Knemiceras gracile DOUVILLÉ, 1916: a misunderstood Early Albian ammonite from north Sinai (Egypt), and considerations on the genus Platiknemiceras BATALLER, 1954

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Abstract
The taxonomic treatment of the Engonoceratoidea HYATT, 1900 (WRIGHT et al., 1996) is problematic and confusing, and recently has gained the attention of many palaeontologists (ROBERT, 2002; BUJTOR, 2010; BULOT, 2010; LATIL, 2011). It appears that most of the described genera within this superfamily were based on morphological features, without stratigraphic and/or phylogenetic control. In particular, the genus Platiknemiceras BATALLER, 1954, seems to represent a classic example of this problem. Knemiceras gracile DOUVILLÉ, 1916, from the Early Albian of Maghara area, north Sinai, Egypt, referred by CASEY (1961) to Platiknemiceras, appears to be an often misinterpreted species. Species identified as members of the genus Platiknemiceras BATALLER, 1954 in the literature, from Iran, Lebanon, Egypt, Tunisia, Algeria, Spain, France Peru, Colombia, Venezuela, USA and Japan are discussed herein, in order to revise their taxonomic positions. The type species, Platiknemiceras bassei BATALLER 1954, is redescribed. A re-examination of the relationships between Knemiceras gracile and other members of the genus Platiknemiceras strongly suggests that this latter genus is polyphyletic.

Keywords
Albian, Ammonites, Engonoceratoidea, Platiknemiceras, Parengonoceras, Knemiceras, Egypt, Spain, Tethys.

I. INTRODUCTION
Knemiceras gracile DOUVILLÉ, 1916 was described from the Albian of the Maghara area, north Sinai, Egypt from a single specimen. Since that time, many specimens have been reported in the literature as belonging to this species. It has even been regarded as an index species for a regional biozone of the Early Albian (ABU-ZIED, 2008). Since CASEY (1961), it has been placed within the genus Platiknemiceras BATALLER, 1954, and it seems that this taxon has been often misinterpreted and its application in the literature is confusing.

The genus Platiknemiceras was originally created by BATALLER (1954) as a subspecies of Knemiceras for Knemiceras (Platiknemiceras) bassei BATALLER, 1954 (p. 175, fig. 1): A species that have a compressed section, narrow umbilicus and feeble, flexuous costation. It was interpreted by CASEY (1961) as a genus close to ParengonocerasSPATH, 1924, but was characterized by a thinly discoidal shell, accompanied by an extreme reduction of sculpture. It should be noted that Platiknemiceras bassei is known only from juvenile specimens, which are morphologically very close to the juvenile stages of growth of Parengonoceras species. CASEY referred several tethyan ammonites to this genus for which their taxonomic positions are discussed below. Many ammonites with compressed whorl section and reduced ornament, have been subsequently attributed to this morphological genus, including: Platiknemiceras sequanense DESTOPMENSE, 1979; Platiknemiceras colombiana ETAYO-ŞRNA, 1979; Platiknemiceras caseyi MATSUMOTO 1980; Platiknemiceras valencianum MAS & WIEDMANN, 1980; and Platiknemiceras flexuosum KENNEDY et al., 1998. The taxonomic positions of all this material are herein reconsidered.

BULOT (2010, p. 171) pointed out that the genus Platiknemiceras was most probably polyphyletic and retained only the following species: Platiknemiceras bassei BATALLER, 1954; Platiknemiceras hachouri (DUBOURDIEU, 1953); and Platiknemiceras flexuosum KENNEDY, LANDMAN & COBBAN, 1998. BUJTOR (2010, p. 13) adopted an even more conservative conception of the genus, close to that of CASEY (1961). LATIL (2011, p. 349) regards the type species of Platiknemiceras as a direct ancestor of the genus Parengonoceras s.str. and placed it within this latter genus. Both Knemiceras gracile and Platiknemiceras bassei are herein redescribed and discussed, in order to clarify the phylogenetic relationships between the Albian species previously referred to the genus Platiknemiceras BATALLER, 1954.

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II. CONVENTIONS

All dimensions of specimens are given in millimetres: 
D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilical diameter, v = distance between the two ventrolateral edges. Figures in parentheses are dimensions as a percentage of the diameter at the point of measurement.

The following conventions are used to indicate the repositories of specimens mentioned in the text: UJF.ID, Institut Dolomieu, Grenoble, France; FSL, Paleontological collections of the Université Claude Bernard, Lyon, France; MHNP, Museum National d’Histoire Naturelle de Paris, France; MGSB, Museo Geológico del Seminario de Barcelona, Spain; NHML, Natural History Museum of London, England; UNCMHN, Universidad Nacional de Colombia, Museo de Historia Natural, Bogota, Colombia.

III. SYSTEMATIC PALEONTOLOGY

Order Ammonoidea ZITTEL, 1884
Suborder Ammonitina HYATT, 1889
Superfamily Engonoceratoidea HYATT, 1900
Family Knemiceratidae HYATT, 1903
Genus Knemiceras BÖHM, 1898
[= Iranoknemiceras COLLIGNON, 1981a, 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.

See full discussions in BULOT (2010) and LATIL (2011).

Knemiceras gracile H. DOUVILLÉ, 1916
Figs 1, 2

1916. Knemiceras gracile H. DOUVILLÉ, p. 128, pl. 16, fig. 9; text-fig. 42.

? 1940. Engonoceras gracile DOUVILLÉ & BASSE, p. 438, pl. 4, fig. 1; text figs 9, 10.


non 2006. Knemiceras gracile DOUVILLÉ, 1916.–ABU-ZIED, fig. 2r, pl. 6, figs 10-12.


Holotype: The holotype by monotypy is the specimen figured by H. DOUVILLÉ (1916, pl. 9, text-fig. 42), from NW of Talat el Fellahin (now Gabal Maaza), SE of Gabal Maghara, north Sinai, Egypt. The holotype, herein re-figured (Figs 1, 2), is deposited in the paleontological collections of the Université Claude-Bernard, Lyon as FSL.EM.1788 (former collections of the École des Mines de Paris).

Dimensions of the holotype:
FSL.EM.1788: D: 53.0 (100) – Wh: 30.0 (57) – Wb: 16.0 (30) – U: 5.0 (9) – v: 2.4 (5) – Wb/Wh: 0.53
FSL.EM.1788: D: 70.0 (100) – Wh: 38.0 (54) – Wb: 21.0 (30) – U: 6.5 (9) – v: 3.7 (5) – Wb/Wh: 0.55

Description: A single specimen preserved as calcareous internal mould of a subadult phragmocone, 70 mm in diameter, with an estimated total diameter of at least 140 mm. The discoidal shell shows involute coiling with

Fig. 1: The holotype of Knemiceras gracile H. DOUVILLÉ, 1916, FSL.EM.1788, NW of Talat el Fellahin (now Gabal Maaza), SE of Gabal Maghara, north Sinai, Egypt, Early Albian.
**Knemiceras gracile** DOUVILLE, 1916: a misunderstood Early Albian ammonite (Egypt)

a very narrow umbilicus, comprising 9% of the diameter. The umbilicus increases in diameter on the last stages of ontogenesis, as suggested by traces on the flanks of the last whorl of the phragmocone. The umbilical wall is shallow and vertical with sharp umbilical shoulder. The whorl section is compressed, subtriangular (Wb/Wh between 0.53 and 0.55), with maximum width at about the inner third of the flanks. The flanks are gently convex, converging to a very narrow venter (ventral thickness comprising less than 5% of the diameter). The ventral area is grooved and smooth, limited by rows of weak ventrolateral bullae, forming sharp, crenulated ventrolateral edges. The lateral ornament is almost nonexistent and restricted to weak, broad, coarse, regularly alternating primary and intercalatory ribs, up to a diameter of 40-50 mm. The ribbing style, while not well expressed, is characteristic of the genus. Beyond 50 mm in diameter, the lateral ribbing becomes inconspicuous, and tends to disappear altogether. The body chamber is unknown from the holotype. The suture shows entire saddles and feebly indentated lobes (Fig. 2).

**Discussion:** This species remains poorly known, but seems to represent a primitive morphology of the genus *Knemiceras* BÖHM, 1898, characterized by an almost lack of lateral ornament, a very narrowly grooved ventral area, and a suture with entire saddles and feebly indentated lobes.

The holotype seems to co-occur with an unequivocal juvenile representative of the genus *Douvilleiceras* de GROSOUVRE, 1894 (DOUVILLE, 1916, p. 120; pl. 15, fig. 7). MAHMoud (1956: p. 66) does not provide details about the locality or stratigraphic level of the specimen he figured, but MORET & MAHMoud (1953, p. 268 and 269) mentioned the species within their Levels 2 and 4, indicating an Early Albian age.

The specimens figured by BASSE (1940, pl. 4, fig. 1; text-figs 9, 10), from an unknown stratigraphic level of the Albian of Mdereidj, Lebanon, seem to be close to the present species by their general shape, suture and narrow concave ventral area, but the photographed specimen, herein figured (Fig. 3) is too weathered and corroded to be specifically identified. The specimens figured by ARNOULD-SAGET (1956, p. 16, text-fig. 10; pl. 3, figs 3, 4), from the Early Albian of southern Tunisia, are too weathered to be fully identified. Furthermore, the Tunisian specimens have a wider and flatter ventral area, and less convex flanks than the holotype.

**Occurrence:** Gabal Maaza, SE of the great Maghara Dome, north Sinai, Egypt, Early Albian (After DOUVILLE, 1926).

**Fig. 2:** Suture of the holotype of *Knemiceras gracile* H. DOUVILLE, 1916, FSL.EM.1788, NW of Talat el Fellahin (now Gabal Maaza), SE of Gabal Maghara, north Sinai, Egypt, Early Albian (After DOUVILLE, 1926).

**Fig. 3:** *Knemiceras* sp. ind., the specimen figured by BASSE (1940, pl. 4, fig. 1; text-fig. 9, 10), as *Knemiceras gracile*, from unknown stratigraphical level of the Albian of Mdereidj, Lebanon.
the original designation of SPATH, 1924, p. 508. ROBERT (2002, p. 100) selected the specimen figured by LORIOL (1882, pl. 1: MHNG.035492, EBRAY collection) as lectotype (Pl. III, figs 1-4). The species was revised by LATIL (2008).

See full discussions in BULOT (2010) and LATIL (2011).

**Parenongonoceras bassei (BATAILLER, 1954)**

**Fig. 4**

1949. *Knemiceras compressum* HYATT.- DUBOURDIEU, p. 26, figs 1, 2.

1954. *Knemiceras* (Platiknemiceras) *bassei* BATAILLER, p. 175, fig. 1.


1959. *Platyknemiceras bassei* BATAILLER, p. 65, fig. 826.


? 1982. *Parenongonoceras hachourii* (DUBOURDIEU, 1953).- RENZ, p. 31, pl. 3, fig. 4; text fig. 19c-d.


1994. *Platyknemiceras* *bassei* BATAILLER.- MARTINEZ, GRAUGES & SALAS, pl. 3, fig. 4.


1996. *Platyknemiceras* sp.- WRIGHT, CALLOMAN & HOWARTH, p. 130, fig. 100: 5c.


**Type material:** The lectotype (MGSB.11478), designated by CASEY (1961, p. 23), has been figured by BATAILLER (1954, p. 175, figs 1, 2); BATAILLER (1959, p. 65, fig. 826); CAZALDA & URQUIOLA (1992, p. 74, photo on page 75), herein figured (Fig. 4).

**Dimensions of the lectotype:**

D: 60 (100) – Wh: 32 (53) – Wb: 17 (28) – U: 6 (10) – v: 3 (5) – Wb/Wh: 0.53

**Description:** The species was described on the basis of two specimens identified from the Early Albian of NE Spain (Tarragona). The lectotype is preserved as a calcareous internal mould of a non-adult phragmocone. The coiling is involute, with a narrow umbilicus comprising 10% of the diameter. The umbilical wall is shallow and almost vertical. The whorl section is subtriangular, compressed, with a maximum width at the umbilical seam. The flanks are feebly convex, converging to a narrow, bicarinate, slightly concave venter. Strongly, prorsiradiate, faint ribs arise to umbilical seam, tending to blunt on the inner third of the flanks. The ribs curve backward at mid flanks, becoming radial on the outer third of the flanks and tending to be projected outward near the ventrolateral edge. The ribs, becoming fainter at the end of the preserved last whorl, are replaced by growth striae. Both the body chamber and the adult growth stages are unknown. The knemiceratid suture line is diagnostic, with broad first lateral lobe, frilled lobes and indented saddles. This species seems to show a low rate of growth, with short distance between two sutures, even on the internal whors. MARTINEZ et al. (1994, pl. 3, fig. 4) figured a specimen from Les Ventoses, Marmellà, Barcelona (MGSB 1044, probable paralectotype). This juvenile specimen, 28 mm in diameter, shows rather strong, prorsiradiate, sinuous riblets, rising on umbilical wall. An additional fragment, MGSB 8689, a 180° sector of a phragmocone, about 80 mm in diameter, is characteristic of the species, with the ornament that tends to be effaced with age. The venter remains very narrow with age (v/D = 0.045), becoming slightly convex.

**Discussion:** This species represents the oldest known representatives of the genus *Parenongonoceras* SPATH, 1924. It resembles superficially *Knemiceras gracile* H. DOUVILLE, 1916 (p. 128, pl. 16, fig. 9), which has ventrolateral bullae, coarse and wide ribs on the flanks of the juvenile, and a suture with entire saddles. *Knemiceras deserti* MAHMoud, 1956 (p. 63, pl. 4, figs 3-5; text-figs 39-41) also shows a suture with entire saddles. These two last species show strong affinities with the genus *Knemiceras* s.str. *Parenongonoceras bassei* is very similar in shape to *Knemiceras hachourii* DUBOURDIEU, 1953 (p. 23, pl. 2, fig. 10-18; pl. 3, fig. 1-5) and differs mainly by its grooved ventral area, the lack of true ventrolateral tubercles at a similar diameter. *Parenongonoceras cf. hachourii* (DUBOURDIEU) (RENZ, 1982, p. 31, pl. 3, fig. 4; text-fig. 19 c-d) from the upper...
part of Machiques Formation (transition Aptian-Albian), Quebrada Maraca, Venezuela, is characterized by a lack of lateral tuberculation, falconoid growth striae and bicarinate ventral area, and probably belongs to *Parengonoceras bassei*, differing only by its strongly frilled suture.

The specimen recently figured by Bulot (2010, pl. 1, fig. 1) as *Platiknemiceras aff. bassei* Bataller, 1954, from the Aptian-Albian transition of Kuh-e-Bangestan (Iran) is too poorly preserved to allow a determination. Bujtor (2010) re-figured two drawings of Casev (1961, fig. 1a, c) as “reproduction of the figure of Basse (1954, p. 175)” (sic!). The lateral view corresponds to a drawing by Casev (1961, fig. 1a) of the original figure of Bataller (1954, fig. 1), while the ventral view is a drawing of a Peruvian specimen, identified by Casev (1961, fig. 1c) as *Platiknemiceras* sp. The same mistake is recorded in Wright et al. (1996, p. 130).

**Age:** The type species *Knemiceras* (*Platiknemiceras*) *bassei* Bataller, 1954 is known from Marmella, Montmell Formation (Salou-Garraf, Tarragona). No other ammonites co-occur with this species in its type locality. Findings in the laterally equivalent Escucha Formation, comprising "*Hypacanthoplites milletianus* (d’Orbigny), *Hypacanthoplites milletoides* CASEY and *Sonneratia subglabra* CASEY” (Martínez, Graües & Salas, 1994; Moreno-Bedmar et al., 2008), allow to assign an Early Albian age to *Platiknemiceras bassei* (Leymeriella tardefurcata Zone to *Sonneratia chalensis* Zone). Moreno-Bedmar et al. (2008) mention co-occurrence of "*Hypacanthoplites*’ and *Parengonoceras bassei* within the same bed in the basal Escucha Formation (Puntarrio de Traiguera section, Cuenca del Maestrat, E Cordillera Ibérica). This strongly suggests a basal Early Albian age for *Parengonoceras bassei*.

**Occurrence:** Early Albian of Spain (Bataller, 1954), Tunisia (Latil, 2011) and maybe Venezuela (Renz, 1982).

**IV. DISCUSSION ABOUT THE TAXONOMIC POSITION OF THE TAXA FORMELY REFERRED TO THE GENUS *PLATIKNEMICERAS***

**Iran:** Casev (1961, p. 354) reported three specimens from the Albian of Hamiran, south Iran (Spath, 1931, p. 339, text-fig 111f-h; Casev, 1961, text-fig. 1c: suture lines). Spath attributed these three specimens to *Knemiceras* of the group of *attenuatum-gabbi* (sensu lato). He interpreted them as probable new species, and considered them as passage-forms between *Knemiceras* and *Engonoceras*, following Pervinquière’s opinion (1907). These specimens are housed in the collections of the Natural History Museum of London under the numbers C68402, C68403 and C648406 (Figs 5, 6). These specimens, represented by rather large-sized phragmocones, show a compressed whorl section, narrow umbilicus, slightly convergent flanks and a narrow, bicarinate venter. The ventrolateral edges are crenate to tuberculate, and ventrolateral tubercles, when present, are opposite on the venter. One specimen (NHML-C68406, Fig. 6d-f) has radially elongated, periumbilical swellings, from which arise single, slightly flexuous, narrow, coarse ribs that tend to be effaced with age. Morphological features of this material strongly suggest close affinities to the genus *Knemiceras*. Pending a revision of the south Iranian engonoceratid faunas, and following Spath’s opinion, we herein consider this material as belonging to one or several undescribed new species.

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**Fig. 5:** *Knemiceras* sp. nov., NHML-C68403, Albian of Hamiran, south Iran.
Fig. 6: *Knemiceras* sp. nov. a–c, NHML.C68402, Albian of Hamiran, south Iran; d–f, NHML.C68406, Albian of Hamiran, south Iran.
Lebanon: *Knemiceras subcomplicatum* BASSE, 1940, p. 434, pl. 3, fig. 2, 3, from the Albian of Lebanon, is based on two specimens. The holotype (MHNP.R052050: pl. 3, fig. 2), from Bhamdoun, is a crushed, distorted and weathered fragment of an adult phragmocone, about 130 mm diameter, with a compressed whorl section, narrow umbilicus and narrow venter. No ornament can be observed because of weathering. According to BASSE, the main features of this species are based mainly on the suture line, which is supposed to be characterized by deep lobes, strongly frilled saddles and numerous accessory elements. The suture being strongly weathered, cannot be clearly studied. In addition, we agree with YOUNG’s statement (1957, p. 2): “In my opinion, authors who designate genera and/or species on sutures only are daydreaming”.

The paratype (MNHP.R52057, pl. 3, fig. 3), from Maaser-ech-Chouf, is a complete specimen, preserved as a weathered, slightly distorted, calcareous internal mould, 115 mm diameter, comprising a 180° sector of body chamber. The whorl section is compressed, with a maximum width at about mid flanks. The umbilicus is narrow, with a shallow steep umbilical wall. The flanks are slightly convex, the venter is narrow and bicarinate, tending to become convex and wider on the end of body chamber. The ornament on ventrolateral edges is obscured, probably because of weathering. The inner part of the last whorl (end of the phragmocone) shows feeble, coarse ribs arising by two or three from coarse umbilical bullae. BASSE (1940, p. 434) mentions numerous tiny, ventrolateral tubercles on the phragmocone.

*Knemiceras subcomplicatum* BASSE, 1940, is referred to the genus *Platiknemiceras* by CASEY (1961, p. 354) without justification. From the main features of the paratype, this species should be placed within the genus *Knemiceras*, but we are not even sure that the two specimens described by BASSE belong to the same species. The state of preservation of the holotype leads us to regard the present species as a *nomen dubium*.

Egypt: *Knemiceras deserti* MAHMOUD, 1956 (p. 63, pl. 4, fig. 3-5, text fig. 39-41), was described from the Early Albian of Gabal Manzour, north Sinai, Egypt (see also CASEY, 1961, p. 354), for small sized, compressed ammonites, with subtriangular whorl section, narrow umbilicus, steep umbilical wall, nearly smooth flanks, narrow venter, slightly crenate ventrolateral edges and faint ventrolateral bullae that are opposite on venter. This species is in need of a revision, but its suture suggests strong affinities with the genus *Knemiceras*. A careful examination of the paleontological collections in Geology Department of Cairo University (Egypt), has convinced us that *Knemiceras deserti* represents an extreme, compressed morphology of *Knemiceras douvillei* BASSE, 1940.

Algeria: *Engonoceras jullieni* BASSE, 1940, p. 439, text-fig. 11; pl. 4, fig. 4, from the Albian of Khencela, Algeria, is based on a poorly preserved, eroded and distorted specimen, from an unknown locality and stratigraphic level. This taxon is herein regarded as a *nomen dubium*. GEYER (1995, p. 8), placed *Platenticeras saadiensis* PERON, 1890, p. 19; pl. 16, figs 3-7, within the genus *Platiknemiceras*. BREISTROFFER (1940a and b) regarded this species as a *Knemiceras*. On the other hand, LATIL (1989) identified it as an *Engonoceras*. This Late Albian species from Algeria and Tunisia would be better placed within the genus *Hypengonoceras* SPATH, 1922, as a result of its age and its sutral similarities.

Tunisia: CASEY (1961, p. 354), placed *Knemiceras hachourii* DUBOURDIEU, 1953 (p. 23, text-fig. 7; pl. 2, figs 10-18; pl. 3, figs 1-5) within the genus *Platiknemiceras*. LATIL (2011, p. 351) attributed this species to *Paren gonoceras*.

Spain: *Platiknemiceras valencianum* MAS & WIEDMANN (1980, p. 265, figs 6, 7A, 8A) from La Ermita de Chera section, Valencia Province, Spain (Late Albian), is based on a poorly preserved fragment, but its suture shows strong affinities with sutures of *Knemiceras sensu lato*, such as *Knemiceras uhlgi* (CHOFFAT, 1886). Furthermore, the ventrolateral clavi of *Platiknemiceras valencianum* are alternating on the ventral area. The present authors are satisfied to exclude this species from either *Knemiceras* or *Platiknemiceras auctorum*.

France: *Platiknemiceras sequanense* DESTOMBES, 1979, p. 114, pl. 4, fig. 3, was described from a single specimen from Quarry West, Bois du Perchois, Aube, France, level 1b (Early Albian, *Sonneratia dutempleana* zone, *Cleoniceras floridum* Subzone of *DESTOMBES*). The holotype is a crushed and distorted fragment, represented by the end of the phragmocone and a 270° sector of body chamber. The body chamber has been crushed before fossilisation. The umbilicus is very narrow, with rather deep, rounded umbilical wall. The whorl section is subtriangular, with maximum width just above the umbilical seam. Then the flanks are convergent to a narrow, slightly concave bicarinate venter (v/D = 0.05). The author mentions smooth flanks, but an in-deep examination of the type reveals the presence of faint, flexuous growth striae on the body chamber. The suture is poorly preserved, showing numerous, frilled elements. From the same level, TOUCH & MATRION (1995, pl. 3, fig. 5) have figured an unregistered specimen identified as *Platiknemiceras* sp. This incomplete specimen, 55 mm in diameter, is characterized by a flat, narrow, bicarinate venter and strongly flexuous growth striae. MATRION (2010, p. 162, figs 116A-C) has figured two additional specimens from le Perchois quarries of *Platiknemiceras sequanense*. This species could be phylogenetically related to *Paren gonoceras bassei* (BATALLER, 1954).

USA: *Platiknemiceras flexuosum* KENNEDY, LANDMAN & COBBAN, 1998, p. 38, fig. 51, 52 (Knemiceras sp. nov., CASEY, 1961, p. 355), from the Glen Rose Limestone (Early Albian) of Texas, is characterized by its strongly flexuous ribs, its convergent outer flanks and its narrow, slightly concave, bicarinate venter. This species is
herein regarded as a primitive morphology of Texan engonoceratoids and is provisionally placed within the genus *Parengonoceras*. However, we believe that the north american engonoceratids most probably derive from some obscure Early Albian, tethyan stock, and have evolved in isolation, on the Texan platforms. In our opinion, this group deserves a separate generic status. It should be noted that this species and *Parengonoceras roemeri* (CrAsin, 1893) are contemporaneous.

**Venezuela:** Some discoidal specimens with a compressed whorl section and feeble ornament have been reported from the Early Albian of Venezuela (REnZ, 1982).

*Parengonoceras* cf. *hachourii* (DUBOuRDIEU) (REnZ, 1982, p. 31, pl. 3, fig. 4; text-fig. 19c, d: specimen MB.Re2439), from the upper part of Machiques Formation in the Quebrada Maraca (Pevrijá river, Venezuela), characterized by the lack of lateral tuberculation, biconcave ventral area, and prorsiradiate flexuous striae. It differs from *Parengonoceras bassei* mainly by its suture with strongly frilled saddles and somewhat less convex flanks. This ammonite was collected in the same stratigraphic levels of *Prolyelliceras gevei* (JACOB, 1907), providing an Early Albian age, *Leymeriella tardefurcata* Zone to base of *Dowvilleceras mammatum* Superzone.

*Parengonoceras* sp. (REnZ, 1982, p. 32, pl. 4, fig. 2), from the top of Machiques Formation, Quebrada Macoita, Venezuela, is probably contemporaneous to *Prolyelliceras gevei* (JACOB, 1907). This specimen, with compressed section, umbilical tubercles and flexuous striae, is close to *Parengonoceras caneroti* COLLIGNON, 1981b, from which it differs by its strong ventrolateral clavi that are opposite on the ventral area.

**Colombia:** *Platiknemiceras colombiana* ETAYO-SERNA, 1979 from Cerro Bejucal, Colombia, basal part of the Capotes Member (?Middle Albian), is poorly figured (p. 76, pl. 11, fig. 7: holotype by monotypy C-169/ UNCMHCNP05.N85). It is characterized by “A) finely crenate ventrolateral carinae, B) the trend of the bundles of lirae, radial on the central and adumbilical third of the flank, adorally concave on the adventral third” (ETAYO-SERNA, 1979, p. 76).

BREISTROFFER (1952, p. 2634) mentioned from the basal Middle Albian of Cundinamarca, Colombia, discoidal, compressed and involute specimens attributed to the genus *Knemiceras*, with a costation reduced to very fine striae and a narrow bicipitate venter. This material, placed by CASEY (1961, p. 355) in *Platiknemiceras*, has been borrowed by us from the collections of the Université Joseph Fourier (Grenoble, France). This material consists of two fragments from Quipilé, and an additional one from Viota, Quebrada Tasajera (Cundinamarca, Colombia). A small fragment of an internal mould of a juvenile specimen from Quipilé (UJF.ID10886), about 30 mm long, shows a narrow, flat, bicornicate venter. It has a compressed, subtriangular whorl section, with subparallel flanks (Fig. 7d, e). The internal mould shows only inconspicuous riblets on the flanks. Some pieces of shell are preserved on the flank and venter, showing numerous fine lirae, crossing over the ventral area. The suture, partly preserved, shows a wide, deeply serrated external lobe and frilled saddles, the successive sutures overlapping on mid-flank (Fig. 7f). Another fragment of a body chamber, from the same locality (UJF.ID10885), with Wh at about 45 mm, has preserved the shell, which is covered with fine lirae. These lirae are straight on the inner part of the flank, slightly concave adorally on the outer third, and crossing over the ventral area. The venter is relatively broad, slightly convex and bicornicate (Fig. 7e). A larger fragment of body chamber from Viota (UJF. ID10884), measuring 110 mm of length, and preserved as an internal mould, shows an almost flat, bicornicate venter and inconspicuous lirae on the flanks (Fig. 7a, b).

This material collected by BREISTROFFER (1952) seems to be very close to the unfigured specimen described as *Platiknemiceras* sp. A by ETAYO-SERNA (1979, p. 76, text-figs 8A, K). The poorly figured *Platiknemiceras colombiana* ETAYO-SERNA, 1979 seems to differ from both *Platiknemiceras* sp. A and the BREISTROFFER’S material, only by its finely crenate ventrolateral edges.

The taxonomic position of those colombian ammonites remains unclear. Pending a revision of this group on the basis of new material, the morphological features of the suture line has led us to exclude these ammonites from either *Platiknemiceras auctorum* or *Knemiceras*.

**Peru:** CASEY (1961, p. 354, fig. 1c, d) published drawings of the ventral and cross-section views of a specimen attributed to *Platiknemiceras*, which was collected by HARRISON (1953, p.15) from the Early Albian of Canta, Peru (C.W. WRIGHT collection). We were unable to locate this specimen, which is supposed to be housed in the collections of the Natural History Museum of London. ROBERT (2002, pl. 16, figs 3, 4) and ROBERT & BULOT (2004, pl. 2, fig. 4) have identified a specimen from the upper part of the Early Albian of Paria Puquio, Peru as *Platiknemiceras* cf. *flexuosum* KENNEDY, LANDMAN & COBBAN, 1998. This poorly preserved ammonite, about 150 mm diameter, with a compressed whorl section, a narrow umbilicus, rounded and shallow umbilical wall, convex flanks, extremely narrow flat to slightly concave venter and lack of ornament, cannot be identified specifically, and may represent a primitive morphology of the genus *Glottoceras* HYATT, 1875.

**Japan:** *Platiknemiceras caseyi* MATSUMOTO, 1980 (in MATSUMOTO, KANMERA & OHTA, p. 333, pl. 37, fig. 5), from the middle member of the Yatsushiro Formation, Kyushu, Japan, (?Early Albian) was described on the basis of a single specimen, 27 mm in diameter. It has a compressed whorl section, a narrow umbilicus and a bicornicate venter, and it is characterized by flexuous low ribs on the outer part of the flank, ending with ventrolateral clavi. This ribbing style is not characteristic of the genus *Platiknemiceras*, and it seems that this enigmatic specimen of inaccurate age does not belong to the Engonoceratoidea.
Knemiceras gracile Douvillé, 1916: a misunderstood Early Albian ammonite (Egypt)

Fig. 7: ?Parengonoceras sp. nov. a, b, UJF-ID10884, Albian of Quebrada Tasajera, Viota, Cundinamarca, Colombia; c, UJF-ID.10885, Quipilé, Cundinamarca, Colombia; d-f, UJF-ID.10886, Quipilé, Cundinamarca, Colombia.
V. CONCLUSION

A careful examination of the material previously referred in the literature to the genus Platiknemiceras, strongly suggests that this latter genus is polyphyletic. Some species are herein placed within the genus Parengonoceras Spath, 1924:

- Knemiceras (Platiknemiceras) basseti Bataller, 1954 (p.175, fig. 1).
- Knemiceras hachourii Dubourdieu, 1953 (p. 23, text-fig. 7; pl. 2, figs 10-18; pl. 3, figs 1-5).
- Platiknemiceras sequanense Destombes, 1979 (p. 114, pl. 4, fig. 3).

Two species are referred to the genus Knemiceras Böhm, 1898:

- Knemiceras gracile H. Douvillé, 1916 (p. 128, pl. 16, fig. 9; text-fig. 42).
- Knemiceras deserti Mahmoud, 1956 (p. 63, pl. 4, fig. 3-5; text-fig. 39-41)

One species seems to be closely related with the Late Albian genus Hypengonoceras Spath, 1922:
- Placenticeras saadensis Peron, 1890 (p. 19; pl. 16, figs 3-7).

Two species are regarded as nomen dubium
- Knemiceras subcomplicatum Basse, 1940 (p. 434, pl. 3, fig. 2, 3).
- Engonoceras jullieni Basse, 1940 (p. 439, text-fig. 11; pl. 4, fig. 4).

The taxonomic position of the following species has yet to be precised:
- Platiknemiceras vauxianum Mas & Wiedmann, 1980 (p. 265, figs 6, 7A, 8A).
- Platiknemiceras flexuosum Kennedy, Landman & Cobban, 1998 (p. 38, fig. 51, 52).
- Platiknemiceras columbiana Eyatio-Serna, 1979 (p. 76, pl. 11, fig. 7).
- Platiknemiceras caseyi Matsumoto, 1980 (in Matsumoto, Kanmera & Ohta, p. 333, pl. 37, fig. 5).

Furthermore, the Iranian material reported by Spath (1931) and Casey (1961) as belonging to Knemiceras of group of attenuatum-gabbi (sensu lato) may represent a new species of Knemiceras. The Peruvian material identified by Robert (2002) and Robert & Bulot (2004) as Platiknemiceras cf. flexuosum Kennedy, Landman & Cobban, 1998, probably belongs to the genus Glottoceras Hyatt, 1875.

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