional differences (see BECKER & HOUSE 1994a, fig. 17). Characteristic for I-J are advanced oxyconic gephuroides, such as *Virginoceras* (Australia, Timan) and *Neomanticoceras* (Büdesheim), as well as *Clausenicerias*, a relative of *Manticoceras* with (sub)convex growth ornament (BECKER & HOUSE 1993). Both in the Rhenish Massif (WEDEKIND 1913a: classical do Iy fauna) and in the Anti-Atlas (BECKER & HOUSE 2000a; BECKER et al. 2018a), the compressed *Mant. carinatum* enters abundantly as an index fossil in limestones of UD I-J. The species is characterized by a wide and subsymmetric flank saddle and a late ontogenetic sharpening of the lateral lobe (see BECKER & HOUSE 1994a, fig. 15C). The ventral carina of the types (see HOUSE & ZIEGLER 1977) is not regarded as a meaningful character, which was already noted in the first revision by WEDEKIND (1913a). Consequently, we assign

the Boudouda succession from Bed 14a on to UD I-J, a regional *M. carinatum* Zone.

In Germany (WEDEKIND 1913a; MATERN 1931b, HOUSE & ZIEGLER 1977), SW England (HOUSE 1963; GAUSS & HOUSE 1972) and in Australia (GLENISTER 1958; BECKER & HOUSE 2009), regionally different species of *Ponticeras* bloomed in UD I-J. The fragmentary *Ponticeras* found in Beds 17a and 19a agree with this distribution patterns. BECKER & HOUSE (1993, p. 122) emphasized that “*Ponticeras*” *prumiense*, another Büdesheim species, found at Boudouda in Beds 15a and 25 (Tab. 1, Fig. 2), belongs to a distinctive side-branch of ponticeratid evolution. Closely related forms occur in SW England (GAUSS & HOUSE 1972) and NW Australia in the upper part of UD I-I (BECKER & HOUSE 2009) but the species may range throughout I-I/J in Germany.

3. Palaeobiogeography (Tab. 2)

As noted in the introduction, upper Frasnian goniatite faunas are sparse in the Moroccan Meseta and come mostly from extremely condensed cephalopod limestone facies, which is dominated by manticoceratids and beloceratids. *Beloceras* is generally very rare in hypoxic, organic-rich facies, with single exceptions from the “*Archoceras*” Zone (UD I-K) of Büdesheim (KORN et al. 2013), the Dra Valley (UD I-I, BECKER et al. 2004a), and from Kellwasser facies of the southern Tafilalt (specimen overgrown by *Prosochasma bickense* from El Atrous = Takhat ou Heyene, see section of BECKER et al. 1989a). The absence of *Beloceras* from the Boudouda fauna has biofacies, not palaeobiogeographic reasons.

A moderately diverse, only partly described upper Frasnian manticoceratid fauna occurs in the Mrirt region (BECKER et al. 2020b, UD I-I to I-L), which represents an allochthonous nappe derived from the east. Its

fauna consists mostly of *Manticoceras* groups; other genera of the Gephuroceratidae are not known with certainty (one questionable “*Maternoceras*”). Again, this is thought to reflect a strong biofacies difference to Boudouda. The restricted number of sufficiently preserved specimens has to be taken into consideration, too, but genera, such as *Costamanticoceras*, *Trimanticoceras*, *Ponticeras*, and *Aulatonoceras*, are well-known from German cephalopod limestone facies. Interestingly, *M. cordatum* (s.str.) and *M. carinatum* have not yet been recorded from the Mrirt region. The poorly preserved *Aulatonoceras* and *Tornoceras* of Bou Ounebdou are from younger (Kellwasser) levels than the Boudouda faunas and cannot be compared until further investigation. In summary, the differences between upper Frasnian goniatite faunas of the Benahmed region and Mrirt-Azrou Nappe may reflect a combination of dominant biofacies and subordinate palaeogeographic patterns.

The goniatite faunule from UD I-J goniatite shale of Immouzer-du-Kandar (Middle Atlas basement, ABOUSSALAM et al. 2020) is too small for detailed comparisons. But the presence there of *M. cordatum* and *Sph. orbiculum* give biogeographically relevant similarities.

At Boudouda, three of 18 species are endemic according to current knowledge: *Costornoceras multiseptatum* n. gen. n. sp., *Crassotornoceras boudoudense* n. sp., and *Costamanticoceras hybris* n. sp. The spatial range of *Trimanticoceras* n. sp. is not yet known since similar forms occur in other regions but have not yet been described; all other taxa are more or less cosmopolitan (Tab. 2). The local genus-level endemism is especially significant.

From the Tafilalt and Maïder of the eastern Anti-Atlas, which was not separated from the Meseta by a plate tectonic suture (BAIDDER et al. 2008; FERONI et al. 2010; RYTINA et al.

2013), only ca. a third of the Boudouda species are known, and not necessarily from faunas of the same zones. There are occurrences of *Aul. auris*, *Aul. constrictum*, *Lobo. ausavense*, *M. cordatum*, *M. carinatum*, and close relatives of the Australian *T. contractum* (e.g., BECKER & HOUSE 2000a; BECKER et al. 2018b, 2018c; Tab. 2). A poorly preserved, not yet illustrated *Costamanticoceras* from Jebel Amelane (BECKER & HOUSE 2000b) could be added. As in the case of the Mriert area, biofacies differences can account for a good deal of the distinction. All UD I-I/J goniatites of the eastern Anti-Atlas are from condensed, dark-grey Kellwasser-type facies. Originally pyritic faunas are only known (but not yet described) from the “*Archoceras*” Zone (UD I-K, Tafilalt Basin: Ouidane Chebbi and Hassi Nebech regions).

In the eastern Dra Valley, goniatite shales of UD I-I occur at Oued Mzerreb SE of Tata (BECKER et al. 2004a). The fauna of the “*Carinoceras* Beds” shares with Boudouda three or four species: *Trimanticoceras* n. sp., close relatives of *T. contractum*, *Aul. auris*, and *Lobo. ausavense*. In this case, the large difference of the associated geophuroceratids is interesting; at Oued Mzerreb an oxyconic species of *Gephyroceras* (= *M. rhynchostomum* Group) dominates. Different compositions apply also to Oued Mzerreb faunas from the middle Frasnian (UD I-G) and top upper Frasnian (UD I-K/L), with the exception that *M. carinatum* enters abundantly with the Lower Kellwasser level. Since the northern margin of the Tindouf Basin was palaeogeographically not more remote from the central Meseta than the eastern Anti-Atlas, it must be concluded that the Dra Valley “*Carinoceras* Beds” represent a different goniatite shale ecosystem than the Boudouda Formation. This view is supported by the unusual grading upwards into a crinoid shale (WEBSTER & BECKER 2009). Few upper

Frasnian sediments are known from the southern Meseta regions, such as the Rehamna, Jebilet, High Atlas, and Skoura. A major phase of Eovariscan block faulting started in the middle/upper Givetian (BECKER et al. 2015) and may have created a barrier. However, a questionable *Ponticeras* from Taliouine (see Skoura chapter) indicates that upper Frasnian goniatite shale facies did exist locally.

Going northwards from the Meseta, the next crustal block with described upper Frasnian ammonoid faunas is the Montagne Noire of southern France (e.g., FRECH 1887; HOUSE et al. 1985; BECKER & HOUSE 1994a). While faunas from condensed cephalopod limestones, e.g., of the Frasnian-Famennian GSSP at Coumiac and other sections of the Mt. Peyroux Nappe (BECKER et al. 1989b), differ strongly, with only *M. cordatum*, *Aul. auris*, and perhaps *T. contractum* Gp. in common, the goniatite shale assemblages of the Cabrières region have not been revised. They share with Boudouda occurrences of *Sphaeromanticoceras* (probably both species) and *Serramanticoceras*.

The largest congruence of the Boudouda succession are with contemporaneous faunas from the Rhenish Massif. From the 18 species at Boudouda, at least 12 (2/3) are known from the Rhenish Massif. These are all abundant at Büdesheim, Germany (e.g., CLAUSEN 1969). Further similarity comes from the associated bactritids and bivalves. This points to very similar ecosystems developed contemporaneously despite a considerable palaeolatitudinal distance and despite a complex of intervening terrains (chain of South European blocks and the Armorican Terrain Assemblage) and oceanic passages. The only significant difference requiring an explanation is the lack of *Linguatormoceras* at Boudouda. Despite the extinctions associated with the Lower Kellwasser Event (e.g., of most Ponticeratidae and *Costamanticoceras*),

similarity continued upwards, with the presence of nine common species still found in UD I-K at Bergisch Gladbach-Sand (SÖTE et al. 2021). In Rhenish cephalopod limestone facies (e.g., WEDEKIND 1913a; MATERN 1931b; HOUSE & ZIEGLER 1977), the similarity decreases to ca. 40 % (Tab. 2), a similar value as for Anti-Atlas limestones. However, one has to acknowledge the limited knowledge of tornoceratids in the latter facies.

MATERN (1931a), MAILLIEUX (1936), and GATLEY (1983) documented faunas from the Ardennes, where goniatite shales dominate the upper Frasnian. TERMIER & TERMIER (1951b, p. 20) compared the pyritic “Sidi Bou Chatah” fauna with the Matagne Shale. Again, the Belgian tornoceratid knowledge is much more restricted than that of gephuoceratids. At species-level, ca. 50 % of the Boudouda taxa may be present. A significant distinction, which does not occur at Büdesheim, are the various carinoceratids (s.l.) of the Ardennes Shelf basin. This gives an interesting parallel to the hypoxic Dra Valley fauna. Westwards, the goniatite shales of UD I-I/J of North Cornwall (Lower Merope Island Shale) have been compared by HOUSE (1963) and GAUSS & HOUSE (1972) with the Büdesheim Goniatite Shale. At least more than a third of the Boudouda taxa are present but the fauna, especially the tornoceratids, has been poorly documented so far. The biogeographic trend continues in the younger (UD I-K/L) goniatite shale fauna of Waterside Cove, South Devon (HOUSE 2002), resembling the Rhenish trend.

Much further away, rich upper Frasnian ammonoid faunas are known from eastern North America (revised by HOUSE & KIRCHGASSER 2008), the Timan of northern Russia (revised by BECKER et al. 2000), southern Siberia (BOGOSLOVSKIY 1969), and the Canning Basin of NW Australia (GLENISTER 1958; BECKER et al. 1993; BECKER & HOUSE 2009). The Appalachian Basin shares only two taxa (*Aul. auris* and

Lobo. hassoni; compare HOUSE & KIRCHGASSER 2008). Interestingly, *Lobo. hassoni* is currently only known from the Appalachian Mountains and Morocco, suggesting a limited breakdown of faunal isolation with the basal upper Frasnian *semichatovae* Transgression. Sporadic occurrences of upper Frasnian goniatites in the west (Missouri, Iowa), in the Great Basin (Utah), and in the Canadian Rocky Mountains do not include any Boudouda forms.

In the Timan, on the eastern tropical shelf of Laurussia, four Boudouda species occur in the calcareous, upper Frasnian Lyaiol Formation: *Aul. auris*, *Aul. constrictum* (= *Aul. bickense* in BECKER et al. 2000), *M. cordatum*, and *M. carinatum*. In the middle Frasnian Domanik Formation, *T. contractum* is widespread and *Lobo. strangulatum* is a close relative of *Lobo. ausavense*. This gives a similarity with Boudouda in the range of Anti-Atlas and Rhenish cephalopod limestones. A single biogeographic province (biochore) stretched from NW Gondwana to the shelf belt around the southern and eastern margin of Laurussia.

Upper Frasnian ammonoids from Novaya Zemlya, other regions of Arctic Russia, Iran, and South China are very poorly known. With respect to the enormous spatial distance between the western and eastern Protethys, there are surprisingly intensive links between the ammonoid faunas of Boudouda and those of the Canning Basin (8-9 common species, Tab. 2). This is even more remarkable considering that the latter region does not include upper Frasnian goniatite shales.

In conclusion, the composition of upper Frasnian ammonoid faunas is generally controlled more strongly by biofacies than by biogeographic barriers. The total Boudouda assemblage is dominated by taxa with wide to even cosmopolitan distribution, for example across the Variscan Sea towards the Rhenish Massif and beyond, and along the Prototethys

towards Western Australia. With *Costornoceras* n. gen., there is one endemic genus distinctive for Boudouda. The rather strong difference to Anti-Atlas faunas may reflect a barrier caused by the top-Givetian Eovariscan block tectonics and uplift characteristic for the southern Meseta. The Boudouda record of *Lobo. hassoni* suggests an episodic and partial viability of the Afro-Appalachian Seaway during times of transgression.

4. Taxonomic Notes

4.1. Ammonoidea

Abbreviations: Dm = diameter, wh = whorl height, ah = apertural height, ww = whorl width, uw = umbilical width, WER = whorl expansion rate, E = external or ventral lobe, A = adventitious flank lobe, L = lateral lobe at the umbilical seam (in the Tornoceratidae), I = inner or dorsal lobe.

Suborder Tornoceratina WEDEKIND in POMPECKJ, 1912

Discussion: In many publications, the authorship of the suborder Tornoceratina is given rather variably to WEDEKIND (1914a) or WEDEKIND (1918). However, the correct suborder term appeared for the first time in the systematics of POMPECKJ (1912, p. 291), who gave credits to an unpublished paper by R. WEDEKIND. As a consequence, there was also no first correction (“nom. transl.”) of the suborder term in RUZHENCEV (1957), as quoted sometimes.

Superfamily Tornoceratoidea WEDEKIND, 1910

Family Tornoceratidae WEDEKIND, 1910

Subfamily Tornoceratinae WEDEKIND, 1910

Genus *Tornoceras* HYATT, 1884

***Tornoceras aequilobum* SÖTE, BECKER, HERD & BOCKWINKEL, 2021**

Figs. 3a-b, Tabs. 1-3

Discussion: There are 14 more or less well-preserved specimens with the typical,

symmetrically rounded A-lobe and rounded, tegoid whorl form. The umbilicus of the moulds is so narrow that it was closed by the shell. The figured specimen GMM B6C.54-122 from Bed 16a is larger than the slightly younger (UD I-K) types from Bergisch Gladbach-Sand, but the cross-section and shell parameters agree well.

***Tornoceras* aff. *contractum* GLENISTER, 1958**

Figs. 3c-d, 7a-b, Tabs. 1-3

Description: Twelve specimens from Beds 9a to 20a are characterized by strongly tegoid cross-section with high (wh/dm ca. 0.58) and compressed whorls (ww/wh = 0.80 at ca. 12 mm dm). Impressed traces of the ornament (Fig. 3d) suggest a well-developed ocular sinus and moderately high and wide ventrolateral salient. Sutures are characterized by a moderately wide, asymmetric, relatively low dorsolateral saddle, a wide and asymmetric A-lobe, and a wide and low (< 50 % dorsolateral saddle), asymmetrically ascending ventrolateral saddle.

Discussion: There are many similarities with *T. contractum*, which types are from the much older Timanites Zone (UD I-C, high lower Frasnian) of the Canning Basin. The main difference, which leads to an aff. identification, are the narrower A-lobes and ventrolateral saddles of the *contractum* holotype. We currently apply open nomenclature for the younger Boudouda form since the intraspecific variability of the Australian species is not yet established. This is especially relevant for stratigraphically intermediate specimens from middle Frasnian goniatite shales of the Bugle Gap region (sections 365, 367, McWhae Ridge Graben; BECKER & HOUSE 2009). BOGOSLOVSKIY (1971) illustrated typical *T. contractum* from the middle Frasnian of the Timan as “*T. simplex*” (see the *T. contractum* illustrated by BECKER et al. 2000, pl. 2, figs. 5-6).

REGION	Bou	Mr	IdK	Taf	Dra	MN	Büd	RhM	Ard	Eng	App	Tim	RA	CB
<i>T. aequilobum</i>	x						x							
<i>T. contractum</i> Gp.	x	?		x	x	?		x	?	?		x		x
<i>Lobo. hassoni</i>	x				cf.						x			
<i>Lobo. ausavense</i>	x			x	x		x					(str.)		
<i>Crasso. boudoudense</i> n. sp.	x													
<i>Crasso. hetzeneggeri</i>	x						x							
<i>Cost. multiseptatum</i> n. sp.	x													
<i>Aul. auris</i>	x	x		x	x	x	x	x	x	x	x	x		x
<i>Aul. constrictum</i>	x			x			x	x	?	cf.		x		
<i>M. cordatum</i>	x	aff.	x	x		x	x	x	x	x		x		x
<i>M. carinatum</i>	x			x	x		x	x	x			x	x	
<i>Sph. orbiculum</i>	x		x			x	x		x					
<i>Sph. affine</i>	x					x	x	?	x	cf.			?	x
<i>Serr. serratum</i>	x					aff.	x	x	x					x
<i>Trimanticoceras</i> n. sp.	x				cf.			cf.		cf.				cf.
<i>Costam. hybris</i> n. sp.	x			?										?
<i>Ponticeras</i> sp.	x						x	x	x	x				x
"Pont." <i>prumiense</i>	x						x		x	x				x
common species [%]		< 10	?	33	cf. 33	22- 33	67	ca. 40	ca. 50	?44	11	ca. 33	<10	40- 50

Tab. 2: Distribution of Boudouda ammonoids in other regions. Bou = Boudouda, Mr = Mrirt region, Meseta, IdK = Imouzzer-du-Kandar, Middle Atlas basement, Taf = Tafilalt/Maïder, eastern Anti-Atlas, Dra = Tata region, eastern Dra Valley, MN = Montagne Noire, southern France, Büd = Büdesheim, Eifel Mts., Germany, RhM = cephalopod limestone facies of Rhenish Massif, Ard = Ardennes, Eng = Devon/Cornwall, SW England, App = Appalachian Foreland (New York State to West Virginia), Tim = Timan, northern Russia, RA = Rudnyi Altai, southern Siberia, CB = Canning Basin, Western Australia, (str.) = *Lobo. strangulatum*.

species	GMM B6C.54	bed no.	dm	wh	ah	ww	uw	wh/ dm	ww/ wh	uw/ dm	ww/ dm	WER	IZR
<i>T. aequilobum</i>	54-122	16a	12.40	7.84	-	6.49	0.05	0.63	0.83	0.00	0.52	-	-
<i>T. aff. contractum</i>	54-132	15a	9.37	5.33	-	-	0.60	0.57	-	0.06	-	-	-
<i>T. aff. contractum</i>	54-133	15a	11.83	6.82	-	5.45	0.62	0.58	0.80	0.05	0.46	-	-
<i>Lobo. hassoni</i>	54-61	6a	9.10	5.75	3.37	3.80	0.10	0.63	0.66	0.01	0.42	2.52	0.41
<i>Lobo. hassoni</i>	54-64	-	11.27	6.57	3.90	4.25	0.05	0.58	0.65	0.00	0.38	2.34	0.41
<i>Crasso. boudoudense</i> n. sp. *	54-46	3a	5.80	3.14	1.75	3.15	0.76	0.54	1.00	0.13	0.54	2.05	0.44
<i>Cost. multiseptatum</i> n. sp. *	54-35	4a	9.52	4.75	2.70	4.43	1.10	0.50	0.93	0.12	0.47	1.95	0.43
<i>Cost. multiseptatum</i> n. sp.	54-42	-	8.02	4.01	2.45	3.70	1.20	0.50	0.92	0.15	0.46	2.07	0.39
<i>Cost. multiseptatum</i> n. sp.	54-43	-	5.35	2.66	1.62	2.79	0.96	0.50	1.05	0.18	0.52	2.06	0.39
<i>Aul. auris</i>	54-7	17/18	8.65	4.16	2.60	4.54	1.58	0.48	1.09	0.18	0.52	2.04	0.38
<i>Costam. hybris</i> n. sp. *	54-34	21a	12.5	6.10	5.90	5.93	2.50	0.49	0.97	0.20	0.47	2.47	-
<i>Costam. hybris</i> n. sp. *	54-34	21a	8.63	4.07	3.15	4.17	2.22	0.47	1.02	0.26	0.48	2.48	-
<i>Costam. hybris</i> n. sp. *	54-34	21a	5.35	2.50	2.00	2.81	1.91	0.47	1.12	0.36	0.53	2.55	0.20

Tab. 3: Shell parameters of some Boudouda ammonoids (* = holotype).

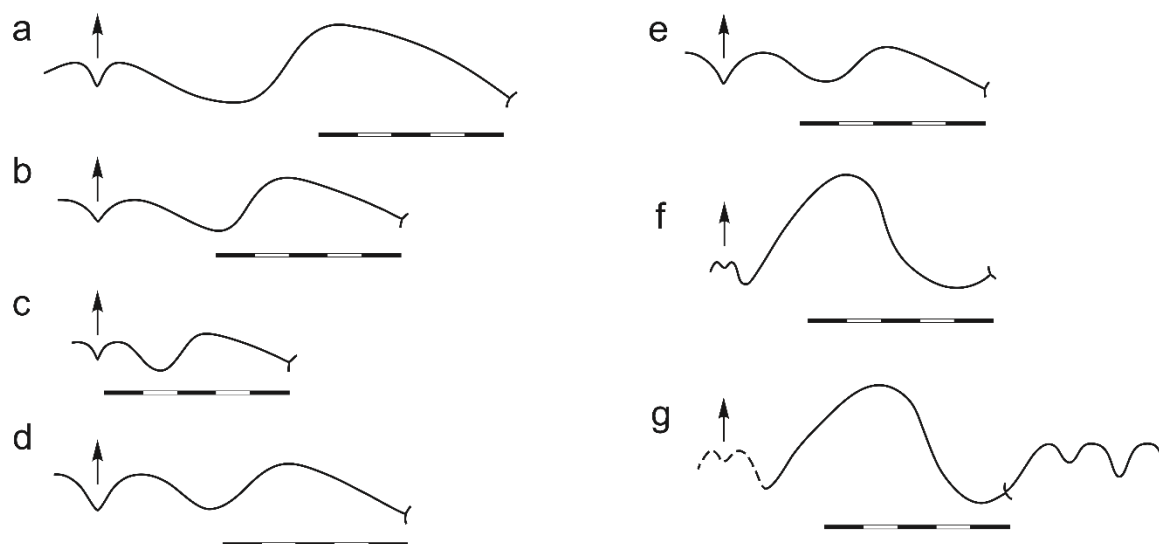


Fig. 7: Sutures of upper Frasnian ammonoids from Boudouda. Scale bar = 2 mm. **a.** *Tornoceras* aff. *contractum*, GMM B6C.54-133, Bed 15a; **b.** *T.* aff. *contractum*, GMM B6C.54-132, Bed 15a; **c.** *Crassotornoceras boudoudense* n. sp., holotype GMM B6C.54-46, Bed 3a; **d.** *Costornoceras multiseptatum* n. gen. n. sp., holotype GMM B6C.54-35, Bed 4a; **e.** *Cost. multiseptatum* n. gen. n. sp., paratype GMM B6C.54-41, Bed 21a; **f.** *Costamanticoceras hybris* n. sp., holotype GMM B6C.54-34, Bed 21a; **g.** *Trimanticoceras* n. sp., GMM B6C.54-152, Bed 14a.

BECKER et al. (2004a) noted previously that close relatives of *T. contractum* range in Morocco into the upper Frasnian.

Genus *Lobotornoceras* SCHINDEWOLF, 1936

Lobotornoceras ausavense (STEININGER, 1849)

Figs. 3i-j, Tabs. 1-2

Discussion: The four available specimens from Boudouda strongly resemble the type material from the Rhenish Massif. As common in the species, varices have variably a slightly biconvex to convex course. The figured specimen displays at the aperture a seventh varix on the last whorl, which is one more than previously known for the taxon. Their spacing is not regular.

Lobotornoceras hassoni (HOUSE, 1978)

Figs. 3k-l, Tabs. 1-3

Discussion: Three ammonoids from Boudouda are assigned to *Lobo. hassoni*, which was so far only known from the lower

Frasnian Harrel Shale of the Appalachian Mountains (UD I-C, West Virginia, HOUSE, 1978). Our specimens are identical with the types in terms of suture, strongly compressed conch form, and ornament. The shell parameters (Tab. 3), which are somewhat variable in the holotype (USNM 239891) and best preserved in paratype (USNM 239893), e.g., $wh/dm = 0.54$ to 0.63 , and $ww/wh = 0.54$ to 0.68 , provide no reason for distinction. *Lobotornoceras* aff. *hassoni* described by HOUSE & KIRCHGASSER (2008) from the lower Frasnian West River Shale (UD I-C) of New York State differs in a slight flattening of the venter and subangular ventrolateral shoulders.

The Boudouda record increases significantly the geographical range of *Lobo. hassoni* and expands its stratigraphical range to the upper Frasnian.

Crassotornoceratinae n. subfam.

Diagnosis: Small-sized (micromorphic), shell thinly pachyconic, with rounded flanks and

venter, umbilicus narrow but open throughout ontogeny, with or without varices, growth ornament biconvex, with low or high ventrolateral salient, mostly without, rarely with faint ventrolateral furrows. Sutures with moderately wide to narrow, rounded A-lobe and low ventrolateral saddle. Suture formula: EALI or ELI.

Included genera:

Crassotornoceras HOUSE & PRICE, 1985

Retrotornoceras HOUSE, 2002

Costornoceras n. gen.

Discussion: BECKER (1993) subdivided the Tornoceratinae into three tribes, which were elevated by KORN & KLUG (2002) to full subfamilies of the Tornoceratidae. The Tornoceratinae comprise all genera, which are involute after the 2nd whorl and which lack juvenile ventrolateral furrows. The ventrolateral growth line salient, if developed (not in *Domanikoceras*), is normally broad, the venter may be oxyconic, and the L-lobe is subdivided in *Lobotornoceras*. The Falcitornoceratinae are characterized by involute early stages with ventrolateral furrows. A phylogenetic subdivision into genera with undivided (*Phoenixites*, *Nebechoceras*) and divided L-lobe (*Falcitornoceras*, *Kourazoceras*, *Gundolficeras*, “*G.*” *fezzouense* Group, *Exotornoceras*) is possible. The Aulotornoceratinae include mostly small-sized, open umbilicate genera. Again, there are two groups, the Frasnian and lower Famennian typical forms with projecting, very high ventrolateral salients lying in narrow furrows (*Aulotornoceras*, *Truyolsoceras*, *Polonoceras*, *Immenites*), and mostly middle Famennian genera without prominent salient furrows (*Armatites*, *Protornoceras*, *Tornia*, *Pernoceras*, *Planitornoceras*).

In this scheme, there is no clear place for the micro- and paedomorphic *Crassotornoceras* and its two related genera, which possess an open but narrow umbilicus

and which normally lack a projecting ventrolateral apertural margin stiffened by furrows. Therefore, we introduce for this independent and long-lived side-branch of tornoceratid evolution a new subfamily. It is likely that the Crassotornoceratinae and Aulotornoceratinae have a common paedomorphic ancestor in the lower/middle Frasnian, which Tornoceratidae have hardly been studied.

Stratigraphical range: Middle Frasnian (UD I-E) to high in the lower Famennian (UD II-D).

Geographical distribution: Eastern North America (New York State), North Africa (Moroccan Meseta), Europe (Montagne Noire, Rhenish Massif, Ardennes, South Devon), Western Australia (Canning Basin). Specimens from the Holy Cross Mountains (Poland) identified by DZIK (2002) as “*Aulotornoceras belgicum*” are aulotornoceratids, not *Crasso. belgicum*.

Genus *Crassotornoceras* HOUSE & PRICE, 1985

Crassotornoceras boudoudense n. sp.

Figs. 3e-f, 7c, Tab. 3

Types: Holotype GMM B6C.54-46 (Figs. 3e-f, 7c) is an internal mould displaying well the conch morphology as well as suture and ornament. There are two additional paratypes (GMM B6C.54-47 and 48).

Type level and locality: Type locality of Boudouda Formation, Benahmed region, Bed 3a, UD I-I, local *Aul. auris-Serr. serratum* Zone.

Derivation of Name: After the locality Boudouda.

Diagnosis: Very small-sized, with weakly depressed (ww/wh 1.00 at 5.80 mm dm) and thickly discoidal (ww/dm 0.54 at 5.80 mm dm) whorls, high WER (2.05 at 5.80 mm dm), and narrow umbilicus (uw/dm 0.13 at 5.80 mm dm). Ornament with characteristic,

straight ribbing on the lower flanks (7-10 per whorl), broad ocular sinus of growth lines and moderately high, subtriangular ventrolateral salient, which apex lies in incipient furrows. No varices. Sutures with low ventrolateral saddle, shallow, wide A-lobe, and asymmetrically arched, relatively low dorsolateral saddle.

Description: All three specimen share the characteristic ribbing, which are not following the course of the bundled growth lines (Fig. 3f). The broadly rounded venter is smooth, lacking a ventral band (Fig. 3e). Faint, very narrow ventrolateral furrows are best visible in the holotype and connect spirally the apexes of the ventrolateral growth line bundles. They are lacking in paratype GMM B6C.54-48, which also displays a wide subsymmetrical A-lobe. Paratype GMM B6C.54-48 is roughly the same size as the holotype but rather poorly preserved. Nonetheless, it shows an open umbilicus, rounded venter, and lateral ribbing.

Suture differs from that in typical *Crassotornoceras* by a relatively wide A-lobe (Fig. 7c). The ventrolateral saddle is slightly lower than the inner flank saddle:

Discussion: The new species differs from the also ribbed *Crasso. belgicum* MATERN, 1931a by the lack of prominent varices, the incipient ventrolateral furrows, and much wider A-lobe. *Crassotornoceras nudum* lacks any ornament (ribbing and furrows), while *Crasso. hetzeneggeri* differs by its thicker conch (ww/wh ca. 1.30 at 5.80 mm dm) and lack of ventrolateral furrows (see below). *Crassotornoceras* aff. *belgicum* sensu SÖTE et al. (2021) resembles *Crasso. boudoudense* n. sp. in the combination of weak furrows and dorsolateral folds but has a markedly different suture, with higher suture relief, a low but rounded ventrolateral saddle, and smaller A-lobe. Furthermore, it possesses a higher whorl expansion rate at the same size (2.38 versus 2.05) and ventral varices. The ribbed lower Famennian *Crasso. isolatum* BECKER, 1993

has rursiradiate inner flank folds, a narrower venter, and sutures with higher relief.

Species, such as *Crasso. boudoudense* n. sp. and *Crasso. aff. belgicum*, lack the ventral band of *Aulatonoceras* but their faint ventrolateral furrows support the idea that both paedomorphic genera had a common origin.

Geographic and stratigraphic range: Restricted to lower parts of the upper Frasnian (UD I-I) of the west-central Moroccan Meseta.

Crassotornoceras hetzeneggeri SÖTE, BECKER, HERD & BOCKWINKEL, 2021

Figs. 3g-h, Tabs. 1-2

Discussion: Four Boudouda goniatites assigned to *Crasso. hetzeneggeri* show the faint, undulose ribbing on the inner flanks (Fig. 3g), the rounded, thick conch, a lack of varices, and a punctiform umbilicus, as in the type material from the Rhenish Massif. The typical crassotornoceratid suture with a low ventrolateral saddle and small A-lobe is present. *Crassotornoceras boudoudense* n. sp. is easy to distinguish by its incipient ventrolateral furrows and different, straight dorsolateral ribs. All other Frasnian *Crassotornoceras* species either possess prominent varices (e.g., *Crasso. crassum*, *Crasso. belgicum*, *Crasso. anissi*) or differ in terms of conch morphology and ornament (*Crasso. nudum*).

Costornoceras n. gen.

Derivation of name: After the characteristic ribbing.

Type species: *Costornoceras multiseptatum* n. sp.

Diagnosis: Small-sized (micromorphic), with compressed (from ca. 5 mm dm on), moderately high whorls, small open umbilicus, and towards maturity with increasingly regular, dense, biconvex flank ribbing characterized by a low ventrolateral

salient. Suture with small, v-shaped ventral lobe, low ventrolateral saddle, wide, rounded A-lobe, and asymmetric, low ventrolateral saddle. Suture formula: EALI.

Discussion: The ontogenetically increasing prominent ribbing of the outer flanks separates the new genus from most other genera of the Tornoceratinae. Similar ribbing characterizes in the lower Famennian the two genera *Falcitornoceras* HOUSE & PRICE, 1985 and *Kourazoceras* BECKER in BECKER et al. (2002). The first has marked juvenile falcate ribs with high, narrowly triangular ventrolateral projection, lying often in spiral furrows. The second is strongly paedomorphic (as *Costornoceras* n. gen.) and develops regular ribs with low ventrolateral salient at maturity (at only ca. 10 mm dm). Both genera have closed umbilici and divided L-lobes, as typical for advanced Falcitornoceratinae.

Costornoceras n. gen. is closely related to *Crassotornoceras* but differs by its biconvex ribbing combined with a low ventrolateral salient and early ontogenetic shell compression.

Geographic and stratigraphic range: Restricted to lower parts of the upper Frasnian (UD I-I) of the west-central Moroccan Meseta.

***Costornoceras multiseptatum* n. gen. n. sp.**

Figs. 3m-p, 7d-e, Tab. 3

Types: Holotype GMM B6C.54-35 (Figs. 3m-n), a well-preserved internal mould showing all features. There are eleven paratypes (GMM B6C.54-36-45; see Appendix).

Type locality and level: Type locality of Boudouda Formation, Benahmed region, Bed 4a, UD I-I, local *Aul. auris-Serr. serratum* Zone.

Derivation of name: After the dense septal spacing.

Diagnosis: Very small-sized, whorls weakly depressed before 5-6 mm dm, afterwards

weakly compressed, thickly discoidal (ww/dm slightly decreasing from 0.55 at 5 mm dm to 0.47 at 9.50 mm dm), moderately to fast expanding (WER = 1.90-2.10), in early ontogeny subinvolute (uw/dm = ca. 0.20 at 5 mm dm), later involute (uw/dm ca. 0.10 at 10 mm dm); with characteristic, densely spaced ribs on the outer flank half, following the biconvex growth lines, and with a low ventrolateral salient. Sutures with dense spacing, broad and moderately high, asymmetrically rounded dorsolateral saddle, widely rounded A-lobe, small, rounded and low ventrolateral saddle, and v-shaped E-lobe.

Description: The species is paedomorphic. The maximum known diameter is seen in the holotype at ca. 9.5 mm dm (Tab. 3). It features the most prominent ribs (ca. 25) on the last half whorl. Smaller specimens, such as paratype GMM B6C.54-42 (Figs. 3o-p), have visible but more undulose ribs. The ontogenetic change to prominent ribs starts around 5 mm dm. One specimen displays weak spiral depressions on the outer flank, outside the ventrolateral salient. Every specimen features dense sutural-spacing ranging between 30 to 40 sutures per whorl (compare Figs. 3n-o). At very small size, the ventrolateral saddle is almost flat. The uw/dm ratio decreases during ontogeny while the whorl expansion fluctuates around 2.0.

Discussion: The ribbing type is very different in some *Crassotornoceras* species. They display widely spaced minor folds restricted to the subumbilical area (*Crasso. boudoudense* n. sp., *Crasso. isolatum*), not on the outer flanks, often not in parallel with the growth ornament, or in conjunction with varices (*Crasso. belgicum*). All Frasnian *Crassotornoceras* species with marked dorsolateral folds display high, projecting ventrolateral salients of the ornament.

Geographic and stratigraphic range: As for the genus.

Subfamily Aulaternoceratinae KORN & KLUG, 2002

Genus *Aulaternoceras* SCHINDEWOLF, 1922

***Aulaternoceras auris* (QUENSTEDT, 1849)**

Figs. 4a-b, Tabs. 1-2

Discussion: The eight specimens assigned to *Aul. auris* belong to a morphotype with only weakly developed growth line bundles on the flank (Fig. 4b) and ventral festoons (Fig. 4a). In the Rhenish Massif, at Büdesheim, morphotypes with both weak or strong bundles and ventral band are abundant. Apart from this feature, the suture, ornament and conch morphology of the Boudouda specimens are identical. Previously, no Moroccan *Aul. auris* has been illustrated.

***Aulaternoceras constrictum* (STEININGER, 1849)**

Figs. 4c-d, Tabs. 1-2

Discussion: Characteristic are the regularly-spaced strong varices, narrow and strong ventrolateral furrows (Fig. 4c), and the weak ventral band (Fig. 4d). All six specimens from Boudouda are identical to material from the German type region (see SÖTE et al. 2021).

***Aulaternoceras* sp.**

Fig. 4o, Tab. 1

Discussion: There is one fragment, which resembles *Aul. auris*, especially in its strongly bundled flank ornament, but it seems to lack a ventral band. This feature is typical for the lower Famennian genus *Truyolsoceras* MONTESINOS, 1988, which, however, is also characterized by regular ventral ribbing (see revision by BECKER, 1993). Since there is only one small fragment, since the ventral part is not preserved well enough, and since all Boudouda aulaternoceratids have weak ventral bands, we allocate the specimen to *Aulaternoceras* in open nomenclature.

Suborder Gephuroceratina RUZHENCEV, 1957

Superfamily Gephuroceratoidea FRECH, 1897

Family Gephuroceratidae FRECH, 1897

Subfamily Trimanticoceratinae KORN in KORN & KLUG, 2002

Genus *Costamanticoceras* BECKER & HOUSE, 1993

***Costamanticoceras hybris* n. sp.**

Figs. 4m-n, 7f, Tabs. 1-3

Derivation of name: After the hybrid morphology of early and median ontogenetic stages.

Types: Only holotype GMM B6C.54-34.

Type level and locality: Type locality of Boudouda Formation, Benahmed region, Bed 21a, UD I-J, *M. carinatum* Zone.

Diagnosis: Early whorls between ca. 2.5 and 3.5 mm dm depressed, subevolute, and with dense, biconvex ribbing on the flanks and venter, apart from a smooth mid-ventral zone, subsequently without ribbing, whorls very high (WER = ca. 2.5), increasingly subinvolute and weakly compressed (uw/dm = 0.20 and ww/wh = 0.97 at 12.5 mm dm), tegoid, with narrowly rounded venter. Sutures with a relatively wide, subsymmetric ventrolateral saddle, rounded L-lobe and well-developed U-lobe of early stages.

Description: The only available specimen shows the early ontogeny and different median stage. The exposed inner whorl between ca. 2.5 and 3.5 mm dm bears ca. 15 dense, rounded, biconvex flank ribs (per half whorl) with a broad ventrolateral salient. Ribs and interspaces are equally wide; the ribs do not cross the mid-ventral field (Fig. 3n). They disappear rapidly until 5 mm dm, where the conch is still subevolute (uw/dm = ca. 0.35, Tab. 3) and depressed (ww/wh = 1.12). Later whorls become subinvolute, weakly compressed, with well-rounded, tegoid cross-section. The whorl expansion is very high (WER = ca. 2.5) from early on. The septal face at ca. 5.5 mm dm shows a rather deep and rounded, internal U-lobe and broad flank

saddle (Figs. 4n, 6f). On the last preserved whorl, the latter become subsymmetric and moderately high (Fig. 4n).

Discussion: The regular ribbing at small size suggests that the new species belongs to *Costamanticoceras*. Typical species of the genus, however, retain ribbed and subevolute stages much longer during ontogeny. Since the ribs are rounded, not thin and sharp, the Boudouda form does not belong to *Gephyroceras* (compare the revision of North American typical species by HOUSE & KIRCHGASSER 2008).

Our new Boudouda form is isolated in terms of morphology and palaeogeography, which justifies to name it. It is not close to the *Costamanticoceras* illustrated from Immouzer-du-Kandar in ABOUSSALAM et al. (2020); this form is a more typical *Costamanticoceras*. A single *Costam.* cf. *nodulosum* from the Tafilalt mentioned by BECKER & HOUSE (2000b, p. 54) also refers to the typical group around the type-species.

Geographic and stratigraphic range: Restricted to type level and locality.

Genus *Trimanticoceras* HOUSE in HOUSE & ZIEGLER, 1977

***Trimanticoceras* n. sp.**

Figs. 5a-b, 7h, Tabs. 1-2

Description: Three small whorl fragments from Beds 14a and 15a are characterized by subinvolute, moderately high, very weakly depressed ($ww/wh = 1.03$), well-rounded, tegoid whorls. Most distinctive are strongly biconvex, undulose growth lines with a projecting ventrolateral salient delimited by spiral double furrows. The outer furrow is narrow and more distinctive. On the broadly rounded venter, a weak ventral band is developed. The adapical septal face of GMM B6C.54-152 shows a rounded L-Lobe, asymmetric, moderately wide and high ventrolateral saddle, a deep, asymmetrically

pointed E-lobe, and low median saddle (Fig. 7h).

Discussion: So far, there are only two valid species in *Trimanticoceras*, the rather evolute *Tri. cinctum* (GLENISTER, 1958), the generotype from the Canning Basin and Germany (BECKER & HOUSE 1993), and the very poorly known, more compressed *Tri. retrorsum* (von BUCH, 1832) from Martenberg, Germany, which type (selected by WEDEKIND 1913a, p. 54) has never been illustrated and probably been lost. Based on very early juvenile furrows documented by CLAUSEN (1969) in Budesheim specimens (not in type material), BECKER & HOUSE (2009) re-assigned *M. bullatum* WEDEKIND, 1913a to *Trimanticoceras*. However, it is now known that juvenile *Sphaeromanticoceras* s.str. are characterized by this feature (see BECKER & HOUSE 1994a; SÖTE et al. 2021).

The Boudouda specimens do not belong to either of the two named species, due to the double furrows and ventral band alone. BECKER et al. (1993) and BECKER & HOUSE (2009) listed several new trimanticoceratids from Western Australia. Since we only have fragments from Boudouda, it is better to leave them in open nomenclature until the general knowledge of the genus is improved.

Geographic and stratigraphic range: Restricted to lower parts of the upper Frasnian (UD I-J, *M. carinatum* Zone) of the west-central Moroccan Meseta.

4.2. Gastropoda

Family uncertain

***Goniphilus* n. gen.**

Derivation of name: After the regular co-occurrence with goniatites in hypoxic goniatite shale facies.

Type-species: *G. delicatulus* n. sp.

Other species: *Natica ausavensis* STEININGER, 1953, other un-named species, such as the lower Famennian “*Platyostoma*

aff. *lineata*” sensu JUX & KRATH (1974), possibly also *Diaphorostoma* (*Naticopsis*) *rotundata* CLARKE, 1904 from the Angola Shale (lower part of upper Frasnian) of New York State.

Diagnosis: Small-sized, thin-shelled, with three whorls at maturity; whorls very fast expanding, low- to slightly inverse-spired, laterally inflated, apex region plain or slightly inserted (heterostrophic), umbilicus very deep and narrow, peristome subcircular to oval. First whorl gyroconic (open), with protoconch not overlapping the second whorl. Delicate ornament consisting of arched, biconvex growth lirae and non-bifurcating ribs are always impressed on internal moulds.

Discussion: The new genus forms a well-defined group of morphologically similar species that are restricted to pelagic ammonoid facies. *Goniphilus* n. gen. differs from the platyceratid *Platyostoma* in smaller size, with a lower number of even lower spired whorls. In *Platyostoma*, the apex and first whorls are standing out in apertural view. In *Goniphilus* n. gen., the first whorl may be even “inserted” into the later ones, giving a slight heterostrophic coiling (Figs. 5g-h). The protoconch and perforate first whorl are not cyrtoneritimorph as in various Palaeozoic platyceratids (FRÝDA et al. 2009) but resemble that in some euomphalids (see BANDEL & FRÝDA 1998). PAECKELMANN (1913) had placed STEININGER’s species in *Platyceras*, which we do not agree with based on the early ontogeny alone.

The much younger (Triassic) genus *Planospirina* KITTL, 1899 shows a somewhat similar shell whorl form but is thick-shelled, larger, lacks ribbing or sharp growth lirae, and also the well-developed lateral sinus of the ornament.

Stratigraphic and geographical range: Upper Frasnian (UD I-I) to lower Famennian (ca. UD II-D) of Germany, the Montagne

Noire (juveniles, BECKER 1993), eastern North America, and the Moroccan Meseta.

***Goniphilus delicatulus* n. sp.**

Figs. 5j-m, 8

Types: Holotype GMM B6B.11-1, paratypes GMM B6B.11-2 and 3.

Derivation of name: After the delicate ribbing.

Type level and locality: Type locality of Boudouda Formation, Benahmed region, Bed 18a, UD I-J, *M. carinatum* Zone.

Diagnosis: Small-sized, low, fast expanding whorls (WER in apical view = ca. 4.2) with short, steep-sided, subangular sutures, ovoid aperture, and fine, rursiradiate, biconvex, non-bifurcating ribs (ca. 45 on last whorl) consisting of bundled growth lirae.

Description: The holotype is the largest specimen with a diameter of near 10 mm and three completed whorls. The paratypes are slightly smaller or incomplete, and several other fragments do not suggest that the species reached larger size. The whorls increase apically measured (Fig. 5j) fast in width but remain low. At the fully rounded aperture, whorl height and width are similar. The “umbilical width” of the apical view is 25-27 % of the dm. On the underside, the umbilicus is very deep and narrow (ca. 15 % dm in paratype GMM B6B.11-3). The early whorls and apex are hardly visible in lateral or apertural view (Figs. 5l-m). The first whorl leaves a minor apical opening but the minute protoconch does not touch or overlap the second whorl (Fig. 8).

The delicate and regular ribs consist of bundled, fine growth lirae that are partly also recognizable in the rib interspaces. They run undivided all around the whorl and consist typically of one strong lira bordered by two smaller lirae. They begin ca. after the first half whorl and increase in strength with growth. On the upper whorl they are strongly convex (Fig. 5j), form a broad sinus on the flanks (Fig.

5m), followed by a wide salient that runs into the umbilicus (Fig. 5k). Since all specimens are internal moulds, it is remarkable that finest ornament details are preserved. Based on the width of the whorl sutures interspace (Fig. 8), the probably aragonitic adult shell was not more than 0.2 mm thick.



Fig. 8: Apical view of the holotype of *Goniphilus delicatulus* n. gen. n. sp. (GMM B6B.11-1), showing the perforate coiling and onset of ornament of the first whorl. Whorl sutures were originally filled by shell but leave an open apex in the center.



Fig. 9: Apical view of the topotype (potential neotype) of *Goniphilus ausavensis* n. gen. (STEININGER, 1853) from Büdesheim (GMM B6B.11-6), showing the perforate coiling and onset of ornament of the first whorl. Whorl sutures were originally filled by shell but leave an open apex in the center.

Discussion: Based on the examination of several topotypes (Figs. 5g-i, 9), *G.*

ausavensis n. gen. from Büdesheim is similar but differs in more undulose, less sharply defined ribs, and convexly rounded, not flattened upper whorl sides. Consequently, the whorl sutures lie beneath rounded whorl shoulders (Fig. 5h). In addition, the first whorl sits in a lower position than the second one (in a minor depression), causing incipient heterostrophy (Fig. 5g). The first whorl seems to be slightly larger (Fig. 9) than in *G. delicatulus* n. gen. n. sp. (Fig. 8) but the open coiling is very similar. The still un-named lower Famennian species of the Knoppenbissen Formation (“*Platyostoma* aff. *lineata*” sensu JUX & KRATH, 1974) and Nehden Goniatile Shale (Nehden Formation, BECKER et al. 2016) is characterized by fine reticulate ornament, featuring numerous longitudinal lirae. *Diarophostoma (Naticopsis) rotundatum* CLARKE, 1904 comes from upper Frasnian shales with goniatites (Angola Shale) of New York State. It differs from both *G. delicatulus* n. gen. n. sp. and *G. ausavensis* n. gen. in more globose, evenly rounded whorls, only very weak ribbing restricted to the outer whorl margin, and an apex of the first whorls that slightly stands out.

Stratigraphical and geographical range: Restricted to the lower part of upper Frasnian (UD I-I/J) of the west-central Meseta.

Appendix:

Boudouda Frasnian fossil specimen list (* = holotypes)

„Pont.“ <i>prumiense</i>	Fr-15a	B6C.54-1
„Pont.“ <i>prumiense</i>	Fr-25	B6C.54-2
<i>Aulaternoceras</i> sp.	Fr-17a	B6C.54-3
<i>Aul. auris</i>	Fr-02a	B6C.54-4
<i>Aul. auris</i>	Fr-13a	B6C.54-5
<i>Aul. auris</i>	Fr-15a	B6C.54-6
<i>Aul. auris</i>	Fr-17a	B6C.54-7
<i>Aul. auris</i>	Fr-17a	B6C.54-8
<i>Aul. auris</i>	Fr-17a	B6C.54-9
<i>Aul. auris</i>	loose	B6C.54-10
<i>Aul. auris</i>	loose	B6C.54-11
<i>Aul. constrictum</i>	Fr-13a	B6C.54-12
<i>Aul. constrictum</i>	Fr-21a	B6C.54-13

<i>Aul. constrictum</i>	Fr-21a	B6C.54-14	<i>M. carinatum</i>	Fr-23a	B6C.54-70
<i>Aul. constrictum</i>	Fr-25	B6C.54-15	<i>M. carinatum</i>	Fr-15a	B6C.54-71
<i>Aul. constrictum</i>	loose	B6C.54-16	<i>M. carinatum</i>	loose	B6C.54-72
<i>Aul. constrictum</i>	loose	B6C.54-17	<i>M. carinatum</i>	loose	B6C.54-73
<i>Bac. anellus</i>	Fr-21a	B6C.54-18	<i>M. cordatum</i>	Fr-17a	B6C.54-74
<i>Bac. anellus</i>	Fr-21a	B6C.54-19	<i>M. cordatum</i>	Fr-20a	B6C.54-75
<i>Bac. anellus</i>	Fr-23a	B6C.54-20	<i>M. cordatum</i>	Fr-25	B6C.54-76
<i>Bac. anellus</i>	loose	B6C.54-21	<i>M. cordatum</i>	Fr-25	B6C.54-77
<i>Bac. anellus</i>	loose	B6C.54-22	<i>M. cordatum</i>	Fr-13a	B6C.54-78
<i>Bac. declivis</i>	Fr-15a	B6C.54-23	<i>M. cordatum</i>	Fr-13a	B6C.54-79
<i>Bac. declivis</i>	Fr-15a	B6C.54-24	<i>M. cordatum</i>	Fr-13a	B6C.54-80
<i>Bac. declivis</i>	Fr-15a	B6C.54-25	<i>M. cordatum</i>	Fr-13a	B6C.54-81
<i>Bac. declivis</i>	Fr-15a	B6C.54-26	<i>M. cordatum</i>	Fr-15a	B6C.54-82
<i>Bac. declivis</i>	Fr-18a	B6C.54-27	<i>M. cordatum</i>	Fr-17a	B6C.54-83
<i>Bac. declivis</i>	Fr-18a	B6C.54-28	<i>Manticoceras</i> sp.	Fr-05a	B6C.54-84
<i>Bac. declivis</i>	Fr-18a	B6C.54-29	<i>Manticoceras</i> sp.	Fr-05a	B6C.54-85
<i>Bac. declivis</i>	Fr-18a	B6C.54-30	<i>Manticoceras</i> sp.	Fr-18a	B6C.54-86
<i>Bac. declivis</i>	Fr-18a	B6C.54-31	<i>Manticoceras</i> sp.	Fr-25	B6C.54-87
<i>Bactrites</i> sp.	Fr-20a	B6C.54-32	<i>Manticoceras</i> sp.	loose	B6C.54-88
<i>Bactrites</i> sp.	Fr-20a	B6C.54-33	<i>Ponticeras</i> sp.	Fr-17a	B6C.54-89
<i>Costam. hybris</i> n. sp. *	Fr-21a	B6C.54-34	<i>Ponticeras</i> sp.	Fr-19a	B6C.54-90
<i>Cost. multiseptatum</i> n. sp. *	Fr-04a	B6C.54-35	<i>Serr. serratum</i>	Fr-03a	B6C.54-91
<i>Cost. multiseptatum</i> n. sp.	Fr-13a	B6C.54-36	<i>Serr. serratum</i>	loose	B6C.54-92
<i>Cost. multiseptatum</i> n. sp.	Fr-15a	B6C.54-37	<i>Sph. affine</i>	Fr-03a	B6C.54-93
<i>Cost. multiseptatum</i> n. sp.	Fr-17a	B6C.54-38	<i>Sph. affine</i>	Fr-04a	B6C.54-94
<i>Cost. multiseptatum</i> n. sp.	Fr-17a	B6C.54-39	<i>Sph. affine</i>	Fr-05a	B6C.54-95
<i>Cost. multiseptatum</i> n. sp.	Fr-20a	B6C.54-40	<i>Sph. affine</i>	Fr-06a	B6C.54-96
<i>Cost. multiseptatum</i> n. sp.	Fr-21a	B6C.54-41	<i>Sph. affine</i>	Fr-08a	B6C.54-97
<i>Cost. multiseptatum</i> n. sp.	loose	B6C.54-42	<i>Sph. affine</i>	Fr-08a	B6C.54-98
<i>Cost. multiseptatum</i> n. sp.	loose	B6C.54-43	<i>Sph. affine</i>	Fr-15a	B6C.54-99
<i>Cost. multiseptatum</i> n. sp.	loose	B6C.54-44	<i>Sph. affine</i>	Fr-15a	B6C.54-100
<i>Cost. multiseptatum</i> n. sp.	loose	B6C.54-45	<i>Sph. affine</i>	Fr-15a	B6C.54-101
<i>Crasso. boudoudense</i> n. sp. *	Fr-03a	B6C.54-46	<i>Sph. affine</i>	Fr-17a	B6C.54-102
<i>Crasso. boudoudense</i> n. sp.	Fr-13a	B6C.54-47	<i>Sph. affine</i>	Fr-20a	B6C.54-103
<i>Crasso. boudoudense</i> n. sp.	loose	B6C.54-48	<i>Sph. affine</i>	Fr-23a	B6C.54-104
<i>Crasso. hetzeneggeri</i>	Fr-09a	B6C.54-49	<i>Sph. affine</i>	loose	B6C.54-105
<i>Crasso. hetzeneggeri</i>	Fr-15a	B6C.54-50	<i>Sph. orbiculum</i>	Fr-02a	B6C.54-106
<i>Crasso. hetzeneggeri</i>	Fr-15a	B6C.54-51	<i>Sph. orbiculum</i>	Fr-02a	B6C.54-107
<i>Crassotormoceras</i> sp.	Fr-15a	B6C.54-52	<i>Sph. orbiculum</i>	Fr-02a	B6C.54-108
<i>Lobobactrites</i> sp.	Fr-15a	B6C.54-53	<i>Sph. orbiculum</i>	Fr-15a	B6C.54-109
<i>Lobobactrites</i> sp.	Fr-15a	B6C.54-54	<i>Sph. orbiculum</i>	Fr-16a	B6C.54-110
<i>Lobobactrites</i> sp.	Fr-15a	B6C.54-55	<i>Sph. orbiculum</i>	Fr-17a	B6C.54-111
<i>Lobobac. timanicus</i>	Fr-19a	B6C.54-56	<i>Sph. orbiculum</i>	Fr-17a	B6C.54-112
<i>Lobo. ausavense</i>	Fr-03a	B6C.54-57	<i>Sph. orbiculum</i>	Fr-17a	B6C.54-113
<i>Lobo. ausavense</i>	Fr-04a	B6C.54-58	<i>Sph. orbiculum</i>	Fr-20a	B6C.54-114
<i>Lobo. ausavense</i>	Fr-04a	B6C.54-59	<i>Sph. orbiculum</i>	Fr-20a	B6C.54-115
<i>Lobo. ausavense</i>	loose	B6C.54-60	<i>Sph. orbiculum</i>	Fr-20a	B6C.54-116
<i>Lobo. hassoni</i>	Fr-06a	B6C.54-61	<i>Sph. orbiculum</i>	loose	B6C.54-117
<i>Lobo. hassoni</i>	Fr-23a	B6C.54-62	<i>T. aequilobum</i>	Fr-03a	B6C.54-118
<i>Lobo. hassoni</i>	Fr-25	B6C.54-63	<i>T. aequilobum</i>	Fr-14a	B6C.54-119
<i>Lobo. hassoni</i>	loose	B6C.54-64	<i>T. aequilobum</i>	Fr-15a	B6C.54-120
<i>Lobo. hassoni</i>	loose	B6C.54-65	<i>T. aequilobum</i>	Fr-15a	B6C.54-121
<i>M. carinatum</i>	Fr-14a	B6C.54-66	<i>T. aequilobum</i>	Fr-16a	B6C.54-122
<i>M. carinatum</i>	Fr-15a	B6C.54-67	<i>T. aequilobum</i>	Fr-17a	B6C.54-123
<i>M. carinatum</i>	Fr-23a	B6C.54-68	<i>T. aequilobum</i>	Fr-19a	B6C.54-124
<i>M. carinatum</i>	Fr-23a	B6C.54-69	<i>T. aequilobum</i>	Fr-23a	B6C.54-125

<i>T. aequilobum</i>	loose	B6C.54-126	<i>Tornoceras</i> sp.	Fr-06a	B6C.54-145
<i>T. aequilobum</i>	loose	B6C.54-127	<i>Tornoceras</i> sp.	Fr-13a	B6C.54-146
<i>T. aequilobum</i>	loose	B6C.54-128	<i>Tornoceras</i> sp.	Fr-15a	B6C.54-147
<i>T. aequilobum</i>	Fr-13a	B6C.54-129	<i>Tornoceras</i> sp.	Fr-16a	B6C.54-148
<i>T. aequilobum</i>	Fr-13a	B6C.54-130	<i>Tornoceras</i> sp.	Fr-13a	B6C.54-149
<i>T. aequilobum</i>	Fr-13a	B6C.54-131	<i>Tornoceras</i> sp.	Fr-13a	B6C.54-150
<i>T. aff. contractum</i>	Fr-15a	B6C.54-132	<i>Tornoceras</i> sp.	Fr-13a	B6C.54-151
<i>T. aff. contractum</i>	Fr-15a	B6C.54-133	<i>Trimanticoceras</i> n. sp.	Fr-14a	B6C.54-152
<i>T. aff. contractum</i>	Fr-15a	B6C.54-134	<i>Trimanticoceras</i> n. sp.	Fr-15a	B6C.54-153
<i>T. aff. contractum</i>	Fr-15a	B6C.54-135	<i>Trimanticoceras</i> n. sp.	Fr-15a	B6C.54-154
<i>T. aff. contractum</i>	Fr-16a	B6C.54-136	athyridid sp.	Fr-2a	B5B.16-1
<i>T. aff. contractum</i>	Fr-20a	B6C.54-137	<i>Glyptohallicardia palmata</i>	Fr-5a	B6A.37-1
<i>T. aff. contractum</i>	loose	B6C.54-138	<i>Goniphilus delicatulus</i> n. sp. *	Fr-18a	B6B.11-1
<i>T. aff. contractum</i>	loose	B6C.54-139	<i>Goniphilus delicatulus</i> n. sp.	Fr-3a	B6B.11-2
<i>T. aff. contractum</i>	loose	B6C.54-140	<i>Goniphilus delicatulus</i> n. sp.	loose	B6B.11-3
<i>T. aff. contractum</i>	Fr-09a	B6C.54-141	<i>Goniphilus delicatulus</i> n. sp.	Fr-4a	B6B.11-4
<i>T. aff. contractum</i>	Fr-14a	B6C.54-142	<i>Goniphilus delicatulus</i> n. sp.	Fr-16a	B6B.11-5
<i>T. aff. contractum</i>	Fr-14a	B6C.54-143	<i>Goniphilus ausavensis</i> (topotype)	Büd	B6B.11-6
<i>Tornoceras</i> sp.	Fr-15a	B6C.54-144	<i>Goniphilus ausavensis</i> (topotype)	Büd	B6B.11-7

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