Exploring the Limits of Morphospace: Ontogeny and Ecology of Late Viséan Ammonoids from the Tafilalt, Morocco

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Editors' choice

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Early late Viséan ammonoid assemblages in Morocco are composed of diverse and well-preserved specimens. The material was found in a plain in the Tafilalt (eastern Anti-Atlas). Here, we describe mass-occurrences of juvenile specimens, in which subadult and adult specimens occur in low numbers. The juveniles of some species display a conch morphology that differs fundamentally from the adult stages. Accordingly, we emend the species diagnoses of *Goniatites lazarus* as well as *Calygirtyoceras darkaouaense*, introduce the species *Entogonites bucheri* sp. nov., and discuss possible ecological implications of the morphologic changes throughout ontogeny. In particular, we compare the changes in conch morphology through ontogeny in the light of Pareto Optimiality according to which the morphology of organisms would fill a polygon or polyhedron in morphospace. Data points in one of the vorteces of the polyhedron indicate optimisation for the corresponding task. Although shape is not a proof of function, it appears plausible that juvenile conchs were selected rather for compactness while adult conchs were positively selected for conchs with improved hydrodynamic properties. This appears plausible because at small conch diameters, swimming movements will not suffice for effective translocation and a planktonic mode of life is likely.

Key words: Ammonoidea, morphospace, palaeoecology, Viséan, Morocco.

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Introduction

The evolution of life has never been a straight line, particularly not for ammonoids. As documented by many authors, the ammonite conch underwent several morphological changes during ontogeny, possibly reflecting changes in habitat and habit (e.g., Drushchits et al. 1977; House 1996; Westermann 1996; Klug 2001; Lukeneder et al. 2010; Ritterbush et al. 2014; Robin et al. 2014; Lukeneder 2015; Mironenko and Rogov 2015; Naglik et al. 2015a). These ontogenetic changes can be profound to subtle. Examining conchs of adult ammonoids bears the advantages for the studying researchers that they commonly formed distinct adult modifications such as constrictions or changes in coiling (e.g., Davis et al. 1996; Klug et al. 2015b) and that intraspecific variability appears to be lower (De Baets et al. 2015), thus facilitating species determination. By contrast, determination of juvenile forms, which are often more common, is sometimes difficult due to the lack of adult characters and because they display a different kind of variability (e.g., higher degree of interspecific overlap, dimorphism is not or poorly expressed; e.g., Davis et al. 1996; De Baets et al. 2013, 2015; Klug et al. 2015a). In any case, knowledge of the whole ontogeny is important to understand ammonoid systematics, phylogeny, and ecology (see De Baets et al. 2013; Klug et al. 2015a).

Ammonoid palaeoecology is difficult to assess, because direct observation of ammonoid behaviour is impossible and we have to rely on inferences that can be drawn from conch and jaw morphology. In this context, Tendler et al. (2015) have recently explored the distribution of shell shapes in morphospace. Based on the topography of this morphospace, they evaluated possible links between conch morphology and the optimisation for certain tasks. These tasks are (i) economy of shell material (see also Raup 1967), (ii) optimal hydrodynamics (Chamberlain 1976; Jacobs 1992; Naglik et al. 2015b), and (iii) rapid shell growth (= high

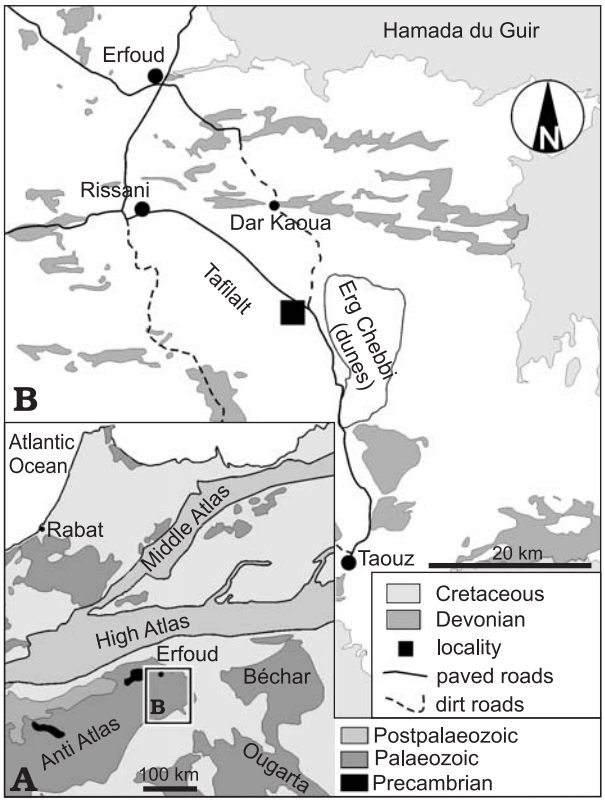

Fig. 1. Geological map of the eastern Anti-Atlas (modified after Korn et al. 2005).

whorl expansion; compare Bucher et al. 1996). However, Tendler et al. (2015) found that the morphospace of adult ammonoid conchs filled a pyramid with five vertices. Accordingly, they interpreted the remaining two vertices as being occupied by shell morphologies optimized for combinations of two tasks, namely compactness with economy of shell material (iv) and compactness with hydrodynamics (v).

In this paper, we want to explore these links using the well preserved Carboniferous materials from Morocco. After some quiescence following the pioneering works on Early Carboniferous (Mississippian) ammonoids from northern Africa (e.g., Delépine 1941; Pareyn 1961; Hollard 1958), research on these fossils is currently experiencing a renaissance (Korn et al. 1999; 2002, 2003a, b, 2005, 2007, 2010, 2014; Ebbighausen et al. 2004, 2010; Bockwinkel and Ebbighausen 2006; Klug et al. 2006; Bockwinkel et al. 2010). Possibly due to the quality of the outcrop (large plains covered in loose gravel with fossils aligned according to their source rock), several Carboniferous ammonoid assemblages (including the *Entogonites*-bearing assemblage described by Korn et al. 2005; see map in Fig. 1) had been overlooked in the eastern Anti-Atlas (Morocco) although they are often well preserved, sometimes rather highly diverse and the contained forms display an impressive disparity. These assemblages yielded both juvenile and adult conchs of several, morphologically quite disparate species. This morphological disparity includes not only differences between different taxa but also within taxa between different growth stages (see also Klug 2001).

In the case of the nodules with *Entogonites*, the fossil-bearing rocks are scarce and not so easy to find. The nodules containing the *Entogonites* assemblage are usually flat, brownish and contain fossils in nearly rock forming numbers. Some of the rocks may actually represent gutter casts, which is supported by the fact that some of the nodules contain only juvenile specimens and that the nodules have a flat cross section and appear to be elongate. It is well visible that the contained ammonoids are reasonably diverse because their morphology differs strongly. The *Entogonites* assemblage contains all of the main types of "monomorphic" (planispirally coiled, bilaterally symmetric) ammonoids including oxyconic (adult *Calygirtyoceras*), serpenticonic (*Nomismoceras*), cadiconic (juvenile *Calygirtyoceras*), quadrate (juvenile *Entogonites*), and globose (adult *Goniatites*) to extremely spindle-shaped forms (juvenile *Goniatites*). A closer look revealed that certain morphologies are absent in the juveniles and others in the adults of this assemblage. This, in turn, led us to question whether this absence of certain conch shapes could be caused by sorting or other taphonomic processes or whether this is a primary signal, where juveniles or adults, respectively, simply did not produce conchs with such shapes.

Accordingly, the aims of our study are to: (i) describe the morphology of the members of the *Entogonites* assemblage, (ii) document, which morphologies are adult-only or juvenile-only, and (iii) discuss potential explanations for the patterns.

Institutional abbreviations.—GPIT, Institut für Geowissenschaften, Eberhard Karls Universität Tübingen, Germany; MB.C, Museum für Naturkunde, Berlin, Germany; PIMUZ, Paläontologisches Institut und Museum, Zürich University, Switzerland.

Other abbreviations.—ah, apertural height; dm, diameter; uw, umbilical width; WER, whorl expansion rate; ww, whorl width (measured between ribs). Conch parameters after Raup (1966: 1294; see below for the equations to determine these values): D, the distance between the generating curve and the coiling axis; S, the shape of the generating curve ("equivalent to the cross-sectional shape of the tube"); W, whorl expansion rate ("the rate of increase in the size of the generating curve per revolution").

Material and methods

The recently collected, well preserved specimens were all found in the pebble-covered reg-like desert (reg: gravel-covered flat area) about 12 km south of the oasis of Dar Kaoua. This assemblage described herein was partially presented by Korn et al. (1999, 2005, 2007) including one of the stratigraphically oldest occurrences of a member of the genus *Goniatites* (*G. lazarus*) and a new species of *Entogonites* (*E. saharensis*). All material was collected in a plain, about 10 to 12 km south of the Kasbah (fortified Moroccan building)

of Dar Kaoua (Tafilalt, SE of Erfoud, Morocco; Fig. 1). The reg-like plain is largely flat with shallow hills covered by scree and very little true exposure. Nevertheless, some fossiliferous layers locally yield well-preserved ammonoids, orthocerids, nautilids, gastropods, trilobites, bryozoans, brachiopods, and crinoids. These layers can be vaguely traced by following the fossil occurrences. The relative abundances of ammonoids are listed in Table 1.

As far as measurements and ratios are concerned, we followed the suggestions published by Korn (2010) as well as Klug et al. (2015a). Also, we use technical terms in the sense used in these two papers. To calculate the classical Raupian parameters W, S, and D, we used the original equations by Raup (1966, 1967). Tendler et al. (2015) repeated the equations needed to determine the values:

$W = a/b$

$D = x/a$

$S = y/z$

where a is the radius from the coiling axis to the venter, b is the same value of the preceding whorl, x is the umbilical width measured as a ratio from the coiling axis, y is the whorl width and z is the whorl height.

Table 1. Quantity of specimens of different taxa in the new material from the early late Viséan, 12 km south of the oasis of Dar Kaoua.

Taxon	Juveniles	(Sub-) Adults	Total	% of ammonoids in the assemblage
Nomismoceras sp.	169	5	174	52
Entogonites saharensis	68	3	71	21
Goniatites lazarus	25	5	30	9
Prolecanites sp.	23	0	23	7
Goniatitidae indet.	16	0	16	5
Entogonites bucheri	6	1	7	2
Calygirtyoceras darkaouaense	5	1	6	2
Beyrichoceras sp.	0	1	1	1
Bollandites sp.	4	0	4	1

Systematic palaeontology

Ammonoidea Zittel, 1884

Family Goniatitidae Haan, 1825

Genus *Goniatites* Haan, 1825

Type species: Conchiliolithus Nautilites (*sphaericus*) Martin, 1809 (nomen nudum) = *Ammonites sphaericus* Sowerby, 1814 (Opinion 420 ICZN, 1956).

Goniatites lazarus Korn, Klug, and Mapes, 2005

Fig. 2−4.

Type material: Holotype GPIT 1851–97 (Korn et al. 2005: figs. 8.1, 8.2); paratypes MB.C. 5307 and MB.C. 5308.

Type locality: 12 km southeast of Dar Kaoua, southeast of Erfoud, eastern Anti–Atlas, Morocco.

Type horizon: Early late Viséan (*Entogonites* assemblage).

Material.—25 juveniles: 6 in PIMUZ 31508, 1 in PIMUZ 31509, 6 in PIMUZ 31510, 2 in PIMUZ 31512, 1 in PIMUZ 31520, 2 in PIMUZ 31518, 7 in PIMUZ 31519. 4; adults: MB.C. 25130, PIMUZ 31514–16.

Emended diagnosis (modified after Korn et al. 2005).—*Goniatites* with an extremely broad spindle-shaped juvenile conch (dm 1.1–6 mm; ww/dm up to 1.76), later with a pachyconic conch up to 40 mm dm (ww/dm 0.70) and thickly discoidal conch at 70–100 mm diameter (ww/dm 0.6–1.00). Umbilicus almost closed (uw/dm 0.01–0.03) in all growth stages. Low aperture, moderate whorl expansion rate (1.7 in juvenile whorls, and nearly 2 near adulthood). The spindle-shaped juvenile whorls carry an umbilical ridge that vanishes at a diameter of about 7 mm. Suture line with V-shaped external lobe with slightly sinuous flanks, moderately high median saddle (one-third of the symmetric, narrowly rounded ventrolateral saddle). Shell ornament with crenulated growth lines with convex course in juvenile to adult whorls.

Table 2. Measurements (in mm) and ratios of *Goniatites lazarus*. Abbreviations: ah, apertural height; D, the distance between the generating curve and the coiling axis; dm, diameter; S, the shape of the generating curve; uw, umbilical width; W, whorl expansion rate; WER, whorl expansion rate; ww, whorl width (measured between ribs).

Specimen	dm	ww	uw	ah	WER	ww/dm	ah/dm	uw/dm	W	D	S
PIMUZ 31514	97	61	1.2	17	1.47	0.63	0.17	0.01	1.40	0.08	1.20
PIMUZ 31510, section 1	6.04	8.5	0.4	1.26	1.56	1.41	0.21	0.07	1.53	0.08	2.67
	4.82	7.38	0.32	1.14	1.61	1.53	0.24	0.07		0.08	3.13
	3.8	6.23	0.28	0.75	1.74	1.64	0.20	0.07		0.05	2.84
PIMUZ 31510, section 2	5.31	7.1	0.35	0.99	1.56	1.34	0.19	0.07	1.57	0.14	3.06
	4.25	6.69	0.2	0.78	1.55	1.57	0.18	0.05		0.10	3.04
	3.41	4.7		0.7	1.60	1.38	0.21				
	2.3	3.37		0.4	1.09	1.47	0.17				
	1.8	2.8		3.8	1.68	1.56	2.11				
PIMUZ 31510, section 3	5.58	7.8	0.31	0.92	1.43	1.40	0.16		1.45	0.06	2.63
	4.88	7		0.85	1.60	1.43	0.17				
	3.86	5		0.8	1.58	1.30	0.21			0.60	2.43
	2.43	3.7		0.66	1.03	1.52	0.27				

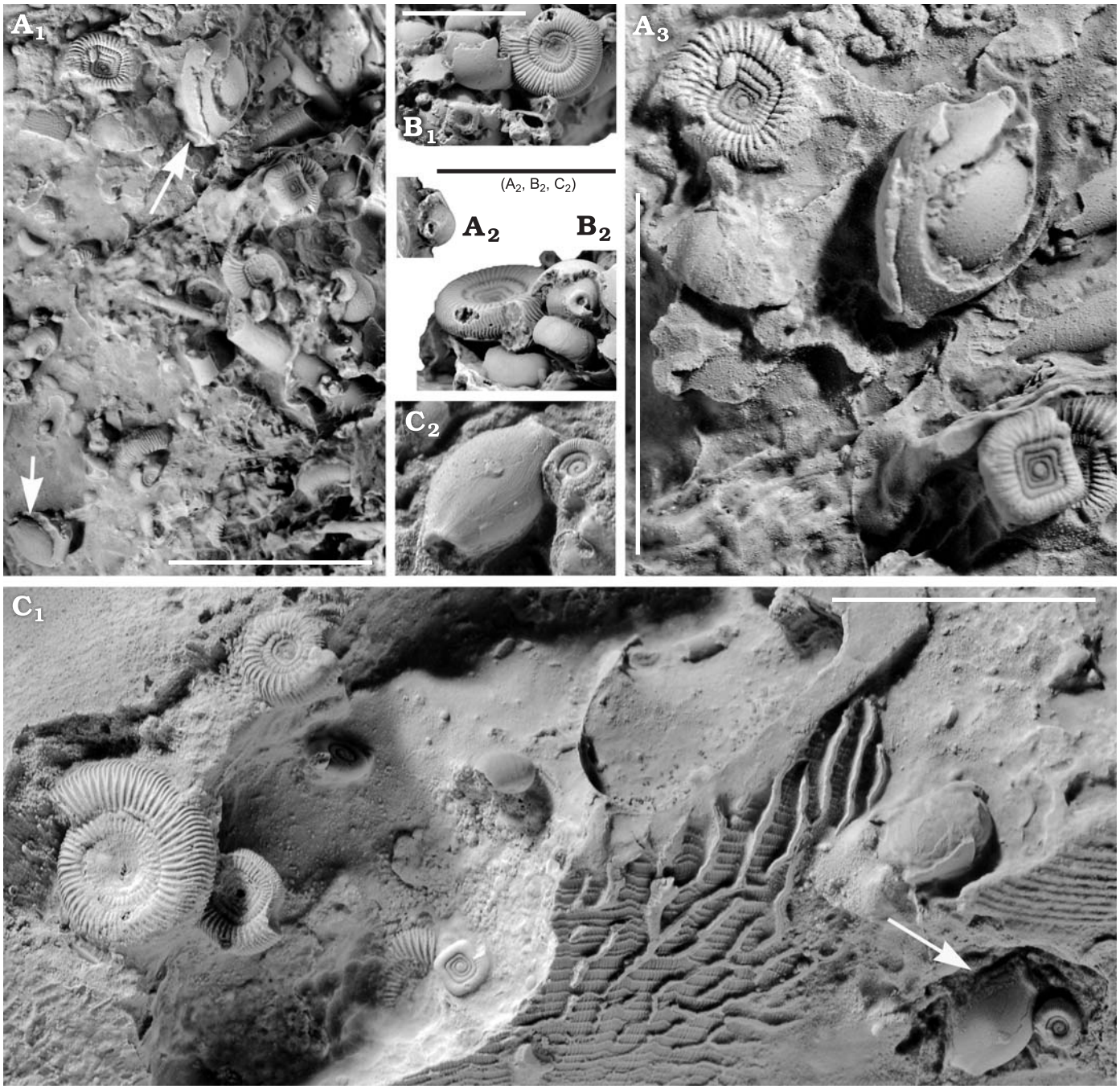

Fig. 2. Juvenile (neanic) specimens of *Goniatites lazarus* Korn, Klug, and Mapes, 2005, *Entogonites saharensis* Korn, Klug, and Mapes, 2005, and *Entogonites bucheri* sp. nov. All from the early late Viséan, 12 km SE of Dar Kaoua (Tafilalt, Morocco). **A**. PIMUZ 31512, two neanic *G. lazarus* specimens (white arrows) in ventral views (A_1), note the associated *E. saharensis* and orthocones. Enlarged *G. lazarus* in lateral view (A_2); the narrow umbilicus and the umbilical ridge (A_3). **B**. PIMUZ 31512, a juvenile *G. lazarus*, a small juvenile and a subadult *E. saharensis*; *G. lazarus* in ventral (B_1) and lateral (B_2) views. **C**. PIMUZ 31520, detail of a fully grown *Maxigoniatites saourensis* (Pareyn, 1961) with *G. lazarus*, 3 juvenile *E. saharensis*, and a subadult *E. saharensis* and a hatchling of *E. bucheri* sp. nov. (arrowed); C_2, detail of C_1, showing *G. lazarus* and *E. bucheri* sp. nov. All specimens whitened with NH_4Cl-sublimate. Scale bars 10 mm.

Description.—At diameters of 2–7 mm, the whorl width/diameter ratio ranges between 1.4 and almost 1.8 (e.g., PIMUZ 31512; Figs. 2–4; Table 2). This ratio lies between 1.4 and 1 in later ontogeny (dm < 70 mm) and further decreases to 0.6 in the still pachyconic adults (PIMUZ 31514, dm 97 mm; Table 2). The umbilicus is very narrow throughout the post-hatching ontogeny. Until a diameter of about 7 mm, the spindle-shaped shell carries an umbilical ridge (PIMUZ 31512; Fig. $2A_3$). Adult conchs are globose with rounded venter and very involute (PIMUZ 31514; Fig. 3). Ornamentation is limited to fine growth lines, which are rather straight in small juveniles (e.g., PIMUZ 31520; Fig. $2C_2$) and can be slightly crenulated in adults (PIMUZ 31514). In PIMUZ 31515, the crenulation consists of 2 minute waves

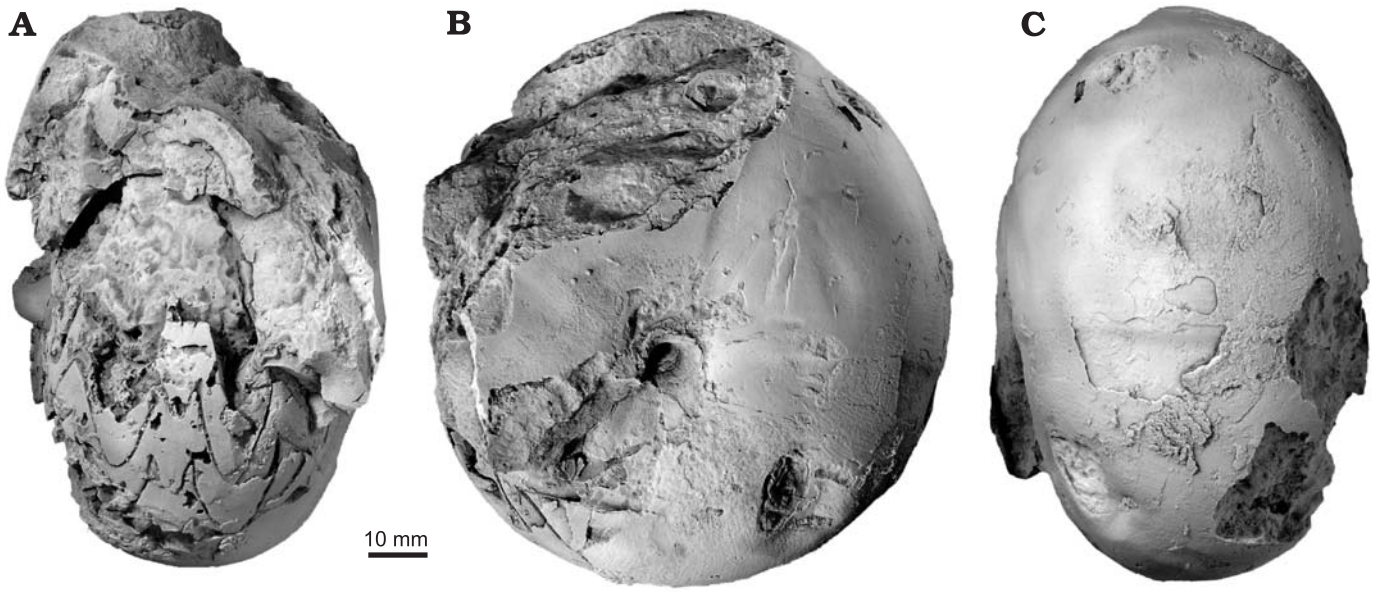

Fig. 3. Adult specimen of *Goniatites lazarus* Korn, Klug, and Mapes, 2005 (PIMUZ 31514) from the early late Viséan, 12 km SE of Dar Kaoua (Tafilalt, Morocco), in dorsal (**A**), lateral (**B**), and ventral (**C**) views. All specimens whitened with NH_4Cl-sublimate

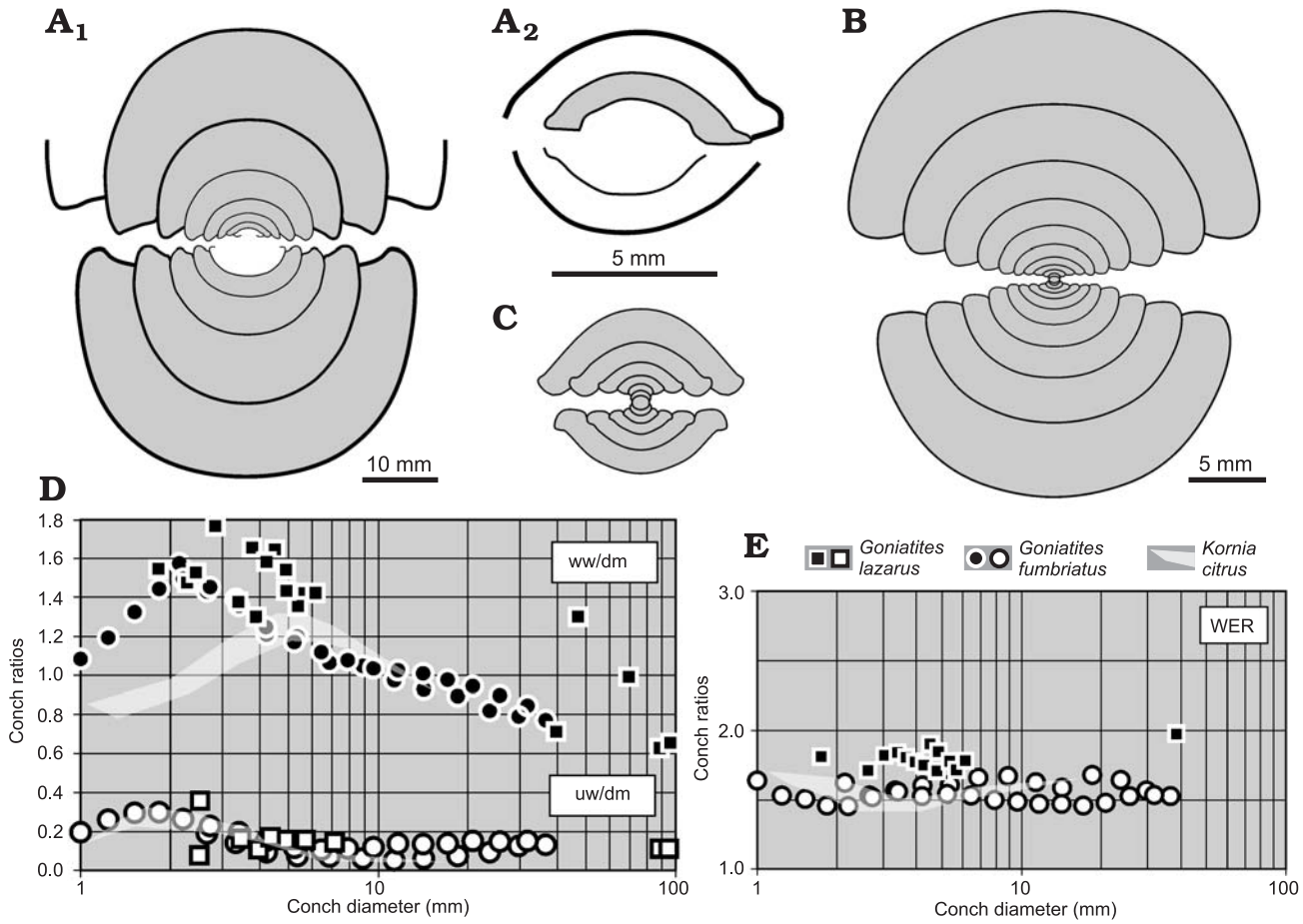

Fig. 4. Comparison of cross sections, measurements, and ratios of *Goniatites lazarus* and other ammonoids. **A**. *Goniatites lazarus*, subadult (MB.C. 25130, A_1) and juvenile (PIMUZ 31510, A_2) from early late Viséan, 12 km SE of Dar Kaoua (Tafilalt, Morocco). **B**. *Goniatites fimbriatus*, MB.C.13299 (after Korn et al. 2008: fig. 23A) from Nehden, Viséan, Rhenish Mountains, Germany. **C**. Juvenile *Kornia citrus*, MB.C.10202.1 (after Ebbighausen and Bockwinkel 2007: fig. 30B) from early Tournaisian, Aguelmous (Tafilalt, Morocco); note the conch shape and umbilical ridge, which is similar to juvenile *G. lazarus*. Whorl width (ww) and umbilical width (uw) indexes (**D**) and whorl expansion rate (WER) (**E**) of *G. lazarus*, *G. fimbriatus*, and *K. citrus*.

on the growth lines or lirae, which are spaced at 0.5–0.8 mm at a diameter of 85 mm. The juvenile suture is poorly visible in PIMUZ 31512; its overall course corresponds to the adult suture, but details are not visible in all juvenile specimens. The adult suture (PIMUZ 31514; Fig. 3) was examined at ca. 77 mm diameter. At this size, the V-shaped external lobe is almost twice as high as wide at the mid of its height. The median saddle measures 0.36 of the E-lobe height. The ventrolateral saddle has a nearly isosceles triangle-shape with shallow bulges near the bases and tops of both flanks and gentle concavity in the middle. Its adapertural tip is slightly asymmetrical and narrowly rounded. The adventive lobe is similar in size and shape, except that it is somewhat lower and broader.

Remarks.—The inner whorls of *G. lazarus* strongly resemble those of *Kornia citrus* Bockwinkel and Ebbighausen, 2006. We cut and polished two subadult *G. lazarus* from the same locality (Fig. 4A), which confirmed that the spindle-shaped juveniles indeed belong to this species and not to *Kornia*. With a conch width index (ww/dm) of up to 1.8, juveniles of this species belong to the ammonoids with the most extreme whorl width/diameter ratio. Similar changes in conch ontogeny have been documented from several goniatitids including, e.g., *G. fimbriatus* (Fig. 4B) and *K. citrus* (Fig. 4C).

Stratigraphic and geographic range.—Early late Viséan, so far only known from the Tafilalt (Morocco).

Family Girtyoceratidae Wedekind, 1918

Genus *Calygirtyoceras* Korn, Klug, and Mapes, 1999

Type species: *Calygirtyoceras darkaouaense* Korn, Klug, and Mapes, 1999, see below.

Calygirtyoceras darkaouaense Korn, Klug, and Mapes, 1999

Fig. 5.

Holotype: GPIT 1851-87; Korn et al. 1999: pl. 1: 7.

Type locality: 12 km southeast of Dar Kaoua, southeast of Erfoud, eastern Anti-Atlas, Morocco.

Type horizon: Early late Viséan (*Entogonites* assemblage).

Material.—6 specimens: three juvenile conchs in PIMUZ 31509, PIMUZ 31516, PIMUZ 31519; two additional juveniles in PIMUZ 31508; an incomplete adult specimen with septal crowding in PIMUZ 31513.

Emended diagnosis (modified after Korn et al. 1999).—*Calygirtyoceras* with a juvenile cadiconic conch (dm 5–10 mm; ww/dm 0.60–0.71), a transitional discoidal, platyconic preadult conch shape and a large, thinly discoidal, oxyconic adult conch (dm 100–150 cm; ww/dm 0.30–0.40). Umbilicus very wide in juvenile growth stages (uw/dm 0.08; dm 5–10 mm) and very narrow near adulthood (uw/dm 0.10–0.15; dm > 50 mm). Whorl expansion rate very low in juvenile whorls (dm < 10 mm) and increasing to almost 3 at > 50 mm diameter. Adult ornamentation with fine, crenulated growth lines with biconvex and slightly rursiradiate course. Suture line with low median saddle (median saddle width/height ratio 0.30), broadly rounded ventrolateral saddle, and narrow external lobe (external lobe width/height ratio 0.55).

Description.—PIMUZ 31516 (Fig. 5B) is a cadiconic juvenile with a thinly to thickly globular, very evolute conch. The whorl cross section is strongly depressed with a hardly vaulted venter; at the thickest part of the flanks, 12–15 small nodes are developed at a diameter below 10 mm per half whorl. In the subsequent ontogenetic stage, the venter becomes more and more vaulted and rounded. At a whorl height of about 30 mm (PIMUZ 31513), the cross section becomes subtriangular with gently rounded flanks. PIMUZ 31513 is a fragment of an adult conch (septal crowding at dm ca. 110 mm). At this stage, the conch is extremely discoidal and involute (Table 3). In this specimen, the external lobe is incompletely visible but V-shaped with a high ventrolateral saddle as present in the type-material. The V-shaped adventive lobe is inclined dorsally with a convex ventral flank.

Remarks.—In the original species diagnosis by Korn et al. (1999), the ontogenetic changes were described in a somewhat misleading way: in the same article, we (Korn et al. 1999: p. 354) had stated that the "Umbilicus [is] very narrow in early growth stages (uw/dm = 0.08 at 20–30 mm dm) and slightly opening during ontogeny (stages (uw/dm = 0.10 to 0.12 at 40–60 mm dm)." When measuring the umbilical width throughout the entire post-hatching ontogeny, a rather constant reduction of the uw/dm ratio from 0.62 to 0.14 was measured. Also, the latest growth stage was unknown previously.

Stratigraphic and geographic range.—Early late Viséan, so far only known from the Tafilalt (Morocco).

Table 3. Measurements (in mm) and ratios of *Calygirtyoceras darkaouaense*. Abbreviations: ah, apertural height; D, the distance between the generating curve and the coiling axis; dm, diameter; S, the shape of the generating curve; uw, umbilical width; W, whorl expansion rate; WER, whorl expansion rate; ww, whorl width (measured between ribs).

Specimen	dm	ww	uw	ah	WER	ww/dm	ah/dm	uw/dm	W	D	S
PIMUZ 31513	83	26	12	35	2.99	0.31	0.42	0.14	2.48	0.10	0.43
PIMUZ 31516	6.5	4.6	4	0.75	1.28	0.71	0.12	0.62	1.26	0.42	4.60
GPIT 1851-88, paratype (from Korn et al. 1999)	21.3	15.1	6.3	5.8	1.89	0.71	0.27	0.30			
	15.5	12.6	6.5	3.5	1.67	0.81	0.23	0.42			
	12	11.2	6.1	2.5	1.60	0.93	0.21	0.51			
	9.5	9	5.1	1.95	1.58	0.95	0.21	0.54			

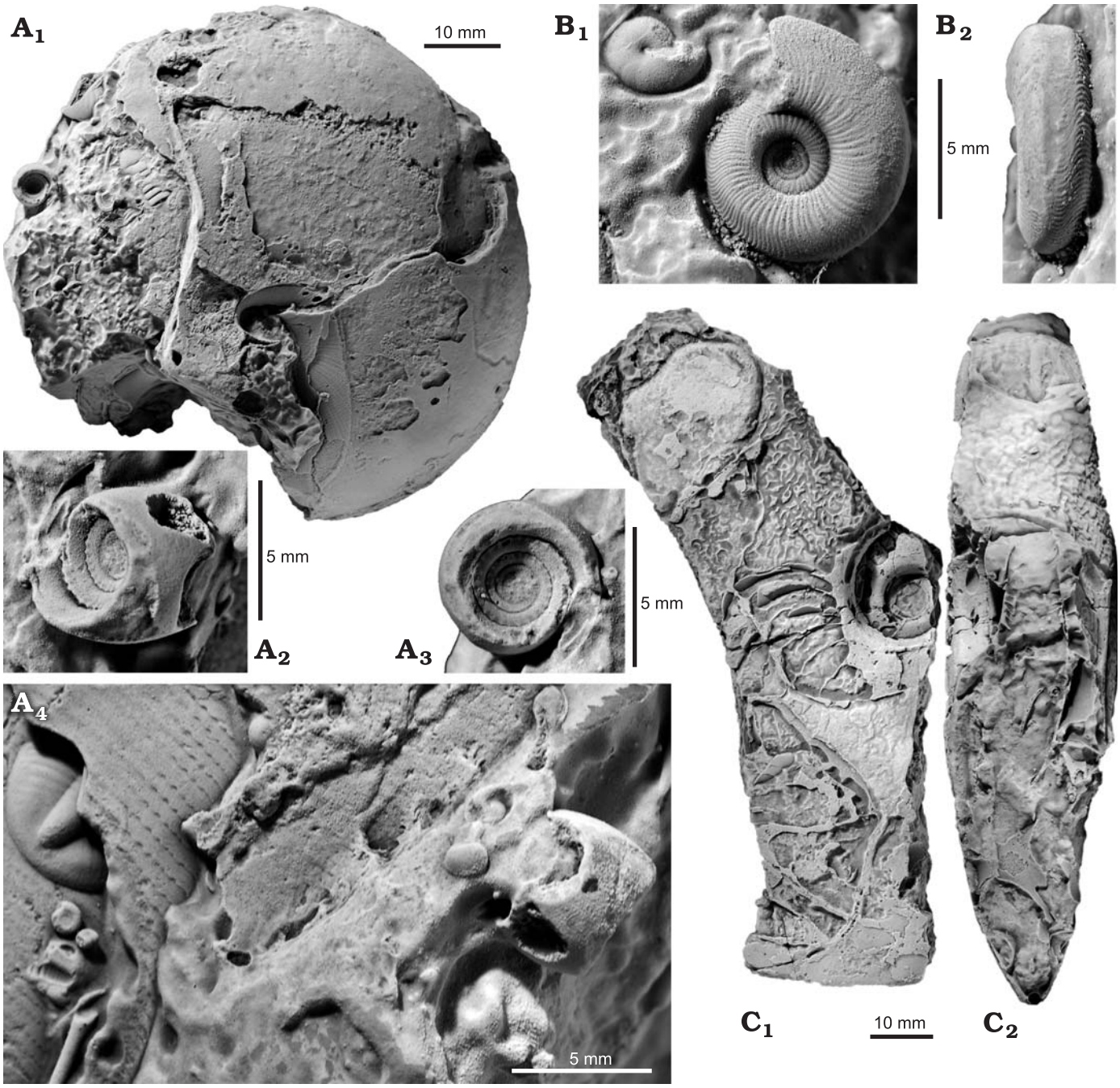

Fig. 5. Ammonoids from the early late Viséan, 12 km SE of Dar Kaoua (Tafilalt, Morocco). **A**, **C**. *Calygirtyoceras darkaouaense* Korn, Klug, and Mapes, 1999. **A**. PIMUZ 31516 (A_1), *Goniatites lazarus* with a juvenile specimen in oblique-ventral (A_2), lateral (A_3), and ventral (A_4) views. **C**. PIMUZ 31513, fragmentary adult in lateral view (C_1), cross section (C_2). **B**. *Entogonites bucheri* sp. nov., PIMUZ 31509, holotype in lateral (B_1) and ventral (B_2) views. All specimens whitened with NH_4Cl-sublimate.

Entogonitidae Ruzhencev and Bogoslovskaya, 1971
Genus *Entogonites* Kittl, 1904

Type species: *Tetragonites grimmeri* Kittl, 1904; by monotypy; Bosnia-Herzegovina, Praca Dolnja, E of Sarajewo, early late Viséan.

Included species: *Entogonites acus* Korn and Titus, 2011: 134, Utah; *Entogonites borealis* Gordon, 1957: 53, Alaska; *Entogonites bucheri* sp. nov., herein, Anti-Atlas; *Entogonites burbankensis* Korn and Titus, 2011: 131, Utah; *Tetragonites grimmeri* Kittl, 1904: 677, Bosnia and Herzegovina; *Pericyclus nasutus* Schmidt, 1941: 151, Harz; *Entogonites saharensis* Korn, Klug, and Mapes, 2005: 363, Anti-Atlas; *Gastrioceras* (*Branneroceratoides*) *tetragonum* Kullmann, 1962: 88, NW Serbia.

Diagnosis.—Entogonitidae with simple ontogeny. Adult whorls slightly narrower umbilicate; inner whorls tetrangularly coiled (from Korn et al. 2010).

Stratigraphic and geographic range.—Mississippian (Late Viséan) of Alaska, Bosnia, Germany, Morocco, Poland, Serbia, United Kingdom, and Utah.

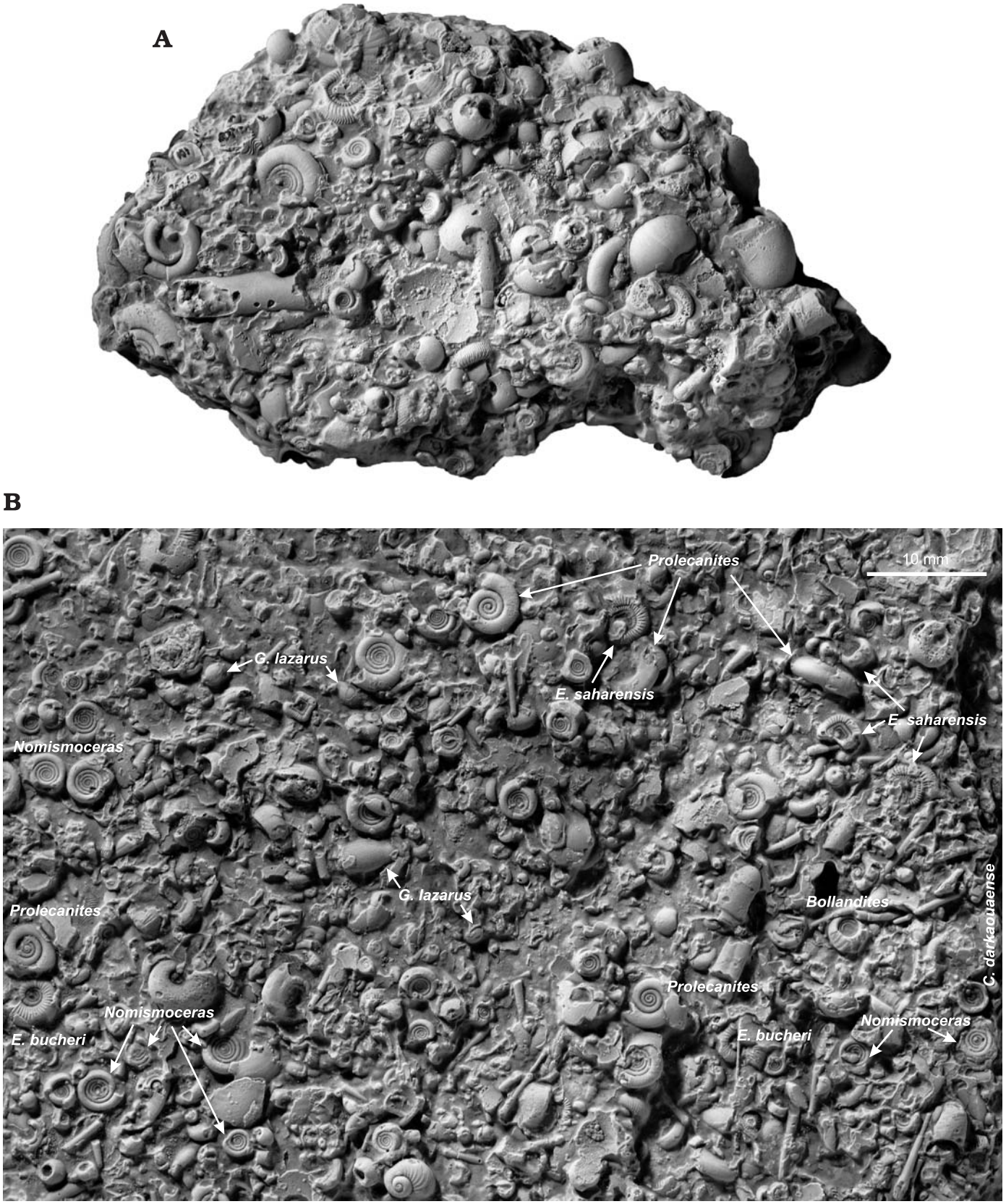

Fig. 6. Mass occurrence of juvenile ammonoids from the early late Viséan, 12 km SE of Dar Kaoua (Tafilalt, Morocco). **A**. PIMUZ 31518 with 4 specimens of *Nomismoceras* sp., 3 *Prolecanites* sp., 4 *Entogonites saharensis* Korn, Klug, and Mapes, 2005, 1 *Calygirtyoceras darkaouaense* Korn, Klug, and Mapes, 1999, and 2 *Bollandites* sp. **B**. PIMUZ 31508, overview; many taxa are indicated in the figure. All specimens whitened with NH_4Cl-sublimate.

Entogonites saharensis Korn, Klug, and Mapes, 2005

Figs. 6, 7.

Type material: Holotype MB.C.5301; paratypes MB.C.5302–06.

Type locality: 12 km southeast of Dar Kaoua, southeast of Erfoud, eastern Anti–Atlas, Morocco.

Type horizon: Early late Viséan (*Entogonites* assemblage).

Material.—68 specimens displaying several ontogenetic stages 2 specimens in PIMUZ 31509; 2 specimens in PIMUZ 31509; 4 specimens in PIMUZ 31510; 5 specimens in PIMUZ 31511; 16 specimens in PIMUZ 31512; 2 specimens in PIMUZ 31517; 4 specimens in PIMUZ 31518; 9 specimens in PIMUZ 31519; 5 specimens in PIMUZ 31520).

Remarks.—In terms of ontogenetic morphologic data, not much can be appended to the original descriptions (Korn et al. 2005). We add that the number or primary ribs varies on the quadratic whorls between 15 and 22 per half whorl. Not all ribs are dichotomous.

Stratigraphic and geographic range.—Early late Viséan, so far only known from the Tafilalt (Morocco).

Entogonites bucheri sp. nov.

Figs. 2C, 5A, 6C.

Etymology: Honoring Hugo Bucher (Zürich) for his numerous, thorough and profound contributions to ammonoid paleobiology and stratigraphy.

Type material: Holotype, subadult specimen, PIMUZ 31509, paratype, juvenile specimen, PIMUZ 31508.

Type locality: 12 km southeast of Dar Kaoua, southeast of Erfoud, eastern Anti–Atlas, Morocco.

Type horizon: Early late Viséan (*Entogonites* assemblage).

Material.—6 individuals: 2 specimens in PIMUZ 31509 (the subadult holotype and a smaller individual); 3 juvenile to subadult specimens in PIMUZ 31512 (associated with about 100 other juvenile ammonoid conchs); a very small juvenile conch in PIMUZ 31520 (in the body chamber of a mature conch of *Maxigoniatites*).

Diagnosis.—*Entogonites* with largely regularly coiled whorls. Only the third whorl displays faint tetragonal coiling. Expansion rate of juvenile and adult whorls exceeds 2.0. The uw/dm ratio is below 0.4. Ornamentation begins after the nepionic constriction with simple ribs, followed by bifurcating and intercalatory ribs (>30 per whorl).

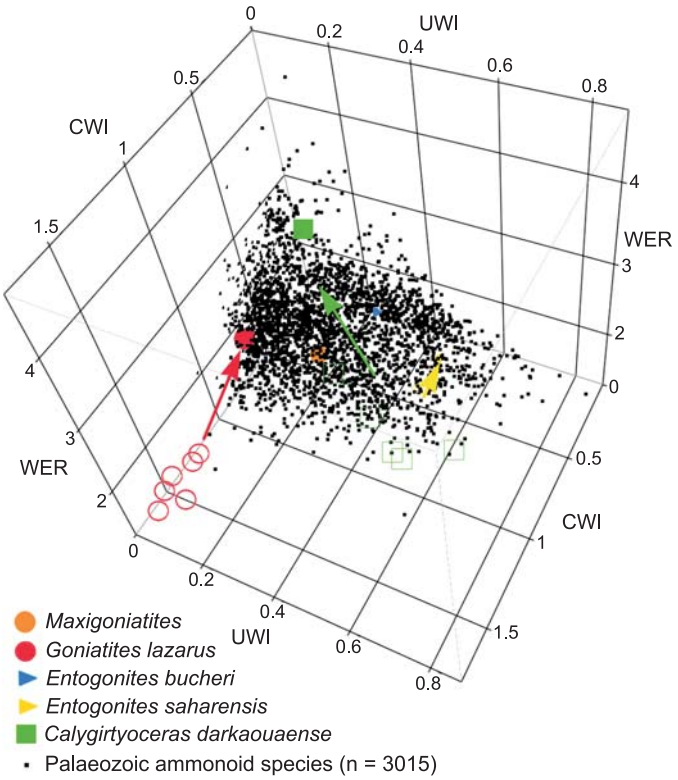

Fig. 7. Morphospace (UWI, umbilical width index; WER, whorl expansion rate; CWI, conch width index) with data of 3015 species of Palaeozoic ammonoids with additional points of the ammonoids from the early late Viséan of the Tafilalt (Morocco). Note that data points of juveniles (empty symbols) of *Calygirtyoceras darkaouaense* and *Goniatites lazarus* lie at the edge or outside of the cloud of 3015 species. Graph produced using JMP 11.

Description.—The small subevolute specimen PIMUZ 31520 measures about 1.8 mm in diameter. It comprises the initial chamber and the initial 2.5 whorls (Fig. 2C). The embryonic shell measures less than 1 mm and has a smooth surface. Only one side is exposed and thus, the thickness cannot be measured. At the presumed position of the nepionic constriction, the fine ornament commences. At 1.8 mm diameter, there are 25 simple and rectiradiate ribs per half whorl.

The ontogenetically slightly older specimen PIMUZ 31508 measures 5 mm in diameter. Its conch is subinvolute with a high whorl expansion rate (Table 4). As in the other specimen, the conch is only partially exposed and hence, conch thickness is unknown. The tetragonal coiling is only

Table 4. Measurements (in mm) and ratios of *Entogonites saharensis* and *E. bucheri* sp. nov. Abbreviations: ah, apertural height; D, the distance between the generating curve and the coiling axis; dm, diameter; S, the shape of the generating curve; uw, umbilical width; W, whorl expansion rate; WER, whorl expansion rate; ww, whorl width (measured between ribs).

Species	Specimen	dm	ww	uw	ah	WER	ww/dm	ah/dm	uw/dm	W	D	S
Entogonites saharaensis	PIMUZ 31520	7.67		3.60	1.63	1.61		0.21	0.47			
	MB.C.5301, holotype	9.35	3.05	4.55	2.05	1.64	0.33		0.49	1.67	0.49	1.13
	MB.C.5304, paratype	11.2		5.4					0.48			
	MB.C.5305, paratype	2.2	1.15	1.05		1.58	0.52		0.48	1.53	0.43	1.67
Entogonites bucheri	PIMUZ 31509, holotype	8.93	3.1	2.86	2.68	2.04	0.35	0.3	0.32			
	PIMUZ 31512	5.0		1.84	2.37	2.13		0.47	0.37			

very faintly developed in early whorls and the last of the preserved (preadult) whorls is completely regularly coiled. At 5 mm diameter, there are 20 primary ribs per half whorl. Most of these ribs bifurcate near the midflank, but there are a few trifurcating ribs as well (or bifurcating with an associated intercalatory rib).

The holotype PIMUZ 31509 has a diameter of almost 9 mm. At this size, the subevolute conch is thinly discoidal with a high whorl expansion rate. The initial chamber measures approximately 0.4 mm across. The first two whorls are regularly coiled followed by one vaguely tetragonally coiled whorl. The last two whorls are again normally coiled. The ornamentation consists of 34 primary ribs on the last half whorl. Most of these ribs bifurcate in the middle of the flank, some are simple but then often associated with intercalatory ribs. The rib course begins with a deep ventral sinus, which is nearly twice as wide as it is deep measured from the tips of the adjacent ventrolateral projections, which are rounded and asymmetric. The ribs are the most strongly developed in the ventrolateral projections. Most of the flank is covered by a broad and shallow sinus. None of the specimens displays the suture line.

Remarks.—Although the suture is not visible, the combination of coiling, ornamentation and stratigraphic origin confirms the genus assignment. The new species differs from all other species in the extremely reduced tetragonal coiling of the inner whorls. Additionally, it has a clearly higher whorl expansion rate (values partially from the online database GONIAT (http://www.goniat.org, accessed September 7th 2015) and Korn et al. 2010) than all other species (*E. bucheri*, 2.0–2.15; *E. grimmeri*, 1.5–1.7; *E. saharaensis*, 1.5–1.65; *E. tetragonus*, 1.8–1.9) and, as can be expected from the covariation of these characters, the umbilicus is narrower (*E. bucheri*, <0.4; *E. borealis*, 0.41; *E. grimmeri*, 0.45; *E. saharaensis*, >0.48; *E. tetragonus*, 0.5).

Stratigraphic and geographic range.—Early late Viséan, so far only known from the Tafilalt (Morocco).

Discussion

As far as the early late Viséan ammonoid fauna from the Tafilalt is concerned, the extreme morphology of some juvenile shells in combination with the often fundamentally different adult morphology is striking. One might suggest that these differences are rooted in the widely documented juvenile (post-hatching) morphological intraspecific variability of mollusk shells (e.g., Jacobs 1992; Jacobs et al. 1994; Jacobs and Chamberlain 1996; Urdy et al. 2010a, b; De Baets et al. 2013, 2015; Naglik et al. 2015a). This is in contrast with the fact that the conch morphology of some of the juveniles of early late Viséan ammonoids lies at the edge or even outside of the morphospace of adult Palaeozoic ammonoids (Figs. 7, 8). To put it differently: some juvenile morphologies are inexistent in adult ammonoids (at least in the *Entogonites* assemblage; we are not aware of adult ammonoids with a conch morphology remotely similar to juvenile *Goniatites lazarus*). The morphologies (see also the illustrations in Fig. 8; the terminology of Korn 2010 is given in brackets where it differs from the classical terms) we found in the major growth stages of the *Entogonites* assemblage are:

- conch shapes occurring only in juveniles: cadiconic (spindle-shaped, very evolute), spindle-shaped involute, evolute with quadrate coiling;
- conch shapes occurring only in subadults and adults: oxyconic (extremely discoidal, involute);
- conch shapes occurring in juvenile to adult stages: platyconic (discoidal), serpenticonic (discoidal, very evolute), sphaeroconic (pachyconic, involute).

This leads to the question of whether this ontogenetic distribution of shell morphologies roots purely in morphogenetic constraints or whether there are also some aspects that can explain shell morphology, which root in the selection for distinct shapes. There are limits as to how to test these hypotheses since direct observation of these extinct animals is impossible. We can still discuss this issue a bit further by, for example, employing the set of hypotheses published recently by Tendler et al. (2015). In their paper, they explored possible adaptations and trade-offs throughout ammonoid evolution. They followed other authors (e.g.,

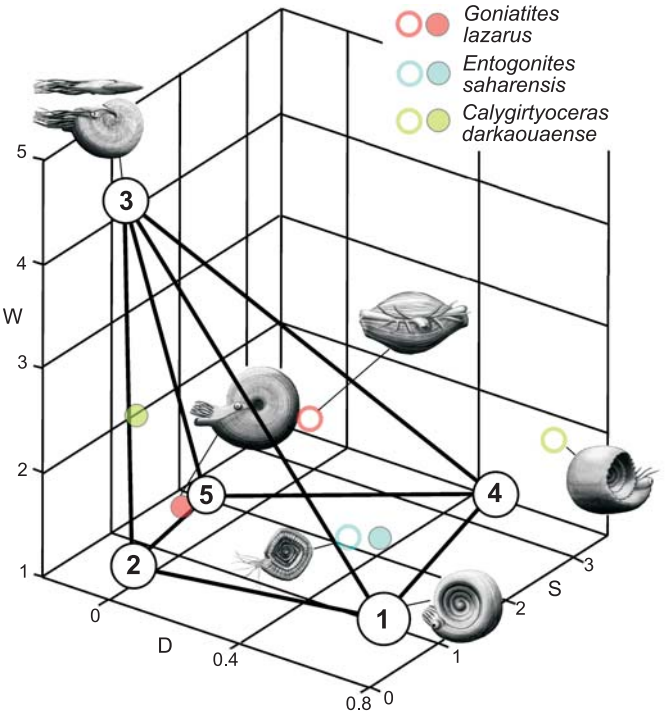

Fig. 8. Ammonoid morphospace after Tendler et al. (2015) using the Raupian parameters W (whorl expansion rate), S (shape of the generating curve), and D (distance between the generating curve and the coiling axis). Note that the juveniles (empty symbols) of *Calygirtyoceras darkaouaense* and *Goniatites lazarus* (in contrast to the respective adults) lie outside of the five-sided pyramid. Juvenile *Nomismoceras* sp. plots near vertex 1, *Entogonites* spp. between 1 and 4, and juvenile *Bollandites* sp. near 4. A Devonian pinacitid is depicted near vertex 3 to illustrate the conch morphology.

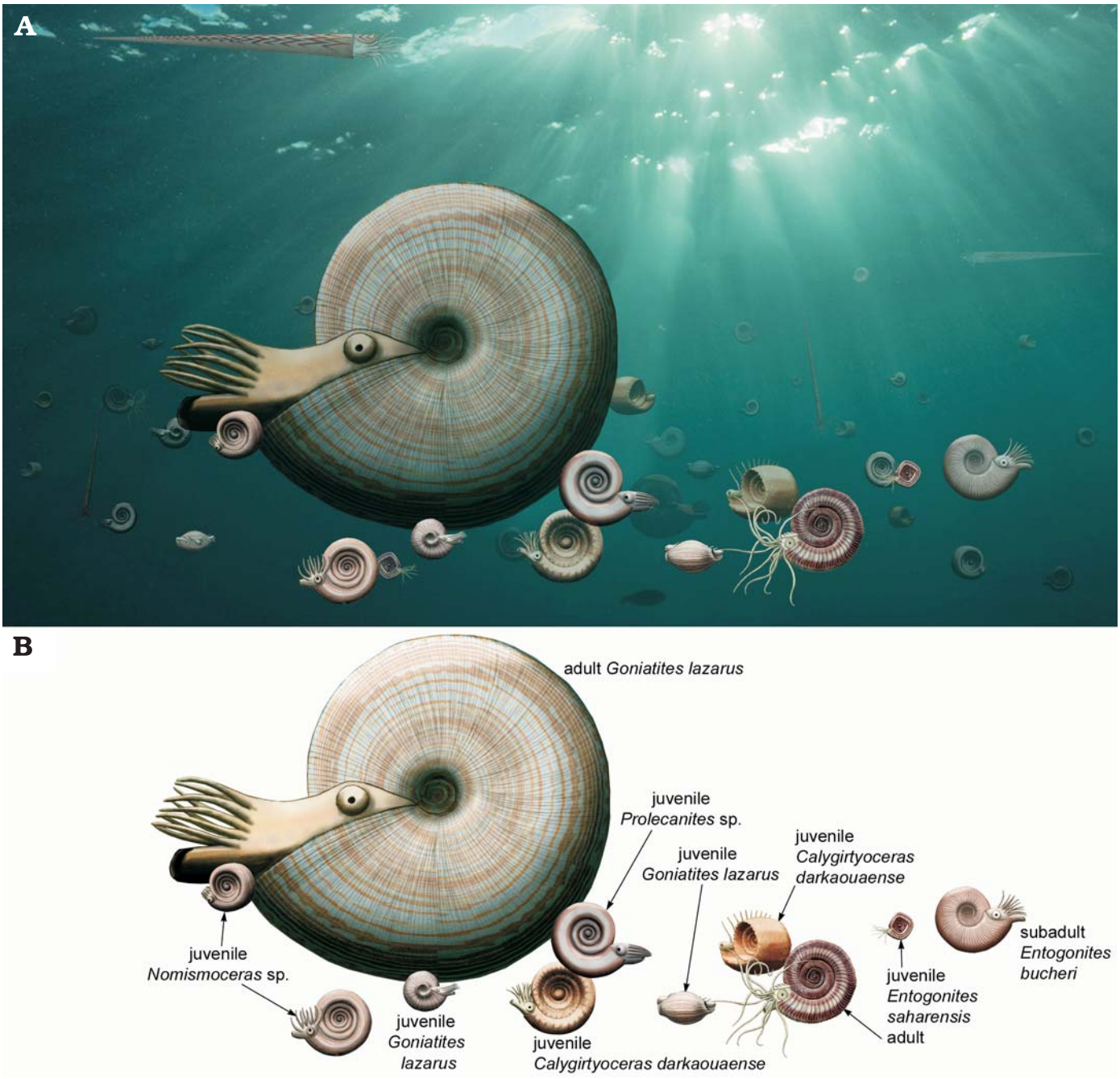

Fig. 9. Reconstruction of the ammonoid fauna from the early late Viséan,12 km SE of Dar Kaoua (Tafilalt, Morocco). **A**. Illustration of the habitat. **B**. The main components of the ammonoid assemblage.

Arnold 1983; Farnsworth and Niklas 1995; Alexander 1996) in the assumption that organisms have to be capable to deal with differing "tasks" that often lead to trade-offs in constructional morphology. Tendler et al. (2015) employed the theory of Pareto Optimality (named after the economist Vilfredo Pareto), which is based on the fields of economy and engineering (Sen 1993; Shoval et al. 2012; Tomoiagă et al. 2013). Accordingly, the morphology of most organism groups would fill a polygon or polyhedron in the morphospace. Data points of specimens that are positioned in a corner of the polygon or polyhedron would represent forms optimized to fulfil one task predominantly. Such forms were dubbed archetypes by Tendler et al. (2015). Consequently, if the shape of a body part of an animal lies between two or more archetype positions, we can assume a limited optimization for several tasks, linked with trade-offs with regard to the others.

In their study, Tendler et al. (2015) applied these ideas to a dataset of mostly adult ammonoids from all major groups. They discovered that ammonoids filled a space in the Raupian W-S-D morphospace (Raup 1966, 1967) that has a shape of a pyramid with five vertices (Fig. 8).

These vertices correspond with morphologies representing optimization for shell growth, hydrodynamics, economy of shell material, compactness + economy of shell material, and compactness + hydrodynamics (i.e., the last two represent combinations of two optimizations each). When applied to the early late Viséan ammonoids from Morocco, this would imply differing optimizations depending on ontogenetic stages:

- optimization only in juveniles: compactness + economy of shell material, compactness + hydrodynamics;
- optimization only in subadults and adults: shell growth, hydrodynamics;
- optimization in juvenile to adult stages: economy of shell material, compactness and hydrodynamics.

The absence of certain optimizations (independent of their functional interpretations) in certain ontogenetic stages might imply that juvenile conch morphologies had to be optimised partially to other tasks than adults. Interestingly, no juvenile of the *Entogonites* assemblage lies close to the vertices representing optimization for hydrodynamics and shell growth. These results coincide with findings of Jacobs (1992), Jacobs et al. (1994), and Jacobs and Chamberlain (1996), according to which the maximum sustainable swimming velocity depends strongly on size and shell morphology (reviewed in Naglik et al. 2015b). Additionally, large ammonoids with compressed shells (e.g., oxycones) could have reached the highest swimming velocities, while at small conch sizes, ammonoids with depressed shells (cadicones and spherocones) could swim faster (although still not fast).

Possibly, the congruence of this conclusion of Jacobs (1992) and Jacobs and Chamberlain (1996) with the distribution of juvenile morphologies versus adult morphologies is a coincidence. Also, Tendler et al. (2015) interpreted the conch morphologies with depressed shells as being optimised for compactness in combination with economy of shell material or hydrodynamics. It thus appears that such a compact conch morphology was advantageous for juvenile ammonoids of the Viséan. Compactness of the conch morphology has effects on swimming velocities and endurance by reducing drag, it has effects on reproduction through the reduction of embryonic shell size (De Baets et al. 2012) and on predation as individuals with similar width have a smaller diameter and thus might be harder to detect and catch. The hypothesis that juvenile conchs were optimized for tasks different from those of adults (or for similar tasks accomplished by different morphological means) finds a further, however weak, support in the fact that some of the slabs from the early late Viséan of the Tafilalt are covered by hundreds of juveniles of various ammonoid species (Figs. 6, 9): on the one hand, these associations could represent taphocoenosis of juveniles that shared habitats different from those of adults, but on the other hand, these assemblages might also have formed by size-sorting due to currents.

Conclusions

Early late Viséan sedimentary rocks of the Tafilalt (Morocco) contain well-preserved and diverse ammonoid assemblages, which enabled us to emend the diagnoses of the two ammonoid species *Goniatites lazarus* and *Calygirtyoceras darkaouaense*. Additionally, we describe the new species *Entogonites bucheri* sp. nov., which shares the tetragonal juvenile whorls with other representatives of the genus (although the tetragonal shape is only weakly developed in the new species).

The locality SE of Dar Kaoua in the Tafilalt occasionally yields blocks full of small, mostly juvenile specimens. These juveniles commonly exhibit shapes that never occur in adult ammonoids. Also, the morphologic change in the corresponding adults is often profound. We discuss this finding in the light of Pareto Optimality, which was applied to ammonoids by Tendler et al. (2015). In accordance with the results of studies by Jacobs (1992) and Jacobs and Chamberlain (1996), we suggest that the different morphospace occupations of juvenile and adult ammonoids might represent optimisations for compactness (and secondarily hydrodynamics) in the juveniles and for hydrodynamics (and secondarily shell growth) in adults. In future studies, it might be interesting to further compare juvenile and adult morphospace occupations and optima, their degree of overlap and separation as well as changes in overlap through time and phylogeny.

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