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Taxonomy, phylogeny and biostratigraphy of the upper Aptian–lower Albian ammonites of the Chott area, southern Central Tunisia.

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Abstract. Four sections were measured and studied in the uppermost Aptian and lower Albian of the Chott Basin (southern Central Tunisia), providing an abundant, bed-by-bed collected paleontological material. The ammonite succession allows precise correlations with the ammonite biozonation established in Central Tunisia. The phylogeny of knemiceratids and acanthohoplitinids of the Chott Basin is investigated and the alleged extreme variability of knemiceratids is questioned. Five new ammonite species are herein described: *Knemiceras sagetae* sp. nov., *Knemiceras lanceolatum* sp. nov., *Knemiceras multicoatum* sp. nov., *Knemiceras tunisiense* sp. nov., *Parengonoceras chottensis* sp. nov., highlighting the highly endemic character of the Chott Basin ammonite faunas.

Keywords. Paleontology, biostratigraphy, ammonites, Aptian, Albian, Tunisia.

1. Introduction

This work follows the recent stratigraphic and sedimentologic studies of the Chott Basin in southern Central Tunisia (Jaillard et al., 2022), which allowed to refine the age of the sedimentary pile of the Chott area, to highlight the sedimentary evolution of the area, and to propose new correlations with northern Central Tunisia. The first paleontological study of the Albian ammonites of the Chott area was carried out by Arnould-Saget (1956), and since that time, very few studies have been carried out (Ben Youssef et al., 1985; Abdallah et al., 1995; Moreno-Bedmar et al., 2008). The aim of the present paper is to focus on the paleontological study of the ammonite faunas collected bed by bed along the studied sections (Fig. 1), and on their biostratigraphical and paleoecological implications. The present revision of the upper Aptian/lower Albian ammonite faunas of the Chott Basin, leads us to confirm the highly endemic character of the engonoceratids and the close relationships between the Acanthohoplitinids of south Central and Central Tunisia.

2. Geological context and biostratigraphic correlations

In Cretaceous times, Tunisia belongs to the south-Tethyan passive margin. It comprises from North to South (Fig. 1A), (1) the deep marine north Tunisian Basin (present Tellian nappes), (2) an outer shelf domain (northern Tunisian Atlas), (3) a shallow, sporadically emergent area (southern Tunisian Atlas), (4) an E-W-trending, shallow marine trough (Chott Basin), and (5) the very shallow marine, frequently emergent Saharan platform (Southern Tunisia).

After a drastic sea level drop around the Aptian-Albian boundary, marine sedimentation resumed in early Albian times. The north Tunisian Basin then received a thick series of mainly argillaceous deposits (Burollet, 1956; Memmi, 1999). These grade southward into

limestone beds with thick marl intervals (Lower Fahdene Mb; Chiahoui et al., 2010; Jaillard et al., 2021), which taper southward. Southern Central Tunisia recorded subaerial to lacustrine deposits to the East (Kebar Fm; Trabelsi et al., 2010; 2021; Houla et al., 2017) and shallow marine limestone and marls to the West (Intermediate series; El Euch, 1993; Jaillard et al., 2021). The Chott Basin received shallow marine deposits, consisting first in clastic to evaporitic beds (Arguib and Foum el Argoub mbs of the Orbata Fm), then in carbonates (“Knemiceras beds” and Radhouane Mb of the Zebbag Fm). Farther South, the Radhouane Mb overlies mainly subaerial clastic deposits (Barale and Ouaja, 2001; Bodin et al., 2010; Fanti et al., 2012; Krimi et al., 2017).

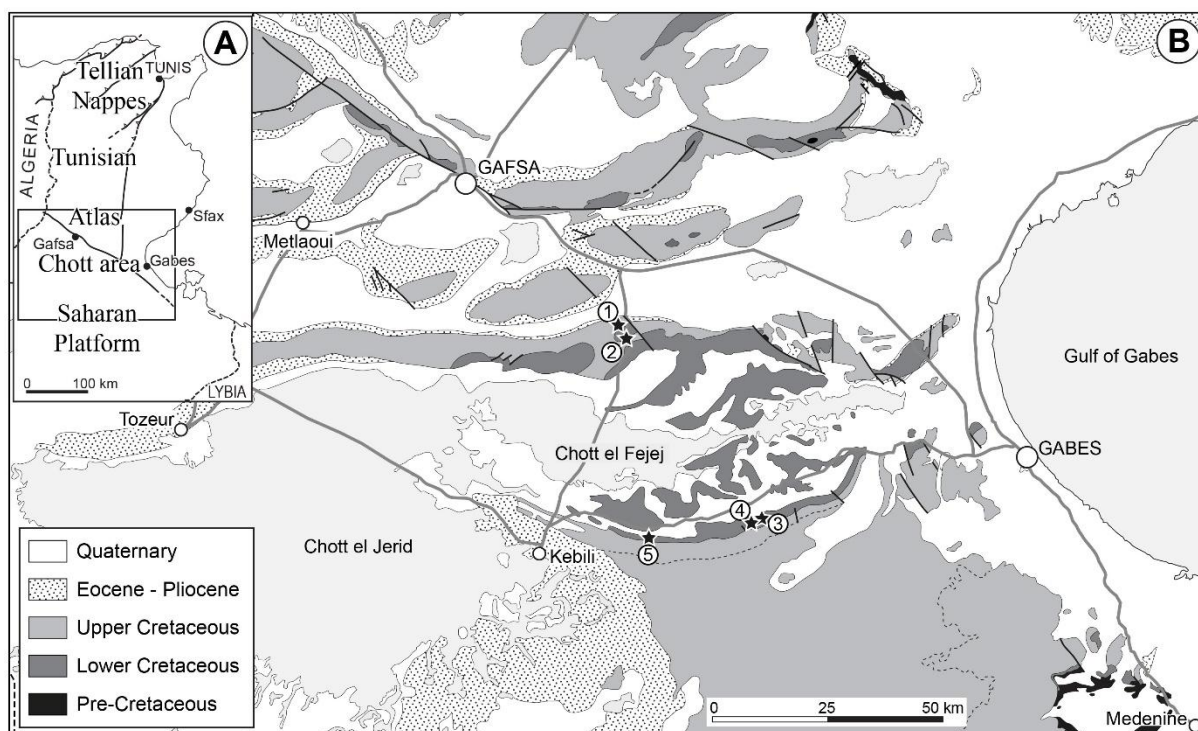


Figure 1. (A) Main structural domains of Tunisia, and location of Fig. 1B. (B) Map of the Chott area, with locations of the sections studied in this work. 1. Bir Oum Ali North, 2. Bir Oum Ali South, 3. Foum el Argoub, 4. Foum el Argoub West, 5. Rhadouane.

The Arguib and Foum el Argoub mbs were first ascribed to the lower Aptian (Abdallah et al., 1995), later revised as latest Aptian (Hfaied et al., 2013; Jaillard et al., 2022). The “Knemiceras beds” were considered late Albian in age (Arnould-Saget, 1956; Abdallah et al., 1995), now revised as lower Albian (Moreno-Bedmar et al., 2008; Jaillard et al., 2022). Consequently, the Radhouane Mb is presently ascribed to the late lower Albian, with a possible extension to the earliest middle Albian (Jaillard et al., 2022).

The taxonomic study of the engonoceratids of the Chotts, as carried out by Arnould-Saget (1956), was based on 59 specimens that had been collected by geologists of the Petroleum Research Society of Tunisia (SEREPT). This approach was purely morphological, and did not take account of the stratigraphic position of the material. Since that time, very few studies have been carried out (Abdallah et al., 1995; Moreno-Bedmar et al., 2008). Before 2008, the engonoceratids faunas of southern Central Tunisia were considered as belonging to the upper Albian (Arnould-Saget, 1956; Abdallah et al., 1995). Moreno-Bedmar et al. (2008) gave an upper lower Albian to middle Albian age to these faunas. After Latil (2011) and the discovery of *Parengonoceras bussoni* Collignon, 1965 below the top of the lower Albian in Jebel El

Hamra (Central Tunisia), it became clear that the age of the ‘*Knemiceras* beds’ of south Central Tunisia had to be revised. Jaillard et al (2022) unequivocally showed that the ‘*Knemiceras* beds’ of the authors was lower Albian in age.

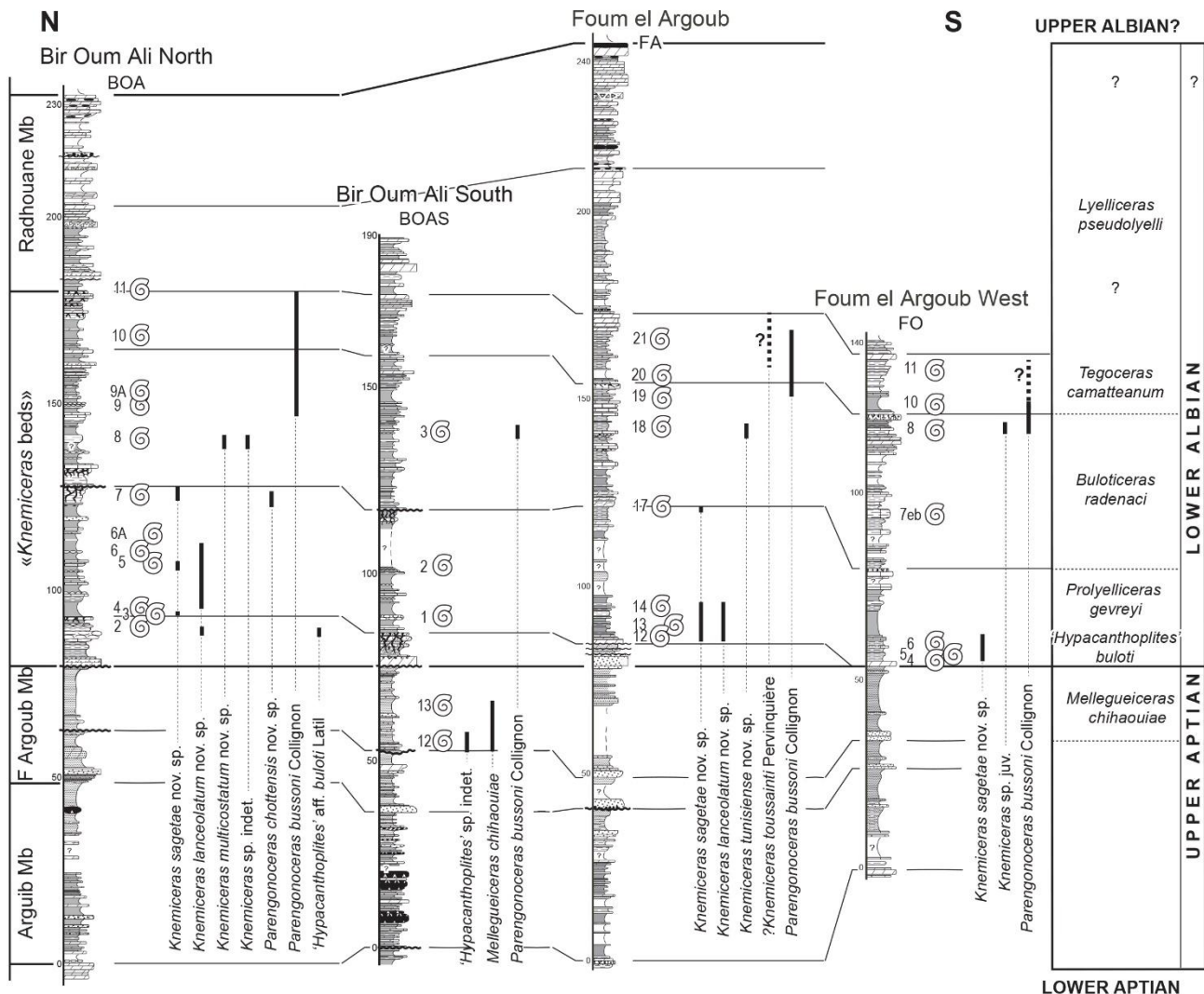


Figure 2. The measured sections of the Chott area, showing the lithological sequence and the ammonite faunas collected during the present study.

The discovery of acanthohoplitinids in the upper Aptian to basal Albian of the Chott Basin is much more recent. The first figured specimen (Abdallah et al., 1995, fig. 22.6), misidentified as *Deshayesites callidiscus* Casey, led the authors to give a lower Aptian age to the upper member of the Orbata Formation at Biroum Ali and Jebel Naïmia. More recent investigations (Hfaiedh et al., 2013; Jaillard et al., 2022), have showed that the acanthohoplitinid faunas are closely related to the faunas of Central Tunisia and indicate an upper Aptian-basal Albian age.

The highly endemic character of the ammonite faunas of the Chott Basin does not facilitate the stratigraphic correlations with Central Tunisia. However, the presence of *Mellegueiceras chihouiaie* Latil, 2011 and '*Hypacanthoplites*' aff. '*H.*' *buloti* Latil, 2011 in the lower part of the series, and *Parengonoceras bussoni* Collignon, 1965 in the upper part of fossiliferous beds, allowed to precise the biostratigraphic correlations (Jaillard et al., 2022), herein modified according to paleontological data (Fig. 2).

3. Systematic paleontology

Dimensions are given in millimetres: D = diameter; Wb = whorl breadth; Wh = whorl height; U = umbilicus; v = width of the venter; dc = distance between two successive ventrolateral tubercles; dc/Wh = ventrolateral tubercles density; v = width of the venter.

Figures in parentheses are dimensions as a percentage of the diameter.

The repositories of specimens are:

UJF-ID: ISTerre, Université of Grenoble Alpes, ex Institut Dolomieu collections.

MNHN: Laboratoire de Paléontologie of the Muséum National d'Histoire Naturelle, Paris.

UCBL-FSL : Université Claude Bernard, Lyon.

Order: Ammonoidea Zittel, 1884

Suborder: Ammonitina Hyatt, 1889

Superfamily Engonoceratoidea Hyatt, 1900

Family Knemiceratidae Hyatt, 1903

Genus *Knemiceras* Böhm, 1898

[=*Cnemidoceras* Haug, 1900, p. 24 (nomen vanum);

=*Cnemioceras* Haug, 1900, p. 85 (nomen vanum);

=*Knemoceras* Krause, 1902, p. 7 (nomen vanum);

=*Omaimaiceras* Mahmoud in Moret & Mahmoud, 1955, p. 271 footnote (nomen nudum);

=*Iranoknemiceras* Collignon, 1981 (p. 258, type species *Knemiceras uhligi* (Choffat) var. *douvillei* Basse, 1940, p. 431, by original designation]

Type species. *Ammonites syriacus* Buch, 1850, p. 20, by the original designation of Böhm, 1898, p. 200. The genus *Knemiceras* is here restricted to the morphologies with opposite ventrolateral tubercles.

Knemiceras sagetae nov. sp.

Figs 3A-C, 4A-G, 5A-D, 6A-E, 7A-I, 8A, B, 9A-E, 10A-C, 11A-C, appendices 2, 3, 4

1956. *Knemiceras aegyptiacum* Mahmoud; Arnould-Saget, p. 7 pars, pl. 1, fig. 1, 4 only.

1956. *Knemiceras syriacum* (von Buch); Arnould-Saget, p. 11, pl. 1, fig. 3, ?pl. 10, fig. 4.

1956. *Knemiceras dubertreti* Basse; Arnould-Saget, p. 10, pl. 1, fig. 2; pl. 3, fig. 2.

1956. *Knemiceras douvillei* Basse; Arnould-Saget, p. 9, pl. 2, fig. 1, 2; pl. 9, fig. 2.

? 1956. *Knemiceras gracile* H. Douvillé; Arnould-Saget, p. 16, pl. 3, fig. 3, 4. (formes usées?)

1956. *Knemiceras* sp.; Arnould-Saget, p. 21, pl. 6, 7, 11.

1956. *Knemiceras compressum* Hyatt; Arnould-Saget, p. 15, pl. 9, fig. 1.

?1995. *Knemiceras compressum* Hyatt; Abdallah et al., fig. 22.5.

?1995. *Knemiceras syriacum* (von Buch); Abdallah et al., fig. 22.3, 4.

2008. *Knemiceras* cf. *compressum* Hyatt; Moreno-Bedmar et al., fig. 1.

2008. *Parengonoceras* sp. 1; Moreno-Bedmar et al., fig. 1.

2022. *Knemiceras* sp.1, Jaillard et al., p. 16, Fig. 13G, H.

2022. *Knemiceras* sp.2; Jaillard et al., p. 16, Fig. 14A-C.

Zoobank identification number. urn:lsid:zoobank.org:act:AA01E92A-6581-40DE129A7C5-6ACBEA78404F

Derivatio nominis. This species is dedicated to Suzanne Arnould-Saget (1920-1989) who first figured *Knemiceras* with two rows of periumbilical tubercles (Appendix 1).

Holotype. UJF-ID.15105 from bed BOA.5 (Fig. 3, Appendix 2).

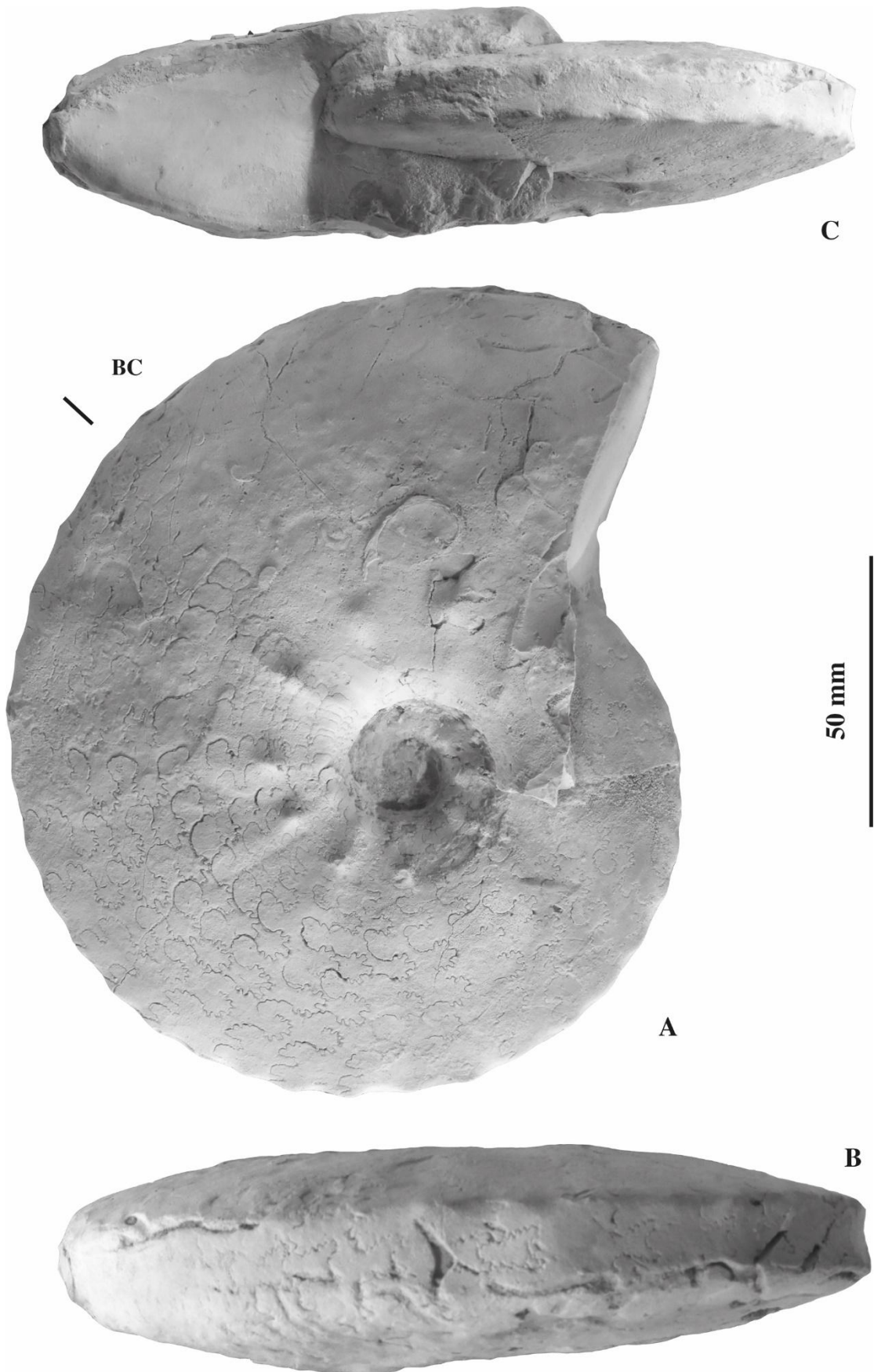


Figure 3. (A-C) *Knemiceras sagetae* nov. sp., UJF-ID.15105, the holotype, morphotype 1 from BOA.5, *Prolyelliceras gevreyi* Zone, lower Albian. Scale bar is 50 mm

Diagnosis. Polymorphic species characterized by a tendency to develop two rows of periumbilical tubercles at some stage of the growth, the external tubercles being stronger than the internal ones

Description of the holotype.

UJF-ID.15105: D. 140.0 – Wh: 73 (0.52) – Wb: 40 (0.29) – U: 19.5 (0.14) – Wb/Wh: 0.55 – dc/Wh; 0.16 – v/Wh: 0.22

UJF-ID.15105, from BOA.5, is an almost complete adult specimen, about 200 mm in diameter, comprising a 200° sector of body chamber, preserved as a calcareous internal mold (Appendix 2). It has a discoidal, involute coiling ($U/D = 0.14$), with narrow, deep umbilicus. The whorl section is compressed ($Wb/Wh = 0.55$), subtrapezoidal, with a maximum of width at the inner third of the flanks. The inner whorls are unknown. On the last whorl of the phragmocone, up to a diameter of 140 mm, the umbilical wall is deep and feebly inclined, the umbilical shoulder is broadly rounded, feebly convex flanks converge to a narrow, flat venter ($v/Wh = 0.22$). There are ten feeble bullae on the umbilical shoulder, followed by stronger, more external tubercles. The more internal tubercles give rise to inconspicuous, coarse primary ribs that are visible on the inner third of the flanks. There is no visible intercalatory rib. There are numerous, small, spirally elongated ventrolateral clavi (dc/Wh at about 0.14) that are opposite on the venter. On the inner part of the body chamber, the venter becomes feebly convex, the ventrolateral clavi tend to disappear and the two rows of periumbilical tubercles are still visible. The outer part of the body chamber seems to be smooth. The suture line is weathered, showing a broad lateral lobe with frilled lobes and entire to only feebly indented saddles (Fig. 3A).

Material. 104 specimens from BOA.3, 5 and 7; FA.12-14 and 17; FO.5 and 6.

As herein understood, *K. sagetae* comprises three morphotypes:

- Morphotype 1 (more than 50%): the typical large-sized ammonite, with a compressed whorl section, high ventrolateral tubercles density, numerous periumbilical tubercles, two rows of periumbilical tubercles on the last whorl of the phragmocone and the inner part of the body chamber;
- Morphotype 2 (about 40%): small-sized ammonite, with a more inflated whorl section, low ventrolateral tubercles density, few, strong, unique, periumbilical tubercles on the phragmocone, increasing in number and radially elongated on the inner part of the body chamber;
- Morphotype 3 (6%): medium sized ammonite, with intermediate characters between morphotypes 1 and 2.

Morphotype 1. Fifty-four specimens preserved as more or less weathered calcareous internal molds (Figs 3A-C, 4A-G, 5D, Appendices 2A, 3A, 4A, B) (Fig. 13 in Jaillard et al., 2022).

1. UJF-ID.15158: D. 60.0 – Wh: 33 (0.55) – Wb: 17 (0.28) – U: 8 (0.13) – Wb/Wh: 0.52 – dc/Wh: ? – v/ Wh: ?
2. UJF-ID.15159: D. 93.0 – Wh: 49 (0.53) – Wb: 26 (0.28) – U: ? (?) – Wb/Wh: 0.53 – dc/Wh: ? – v/ Wh: 0.14
3. UJF-ID.15160: D. 90.0 – Wh: 48 (0.53) – Wb: 22 (0.24) – U: 11 (0.12) – Wb/Wh: 0.46 – dc/Wh: ? – v/ Wh: 0.13
4. UJF-ID.15161: D. 170.0 – Wh: 85 (0.50) – Wb: 40 (0.24) – U: 25 (0.15) – Wb/Wh: 0.47 – dc/Wh: ? – v/ Wh: 0.22

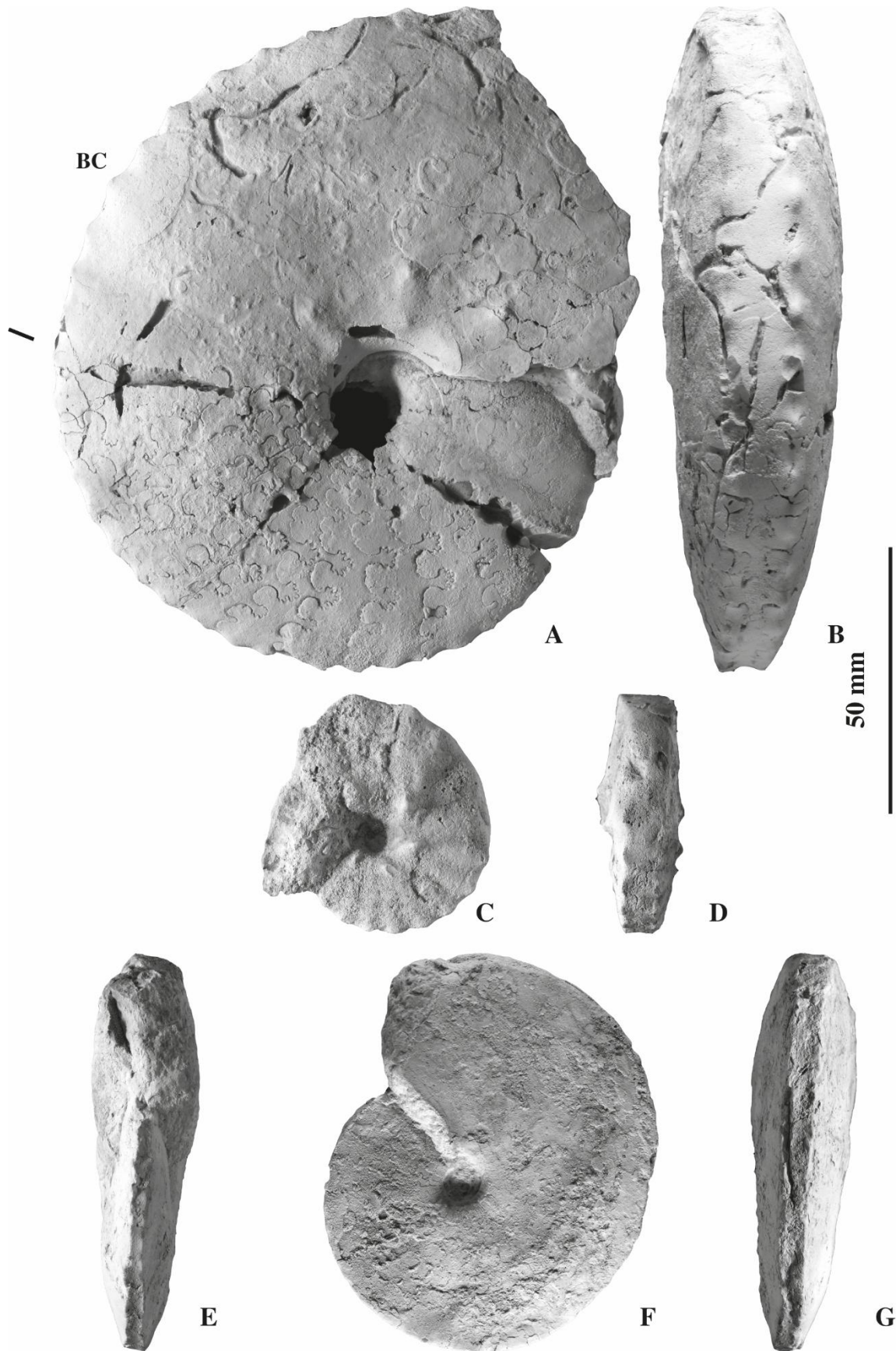


Figure 4. (A-G) *Knemiceras sagetae* nov. sp., Prolyelliceras gevreyi Zone, lower Albian; (A, B) UJF-ID.15190, morphotype 1 from BOA.5; (C, D) UJF-ID.15194, morphotype 1, from BOA.5; (E-G) UJF-ID.15191, morphotype 1, from BOA.5. Scale bar is 50 mm

5. UJF-ID.15192: D. 48.0 – Wh: 24 (0.50) – Wb: 13 (0.27) – U: 8 (0.17) – Wb/Wh: 0.54 – dc/Wh: 0.27 – v/H: 0.27
6. UJF-ID.15190: D. 125. – Wh: 64 (0.51) – Wb: 34 (0.27) – U: 17.5 (0.14) – Wb/Wh: 0.53 – dc/Wh: 0.14 – v/H: 0.17
7. UJF-ID.15105: D. 140.0 – Wh: 73 (0.52) – Wb: 40 (0.29) – U: 20 (0.14) – Wb/Wh: 0.55 – dc/Wh: ? – v/H: 0.22
8. UJF-ID.15191: D. 74.0 – Wh: 38 (0.51) – Wb: 18 (0.24) – U: 8 (0.11) – Wb/Wh: 0.47 – dc/Wh: ? – v/H: 0.21
9. UJF-ID.15195: D. 190.0 – Wh: 91 (0.48) – Wb: 50 (0.26) – U: 32 (0.17) – Wb/Wh: 0.55 – dc/Wh: ? – v/H: 0.19
10. UJF-ID.15222: D. 76.0 – Wh: 40 (0.53) – Wb: 22 (0.29) – U: 10.5 (0.14) – Wb/Wh: 0.50 – dc/Wh: ? – v/H: 0.15
11. UJF-ID.15223: D. 175.0 – Wh: 85 (0.49) – Wb: 48 (0.27) – U: 32 (0.18) – Wb/Wh: 0.56 – dc/Wh: ? – v/H: 0.36

The coiling is discoidal. The phragmocone, up to about 100-110 mm in diameter, has a compressed, subtrapezoidal whorl section, with a maximum of width at the inner third of the flanks (Wb/Wh ranging from 0.46 to 0.54). The umbilic is low and narrow (U/D between 0.12 and 0.17), the umbilical wall is low and smooth, the umbilical shoulder is convex. The flanks are feebly convex, converging to a narrow, flat venter (v/Wh between 0.13 and 0.27). The inner whorls, below a diameter of 20 mm are poorly known but the flanks seem to be smooth. Between a diameter of 20 and 80 mm, when the molds are well-preserved, there are 8-10 tiny periumbilical tubercles per whorl, and 8-10 well marked, small tubercles on the inner part of the flanks, giving rise to inconspicuous, radial ribs, which are only visible on the inner third of the flanks (Fig. 4A-D). Some juvenile specimens have no periumbilical tubercles (Fig. 4E-G) or feeble ones (Fig. 5D). There are numerous ventrolateral clavi, which are opposite on the venter. The ventrolateral tubercles density is high, at about 0.27. The ribs tend to cross the venter on the juvenile, up to a diameter of 20-25 mm. The venter is smooth. On the inner half of the body chamber, the periumbilical tubercles are persisting, the ventrolateral clavi disappears and the venter becomes slightly convex and slightly broader (v/Wh ranging from 0.13 to 0.36). When present, the outer half of the body chamber is weathered and seems to be smooth with a slightly more convex venter (Appendices 3, 4). The adult estimated diameter is about 200 mm. The suture lines are always weathered, showing a broad E, frilled lobes and entire or feebly indented, broad saddles.

Morphotype 2. Forty specimens preserved as more or less weathered calcareous internal molds (Figs 6A-E, 7A-I, 8A, B).

1. UJF-ID.15152: D. 52.0 – Wh: 26 (0.50) – Wb: 21 (0.40) – U: 9 (0.18) – Wb/Wh: 0.80 – dc/Wh: 0.35 – v/ Wh: 0.42
2. UJF-216 ID.15153: D. 62.0 – Wh: 32 (0.52) – Wb: 31 (0.50) – U: 9 (0.15) – Wb/Wh: 0.97 – dc/Wh: 0.31 – v/ Wh: 0.44
3. UJF-ID.15154: D. 76.0 – Wh: 37 (0.49) – Wb: 34 (0.48) – U: 14 (0.18) – Wb/Wh: 0.92 – dc/Wh: 0.46 – v/ Wh: 0.43
4. UJF-ID.15155: D. 87.0 – Wh: 43 (0.49) – Wb: 31 (0.37) – U: 15 (0.17) – Wb/Wh: 0.72 – dc/Wh: 0.14 – v/ Wh: 0.39

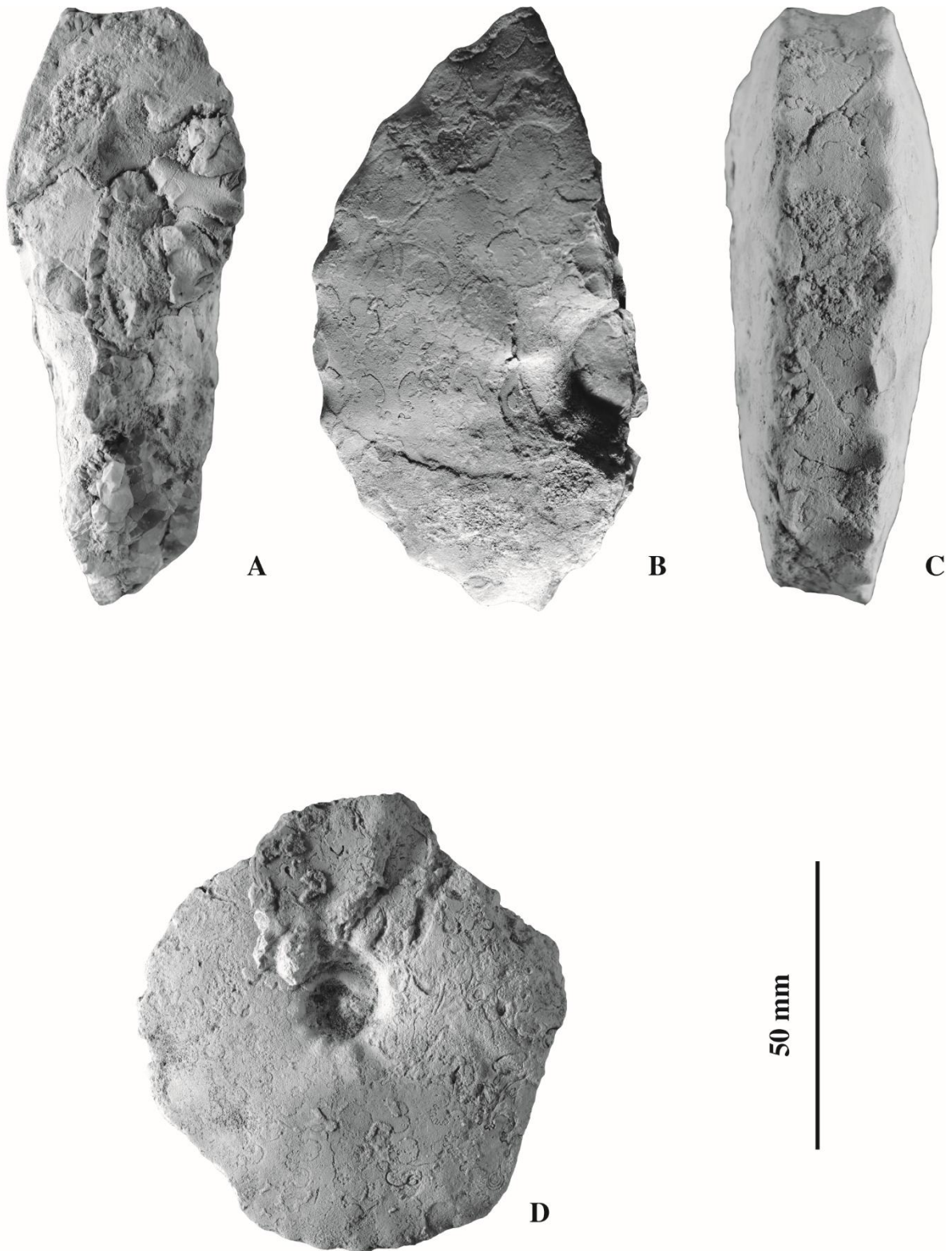


Figure 5. (A-D) *Knemiceras sagetae* nov. sp., *Polyelliceras gevreyi* Zone, lower Albian; (A-C) UJF-ID.15183, morphotype 3, from BOA.5; (D) UJF-ID.15222, morphotype 1, from FA.13. Scale bar is 50 mm

5. UJF-ID.15156: D. 90.0 – Wh: 45 (0.50) – Wb: ? (?) – U: 19 (0.21) – Wb/Wh: ? - dc/Wh: 0.20 – v/ Wh: ?

6. UJF-ID.15174: D. 84.0 – Wh: 38 (0.45) – Wb: 31 (0.37) – U: 19 (0.23) – Wb/Wh: 0.82 – dc/Wh: 0.33 – v/ Wh: 0.39
7. UJF-ID.15175: D. 95.0 – Wh: 44 (0.46) – Wb: 33 (0.38) – U: 22 (0.19) – Wb/Wh: 0.75 – dc/Wh: ? – v/ Wh: 0.50
8. UJF-ID.15176: D. 69.0 – Wh: 33 (0.48) – Wb: 30 (0.43) – U: 14 (0.20) – Wb/Wh: 0.91 – dc/Wh: 0.42 – v/ Wh: 0.42
9. UJF-ID.15176: D. 98.0 – Wh: 50 (0.51) – Wb: ? (?) – U: 19 (0.19) – Wb/Wh: ? – dc/Wh: ? – v/ Wh: 0.42
10. UJF-ID.15177: D. 105.0 – Wh: 52 (0.50) – Wb: 37 (0.35) – U: 14 (0.13) – Wb/Wh: 0.71 – dc/Wh: ? – v/ Wh: 0.44
11. UJF-ID.15180: D. 94.0 – Wh: 44 (0.47) – Wb: 38 (0.40) – U: 18 (0.19) – Wb/Wh: 0.86 – dc/Wh: ? – v/Wh: 0.45
12. UJF-ID.15104: D. 90.0 – Wh: 43 (0.48) – Wb: 39 (0.43) – U: 19 (0.21) – Wb/Wh: 0.91 – dc/Wh: 0.30 – v/ Wh: 0.42
13. UJF-ID.15203: D. 40.0 – Wh: 20.5 (0.51) – Wb: 15 (0.38) – U: 6 (0.15) – Wb/Wh: 0.73 – dc/Wh: 0.29 – v/H: 0.44
14. UJF-240 ID.15204: D. 70.0 – Wh: 35 (0.50) – Wb: 27 (0.39) – U: 12 (0.17) – Wb/Wh: 0.77 – dc/Wh: 0.37 – v/H: 0.37
15. UJF-ID.15205: D. 75.0 – Wh: 37 (0.49) – Wb: 34 (0.45) – U: 14 (0.18) – Wb/Wh: 0.92 – dc/Wh: 0.57 – v/H: 0.51
16. UJF-ID.15206: D. 150.0 – Wh: 70 (0.47) – Wb: 52 (0.35) – U: 32 (0.21) – Wb/Wh: 0.74 – dc/Wh: ? – v/H: 0.37

The coiling is discoidal. The phragmocone, up to about 70-80 mm in diameter, has an inflated, subtriangular to subquadratic whorl section, with a maximum of width at the inner third of the flanks (Wb/Wh ranging from 0.72 to 0.97). The umbilic is almost funnel shaped, deep and narrow (U/D between 0.15 and 0.23), the umbilical wall is deep and smooth, the umbilical shoulder is convex. The flanks are feebly convex, converging to a broad, flat venter (v/Wh between 0.37 and 0.51). The inner whorls, below a diameter of 20 mm are poorly known. Between a diameter of 20 and 80 mm, there are 6-7 strong periumbilical tubercles per whorl on the umbilical shoulder, giving rise to generally two feeble, radial to slightly prorsiradiate, broad, coarse ribs, which end with a ventrolateral clavus (Figs 6A, B, 7A-G, 8A, B). Only one specimen, UJF-ID.15156, has seven tubercles on the last whorl of the phragmocone. The ventrolateral tubercles density (dc/Wh) is predominantly low but shows some variation, ranging from 0.27 to 0.57. The ribs tend to cross the venter on the juvenile, up to a diameter of 20-25 mm. Beyond a diameter of 25-30 mm, the venter is smooth. On the inner half of the body chamber, the periumbilical tubercles are more numerous, but they are feebler and radially elongated (Figs 6D, E, 7H, I). Coarse and weak ribs are visible only on the inner half of the flanks, and the ventrolateral tubercles density is higher, with dc/Wh ranging from 0.14 to 0.30. When present, the outer half of the body chamber is weathered and seems to be smooth with a slightly convex venter. The adult estimated diameter is 150-170 mm. The suture lines are always weathered, showing a broad E, frilled lobes and entire or feebly indented saddles.

Morphotype 3. Six specimens preserved as more or less weathered calcareous internal molds (Figs 5A-C, 9A-E, 10A-C, 11A-C).

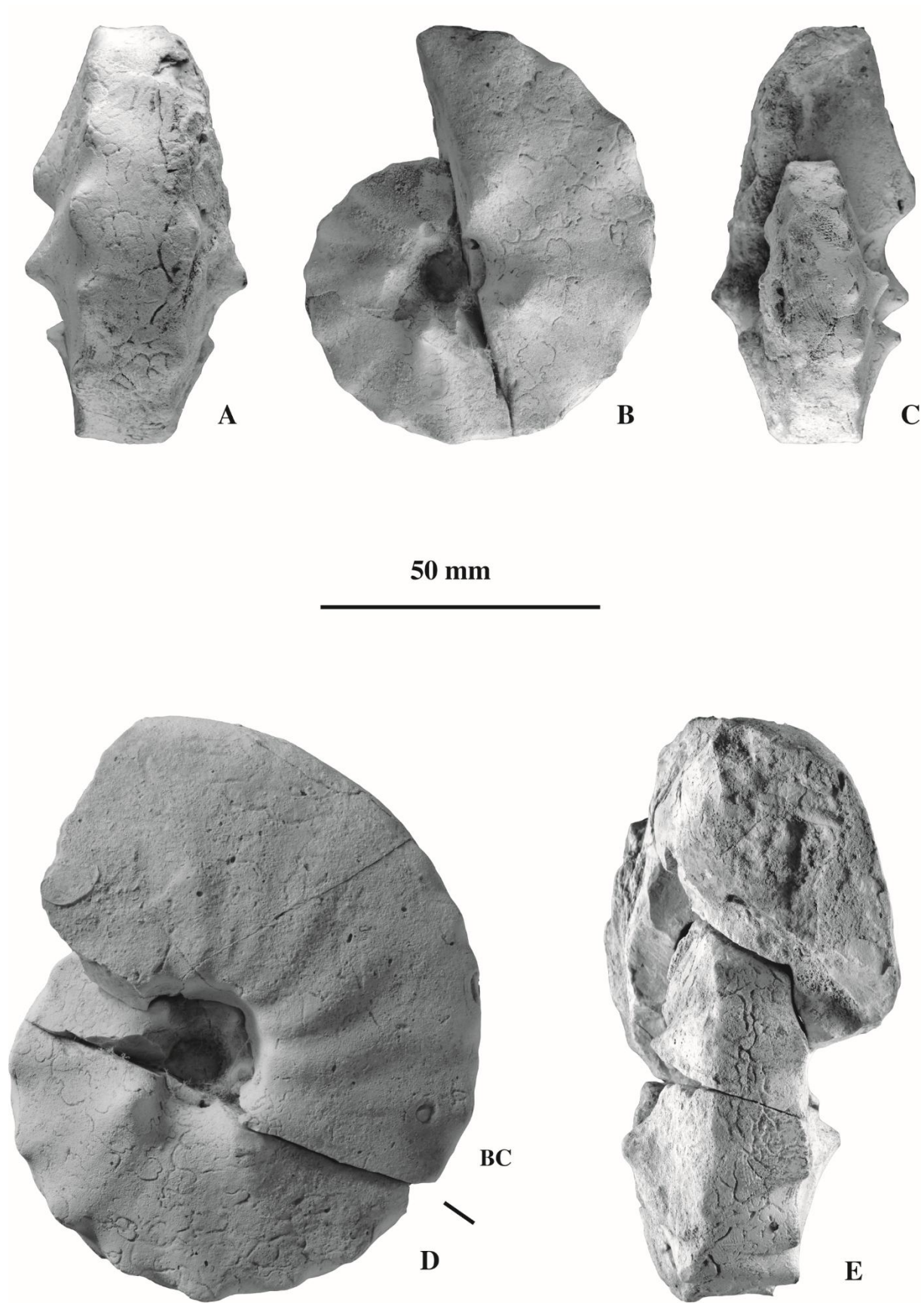


Figure 6. (A-E) *Knemiceras sagetae* nov. sp., *Polyelliceras gevreyi* Zone, lower Albian; UJF1270 ID.15176, morphotype 2, from BOA.5. Scale bar is 50 mm

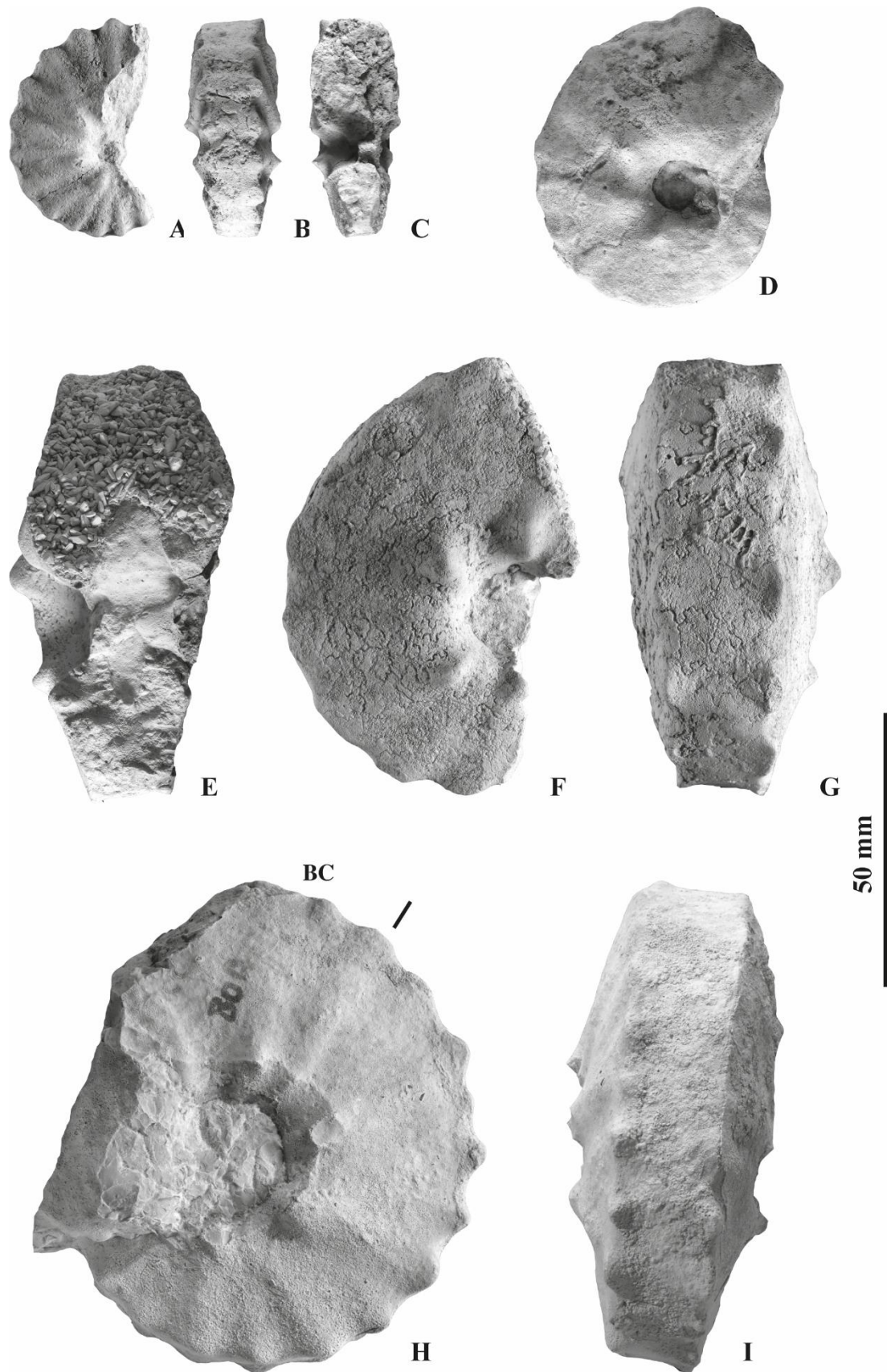


Figure 7. (A-I) *Knemiceras sagetae* nov. sp, *Prolyelliceras gevreyi* Zone, lower Albian.; (A-C) UJF-ID.15203, morphotype 2, from FA.13; (D) UJF-ID.15152, morphotype 2, from BOA.3; (E1273 G) UJF-ID.15205, morphotype 2, from FA.13; (H, I) UJF-ID.15104, morphotype 2, from BOA.5. Scale bar is 50 mm

1. UJF-ID.15178: D. 136.0 – Wh: 70 (0.51) – Wb: 43 (0.31) – U: 21 (0.15) – Wb/Wh: 0.61 – dc/Wh: 0.16 – v/ Wh: 0.25
2. UJF-ID.15179: D. 81.0 – Wh: 41 (0.51) – Wb: 29 (0.36) – U: 15 (0.19) – Wb/Wh: 0.71 – dc/Wh: 0.26 – v/ Wh: 0.28
3. UJF-ID.15194: D. 43.0 – Wh: 21 (0.49) – Wb: 12.5 (0.29) – U: 7 (0.16) – Wb/Wh: 0.60 – dc/Wh: 0.57 – v/H: 0.43
4. UJF-ID.15184: D. 125.0 – Wh: 65 (0.52) – Wb: 44 (0.35) – U: 18.5 (0.15) – Wb/Wh: 0.68 – dc/Wh: ? – v/H: 0.29
5. UJF-ID.15221: D. 53.0 – Wh: 27 (0.51) – Wb: 17 (0.32) – U: 7 (0.13) – Wb/Wh: 0.63 – dc/Wh: 0.37 – v/H: 0.26
6. UJF-ID.15245: D. 125.0 – Wh: 66 (0.53) – Wb: 45 (0.36) – U: 17 (0.14) – Wb/Wh: 0.68 – dc/Wh: ? – v/H: 0.33

The coiling is discoidal. The phragmocone, up to about 90 mm in diameter, has a moderately inflated, subtriangular to subquadratic whorl section, with a maximum of width at the inner third of the flanks (Wb/Wh ranging from 0.60 to 0.71). The umbilic is almost funnel shaped, deep and narrow (U/D between 0.13 and 0.19), the umbilical wall is deep and smooth, the umbilical shoulder is convex. The flanks are feebly convex, converging to a moderately broad, flat venter (v/Wh between 0.25 and 0.43). The inner whorls, below a diameter of 20 mm are not known. Between a diameter of 20 and 80 mm, there are 6-7 strong periumbilical tubercles per whorl on the umbilical shoulder, giving rise to generally two radial to slightly prorsiradiate, broad, coarse ribs, which end with a ventrolateral clavus (Figs 5A-C, 9A-C). The ventrolateral tubercles density (dc/Wh) is predominantly low but shows some variation, ranging from 0.26 to 0.57 (Figs 5A-C, 9A-E). On the inner half of the body chamber, the periumbilical tubercles are more numerous, and there are two rows of periumbilical tubercles (Figs 9D, 10B, 11B). Coarse and weak ribs are visible only on the inner half of the flanks, and the ventrolateral tubercles density is higher, with dc/Wh at about 0.16. When present, the outer half of the body chamber is weathered and seems to be smooth with a slightly convex venter. The adult estimated diameter is 180 mm.

Remarks. A preliminary paleontological approach led us to consider morphotypes 1 and 2 as two distinct species (Jaillard et al., 2022). As a result of further investigations, *Knemiceras sagetae* is herein interpreted as a polymorphic complex with two distinct morphotypes connected one to the other by very few intermediate morphologies (6%).

There is no evidence of sexual dimorphism, and it should be noted, based on morphology and ontogeny, that morphotype 3 could be interpreted as a microconch of morphotype 1 or as a macroconch of morphotype 2.

The specimens described and figured by Arnould-Saget (1956) as *Knemiceras dubertreti* Basse (p. 10, pl. 1, fig. 2; pl. 3, fig. 2), *Knemiceras compressum* Hyatt (p. 15, pl. 9, fig. 1), *Knemiceras* sp. (p. 21, pl. 6, 7, 11), the specimen figured by Moreno-Bedmar et al. (2008, fig. 1) as *Parengonoceras* sp. 1, and the specimen described and figured by Jaillard et al. (2022, p. 16, Fig. 14A-C) as *Knemiceras* sp. 2, are herein assigned to the morphotype 1 of *Knemiceras sagetae*. The poorly preserved juvenile specimens figured by Arnould-Saget (1956, p. 16, pl. 3, fig. 3, 4) as *Knemiceras gracile* H. Douvillé, the fragment figured by Abdallah et al. (1995, fig. 22.4 only) as *Knemiceras syriacum* (von Buch), and the specimen figured by Abdallah et al. (1995, fig. 22.5) as *Knemiceras compressum* Hyatt, are doubtfully assigned to *Knemiceras sagetae*.

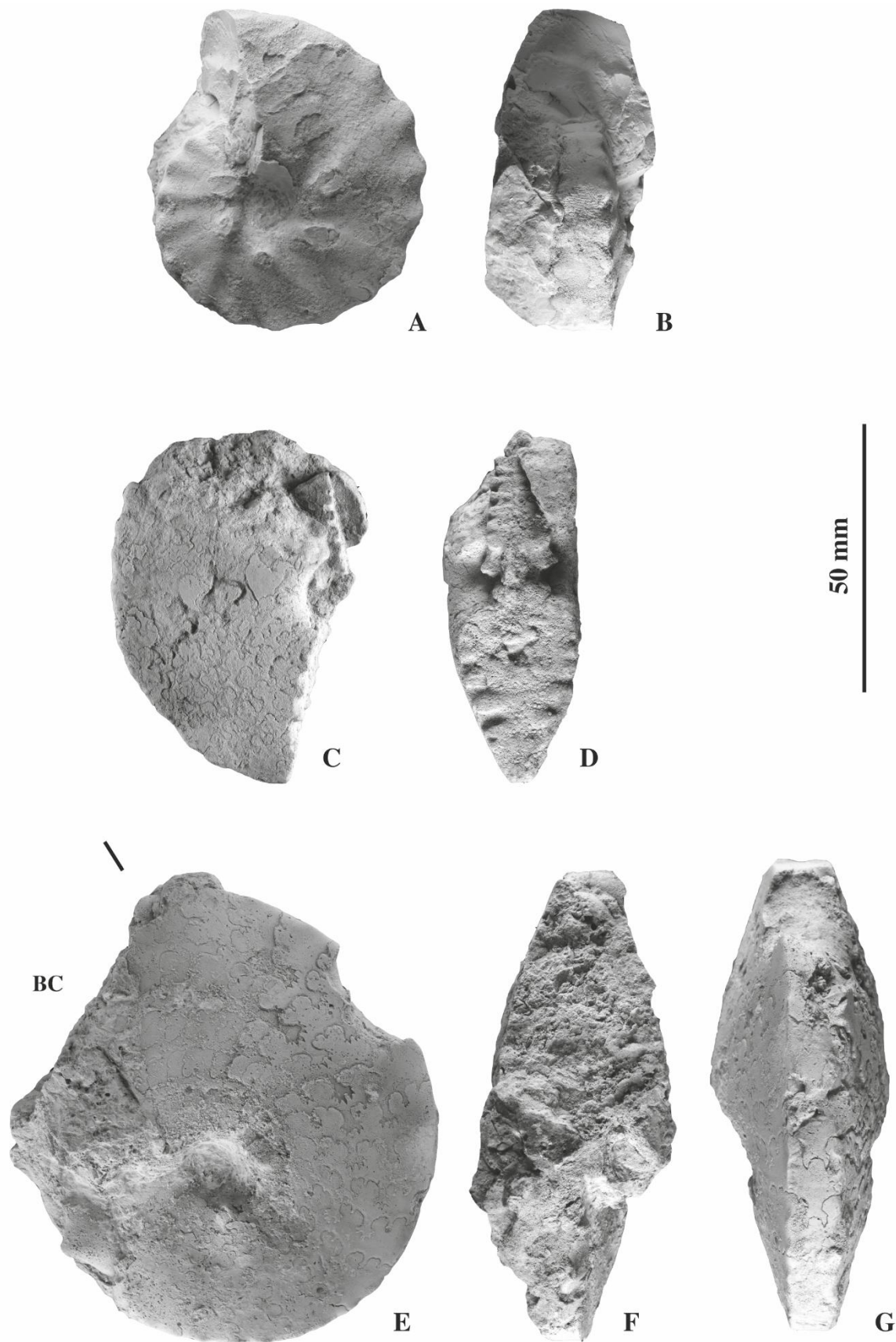


Figure 8. (A, B) *Knemiceras sagetae* nov. sp., *Polyelliceras gevreyi* Zone, lower Albian, UJF-ID.15153, morphotype 2, from BOA.3; (C-G) *Knemiceras lanceolatum* nov. sp., *Polyelliceras gevreyi* Zone, lower Albian; (C, D) UJF-ID.15124, from bed BOA.4; (E-G) the holotype UJF-ID.15127, from bed BOA.6. Scale bar is 50 mm

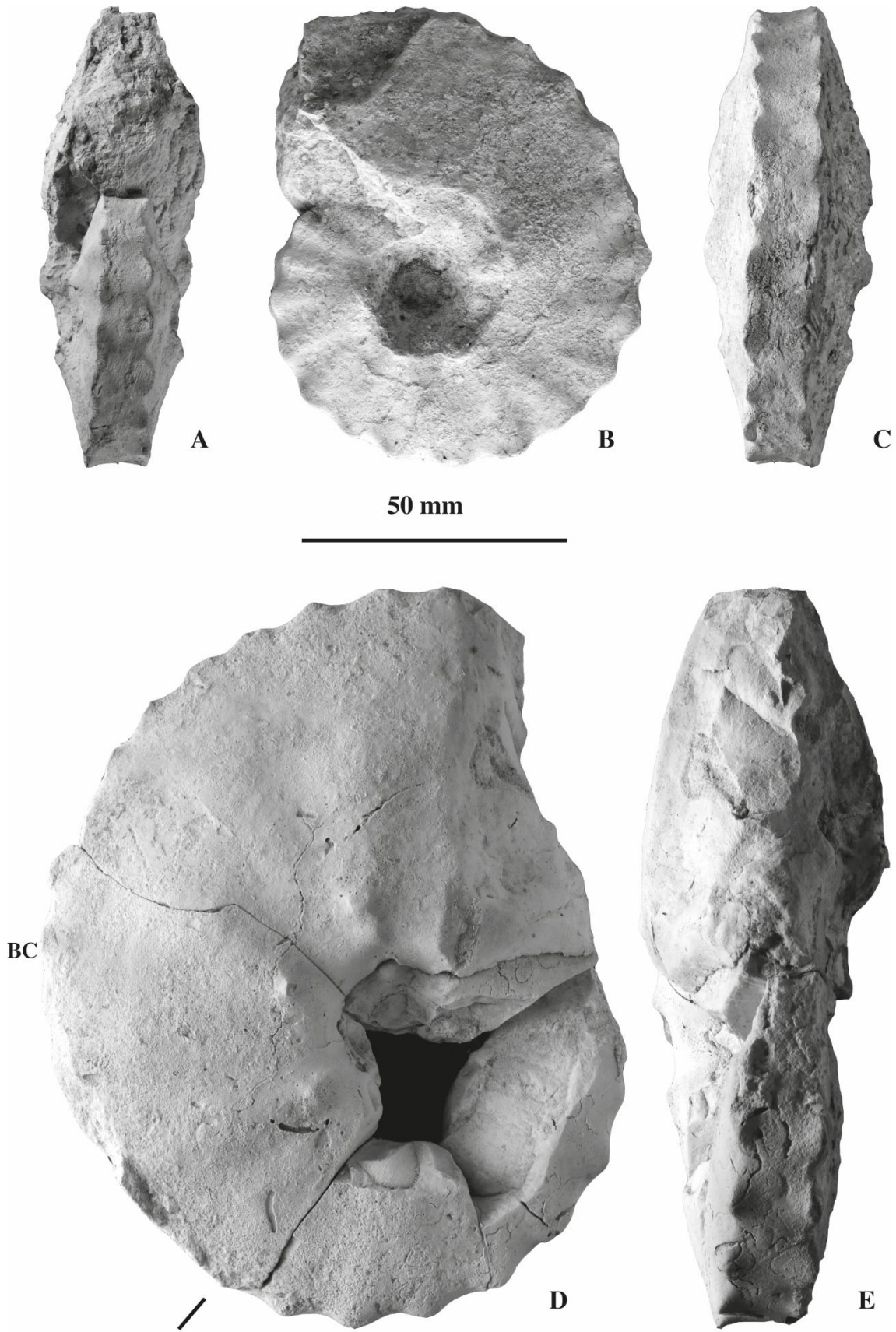


Figure 9. (A-E) *Knemiceras sagetae* nov. sp., *Prolyelliceras gevreyi* Zone, lower Albian; (A-C) UJF-ID.15179, morphotype 3, from BOA.5; D, E) UJF-ID.15178, morphotype 3, from BOA.5. Scale bar is 50 mm

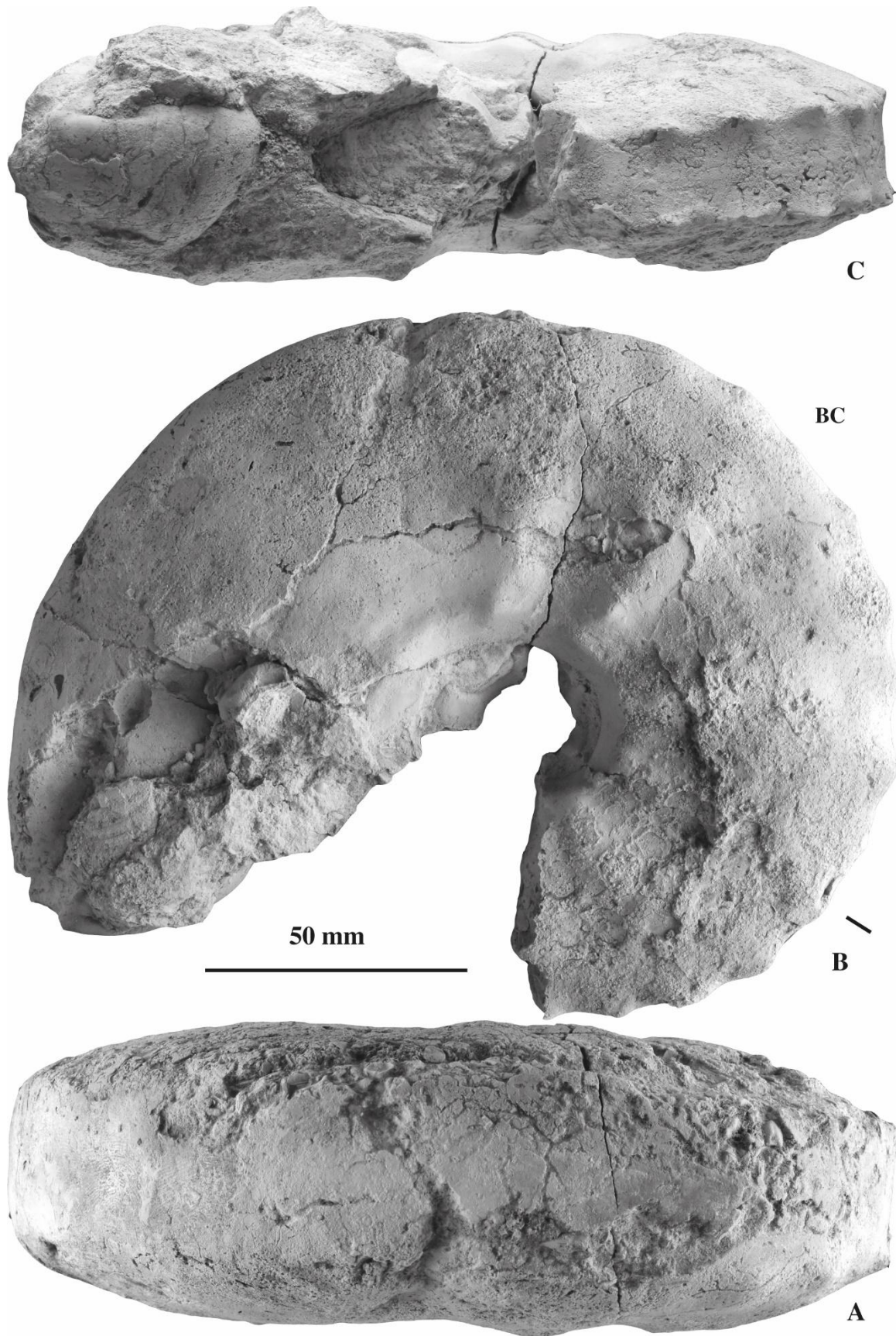


Figure 10. (A-C) *Knemiceras sagetae* nov. sp., *Prolyelliceras gevreyi* Zone, lower Albian; (A-C) UJF-ID.15206, morphotype 3, from FA.13. Scale bar is 50 mm

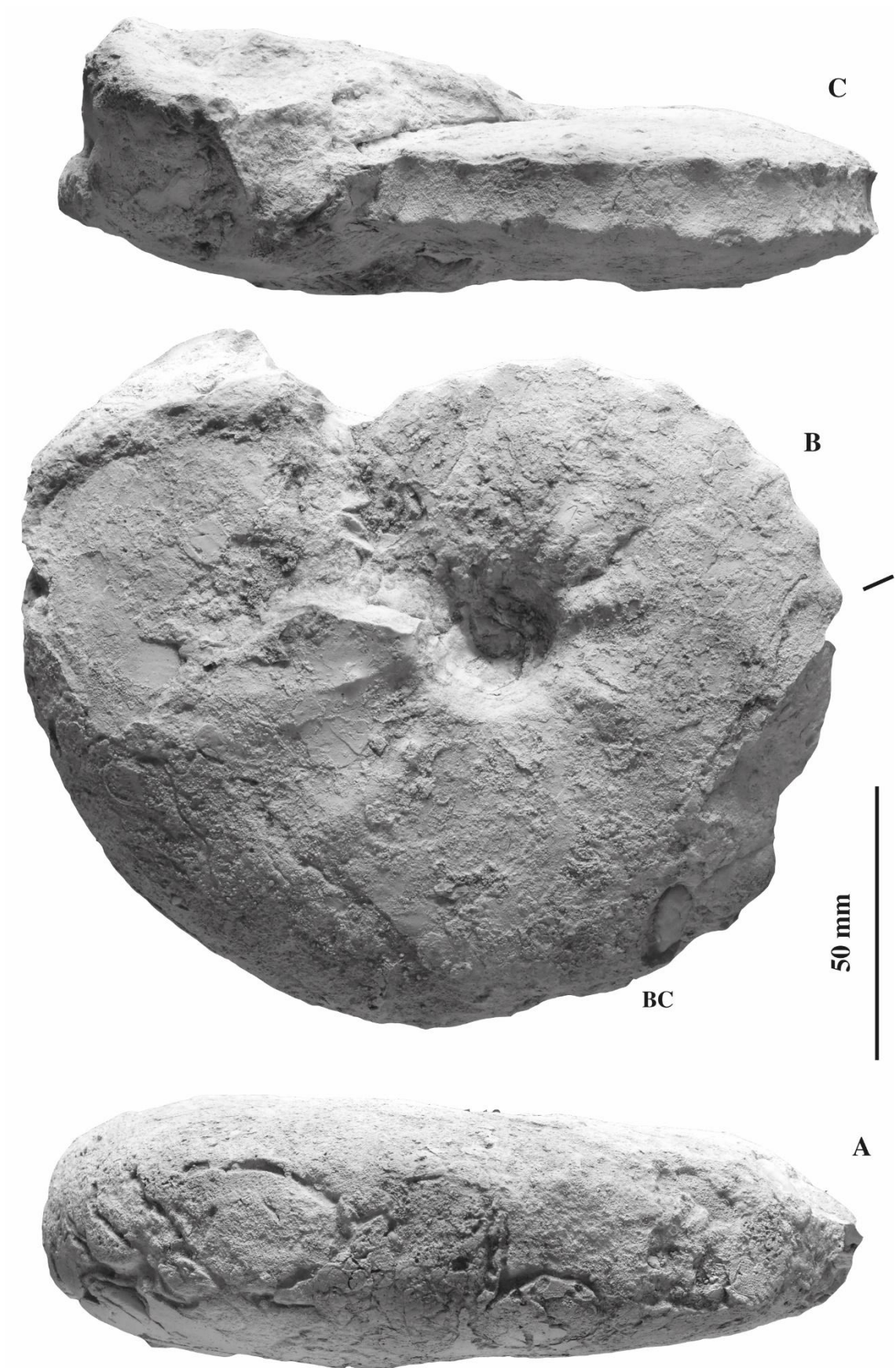


Figure 11. (A-C) *Knemiceras sagetae* nov. sp., *Prolyelliceras gevreyi* Zone, lower Albian; (A-C) UJF-ID.15245, morphotype 3, from FO.4. Scale bar is 50 mm

The specimens described and figured by Arnould-Saget (1956) as *Knemiceras aegyptiacum* Mahmoud (p. 7 pars, pl. 1, fig. 1, 4 only), *Knemiceras douvillei* Basse (p. 9, pl. 2, fig. 1, 2; pl. 9, fig. 2, and *Knemiceras syriacum* (von Buch) (p. 11, pl. 1, fig. 3 only), the specimen figured as *Knemiceras* cf. *compressum* Hyatt by Moreno-Bedmar et al. (2008, fig.1), and the specimen described and figured by Jaillard et al. (2022, p. 16, Fig. 13G, H) as *Knemiceras* sp.1, are herein assigned to the morphotype 2 of *Knemiceras sagetae*. The strongly weathered specimen figured by Abdallah et al. (1995, fig. 22.3 only) as *Knemiceras syriacum* (von Buch), is doubtfully assigned to the morphotype 2 of *Knemiceras sagetae*.

The specimens described and figured by Arnould-Saget (1956, p. 14, pls. 5, 8, 12) as *Knemiceras* cf. *moorei* Knechtel, Richards & Rathbun, and the specimen figured by Moreno-Bedmar et al. (2008, fig. 1) as *Parengonoceras* sp. 2, are herein assigned to the morphotype 3.

The morphotype 2 of *Knemiceras sagetae* shows superficial resemblances with *Knemiceras aegyptiacum* Mahmoud, 1956 from the lower Albian of Sinai (Egypt), from which it differs by slightly less numerous periumbilical tubercles, its stronger and less numerous ventrolateral tubercles, the persistence of tuberculation on the inner part of the body chamber with tubercles increasing in number and tending to be radially elongated, and by its suture line with entire or feebly indented saddles. *Knemiceras douvillei* Basse, 1940 differs from the Tunisian species by its much smaller adult size.

Occurrence. Beds BOA.3, 5, 7; FA.12-14, 17; FO.4-6, most probably the *Prolyelliceras gevreyi* Zone, Lower Albian. Also known from Jebel Smaïa, Jebel Naïmia, Jebel Chemsî, Jebel Asker, Sif el Laham and ?Foum Rhadouane (Arnould-Saget, 1956; Moreno-Bedmar et al., 2008).

Knemiceras lanceolatum nov. sp.

Figs 8C-G, 12a-f, 13a-e

1956. *Knemiceras attenuatum* Hyatt; Arnould-Saget, p. 12, ?pl. 2, fig. 3, pl. 3, fig. 1, text fig. 17 pars.

?1956. *Knemiceras gracile* H. Douvillé; Arnould-Saget, p. 16, pl. 3, fig. 3, 4, text-fig. 10.

1956. *Engonhoplitoïdes vicorpense* Basse; Arnould-Saget, p. 23, pl. 10, fig. 1, text-fig. 14.

2022. *Knemiceras* sp.3, Jaillard et al., p. 16, Fig. 15a-c

Zoobank identification number. urn:lsid:zoobank.org:act:263F52EA-7365-40C8-87D4-DA8C4239B2B6

Derivatio nominis. For its lanceolate whorl section.

Holotype. UJF-ID.15127, from BOA.6 (Figs 8E-G).

Material.

One poorly preserved specimen from BOA.2 (UJF-ID.15122), three specimens from BOA.4 (UJF-ID.15123-5), one specimen (UJF-ID.15103) and one questionable fragment from BOA.5 (UJF-ID.15126), six specimens from BOA.6 (UJF-ID.15127-32), three specimens from FA.12 (UJF-ID.15133-35), four specimens from FA.13 (UJF-ID.15136-39), and three specimens from FA.14 (UJF-ID.15140-42).

Description.

1. UJF-ID.15133: D. 39.0 – Wh: 21 (0.54) – Wb: 12 (0.31) – U: 4.5 (0.12) – Wb/Wh: 0.57 – dc/Wh: ? – v/Wh: 0.14

2. UJF-ID.15140: D. 73.0 – Wh: 40 (0.55) – Wb: 22 (0.30) – U: 7 (0.10) – Wb/Wh: 0.55 – dc/Wh: ? – v/Wh: 0.13

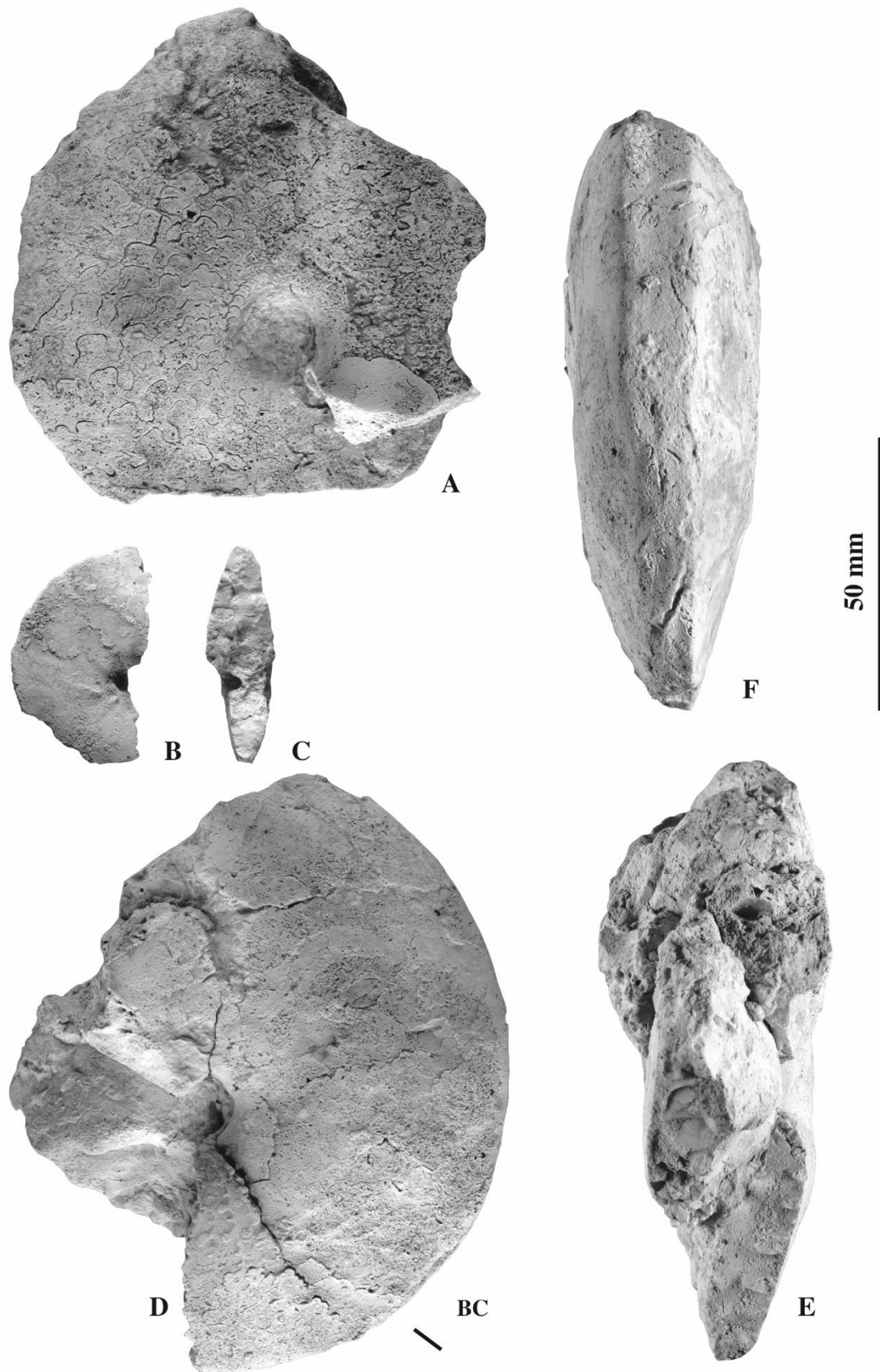


Figure 12. (A-F) *Knemiceras lanceolatum* nov. sp., *Polyelliceras gevreyi* Zone, lower Albian; (A) UJF-ID.15123, from bed BOA.4; (B, C) UJF-ID.15133, from bed FA.12; (D-F) UJF-ID.15128, from bed BOA.6. Scale bar is 50 mm

3. UJF-ID.15127: D. 84.0 – 361 Wh: 46 (0.55) – Wb: 30 (0.36) – U: 8.5 (0.10) – Wb/Wh: 0.65 – dc/Wh: 0.16 – v/Wh: 0.22
4. UJF-ID.15103: D. 87.0 – Wh: 45 (0.52) – Wb: 26 (0.30) – U: 10 (0.12) – Wb/Wh: 0.58 – dc/Wh: 0.16 – v/Wh: 0.22
5. UJF-ID.15128: D. 91.0 – Wh: 47 (0.52) – Wb: 29 (0.32) – U: 10 (0.11) – Wb/Wh: 0.62 – dc/Wh: ? – v/Wh: 0.18
6. UJF-ID.15136: D. 104.0 – Wh: 59 (0.53) – Wb: 33 (0.32) – U: 9 (0.09) – Wb/Wh: 0.56 – dc/Wh: 0.18 – v/Wh: 0.17

The inner whorls are not known. Between 20 and 40 mm of diameter, the whorl section is compressed ($Wb/Wh = 0.57$) and lanceolate with a maximum of width just above the umbilical shoulder. The flanks are smooth and convex, converging to a narrow, flat venter (Fig. 12B, C). When present, feeble periumbilical tubercles appear at a diameter of 40 mm, and there are 4-5, more or less strong periumbilical tubercles on the last whorl of the phragmocone, at the periumbilical shoulder. The umbilicus is very narrow (U/D between 0.09 and 0.12). The umbilical wall is deep, vertical to feebly funnel-shaped. The umbilical shoulder is convex. The flanks are convex, almost smooth, converging to a narrow venter (v/Wh between 0.13 and 0.22). The whorl section is typically lanceolate with a maximum of width just above the umbilical shoulder. The flanks are smooth, and there are numerous, small, spirally elongated ventrolateral clavi (dc/Wh between 0.16 and 0.18) that are opposite on the venter.

The adult phragmocone has a diameter of 90-100 mm (Figs 8C-G, 12A). The body chamber, which is known only by its inner half, is poorly preserved and shows smooth, convex flanks and small, persistent ventrolateral clavi (Figs 12D-F, 13A-E). The suture line is always weathered.

The specimen UJF-ID.15103, from BOA.5 (Fig. 13C-E), is the best-preserved specimen but is atypical. It is an adult with a 90° sector of body chamber (Appendix 4A-C). It has a discoidal, involute coiling ($U/D = 0.12$), with narrow, funnel-shaped deep umbilicus. The whorl section is compressed, subtrapezoidal, with a maximum of width at the inner third of the flanks, feebly convex flanks, and a narrow, flat venter. There are small, peri-umbilical bullae on the juvenile that disappear early. The flanks are smooth, and there are numerous, small, spirally elongated ventrolateral clavi (dc/Wh at about 0.16) that are opposite on the venter. The venter is flat and very narrow. On the inner part of the body chamber, the ventrolateral clavi tend to disappear. This specimen is characterized by its less convex flanks but seems to enter the variability of *K. lanceolatum*.

Remarks. At Bir Oum Ali, this species is absent in BOA.3, very rare in BOA.5 and is dominant in BOA.4 and 6. The beds BOA.4 and 6 are characterized by clayey deposits and a more abundant and diverse associated fauna, with bivalves, gastropods, trigoniidae and *Plicatula* sp., while beds BOA.3 and 5 are characterized by the presence of oysters and ostracods, which suggests a more external environment for beds BOA.4 and 6. At Foum el Argoub, *Knemiceras lanceolatum* is rare but present in beds (FA.12-14) that show a lack of diversity, where oysters are dominant, but contain phosphates, which indicates low rates of sedimentation and/or more external deposits.

The specimen described and figured by Arnould-Saget (1956, p. 12, pl. 3, fig. 1, text-fig. 17A) as *Knemiceras attenuatum* Hyatt, from Foum el Argoub, is an adult phragmocone, 89 mm in diameter. It shows a compressed whorl section with smooth convex flanks with a maximum of width at the inner third of the flanks, a very narrow umbilicus ($U/D = 0.12$), and a weathered narrow venter. This specimen enters the variability of *K. lanceolatum*.

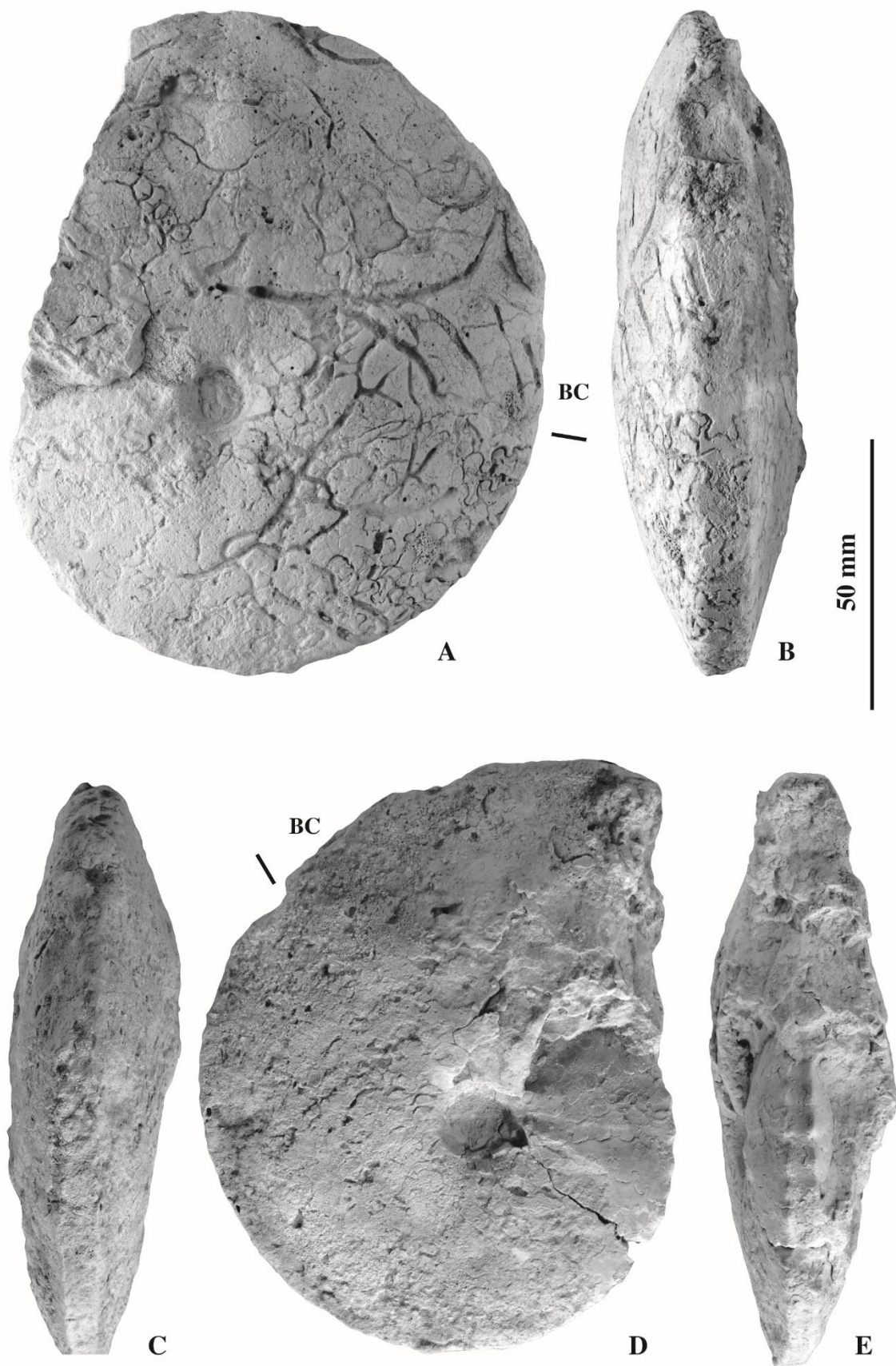


Figure 13. (A-E) *Knemiceras lanceolatum* nov. sp., *Polyelliceras gevreyi* Zone, lower Albian; (A, B) UJF-ID.15136, from bed FA.13; (C-E) UJF-ID.15103, from bed BOA.5. Scale bar is 50 mm

Arnould-Saget has figured another specimen (1956, pl. 2, fig. 3, text-fig. 17D) from Djebel Smaïa, an adult phragmocone, 932 mm in diameter, that has a wider umbilicus ($U/D = 0.18$), a wider, slightly concave venter and a less compressed whorl-section ($Wb/Wh = 0.75$). This specimen is doubtfully referred to *K. lanceolatum*.

The specimen described and figured by Arnould-Saget (1956, p. 23, pl. 10, fig. 1, text-fig. 14) as *Engonhoplitoides vicorpense* Basse, from Oum Krelakril, is an adult phragmocone, with a diameter of 74 mm, that has a very narrow umbilicus ($U/D = 0.12$), a compressed whorl section ($Wb/Wh = 0.57$), with a maximum of width on the inner third of the flanks, convex smooth flanks, and a narrow venter which has finely crenellated shoulders. We consider that this specimen belongs to *K. lanceolatum*.

The specimens described and figured by Arnould-Saget (1956, p. 16, pl. 3, fig. 3, 4, text fig. 10) as *Knemiceras gracile* H. Douvillé, from Fom el Argoub and Djebel Asker, are poorly preserved but seem to have feebly convex flanks. They are doubtfully referred to *K. lanceolatum*.

Occurrence. BOA.2, 4, 5 and 6; FA.12-14, doubtfully present in the ‘*Hypacanthoplites*’ *buloti* Zone and more likely *Prolyelliceras gevreyi* Zone, lower Albian. The species is known also from Oum Krelakril and Djebel Smaïa (Arnould-Saget, 1956).

Knemiceras multicostatum nov. sp.

Figs 14A-F

Zoobank identification number. urn:lsid:zoobank.org:act:7B124CF0-8FCD-4E0D-931C-E84CA256DD1C

Derivatio nominis. With numerous ribs.

Holotype. UJF-ID.15146, from BOA.8 (Figs 14E, F).

Material. Twelve specimens from BOA.8 preserved as calcareous internal molds.

Description.

1. UJF-ID.15146: D. 41.0 – Wh: 20 (0.49) – Wb: 15.5 (0.38) – U: 7.5 (0.18) – Wb/Wh: 0.78 – dc/Wh: 0.32
2. UJF-ID.15147: D. 45.0 – Wh: 22.5 (0.50) – Wb: 12 (0.27) – U: 9 (0.20) – Wb/Wh: 0.53 – dc/Wh: 0.20
3. UJF-ID.15146: D. 70.0 – Wh: 35 (0.50) – Wb: 26 (0.37) – U: 14 (0.20) – Wb/Wh: 0.74 – dc/Wh: 0.25

This species is known from juvenile (Figure 14A-D) and adult phragmocones and the beginning of the body chamber (Figure 14E, F). The coiling is discoidal and involute, with narrow, deep umbilicus (U/D at about 0.20). The whorl section is compressed (Wb/Wh between 0.57 and 0.78), subtrapezoidal, with a maximum of width at the inner third of the flanks, feebly convex flanks, and a relatively broad, flat venter. There are 8-9 strong, coarse, feebly radially elongated periumbilical tubercles on the last whorl of the phragmocone. These tubercles remain close to the umbilical shoulder, give rise to coarse primary ribs that are well-expressed on the inner third of the flanks. There is one intercalatory rib between two primaries on the outer third of the flanks, arising at about mid-flanks or higher, and ending with ventrolateral clavi, which are opposite on the venter. The ornamentation tends to be effaced on the beginning of the body chamber.

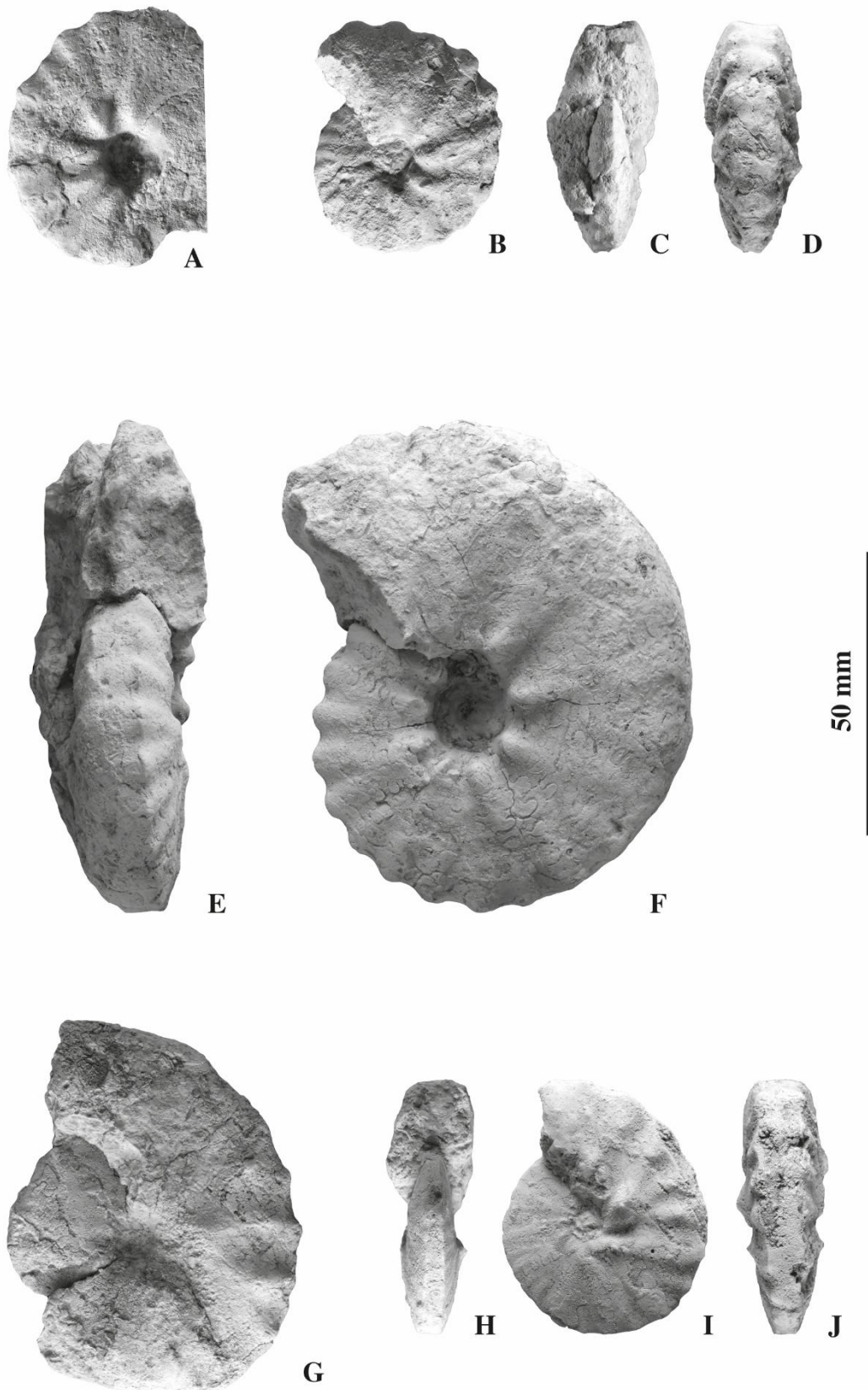


Figure 14. (A-F) *Knemiceras multicostatum* nov. sp., Buloticerias radenaci Zone, Lower Albian; (A) UJF-ID.15147, from bed BOA.8; (B-D) UJF-ID.15148, from bed BOA.8; (E, F) the holotype UJF-ID.15146, from bed BOA.8; (G-J) *Parenгонoceras* cf. *bussoni* Collignon, 1965, Buloticerias radenaci Zone, Lower Albian; (G) UJF-ID.15150, from bed BOA.8; (H-J) UJF-ID.15151, from bed BOA.8. Scale bar is 50 mm

The ventrolateral tubercles density is rather high (dc/Wh between 0.20 and 0.32). The venter is flat to feebly convex and narrow to moderately broad.

Remarks. This species is characterized by its suture with indented saddles, its high ribbing density, with eight to nine primary ribs on the juvenile and the last whorl of the phragmocone, arising from periumbilical tubercles, which is never the case on the material in the underlying stratigraphic levels.

Occurrence. BOA.8, Bir Oum Ali section, *Buloticerias radenaci* Zone, lower Albian.

Knemiceras sp. indet.

Figs 15A-D

1956. *Knemiceras* cf. *raimondi* Lisson, Arnould-Saget, p. 19, pl. 4, fig. 2.

2022. *Knemiceras* sp.4, Jaillard et al., p. 16, Fig. 17a, b

Description.

D. 87.0 – Wh: 45 (0.52) – Wb: 26 (0.30) – U: 10 (0.12) – Wb/Wh: 0.58 – dc/Wh; 0.16

UJF-ID.15107, from BOA.8, is a fragment of a phragmocone, 56 mm in diameter (Fig. 15A, B). It has a discoidal, involute coiling, with narrow, deep umbilicus. The whorl section is compressed, subtrapezoidal, with a maximum of width at the inner third of the flanks, feebly convex flanks, and a relatively broad, flat venter. There are strong, radially elongated periumbilical tubercles that give rise to coarse primary ribs, bearing small conical outer lateral tubercles and strong club-shaped ventrolateral clavi, which are opposite on the venter. There are generally two intercalatories between two primaries, arising at about mid-flanks, and bearing or not feeble outer lateral tubercles. The ventrolateral tubercles density is low (dc/Wh at about 0.36). The venter is flat to feebly convex and moderately broad.

Remarks. Another fragment (UJF-ID.15145), from FA.19, a little higher in the stratigraphic column, shows the same lateral ornamentation but has ventrolateral tubercles that tend to be alternating on the venter, which may be the result of a deformation (Fig. 15C,D).

The specimen described by Arnould-Saget (1956, p. 19, pl. 4, fig. 2) as *Knemiceras* cf. *raimondi* Lisson, from Djebel Smaïa, a poorly preserved phragmocone, 77 mm in diameter, with low umbilical wall, narrow umbilicus (U/D = 0.18), almost flat flanks, broad venter, eight periumbilical tubercles on the last preserved whorl, twelve-fifteen outer lateral tubercles, and about twenty ventrolateral tubercles that are opposite on the venter, looks like very similar to our specimen.

Occurrence. BOA.8, Bir Oum Ali section, *Buloticerias radenaci* Zone, lower Albian. The species is also known from Djebel Smaïa area.

Knemiceras sp. ?juv.

Figs 15E-H

2022. *Knemiceras* sp.5, Jaillard et al., p. 17, Fig. 17c-f

Description.

UJF-ID.15113: D. 20.0 - Wh: 9.5 (0.48) - Wb: 7.5 (0.38) - U: 3 (0.15) - Wb/Wh: 0.79 - dc/Wh; 0.42

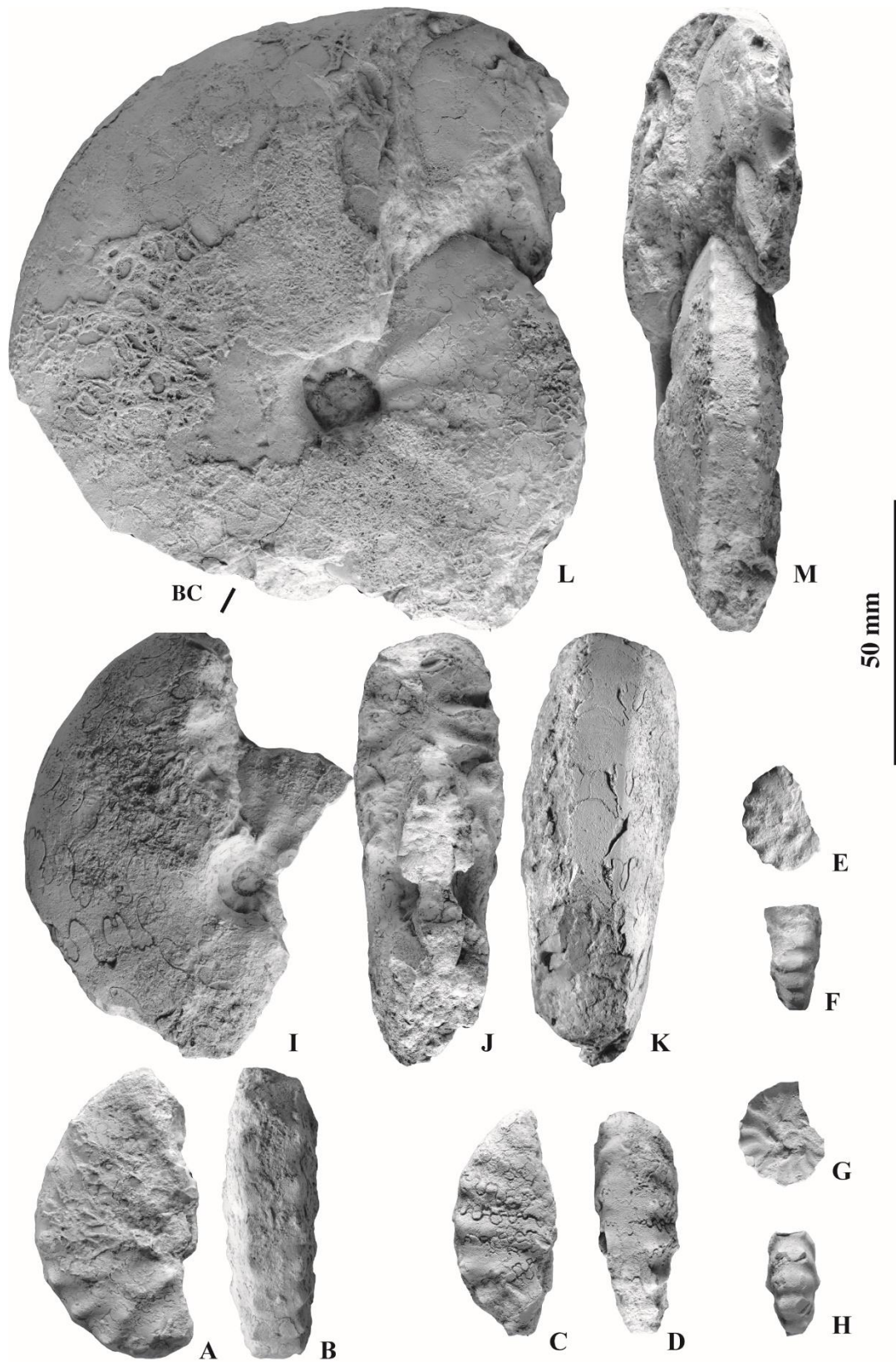


Figure 15. (A-D) *Knemiceras* sp. *indet.*, *Buloticeris radenaci* Zone, Lower Albian; (A, B) UJF-ID.15107, from bed BOA.8; (C, D) UJF-ID.15145, from bed FA.19; (E-H) *Knemiceras* sp. ?*juv.*, *Buloticeris radenaci* Zone, Lower Albian; (E, F) UJF-ID.15109, from FO.8; (G, H) UJF-ID.15113, loose from FO, lower Albian; (I-M) *Knemiceras tunisiense* nov. sp., *Buloticeris radenaci* Zone, Lower Albian; (I-K) the holotype UJF-ID.15143, from bed FA.18; (L, M) UJF-ID.15144, from bed FA.18. Scale bar is 50 mm

Three specimens UJF-ID.15109, from FO.8 (Figs 15E-F), and UJF-ID.15113 (Figs 19G, H) and UJF-ID.15121, loose from the same section but very probably from the same stratigraphic level. All are preserved as small fragments, between 20 and 25 mm in diameter, without it being possible to say whether they are juveniles or micromorphs. The shell is discoidal, involute, with narrow umbilicus. The whorl section is compressed, subtrapezoidal, with a maximum of width at the inner third of the flanks, feebly convex flanks, and a moderately broad, flat venter. There are 5 strong, conical periumbilical tubercles that give rise to coarse, broad, prorsiradiate, convex, primary ribs, bearing strong, spirally elongated ventrolateral clavi, which are opposite on the venter. There is an intercalatory rib between two primaries, arising on the inner third of the flanks and tending to be branched to the primary. All ribs cross the venter without interruption. The ventrolateral tubercles density is low (dc/Wh at about 0.42).

Remarks. This morphology represents the youngest known representatives of the genus *Knemiceras* in the Chott area; it is characterized by its ribs that cross the venter without interruption. A poorly preserved fragment of a specimen from BOA.8 (UJF-ID.15149), which presents a 90° sector of body chamber, with a whorl height of 14 mm, a feebly compressed whorl section ($Wb/Wh = 0.86$), a low ventrolateral tubercle density ($dc/Wh = 0.50$), and ribs that tend to cross the venter, is possibly referred to the present species.

Occurrence. FO.8, Fom el Argoub Ouest section, *Buloticerias radenaci* Zone, lower Albian.

Knemiceras tunisiense nov. sp.

Figs 15I-M

Zoobank identification number. urn:lsid:zoobank.org:act:4F45D7CF-106C-4232- A1AD-081711D6A8F1

Derivatio nominis. From Tunisia.

Holotype. UJF-ID.15143, from FA.18 (Figs 15I-K).

Description.

1. UJF-ID.15143: D. 39.0 - Wh: 22 (0.56) - Wb: 13 (0.33) - U: 7 (0.18) - Wb/Wh : 0.59 – v/Wh : 0.20
2. UJF-ID.15143: D. 65.0 - Wh: 30 (0.46) - Wb: 22 (0.34) - U: 11 (0.17) - Wb/Wh : 0.73 – v/Wh : 0.30
3. UJF-ID.15144: D. 109.0 - Wh: 57 (0.52) - Wb: ? (?) - U: 12 (0.11) - Wb/Wh : ?

Two specimens UJF-ID.15143-44, from FA.18. UJF-ID.15143 is an adult phragmocone, about 80 mm in diameter, preserved as weathered internal mold (Figs 15I-K). The juvenile, up to a diameter of about 40 mm, has a lanceolate, compressed whorl section ($Wb/Wh = 0.59$), with a maximum of width at the inner third of the flanks. The flanks are slightly convex, converging to a narrow, flat venter ($v/Wh = 0.20$). The umbilicus is narrow (U/D between 0.17 and 0.18), the umbilical wall is deep and almost vertical and the umbilical shoulder is broadly rounded. At a diameter of about 40 mm, twelve fine ribs arise at the umbilical seam on the last whorl, and develop small clavi just above the umbilical shoulder. The ribs are fine and radial on the inner whorls, and are prorsiradiate, feeble and coarser on the outer part of the juvenile. There are ventrolateral clavi that are opposite on the venter. The adult phragmocone has a diameter of about 80 mm. At 60 mm, the ornamentation on the flanks has almost disappeared, with only feeble coarse ribs on the inner part of the flanks and inconspicuous, periumbilical tubercles. The venter broadens with age ($v/wh = 0.30$ at a diameter of 65 mm), correlatively to the broadening of the whorl section. At the end of the

phragmocone, the flanks are smooth and the ventrolateral clavi are effaced. The body chamber is known only from a 90° sector of body chamber with feebly convex, smooth flanks, convex, smooth venter, and very narrow umbilicus (U/D = 0.11) (Figs 15L, M). The suture line is not well preserved but shows frilled lobes and deeply incised saddles

Remarks. This species is characterized by a juvenile stage with numerous, fine ribs (12 per whorl), that arise at the umbilical seam and develop small periumbilical clavi, and the early disappearance of the ornament on the flanks, before the end of the phragmocone.

Occurrence. FA.18, Foug el Argoub section, *Buloticerias radenaci* Zone, lower Albian.

?*Knemiceras toussainti* (Pervinquière, 1907)

Appendix 5A-E

1907. *Engonoceras Toussainti* Pervinquière, p. 205, pl. 9, fig. 7.

Non1956. *Engonoceras toussainti*, Arnould-Saget, p. 22, pl. 10, fig. 2.

?1965. *Knemiceras saharae* Collignon, p. 167, pl. B, fig. 1.

1989. *Engonoceras toussainti* Pervinquière, Latil, p. 52.

?1995 *Engonoceras toussainti* Pervinquière, Abdallah et al., fig. 22.7.

Non 2003. *Engonoceras toussainti* Pervinquière, Hewaidy et al., p. 339, pl. 1, figs. 3-5.

?2014. *Knemiceras saharae* Collignon, Klein, p. 180.

2014. *Engonoceras toussainti* Pervinquière, Klein, p. 205 pars.

Holotype. The type, from the former collections of the Sorbonne University has not been recovered. The original figure is herein refigured (Appendix 5A-C). According to Pervinquière, the measurements of the holotype of *Engonoceras toussainti*, from the Albian of Foug el Argoub, are as follow:

D: 35 - Wh: 19 (.55) - Wb: 11 (.31) - U: ? - Wb/Wh: 0.58

D: 70 - Wh: 38 (.54) - Wb: 29 (.41) - U: 13 (.19) - Wb/Wh: 0.76

The shell is discoidal. The umbilicus is narrow and shallow. The whorl section is compressed, especially on the juvenile. The flanks are feebly convex. The venter is flat and there are ventrolateral clavi that alternate on the venter. Up to a diameter of 35 mm, the ornament is made of weak, coarse, falcate ribs. Beyond a diameter of 35 mm, the ribs become stronger, straight and radial, developing bulges just above the umbilical shoulder. There are eight ribs on the last preserved whorl. According to Pervinquière, the suture is poorly preserved.

Remarks. The type of *Knemiceras saharae* (Collignon, 1965) herein refigured, appendix 5D, E), is preserved as a distorted, calcareous internal mold of a phragmocone, about 140 mm in diameter. The shell is discoidal, the whorl section compressed (Wb/D at about 0.30) with a maximum of width at the inner third of the flanks. The umbilical wall is broadly rounded. The flanks are convex, converging to a narrow, flat venter. There are eight coarse, inconspicuous, primary ribs that develop radially elongated bulges on the umbilical wall. There are coarse, inconspicuous intercalatory ribs on the outer part of the flanks. The juvenile bears numerous ventrolateral clavi that alternate on the venter, which tend to disappear on the outer part of the last preserved whorl, the venter becoming convex. *Knemiceras saharae* might represent the adult stages of ?*Knemiceras toussainti*. The poorly preserved specimen figured by Arnould-Saget (1956, p. 22, pl. 10, fig. 2) as *Engonoceras toussainti* Pervinquière is herein interpreted as a juvenile of *Paragonoceras bussoni* (see below).

The specimen figured by Abdallah et al. (1995, fig. 22.7), from Oued Zitoun, with a diameter of about 70 mm, seems to show the typical ribbing style of ?*Knemiceras toussainti*, with coarse ribs arising on the umbilical wall and well-marked on the inner half of the flanks.

The specimen figured by Hewaidy et al. (2003, pl. 1, figs. 3-5), from the Turonian of Egypt, is definitively not related to the present species. Both ?*K. toussainti* and ?*K. saharae* are herein interpreted as offshoots of the genus *Knemiceras* that announce the middle and upper Albian ‘*Knemiceras*’ with ventrolateral clavi that alternate on the venter, whereas the *Knemiceras* lineages with opposite ventrolateral tubercles are not extinct. They should be excluded from the genus *Knemiceras*.

Occurrence. This poorly known species is reported only from Tunisia and seems to be slightly younger than *Parengonoceras bussoni* in the upper part of the *Bulotoceras radenaci* Zone and *Tegoceras camatteanum* Zone or a little higher, lower Albian. It should be noted that ?*Knemiceras saharae* (Collignon, 1965) has been found by Busson (1965) at Foug el Argoub, about ten meters above the holotype of *Parengonoceras bussoni*, therefore well above FA.19 and FO.8.

Genus *Parengonoceras* Spath, 1924

[= *Platiknemiceras* Bataller, 1954. Type species, *Knemiceras (Platiknemiceras) bassei* Bataller, 1954, p. 175, by original designation; *Platyknemiceras* Bataller, 1959, p. 65, nom. null.]

Type species. *Amaltheus ebrayi* de Loriol, 1882, p. 7, by original designation by Spath, 1924, p. 508. Robert (2002, p. 100) selected the specimen figured by de Loriol (1882, pl. 1: MHNG.035492, Ebray collection) as lectotype (Pl. III, fig. 1-4). The species was revised by Latil (2008).

Parengonoceras chottensis sp. nov.

Figs. 16A-C

2022. *Parengonoceras* sp. indet., Jaillard et al., p. 18, Figs. 14d, e, 16a.

Zoobank identification number. urn:lsid:zoobank.org:act:D98D8B79-0A61-4466-8B02-79DB285007BC

Holotype. The specimen UJF-ID.15106, from BOA.7 (Figs. 16A-C)

Derivatio nominis. From the Chott area, southern Central Tunisia.

Description.

D. 120.0 – Wh: 61 (0.51) – Wb: 32 (0.27) – U: 15 (0.13) – Wb/Wh: 0.52

The holotype (Figures 16A-625 C), is a small-sized adult, about 140 mm in diameter, comprising a 180° sector of body chamber. The shell is discoidal, involute ($U/D = 0.13$), with shallow umbilicus, and convex umbilical wall. The whorl section is compressed, elliptical, with a maximum of width at about mid-flanks, convex flanks, and a narrow, flat venter, which becomes convex on the body chamber. There are 8, small, conical periumbilical tubercles that give rise to almost inconspicuous, low, coarse, radiate, primary ribs. There is an intercalatory rib between two primaries, arising on the inner third of the flanks and tending to be branched to the primary. There are numerous, spirally elongated ventrolateral clavi, which are alternating on the venter of the phragmocone. They tend to disappear on the body chamber. The ribs do not cross the venter. The ventrolateral tubercles density is high on the phragmocone (dc/Wh at about 0.16).

Remarks. This species is herein considered as an ancestor of *Parengonoceras bussoni*, from which it differs by its smaller size and the lack of both inner and outer lateral tubercles.

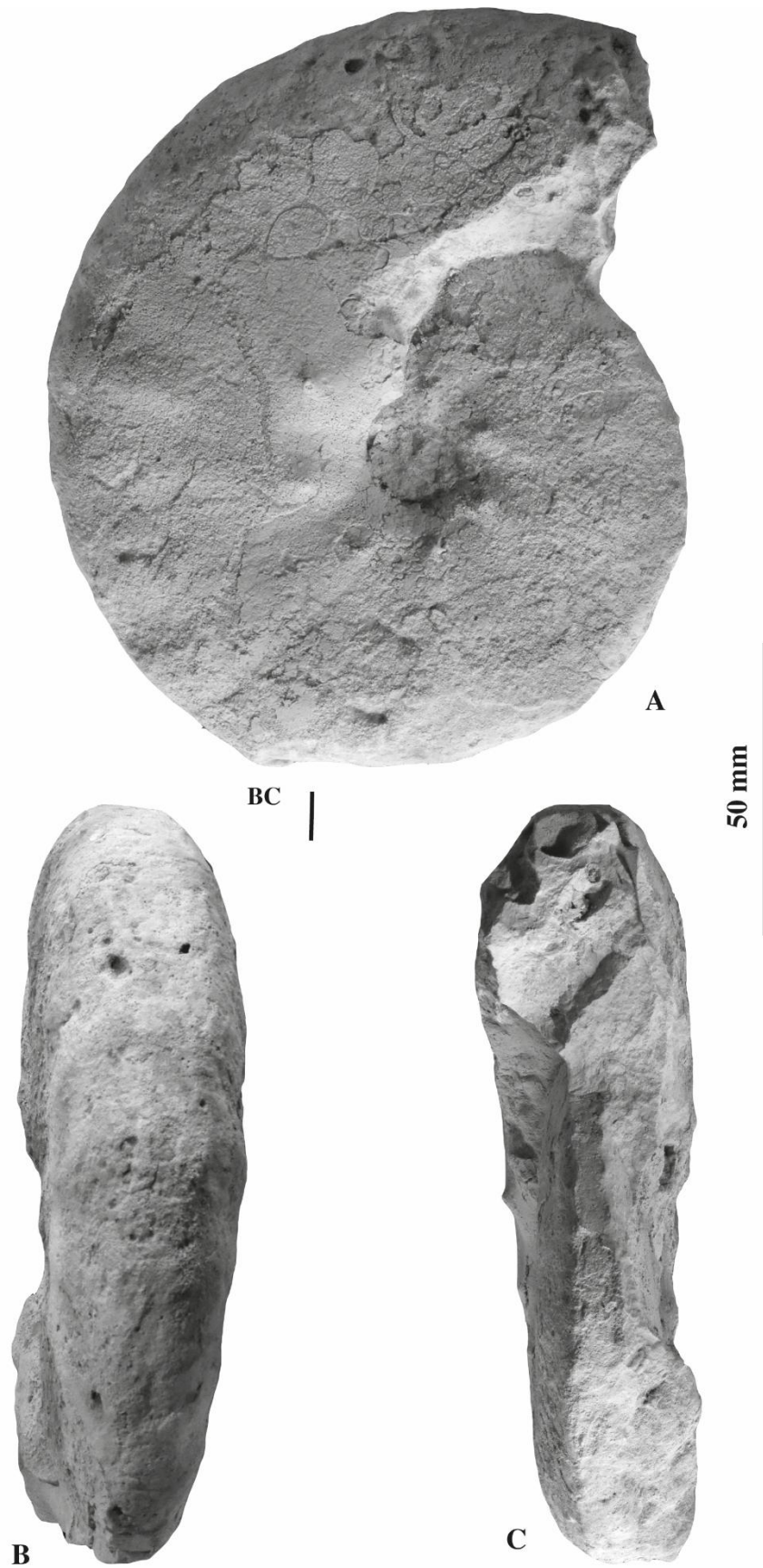


Figure 16. (A-C) *Parenгонoceras chottensis* sp. nov., the holotype UJF-ID.15106, from Bed BOA.7 of Bir Oum Ali, most probably at the transition of the *Prolyelliceras gevreyi* and *Bulotoceras radenaci* Zones, lower Albian. Scale bar is 50 mm

Occurrence. Bed BOA.7 of Bir Oum Ali, most probably at the transition of the *Prolyellicerus gevreyi* and *Buloticerus radenaci* Zones, lower Albian.

Parengonoceras bussoni Collignon, 1965

Figs 17A-I, 18A-C, 19A, B, 20A, appendices 6A,B, 7A,B, 8A, B, 9A

1956. *Knemiceras* cf. *crassinodosum* Sommermeier, Arnould-Saget, p. 17, text-fig. 11, pl. 4, fig. 1.

?1956. *Engonoceras toussainti* Pervinquière, Arnould-Saget, p. 22, pl. 10, fig. 2.

1965. *Parengonoceras bussoni* Collignon, Busson, p. 158.

1965. *Parengonoceras bussoni* Collignon, p. 168, pl. A, fig. 1.

1995. *Knemiceras* aff. *saharae* Collignon, Abdallah et al., fig. 22.1.

2011. *Parengonoceras bussoni* Collignon, Latil, p. 353, text-figs 27, 28; Pl. 6, figs 1, 2.

2014. *Parengonoceras bussoni* Collignon, Klein, p. 187.

2022. *Parengonoceras bussoni* Collignon, Jaillard et al., p. 18, Figs 15g, h, 16c-e.

Holotype. MNHN.F.R53919, collected by Busson at Foum el Argoub, Tebaga de Kebili, locality TU2051 of Busson (1965), 15 meters below the presumed Cenomanian; described and figured by Collignon (1965, p. 168, pl. A, fig. 1), refigured by Latil, 2011, text-fig. 27, 28) and herein (Appendices 6A, B, 7A, B).

Material. One fragment from BOAS.3; one fragment from BOA.9; five specimens from BOA.10; two poorly preserved fragments from BOA.11; two fragments from FO.8, two fragments loose in FO.8; one fragment from FO.10; eight specimens from Rhadouane section.

Description. A series of seven well-preserved specimens (UJF-ID.15114-15120), collected in the *Parengonoceras bussoni* beds of Rhadouane section, allows a better understanding of the ontogeny of the species.

1. UJF-ID.15114: D: 64.0 – Wh: 36 (0.56) – Wb: 18 (0.28) – U: 8.5 (0.13) – Wb/Wh: 0.50 – dc/Wh: 0.20

2. UJF-ID.15115: D: 73.0 – Wh: 41 (0.56) – Wb: ? (?) – U: 7.0 (0.10) – Wb/Wh: ? – dc/Wh: 0.28

3. UJF-ID.15116: D: 77.0 – Wh: 38 (0.49) – Wb: 20 (0.26) – U: 11.0 (0.14) – Wb/Wh: 0.59 – dc/Wh: 0.28

4. UJF-ID.15117: D: 105.0 – Wh: 50 (0.48) – Wb: 37 (0.35) – U: 16.0 (0.15) – Wb/Wh: 0.74 – dc/Wh: ?

5. UJF-ID.15117: D: 136.0 – Wh: 66 (0.49) – Wb: 43 (0.32) – U: 27.0 (0.20) – Wb/Wh: 0.65 – dc/Wh: ?

6. UJF-ID.15119: D: 141.0 – Wh: 74 (0.52) – Wb: 45 (0.32) – U: 22.0 (0.16) – Wb/Wh: 0.61 – dc/Wh: ?

676 7. UJF-ID.15120: D: 141.0 – Wh: 70 (0.50) – Wb: 49 (0.35) – U: 26.5 (0.19) – Wb/Wh: 0.59 – dc/Wh: ?

8. UJF-ID.15120: D: 188.0 – Wh: 82 (0.43) – Wb: 59 (0.31) – U: 42.0 (0.22) – Wb/Wh: 0.72 – dc/Wh: ?

The inner whorls are not known prior to a diameter of 33 mm. Between 33 and about 50 mm in diameter, the ammonites are discoidal, with a compressed whorl section (Wb/Wh at about 0.50), the umbilicus is narrow (U/D at about 0.15) (Figs. 17A-F). The umbilical wall is low, the umbilical shoulder is broadly rounded. The flanks are slightly convex, converging to a narrow, flat venter. The ornament is weak; there are about six coarse periumbilical bullae that give rise to coarse, inconspicuous, prorsiradiate ribs. There are numerous, clavate, ventrolateral tubercles that alternate on the venter.

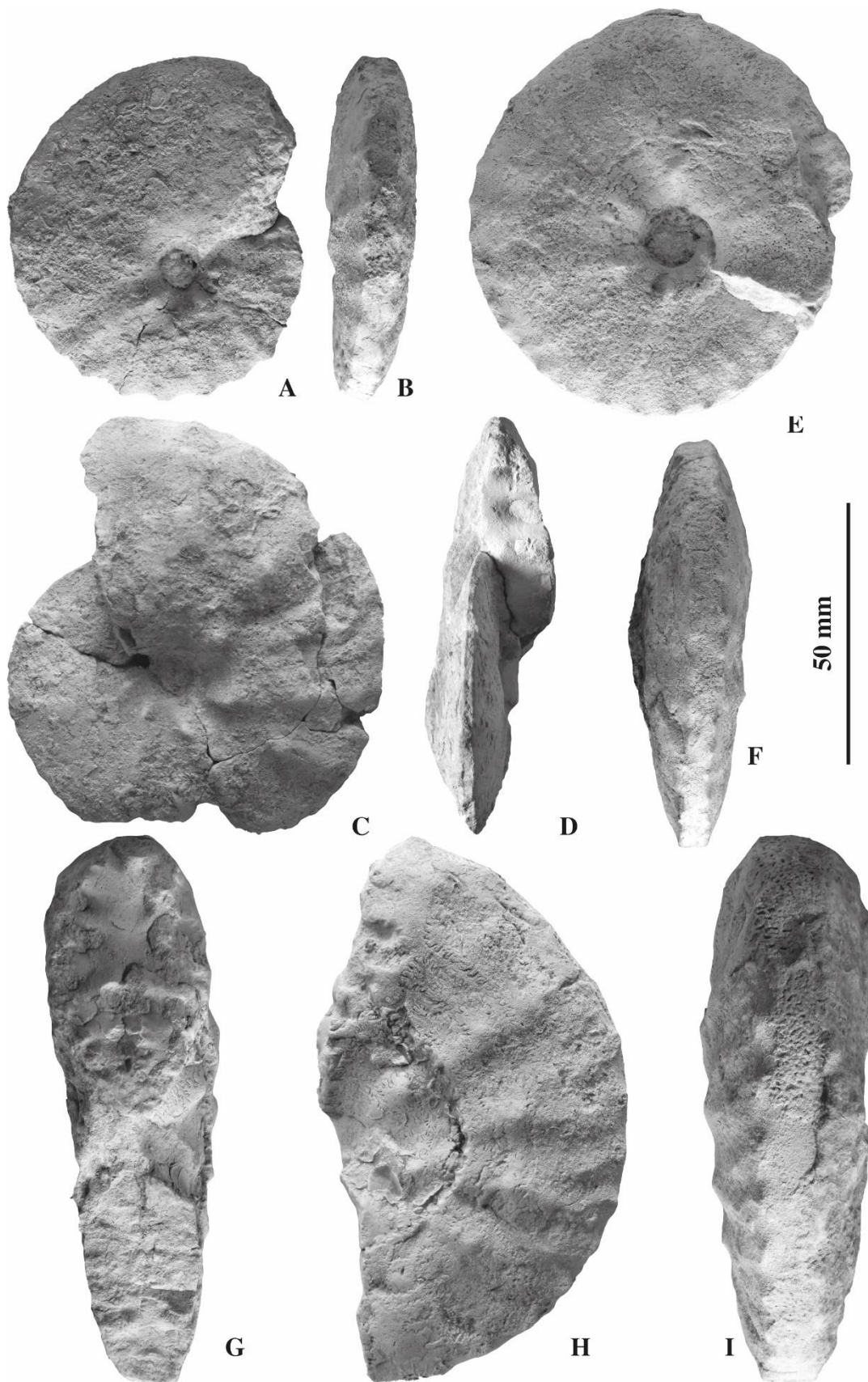


Figure 17. (A-I) *Parengonoceras bussoni* Collignon, 1965; (A, B) UJF-ID.15115 from Rhadouane, (C, D) UJF-ID.15114 from Rhadouane, (E, F) UJF-ID.15116 from Rhadouane, (G-I) UJF-ID.15108, loose in FO.8, upper part of *Bulotoceras radenaci* Zone - *Tegoceras camatteanum* Zone, Lower Albian. Scale bar is 50 mm

Small inner and outer lateral tubercles appear at a diameter of about 60 mm on primary and intercalatory ribs. Inner lateral tubercles, which are twice as numerous as periumbilical ones, are present on primary ribs and between two primaries, giving rise to intercalatory ribs. The outer lateral tubercles are about twice as numerous as inner lateral ones. They are discrete and located on the upper part of the flanks (Figs. 17G-I, 18A-C).

The adult phragmocone has a diameter of about 120-150 mm. At that size, the umbilicus starts to increase in size, the periumbilical and inner lateral tubercles are well expressed, the outer lateral tubercles remain discrete and the ventrolateral clavi are still present (Figs. 18A-C, Appendix 8A, B).

The ventrolateral tubercles disappear at the beginning of the body chamber when the venter becomes convex. When the ornament is well-preserved, the periumbilical, inner lateral and outer lateral tubercles are still present on the body chamber (Figs. 19A, B, 20A, Appendices 6A, B, 7A, B, 8A, B). The coiling is subscaphitoid on the body chamber (U/D between 0.10 and 0.15 on the phragmocone and between 0.16 and 0.22 on the body chamber), which seems to be correlated with a decrease in whorl height.

Remarks. *Parengonoceras bussoni* differs from *Parengonoceras ebrayi* (de Loriol, 1882) (see Latil, 2008), by its smaller adult size, its stronger ornamentation that appears earlier on ontogeny, and its less compressed whorl section. The specimen figured by Matrimon (2010, Fig. 115A) as *Parengonoceras ebrayi*, from the lower Albian, *Cleoniceras floridum* Zone of the Perchois-Ouest (Aube, France), which presents a 180° sector of body chamber, 170 mm in diameter, differs from *P. bussoni* by its more compressed whorl section, its finer ribbing, its much smaller inner lateral tubercles and its extremely feeble outer lateral tubercles that disappear at the beginning of the body chamber.

The specimens described and figured as *Knemiceras* cf. *crassinodosum* Sommermeier by Arnould-Saget (1956: p. 17, text-fig. 11, pl. 4, fig. 1) from Sif el Laham and El Guettar; with their four rows of tubercles, are characteristic of *P. bussoni*.

The poorly preserved specimen figured by Arnould-Saget (1956, p. 22, pl. 10, fig. 2) as *Engonoceras toussainti* Pervinquière, a phragmocone from Djebel Rhadouane, 73 mm in diameter, with weak ribs, umbilical tubercles above the umbilical shoulder, and ventrolateral tubercle that alternate on the venter, is probably a juvenile of *P. bussoni*.

The specimen figured by Abdallah et al (1995, fig. 22.1) as *Knemiceras* aff. *saharae* Collignon, about 80 mm in diameter, from Fom el Argoub, shows the characteristic ornamentation of *P. bussoni*.

Hypengonoceras ibericum Arias and Wiedmann (1977, p. 9, fig. 5), from the presumed upper Albian of South East Spain, with four rows of tubercles is very probably a lower Albian *Parengonoceras* that differs from our material by its more compressed whorl section, and its periumbilical tubercles that are feebler than the lateral and outer lateral ones.

Two specimens from unknown localities of Aïn Rich area, Algeria, are housed in the collections of the Université Claude Bernard, Lyon (UCBL-FSL 85571 and 85582). They have been collected when geological explorations were carried out in preparation for the geological map of Aïn Rich in the late 1960'. Specimen UCBL-FSL 85571, a well preserved adult, about 200 mm in diameter, comprising a 90° sector of body chamber, is figured herein (Appendix 9A). In comparison to the Tunisian material, it shows a more compressed whorl section and a similar ornamentation but with effaced ribs, slightly more numerous tubercles and stronger outer lateral tubercles (UCBL-FSL 85571: D: 200.0 – Wh: 101 (0.51) – Wb: 47 (0.24) – U: 35.0 (0.18) – Wb/Wh: 0.47). Specimen UCBL-FSL 85582, a 90° sector of the end

of phragmocone and beginning of body chamber, with a whorl height of about 60 mm, is closely related to the Tunisian material.

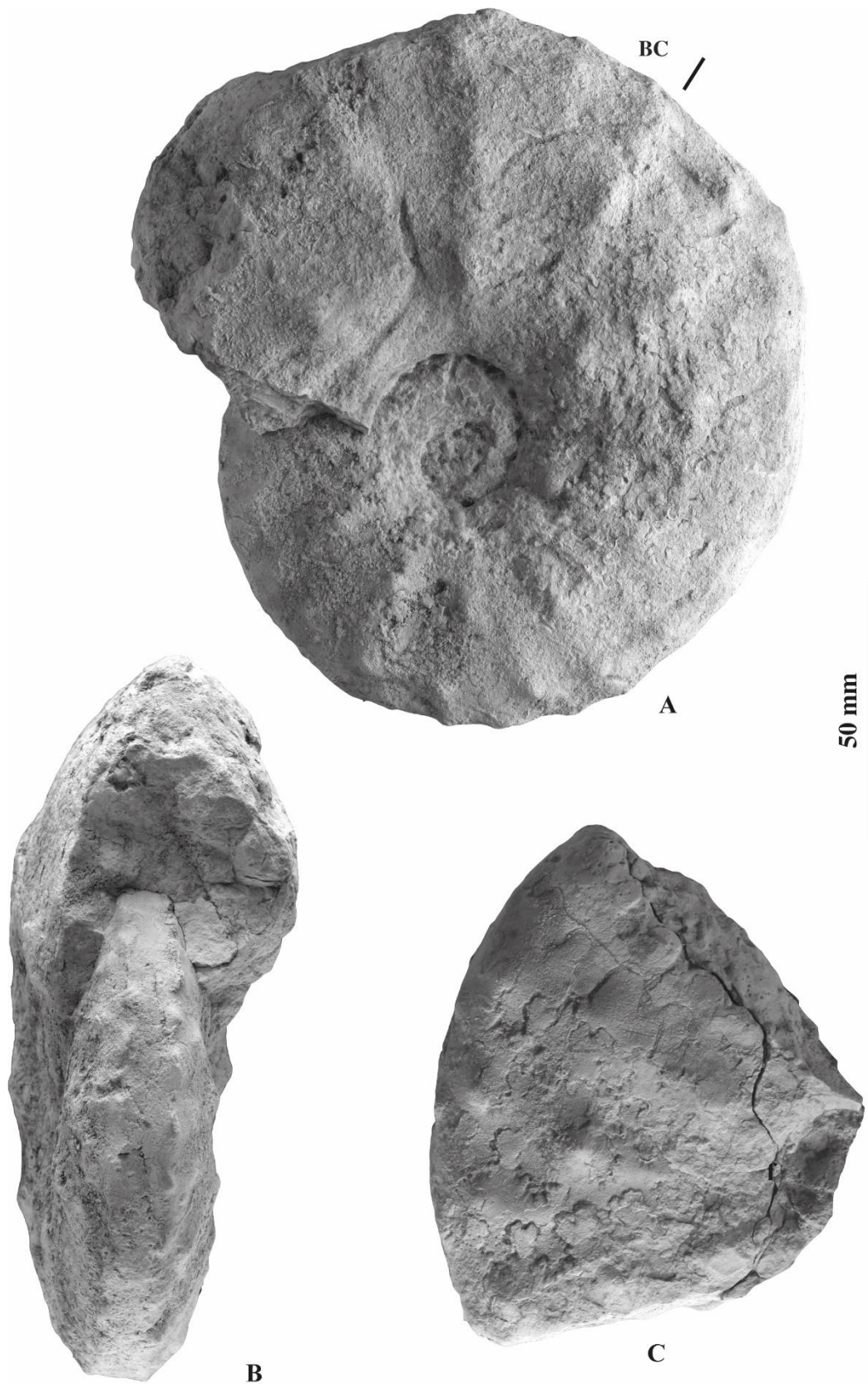


Figure 18. (A-C) *Parengonoceras bussoni* Collignon, 1965; (A, B) UJF-ID.15117 from Rhadouane, (C) UJF-ID.15111, from BOA.10, upper part of *Bulotoceras radenaci* Zone - *Tegoceras camatteanum* Zone, Lower Albian. Scale bar is 50 mm

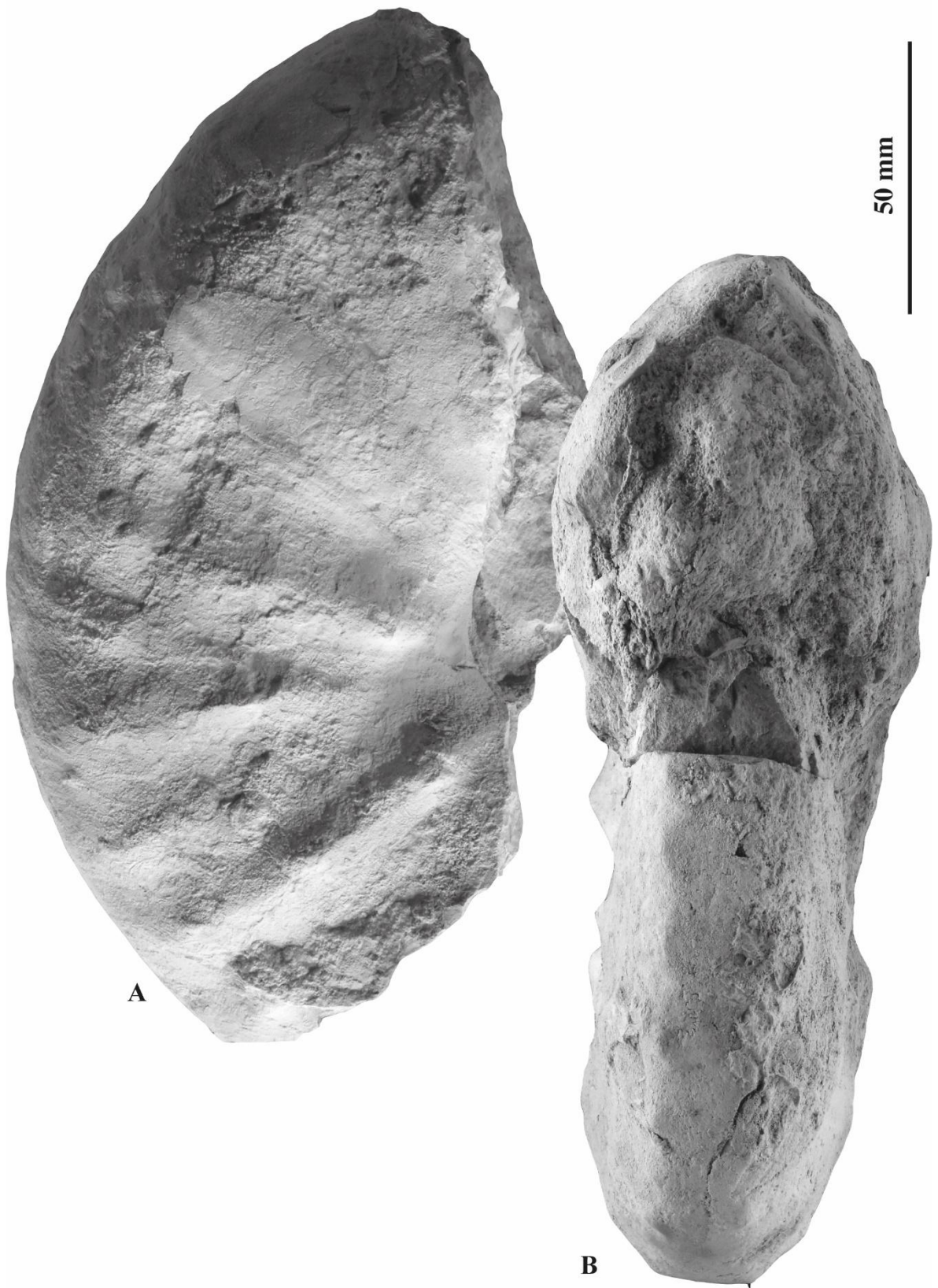


Figure 19. (A, B) *Parengonoceras bussoni* Collignon, 1965, (a) UJF-ID.15110, from BOA.10, (b) UJF-ID.15120 from Rhadouane, upper part of *Buloticerus radenaci* Zone - *Tegoceras camatteanum* Zone, Lower Albian. Scale bar is 50 mm

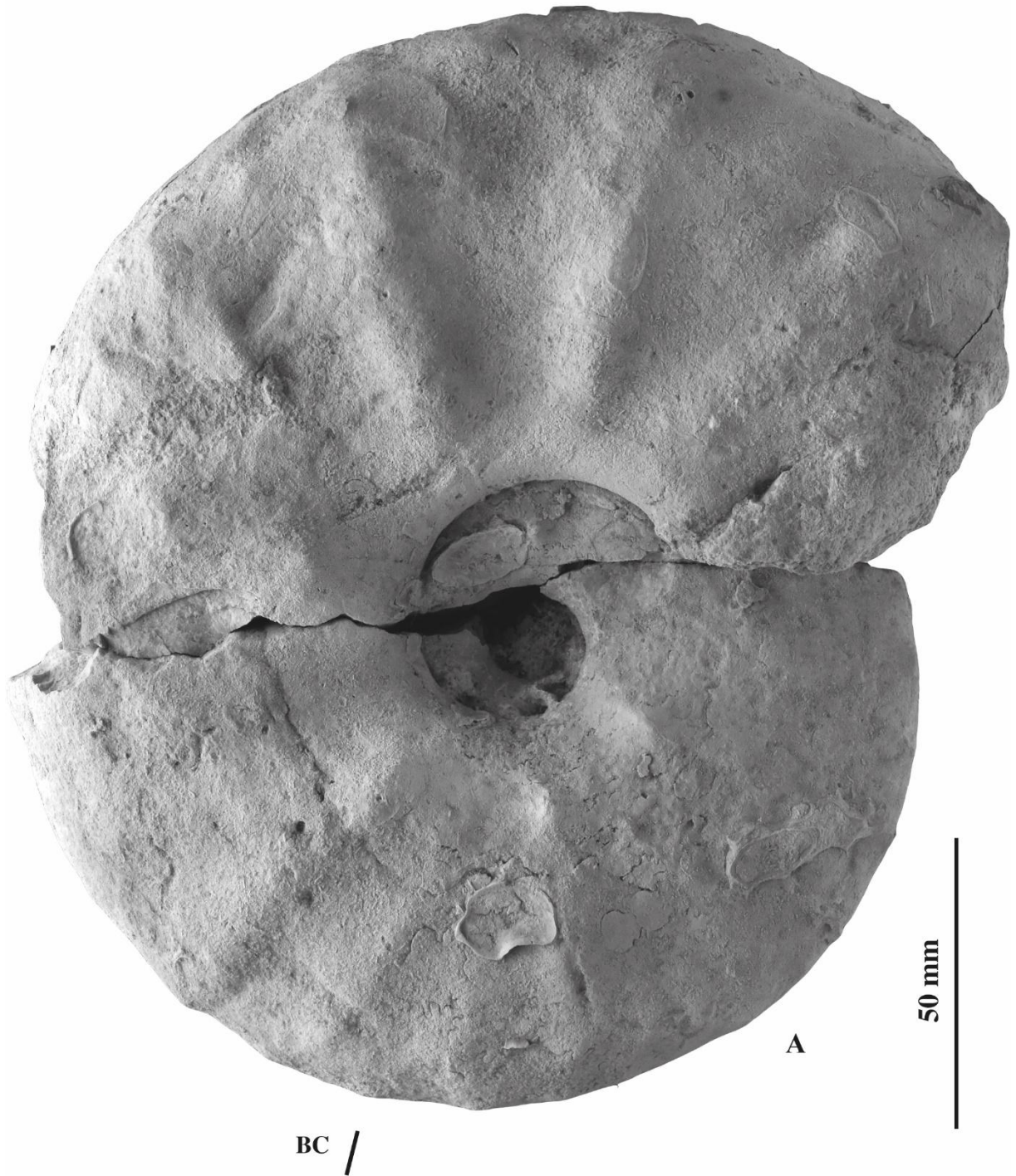


Figure 20. (A) *Parengonoceras bussoni* Collignon, 1965, UJF-ID.15120 from Rhadouane, upper part of *Bulotoceras radenaci* Zone - *Tegoceras camatteanum* Zone, Lower Albian. Scale bar is 50 mm

According to Latil (2011, p 353), ‘Recent investigations in south Tunisia have convinced me that *Parengonoceras bussoni* is an Albian species that derives from the genus *Knemiceras*. This species may be considered as a homeomorph of *Parengonoceras ebrayi* that very probably does not belong to the genus *Parengonoceras*.’ The subsequent discovery of *Parengonoceras chottensis* (see above), which is herein interpreted as a probable ancestor of *P. bussoni*, raises questions concerning this hypothesis.

There are six poorly preserved, juvenile specimens in BOA.8 that could be interpreted as intermediate morphologies between *Parengonoceras chotti* and *Parengonoceras bussoni* (Fig. 14G-J). The inner whorls have a compressed section and smooth flanks. The periumbilical tubercles appear at a diameter of 20-25mm. At a diameter of about 35 mm, outer lateral tubercles appear on the outer third of the flanks and are twice as numerous as periumbilical ones. The largest specimen has a diameter of 65 mm and there is no change in the ornamentation. All these specimens have ventrolateral tubercles that alternate on the venter but one specimen, 45 mm in diameter, shows ventrolateral tubercles that become opposite on the last preserved quarter-whorl. All of this argues in favor of a phylogenetic proximity of *Parengonoceras chotti/bussoni* and *Knemiceras*.

Occurrence. Beds BOAS.3, BOA.9 to 11, FA.19-21, FA.8 and 10, and ‘*bussoni* beds’ of the Rhadouane section, upper part of the *Bulotoceras radenaci* Zone and *Tegoceras camatteanum* Zone, lower Albian. The species is also reported from the Albian of Algeria.

Suborder Ancyloceratina Wiedmann, 1966

Superfamily: Acanthohoplitoidea Stoyanow, 1949

Family: Acanthohoplitidae Stoyanow, 1949

Subfamily: Acanthohoplitinae Stoyanow, 1949

See Latil and Robert (2019) for discussion.

Genus *Hypacanthoplites* Spath, 1923

Type species. *Acanthoceras milletianum* (Orbigny) var. *plesiotypica* Fritel, 1906, by the original designation of Spath, 1923, p. 64.

Lately Latil (2011) discussed the genus *Hypacanthoplites*, which is herein understood as described by Wright et al. (1997): ‘... Early whorl hexagonal or rectangular in section, with flat or concave venter and angular shoulder; primary ribs straight or flexuous, tuberculate at umbilical margin, and branching at lateral tubercle; secondary ribs intercalated or branching; all ribs nodose on shoulders...’. This is a trash genus and a lot of uppermost Aptian-earliest Albian acanthohoplitinids with young stages that do not match the characteristics of the genus have been identified as *Hypacanthoplites* in the literature.

Hypacanthoplites cf. *H. plesiotypicus* (Fritel, 1906) *sensu* Casey (1965), non Fritel (1906)

Appendix 10B-D

2022 *Hypacanthoplites* aff. *H. plesiotypicus* (Fritel, 1906) *sensu* Casey (1965), non Fritel (1906); Jaillard et al., p. 18, Fig. 12B-D.

Material and description. UJF-ID.15099: a juvenile phragmocone, 50 mm in diameter, preserved as a calcareous internal mold, from BOAS.12 (Appendix 10B-D).

D. 45.0 – Wh: 20 (0.44) – Wb: 17 (0.38) – U: 14 (0.31) – Wb/Wh: 0.85 – dc/Wh: 0.14

The inner whorls, prior to a diameter of 20 mm, are not preserved. The coiling is moderately involute ($U/D = 0.31$). The umbilical wall is almost vertical and moderately deep, the umbilical edge is narrowly rounded. The whorl section is higher than broad, rectangular with a maximum of width at mid-flanks, becoming subtetragonal, with a maximum of width at the

inner third of the flanks. The flanks are slightly convex, converging to a narrow, convex venter. The ribbing is moderately dense ($dc/Wh = 0.14$). The primary ribs are straight and radial, arising on the umbilical wall, strengthening at the periumbilical edge, developing tiny, but distinct, radially elongated tubercle. They bifurcate at mid-flank from a small, conical tubercle which tend to disappear at a diameter of 45 mm. Intercalatory ribs may occur, arising at about mid-flank. All the ribs cross the venter radially and are somewhat angular at the ventrolateral shoulders, due to an elevation of the ribs, without any trace of ventrolateral tubercles. The ribs are as wide as the intercostal spaces. The venter is slightly convex.

Remarks. Among the hundreds of acanthohoplitids we collected from the uppermost Aptian and earliest Albian of Tunisia, this is the only specimen that can be assigned to the genus *Hypacanthoplites* as defined by Wright et al. (1997). Our specimen differs from *H. clavatus* (Fritel, 1906) by its less dense and more rigid ribbing, the lack of ventrolateral tubercles and by its less pronounced tuberculation at the same size. It differs from *H. plesiotypicus* (Fritel, 1906) = *H. jacobii* (Collet, 1907), by its persisting lateral tuberculation, the lack of ventrolateral tubercles and a less dense and more rigid ribbing.

Occurrence. Bed BOAS.12 of Bir oum Ali, Tunisia, upper Aptian, *Mellegueiceras chihaouiae* Horizon, *Hypacanthoplites elegans* Zone of Szives et al. (2023).

Genus '*Hypacanthoplites*'

Generic remarks: Acanthohoplitinae with regular ribbing, no tuberculation, convex venter excepted occasionally on the very young stages, lacking the juvenile *Hypacanthoplites* growth stages, and thus inconsistent with the diagnosis of the genus *Hypacanthoplites*. These forms are herein provisionally placed within the genus '*Hypacanthoplites*'.

'*Hypacanthoplites*' sp. indet.

Appendix 10A

'*Hypacanthoplites*' sp. indet., Jaillard et al., p. 18, Fig. 12A.

Material and description. UJF-ID.15100: a fragment of a juvenile phragmocone, 38 mm long, preserved as a calcareous internal mold, from BOAS.12 (Appendix 10A).

The umbilical wall poorly preserved. The whorl section is subtetragonal, compressed ($Wb/Wh = 0.80$) with a maximum of width at the inner third of the flanks. The flanks are slightly convex, converging to a narrow, convex venter. The ribbing is moderately dense ($dc/Wh = 0.18$). The primary ribs arise at or below the periumbilical shoulder, and are straight and radial to slightly prorsiradiate. Between two primaries, there are generally one, sometimes two, intercalatory ribs, arising at about mid-flank or lower. All the ribs cross the venter radially.

Remarks. This specimen differs from *Hypacanthoplites* cf. *H. plesiotypicus* (Fritel, 1906), described above, by its more flattened flanks, broader venter, lack of tuberculation and less prominent ribs. It differs from '*H. paucicostatus*' (Breistroffer, 1953) by its straight ribs and the lack of any kind of swelling/raising of the ribs at periumbilical edge and at ventrolateral shoulders.

Occurrence. Bed BOAS.12 of Bir oum Ali, Tunisia, upper Aptian, *Mellegueiceras chihaouiae* Horizon, *Hypacanthoplites elegans* Zone.

'*Hypacanthoplites*' aff. '*H. buloti*' Latil, 2011

Appendix 10G

2011 '*Hypacanthoplites*' *buloti* Latil, p. 377, figs 41, 42; pl. 22, figs 1-26; pl. 23, figs. 1-5; pl. 23, fig. 1.

2013 *Hypacanthoplites?* *buloti* Latil; Klein and Bogdanova, p. 185.

2022 '*Hypacanthoplites*' aff. *buloti* Latil; Jaillard et al., p. 23, Fig. 16B.

Material and description. UJF-ID.15112: a poorly preserved fragment of an imprint, 75 mm long, with a maximum whorl-height of 55 mm, from BOA.2 (Appendix 10G).

The umbilical wall is not preserved. The flanks are weathered, showing only the basal part of the ribs, which are regularly alternating, one primary for one intercalatory. The ribs are coarse, broad, slightly flexuous, the intercalatories arising at about mid-flanks or lower. This specimen, with its broad ribs on the ventral area, is very close to '*H.*' *buloti*.

Occurrence. Bed 841 BOA.2 of Bir oum Ali, Tunisia, lower Albian, '*Hypacanthoplites*' *buloti* Zone.

Genus *Mellegueiceras* Latil, 2011

Type species. *Mellegueiceras ouenzaensis* (Breistroffer, 1953, p.13, pl. 1 fig. 1-6), by the original designation of Latil, 2011, p. 371.

Remarks. According to Lehman et al. (2020) '...Therefore, it possibly makes sense to accommodate *H. elegans* in *Mellegueiceras*.' However, the juvenile morphology of *H. elegans* has nothing in common with the genus *Mellegueiceras*. As understood by Kennedy (2000, p. 695, Figures 38a–m, 53j, k, 57a–i, k–q), *Hypacanthoplites elegans* (Fritel, 1906) shows a juvenile morphology with sharp periumbilical bullae, bullate ventrolateral tubercles, and occasional lateral tubercles, characters that are supposed to be diagnostic of the genus *Hypacanthoplites* and that are never present in the genus *Mellegueiceras*.

One juvenile acanthohoplitinid from the uppermost Aptian of Jebel Oust, Tunisia (level JOE.8, unpublished section, about 15 meters below the Aptian/Albian boundary) (unnumbered UJF-ID. specimen, Appendix 10H-J) is strictly contemporaneous of *Mellegueiceras chiahouiae* and is interpreted as a juvenile of this species. This specimen clearly shows a convex venter, narrowly rounded ventrolateral shoulders, and no trace of tuberculation.

According to Lehmann et al. (2020): 'The thickened ribs at the umbilical margin of the inner whorls in *Mellegueiceras* are very close to be called bullae...'; everything is said in this sentence: there are not bullae. Lehmann et al. (2020) discussed separately the different characters and conclude that none of these characters (irregular versus regular ribbing, tuberculation) constitutes a unique feature. However, the combination of these characters is diagnostic of the genus: irregular ribbing, non tuberculated ribs at any stage of the growth, convex venter excepted occasionally at very juvenile stages of growth. The juvenile *Mellegueiceras* have nothing in common with those of the genus *Hypacanthoplites*, as defined by Wright et al. (1997): '...Early whorl hexagonal or rectangular in section, with flat or concave venter and angular shoulder; primary ribs straight or flexuous, tuberculate at umbilical margin, and branching at lateral tubercle; secondary ribs intercalated or branching; all ribs nodose on shoulders...' (Wright et al., 1997).

Mellegueiceras chiahouiae Latil, 2011

Appendices 10E, F, 11A, 12A-D

1995 *Deshayesites callidiscus* Casey; Abdallah et al., fig. 22.6.

2011 *Mellegueiceras chihaouiae* Latil, p. 371, pl. 10, fig. 1, pl. 11, figs 1-4, pl. 12, figs 1-5 (with synonymy).

2013 *Mellegueiceras chihaouiae* Latil; Klein and Bogdanova, p. 209.

2013 *Mellegueiceras* sp., Hfaied et al., fig. 14A, B.

2019 *Mellegueiceras chihaouiae* Latil; Latil and Robert, p. 588, F6, Fig. 9B.

2020 “*Mellegueiceras*”? sp., Lehmann et al., figs 3F, G, I, J.

2020 “*Mellegueiceras*”? cf. *chihaouiae*, Lehmann et al., Fig. 3H.

2022 *Mellegueiceras chihaouiae* Latil; Jaillard et al., p. 23, Fig. 12E, F.

Material and description. UJF-886 ID. 10887 (Appendix 12A-C), 10888 (Appendices 11A, 12D) and two unnumbered specimens from SOA.29 (Hfaied et al., 2013); UJF-ID.15101 (Appendix 10E), 15102 (Appendix 10F) and one unnumbered specimen from BOAS.13. UJF-ID.15101, from BOAS.13 (Appendix 10E), is a weathered and distorted juvenile, 75 mm in diameter with feebly flexuous ribs and a ribbing density (dc/Wh) of 0.14. UJF-ID.15102, from BOAS.13 (Appendix 10F), is a 90° sector of a phragmocone, with a maximum whorl height at about 60 mm, which is in all aspects, similar to the material described by Latil (2011) from Jebel Harraba: strong, coarse, straight to feebly flexuous, radiate to feebly prorsiradiate, irregularly alternating primary and intercalary ribs; primaries arising at the umbilical seam, developing a radially elongated swelling at the shoulder, bifurcating or trifurcating near mid-flank, while there are occasionally intercalated ribs that arise at mid-flank. Coarse ribs cross over the ventral area with intercoastal spaces narrower than ribs. Ribbing density (dc/Wh) is 0.11. UJF-ID.10887 (Appendix 12A-C), is a strongly weathered and distorted fragment of phragmocone with a ribbing density of 0.11. UJF-ID.10888 (Appendices 11A, 12D) is an adult phragmocone, with an estimated diameter of 200 mm. With age, the primary ribs tend to trifurcate at the inner third of the flanks and the ribs become more flexuous. The whorl section is high, oval, with a maximum width at about the inner third of the flanks. The sutures are always strongly weathered.

Remarks. The specimens figured as *Mellegueiceras* sp. by Hfaied et al. (2013, Fig. 14A, B), were originally interpreted as a possible ancestor of *M. chihaouiae*. Actually, the whole material from Bir Oum Ali is very close to *M. chihaouiae*, and seem to enter the variability of *M. chihaouiae*. We herein consider that the material figured by Lehmann et al. (2020, fig. 3F-J) as “*Mellegueiceras*”? sp. and “*Mellegueiceras*”? cf. *chihaouiae* falls within the variability of *Mellegueiceras chihaouiae*.

At Bir Oum Ali, Ben Youssef et al. (1985) mentioned *Deshayesites callidiscus*, *D. cf. planus*, *D. weissii* and *D. furcata* at about 20 meters below the first *Knemiceras* bed. This level is very probably equivalent to the bed BOAS.13 in Jaillard et al. (2022). One of these specimens is figured by Abdallah et al. (1995, fig. 22.6) as *Deshayesites callidiscus* Casey. This specimen, an adult phragmocone with a diameter of about 130 mm, is closely related to our material. It seems to differ only by its finer ribs, which is probably due to its preservation with a thin layer of calcified shell.

4. Biostratigraphic and phylogenetic discussions

The Aptian-Albian Ammonite zonation used herein are the regional biozonation established by Latil (2011) and the zonation proposed by Szives et al. (2023) to be the Standard Mediterranean Ammonite Zonal Scheme proposed by Szives et al. (2023).

The Aptian-Albian boundary as defined by Kennedy et al. (2014, 2017) cannot be used in Tunisia. On the basis of the ammonite successions, this boundary probably occurs within the interval between the top of the *Mellegueiceras chihaouiae* Horizon and the first occurrence of

the genus *Douvilleicer* (*Douvilleicer* sp. nov.? in Latil, 2011). This interval is herein interpreted as the Aptian/Albian transition.

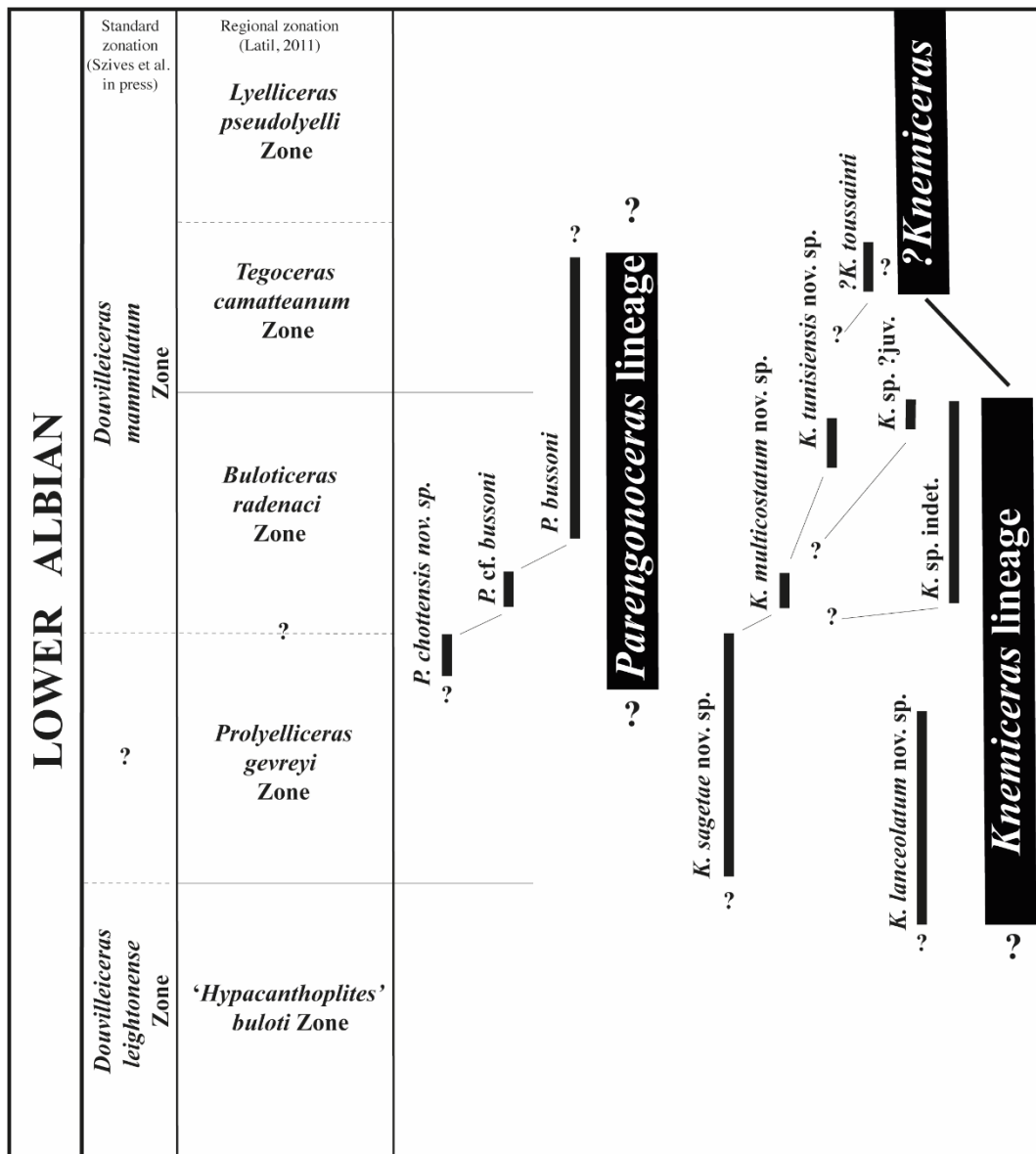


Figure 21. Phylogeny of knemiceratid ammonites of the lower Albian of southern Central Tunisia.

4.1 Comments about the phylogeny and intraspecific variability of knemiceratids.

According to Klinger and Kennedy (1989, p. 383): ‘Arnould-Saget (1956) attempted to explain the extreme intraspecific variation in *Knemiceras* from southern Tunisia. Here both ornament and suture lines are very variable. According to her, the variations are individual and irrational; their systematic study is sterile from an evolutionary point of view, and variation is ascribed to paleobiological causes. The Tunisian *Knemiceras* lived in a stable environment in the neritic zone at the margins of the old Saharan mainland, without important detritus deposits and without violent perturbation. These optimum conditions did not create any need for adaptation; the life potential of *Knemiceras* wasted itself in a useless and directionless polymorphism, but also underlines the mode of life of these animals-more benthic than neritic!’ As mentioned above, the taxonomic study of the engonoceratids of the

Chotts, as carried out by Arnould-Saget (1956), was based on 59 specimens that had been collected by geologists of the Petroleum Research Society of Tunisia (SEREPT). This approach was purely morphological, and did not take in account the stratigraphic position of the material. The alleged extreme intraspecific variation in knemiceratid faunas of Tunisia by Arnould-Saget is simply the result of a total lack of stratigraphic control. Not only is there no extreme intraspecific variation in *Knemiceras*, there is also a biological diversity and evolutionary trends among two different ammonite lineages: *Knemiceras* and *Parengonoceras* (Fig. 21).

The genus *Knemiceras* appears at Bir Oum Ali at the top of the fourth depositional sequence (SA; base of ‘*Knemiceras* Beds’, ‘*Hypacanthoplites*’ *buloti* Zone) during a significant transgressive trend in a low energy shallow marine environment (Jaillard et al., 2022), and reaches its highest abundance in the fifth depositional sequence (lower part of ‘*Knemiceras* Beds’, *Prolyelliceras* *gevreyi* Zone). Slight periodical, environmental changes (internal to slightly more external platform), allowed us to separate two different species of *Knemiceras*: *K. sagetae* nov. sp. and *K. lanceolatum* nov. sp. The genus *Knemiceras* is scarcer in the sixth depositional sequence (*Bulotoceras* *radenaci* Zone), and is lacking in the seventh depositional sequence (*Tegoceras* *camatteanum* Zone), seeming to disappear before the end of the lower Albian, probably at the transition between the *Tegoceras* *camatteanum* and *Lyelliceras* *pseudolyelli* zones. It probably gives rise to new, obscure morphologies with ventrolateral tubercles that alternate on the venter, represented by ?*Knemiceras* *toussainti* Pervinquière. The local apparition and flourishing of *Parengonoceras* is concomitant with the rarefaction of *Knemiceras* in a very shallow marine, subtidal to intertidal platform, which, however, represents the deepest, most open marine depositional environments in the studied interval (Jaillard et al. 2022). This is consistent with the extreme scarcity of *Knemiceras* and the flourishing of *Parengonoceras* in more external environments of Central Tunisia (Latil, 2011).

This approach shows that we should be extremely careful with the temptation to interpret knemiceratid faunas as a single extremely variable species in the absence of stratigraphical and/or ecological control (Arnould-Saget, 1956; Kennedy et al., 2009).

4.2. Remarks about the age of *M. chihaouiae*.

According to Lehmann et al. (2020): ‘A stratigraphic position as lowermost Albian and not upper Aptian (Latil, 2011) is confirmed by data from Morocco where “*Mellegueiceras*” (sic!) *chihaouiae* is associated with *Douvilleiceras* (Luber et al., 2017; 2019)’. This is no more than an assertion, unsubstantiated by relevant evidence. As pointed out by Giraud et al. (2020), ‘The use of *Mellegueiceras* *chihaouiae* as an index of a lower Albian zone by Luber et al. (2017) is erroneous. As matter of fact, according to Latil (2011) and Ben Chaabane et al. (2019), *M. chihaouiae* cannot be restricted to the lower Albian but rather characterizes the Aptian-Albian transition’. The co-occurrence of *M. chihaouiae* and *Douvilleiceras* *leightonense* is totally excluded since *M. chihaouiae* is replaced by the derived species *Mellegueiceras* *hameimaensis* Latil, 2011 in the ‘*Hypacanthoplites*’ *paucicostatus* Zone of Tunisia.

Furthermore, *Mellegueiceras* *chihaouiae* has been found in many places in Tunisia at the same stratigraphic interval, much below the first record of the genus *Douvilleiceras*. The specimens identified as *Mellegueiceras* *chihaouiae* by Luber et al. (2017 and 2019) are not figured and the specimen figured as *Mellegueiceras* cf. *chihaouiae* by Luber et al. (2019, fig. 12.9,10) is a poorly preserved specimen that comes from a condensed level. The co-occurrence of *Mellegueiceras* *chihaouiae* and ‘*Hypacanthoplites*’ *paucicostatus* in the same stratigraphical level is not documented in Tunisia (Latil, 2011 and this work, Fig. 22).

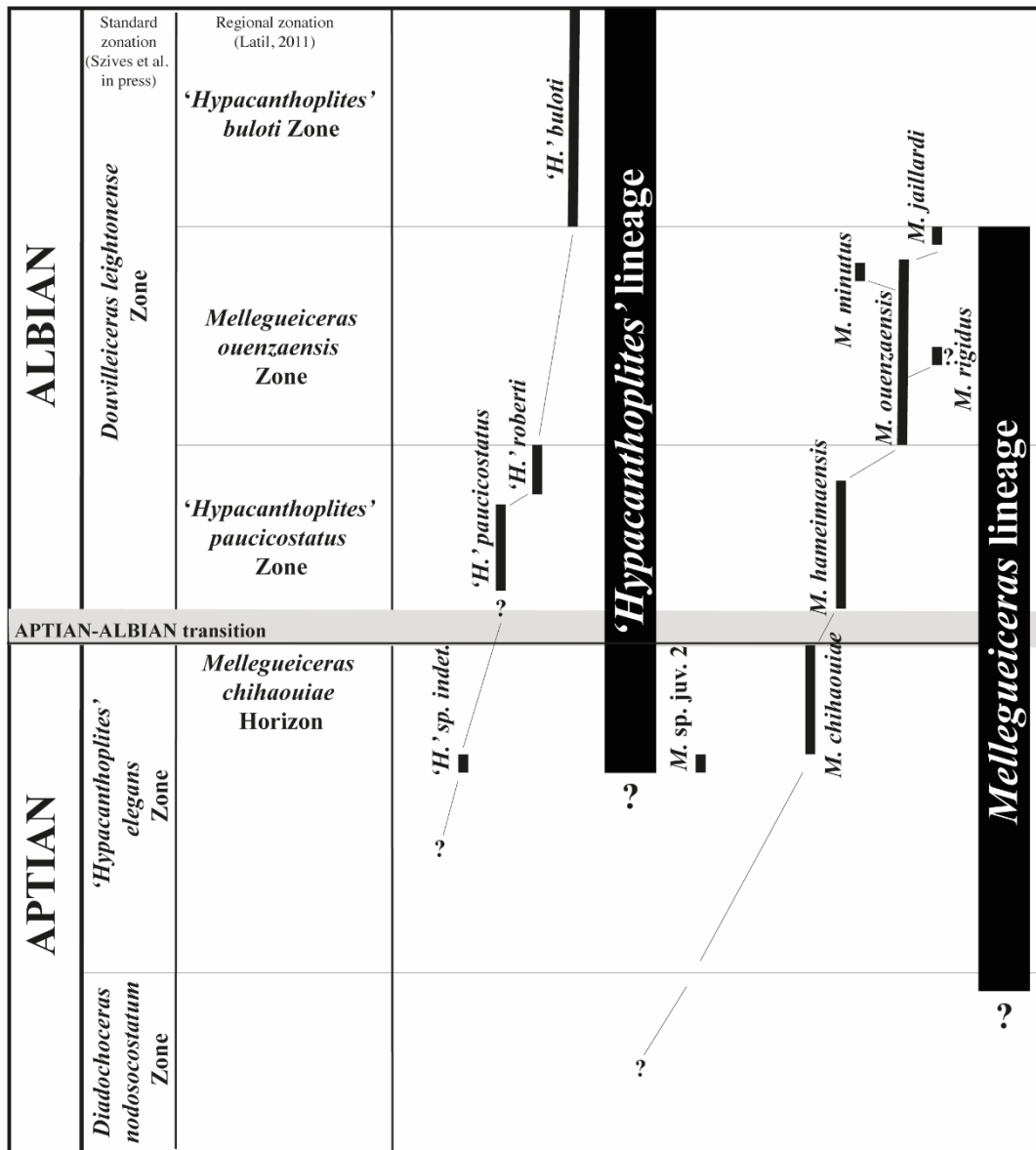


Figure 22. Phylogeny of uppermost Aptian and lower Albian acanthoplitinid ammonites in Tunisia.

Another unfounded assertion in the paper by Lehmann et al. (2020) is: ‘An alleged condensation by “reworked phosphatised *Epicheloniceras*” (Latil, 2011: 372), respectively “Reworked, phosphatised, juvenile *Epicheloniceras* sp.” (Ben Chaabane et al., 2019: 588) is actually based on a misidentification. These reported cheloniceratids are actually douvilleiceratids, possibly of a hitherto new genus (pers. obs. by one of us: LGB)’. These two specimens, comes from reworked phosphatized nodules, and are herein identified as *Epicheloniceras* sp. aff. *buxtorfi* (Jacob and Tobler, 1906, Fig. 33E, F). These fragments of juvenile phragmocones, preserved as more or less weathered internal molds, have a depressed whorl section ($Wb/Wh = 1.37$). The inner whorls are known only by the ventral area, bearing small ventrolateral tubercles.

The best-preserved fragment (UJF-ID.15257), 33 mm long (estimated diameter of 50mm), bears about 6 radial, straight ribs to quarter-whorl, consisting mainly in primaries with few intermediates in uniform relief, all of them being strongly elevated on the venter and separated by wide concave interspaces. The primaries arise on the umbilical wall, the

intermediaries arise just above the periumbilical edge. At this stage of the growth, no umbilical tubercle can be seen, there are small, coarse radially elongated lateral tubercles, and small, coarse ventrolateral tubercles that tend to weaken with age. The ribs are only slightly concave on the venter. This specimen differs from *Epicheloniceras buxtorfi* (Jacob and Tobler, 1906) only by its coarser ribs, its broader venter and its slightly more depressed whorl section. At Bir Oum Ali, *Mellegueiceras chihaouiae* has been found in the third sequence, below the major basal discontinuity of S4. According to Hfaiedh et al. (2013), Jaillard et al. (2022) and this work, the age of this level is undoubtedly upper Aptian.

Occurrence. Bed BOAS.13 of Bir Oum Ali, Tunisia, Aptian, *Mellegueiceras chihaouiae* Horizon, top of the *Hypacanthoplites elegans* Zone. The species has been found in many places of Tunisia within the same stratigraphic interval (Latil, 2011; Ben Chaabane et al., 2019; this work).

4.3. Comments about the phylogeny of Tunisian acanthoplitid ammonites

Two parallel lineages have been identified in the uppermost Aptian and earliest Albian of Tunisia (Latil, 2011 and this work) (Fig. 22):

1. A *Mellegueiceras* lineage with *M.* sp. juv., *M. chihaouiae*, *M. hameimaensis*, *M. ouenzaensis-rigidus-minutus* and *M. jaillardi*;
2. A ‘*Hypacanthoplites*’ like lineage with ‘*H.*’ sp., ‘*H.*’ *paucicostatus*, ‘*H.*’ *roberti*, surviving everywhere to the *Mellegueiceras* lineage with *H. buloti*.

These two lineages most probably take root within an old stock in the *Diadochoceras nodosocostatum* Zone, a point that remains to be investigated. It seems obvious that these two lineages belong to two different genera having nothing in common with European faunas but superficial resemblances and probable common ancestors. The true *Hypacanthoplites* are very rare and are known only by four juvenile specimens from the lower Albian (‘*Hypacanthoplites*’ *buloti* Zone) of Hameima, identified as ‘*Hypacanthoplites*’ cf. *inflatus* Sornay, 1955 (Latil, 2011, p. 379, figs 43, 44, pl. 25, figs 1-9), and by three juvenile specimens from the upper Aptian (*Mellegueiceras chihaouiae* horizon) of Bir Oum Ali, herein identified as *Hypacanthoplites* cf. *H. plesiotypicus* (Fritel, 1906) *sensu* Casey (1965), non Fritel (1906) (Appendix 11B-D).

5. Concluding remarks.

Our paleontological approach of the ammonite faunas of the Chott Basin, based on an abundant bed-by-bed collected material, allows us to reinterpret the taxonomy of the engonoceratids of southern Central Tunisia as follows:

1. The concept of intraspecific variability is revisited and the alleged huge variability of lower Albian engonoceratids is tempered by the fact that both ecological and stratigraphical controls have a significant impact on taxonomy.
2. Two parallel lineages are documented with a possible common origin at the base of the Albian: a *Knemiceras* lineage with their older known representants that are contemporaneous of ‘*Hypacanthoplites*’ *buloti* and evolve during the early Albian before giving rise to new morphologies (?*Knemiceras toussainti*); and a *Parengonoceras* lineage that is closely related to the genus *Knemiceras*.
3. The distinction between the two contemporaneous species *Knemiceras sagetae* nov. sp. and *Knemiceras lanceolatum* nov. sp. is clearly due to environmental constraints, as *K. lanceolatum* represents more external deposits than *K. sagetae*.

4. *Knemiceras sagetae* nov. sp. is interpreted as a polymorphic species comprising three morphotypes.

5. There is no evidence of sexual dimorphism. The hypotheses concerning the evolution of the acanthohoplitinids of Tunisia (Latil, 2011; Latil and Robert, 2019) are supported by the data in south Central Tunisia:

1. The presence of two lineages of acanthohoplitinids (*Hypacanthoplites* and *Mellegueiceras*) is confirmed, as well as
2. the presence of true *Hypacanthoplites* in the uppermost Aptian of Tunisia;
3. The upper Aptian age of *Mellegueiceras chihaouiae* is also confirmed.

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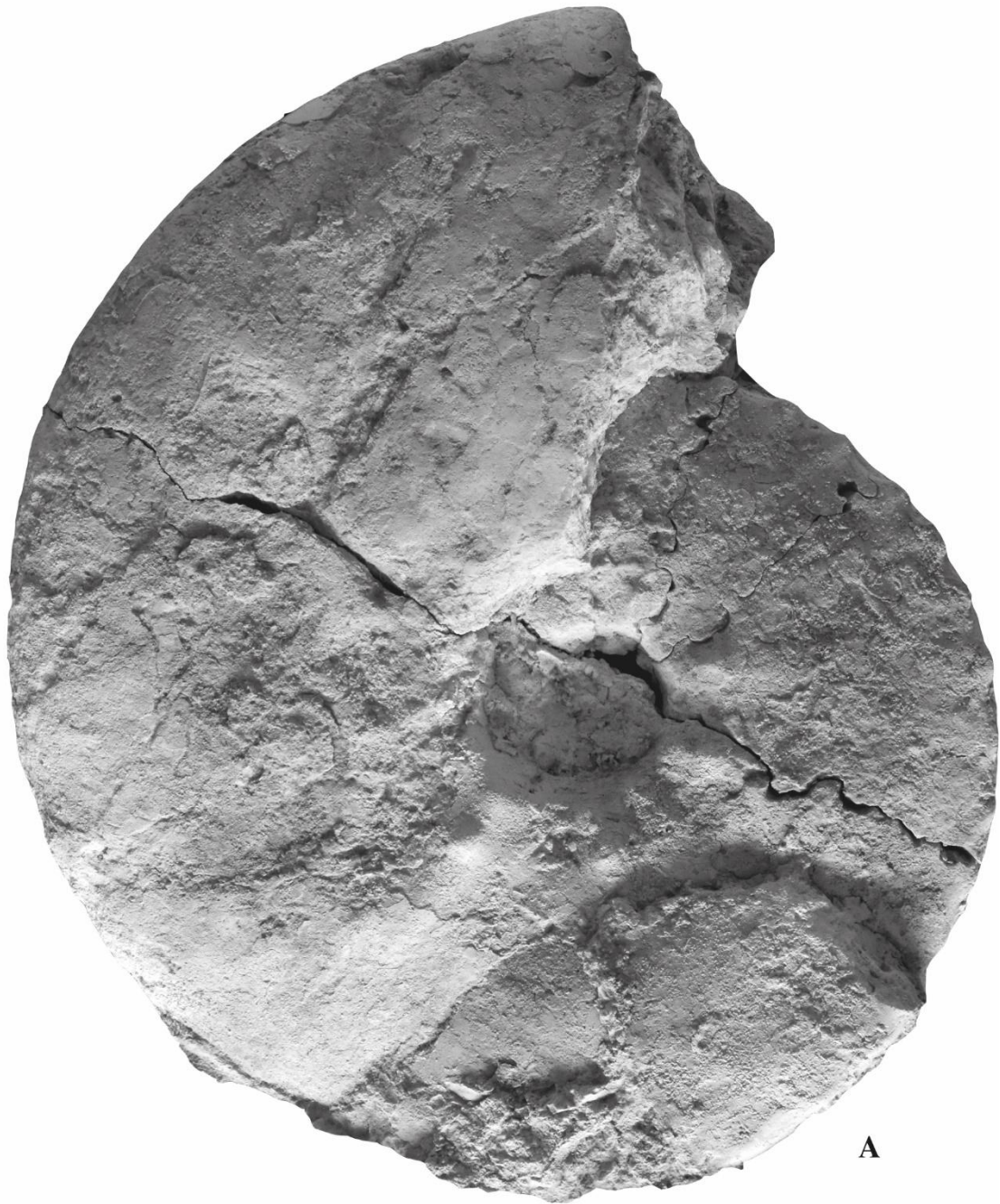
Appendix



*Appendix 1. A portrait of Suzanne Arnould-Saget (1920-1989) who first figured *Knemiceras* with two rows of periumbilical tubercles (1956), thanks to Mme Dominique Arnould.*

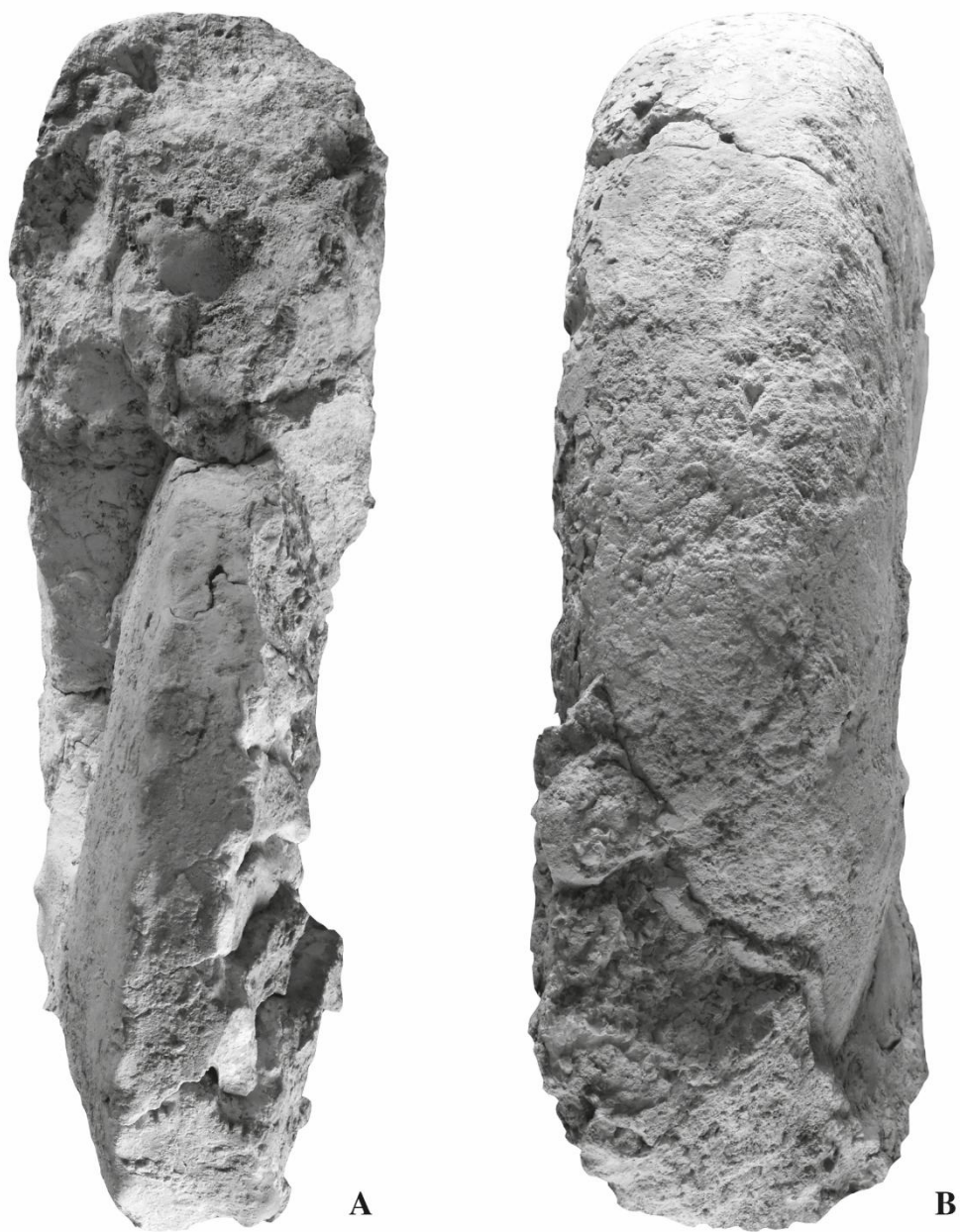


Appendix 2. (A) *Knemiceras sagetae* nov. sp., UJF-ID.15105, the holotype, morphotype 1 from BOA.5, *Polyelliceras gevreyi* Zone, lower Albian. Scale bar is 50 mm

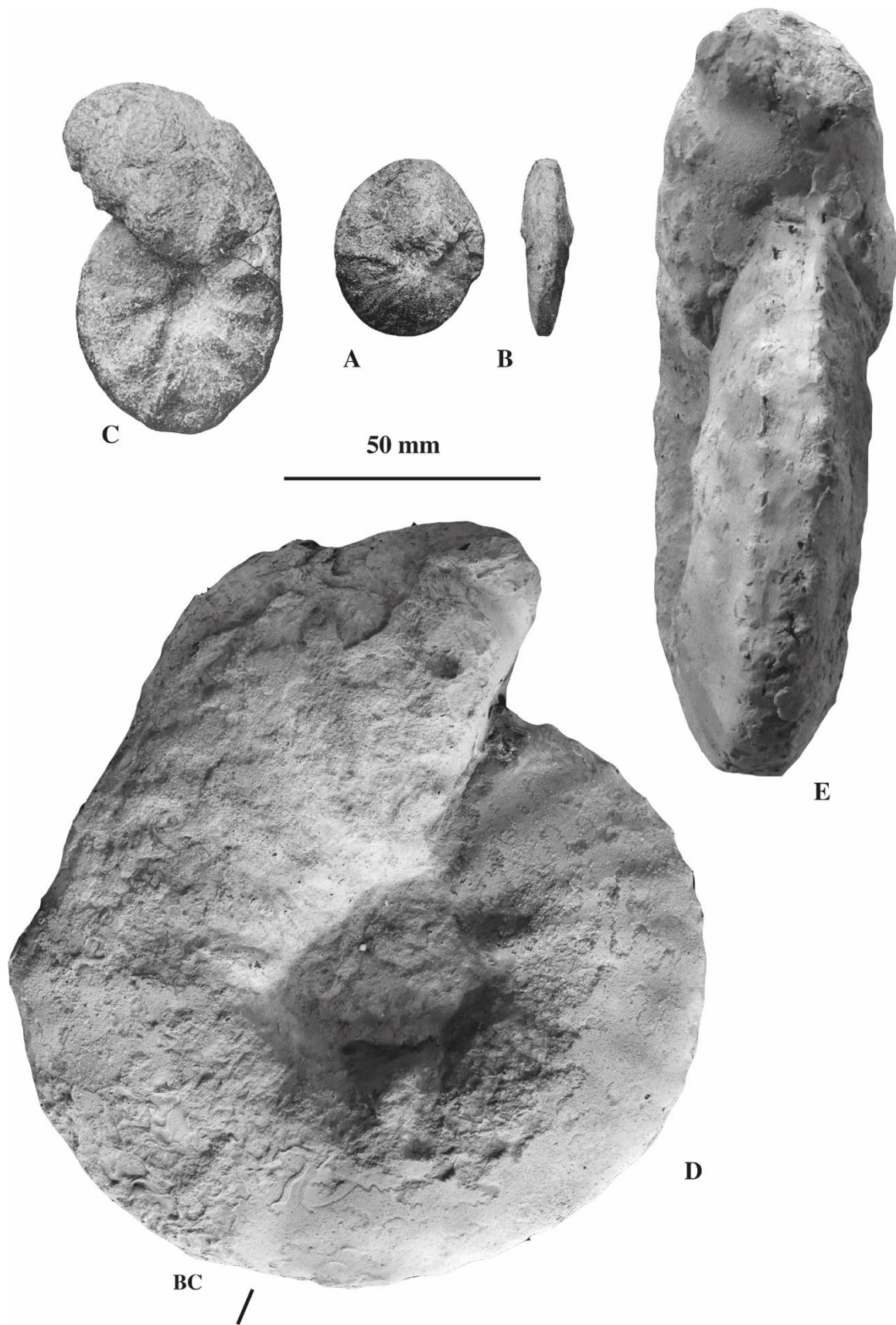


50 mm

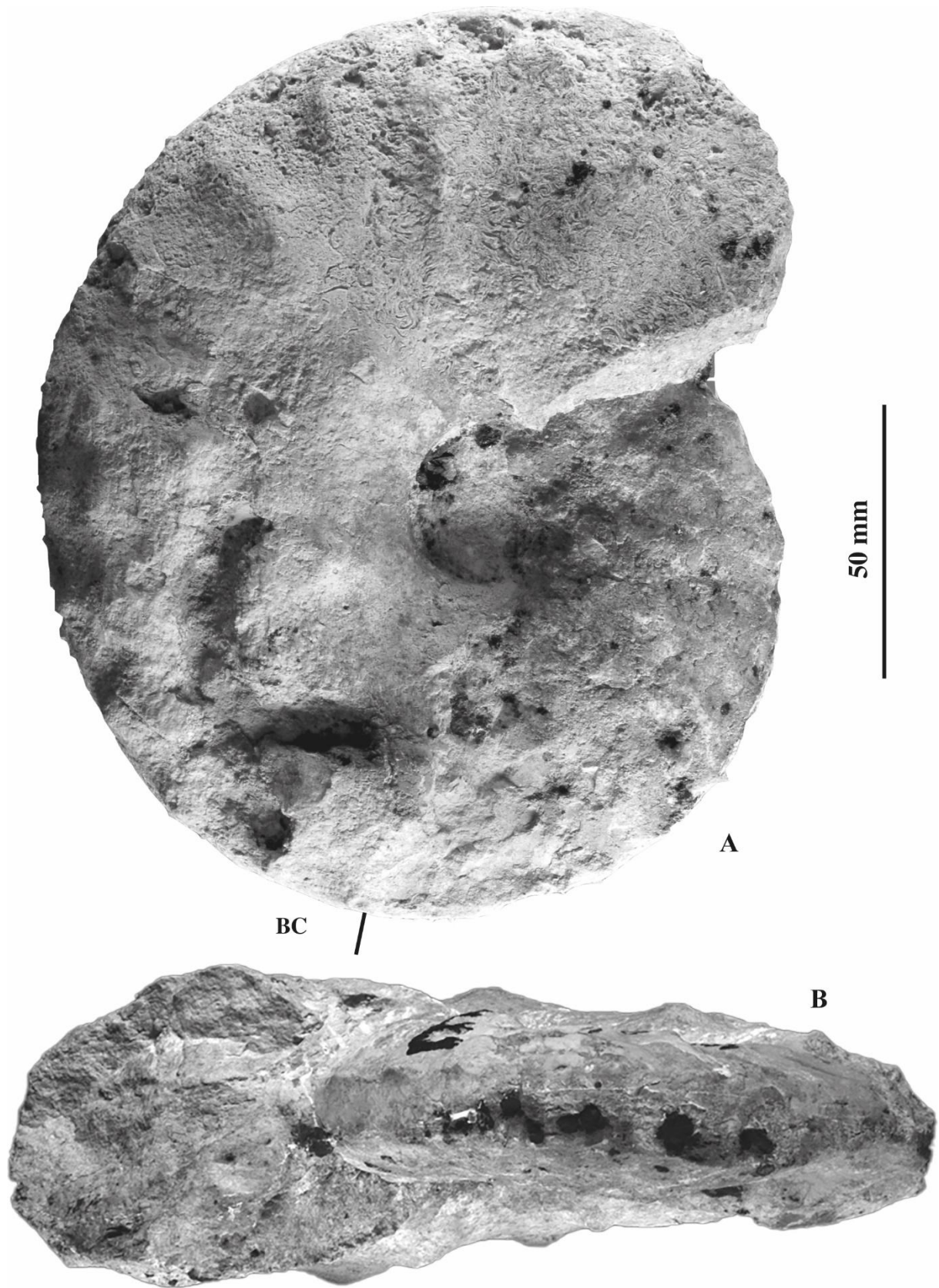
Appendix 3. (A) *Knemiceras sagetae* nov. sp., *Polyelliceras gevreyi* Zone, lower Albian; (A-C) UJF-ID.15223, morphotype 1, from FA.13. Scale bar is 50 mm



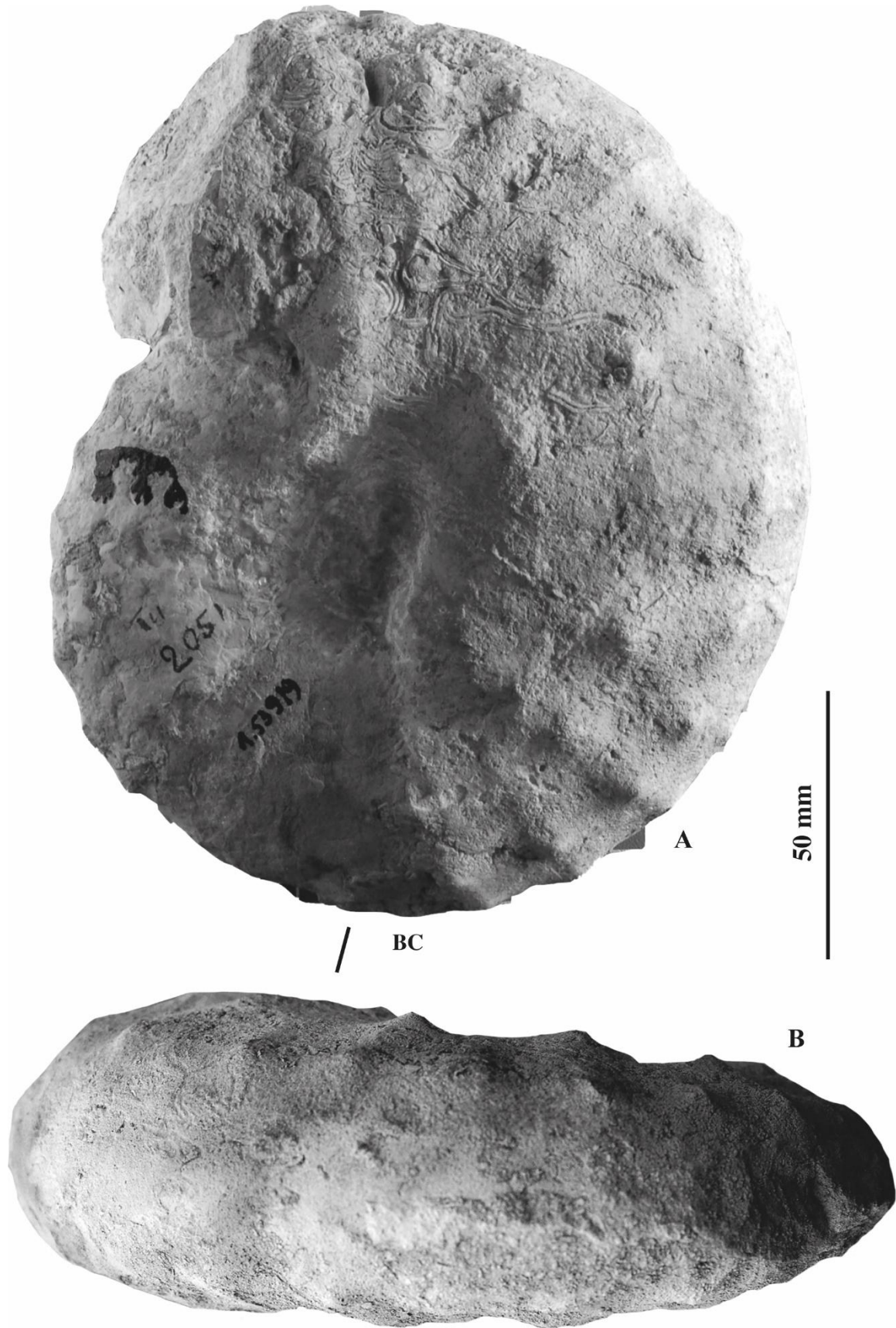
Appendix 4. (A, B) *Knemiceras sagetae* nov. sp., Prolyelliceras gevreyi Zone, lower Albian;
(A-C) UJF-ID.15223, morphotype 1, from FA.13. Scale bar is 50 mm



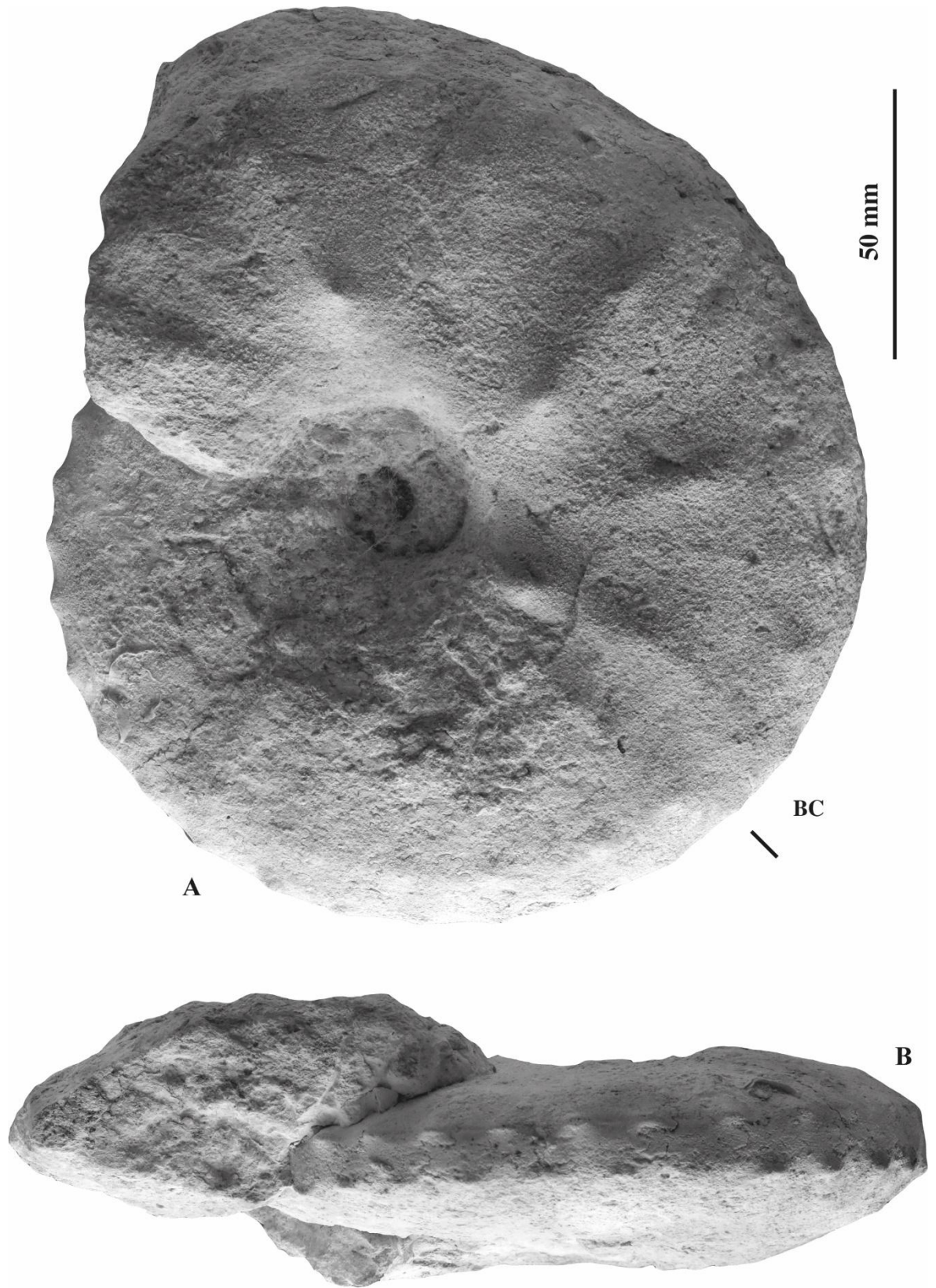
Appendix 5. (A-E) ?*Knemiceras toussainti* (Pervinquière, 1907); (A-C) the original figuration of Pervinquière, pl. 9, fig. 7, from the Albian of Foug el Argoub; (D, E) the holotype of *Knemiceras saharæ* Collignon, 1965, pl. B, fig. 1, MNHN-R53932, from the Albian of Foug el Argoub. Scale bar is 50 mm



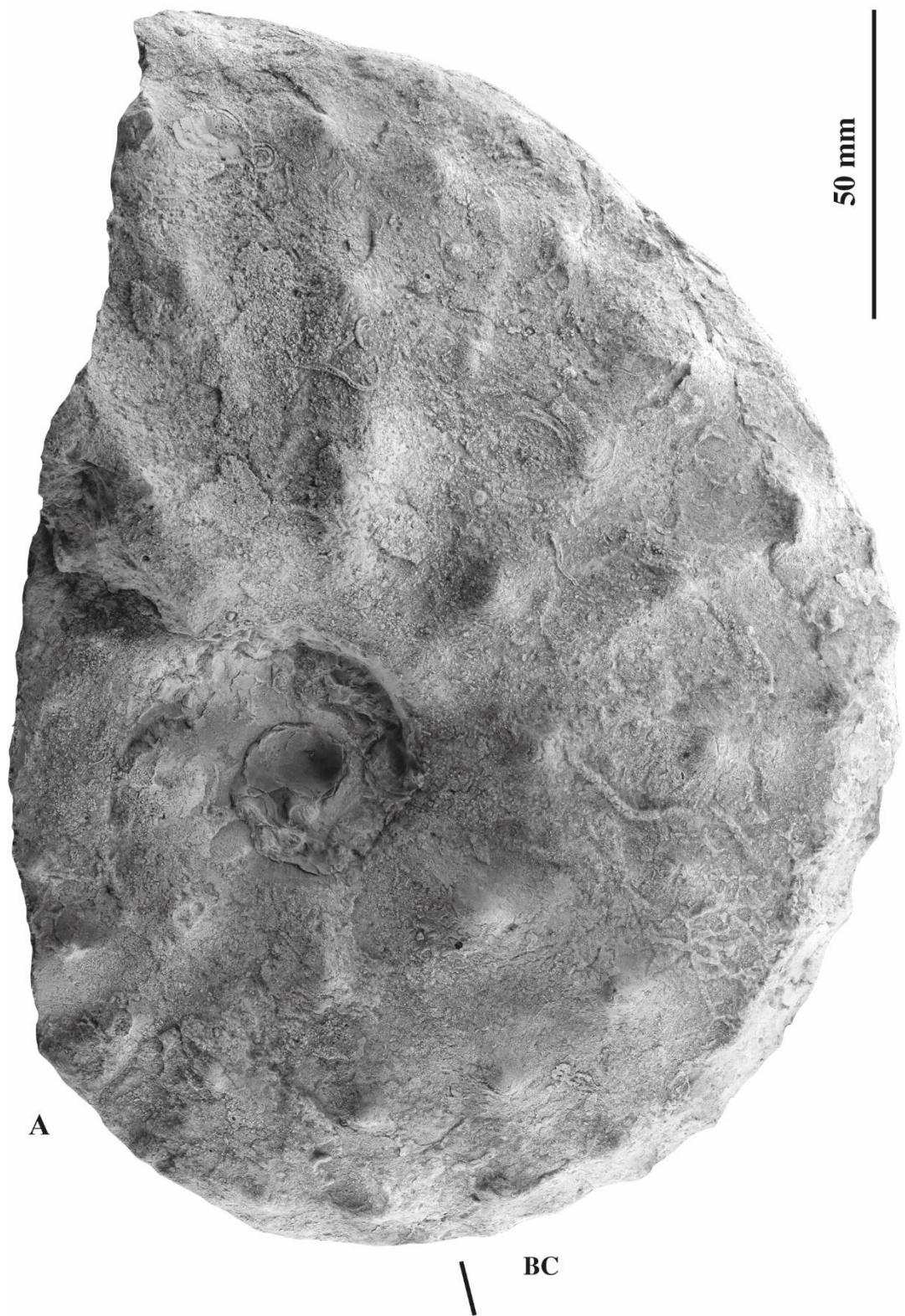
Appendix 6. (A, B) *Parengonoceras bussoni* Collignon, 1965, MNHN-R53919, the holotype, from Foum el Argoub, at or slightly above FA19 or FO.8, upper part of *Buloticerus radenaci* Zone - *Tegoceras camatteanum* Zone, Lower Albian. Scale bar is 50 mm



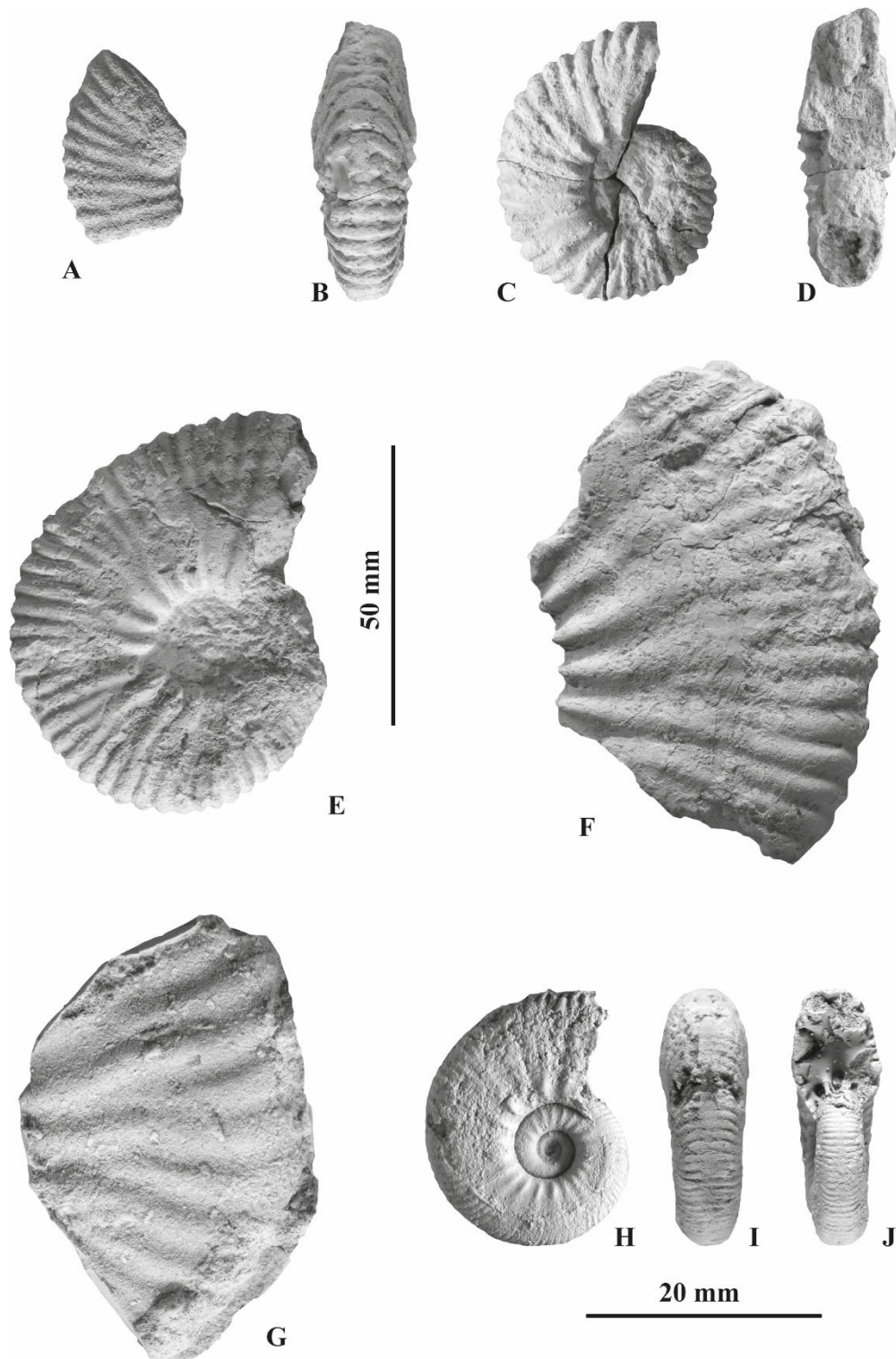
Appendix 7. (A, B) *Paregonoceras bussoni* Collignon, 1965, MNHN-R53919, the holotype, from Foug el Argoub, at or slightly above FA19 or FO.8, upper part of *Bulotoceras radenaci* Zone - *Tegoceras camatteanum* Zone, Lower Albian. Scale bar is 50 mm



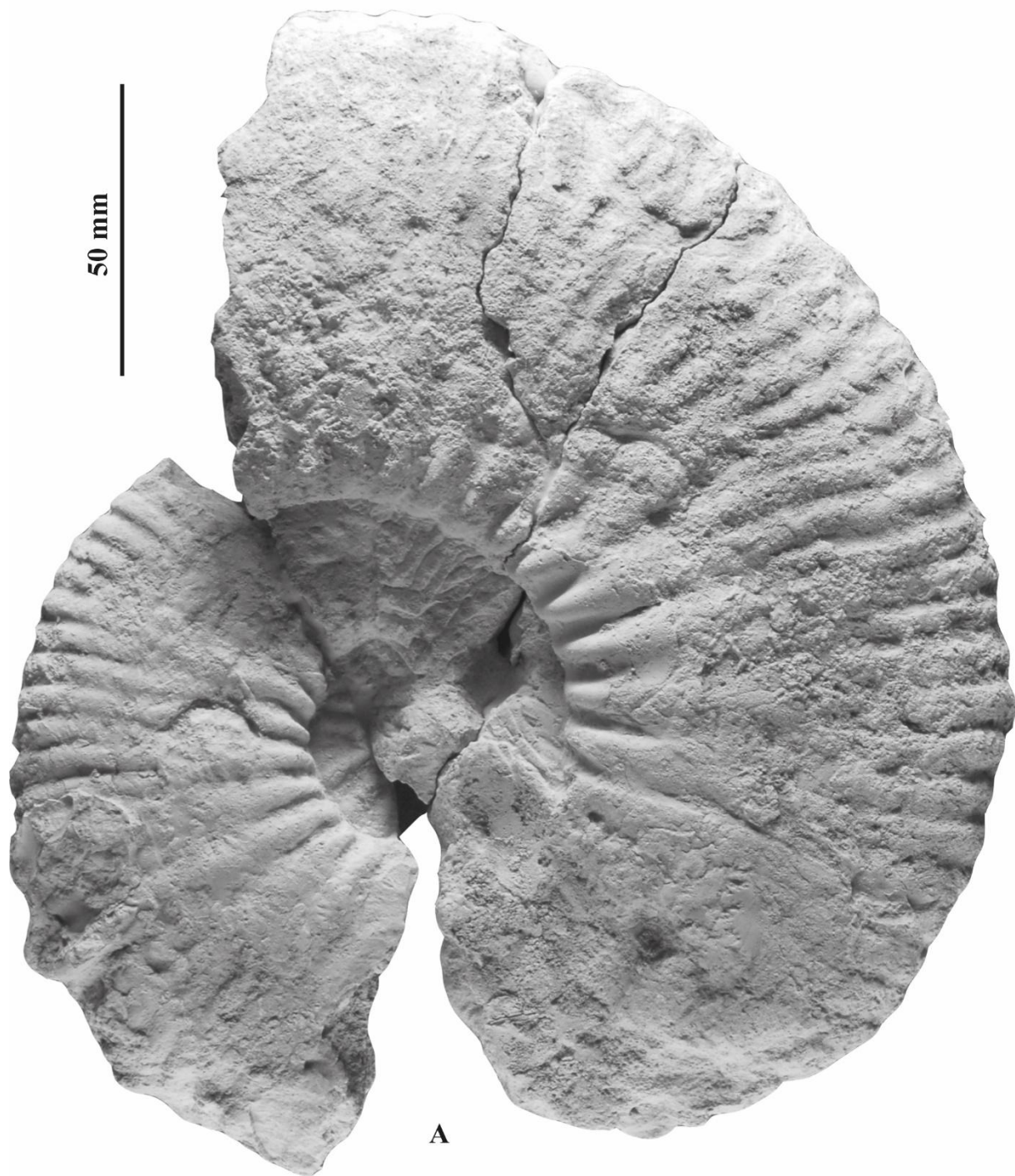
Appendix 8. (A, B) *Parengonoceras bussoni* Collignon, 1965, UJF-ID.15119 from Rhadouane, upper part of *Buloticerias radenaci* Zone - *Tegoceras camatteanum* Zone, Lower Albian. Scale bar is 50 mm



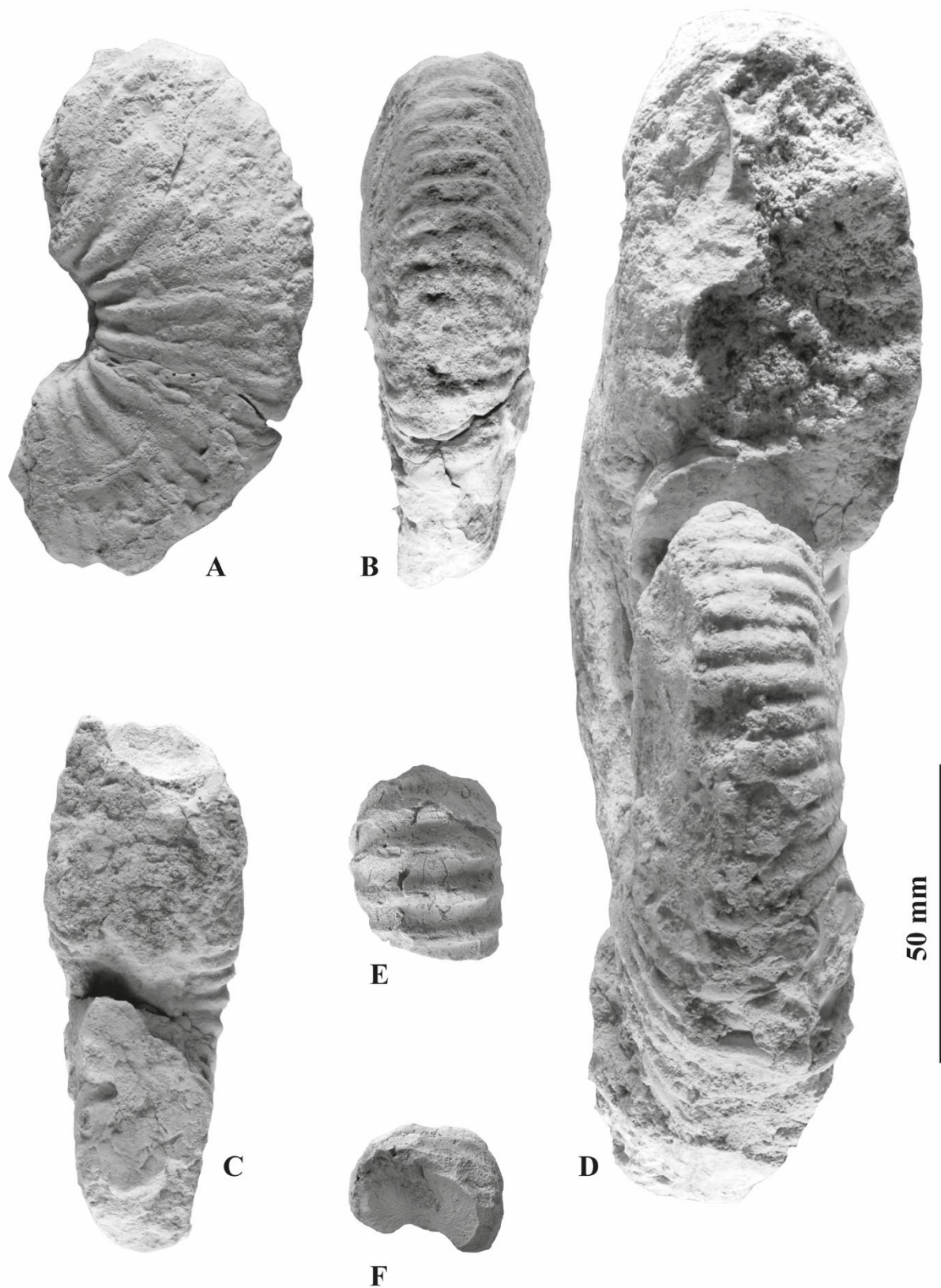
Appendix 9. (A) *Parengonoceras bussoni* Collignon, 1965, UCBL-FSL 85571 from the Albian of Algeria, unknown locality of Aïn Rich area. Scale bar is 50 mm



Appendix 10. (A) ‘Hypacanthoplites’ *sp. indet.*, UJF-ID.15100, from BOAS.12; (B-D) Hypacanthoplites *cf.* *H. plesiotypicus* (Fritel, 1906) *sensu* Casey (1965), *non* Fritel (1906), UJF-ID.15099, from BOAS.12, Mellegueiceras *chihaouiae* Horizon, Hypacanthoplites *elegans* Zone; (E, F) Mellegueiceras *chihaouiae* Latil, 2011, (E) UJF-ID.15101, from BOAS.13, Mellegueiceras *chihaouiae* Horizon, Hypacanthoplites *elegans* Zone; (F), UJF-ID.15102, from BOAS.13; (G) ‘Hypacanthoplites’ *aff.* ‘H.’ *buloti* Latil, 2011, UJF-ID.15112, from BOA.2, lower Albian, ‘Hypacanthoplites’ *buloti* Zone; (H-J) Mellegueiceras *chihaouiae* Latil, 2011, unnumbered specimen from UJF-ID, from JOE.8, Jebel Oust, Tunisia, uppermost Aptian, Mellegueiceras *chihaouiae* Horizon. Scale bar is 50 mm for A-G, 20 mm for H-J



Appendix 11. (A) *Mellegueiceras chihaouiae* Latil, 2011, UJF-ID.10888, from SOA.29, *Mellegueiceras chihaouiae* Horizon, *Hypacanthoplites elegans* Zone. Scale bar is 50 mm



Appendix 12. (A-D) *Mellegueiceras chihaouiae* Latil, 2011, (A-C) UJF-ID.10887, from SOA.29; (D) UJF-ID.10888, from SOA.29, both from the *Mellegueiceras chihaouiae* Horizon, *Hypacanthoplites elegans* Zone; (E, F) *Epicheloniceras* sp. aff. *buxtorfi* (Jacob and Tobler, 1906), UJF-ID.15257, reworked phosphatized ammonite from Jebel Harraba, Central Tunisia. Scale bar is 50 mm