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REGULAR RESEARCH ARTICLE

The oldest ammonoids of Morocco (Tafilalt, lower Emsian)

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Abstract

During a fieldtrip of the 10th International Cephalopod Symposium to the Tafilalt (SE Morocco), a fauna with the so far oldest ammonoid of the region was discovered at the top of the basal Emsian *Deiroceras* Limestone of Jebel Mech Irdane. The new material confirms the record of a single, poorly preserved specimen of the same age from Ras El Kebbar in the northwestern Tafilalt. All specimens are assigned within the Chebbitinae n. subfam. (Mimosphinctidae) to *Praechebbites debaetsi* n. gen. n. sp., which differs from the slightly younger *Chebbites reisdorfi* mostly in the lack of a dorsal lobe and dorsal imprint zone. In the conodont succession, the new species and genus falls in the top of the *Eolinguipolygnathus excacatus* M114 Zone, which has been proposed to define in future the base of the Emsian. Since the new taxon is morphologically already advanced, it is likely that even older ammonoids with loosely coiled conchs will be discovered in the future. A block from a Lower Carboniferous olistostrome of the adjacent Tinerhir region contained the gyroconic *Ivoites* n. sp. only. The global comparison of oldest ammonoid faunas shows the rarity of assemblages assigned to Lower Devonian (LD) III-B, often dated by conodonts and dacryoconarids. These faunas display a high level of endemism, which suggests that ammonoid origin and early evolution took place in regional populations with a restricted dispersal of genera and species.

Keywords Ammonoids · Emsian · Taxonomy · Stratigraphy · Morocco

Introduction

Ammonoids are among the fossil groups with the richest, in terms of abundance and palaeobiodiversity, and stratigraphically most refined global fossil record. Despite this, the ancestry and early evolution of the superorder is still enigmatic, mostly because of a surprisingly incomplete knowledge of transitional forms from the ancestral bactritids. The morphological changes that occurred around the evolution from slender orthoconic, compressed *Lobobactrites* with ventral siphuncle and ventral lobes of septa via cyrtocones and gyrocones ultimately to fully coiled goniatites are well documented (e.g., Schindewolf 1932; Erben 1964, 1966; De Baets et al. 2012; Klug et al. 2015),

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including palaeoecological implications of this transformation (e.g., Klug and Korn 2004). However, there are almost no fossil successions that directly document the assumed evolutionary trends in a geological time framework. Early ammonoids had a near-global distribution in the palaeo(sub)tropics (see recent literature compilation in Klug 2017). Relative high numbers of species are known from the Rhenish Massif of Germany, Bohemia, the southern Tien Shan of Uzbekistan, and South China (Guangxi). The perhaps best stratigraphical control for a series of lower Emsian faunas comes from southern Morocco (Becker and House 2000a; Klug 2001, 2017; Klug et al. 2008; De Baets et al. 2010; Becker et al. 2018b). In this region, early goniatite zones have been precisely correlated with the conodont and dacryoconarid succession (e.g., Aboussalam et al. 2015). Here, we report on the discovery of the currently oldest goniatite level of the central Tafilalt, which confirms an earlier record from the northwestern Tafilalt (Ras El Kebbar), which consisted of a heavily corroded specimen only (Klug 2001). The Jebel Mech Irdane locality contains a single new species assigned to a new genus, which is compared with slightly younger relatives from the region and species from Russia. The new faunule is discussed in the context of lower Emsian records from other Moroccan areas, including *Metabactrites* material mentioned by Rytina et al. (2013) from Taourirt n'Khellil (Tinerhir region, southern Variscan Front), which is re-assigned here to *Ivoites* n. sp., and from far distant regions, with implications for our understanding of earliest ammonoid phylogeny.

Locality and stratigraphy

The new goniatite material was collected on the 31st of March 2018 jointly by the authors during the Atlas/Anti-Atlas field excursion of the 10th International Cephalopod Symposium (ICS). All specimens derived from a single thin limestone layer, probably near the top of the *Deiroceras* Limestone (ca. middle Seheb El Rhassel Formation), which crops out in ca. W–E direction along the northern slope of the Jebel Mech Irdane in the western Tafilalt (Fig. 1). For a recent overview of Emsian regional litho- and biostratigraphy see Aboussalam et al. (2015; Fig. 2). The overall Jebel Mech Irdane Lower/Middle Devonian stratigraphy and research history has been summarized in the published field guidebook of the 10th ICS (Becker et al. 2018a).

Walliser (2000) first mentioned lower Emsian limestones with early goniatites ("*Anetoceras* Group") from outcrops in the plain ca. 200 m north of the basal Givetian GSSP section. Klug (2001) illustrated a lower Emsian section log for the succession near the eastern end of the northern limb of the Mech Irdane Anticline, where the Palaeozoic rocks were intruded by a dolerite sill (Fig. 1). He showed the presence of *Erbenoceras advolvens, Anetoceras obliquecostatum,* and *Irdanites korni* near the base of the *Anetoceras* Limestone, in the lower part of his Unit

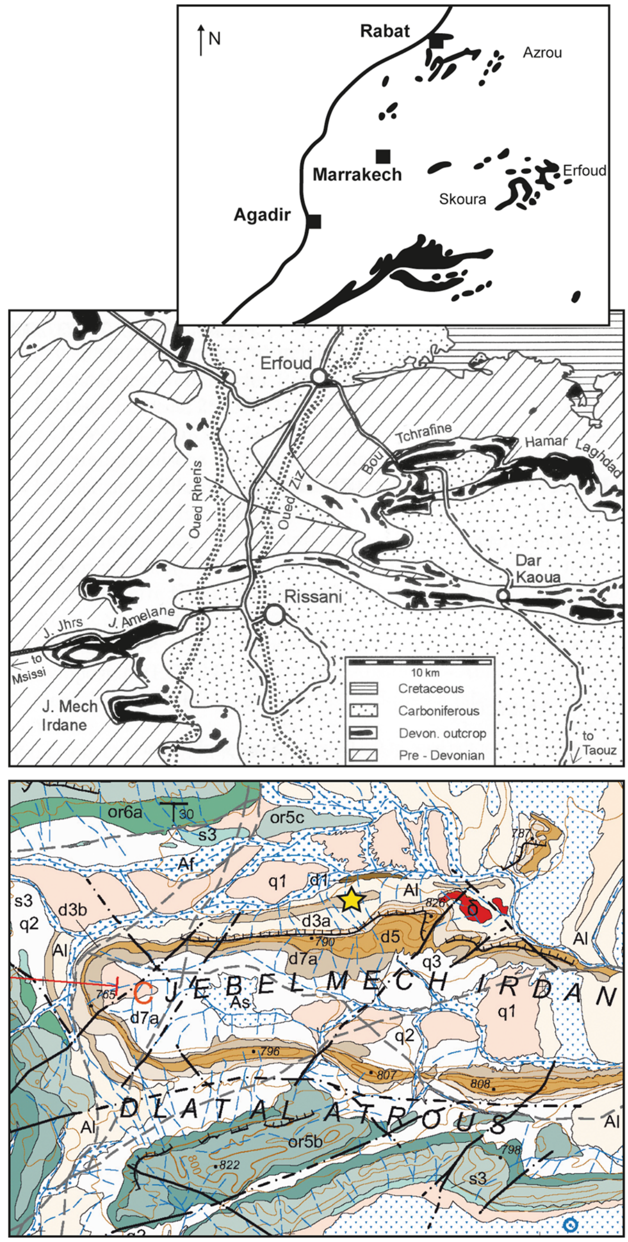

Fig. 1 Position of the ammonoid locality SW of Erfoud (Tafilalt, eastern Anti-Atlas), near the NE end of Jebel Mech Irdane, showing the regional geology in an extraction from the geological map, 1:50,000, sheet Irara (Alvaro et al. 2014); or 5b = Lower Ktaoua Formation (Caradoc), or 5c = Tiouririne Formation (Caradoc/lower Ashgill), or6a = Bani Group (top Ordovician), s3 = Ludlow, d3a = Amerboh Formation (s.l.), Lower Member (lower Emsian), d3b = Amerboh Formation (s.str.), Upper Member (upper Emsian), d5 = Boutchrafine Formation, Upper Member (Givetian), d7a = Achguig Formation, Middle Member (middle Famennian), AI and q1-2 = Quaternary terraces, As = Sebkha, o (red) = dolerite

D (= Unit I sensu Becker et al. 2013, 2018c). Higher, a more solid limestone of his Unit E, the *Mimagoniatites* Limestone (Unit J sensu Becker et al. 2013, 2018d), yielded the upper lower Emsian index goniatite *Mimagoniatites fecundus*.

Our new faunule comes from the same section, from the thin-bedded limestones at the top of Klug's Unit A (= Unit G sensu Becker et al. 2013, 2018d; Fig. 2). This level was originally called "*Jovellania* Limestone" in the Tafilalt (e.g., Bultynck and Walliser 2000) but it was re-named as *Deiroceras* Limestone by Kröger (2008), due to the corrected taxonomic assignment of its common, large orthocones. The discovery of our new goniatites was eased by the wide exposure of the goniatite-bearing bedding plane; additionally, extraction of the reasonably well-preserved and abundant material was facilitated by the comparatively deeply weathered marly limestones, which apparently have a lower carbonate content than seen in the massive limestones of the same layer elsewhere (presuming our correlation is correct). The overlying *Metabactrites* Shale (Unit B of Klug 2001, Unit H of Becker et al. 2013, 2018d) is locally rather unfossiliferous, which is partly a consequence of poor exposure and probably also differences in the degree of pyritization of the internal moulds. Only a few fragmentary *Erbenoceras* of "Faunule 2" sensu Klug et al. (2008) were collected at the same locality. Klug's fauna from the subsequent lower *Anetoceras* Limestone was not re-sampled. A poor, smooth fragment indicates that the index species *Klugites gesinae* occurs in the main *Anetoceras* Limestone, as at Bou Tchrafine (Becker et al. 2018a) and Ouidane Chebbi (Klug 2001) to the east. Near the top of the lower Emsian, several *Mimagoniatites* were collected from solid bluish-grey limestone, which includes localized small coral biostromes.

Becker and House (1994, 2000b) introduced a refined Lower/Middle Devonian ammonoid zonation, with the lower Emsian being called LD (= Lower Devonian) III. The first zone, LD III-A, is characterized by bactritids that abundantly occur in the *Devonobactrites* Shale of the Tafilalt (with "Faunule 1" sensu Klug et al. 2008 and Frey

lithological units		ammonoid zones / subzones	key	polygnathid zones/subzones	icriodid zones	dacryoconarid zones
J	*Mimagoniatites* Limestone	*Mimosphinctes karltschanzi*	III-E	*Eol. laticostatus*	(poor record)	*Now. (Now.) cancellata* *Nowakia (Now.) elegans*
		Mimagoniatites fecundus	III-D	*L. inversus* (record gap)		
I	*Anetoceras* Limestone	*Klugites gesinae*	III-C2	(*Criteriognathus steinhornensis*)	*Latericriodus beckmanni beckmanni*	*Nowakia (Now.) barrandei*
		Anetoceras obliquecostatum	III-C1	*Eolinguipolygnathus catharinae*	*Latericriodus latus*	*Nowakia (Dmitriella)* cf. *praecursor*
H	*Metabactrites* Shale	*Erbenoceras advolvens* *Metabactrites formosus*	III-B2	(record gap)	(record gap)	(record gap)
G	*Deiroceras* Limestone	*Praechebbites debaetsi* n.g. n.sp.	III-B1	*Eol. excavatus* Morphotype 114	*Lat. bilatericrescens bilatericrescens* *Lat. bil. gracilis*	*Nowakia (Now.) zlichovensis maghrebiana*
F	*Devonobactrites* Shale	*Devonobactrites obliquiseptatus*	III-A	(record gap)	(record gap)	*Guerichina africana*
E	Pragian Limestone	–	II		*Caudicriodus celtibericus*	

Fig. 2 Lower Emsian litho- and biostratigraphy of the central Tafilalt, showing the position of the new, oldest goniatite fauna in relation to the conodont and dacryoconarid succession

et al. 2014; *Devonobactrites obliqueseptatus* Zone), which underlies the *Deiroceras* Limestone (Fig. 2). The onset of the oldest ammonoids defines LD III-B, which now can be subdivided in the Tafilalt into two regional subzones. The top of the *Deiroceras* Limestone is assigned to the new *Praechebbites debaetsi* Subzone (LD III-B1), whilst LD III-B2 comprises "Faunule 2" (sensu Klug et al. 2008) of the *Metabactrites* Shale, the main part of the *Erbenoceras advolvens* Subzone. The oldest *Chebbites*, *Gyroceratites*, and *Oculoceras* are alternative index genera (e.g., Klug 2001; Klug et al. 2008; Becker et al. 2018b). The onset of the tightly gyroconic *Anetoceras* defines LD III-C1 (*Anetoceras obliquecostatum* Zone and Subzone) low in the *Anetoceras* Limestone (Unit I sensu Becker et al. 2013, 2018d). At this level, large-sized *Erbenoceras* are often dominant and *Teicherticeras* enters locally (De Baets et al. 2010). The entry of *Klugites* near the middle of the *Anetoceras* Limestone characterizes a regional upper subdivision (LD III-C2, *Klugites gesinae* Subzone; Klug 2001; Aboussalam et al. 2015). *Weyeroceras angustus* occurs as a rare form in this subzone (Klug 2001; De Baets et al. 2010). In some sections of the southern Tafilalt (e.g., at the Jebel el Mrier), *Teicherticeras* (s.str.) replaces *Klugites* (Aboussalam and Becker 2015). Within the subsequent *Mimagoniatites* Limestone (Unit J sensu Becker et al. 2013, 2018d), *Mimagoniatites* and *Mimosphinctes* are the international markers of zones LD III-D (*Mimag. fecundus* Zone) and LD III-E (local level of *Mimosph. karltschanzi*), respectively. The latter is a very rare genus in southern Morocco (Klug 2017); it occurs in the last limestone below the thick equivalents of the basal upper Emsian Daleje Shales (Unit K sensu Becker et al. 2013, 2018d). Due to its extreme rarity, it does not really justify the separation of a regional zone.

In terms of the conodont zonation, the upper *Deiroceras* Limestone falls in the *Eolinguipolygnathus excavatus* Morphotype 114 Zone or in the *Latericriodus bilatericrescens bilatericrescens* Zone of the alternative icriodid scheme (Aboussalam et al. 2015). Both zones represent the basal part of a proposed future revised Emsian stage (e.g., Carls et al. 2008). The adjacent Jebel Ihrs section yielded both index species at the top, in association with more dominant *Lat. bilatericrescens multicostatus*, typical morphotypes of *Eol. excavatus*, and the last *Eol. radula*. In the *Deiroceras* Limestone, there is no evidence for true *Eol. gronbergi*, the index species of the next younger polygnathid zone. A previous record in Belka et al. (1999) has been re-identified as a transitional form from *Eol. excavatus* towards *Eol. gronbergi* (Aboussalam et al. 2015, p. 914), which suggests that the new goniatite level falls in the top of the *Eol. excavatus* M114 Zone. The dominance of latericriodids indicates a moderately shallow hemipelagic setting. Belodellids, typical neritic conodonts, which characterize the underlying Pragian Limestone or large parts of the *Mimagoniatites* Limestone above, are rare to absent.

Based on the revised succession at the neighbouring Jebel Ihrs (Alberti 1998, re-illustrated in Becker et al. 2018c: Fig. 4), the *Praechebbites* level falls in the dacryoconarid interval with *Nowakia* (*Now.*) *zlichoviensis maghrebiana* and *Now.* (*Now.*) cf. *praesulcata*.

Taxonomy (RTB and CK)

Abbreviations dm = diameter in mm, wh = whorl height in mm, ww = whorl width in mm, uw = umbilical width in mm, WER = whorl expansion rate (in advolute forms = $(dm–wh)^2$), r_x = number of ribs on the previous quarter whorl (at the given wh = x), ARI_{20} = rib index sensu De Baets et al. (2013b, p. 8) = number of ribs measured on the mid-flanks at a given whorl height and with a radius of 20 mm; E = external or ventral lobe, L = lateral lobe (on the flanks), I = internal or dorsal lobe. Measurements were taken where preservation is sufficient, not necessarily at the end of the last whorl.

Repository Specimens B6C.51-1 to 17 are kept in the Geomuseum Münster, Germany, specimens PIMUZ 36651 to 53 in the Paläontologisches Institut und Museum der Universität Zürich, Switzerland; GPIT stands for the collection of Tübingen University (originals of Klug 2001).

Order Agoniatitida Ruzhencev, 1957.
Suborder Agoniatitina Ruzhencev, 1957.
Superfamily Mimoceratoidea Steinmann in Steinmann and Döderlein (1890).
(nom. transl. Ruzhencev 1957, nom. corr. Klug 2001).
Family Mimosphinctidae Erben, 1953.
Subfamily Chebbitinae Becker and Klug n. subfam.

Diagnosis Small–large-sized, advolute or evolute, rarely with slight mature uncoiling, without or with shallow imprint zone, extremely discoidal, venter rounded or flattened at maturity, umbilicus wide (uw/dm ca. 0.45–0.55), umbilical window moderately large–small (< 5 mm), whorl expansion moderately high (WER between ca. 1.8 and 2.2). Ornament rursiradiate convex, with or without marked flank ribs, venter ribbed or with regularly spaced bean-shaped impressions. Sutures with small, narrow or shallow ventral lobe, deeply rounded, subsymmetric lateral lobe, and without or with very shallow dorsal lobes; suture formula: EL to EL(I).

Included genera Chebbites Klug, 2001, *Praechebbites* n. gen., and possibly an un-named genus represented by the enigmatic *Convoluticeras lanxuense* Chu, 1982.

Discussion When Klug (2001) introduced the genus *Chebbites*, he noted that it does not fall easily into the established families/subfamilies of early ammonoids (Mimoceratoidea) but left it with the Mimosphinctinae. The Anetoceratidae differ in their extremely low to low, very strongly ribbed gyroconic whorls. In the most advanced group of the family, the erbenoceratids, which comprise several genera/subgenera (e.g., *Haletoceras*) and could be separated at subfamily level, whorls become at least partially advolute but the umbilical window remains very large (> 4–5 mm). The Teicherticeratidae are only weakly ornamented, without ventral ribbing, and are characterized by a smaller umbilical perforation (< 2.5 mm) and fast expanding whorls (WER > 2.5). The latter feature applies also to the Palaeogoniatitinae, which display rounded whorls and a distinctive, fasciculate ornament. Typical Mimosphinctidae are characterized by branching or intercalated ribs and include the three genera *Talenticeras* (with bifurcating ribs only in early whorls, Erben 1965), Gen. aff. *Mimosphinctes* sensu Becker et al. (2010) ("*Erbenoceras*" *khanakasuense* Group), and *Mimosphinctes*. Nikolaeva (2007) suggested that the *M. rudicostatus* Group with very fine intercalated ribs could be assigned to a new genus (Naglik et al. 2019). The Mimoceratidae have very different, strongly compressed conchs with tabulate to bicarinate venter and rectiradiate, strongly concavo-convex growth lines.

The discovery of an ancestor of *Chebbites* enables us to separate a new mimosphinctid subfamily characterized by a small umbilical window, no branching of ribs or intercalated ribbing, and moderately fast expanding whorls. Apart from *Chebbites and Praechebbites* n. gen., the new subfamily may also house the unique, monotypic, and poorly known "*Convoluticeras*" *lanxuense* Chu, 1982. It appears to differ from all other known lower Emsian ammonoids in a depressed first whorl (see Chu 1982, pl. 17, Fig. 5a, b). Unfortunately, the very small holotype (8 mm dm) could not be traced at Beijing University (pers. comm. Ma Xueping). In addition, the species is an invalid homonym of *C. lanxuense* Wang in Xian et al. 1980.

Klug (2001) included two Russian species, *Teicherticeras* (*T.*) *lissovi* Bogoslovskiy, 1969 and *T.* (*T.*) *pyshmense* Bogoslovskiy, 1969, in his new genus *Chebbites*. However, as emphasized by Nikolaeva (2007), both weakly ribbed forms lack ventral ornament and their WER ratio is higher than in *Chebbites* (> 2.3) whilst the umbilicus is narrower (uw/mm < 0.50). Both taxa are better retained in the Teicherticeratidae. We agree with Nikolaeva (2007) that at least *T. pyshmense* differs too much from the strictly advolute (Becker et al. 2010) type-species of *Teicherticeras* to be placed in the same genus. This taxonomic problem is left for the ongoing teicherticeratid revision. *Convoluticeras tianlinense* Wang in Xian et al. (1980) and *Convoluticeras* sp. A in Chu (1982) are very close to if not conspecific with *T. pyshmense* (compare Chinese specimens illustrated in Kuang et al. 1989 and Yu et al. 2017; two additional specimens collected at Liujing and Wuxiangling by RTB in 1992).

Klug (2001) referred also *Teicherticeras nantanense* Shen, 1975 to *Chebbites*. Its squashed flat holotype is only very weakly ornamented and apparently advolute, with uw/dm = ca. 0.45, and a WER ratio of ca. 2.0, a typical value for the Chebbitinae n. subfam. Since the venter is unknown and in the absence of a whorl overlap, the species is reassigned with strong reservations to *Praechebbites* n. gen. The whorl expansion is not rapid enough for an inclusion in *Teicherticeras*, as considered by De Baets et al. (2010, 2013b). However, a supposed *nantanense* specimen illustrated by Ruan (1996) has a WER ratio of ca. 2.3 and may represent a true *Teicherticeras*. A rather similar, somewhat more evolute (uw/dm = 0.53) and more regularly ribbed species is *T. ilanense* Shen, 1975. In its also squashed, advolute holotype, the WER is ca. 1.8. Therefore, it is also placed with reservations in our new genus. However, the supposed *ilanense* specimen figured by Ruan (1996) is a true *Teicherticeras* (rather smooth, advolute, WER = ca. 2.55; compare a specimen identified as "*T. nandanense"* in Kuang et al. (1989) with WER = ca. 2.55). Übelacker et al. (2016) kept both Chinese taxa with some reservation in *Teicherticeras* but emphasized the need of further revisions of that genus.

The two Tafilalt species of *Chebbites* are characterized by marked, regular impressions on their flattened venter (Klug 2001; De Baets et al. 2013b). The same unusual feature is found in the smooth, strongly compressed *Gracilites maghribensis* Klug, 2001. The Russian type-species of *Gracilites* as well as *Gr. talyndzhensis* Yatskov, 1992 are characterized by very high, suboxyconic whorls (WER > 2.8) with marked ventral serrations or crenulations. *Gracilites maghribensis* lacks these but displays a flat venter with regular impressions as in *Chebbites*. However, it resembles a supposed median-sized fragment of *Gr. svetlanae* illustrated by Bogoslovskiy (1972, pl. 5, Fig. 4), possibly a Novaya Zemlya representative of *Chebbites*. Since *Gr. maghribensis* has a WER of only 2.1–2.2, it is re-assigned to the latter genus. Its smooth flanks do not isolate the species since there is significant ornament variation in the type-species, *Ch. reisdorfi*, including a morphotype with weak flank ribs (Becker et al. 2018b; Fig. 3g–i). Some specimens of *Ch. maghribensis* are transitional towards smooth *Ch. reisdorfi* (Fig. 3m–o). A weakly ornamented cf. specimen (B6C.51-11, Fig. 3p–r) shows a transition towards the Teicherticeratidae.

As noted by Klug (2001), regular ventral impressions occur also in the holotype of *Lenzites lenzi* (House and Pedder 1963). The genus differs from *Chebbites* in the lack

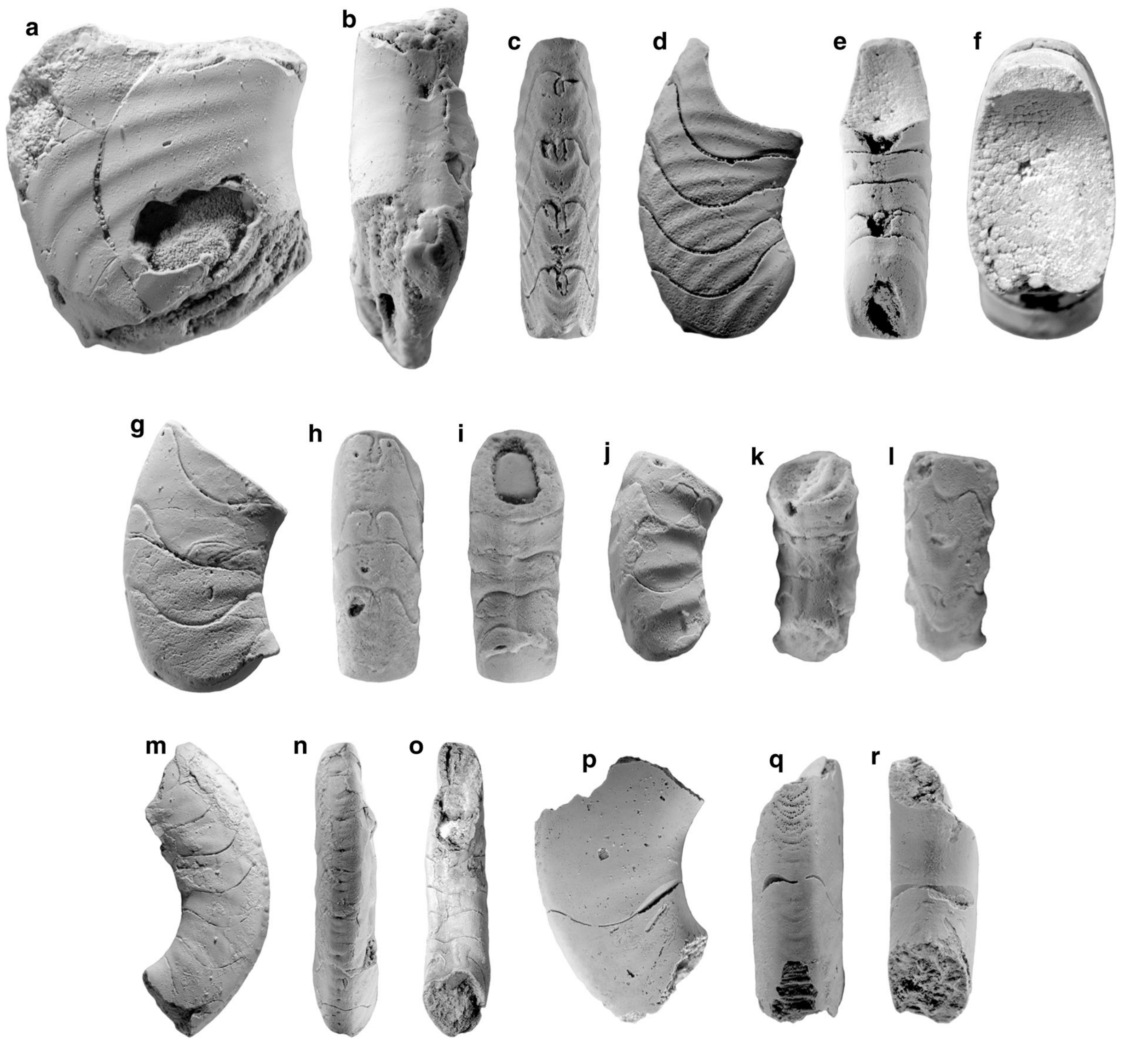

Fig. 3 Fragmentary Tafilalt topotypes of *Chebbites* from the *Metabactrites* Shale. **a–c** *Ch. reisdorfi* Morphotype 2 (typical morphotype with marked ribs), B6C.51-6, Bou Tchrafine Pass (for locality description see Becker et al. 2018d), lateral and dorsal view, showing the dorsal sinus of growth lines at 20 mm wh, × 2. **d–f** *Ch. reisdorfi* Morphotype 1 (with dense ribbing), B6C.51-7, Bou Tchrafine West, ventral, lateral, dorsal, and septal views showing the narrow E-lobe and ventral ribbing, the deep flank lobe, a rather weak imprint zone with incipient dorsal lobe, and the typical, compressed cross-section, × 2. **g–i** Juvenile *Ch. reisdorfi* Morphptype 3 (weakly ribbed), B6C.51-8, Bou Tchrafine Pass, lateral, ventral, and dorsal views, showing a pouched E-lobe, deep L-lobe, and well-developed I-lobe, ×3. **j–l** Juvenile *Ch. reisdorfi* Morphotype 2, B6C.51-9, Bou Tchrafine Pass, lateral, slightly oblique dorsal, and ventral views, showing coarse ribbing, a narrow imprint zone, shallow I-lobe, and ventral impressions, ×4. **m–o** *Ch. maghribensis*, B6C.51-10, Ouidane Chebbi (for section description see Belka et al. 1999; Klug 2001, and Klug et al. 2008), somewhat transitional towards *Ch. reisdorfi*, lateral, ventral, and dorsal views, showing weak flank ribbing, typical ventral impressions, a wide E-lobe, and well-developed I-lobes, ×2. **p–r** *Ch.* cf. *maghribensis*, B6C.51-11, Ouidane Chebbi, lateral, ventral, and dorsal views, showing a completely smooth flank, very weak ventral ornament, a shallow but wide E-lobe, and very incipient imprint zone and I-lobe, ×2.5

of whorl overlap and in a well-developed ocular sinus of its rursiradiate, lamellose growth lines. Becker and House (1994) noted the transitional morphology of *Lenzites* towards either *Gyroceratites* or *Taskanites* and argued that it could be placed either in the Mimoceratidae (see Klug 2001) or Teicherticeratidae (preferred here), which is both supported by a WER > 2.5. The Canadian species suggests that regular ventral impressions evolved convergently twice in early goniatite evolution. The Moroccan *L. gesinae* Klug, 2001, which was later selected as the type-species of *Klugites* Becker in Aboussalam et al. (2015) (Mimoceratidae), does not develop these ventral impressions (Klug 2001; Becker et al. 2018b).

Based on a WER of 2.1–2.2, De Baets et al. (2009) suggested that *Anetoceras (Erbenoceras) mattei* Feist, 1970a could belong to *Chebbites*. This is contradicted by its rather large umbilical perforation (ca. 4 mm) and the lack of a whorl imprint zone. Until more is known about this species, we include it with strong reservation in *Praechebbites* n. gen. The French species may fall in the morphological transition from advanced erbenoceratids with fully advolute whorls (*Erb. elegantulum* Group, WER ca. 1.8) to the Chebbitinae n. subfam.

A supposed *Chebbites* sp. described by De Baets et al. (2013a, b) from the Kaiser Quarry of the Gemünden area (Hunsrück Slate) differs from true members of the genus in its rectiradiate, widely spaced ribs and poorly preserved remnants of ventrolateral intercalatory riblets. The species probably belongs to some type of mimosphinctid; *Mimosphinctes* occurs commonly in the same outcrop.

Stratigraphical range Restricted in Southern Morocco to the lower Emsian LD III-B/C (regional *Praechebbites debaetsi* Subzone to *Klugites gesinae* Subzone) but possibly overlapping with *Mimagoniatites* (LD III-D) in South China (Ruan 1996).

Geographical distribution Southern Morocco (Klug 2001), ? southern France (Feist 1970a), ? Novaya Zemlya (Bogoslovskiy 1972), ? South China (Shen 1975).

Praechebbites Becker and Klug n. gen.

Derivation of name Referring to the ancestral position to *Chebbites* with respect to age and morphology.

Type-species Pr. debaetsi n. sp.

Other included species ? Pr. mattei (Feist, 1970a), *? Pr. nantanense* (Shen, 1975), *? Pr. ilanense* Shen, 1975 (see discussion above).

Diagnosis Large, advolute, without or with slight gyroconic uncoiling of the last whorl, without dorsal imprint zone, thinly discoidal, in typical forms venter flattened from median stages onward, umbilicus wide (uw/dm ca. 0.45–0.55), whorl expansion moderately high (WER = 1.8 − 2.1). Ornament with arched, rursiradiate, convex, weak to moderately distinctive ribs forming a deep, ventral sinus. Sutures with small, narrow ventral lobe, rounded, subsymmetric lateral lobe, and undivided dorsal saddle; suture formula: EL.

Discussion The new genus can be easily distinguished from *Chebbites* by its advolute coiling and the lack of a dorsal lobe throughout ontogeny. The venter displays dense ribbing; only when strongly corroded, sculpture remnants may resemble the ventral impressions of *Chebbites*.

Stratigraphical range: Lower Emsian, LD III-B to possibly III-D (South China).

Geographical distribution: Southern Morocco, ? southern France, ? South China.

Praechebbites debaetsi Becker and Klug n. gen. n. sp.
Figures 4a–k, 5a–f, 6a–c, 7a.
2001 *Chebbites* cf. *reisdorfi* Klug: 497, Fig. 8

Derivation of name In honor of Dr. Kenneth De Baets, Erlangen, for his outstanding contributions to the knowledge of early ammonoids.

Types Holotype is B6C.51-1, an incomplete specimen with two half-whorls showing best the whorl form, sculpture, sutures, and slight mature uncoiling (Fig. 4g–i). All other specimens (B6C.51-2 to 5, PIMUZ 36651 to 53), including GPIT 2040 (Tübingen University collection), the original of *Ch.* cf. *reisdorfi* in Klug (2001) from Ras El Kebbar (southwest of Jorf), are designated as paratypes.

Type locality Jebel Mech Irdane, western Tafilalt, Anti-Atlas, Morocco, plain in the NE.

Type level Top of *Deiroceras* Limestone, top *Eol. excavatus* M114 Zone, lower part of lower Emsian.

Diagnosis Large-sized, advolute, without or with slight gyroconic uncoiling of the last whorl, thinly discoidal (mature ww/dm = ca. 0.18, ww/wh = 0.60), venter flattened, umbilicus wide (uw/dm ca. 0.50–0.54), whorl expansion moderately high (WER ca. 1.9–2.0). Ornament consisting of arched, densely spaced, rursiradiate convex flank ribs that weaken at maturity; venter with dense, bundled ribs forming a deep, lingulate sinus until late maturity. Sutures with narrow ventral lobe, shallow, rounded, lateral lobe, and moderately high, wide dorsal saddle.

Description All specimens are corroded and rather poorly preserved but in summary, they enable the recognition of the full set of important morphological features. In the absence of tectonic deformation, there is no elliptical distortion. The holotype and paratype B6C.51-4 show that the characteristic strong whorl compression, with a flattening of flanks and venter, develops early in ontogeny (at least after ca. 12 mm dm). Mature ww/wh ratios fluctuate between 0.57 (last whorl of the holotype, Fig. 7b), 0.62 (paratype PIMUZ 36651), and 0.63 (paratype B6C.51-5, at 16 mm wh). The umbilical width is somewhat variable (Table 1, uw/dm = 0.49 − 0.54), with the holotype falling on the more evolute side. However, there is no ontogenetic change of uw/dm ratios between ca. 20 and 100 mm dm. In the Ras El Kebbar paratype (from ca. 57 mm dm on) and in the holotype (Fig. 4g), the last preserved whorl detaches slightly, leading to very incipient mature uncoiling. However, this is not seen in the largest paratype PIMUZ 36651 (Fig. 5c). None of the specimens shows evidence of whorl

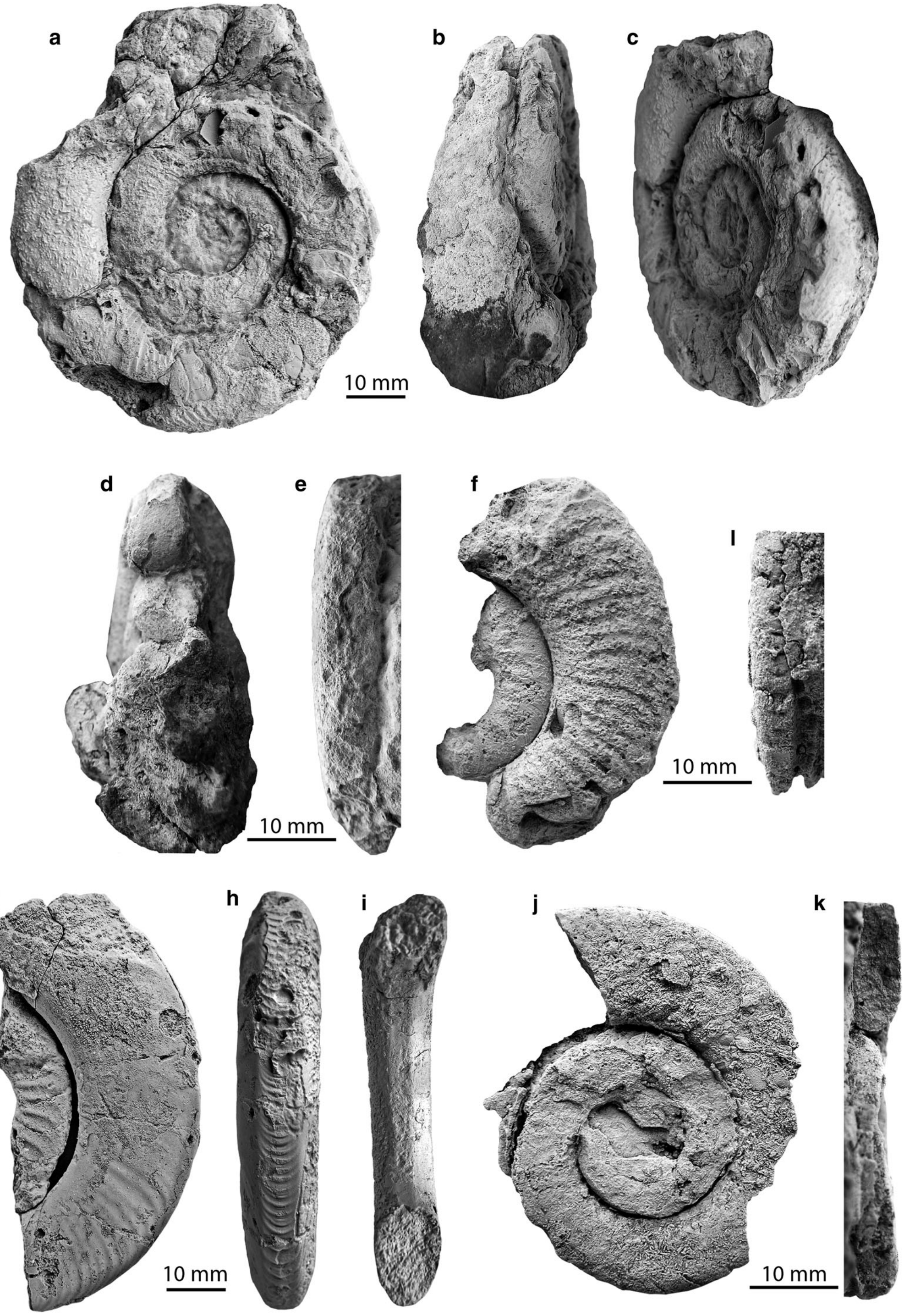

Fig. 4 *Praechebbites debaetsi* n. gen. n. sp. **a–c** Partly corroded paratype B6C.51-2, lateral, ventral, and oblique views, showing sutures, regularly spaced rursiradiate, convex ribbing, and tight advolute coiling until ca. 60 mm dm, ×1. **d–f** Incomplete paratype B6C.51-3, septal, ventral, and lateral views, showing the typical, regular flank ribbing until ca. 45 mm dm and the lack of whorl overlap at an apical septal face, ×1.5. **g–i** Holotype B6C.51-1, lateral, ventral, and dorsal views, showing slight uncoiling and narrow whorl interspace at maturity (60–70 mm dm), reduced mature flank ribbing, ventrolateral edges, regular ventral ribbing, and the mature dorsal whorl flattening, ×1. **j–l** Paratype B6C.51-4, lateral, adoral, and ventral views, corroded specimen with advolute, non-overlapping whorls, and remains of regularly-spaced impressions on the flattened venter, ×1.5

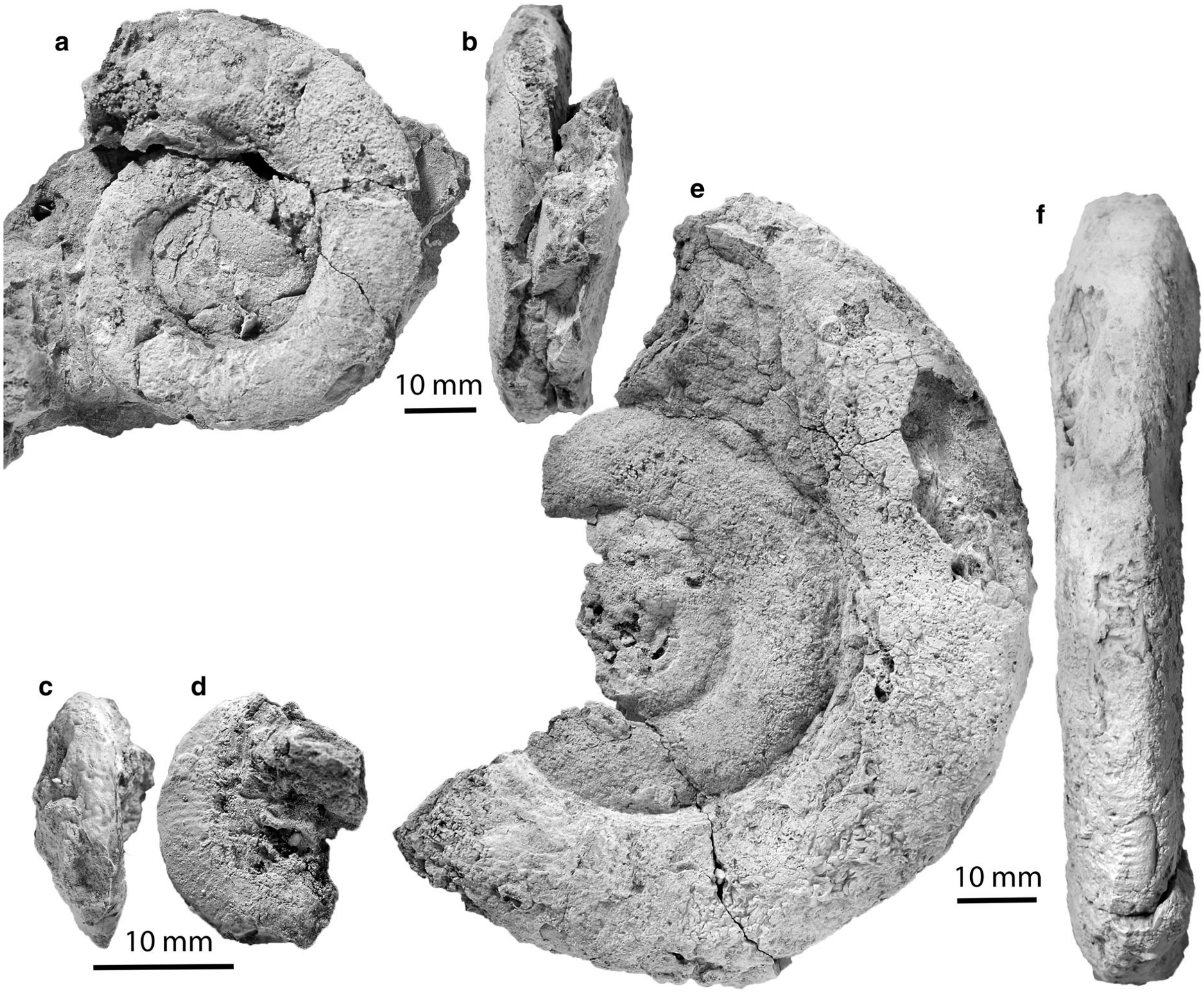

Fig. 5 *Praechebbites debaetsi* n. gen. n. sp. **a**, **b** Corroded paratype PIMUZ 36652, lateral and ventral views, showing regular ribbing on the flattened venter at ca. 50 mm dm, ×1. **c**, **d** Poorly preserved paratype PIMUZ 36653, ventral and lateral views, showing regularly-spaced, convex flank ribbing, ×1.5. **e**, **f** Corroded paratype PIMUZ 36651, ventral and lateral views, showing traces of ribbing on the flattened venter and advolute coiling at maturity (dm almost 100 mm), ×1

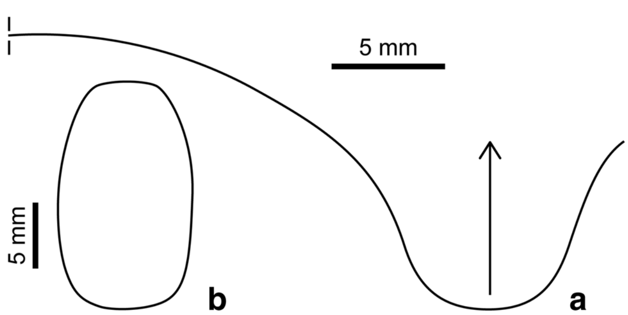

Fig. 6 Growth ornament and cross-section at 18 mm wh in the holotype of *Praechebbites debaetsi* n. gen. n. sp. **a** Strongly rursiradiate course of ornament. **b** Cross-section, showing the flattening of venter, flanks, and dorsal side

overlap or of a dorsal imprint zone. The dorsal whorl may become slightly flattened (only in the holotype, Figs. 4i, 6b) but is never concave (paratype B6C.51-2, paratype B6C.51-3, Fig. 4d, paratype B6C.51-4, Fig. 4k, paratype B6C.51-5). The venter of adult specimens is bordered by angular edges (holotype, Fig. 4h, paratype PIMUZ 36651, Fig. 5d).

Until ca. 18 mm wh (holotype, Fig. 4g), flanks bear very regular, fine ribs with narrow interspaces. Their strongly rursiradiate course leading to a lingulate ventral sinus is depicted in Fig. 6a. In paratype B6C.51-3 there are ca. 15 ribs/quarter whorl before wh = ca. 15 mm (r_{15} = 20; Fig. 4f); ARI_{20} = 10–11. In the holotype, the flanks ribs are gradually subdued on the last half whorl (Fig. 4g) but there is no corresponding reduction on the venter (Fig. 4h). There are more than 35 ventral, deeply lingulate ribs on the last quarter whorl (r_{21} = 35; ARI_{20} = 12 at 20 mm wh). By erosion, more widely spaced (ca. 2.5 mm long) rib bundles appear apically. Paratypes PIMUZ 36651 (Fig. 5d) and PIMUZ 36652 (Fig. 5b) show less well-preserved, similar

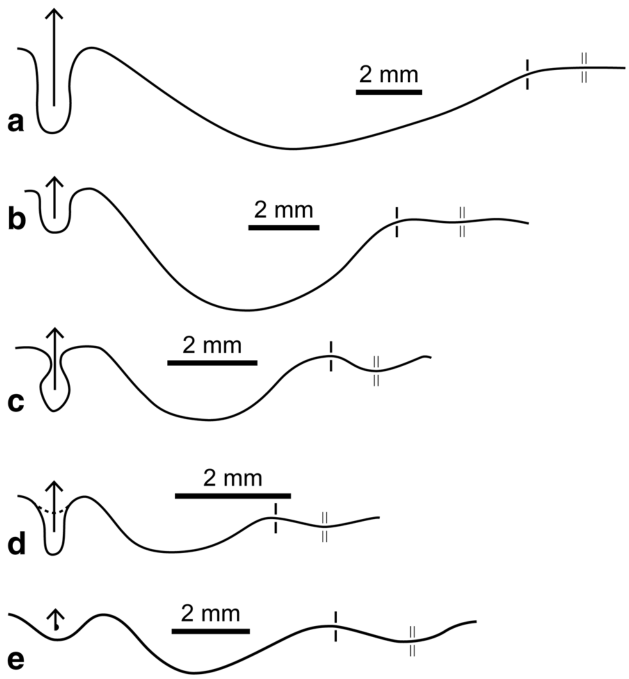

Fig. 7 Sutures of various Chebbitinae n. subfam. from the Tafilalt. All scale bars = 2 mm. **a** *Praechebbites debaetsi* n. gen. n. sp., paratype B6C.51-5 at 15 mm wh. **b** *Ch. reisdorfi* Morphotype 2, B6C.51-7, Bou Tchrafine West, at 10.5 mm wh. **c** Juvenile *Ch. reisdorfi* Morphotype 3, B6C.51-8, Bou Tchrafine Pass, at 6.3 mm wh. **d** Juvenile *Ch. reisdorfi* Morphotype 2, B6C.51-9, Bou Tchrafine Pass, at 3.6 mm wh. **e** *Ch. mahgribensis*, B6C.51-10, Ouidane Chebbi, at 8.8 mm wh (mirrored for comparison)

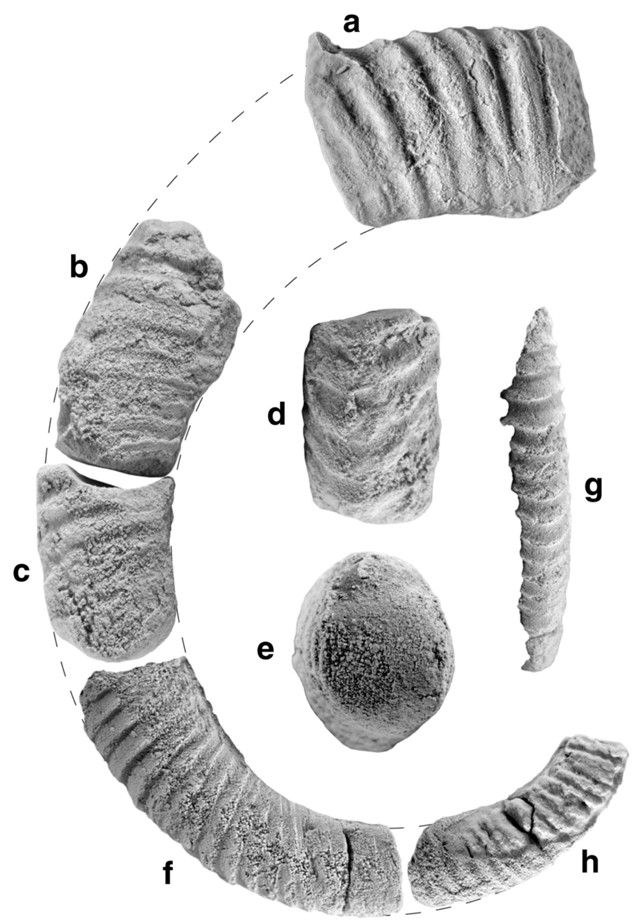

Fig. 8 *Ivoites* n. sp. from an isolated olistolite in the olistostrome at Taourirt n'Khellil (Sample E-Tin 2 of Rytina et al. 2013), five fragments arranged to form a reconstruction, all (except e) ×2.5. **a** B6C.51-12 (mirrored for comparison). **b** B6C.51-13. **c–e** B6C.51-14, lateral, ventral, and apical views (e × 3.7). **f**, **g** B6C.51-15, lateral and ventral views. **h** B6C51-16

ventral ribs, whilst paratypes B6C.51-2 (Fig. 4a) and PIMUZ 36653 (Fig. 5f) display the same flank ribbing as in paratype B6C.51-3. In the strongly corroded paratype B6C.51-4, the lateral ribs have disappeared (Fig. 4j) but the venter shows impression-like remnants of rib bundles (Fig. 4l). None of the specimens has sufficiently well-preserved ornament to measure the DWRA values sensu De Baets et al. (2013a, b), which is the angle between ribs that are half a whorl apart. However, the holotype (Fig. 4g) and paratype B6C.51-3 (Fig. 4f) shows that the inclination of ribs towards the venter does not change between successive whorls. The total evidence suggests rather little variability of the ornament apart from a mature reduction on the flanks.

Sutures are mostly poorly preserved. The rounded flank lobe and narrow ventral lobe are visible in the inner whorl of the holotype. Paratype B6C.51-2 shows the well-rounded, subsymmetric flank lobe, which is deepened by erosion (Fig. 4a). Paratype B6C.51-3 provides an apical view on the septal face (Fig. 4d). The complete suture, with a narrow, relatively deep ventral lobe, widely rounded flank lobe, and wide dorsal saddle, which is lower than the ventral saddle, is preserved in whorl fragments of paratype B6C.51-5 (Fig. 7a).

Discussion: In terms of shell form, umbilical width, WER ratios, ribbing, and whorl compression, *Pr. debaetsi* n. gen. n. sp. is similar to *Ch. reisdorfi*. The latter includes some specimens that are more evolute (uw/dm up to 0.57) and many new topotypes have more strongly flattened flanks, with ww/dm around 0.50 (but ca. 0.60 in B6C.51-12, Fig. 3f). The largest known *Ch. reisdorfi* fragments reach 34.5 mm wh (Klug 2001: GPIT 1849-121). The smaller size of most *Ch. reisdorfi* is very likely to reflect facies conditions. As discussed in Pohle and Klug (2018), specimens preserved in argillaceous sediments with primarily pyritic internal moulds (weathered to goethite in Southern Morocco) are small, because the outer whorls of larger specimens usually get crushed early in diagenesis and are lost when weathering out of the sediment. Therefore, we assume that there was no size difference between *Ch. reisdorfi* and *Pr. debaetsi* n. gen. n. sp. The main distinction between both are the imprint zone and dorsal lobe of

Table 1 Conch parameters of *Praechebbites debaetsi* n. gen. n. sp

Specimen	dm	wh	ww	uw	wh/dm	ww/dm	ww/wh	uw/dm	WER
PIMUZ 36651	100.8	29.4	19.2	51	0.29	0.19	0.65	0.51	2.01
B6C.51-2	72.5	c. 18	?	39	c. 0.25	?	?	0.54	c. 1.8
PIMUZ 36651	71.0	19.4	14.0	36.2	0.27	0.20	0.72	0.51	1.94
Holotype	c. 70	21.0	12.0	c. 38	0.30	0.18	0.57	0.54	c. 2.0
GPIT 2040	60.8	c. 15	?	c. 33	c. 0.25	?	?	0.54	c. 1.8
PIMUZ 36652	59.9	17.2	11.3	28.7	0.29	0.19	0.66	0.48	2.03
B6C.51-2	59.0	16.8	c. 10	29.9	0.28	0.17	0.60	0.51	1.95
PIMUZ 36651	51.0	15.4	10.2	27	0.30	0.20	0.66	0.53	1.98
B6C.51-3	c. 45	14.0	8.0	c. 22	0.31	0.18	0.57	0.50	c. 2.0
B6C.51-4	43.9	12.3	c. 7.5	21.5	0.28	0.17	0.61	0.49	1.93
PIMUZ 36652	42.0	13.4	?	20.1	0.31	?	?	0.48	2.14
PIMUZ 36651	36.2	12.2	?	19.3	0.34	?	?	0.53	1.94
PIMUZ 36653	17.5	5.0	?	8.7	0.29	?	?	0.50	1.96

the first, which can be observed from juvenile stages onward (e.g., at 6.3 mm wh in B6C.51-8, Figs. 3i, 7c). In a few larger *reisdorfi* fragments, the imprint zone and dorsal lobe are shallower but still present (B6C. 51-7, Figs. 3e, 7b). In Figs. 3h and 7c we illustrate a *reisdorfi* representative with somewhat unusual, pouched E-lobes in successive septa. This pattern may result from a slight shift of the siphuncle and seems to have no taxonomic value. The ribbing is also more variable in *Ch. reisdorfi*, which led to the distinction of three morphotypes in Becker et al. (2018b; Figs. 3a, d, g).

Apart from its imprint zone and well-developed I-lobe (at 3.6 mm wh, B6C.51-9; Fig. 3k, 7d), *Ch. undosus* differs from *Pr. debaetsi* n. gen. n. sp. in its thicker, more rounded whorls (Fig. 3l) and very coarse ribbing (Fig. 3j). The ventral lobe is variably shallow or deep and narrow, as it can be observed in two successive septa of the juvenile fragment B6C.51-9 (Figs. 3l, 7d). Again, this reflects probably a slightly fluctuating siphuncle position. *Chebbites maghribensis* is distinguished by its smooth flanks (Fig. 3m), narrow, tabulate venter without ribs (Fig. 3n), wider E-lobe (Fig. 7e), and the well-developed imprint zone with wide, shallow I-lobe (Figs. 3o, 7e).

In the two questionable Chinese species of *Praechebbites* n. gen., the whorl form and ventral ornament are unknown; both lack well-defined flank ribs and *? Pr. nantanense* is more involute (uw/dm = ca. 0.45) whilst *? Pr. ilanense* shows a somewhat lower WER ratio (ca. 1.8). In *? Pr. mattei*, the venter was described to be rounded but it has been eroded in the holotype (Feist 1970a, pl. 1, Fig. 1) and its ornament is unknown. Umbilical width and whorl expansion are comparable with *Pr. debaetsi* n. gen. n. sp. The French form is additionally distinguished by the flexure of the inner limb of the flank lobe, resulting in a well-developed saddle near the umbilical shoulder. Clarification of the precise taxonomic position of *? Pr. mattei* requires additional material.

Stratigraphical range: Restricted to the type level.
Geographical distribution: Restricted to the Tafilalt (localities Jebel Mech Irdane and Ras El Kebbar).

Ivoites De Baets et al., 2009
Ivoites n. sp.
Figure 8a–h.

V 2013 *Metabactrites* sp., Rytina et al.: 13

Material Six fragments (B6C.51-12 to 51-17) from a single, ca. 15 cm large olistolite of Taourirt ńKhellil SE of Tinerhir, geological map, 1:50,000, sheet Taghazout (Dal Pias et al. 2007), Sample E-Tin 2 of Rytina et al. (2013).

Description Based on different whorl heights, five of the fragments can be aligned to reconstruct ca. 2/3 of the whorl of a medium-sized (ca. 48 mm dm), widely gyroconic (uw/dm = ca. 0.70) goniatite with compressed (ww/wh = 0.71 in B6C.51-12 at 10 mm wh, = 0.75 in B6C.51-14 at 6.6 mm wh), oval cross-section, relatively high whorl expansion rate for the group (WER = ca. 1.6), and strong, rursiradiate, dense ribbing (r_8 = ca. 20). Rib interspaces are much narrower than the rib width, which doubles on the last whorl from ca. 0.7 – 1.4 mm. Ribs are markedly rursiradiate and very pronounced on the venter; its sinus deepens during ontogeny (Fig. 8d, g). B6C.51-15 has an ARI_{10} = 10 at ca. 6 mm wh. The reconstruction of Fig. 8 suggests that the DWRA sensu De Baets et al. (2013b), which is the angle between the course of ribs that are half a whorl apart, is near 170° at ca. 35 mm dm. Values < 180° are a good indicator for the onset of cyrtoconic coiling, as it is typical for the genus. An apical septal face of B6C.51-14 (at 6.6 mm wh) suggests a very small E-lobe (very poorly preserved), a deeply rounded flank lobe, and a rounded dorsal saddle, which is lower than the ventral saddle.

Discussion The combination of open, extremely evolute coiling and a relatively high WER ratio separate this obviously new species from *Metabactrites* (see first identification in Rytina et al. 2013) and place it in *Ivoites*. The very narrow rib interspaces and rounded dorsal saddle give a clear distinction from *Metabactrites ernsti* Klug et al., 2008 from "Faunule 2" of the Tafilalt, which was questionably re-assigned to *Ivoites* by De Baets et al. (2013b). Typical *Ivoites* are characterized by finer ribbing, which may be influenced by preservation in deformed material.

There are currently three species groups within the genus, variably with only 1.3 to more than 2.5 whorls (De Baets et al. 2013a, b). It may become useful to restrict the genus to forms close to the type-species, *I. hunsrueckianus* (Erben, 1960). This group is characterized by a maximum of 1.5 whorls, uw/dm ratios > 0.65, a WER of 1.5–1.6, and strongly increasing adult whorl interspace. Apart from the type-species, the Bohemian *I. tenuis* (Barrande, 1865), the Chinese *I. tangdingensis* (Ruan, 1981), the Uzbek *I.* cf. *hunsrueckianus* described by Becker et al. (2010), and *I. medvezhensis* (Yatskov, 1990) from Novaya Zemlya are typical representatives. Mostly based on the assumed uw/dm ratio, *Ivoites* n. sp. is provisionally assigned to the *I. hunsrueckuanus* Group but its ribbing differs from all named *Ivoites* species. We abstain from naming it since our knowledge is based on a reconstruction. Specimen B6C.51-17 (not figured) has about the same wh as B6C.51-16 (Fig. 8h) and proves that not all fragments of the olistolite belonged originally to one specimen.

Stratigraphical range The precise level within the lower Emsian is currently unclear since there were no associated conodonts and since the numerous co-occurring dacryoconarids are too poorly preserved for identification.

Geographical distribution Restricted to the Tinerhir region, southern Morocco.

Comparisons with the oldest ammonoids of other regions

As emphasized in the introduction, there is still a very limited number of regions and localities were the oldest, basal Emsian ammonoids have been found. These should be assigned to division LD III-B sensu Becker and House (1994, 2000b), with *Metabactrites*, *Ivoites*, and *Erbenoceras* as characteristic genera, and still without *Anetoceras*, the index genus of LD III-C. Such faunas should correlate with the *Eolinguipolygnathus excavatus* M114 Zone to lower *Eol. gronbergi* Zone (*gronbergi* Subzone) of the conodont succession, predating the entry of *Eol. perbonus, Eol. nothoperbonus, Eol. catharinae*, *Latericriodus latus*, and *Criteriognathus steinhornensis* (see Aboussalam et al. 2015), and with the upper *Nowakia (Now.) zlichovensis* to lower *Now. (Dmitriella) praecursor* zones of the dacryoconarid succession (e.g., Alberti 1998).

Morocco

- In southern Morocco and to the NW of the Tafilalt, *Erb. advolvens* occurs abundantly in the upper member of the Bou Tiskaouine Formation of the northern **Maïder** (e.g., Hollard 1974), which has been correlated with the *Anetoceras* Limestone (UD III-C) of the Tafilalt (Aboussalam et al. 2015). This is supported by *Anetoceras* records illustrated as *Erbenoceras* sp. and *? Ruanites* sp. in Becker and House (1994). Plodowski et al. (2000) listed "*Anetoceras* sp., ex gr. *A. arduennensis*" from the older *Now. (Dm.) praecursor* Zone of the Jebel Issimour. This material probably corresponds to *Erbenoceras* of the *Metabactrites* Shale of the Tafilalt (LD III-B2).
- In the **eastern Dra Valley**, *Erb. advolvens* enters in the Lower Member of the Mdâouer-el-Kbír Formation (Hollard 1963; De Baets et al. 2010), together with *Now. (Now.)* cf. *zlichovensis* and *Now. (Dm.)* cf. *praecursor* (Hollard 1978). This fauna predates a level with *Anetoceras* and *Klugites*, as in the Tafilalt (De Baets et al. 2010), which suggests a wide regional distribution of the *Erb. advolvens* Zone.
- The so far only *Erbenoceras* of the **western Dra Valley** illustrated by Becker et al. (2008) comes from the upper part of the Akhal Tergoua Member (lower Oui-n-Mesdoûr Formation). Its level post-dates the entry of *Latericriodus beckmanni beckmanni*, an alternative index species of the *Lat. latus* Zone (Aboussalam et al. 2015). The isolated goniatite record, therefore, correlates with the Tafilalt *Anetoceras* Limestone, probably with its higher part (higher LD III-C).
- Hollard (1974) mentioned "*Anetoceras*" (probably *Erbenoceras*) from the **Skoura Devonian**, just S of the High Atlas, which was confirmed by recent re-sampling at Taliouine, jointly with O. Mayer and H. Hüneke (both Greifswald). The precise position of this faunule within the lower Emsian is the subject of ongoing research.
- Within a Lower Carboniferous olistostrome of the **Tinerhir region** within the southern Variscan Front, Rytina et al. (2013) discovered a single olistolite of reddish limestone with several fragmentary *Metabactrites* sp., which are here re-assigned to *Ivoites* n. sp. (see above, Fig. 8). The pebble differs in terms of

lithology/microfacies from lower Emsian strata of the northern Maïder and Tafilalt. It may represent a very early goniatite interval (lower LD III-B) dominated by gyroconic taxa. Unfortunately, all attempts to re-collect the macroscopically distinctive lithology within the huge breccia unit at Taourirt n'Khellil failed.

Europe

- In the SW of the **Rhenish Massif** of Germany, the Hunsrück Slate (s.l.) is now known to comprise a succession of ammonoid assemblages and zones (De Baets et al. 2013b). Well-dated faunas from the Kühstabel to Bocksberg members include only species of *Ivoites*, reminiscent of the Tinerhir olistolite. A tentative correlation of the Rhenish *Ivoites hunsrueckianus* Zone with the *Metabactrites* Shale of the Tafilalt is based on the range of associated *Now. (Dm.) praecursor*. The next younger Rhenish fauna from the Wingertshell Member may correlate with higher parts of the Tafilalt *Erbenoceras advolvens* Subzone. Both contain a very similar early *Gyroceratites* as well as *Metabactrites*. Apart from this, the two faunas have not much in common. Since both come from hypoxic outer shelf shale, the difference probably reflects a palaeobiogeographic barrier, perhaps related to the contemporaneous closure of the true Rheic Ocean (Franke et al. 2017).
- *Ivoites* occurs also in the **Belgian Ardennes** (De Baets et al. 2013a, b). Associated brachiopods, however, suggest a correlation with beds in the **Eifel Mountains** that yielded *Anetoceras* (De Baets et al. 2009), the index genus for LD III-C.
- The type material of *? Pr. mattei* comes from the Pic de Bissous area of the **Montagne Noire** (Feist 1970a). Based on associated "*Polygnathus linguiformis foveolata*" (= *Eol. perbonus*) and *Criteriognathus steinhornensis steinhornensis* (Feist 1970b), the goniatite species derived from equivalents of the *Anetoceras* Limestone (LD III-C, *catharinae* Subzone/*steinhornensis* Zone).
- In **Bohemia**, there is so far no ammonoid record from LD III-B. The regional succession starts with *Anetoceras oriens* and *Teicherticeras senior* (Chlupáč and Turek 1983; LD III-C), which, at the generic level, resembles the *Anetoceras* Limestone assemblages of the Tafilalt (De Baets et al. 2010).
- In the famous La Grange Limestone of the **Armorican Massif**, the oldest limestones fall already in the *Latericriodus latus* Zone or *Eol. nothoperbonus* (Sub)-Zone (Bultynck 1989), the level of the Tafilalt lower *Anetoceras* Limestone (LD III-C1).
- All lower Emsian ammonoids from the Cantabrian Mountains, Pyrenees, and Celtiberian Chains of **Spain** fall in the *barrandei* to *elegans* zones (LD III-D/E; Montesinos and Truyols-Massoni 1987; Carls 1989; Carls and Valenzuela-Ríos 1997; Montesinos and Sanz López 1999).
- Yatskov (1994) separated two lower Emsian ammonoid zones of **Novaya Zemlya**. The lower *Teneroceras hunsrueckianum* Zone has to be re-named as regional *Ivoites medvezhense* Zone (*Teneroceras* Chlupáč and Turek 1983 is an invalid homonym). It comprises *Borivites elegans* (probably a *Metabactrites* species), *I. medvezhense, Erbenoceras, Taskanites*, and various, still un-named *Anetoceras* species. The latter suggest a placing in LD III-C, unless the regional zone can be subdivided. Support for this interpretation comes from the reported association of *Anetoceras* and *Erbenoceras* with *Now. (Now.) barrandei* and *Eol. gronbergi* (Cherkesova et al. 1988). The type-level of *Metabactrites* is even younger, despite the ancestral morphology of its type-species *M. formosus* (*Gracilites svetlanae* Zone, see Bogoslovskiy 1972).
- None of the lower Emsian assemblages from various regions of the **Urals** or **Caucasus** can be assigned to LD III-B. All contain *Mimagoniatites, Mimosphinctes,* advanced Teicherticeratidae, or members of the Auguritidae. Possible exceptions of the Sverdlovsk region (NE Urals) could be the isolated localities with *T. pyshmense* (Bogosloskiy 1969) along the Pyshma River. However, that species is morphologically more advanced than the *Teicherticeras* that occur in the Tafilalt in the *Anetoceras* Limestone (LD III-C). In South China, the same or very closely related forms occur in the upper *Eol. nothoperbonus* and *Now. (Now.) barrandei* Zone (e.g., "*T. pyshinense*" from the Moding Formation in Yu et al. 2017).

Asia

- The oldest, very sparse goniatite fauna of the Zeravshan Range of **Uzbekistan** consist of questionable *Gyroceratites* and *Erbenoceras* (s.l.; reviewed by Becker et al. 2010; Naglik et al. 2019). However, it comes from above the entry of *Eol. nothoperbonus* (conodont record of Yolkin et al. 2008), and, therefore, correlates with the Tafilalt *Anetoceras* Limestone (LD III-C).
- Ruan (1996) reviewed the lower Emsian ammonoid succession of **China**. For the correct understanding of Chinese papers, it is important to know that *Erbenoceras* species were often included in *Anetoceras (Anetoceras)*, whilst true *Anetoceras* species were

recorded as *A. (Nandanoceras)*, a nom. nud. (Yu and Ruan 1989), or, later, as *Ruanites* (Ruan 1996). Forms listed as *A. (Teneroceras)* (e.g., in Yu and Ruan 1989) refer to *Ivoites* occurrences.

The oldest regional level, the *Luofoceras multicostatum* Zone, is represented by a fauna from Luofu, northern **Guangxi**, with *Luofoceras* (an intermediate form between *Metabactrites* and *Ivoites*) and *? Pr. nantanense* (Bed ACE 23, Ruan 1981). It comes from very low in the *Now. (Dm.) praecursor* Zone (Mu and Ruan 1983) and can be placed in LD III-B.

Anetoceras, the LD III-C marker (regional *A. obliquecostatum* Zone), enters above in the higher part of the *praecursor* Zone (beds ACE 24-27), together with the advanced teicherticeratid *Convoluticeras aphelum* and supposed *Erb. solitarium*. The *Anetoceras* level is also known from Hanshan in NW Guangxi (Ruan and He 1974; Xian et al. 1980).

The subsequent and regionally more widespread *Erb. elegantulum* Zone contains in several localities (including Luofu) *Mimagoniatites* and *Now. (Now.) barrandei* (e.g., Shen 1975; Kuang et al. 1989; Yu and Ruan 1989; Zhong et al. 1992), which places such faunas in LD III-D. But supposed *Erb. elegantulum* enter at Sanchahe, Napo County, Guangxi, already in the upper *Now. (Dm.) praecursor* Zone and below typical *Eol. perbonus* (Mu et al. 1982; Yu and Ruan 1989), showing that the *elegantulum* Zone may begin locally much lower. Zhong et al. (1992, p. 365) listed supposed *Erb. elegantulum* together with *? Pr. ilanense* even from the upper *Now. (Now.) zlichovensis* Zone of Luofu. The regional *elegantulum* Zone is heterochronous and should be abandoned. Its main (LD III-D) part should be replaced by a *Mim. fecundus* Zone. Further work has to clarify whether there is a succession of different erbenoceratids in South China.

Ivoites is regionally restricted to the *Now. (Now.) elegans* Zone (LD III-E, regional *I. tangdingensis* Zone or *Mimosphinctes discordans* Zone, updating the taxonomy of Ruan 1996).

- An early part of the "*elegantulum* Zone" (LD III-C) is probably represented by *Erbenoceras* from **Tibet** (Ruan 1984; Rao and Yu 1985; Yu and Ruan 1989), based on the co-occurrence with *Eol. perbonus* below the onset of *Now. (Now.) barrandei*.
- Records of *Erb. elegantulum* and "*Teicherticeras* sp." from **Yunnan** (Daliangtan section, Liao et al. 1978; Yu and Ruan 1989) are associated with *Now.* (*Now.*) *barrandei* and may fall in the main part of the zone (LD III-D). This is also assumed for "*Teicherticeras* sp." from **Sichuan** (Chen et al. 1994; Ruan 1996).
- *Erbenoceras* faunas occur also in **Vietnam** (*Erb. halangense* (Mansuy, 1921)) and in the adjacent NE of **Laos** (Tóng-Dzuy 1993). These isolated and poorly known occurrences cannot be assigned to a specific lower Emsian level.

Australia

- In **Victoria**, Australia, the earliest *Teicherticeras* (sp. D and E sensu Erben 1965) and *Talenticeras* enter below *Eol. perbonus* and *Eol. nothoperbonus* in the upper range of the locally endemic *Eol. abyssus* (upper part of the regional *Eol. dehiscens* Zone, Mawson 1987). Based on the projection of the *nothoperbonus* (Sub)Zone into the lower *Anetoceras* Limestone (Aboussalam et al. 2015), the oldest, highly endemic Buchan fauna can be correlated with the Tafilalt *Metabactrites* Shale. This is significant because it suggests an entry of early Teicherticeratidae and Mimosphinctidae in equivalents of the *Erb. advolvens* Subzone (LD III-B2), contrary to the current evidence from southern Morocco and Germany.

North America

- Isolated records of *Erbenoceras* from **Alaska** (Becker and House 1994) or of *Lenzites* from **Yukon** (House and Pedder 1963) are currently very difficult to compare with the Moroccan ammonoid sequence but a correlation with the *Erb. advolvens* Subzone is possible.
- The **Nevada** records of *Haletoceras erbeni, "Teicherticeras" desideratum,* and *Gracilites nevadense* (e.g., Miller 1938; House 1965) may represent LD III-C/D levels but have not yet been placed in the context of conodonts or dacryoconarids.

Conclusions

Ammonoids from the lowermost Emsian (LD III-B) have an extremely poor record on a global scale. Apart from the two subzones recognized in the Tafilalt, corresponding faunas are only known from other regions of southern Morocco (northern Maïder, eastern Dra Valley), the German Hunsrück Slate, South China, and from Victoria. The currently oldest known taxa are *Pr. debaetsi* n. gen. n. sp., *Ivoites* n. sp. from an allochthonous olistolite block of the Tinerhir region, and possibly *Luofoceras, Erbenoceras, ? Pr. ilanense,* and *? Pr. nantanense* from Guangxi, South

China. The entry of *Chebbites* (Morocco), possibly *Lenzites* (Yukon), *Gyroceratites* (Morocco, Germany), *Oculoceras* (Morocco), *Teicherticeras* (Victoria), and *Talenticeras* (Victoria) occurred higher in LD III-B. Since *Praechebbites* n. gen. is morphologically already rather advanced, well-dated oldest faunas containing only gyroconic Anetoceratidae still have to be discovered in the main *Eol. excavatus* M114 or *Now. (Now.) zlichovensis* zones. The endemism differentiating the ammonoid faunas of NW Gondwana (Morocco), southern Laurussia (Rhenish Massif), South China, and Australia suggests that their evolution occurred in partly isolated populations and regions. From the *Anetoceras* Zone (LD III-C) onward, genera had a more cosmopolitan distribution but with continuing endemism at the species-level.

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