Systematics, phylogeny and homeomorphy of the Engonoceratidae HYATT, 1900 (Ammonoidea, Cretaceous) and revision of *Engonoceras duboisi* LATIL, 1989

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Abstract: The Engonoceratidae may well have originated on the shallow marine carbonate platforms of the southern margin of the Mediterranean Province of the Tethyan Realm during the earliest Albian (?latest Aptian). In the entire Tethyan Realm and beyond adaptive radiation of the group was rapid and successful during the early Albian as indicated by endemic centres in the Peruvian Basin and the Western Interior Sea (USA). Later the group successfully enlarged its distribution, and invaded some provinces (Mowry Sea, Canada) of the Boreal Realm. The mode of life of engonoceratids seems to have been nektoplanktonic, epipelagic, and stenohaline, restricted to shallow water and platform or in some cases extremely shallow (littoral and lagoonal) facies which may have helped their radiation. The group is distinctive and consists of nine genera and up to a hundred species, although its origin is still obscure. Their appearance may have been triggered by the oceanic anoxic event (OAE 1b) and their rapid rise may have been helped by their shallow water mode of life and the global mid-Cretaceous warming and rise in sea level. The fall of the engonoceratids coincides with the end-Cenomanian rapid transgression, which may have changed their shallow water habitats. Today the group is considered to have been a successful colonizer, a reliable stratigraphical indicator for shallow marine environments and a pioneer taxon for recognition of transgressive phases.
Based on new material and sutural analysis, *Engonoceras duboisi* is revised and assigned to *Parengonoceras*. A set of features consisting of a simplified ceratitid suture, lanceolate and compressed oxycone shell together comprising a shallow marine ecotype is pointed out as a successful and repeated morphotype among Mesozoic Ammonoidea, for it was repeated three times during ammonoid evolution.

Key Words: Ammonites; Albian; Cenomanian; phylogeny; systematics; homeomorphy.

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Résumé : ***Systématique, phylogénie et homéomorphie des Engonoceratidae HYATT, 1900 (Ammonoidea, Crétacé) et révision de*** **Engonoceras duboisi** ***LATIL, 1989.-*** Les Enganoceratidae apparaissent à l'Albien basal (ou peut-être dès l'Aptien terminal) dans les séries de plates-formes carbonatées de la marge sud de la province méditerranéenne du domaine téthysien. Leur efficacité évolutive leur permet de coloniser rapidement l'ensemble du domaine téthysien et même au delà comme le montre la présence de groupes endémiques dans le Bassin Péruvien et dans la mer intérieure occidentale des États-Unis. Plus tard, le groupe élargira encore plus son aire de distribution en envahissant certaines régions du domaine boréal (mer de Mowry, Canada). Les Enganoceratidae semblent avoir eu un mode de vie nectoplanctonique, épipélagique et sténohalin au sein de mers chaudes peu à très peu profondes (rivages, lagons), dont la fréquence a favorisé leur évolution. Ce groupe, dont l'origine est obscure, est bien individualisé. Il comprend neuf genres et une centaine d'espèces. Leur apparition semble avoir été provoquée par la crise anoxique OAE 1b et leur rapide expansion favorisée par l'extension progressive des mers chaudes et épicontinentales qui accompagne la montée des eaux du milieu du Crétacé. Le déclin des Enganoceratidae semble lié à l'accélération de la montée des mers qui caractérise la fin du Cénomanien, sans doute par modification substantielle de leurs habitats peu profonds. Ce groupe est considéré comme un colonisateur efficace et un bon indicateur de milieux de faible profondeur en ambiance transgressive.
À partir de nouvelles études stratigraphiques et structurales, il est proposé une révision de l'espèce *Engonoceras duboisi* qui doit être rattachée au genre *Parengonoceras*. Par ailleurs, il est mis en évidence que le fait de présenter des sutures simplifiées de type Cératite et une coquille lancéolée à oxycône comprimé est symptomatique d'ammonites adaptées à des milieux marins peu profonds. Ce modèle est, en effet, répété trois fois au long de l'évolution des Ammonoïdes mésozoïques.

Mots-Clefs : Ammonites ; Albien ; Cénomanien ; phylogénie ; systématique ; homéomorphie.

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Introduction

Engonoceratid ammonites form a distinct but perplexing group among Cretaceous Ammonoidea. Their systematics is still confusing and their origin is obscure. After the period of great monographs on engonoceratid ammonites (HYATT, 1903; PERVINQUIÈRE, 1907; SOMMERMEIER, 1910; BASSE, 1940; KNECHTEL *in* KNECHTEL *et alii*, 1947; DUBOURDIEU, 1953; MAHMOUD, 1955; BENAVIDES-CÁCERES, 1956; RENZ, 1970, 1982; ETAYO-SERNA, 1979), twelve new species have been introduced and forty species invalidated. This prompts a review of the group, and a discussion on the ecology and facies dependency of certain of its taxa. Recent debates on the systematics of Engonoceratidae also invite a review of the systematic position, ecology, distribution, phylogeny and homoeomorphy of this group of fossils and of the species assigned it.

Materials and methods

The following abbreviations indicate the repositories of specimens mentioned in the text: HNHM, Hungarian Natural History Museum, Budapest, Hungary; LC, Lumachella Collection (private collection of Mr. Zoltán EVANICS, 29 Szatmár Street, Budapest, H-1194 Hungary); MHNG-GEPI, Collection Muséum d'Histoire naturelle de Genève, Switzerland. Suture terminology is after KULLMANN & WIEDMANN (1970): E, external lobe; L, lateral lobe; U, umbilical lobe; I, internal lobe. Note that KORN *et alii* (2003) revised the sutural terminology of the Paleozoic prolecanitid ammonites, which implies its modification for Mesozoic ammonoids too, but this modification has not been published yet. All dimensions are in millimetres: D, diameter; Wb, whorl breadth; Wh, whorl height; U, umbilicus; myr: million year. Species names in brackets indicate invalidation.

Historical overview of the concept of Engonoceratidae

The name *Ceratites* was introduced by de HAAN (1825) for a group of Triassic ammonites with simplified suture lines. As early research developed, *Ceratites*-like fossils of Cretaceous age were discovered, so early palaeontologists included these fossils into the ceratitid group, naming them as Cretaceous *Ceratites* (BUCH, 1848, p. 30) or "pseudo-ceratites based on an apparent resemblance between the sutures of Triassic ceratitids and those of Cretaceous engonoceratids" (HYATT, 1903; G. SCOTT, 1940a, 1940b; KENNEDY & COBBAN, 1976; RAWSON, 1981; KENNEDY *et alii*, 1998a). The first engonoceratid ammonite was published by d'ORBIGNY (1841) as *Ammonites Vibrayeanus* [= *Neolobites vibrayeanus*] from France, and by BUCH (1848) as *Ammonites Syriacus* [= *Knemiceras syriacum*] from Lebanon, and *Ammonites pierdenalis* [= *Engonoceras pierdenalis*] from Texas. BUCH (1848) also called attention to the importance of the group referring to them as Cretaceous ceratitids ('Kreide-Ceratit'). Although BUCH (1848) reported other "ceratitids" (whose suture lines superficially resemble those of the Triassic *Ceratites*) such as *Ammonites Ewaldi* and *Ammonites Robini* [= *Metatissotia ewaldi* and *M. robini*], these species belong to discrete taxa (Acanthoceratoidea) with no direct phyletic connection to the engonoceratids. The family name Engonoceratidae was introduced by HYATT (1900, p. 585) to include *Protengonoceras, Engonoceras, Metengonoceras*, and *Neolobites*. Later HYATT (1903, p. 144) established the family Knemiceratidae for *Knemiceras*. Based on the suture line DOUVILLÉ (1912, 1928, 1931) placed the group in the Pulchelliidae, an assignment accepted by G. SCOTT (1940b, p. 1066). SPATH (1922, 1924) introduced *Hypengonoceras*, and *Parengonoceras*. The last described member of the family is *Platiknemiceras* (BATALLER, 1954).

In the mid 1900's CHIPLONKAR (1941) and MOREMAN (1942) referred certain placenticeratid ammonites (*Placenticeras mintoi*, and *P. planum*) to the Engonoceratidae and BENAVIDES-CÁCERES (1956, p. 486) regarded *Neolobites* as *incertae sedis* again an indication of taxonomic uncertainty. *Hypengonoceras* was regarded as a placenticeratid ammonite (CASEY, 1960) at that time the only known Lower Cretaceous placenticeratid. Later RENZ (1970) summarized the systematic debates and content of the family, and KLINGER & KENNEDY (1989, p. 365) revised the systematic position of the most discussed member, *Hypengonoceras*, which they regarded as having been derived probably from *Parengonoceras*. WRIGHT *et alii* (1996, p. 126) did not accept this rationale proposing a different origin for the genus: "*Hypengonoceras*, despite some resemblances to Engonoceratidae, seems to belong here" [= Placenticeratidae HYATT, 1900] and confirmed that the family had an uncertain origin, "but some genera closely resemble Pulchelliidae but are probably not closely related" (WRIGHT *et alii*, 1996, p. 130) and placed the family in the Hoplitoidea with these eight genera included: (*Engonoceras, Hypengonoceras, Knemiceras, Metengonoceras, Neolobites, Parengonoceras, Platiknemiceras*, and *Protengonoceras*). At present, the systematic position of *Hypengonoceras* is again disputed (ROBERT & BULOT, 2004). ROBERT (2002) resurrected the genus *Glottoceras* HYATT 1875, a view supported by ROBERT & BULOT (2004, p. 20). As yet there is no unequivocal approach regarding the systematic position of the group. SCHINDEWOLF (1968, p. 747) had already emphasized the impossibility of placing the group properly until its sutural development is clearly known. He refers this family doubtfully to the Pulchelliidae or the Hoplitidae. RENZ (1970) gave a detailed analysis of the engonoceratid sutural history. In the past forty years many species were introduced but no significant work was done on the sutural ontogeny of the Engo-

noceratidae. Although ROBERT & BULOT (2004) discussed the systematic position of the group placing it in the Pulchelliatoidea, this attribution is not yet widely accepted. KENNEDY *et alii* (2004), YACOBUCCI (2004), MEISTER & ABDALLAH (2005), SZIVES *et alii* (2007), and ALY *et alii* (2008) place the group in the Hoplitoidea, while LATIL (2008) refers it to the Pulchelliatoidea. Most recently, BULOT (2010, p. 169) rejects the pulchelliatoid origin of Engonoceratidae, suggesting that the genus *Subpulchellia*/*Mogharaeceras* is most likely an endemic offshoot of *Barremites* so cannot be the ancestor of the Engonoceratidae. Further uncertainty is indicated by LATIL (*in* MORENO-BEDMAR, 2008b, p. 160) regarding the systematic position of European *Engonoceras sensu stricto*. ROBERT & BULOT (2004, p. 11) stressed a pulchelliatoid origin based on a probable relation with the Barremian/Aptian *Subpulchellia*, but did not include a thorough discussion. BULOT (2010) proposes a new taxonomic rank for engonoceratid ammonites, the Superfamily Engonoceratoidea HYATT, 1900. This taxonomic approach has certain advantages: on one hand it emphasizes the integrity of the group, thus highlighting its morphological independence. On the other hand this approach leaves open the problem of the origin of the group. As mentioned, BULOT (2010) rejected the pulchelliatoid origin of engonoceratid ammonites. If so, the most plausible explanation for its origin is the hoplitoids. This view may be strengthened by new data on the ecology of Aptian *Parahoplites* (LEHMANN *et alii*, 2009). Consequently, the systematics and origin of Engonoceratidae are still open issues. Recently Engonoceratidae was considered to consist of nine genera (*Engonoceras, Glottoceras, Hypengonoceras, Knemiceras, Metengonoceras, Neolobites, Parengonoceras, Platiknemiceras*, and *Protengonoceras*), and 143 species (Table 1) of which 38 are invalid. They are listed in the section discussing the described genera and their species. The genus *Pseudengonoceras* referred to by RAWSON (1981, p. 517) is a typing error for *Parengonoceras* (P. RAWSON, pers. comm., 2009).

Systematic paleontology

Order Ammonitida ZITTEL, 1884
Suborder Ammonitina HYATT, 1889
Superfamily Hoplitoidea DOUVILLÉ, 1890
Family Engonoceratidae HYATT, 1900
= Knemiceratidae HYATT, 1903, p. 144;
Neolobitinae LUPPOV & MIKHAILOV, 1958, p. 125

Genus *Glottoceras* HYATT, 1875, p. 372
(Fig. 1)

Type species. *Glottoceras attenuatum* HYATT, 1875, from the Lower Albian of Peru.

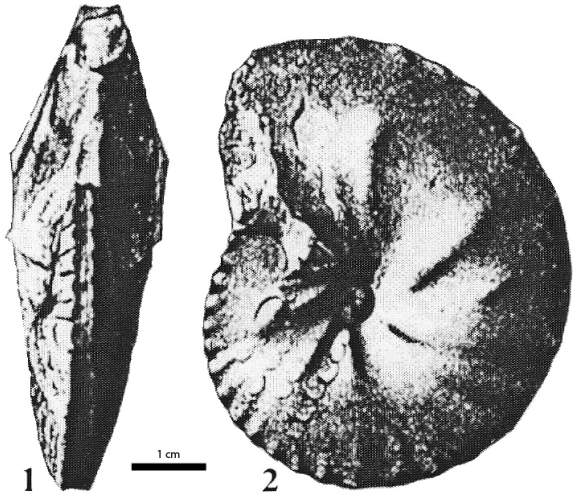


Figure 1: *Glottoceras attenuatum* (HYATT, 1903). Reproduction of the original specimen of HYATT (1903, pl. 17, figs. 13-14).

Diagnosis. Typical engonoceratid coiling with narrow umbilicus. Cross section is rather compressed and pentagonal, or oval in some species. Venter is flat to slightly concave or rounded in adult stage. Ornamentation consists of rather strong, sometimes coarse prorsiradiate ribs, which may originate at the umbilical shoulder from bullae. Ventrolaterally bullae may also appear. Suture consists of many adventive and auxiliary elements. Relative breadth of saddles and lobes are similar. Saddles are bifid, lobes are finely frilled.

Occurrence. *Glottoceras* (*sensu* ROBERT, 2002) is restricted to the Albian of South America.

Included species:

- *Knemiceras andinum* RENZ, 1970: p. 1047, pl. 10, figs. 1a-b, 3; text-fig. 10a-b.
- *Glottoceras attenuatum* HYATT, 1875: p. 372.
- [*Knemiceras bassleri* KNECHTEL *in* KNECHTEL *et alii*, 1947: p. 90, pl. 17, figs. 1-2 = synonym of *G. gabbi* (BENAVIDES-CÁCERES, 1956, p. 451; RENZ, 1970, p. 1048; ROBERT & BULOT, 2004, p. 20)].
- *Knemiceras crassicostatum* SOMMERMEIER, 1910: p. 343, pl. 10, fig. 4; Pl. 11, figs. 1-3.
- *Knemiceras crassinodosum* SOMMERMEIER, 1910: p. 361, pl. 13, figs. 1-2.
- *Knemiceras gabbi* HYATT, 1903: p. 152, pl. 18, figs. 1-3.
- [*Knemiceras gracilecostatum* SOMMERMEIER, 1910: p. 343, pl. 10, figs. 2-3 = synonym of *G. semicostatum* (ROBERT & BULOT, 2004, p. 20)].
- *Knemiceras laraense* RENZ, 1970: p. 1049,

pl. 12, fig. 1; text-fig. 11a-c.
- *Glottoceras raimondii* var. *largum* ROBERT, 2002: p. 125, pl. 12, figs. 4-8; Pl. 13, figs. 1-2.
- [*Knemiceras libertadense* BREISTROFFER, 1952: p. 2633 = synonym of *G. crassinodosum* (ROBERT & BULOT, 2004, p. 20)].
- *Knemiceras moorei* KNECHTEL *in* KNECHTEL *et alii*, 1947: p. 98, pl. 21, figs. 1-2.
- *Ammonites ollonensis* GABB, 1877: p. 271, pl. 38, fig. 4.
- *Knemiceras ovale* BENAVIDES-CÁCERES, 1956: p. 452, pl. 52, figs. 1, 4.
- *Knemiceras raimondii pacificum* BENAVIDES-CÁCERES, 1956: p. 455, pl. 49, fig. 1.
- [*Knemiceras pegnai* ETAYO-SERNA, 1979: p. 77, pl. 12, fig. 2; text-figs. 8d, 8f) = synonym of *G. tardum* (ROBERT & BULOT, 2004, p. 20)].
- *Knemiceras raimondii* LISSÓN, 1908: p. 4a, pl. 4, figs. 1a-e, 2.
- *Knemiceras semicostatum* SOMMERMEIER, 1910: p. 342, pl. 9, fig. 3; Pl. 10, fig. 1.
- [*Knemiceras seminodosum* SOMMERMEIER, 1910: p. 344, pl. 12, figs. 1-3 = synonym of *G. semicostatum* (ROBERT & BULOT, 2004, p. 20)].
- *Knemiceras sommermeieri* (KNECHTEL *in* KNECHTEL *et alii*, 1947: p. 96, pl. 18, figs. 5-6.
- [*Knemiceras spinosum* SOMMERMEIER, 1910: p. 347, pl. 9, fig. 2 = synonym of *G. semicostatum* (ROBERT & BULOT, 2004, p. 20)].
- *Knemiceras raimondii* var. *tardum* BENAVIDES-CÁCERES, 1956: p. 455, pl. 48, figs. 6-7.
- *Knemiceras triangulare* BENAVIDES-CÁCERES, 1956: p. 451, pl. 47, figs. 1-2.
- [*Knemiceras typicum* SOMMERMEIER, 1910: p. 341 = synonym of *G. semicostatum* (ROBERT & BULOT, 2004, p. 20)].

Remarks. BENAVIDES-CÁCERES (1956, p. 449) had already pointed out that South American '*Knemiceras*' are different from the *Knemiceras attenuatum* described by BASSE (1940). On the basis of Art. 23.9 of ICZN (1999), ROBERT (2002) resurrected *Glottoceras* to group the South American species of *Knemiceras*. ROBERT (2002) and ROBERT & BULOT (2004, p. 20) consider the genus *Glottoceras* to be restricted to these Andean species. In the assignment of species to this group, *Knemiceras andinum* RENZ must be included in *Glottoceras* if the rationale of ROBERT & BULOT (2004, p. 20) is accepted.

Genus *Engonoceras* NEUMAYR & UHLIG, 1881, p. 140 = *Engonhoplitoides* BASSE, 1940, p. 441; *Epigonoceras* PACKARD, 1956, p. 400

(Fig. 2)

Type species. *Ammonites pierdenalis* BUCH, 1848, from the Cretaceous of Fredericksburg, Texas.

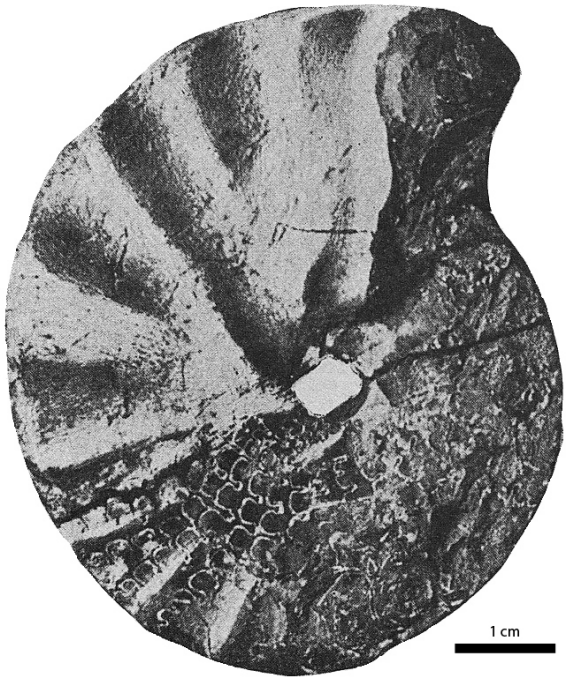


Figure 2: *Engonoceras pierdenalis* (BUCH, 1848). Reproduction of the original figure of BUCH (1848, p. 31, pl. 6, figs. 8-10).

Diagnosis. Diagnosis is after WRIGHT *et alii* (1996, p. 130): "Involute, inner whorls very compressed with narrow, flat or sulcate venter; later flexuous striae normally repeated by weak, flat, flexuous or straight ribs ending in small ventrolateral clavi placed alternately and, in some shells, joined across venter by zig-zagging ribs; umbilical and lateral tubercles may be present, and venter of last whorl may be rounded. Suture with more elements than *Knemiceras* and with saddles normally all entire except that outermost are bifid; external lobe normally with strongly divergent branches."

Occurrence. *Engonoceras* is widespread in its distribution. It is abundant with many species in North America (Colorado, Kansas, New Mexico, Oregon, Texas) and in Mexico (Sonora) and South America (Colombia, Peru) but also in the Tethys: North Africa (Algeria, Morocco, Tunisia), the Near East (Lebanon, Syria) and Asia (Borneo). It is also reported from Europe (England). Stratigraphically it ranges from the Early Albian to the Middle Cenomanian.

Included species:

- *Ammonites belviderensis* CRAGIN, 1894: p. 369, pl. 1, figs. 3-5.
- *Engonoceras pierdenale* var. *commune* HYATT, 1903: p. 165, pl. 21, fig. 1.
- *Engonoceras complicatum* HYATT, 1903: p. 175, pl. 24, figs. 6-8.
- [*Engonoceras duboisi* LATIL, 1989: p. 56, pl. 2, figs. 1-3 = *Parengonoceras duboisi* (this paper)].
- *Engonoceras elegans* KENNEDY *et alii*, 1998a: p. 5, figs. 2-4.
- *Sphenodiscus emarginatus* CRAGIN, 1893: p.

245.
- *Engonoceras gibbosum* HYATT, 1903: p. 171, pl. 22, figs. 6-10; pl. 23, figs. 1-6.
- *Engonoceras grimsdalei* SPATH, 1931: p. 345, pl. 36, fig. 7.
- *Engonoceras hilli* BÖHM, 1898: p. 192, text-fig. 5.
- *Engonoceras iris* SPATH, 1924: p. 506, pl. 35, figs. 5a-b; text-fig. 113.
- *Engonoceras jezzinense* BASSE, 1940: p. 437, pl. 3, fig. 4a-b; text-fig. 7.
- *Engonhoplitoides khenchelaense* BASSE, 1940: p. 442, pl. 4, figs. 5-6; text-fig. 12.
- *Engonoceras olgaluciae* ETAYO-SERNA, 1979: p. 130.
- *Ammonites pierdenalis* BUCH, 1848: p. 30a, pl. 6, figs. 8-10.
- *Knemoceras pinax* KRAUSE, 1902: p. 10, pl. 1, figs. 1-3; Pl. 2, figs. 1-8 [= *Engonoceras pinax* (WRIGHT, 1963, p. 612)].
- *Engonoceras retardum* HYATT, 1903: p. 160, pl. 19, figs. 15-17.
- *Sphenodiscus belviderensis* var. *serpentinus* CRAGIN, 1900: p. 31, pl. 2, figs. 4-6.
- *Engonoceras subjectum* HYATT, 1903: p. 168, pl. 21, figs. 2-6; Pl. 22, figs. 1-5.
- *Engonoceras stolleyi* BÖHM, 1898: p. 188, pl. 5, fig. 3a-c; Pl. 6, fig. 1; text-figs. 2-4.
- *Engonoceras thomasi* PERVINQUIÈRE, 1907: p. 302, pl. 9, fig. 8.
- *Engonoceras toussainti* PERVINQUIÈRE, 1907: p. 305, pl. 9, fig. 7a-c.
- [*Sphenodiscus belviderensis* var. *uddeni* CRAGIN, 1900: p. 30, pl. 1, figs. 3-4 = synonym of *E. belviderense* (R.W. SCOTT, 1970)].
- *Engonhoplitoides vicorpense* BASSE, 1940: p. 443, pl. 5, figs. 2-3.
- *Engonoceras wilkinsoni* PACKARD, 1956; p. 399, text-fig. 1a-c.
- *Engonhoplitoides zumoffeni* BASSE, 1940: p. 443, pl. 5, fig. 1.

Remarks. Although BUCH (1848, pl. 6, fig. 10) in his description of the type species indicates that all the saddles of the suture are bifid: "the saddle is rounded, however with one small secondary lobe in the middle", subsequent designations refer to entire or nearly entire saddles with only one bifid element being typical for *Engonoceras* (WRIGHT *et alii*, 1996; KENNEDY *et alii*, 1998a, p. 5). According to BENAVIDES-CÁCERES (1956, p. 444) most species of *Engonoceras* have sutures with entire saddles and are ornamented with three or two rows of tubercles. In some species (e.g. *E. complicatum*) there are more (up to five) bifid or sometimes trifid saddles (*E. elegans*). Saddles are generally rounded, lobal necks are narrow. Saddles are always broader than lobes. BASSE (1940, p. 441) established *Engonhoplitoides* on the basis of the subdivision of the lateral lobe of the suture line, remarking that the shell morphology of *Engonhoplitoides* is closer to that of *Engonoceras*, while its suture line is more nearly like that of *Knemiceras*. This separation was discredited by WRIGHT *et alii* (1996).

Genus *Neolobites* FISCHER, 1882, p. 389

(Fig. 3)

Type species. *Ammonites Vibrayeanus* d'ORBIGNY, 1841, p. 322, from the Cretaceous of Sarthe (France).

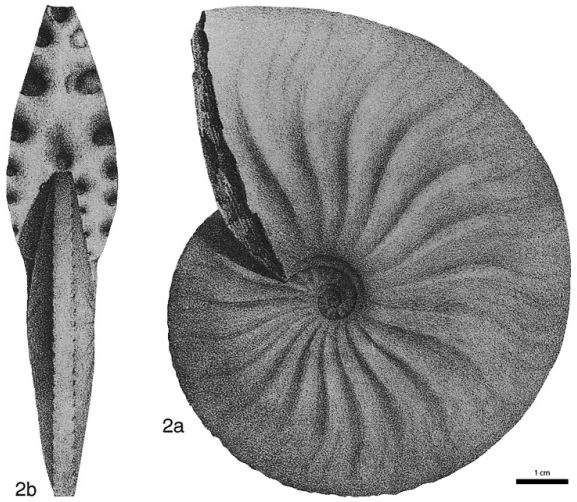


Figure 3: *Neolobites vibrayeanus* (d'ORBIGNY, 1841). Reproduction of the original figure of d'ORBIGNY (1841, p. 322, pl. 96, figs. 1-3).

Diagnosis. Highly variable, oxycone and lanceolate engonoceratid, with small, shallow umbilicus. Suture is extremely simplified consisting of rounded, narrow lobes and wide rounded saddles. Cross section is variable from compressed to slightly inflated. Venter is variable from wide to narrow trapezoidal or simply rounded and in some species ornamented by fine crenulations. Sculpture is variable, too, ranging from smooth, unornamented forms to flexuous and ventrally ornamented forms.

Occurrence. *Neolobites* is restricted to the Middle (*N. fourtaui*) and Late (*N. vibrayeanus*) Cenomanian being a successful shallow marine taxon among Engonoceratidae. The genus is characterized by distinct morphotypes and populations in the Tethyan Realm and seamingly preferred lower latitudes and subtropical/tropical settings (WIESE & SCHULZE, 2005, p. 942). It is reported from South America (Bolivia, Colombia, Peru, and Venezuela), Africa (Algeria, Egypt, Libya, Morocco, Niger, and Tunisia), Europe (France, Portugal, and Spain), and the Near and Middle East (Israel, Jordan, Lebanon, Oman, and Syria).

Included species:
- [*Neolobites bassleri* BOIT, 1926: p. 39, pl. 1, figs. 1-3 = intraspecific variety of *N. vibrayeanus* (WIESE & SCHULZE, 2005, p. 935)].
- [*Neolobites brancai* STAFF & ECK, 1908: p. 277, fig. 5 = subspecies of *N. vibrayeanus* (MEISTER & ABDALLAH, 2005, p. 123); =

intraspecific variety of *N. vibrayeanus* (KENNEDY & JUIGNET, 1981, p. 24; MEISTER *et alii*, 1994; MEISTER & ABDALLAH, 1996; MEISTER & RHALMI, 2002; WIESE & SCHULZE, 2005, p. 935)].

- [*Neolobites bussoni* COLLIGNON, 1965: p. 170, pl. C, fig. 1a-c = intraspecific variety of *N. vibrayeanus* (WIESE & SCHULZE, 2005, p. 935)].
- [*Neolobites choffati* HYATT, 1903: p. 178, pl. 25, figs. 1-4 = intraspecific variety of *N. vibrayeanus* (KENNEDY & JUIGNET, 1981: p. 24; WIESE & SCHULZE, 2005, p. 935)].
- *Neolobites fourtaui* PERVINQUIÈRE, 1907: p. 209, pl. 8, figs. 2-6.
- [*Neolobites isidis* GRECO, 1915: p. 206, pl. 17, fig. 4 = intraspecific variety of *N. vibrayeanus* (KENNEDY & JUIGNET, 1981, p. 24; MEISTER *et alii*, 1992, p. 62; WIESE & SCHULZE, 2005, p. 940)
- [*Neolobites kummeli* BENAVIDES-CÁCERES, 1956: p. 486, pl. 66, figs. 5-6 = synonym of *N. vibrayeanus* (KENNEDY & JUIGNET, 1981, p. 24; WIESE & SCHULZE, 2005, p. 940)].
- [*Ceratites maresi* COQUAND, 1862: p. 168, pl. 32, figs. 1-2 = *N. vibrayeanus* (PERVINQUIÈRE, 1907, p. 307)].
- [*Neolobites medeninensis* BASSE, 1954: p. 197, pl. 32, figs. 1-11 = intraspecific variety of *N. fourtaui* (WIESE & SCHULZE, 2005, p. 940)].
- [*Neolobites peroni* HYATT, 1903: p. 179 = synonym of *N. vibrayeanus* (BENAVIDES-CÁCERES, 1956, p. 486) = intraspecific variety of *N. vibrayeanus* (GRECO, 1915, p. 205; KENNEDY & JUIGNET, 1981, p. 24)].
- [*Neolobites pervinquieri* STAFF & ECK, 1908: p. 279 = intraspecific variety of *N. vibrayeanus* (KENNEDY & JUIGNET, 1981, p. 24; WIESE & SCHULZE, 2005, p. 940)].
- [*Neolobites schweinfurthi* STAFF & ECK, 1908: p. 284, text-fig. 13 = intraspecific variety of *N. vibrayeanus* (KENNEDY & JUIGNET, 1981, p. 24; MEISTER *et alii*, 1992, p. 62; MEISTER & RHALMI, 2002; WIESE & SCHULZE, 2005, p. 935)].
- *Ammonites Vibrayeanus* d'ORBIGNY, 1841: p. 322, pl. 96, figs. 1-3.

Remarks. WIESE & SCHULZE (2005) stated that only *N. vibrayeanus, N. fourtaui* and *N. peroni* deserve discrete specific status. KENNEDY *et alii* (1981, p. 28) convincingly ruled out *N. bedoti* from *Neolobites*. It was placed in *Metengonoceras* (MEISTER *et alii*, 1992). Reported new species are based on fragmented and worn specimens. Therefore the sculpture and suture appear to be simplified (e.g. *N. bassleri, N. kummeli*). KENNEDY & JUIGNET (1981, p. 24) argued that *N. peroni* is also no more than an intraspecific variety of *N. vibrayeanus*. WIESE and SCHULZE (2005) did not discuss the earlier authors' opinion, but maintain *N. peroni* as a distinct species based on slight morphological differences between *N. vibrayeanus* and *N. peroni*. Taking into consideration the extreme morphological variety of the populations of *Neolobites*, the present author accepts the opinion of KENNEDY & JUIGNET (1981) on *N. peroni*, and considers this species an intraspecific variety of *N. vibrayeanus*. It is possible that *N. fourtaui* will also be found to fall into the intraspecific range of *N. vibrayeanus*, especially taking into consideration the eco-morphological analysis of WIESE & SCHULZE (2005). The other possibility, that future research will elucidate, is that *N. fourtaui* and *N. vibrayeanus* form two discrete chronospecies, namely *N. fourtaui* is older and *N. vibrayeanus* is younger. The Early Cenomanian *N. bedoti* of GROSSOUVRE (1912, p. 31) has been assigned to *Metengonoceras* by KENNEDY & JUIGNET (1984, p. 105) because of the very similar morphologies of *Neolobites* and *Metengonoceras*. Based on these similarities, the most probable ancestor of *Neolobites* is *Metengonoceras* (LEHMANN & MURPHY, 2001).

Genus *Knemiceras* BÖHM, 1898, p. 200 = *Cnemidoceras* HAUG, 1900, p. 24; *Cnemioceras* HAUG, 1900, p. 85; *Knemoceras* KRAUSE, 1902, p. 7; *Omaimaiceras* MAHMOUD, 1955; *Iranoknemiceras* COLLIGNON, 1981, p. 258

(Figs. 4 - 5)

Type species. *Ammonites Syriacus* BUCH, 1848, from the Neocomian of Lebanon

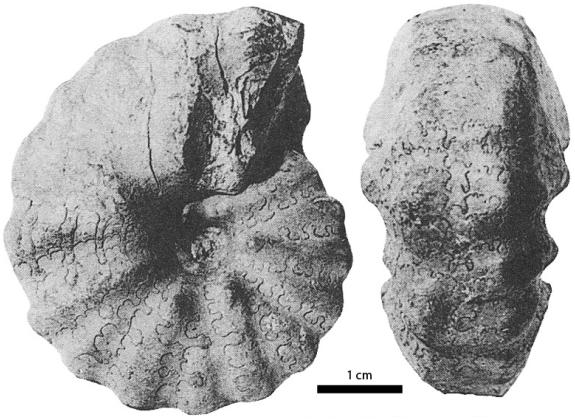


Figure 4: *Knemiceras syriacum* (BUCH, 1848). Reproduction of the original figure of BUCH (1848, p. 21, pl. 6, figs. 1-3).

Diagnosis. Diagnosis is after WRIGHT *et alii* (1996, p. 130): "compressed to moderately inflated; sides flat and parallel or converging; venter flat or slightly concave; ribs moderately to very strong, sparse, rounded or flat, arising singly or in pairs from stout umbilical tubercles; ending in ventrolateral clavi or crossing venter. Suture with frilled lobes and slightly frilled, rarely entire saddles; commonly irregular."

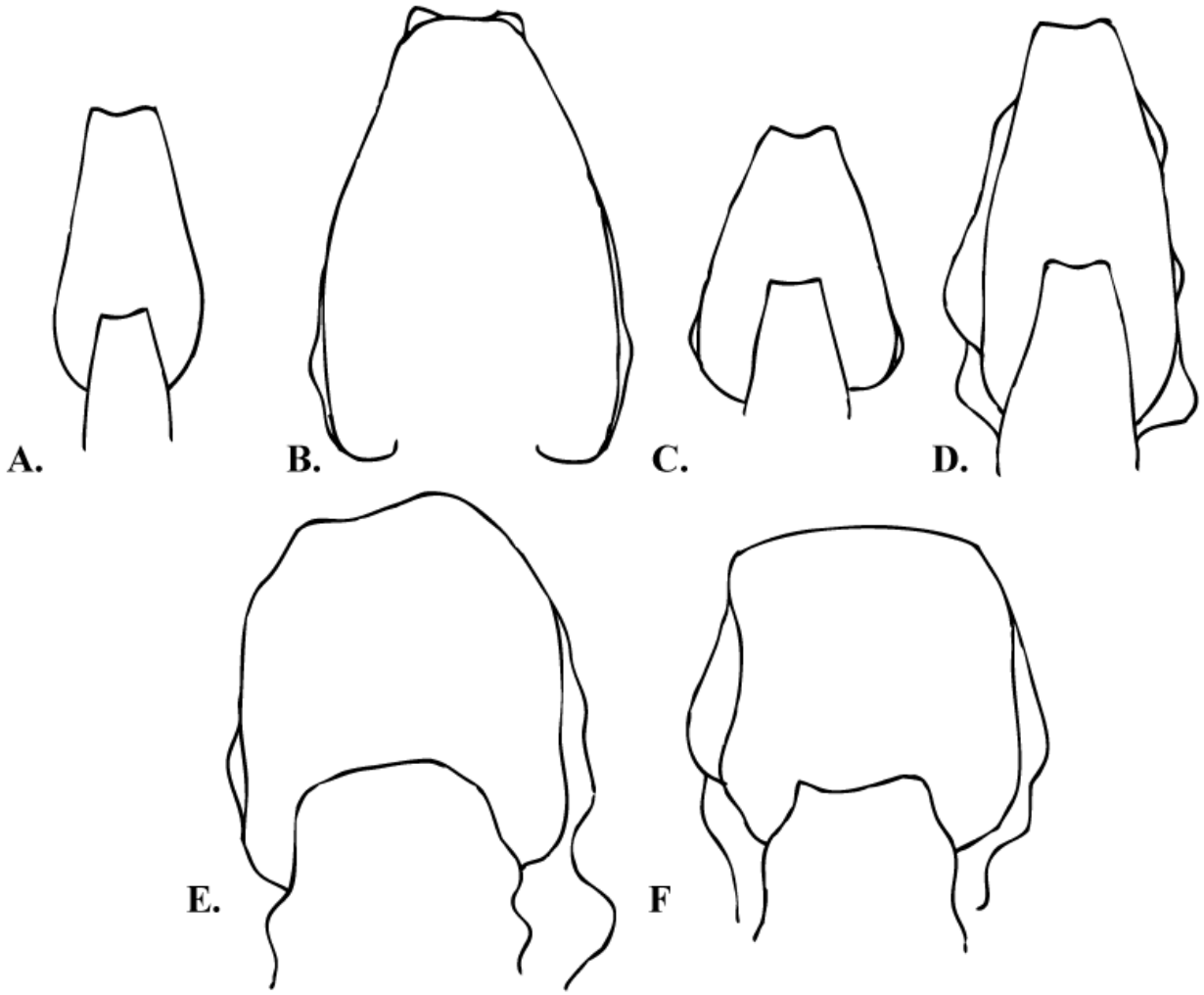


Figure 5: Highly variable cross sections of *Knemiceras* species. A.) *K. compressum* (HYATT, 1903, pl. 16, fig. 16); B.) *K. compressum* (RENZ, 1970, text-fig. 9c); C.) *K. subcompressum* (GEYER *et alii*, 1997, fig. 2f); D.) *K. kazhdumiense* (COLLIGNON, 1981, pl. 3, fig. 1c); E.) *K. douvillei* (COLLIGNON, 1981, pl. 4, fig. 1b); F.) *K. persicum* (COLLIGNON, 1981, pl. 5, fig. 1b).

Occurrence. Separation of South American forms of *Knemiceras* as *Glottoceras* by ROBERT (2002) does not restrict the geographic distribution of the remaining *Knemiceras* species, which are reported from Europe (France, Portugal, Spain), North Africa (Algeria, Egypt, Tunisia), Near East (Israel, Lebanon, Syria), Middle East (Iraq, Iran, Oman), and also from South America (Colombia, Peru). Stratigraphically, *Knemiceras* appears in the earliest Albian (?latest Aptian) and disappears in the Early Cenomanian.

Included species:

- *Knemiceras aegyptiacum* MAHMOUD, 1955: p. 56, pl. 3, fig. 1.
- *Knemiceras arambourgi* BASSE, 1940: p. 426, pl. 1, fig. 2.
- *Knemiceras collignoni* MAHMOUD, 1955: p. 57, pl. 3, figs. 2-3; text-figs. 31-34.
- *Knemiceras compressum* HYATT, 1903: p. 149, pl. 16, figs. 9-10, 15-18.
- *Knemiceras douvillei* BASSE, 1940: p. 431, pl. 3, fig. 1; text-fig. 5.
- *Knemiceras dubertreti* BASSE, 1940: p. 427, pl. 1, figs. 3-4; Pl. 2, figs. 1, 2; text-fig. 2a-b.
- *Knemiceras flexiloculosum* BASSE, 1940: p. 430, pl. 2, fig. 3a-b.
- ? *Hypengonoceras ibericum* ARIAS & WIEDMANN, 1977: p. 9, fig. 5 [see *H. ibericum*].
- *Knemiceras iraniense* COLLIGNON, 1981: p. 254, pl. 1, fig. 1; Pl. 2, fig. 1.
- *Knemiceras kazhdumiense* COLLIGNON, 1981: p. 255, pl. 3, fig. 1.
- [*Knemiceras mintoi* (VREDENBURG, 1907: p. 111, pl. 14, figs. 14-15) of CHIPLONKAR (1941, p. 271) is a synonym of *Placenticeras mintoi* VREDENBURG, 1907 (GANGOPADHYAY & BARDHAN, 2007, p. 101)].
- [*Knemiceras orientalis* MAHMOUD, 1955: p. 54, pl. 2, figs. 2-7; text-figs. 28-29 = synonym with *K. spathi* (BULOT, 2010)].
- *Knemiceras persicum* COLLIGNON, 1981: p.

259, pl. 5, fig. 1.
- [*Knemiceras priscum* DOUVILLÉ, 1916: p. 122 = *Subpulchellia prisca* (WRIGHT *et alii*, 1996, p. 114); = *Mogharaeceras priscum* (BULOT, 2010, p. 168)].
- *Knemiceras (Omaimaiceras) rittmanni* MAHMOUD, 1955: p. 63, pl. 3, fig. 5.
- *Placenticeras saadense* PERON & THOMAS, 1890: p. 19, pl. 16, figs. 3-7.
- *Knemiceras saharae* COLLIGNON, 1965: p. 167, pl. B, fig. 1a-b.
- ? *Knemiceras sinaiticum* is cited by ABDALLAH *et alii* (2008). Without an original diagnosis it is considered here to be a *nomen nudum*
- [*Knemiceras spathi* MAHMOUD, 1955: p. 48, pl. 1, figs. 1-11; Pl. 2, fig. 3; text-figs. 18-27 = synonym with *K. syriacum* (GEYER *et alii*, 1997)].
- [*Knemiceras compressum* var. *subcompressum* HYATT, 1903: p. 150, pl. 16, figs. 11-14, 19 = subspecies of *K. uhligi* (GEYER, 1995a, p. 12, GEYER *et alii*, 1997, p. 226)].
- *Ammonites Syriacus* BUCH, 1848: p. 20, pl. 6, figs. 1-3; Pl. 7, fig. 1.
- *Placenticeras Uhligi* CHOFFAT, 1886: p. 4, pl. 2, figs. 3-5.

Remarks. Resurrection of *Glottoceras* by ROBERT (2002) did not solve the systematic uncertainties around *Knemiceras*. He considered the genus to be a geographical variant and leaves open the problem of the systematic position of the remaining *Knemiceras* species (e.g. *K. attenuatum spinosum* from Australia: WRIGHT, 1963). Other occurrences of '*Knemiceras*' *attenuatum* from Tunisia (ARNOULD-SAGET, 1956, pl. 2, fig. 3a-b) and Iran (COLLIGNON, 1981, pl. 6, fig. 2) should be convincingly placed somewhere in the Engonoceratidae. KLINGER & KENNEDY (1989, p. 364) proposed that *Hypengonoceras ibericum* be placed in *Knemiceras* on the basis that quadrituberculate ornament is unknown in *Hypengonoceras*. Bifid (e.g. *K. compressum, K. subcompressum*) or irregular (*K. douvillei, K. iraniense*) saddles are present in the suture line at any growth stage, distinguishing all *Knemiceras* species from *Engonoceras* and *Platiknemiceras*. The extreme intraspecific variation seen in *Knemiceras* (KLINGER & KENNEDY, 1989, p. 383) especially in its inflation and ornamentation (REYMENT & KENNEDY, 1991) is easily observable in the cross- sections of the body chambers of various species (Fig. 5). Cross-sections of *Knemiceras* range from the slender lanceolate forms (*K. compressum*) through wider (*K. kazhdumiense, K. subcompressum*) and subcircular (*K. douvillei*) and rectangular (*K. persicum*) forms. CASEY (1961) decreased this great variation within the genus by distinguishing the thin, unsculptured and less ornamented forms as *Platiknemiceras*. The extreme variability of shell morphology of *Knemiceras* may have been linked to the mode of life.

Genus *Protengonoceras* HYATT, 1903, p. 153
(Fig. 6)

Type species. *Engonoceras Gabbi* BÖHM, 1898, p. 197, from the Cretaceous of Texas (USA).

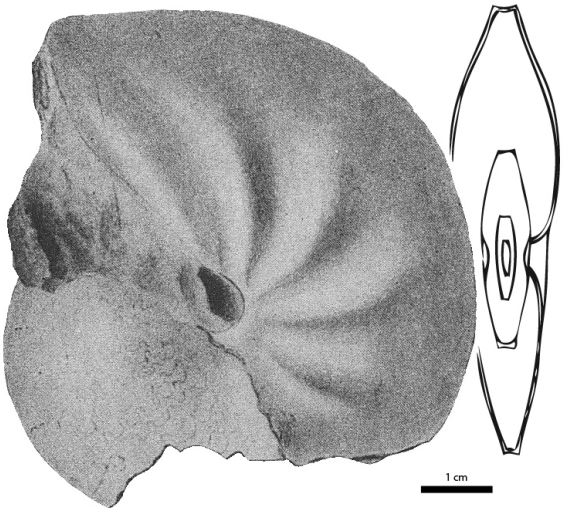


Figure 6: *Protengonoceras gabbi* (BÖHM, 1898). Reproduction of the original specimen of BÖHM (1898, p. 197).

Diagnosis. Diagnosis is after WRIGHT *et alii* (1996) and KENNEDY *et alii* (1998a). Conch is like *Engonoceras* but lacks tubercles at any stage and has feeble, smooth ribs only on adult stage. Cross section is compressed to very compressed and tabulate or may be rounded at adult stage. Where ventrolateral shoulder is present, it is always sharp. The suture line is almost straight and consists of many low adventive saddles, which are entire. Adventicious lobes are narrow and incised.

Occurrence. *Protengonoceras* is reported from the Early and Middle Albian of Peru, Texas, Mexico and Egypt. COLLIGNON (1981) reported two species from the latest Albian and earliest Cenomanian of Iran.

Included species:
- *Protengonoceras dufaurei* COLLIGNON, 1981: p. 261, pl. 5, fig. 2.
- [*Protengonoceras emarginatum* (CRAGIN, 1893): p. 245. referred by HYATT (1903, p. 177) is a synonym of *Engonoceras emarginatum* (HYATT, 1903, p. 157)].
- *Engonoceras Gabbi* BÖHM, 1898: p. 197.
- *Protengonoceras planum* HYATT, 1903: p. 156, pl. 18, figs. 6-9.
- ? *Protengonoceras prestati* COLLIGNON, 1981: p. 262, pl. 6, fig. 3.

Remarks. HYATT (1903, p. 157) referred CRAGIN's *Sphenodiscus emarginatus* to both *Protengonoceras* and *Engonoceras*. Without detailed description it can only be considered a *nomen nudum* so cannot be maintained. HYATT (1903, p. 157) referred to this ambiguity: "not having

seen any specimens of the species, I can not say positively that it is a member of this genus", therefore this reference is omitted. COLLIGNON (1981) reported two new species from the Late Albian-Early Cenomanian of Iran. However, all other species are reported from the Early and Middle Albian, and no occurrences are known from the Late Albian or younger. COLLIGNON (1981) introduced *P. prestati* possessing well preserved dorsolateral and lateral bullae and a suture line with bifid saddles typical of *Knemiceras*. *Protengonoceras* lacks tubercles and never presents bifid and/or incised saddles. On that basis, *P. prestati* belongs rather to *Knemiceras*; however the single figured specimen (COLLIGNON, 1981, pl. 6, fig. 3a-b) does not permit a reliable revision.

Genus *Metengonoceras* HYATT, 1903, p. 179 = *Epengonoceras* SPATH, 1924, p. 508

(Fig. 7)

Type species. *Metengonoceras inscriptum* HYATT, 1903, from the Albian of Decatur, Texas.

Figure 7: *Metengonoceras inscriptum* HYATT, 1903. Reproduction of the original figure of HYATT (1903: p. 180, pl. 25, figs. 5-9).

Diagnosis. Diagnosis is after COBBAN (1987, p. C2). *Metengonoceras* includes very compressed, almost smooth ammonites having very narrow umbilicus and narrow, flattened venters, which may be rounded on the adult body chamber. Sculpture consists of falcoid growth lines. On some species, weak arcuate ribs appear a little above the midflank. Rarely faint umbilical bullae may appear. Suture is simplified, consisting of closely shaped numerous auxiliary and adventive elements. Most of the saddles are wide, being undivided and rounded. Larger lobes may be frilled moderately.

Occurrence. *Metengonoceras* occurred in the Gulf of Mexico during the Middle Albian (COBBAN & KENNEDY, 1989). Many species flourished in the Western Interior of the USA. Repeated speciation took place there (R.W. SCOTT, 2007) from which certain *Metengonoceras* species invaded northward (Mowry Sea, Canada) and eastward (Normandy, France). During the Cenomanian *Metengonoceras* enlarged its territory outside North America. It is reported from Europe (France, Germany), Africa (Algeria, Egypt, Niger, Nigeria, Tunisia), and the Middle East (Jordan) as well as from South America (Brazil, Ecuador) reached through the Saharan seaway. *Metengonoceras* tended to become more acute and sharply keeled during the Cenomanian.

Included species:

- *Metengonoceras acutum* HYATT, 1903: p. 184, pl. 26, fig. 8; pl. 27, figs. 1-2.
- *Metengonoceras ambiguum* HYATT, 1903: p. 183, pl. 26, figs. 5-7.
- *Metengonoceras arnaudi* GROSSOUVRE, 1912: p. 30.
- *Epengonoceras aspenanum* REESIDE & WEYMOUTH, 1931: p. 16, pl. 1, fig. 15; pl. 2, figs. 2-5; pl. 3, figs. 5-7.
- *Neolobites bedoti* GROSSOUVRE, 1912: p. 31, pl. 3, fig. 2; text-fig. 4.
- *Engonoceras bravoense* BÖSE, 1928: p. 229, pl. 7, figs. 31-35: pl. 8, figs. 1-8.
- ? *Metengonoceras dibbleyi* is cited by GROSHENY *et alii* (2008, p. 594) referring to HERKAT (1999, p. 270), however both citations are considered to be *nomen nudum* because of a lack of original designation
- [*Metengonoceras douvillei* GROSSOUVRE, 1912: p. 34, pl. 3, fig. 3 = synonym of *M. dumbli* (KENNEDY *et alii*, 1981, p. 36; KENNEDY & JUIGNET, 1984, p. 100)].
- *Sphenodiscus dumbli* CRAGIN, 1893: p. 243, pl. 44, fig. 6.
- *Metengonoceras inscriptum* HYATT, 1903: p. 180, pl. 25, figs. 5-9; pl. 26, figs. 1-4.
- [*Metengonoceras nigeriensis* FURON, 1935: p. 55, pl. 3, fig. 1 = synonym of *M. dumbli* (KENNEDY *et alii*, 1981, p. 36; MEISTER & ABDALLAH, 2005, p. 123)].
- *Metengonoceras oliveirai* BRITO, 1967: p. 71, pl. 1, figs. 1-2.
- *Metengonoceras teigenense* COBBAN & KENNEDY, 1989: p. L6, pl. 2, figs. 1-7; Pl. 3, figs. 1-8; Pl. 4, figs. 1-8; Pl. 5, figs. 1-3; text-fig. 4.
- [*Metengonoceras tolveiense* GROSSOUVRE, 1912: p. 36 = synonym of *M. dumbli* (KENNEDY *et alii*, 1981, p. 36)].

Remarks: STEPHENSON (1952) extensively reviewed the type species of *Epengonoceras* (*E. dumbli*) and concluded that the genus is not separable from *Metengonoceras*. This view was accepted by KENNEDY & JUIGNET (1984, p. 100)

and is also followed here. R.W. SCOTT (2007) reports stratigraphical ranges of engonoceratid ammonites from North America showing that certain *Metengonoceras* species occur in the Late Albian (*M. teigenense, M. aspenanum*) and Cenomanian (*M. dumbli, M. acutum*) suggesting that in North America *Metengonoceras* species range from earliest Late Albian to the latest Cenomanian.

Genus ? *Hypengonoceras* SPATH, 1922, p. 112
(Fig. 8)

Type species. *Placenticeras Warthi* KOSSMAT, 1895, from the Albian Utatur Group of southern India.

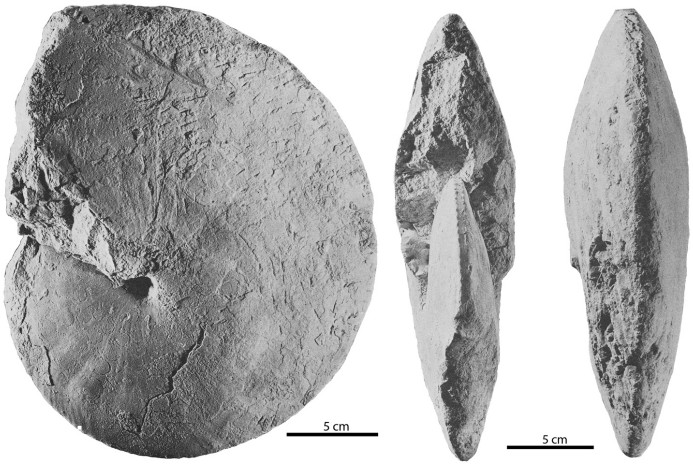


Figure 8: *Hypengonoceras decaryi* (COLLIGNON, 1963). Reproduction of the figures of KLINGER & KENNEDY (1989: figs. 112-113).

Diagnosis. Diagnosis is after KLINGER & KENNEDY (1989, p. 362). "Umbilicus is narrow. The shell compressed, the flanks generally little rounded. Sculpture consists of low falcoid ribs, often very weak and only visible under oblique lighting. Umbilical tubercles may be present, but are never very prominent. Venter is flat to concave with alternating ventral clavi at least at some stage. Dimorphism pronounced, but mainly restricted to differences in size. Suture variable; in typical forms some saddles are little divided and 'pincer-like' with bifid folioles; in others as incised as in a normal placenticeratid pattern."

Occurrence. *Hypengonoceras* is reported from the Late Albian of Europe (France), Africa (Madagascar, Morocco, Mozambique, Zululand), Near East (Israel), India, and probably Sakhalin (Japan). AYYASAMI & BANERJI (1984, Table 1) noted a doubtful occurrence in the Late Cenomanian of the Utatur Group, South India but they did not figure or describe it, so this occurrence is omitted.

Included species:

- *Hypengonoceras chouberti* COLLIGNON, 1966: p. 17, pl. 4, figs. 1-2; Pl. 5, fig. 127.
- *Hypengonoceras decaryi* COLLIGNON, 1963: p. 128, pl. 291, fig. 1269.
- *Hypengonoceras fauremuretae* COLLIGNON, 1966: p. 18, pl. 6, figs. 1-4.
- ? *Hypengonoceras ibericum* ARIAS & WIEDMANN, 1977: p. 9, fig. 5 [= ? *Knemiceras ibericum*, see KLINGER & KENNEDY, 1989, p. 364].
- *Hypengonoceras tarfayense* COLLIGNON, 1966: p. 19, pl. 7, fig. 1.
- [*Hypengonoceras vredenburgi* SARKAR, 1966: p. 144, pl. 11, figs. 1-2 = *Placenticeras vredenburgi* (KLINGER & KENNEDY, 1989, p. 389)].
- *Placenticeras Warthi* KOSSMAT, 1895: p. 80, pl. 20, fig. 8.

Remarks. Although KLINGER & KENNEDY (1989) indicated the placenticeratid-like pattern of the suture of *Hypengonoceras*, they assigned the genus to the Engonoceratidae. This clearly relates to the debate on the systematic position of *Hypengonoceras* for it is the most disputed among the Engonoceratidae and is again under reconsideration (ROBERT & BULOT, 2004). This continuing dispute is based on the general differences between the Engonoceratidae and the Placenticeratidae. The Engonoceratidae are characterized by simplified ceratitic saddles (best seen on all species of *Protengonoceras, Engonoceras, Metengonoceras*, and *Neolobites*) in contrast to the frilled and finely incised saddles and lobes of Placenticeratidae. In this scheme, *Parengonoceras* and *Hypengonoceras* are transitional between the Engonoceratidae and the Placenticeratidae (KLINGER & KENNEDY, 1989, p. 364); however the first-named genus was placed in the Engonoceratidae without dispute - partly because of its known stratigraphical distribution (Early and Middle Albian) and because *Parengonoceras* possesses two true adventive lobes (RENZ, 1970). Only *H. ibericum* is questioned as a member of the genus by KLINGER & KENNEDY (1989, p. 364) because quadrituberculate ornament is unknown in *Hypengonoceras*. They proposed that *H. ibericum* be placed in *Knemiceras*. Since the thorough discussion of *Hypengonoceras* by KLINGER & KENNEDY (1989) no significant progress toward clarifying the position of the genus has been published; therefore the opinion of KLINGER & KENNEDY (1989) is maintained here.

Table 1: Geographical and stratigraphical distribution of engonoceratid species. Type species are indicated in bold.

No.	Species	Stratigraphical distribution	Geographical distribution	References
	Glottoceras HYATT, 1875	Albian	South America	
1	*andinum* (RENZ, 1970)	Upper Albian	Venezuela	RENZ, 1970
2	***attenuatum*** **HYATT, 1875**	?Cenomanian	Celendín, Peru	HYATT, 1903; ROMAN, 1938
		Albian-Cenomanian	Oriente Basin, Ecuador	WOOD & ALEMAN, 1998
		Albian	Une, Une Formation, Colombia	GUERRERO, 2002
		Middle Albian	northern Peru	KNECHTEL *et alii*, 1947; BENAVIDES-CÁCERES, 1956
		Lower Albian	Peru	ROBERT *et alii*, 2003; ROBERT & BULOT, 2004
3	*bassleri* (KNECHTEL *in* KNECHTEL *et alii*, 1947)	Aptian	En Huanco, Celendin, Peru	KNECHTEL *et alii*, 1947
4	*crassicostatum* (SOMMERMEIER, 1910)	Middle Albian	Peru	KNECHTEL *et alii*, 1947
		Lower-Middle Albian	Pongo de Rentemo, Peru	ROBERT *et alii*, 1998
5	*crassinodosum* (SOMMERMEIER, 1910)	Middle Albian	Condebamba, northern Peru	SOMMERMEIER, 1910; KNECHTEL *et alii*, 1947
		Lower-Middle Albian	Peru	ROBERT *et alii*, 2003; ROBERT & BULOT, 2004
6	*gabbi* (HYATT, 1903)	?Cenomanian	Quebrada de Huari, Peru	HYATT, 1903; ROMAN, 1938
		Middle Albian	Celendín, Sunchubamba, northern Peru	BENAVIDES-CÁCERES, 1956
		upper Lower Albian	Peru	ROBERT *et alii*, 2003; ROBERT & BULOT, 2004
7	*gracilecostatum* (SOMMERMEIER, 1910)	Lower Albian	northern Peru	ROBERT *et alii*, 2003
8	*laraense* (RENZ, 1970)	Middle Albian-Upper Albian	Misahualli, Ecuador; Venezuela	BULOT *et alii*, 2007
9	*largum* ROBERT, 2002	Lower Albian	La Cuenca, Peru	ROBERT *et alii*, 2003
10	*libertadense* (BREISTROFFER, 1952)	Albian	Colombia	BREISTROFFER, 1952
11	*moorei* (KNECHTEL *in* KNECHTEL *et alii*, 1947)	upper Middle Albian	Peru	ROBERT *et alii*, 2003; ROBERT & BULOT, 2004
		Middle Albian	Peru	KNECHTEL *et alii*, 1947
			Misahualli, Ecuador	BULOT *et alii*, 2007
12	*ollonense* (GABB, 1877)	Lower Albian	La Cuenca, Peru	ROBERT *et alii*, 2003
			Sunchubamba, northern Peru	BENAVIDES-CÁCERES, 1956; ROBERT *et alii*, 1998
13	*ovale* (BENAVIDES-CÁCERES, 1956)	Middle Albian	Uchupata, northern Peru	BENAVIDES-CÁCERES, 1956
14	*pacificum* (BENAVIDES-CÁCERES, 1956)	Lower Albian	Celendín, Peru	BENAVIDES-CÁCERES, 1956
15	*pegnai* (ETAYO-SERNA, 1979)	Cretaceous	Colombia	ETAYO-SERNA, 1979
16	*raimondii* (LISSON, 1908)	Middle Albian	Cajamarca, Sihuas, Pomachaca, northern Peru	SOMMERMEIER, 1910; KNECHTEL *et alii*, 1947; BENAVIDES-CÁCERES, 1956; ROBERT *et alii*, 1998
		upper Lower Albian	Peru	ROBERT *et alii*, 2003; ROBERT & BULOT, 2004
17	*semicostatum* (SOMMERMEIER, 1910)	Middle Albian	Cochamarca, northern Peru	SOMMERMEIER, 1910; KNECHTEL *et alii*, 1947
		upper Lower Albian	Peru	ROBERT *et alii*, 2003; ROBERT & BULOT, 2004
18	*seminodosum* (SOMMERMEIER, 1910)	Middle Albian	Peru	ROBERT & BULOT, 2004
19	*sommermeieri* (KNECHTEL *in* KNECHTEL *et alii*, 1947)	Middle Albian	Peru	KNECHTEL *et alii*, 1947
			Misahualli, Ecuador	BULOT *et alii*, 2007
20	*spinosum* (SOMMERMEIER, 1910)	Middle Albian	northern Peru	KNECHTEL *et alii*, 1947
		Lower Albian (mammillatum Zone)	Bathurst Island, North Australia	WRIGHT, 1963
21	*tardum* (BENAVIDES-CÁCERES, 1956)	Middle Albian	Sihuas, northern Peru	BENAVIDES-CÁCERES, 1956
		Lower Albian	La Cuenca, Peru	ROBERT *et alii*, 2003
22	*triangulare* (BENAVIDES-CÁCERES, 1956)	Middle Albian	Sihuas, northern Peru	BENAVIDES-CÁCERES, 1956
23	*typicum* (SOMMERMEIER, 1910)	Middle Albian	northern Peru	ROBERT & BULOT, 2004
	Engonoceras NEUMAYR & UHLIG, 1881	Lower Albian-Middle Cenomanian	Tethyan	
1	*belviderense* (CRAGIN, 1894)	Lower Cretaceous	Belvidere, Kansas	HYATT, 1903; COBBAN, 1987
		Upper Albian	Texas, USA	R.W. SCOTT *et alii*, 2003
		Neocomian	Kansas, USA	R.W. SCOTT, 1970; KENNEDY *et alii*, 1998a
		Middle-Upper Albian	Sonora, Mexico	ROMAN, 1938; R.W. SCOTT & GONZÁLEZ-LEÓN, 1991
2	*commune* HYATT, 1903	Cretaceous	Texas	HYATT, 1903
3	*complicatum* HYATT, 1903	Albian	Texas	HYATT, 1903; KENNEDY *et alii*, 1998a
		Upper Albian	El Mizab, Meknes, Atlas, Morocco	COLLIGNON & FAURE-MURAT, 1968
4	*elegans* KENNEDY *et alii*, 1998a	Albian	Texas	KENNEDY *et alii*, 1998a
5	*emarginatum* (CRAGIN, 1893)	Albian	Pleasant Point, Texas, USA	HYATT, 1903
6	*gibbosum* HYATT, 1903	Albian	Texas, USA	HYATT, 1903; KENNEDY *et alii*, 1998a
		Middle Albian		R.W. SCOTT *et alii*, 2003
7	*grimsdalei* SPATH, 1931	Upper Albian	Weymouth, Dorset, England	SPATH, 1931; BENAVIDES-CÁCERES, 1956
8	*hilli* BÖHM, 1898	Albian	Texas, USA	KENNEDY *et alii*, 1998a
			North Peruvian Andes	ROBERT *et alii*, 2003
		Middle-Upper Albian	Texas, USA	R.W. SCOTT *et alii*, 2003
9	*iris* SPATH, 1924	Middle Albian	Folkestone, England	ROMAN, 1938; SPATH, 1924
10	*jezzinense* BASSE, 1940	Albian	Djebel Tebega, Tunisia	ARNOULD-SAGET, 1956
			Jezzine, Lebanon	BASSE, 1940
11	*khenchelaensis* (BASSE, 1940)	Albian-Cenomanian	Syria	KENNEDY *et alii*, 1998a
		Albian	Bhamdoum, Lebanon	CASEY, 1961
12	*olgaluciae* ETAYO-SERNA, 1979	Middle Albian	Colombia	ETAYO-SERNA, 1979
13	***pierdenalis*** **(BUCH, 1848)**	Upper Cretaceous	Fredericksburg, Texas	BUCH, 1848
		Albian	Texas	HYATT, 1903; ROMAN, 1938
		Upper Albian	Chihuahua, Mexico	BÖSE, 1910
		Middle Albian	Sonora, Mexico	GONZÁLEZ-LEÓN, 1988; R.W. SCOTT & GONZÁLEZ-LEÓN, 1991
14	*pinax* (KRAUSE, 1902)	Cenomanian	Temojoh, West Borneo	KRAUSE, 1902; BREISTROFFER, 1940; HAILE, 1955
15	*retardum* HYATT, 1903	lowest Cenomanian	Pottsboro, Texas, USA	HYATT, 1903; COBBAN & KENNEDY, 1989; KENNEDY *et alii*, 2005
16	*serpentinum* (CRAGIN, 1900)	Lower Cenomanian	Texas	MANCINI, 1982
		Upper Albian		ROMAN, 1938; WRIGHT *et alii*, 1996
		uppermost Albian (dispar Zone)		HYATT, 1903; KENNEDY *et alii*, 1998b; KENNEDY, 2004; KENNEDY *et alii*, 2005
17	*subjectum* HYATT, 1903	uppermost Albian (dispar Zone)	Texas	HYATT, 1903; KENNEDY *et alii*, 1998b
18	*stolleyi* BÖHM, 1898	Albian	Texas	KENNEDY *et alii*, 1998a
		Upper Albian	Chihuahua, Mexico	BÖSE, 1910
		Middle-Upper Albian	Sonora, Mexico	R.W. SCOTT & GONZÁLEZ-LEÓN, 1991
		Middle Albian		GONZÁLEZ-LEÓN, 1988
			La Cuenca, Peru	ROBERT *et alii*, 2003
19	*thomasi* PERVINQUIÈRE, 1907	Cenomanian	Rekkame, Middle Atlas, Morocco	LEHMANN & HERBIG, 2009
		U. Albian-L. Cenomanian	Guelta, Tunisia	ROMAN, 1938; LATIL, 1989
20	*toussainti* PERVINQUIÈRE, 1907	U. Albian-L. Cenomanian	Tebaga, Tunisia	ROMAN, 1938; LATIL, 1989
21	*uddeni* (CRAGIN, 1900)	Comanche series, Kiowa shale	Kansas, USA	HYATT, 1903
		Middle Albian	Sonora, Mexico	GONZÁLEZ-LEÓN, 1988
22	*vicorpense* (BASSE, 1940)	Albian-Cenomanian	Syria	KENNEDY *et alii*, 1998a
		Upper Albian	Djebel Naimia, Chotts, Tunisia	MORENO-BEDMAR *et alii*, 2008b
23	*wilkinsoni* PACKARD, 1956	?Upper Albian	Oregon, USA	PACKARD, 1956
24	*zumoffeni* (BASSE, 1940)	Albian-Cenomanian	Syria	KENNEDY *et alii*, 1998a
	Neolobites FISCHER, 1882	Cenomanian	Tethyan	
1	*bassleri* BOIT, 1926	Cenomanian	Caminaca, Peru	BOIT, 1926; CABRERA LA ROSA & PETERSEN, 1936
		Middle-Upper Cenomanian	Altiplano, Peru	JAILLARD, 1995; ROBERT *et alii*, 1998
2	*brancai* STAFF & ECK, 1908	U. Cenomanian- L. Turonian	Egypt	STAFF & ECK, 1908; ECK, 1914; DOUVILLÉ, 1928
		Upper Cenomanian	Central High Atlas, Morocco	MEISTER & RHALMI, 2002
		Upper Cenomanian	Gafsa, Central Tunisia	MEISTER & ABDALLAH, 2005
3	*bussoni* COLLIGNON, 1965	Cenomanian	Tinrhert, Sahara, Algeria	COLLIGNON, 1965; AMARD *et alii*, 1981
		Upper Cenomanian	Ourém, Portugal	BERTHOU & LAUVERJAT, 1978, 1979
4	*choffati* HYATT, 1903	Cenomanian	Portugal	HYATT, 1903
5	*fourtaui* PERVINQUIÈRE, 1907	Cenomanian	Egypt, Tunisia	PERVINQUIÈRE, 1907; GRECO, 1915
		Upper Cenomanian	Tarfa, Arabic Desert	DOUVILLÉ, 1928
			Tinrhert, Sahara, Algeria	COLLIGNON, 1965; AMARD *et alii*, 1981
		Middle-Upper Cenomanian	Palmyrids, Central Syria	MOUTY *et alii*, 2003
6	*isidis* GRECO, 1915	Cretaceous	Egypt	GRECO, 1915
		Upper Cenomanian	Gafsa, Central Tunisia	MEISTER & ABDALLAH, 1996
7	*kummeli* BENAVIDES-CACERES, 1956	base Upper Cenomanian	Celendín, Northern Peru	BENAVIDES-CÁCERES, 1956
			Bolivia	BRANISA, 1968; JAILLARD & SEMPERE, 1992
8	*maresi* (COQUAND, 1862)	Cenomanian	Egypt	COQUAND, 1862; GRECO, 1915; KENNEDY & JUIGNET, 1984
9	*medeninensis* BASSE, 1954	Cenomanian	Tunisia	BASSE, 1954; WIESE & SCHULZE, 2005
10	*peroni* HYATT, 1903	Upper Cenomanian	Tinrhert, Sahara, Algeria	PERVINQUIÈRE, 1910; COLLIGNON, 1965; AMARD *et alii*, 1981
		Cenomanian	North Africa	HYATT, 1903
			Egypt	ECK, 1914; DOUVILLÉ, 1928
			Provence (France), Tunisia	ROMAN, 1938
11	*pervinquieri* STAFF & ECK, 1908	Upper Cenomanian	Egypt	STAFF & ECK, 1908; WIESE & SCHULZE, 2005
	schweinfurthi STAFF & ECK, 1908	U. Cenomanian-L. Turonian	Egypt	STAFF & ECK, 1908; ECK, 1914; DOUVILLÉ, 1928
		Turonian	Egypt	ECK, 1910
12	***vibrayeanus*** **(d'ORBIGNY, 1841)**	Cretaceous	Vibraye, Sarthe, France	d'ORBIGNY, 1841; BUCH, 1848
		Cenomanian	Celendín, Northern Peru	BOIT, 1926
			El Kisba, High Atlas, Morocco	LEHMANN & HERBIG, 2009
			France	GILLARD, 1942; WRIGHT *et alii*, 1996
			France, Portugal	HYATT, 1903
		Upper Cenomanian	Jordan	ALY *et alii*, 2008
			Central Oman	KENNEDY & SIMMONS, 1991
			Estremadure, Lisbon, Portugal	BERTHOU *et alii*, 1979
			Vouillac, France	MOREAU *et alii*, 1983
			Tinrhert, Sahara, Algeria	COLLIGNON, 1965; AMARD *et alii*, 1981; AMÉDRO *et alii*, 1996
			Egypt, Jordan	WIESE & SCHULZE, 2005
			Gafsa, Central Tunisia	MEISTER & ABDALLAH, 2005
			Tanout, Niger	MEISTER *et alii*, 1992
			Burgos, Spain	WIEDMANN, 1979
	Knemiceras BÖHM, 1898	?Upper Aptian-Albian	Tethyan	
	as *Knemiceras* sp.	Upper Albian	Río Aguamulac, Huescar, Spain	BRAGA *et alii*, 1982
		Middle Albian	Aube, France	AMÉDRO & DESTOMBES, 1984
1	*aegyptiacum* MAHMOUD, 1955	Upper Albian-Lower Cenomanian	Kazhdumi, southern Iran	COLLIGNON, 1981
		Upper Albian	Gafsa, Central Tunisia	ABDALLAH *et alii*, 2008
			Oued Zitoun, North Tunisia	KOGBE & MÉHES, 1986
2	*arambourgi* BASSE, 1940	Cretaceous	Syria, Lebanon	BASSE, 1940; KENNEDY & SIMMONS, 1991
3	*collignoni* MAHMOUD, 1955	Cretaceous	Sinai, Egypt	MAHMOUD, 1955
		Upper Albian-Lower Cenomanian	Kazhdumi, southern Iran	COLLIGNON, 1981
4	*compressum* HYATT, 1903	?Cenomanian	Beirut, Lebanon	HYATT, 1903; ROMAN, 1938
		Albian	Nar, Kartang, Jahrum, southern Iran	COLLIGNON, 1981
		Upper Albian	Venezuela	RENZ, 1970
			Oued Zitoun, North Tunisia	KOGBE & MÉHES, 1986
			Djebel Naimia, Chotts, Tunisia	MORENO-BEDMAR *et alii*, 2008b; MARZOUK & BEN-YOUSSEF, 2008
		Middle Albian	Bilbao, northern Spain	LOPEZ-HORGUE *et alii*, 2009
5	*douvillei* BASSE, 1940	Cretaceous	Djebel Dourra Syria	BASSE, 1940
		Upper Albian-Lower Cenomanian	Kazhdumi, southern Iran	COLLIGNON, 1981
		Upper Albian	Lurestan, Iran	BULOT, 2007
6	*dubertreti* BASSE, 1940	Cretaceous	Djebel Dourra, Syria	BASSE, 1940
		Albian	Mderedj, Lebanon	CASEY, 1961
		Upper Albian	Lurestan, Iran	BULOT, 2007
		Lower-Middle Albian	Central Oman	KENNEDY & SIMMONS, 1991
7	*flexiloculosum* BASSE, 1940	Cretaceous	Syria	BASSE, 1940
		Middle Albian	Dead Sea, Israel	WEISSBROD, 2002
		Lower Albian	Guajira, NE Colombia	GUERRERO, 2002
8	*iraniense* COLLIGNON, 1981	U. Albian-L. Cenomanian	Kazhdumi, southern Iran	COLLIGNON, 1981
		Middle-Upper Albian	Bangestan, SW Iran	BULOT, 2010
9	*kazhdumiense* COLLIGNON, 1981	U. Albian-L. Cenomanian	Kazhdumi, southern Iran	COLLIGNON, 1981
		Middle-Upper Albian	Bangestan, SW Iran	BULOT, 2010
10	*orientalis* MAHMOUD, 1955	Middle Albian	Moghara, Egypt	MAHMOUD, 1955
11	*persicum* COLLIGNON, 1981	U. Albian-L. Cenomanian	Kazhdumi, southern Iran	COLLIGNON, 1981
		Lower Albian	Bangestan, Lurestan, Iran	BULOT, 2007, 2010
12	*rittmanni* MAHMOUD, 1955	Middle Albian	Moghara, Egypt	MAHMOUD, 1955; MORET & MAHMOUD, 1955; TAWADROS, 2001
13	*saadense* (PERON & THOMAS, 1890)	Cretaceous	Tunisia	PERON & THOMAS, 1890
		Upper Albian	Salazac, Gard, France	BREISTROFFER, 1940; LATIL, 1989; AMÉDRO, 2008
			Algeria	PERVINQUIÈRE, 1910; ROMAN, 1938; CHIPLONKAR, 1941
14	*saharae* COLLIGNON, 1965	Albian	Tebaga de Kebili, South Tunisia	COLLIGNON, 1965
			Sinai, Egypt	GEYER *et alii*, 1997
15	? *sinaiticum*	Upper Albian	Gafsa, Central Tunisia	ABDALLAH *et alii*, 2008
16	*spathi* MAHMOUD, 1955	U. Albian-L. Cenomanian	Nar, Gavbasht, southern Iran	COLLIGNON, 1981
		Upper Albian	Oued Zitoun, North Tunisia	KOGBE & MÉHES, 1986
		Lower Albian	northern Sinai, Egypt	GEYER *et alii*, 1997; TAWADROS, 2001; ABU-ZIED, 2008
			Bangestan, SW Iran	BULOT, 2010
17	*subcompressum* HYATT, 1903	? Cenomanian	Gilead Mts. Jordan; Mt. Lebanon, Syria	HYATT, 1903; GEYER *et alii*, 1997
18	***syriacum*** **(BUCH, 1848)**	Lower Cretaceous	Lebanon	BUCH, 1848
			Angola	DOUVILLÉ, 1931; ROMAN, 1938
		Cenomanian	Mt. Lebanon, Syria	HYATT, 1903
		U. Albian-L. Cenomanian	Kazhdumi, southern Iran	COLLIGNON, 1981
		Upper Albian	Portugal	ROMAN, 1938
			Lurestan, Iran	BULOT, 2007
			Syria	WRIGHT *et alii*, 1996; MOUTY *et alii*, 2003
		Middle-Upper Albian	northern Sinai, Egypt	GEYER *et alii*, 1997
			Jawan area, NW Iraq	HORBURY, 2006
		Middle Albian	Tebaga, central Tunisia	BEN YOUSSEF *et alii*, 1985
			Moghara, Egypt	DOUVILLÉ, 1916, 1928; MORET & MAHMOUD, 1955
			Dead Sea, Israel	WEISSBROD, 2002
			Cajamarca, Uchupata, Peru	BENAVIDES-CÁCERES, 1956; ROBERT *et alii*, 1998
		Lower Albian	northern Sinai, Egypt	ABU-ZIED, 2008
19	*uhligi* (CHOFFAT, 1886)	? Cenomanian	Portugal	HYATT, 1903; ROMAN, 1938
		Upper Albian	Santander, Cantabria, Spain	WILMSEN, 1996
			Teruel, Valencia, Spain	GEYER, 1995a, 1995b
			Estremadure, Lisbon, Portugal	CHIPLONKAR, 1941; BERTHOU *et alii*, 1979, COLLIGNON, 1981
			Salinas (Angola); Moghara (Egypt)	DOUVILLÉ, 1928, 1931
			Lurestan, Iran	BULOT, 2007
		Middle-Upper Albian	northern Sinai, Egypt	GEYER *et alii*, 1997
			Tebaga, central Tunisia	COLLIGNON, 1965
			Muscat, Oman	IMMENHAUSER *et alii*, 2000
		Lower Albian	Lurestan, Iran	BULOT, 2007
			northern Sinai, Egypt	ABU-ZIED, 2008
	Protengonoceras HYATT, 1903	Lower/Middle Albian-?Lower Cenomanian	Tethyan	
1	*dufaurei* COLLIGNON, 1981	Lower Cenomanian	Kazhdumi, southern Iran	COLLIGNON, 1981
2	***gabbi*** **(BÖHM, 1898)**	Albian	Sonora (Mexico), Texas	HYATT, 1903; KENNEDY *et alii*, 1998a
		Upper Albian	northern Sinai, Egypt	ABU-ZIED, 2008
		Middle Albian	Texas	WRIGHT *et alii*, 1996
			Peru	ROBERT *et alii*, 1998
3	*planum* HYATT, 1903	Upper Cretaceous	Dallas County, Texas	HYATT, 1903; MOREMAN, 1942
4	? *prestati* COLLIGNON, 1981	U. Albian-L. Cenomanian	Kazhdumi, southern Iran	COLLIGNON, 1981
	Metengonoceras HYATT, 1903	Middle Albian-Cenomanian	cosmopolitan	
	as *Epengonoceras* sp.	Upper Albian	Lower Saxony Basin, Germany	OWEN, 2007
	as *Metengonoceras* sp.	uppermost Cenomanian	Sahara, Africa	COURVILLE, 2007
		lower Upper Cenomanian	Sayreville, NJ, USA	COBBAN & KENNEDY, 1990
1	*acutum* HYATT, 1903	Upper Cenomanian	North Central Texas	HYATT, 1903; MOREMAN, 1942; KENNEDY, 1988; KENNEDY & COBBAN, 1990; R.W. SCOTT *et alii*, 2003
2	*ambiguum* HYATT, 1903	Lower Cretaceous	Texas, USA	HYATT, 1903
		Albian		KENNEDY *et alii*, 1998a
		Aptian-Albian		ROMAN, 1938
3	*arnaudi* GROSSOUVRE, 1912	Cenomanian	Touvois, Vendée, France	GILLARD, 1942
			Charentes, France	KENNEDY *et alii*, 1981
4	*aspenanum* (REESIDE & WEYMOUTH, 1931)	Cenomanian	Montana, Wyoming, USA	COBBAN & KENNEDY, 1989; YACOBUCCI, 2004
		uppermost Albian	Montana, USA	R.W. SCOTT *et alii*, 2003
5	*bedoti* (GROSSOUVRE, 1912)	Lower Cenomanian	Vendée, France	GILLARD, 1942; KENNEDY *et alii*, 1981; KENNEDY & JUIGNET, 1984; MEISTER *et alii*, 1992
6	*bravoense* (BÖSE, 1928)	Cenomanian [*M. (P.) rhacioformis* Zone]	Texas	MANCINI, 1979
		lowermost Cenomanian	Texas, USA	KENNEDY *et alii*, 2005
		Albian-Cenomanian	Oriente Basin, Ecuador	WOOD & ALEMAN, 1998
7	? *dibbleyi*	Upper Cenomanian	Ouled nail, Saharan Atlas, Algeria	HERKAT, 1999; GROSHENY *et alii*, 2008
8	*douvillei* GROSSOUVRE, 1912	Cenomanian	Vendée, France	KENNEDY *et alii*, 1981
9	*dumbli* (CRAGIN, 1893)	Cenomanian	Texas, USA	MOREMAN, 1942; WRIGHT *et alii*, 1996
		uppermost Cenomanian	Jordan	ALY *et alii*, 2008
			Benue trough, Nigeria	COURVILLE *et alii*, 1998
		Upper Cenomanian	Mts. Iguellala, Niger	MEISTER *et alii*, 1992
			Sinai, Egypt	ALY & ABDEL-GAWAD, 2001
			Le Mans, France	KENNEDY & JUIGNET, 1984
			Angers, France	KENNEDY *et alii*, 1981
		Middle-Upper Cenomanian	Gafsa, Central Tunisia	MEISTER & ABDALLAH, 2005
			Colorado, USA	COBBAN & G.R. SCOTT, 1972
			North Central Texas	KENNEDY & COBBAN, 1990; R.W. SCOTT *et alii*, 2003
10	***inscriptum*** **HYATT, 1903**	Lower Cretaceous	Texas, USA	HYATT, 1903
		Upper Albian		WRIGHT *et alii*, 1996
		Middle Albian		COBBAN & KENNEDY, 1989
		Albian		KENNEDY *et alii*, 1998a
		Aptian-Albian		ROMAN, 1938
11	*nigeriensis* FURON, 1935	Upper Cenomanian	Niger	KENNEDY *et alii*, 1981
12	*oliveirai* BRITO, 1967	Albian-Cenomanian	Rio Fundo, Sergipe, Brazil	BRITO, 1986; SIMONE, 1994
13	*teigenense* COBBAN & KENNEDY, 1989	Cenomanian	Montana, USA	COBBAN & KENNEDY, 1989; YACOBUCCI, 2004
		Lower Cenomanian	Normandie, France	AMÉDRO *et alii*, 2002
		U. Albian-lowermost Cenomanian	Montana, USA	R.W. SCOTT *et alii*, 2003
14	*tolveiense* GROSSOUVRE, 1912	Cenomanian	Vendée, France	KENNEDY *et alii*, 1981
	Hypengonoceras SPATH, 1922	Upper Albian	Tethyan	
	as *Hypengonoceras* sp.	Upper Albian	Makhtesh Ramon, Israel	LEWY, 1981
	as *Hypengonoceras* sp. ind.	Upper Albian	Salazac, Gard (France)	LATIL, 1989
1	*chouberti* COLLIGNON, 1966	Upper Albian	Tarfaya, Morocco	COLLIGNON, 1966; KLINGER & KENNEDY, 1989
2	*decaryi* COLLIGNON, 1963	Upper Albian	Madagascar	COLLIGNON, 1963
			Zululand, Mozambique	FÖRSTER, 1975; KENNEDY & KLINGER, 1979
			Zuñia, Navarra, Spain	WIEDMANN, 1979
3	*fauremuretae* COLLIGNON, 1966	Upper Albian	Tarfaya, Morocco	COLLIGNON, 1966; KLINGER & KENNEDY, 1989
4	? *ibericum* ARIAS & WIEDMANN, 1977	Albian	Albacete, SE Spain	ARIAS & WIEDMANN, 1977; KLINGER & KENNEDY, 1989
5	*tarfayense* COLLIGNON, 1966	Upper Albian	Tarfaya, Morocco	COLLIGNON, 1966; KLINGER & KENNEDY, 1989
6	***warthi*** **(KOSSMAT, 1895)**	Albian	Albacete, SE Spain	ARIAS & WIEDMANN, 1977
		Upper Albian	South India	CASEY, 1960; WRIGHT *et alii*, 1996
			Diego Suarez, Madagascar	CASEY, 1960
	Parengonoceras SPATH, 1924	Albian	Tethyan	
	as *Parengonoceras* sp. juv.	Upper Albian	Suriname	OWEN & MUTTERLOSE, 2006
	as *Parengonoceras* sp.	Upper Albian	SW Iran	BULOT, 2010
	as *Parengonoceras* sp.	Lower Albian	Kent, England	CASEY, 1957, p. 42
1	*algerianum* (DUBOURDIEU, 1953)	lowermost Albian	Mellégue, Algeria	ROBERT & BULOT, 2004
2	*azlense* (G. SCOTT, 1940b)	Upper Albian	Fort Worth, Texas	G. SCOTT, 1940b
3	*barbacoense* RENZ, 1970	Upper Albian	Barbacoas, Venezuela	RENZ, 1970
4	*bussoni* COLLIGNON, 1965	Upper Albian	Tebaga de Kebili, South Tunisia	COLLIGNON, 1965
5	*caneroti* CANÉROT & COLLIGNON, 1981	uppermost Albian	Castellon, Spain	CANÉROT & COLLIGNON, 1981
		Lower Albian	Maestrat Basin, Spain	MORENO-BEDMAR *et alii*, 2008a
6	*champaraense* BENAVIDES-CÁCERES, 1956	Middle Albian	Sihuas, northern Peru	BENAVIDES-CÁCERES, 1956
		Lower Albian	La Cuenca, Peru	ROBERT *et alii*, 2003
7	*discoides* RENZ, 1970	Upper Albian	Barbacoas, Venezuela	RENZ, 1970
8	*duartei* (ETAYO-SERNA, 1979)	Lower Albian	Corral Quemado, Peru	ROBERT *et alii*, 2003; ROBERT & BULOT, 2004
9	*duboisi* (LATIL, 1989)	Upper Albian	Salazac, Gard, France	LATIL, 1989; AMÉDRO, 2008
			Bakony Mts., Hungary	BUJTOR, 1990a, 1990b
10	*duplicatum* RENZ, 1970	Upper Albian	Barbacoas, Venezuela	RENZ, 1970
			Basque-Cantabrian Basin, N Spain	RENZ, 1970; LOPEZ-HORGUE *et alii*, 2009
11	***ebrayi*** **(LORIOL, 1882)**	Albian	Cosne, France	DOUVILLÉ, 1928, ROMAN, 1938
		Upper Albian	Santander, Cantabria, Spain	WILMSEN, 1996
		Middle Albian	France	WRIGHT *et alii*, 1996
			Perchois, Aube, France	DESTOMBES, 1979; LATIL, 2008
		Lower Albian	Peru	ROBERT *et alii*, 2003; ROBERT & BULOT, 2004
			Maestrat Basin, Spain	MORENO-BEDMAR *et alii*, 2008a
12	*elegans* RENZ, 1970	Upper Albian	Barbacoas, Venezuela	RENZ, 1970
13	*guadaloupeaforme* (SOMMERMEIER, 1910)	Middle Albian	northern Peru	SOMMERMEIER, 1910; ROBERT *et alii*, 1998
			Cajamarca, Condebamba, northern Peru	BENAVIDES-CÁCERES, 1956; ROBERT *et alii*, 1998
		Lower Albian	La Cuenca, Peru	ROBERT *et alii*, 2003
14	*haasi* BENAVIDES-CÁCERES, 1956	Lower Albian	Celendín, northern Peru	BENAVIDES-CÁCERES, 1956
		upper Lower Albian	Peru	ROBERT *et alii*, 2003; ROBERT & BULOT, 2004
15	*icaunensis* (COTTEAU, 1853)	Albian	Ravennes, Yonne, France	COTTEAU, 1853; CASEY, 1978; LATIL, 2008
16	*mahmoudi* (DUBOURDIEU, 1953)	lowermost Albian	Mellégue, Algeria	DUBOURDIEU, 1953; ROBERT & BULOT, 2004
			England	CASEY, 1978
17	*nodosum* (G. SCOTT, 1940b)	Upper Albian	Glen Rose, Texas	G. SCOTT, 1940b
18	*pernodosum* (SOMMERMEIER, 1910)	Lower Albian	Cajabamba, northern Peru	SOMMERMEIER, 1910; ROBERT *et alii*, 2003; ROBERT & BULOT, 2004
		Middle Albian	northern Peru	BENAVIDES-CÁCERES, 1956; ROBERT *et alii*, 1998
			La Cuenca, Peru	ROBERT *et alii*, 2003
19	*roemeri* (CRAGIN, 1893)	Cenomanian	Texas	PRITCHETT, 1905
		Upper Albian	Glen Rose, Texas	G. SCOTT, 1940b
		Albian	Texas	HYATT, 1903; KENNEDY *et alii*, 1998a
20	*tetranodosum* (LISSÓN, 1925)	Middle Albian	Celendín, Cajamarca, northern Peru	BENAVIDES-CÁCERES, 1956
		uppermost Lower Albian	Cajamarca, northern Peru	ROBERT *et alii*, 1998
21	*trinitense* (G. SCOTT, 1940b)	Upper Albian	Fort Worth, Texas	G. SCOTT, 1940b
22	*zagrosiense* COLLIGNON, 1981	? Lower Cenomanian	Kazhdumi, southern Iran	COLLIGNON, 1981
23	*ziczag* (BREISTROFFER, 1952)	Middle Albian	Uchupata, northern Peru	BENAVIDES-CÁCERES, 1956; ROBERT *et alii*, 1998; ROBERT & BULOT, 2004
	Platiknemiceras BATALLER, 1954	uppermost Aptian-Lower Cenomanian	Tethyan	
1	***bassei*** **BATALLER, 1954**	Lower-Middle Albian	Spain	CASEY, 1961
		Lower Albian		WRIGHT *et alii*, 1996
			Maestrat Basin, Cataluna, Spain	MARTÍNEZ *et alii*, 1994; MORENO-BEDMAR *et alii*, 2008a
		uppermost Aptian	SW Iran	BULOT, 2010
2	*caseyi* MATSUMOTO *et alii*, 1980	Lower Albian	Kyushu, Japan	MATSUMOTO *et alii*, 1980
3	*colombiana* ETAYO-SERNA, 1979	upper L. Albian-lower M. Albian	Colombia	ETAYO-SERNA, 1979, 1981; OWEN, 1999
4	*deserti* (MAHMOUD, 1955)	Upper Albian	Utrillas Formation, SE Spain	GIMENEZ *et alii*, 1993
		Lower Albian	Moghara, Egypt	MAHMOUD, 1955; MORET & MAHMOUD, 1955; CASEY, 1961
			Lurestan, Iran	BULOT, 2007
5	*flexuosum* KENNEDY *et alii*, 1998a	Lower-Middle Albian	Texas, USA	KENNEDY *et alii*, 1998a
		upper Lower Albian	Peru	ROBERT & BULOT, 2004
6	*gracile* (DOUVILLÉ, 1916)	Albian	Mderedj, Lebanon	BASSE, 1940; CASEY, 1961
		Upper Albian	Utrillas Formation, Spain	GIMENEZ *et alii*, 1993
			Oued Zitoun, North Tunisia	KOGBE & MÉHES, 1986
			Gafsa, Central Tunisia	MARZOUK & BEN YOUSSEF, 2008
		Middle Albian	Tebaga, central Tunisia	COLLIGNON, 1965; BEN YOUSSEF *et alii*, 1985
			Dead Sea, Israel	WEISSBROD, 2002
		Lower Albian	Moghara, northern Sinai, Egypt	DOUVILLÉ, 1928; MORET & MAHMOUD, 1955; MOUTY & GAUTHIER, 1999; TAWADROS, 2001; ABU-ZIED, 2008
7	*hachourii* (DUBOURDIEU, 1953)	lowermost Albian	Mellégue, Algeria	DUBOURDIEU, 1953; ROBERT & BULOT, 2004
		basal Albian	Guajira, NE Colombia	GUERRERO, 2002
8	*jullieni* (BASSE, 1940)	Upper Albian	El Mizab, Meknes, Atlas, Morocco	COLLIGNON & FAURE-MURAT, 1968
		Albian	Khenchela, Algeria	CASEY, 1961
9	*sequanense* DESTOMBES, 1979	Lower-Middle Albian	Aube, France	DESTOMBES, 1979
10	*subcomplicatum* (BASSE, 1940)	Albian	Lebanon	BASSE, 1940; CASEY, 1961
11	*valencianum* MAS & WIEDMANN, 1980	uppermost Albian-lowermost Cenomanian	Valencia, Spain	MAS & WIEDMANN, 1980; GARCIA *et alii*, 2004

Genus *Parengonoceras* SPATH, 1924, p. 508
(Fig. 9)

Type species. *Amaltheus Ebrayi* LORIOL, 1882, from the Albian of Cosne, Nièvre, France.

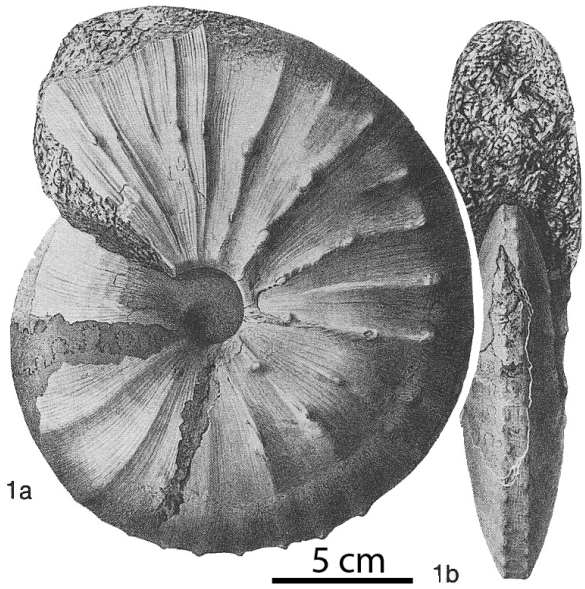


Figure 9: *Parengonoceras ebrayi* (LORIOL, 1882). Reproduction of the original figure of LORIOL (1882, p. 7, pl. 1).

Diagnosis. Coiling is typically engonoceratid. Conch is evolute. At early stages the cross section is lanceolate with tabulate venter. The lanceolate cross-section varies between wide triangular to acute and compressed. At adult stage the cross-section remains lanceolate or becomes oval. Venter is smooth or slightly grooved. Umbilical shoulder is low and always rounded and unornamented. Flanks are smooth in most cases or ornamented by ventrolateral, lateral or dorsolateral bullae. Falcoid ribs may appear ventrolaterally. Venter is usually narrow or in some species wide at adult stage and ornamented by weak tubercles. In some species these tubercles develop strongly. Suture line consists of two adventive and many auxiliary elements. Lobes are always irregularly incised. Saddles are never entire, always weakly or strongly incised.

Occurrence. Although *Parengonoceras* is widely considered to be restricted to the Early and Middle Albian (KLINGER & KENNEDY, 1989, p. 365; WRIGHT *et alii*, 1996, p. 130), many species (mainly South American) are reported from the Late Albian (*P. barbacoense, P. caneroti, P. discoides, P. duplicatum, P. elegans*). Furthermore, in Europe and Asia it is also known from the Late Albian (*P. zagrosiense*). Based on our recent knowledge, the stratigraphical distribution of *Parengonoceras* spans the whole of the Albian.

Included species:

- *Knemiceras algerianum* DUBOURDIEU, 1953: p. 22, pl. 2, figs. 6-9.
- [*Knemiceras azlense* G. SCOTT, 1940b: p. 1067, text-fig. 174 = intraspecific variation of *P. roemeri* (KENNEDY *et alii*, 1998a, p. 21)].
- *Parengonoceras barbacoense* RENZ, 1970; p. 1041, pl. 6, fig. 3a-b; pl. 7, figs. 1-2; text-fig. 7a-c.
- *Parengonoceras bussoni* COLLIGNON, 1965; p. 168, pl. A, fig. 1a-b.
- *Parengonoceras Canéroti* CANÉROT & COLLIGNON, 1981; p. 233, pl. 1, figs. 1a-c, 2a-b.
- *Parengonoceras champaraense* BENAVIDES-CÁCERES, 1956; p. 448, pl. 51, figs. 8-9.
- *Parengonoceras discoides* RENZ, 1970; p. 1032, pl. 1, figs. 1a-b, 2a-c; pl. 2, figs. 1, 2a-b, 3a-b; pl. 4, fig. 2a-b; text-fig. 3a-k.
- *Engonoceras duartei* ETAYO-SERNA, 1979: p. 75, pl. 12, figs. 1, 4.
- *Engonoceras duboisi* LATIL, 1989: p. 56, pl. 2, figs. 1-3.
- *Parengonoceras duplicatum* RENZ, 1970: p. 1038, pl. 5, figs. 1a-c, 2a-b, 3a-b, 4a-b; pl. 6, figs. 1a-c, 2a-b; pl. 7, figs. 3a-b; pl. 8, fig. 2a-b; text-figs. 5a-g, 6.
- *Amaltheus Ebrayi* LORIOL, 1882: p. 7, pl. 1.
- *Parengonoceras elegans* RENZ, 1970: p. 1036, pl. 3, fig. 1a-c, 2a-b; pl. 4, fig. 1, 3a-b; text-fig. 4a-g.
- *Placenticeras guadaloupaeforme* SOMMERMEIER, 1910: p. 333, pl. 7, fig. 2; Pl. 8, figs. 1-2.
- *Parengonoceras haasi* BENAVIDES-CÁCERES, 1956: p. 446, pl. 46, figs. 1-6.
- [*Ammonites Icaunensis* COTTEAU, 1853: p. 330 = *P. ebrayi* (CASEY, 1978, p. 588; LATIL, 2008, p. 252)].
- *Knemiceras mahmoudi* DUBOURDIEU, 1953: p. 19, pl. 1, figs. 18-24; Pl. 2, figs. 1-5.
- [*Knemiceras nodosum* G. SCOTT, 1940b: p. 1069, pl. 67, fig. 6; pl. 68, fig. 6 = intraspecific variation of *P. roemeri* (KENNEDY *et alii*, 1998a, p. 21)].
- *Placenticeras pernodosum* SOMMERMEIER, 1910: p. 330, pl. 7, fig. 1.
- [*Parengonoceras peruvianum = nomen nudum* in lit. (referred by BENAVIDES-CÁCERES, 1956, p. 452; probably misprinting instead of *Prolyelliceras peruvianum* SPATH, 1930)].
- *Sphenodiscus roemeri* CRAGIN, 1893: p. 245, pl. 46, fig. 1.
- [*Knemiceras tetranodosum* LISSÓN, 1925: p. 25, pl. 2, fig. 3= synonym of *P. pernodosum* (ROBERT & BULOT, 2004, p. 20)].
- [*Knemiceras trinitense* G. SCOTT, 1940b: p. 1071, pl. 66, fig. 7; pl. 68, fig. 3= intraspecific variation of *P. roemeri* (KENNEDY *et alii*, 1998a, p. 21)].
- *Parengonoceras zagrosiense* COLLIGNON, 1981; p. 261, pl. 7, fig. 1.
- [*Knemiceras ziczag* BREISTROFFER, 1952: p.

2634= synonym of *Parengonoceras duartei* (ROBERT & BULOT, 2004, p. 20)].

Remarks. In his accurate analysis, RENZ (1970, p. 1030-1032) examined the sutural development of *Parengonoceras* during ontogeny, proving that it has two distinct adventive lobes. *Parengonoceras* has the most complex suture lines among the Early and Middle Albian Engonoceratidae with irregularly and finely frilled deep lobes and saddles. This suture line is distinctive among other Early and Middle Albian engonoceratid ammonites and is considered to be the forerunner of the suture seen in *Hypengonoceras* and therefore, a phylogenetic connection exists between these genera. All species of *Parengonoceras* have rather compressed and smoothly ornamented shells (although fine tubercles may appear on flanks) with frilled suture, which clearly distinguish them from all other genera of Albian and Cenomanian engonoceratids. The proposed *Parengonoceras* - *Hypengonoceras* lineage and the suture remarkably different from those of other engonoceratid species suggest a polyphyletic origin for the Engonoceratidae.

Genus *Platiknemiceras* BATALLER, 1954, p. 174 = *Platyknemiceras* BATALLER, 1959, p. 77

(Fig. 10)

Type species. *Platiknemiceras bassei* BATALLER, 1954, from the Albian of Spain.

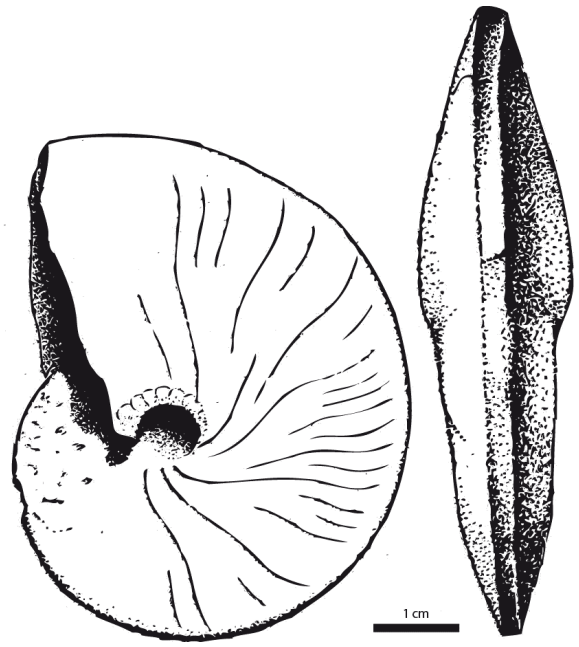


Figure 10: *Platiknemiceras bassei* BATALLER, 1954. Reproduction of the figure of BASSE (1954, p. 175, refigured by CASEY, 1961).

Diagnosis. Diagnosis is after BATALLER (1954, p. 175). Discoidal shape, flanks convex in the middle, being widest next to umbilicus, which is narrow. Umbilical wall is vertical, the last whorl almost entirely embracing. Sculpture is reduced consisting of attenuated ribs that arise at the umbilicus. Ribs may be flexuous in course but not tuberculate. Venter is smooth and forms a shallow groove. Suture is ceratitic.

Occurrence. *Platiknemiceras* appears in the Early Albian. Most species occur in Early-Middle Albian and some range into the Late Albian (*P. deserti, P. jullieni*) and higher, into the earliest Cenomanian (*P. valencianum*). Geographically the genus is reported from Europe (Spain, France), Africa (Algeria, Egypt), South America (Colombia, Peru), North America (Texas, USA), the Middle East (Iran) and Japan.

Included species:

- *Platiknemiceras bassei* BATALLER, 1954: p. 175.
- *Platiknemiceras caseyi* MATSUMOTO *et alii*, 1980: p. 333, pl. 37, fig. 5a-c.
- *Platiknemiceras colombiana* ETAYO-SERNA, 1979: p. 76, pl. 9, fig. 3.
- *Knemiceras deserti* MAHMOUD, 1955: p. 68, pl. 4, figs. 3-5.
- *Platiknemiceras flexuosum* KENNEDY *et alii*, 1998a: p. 38, figs. 51-52.
- *Knemiceras gracile* DOUVILLÉ, 1916: p. 128, pl. 16, fig. 9a-b; text-fig. 42.
- *Knemiceras hachourii* DUBOURDIEU, 1953: p. 23, pl. 2, figs. 10-18; Pl. 3, figs. 1-5.
- *Engonoceras jullieni* BASSE, 1940: p. 439, pl. 4, fig 4a-b.
- *Platiknemiceras sequanense* DESTOMBES, 1979: p. pl. 4, fig. 1.
- *Knemiceras subcomplicatum* BASSE, 1940: p. 434, pl. 3, figs. 2, 3a-b.
- *Platiknemiceras valencianum* MAS & WIEDMANN, 1980: p. 265, text-figs. 6, 7a, 8a.

Remarks. CASEY (1961) discussed the genus thoroughly and grouped some species of *Knemiceras* (*K. deserti, K. gracile, K. hachourii, K. subcomplicatum*, and *K.* sp. nov. [later described as *P. flexuosum* KENNEDY *et alii*, 1998a]), and *Engonoceras* (*E. jullieni*) under *Platiknemiceras* because of common morphological features: thinly discoidal shape with extreme reduction of ornamentation; this grouping restricts the scope of the genus *Knemiceras*. *Platiknemiceras* is close to *Parengonoceras* (CASEY, 1961, p. 354) but it includes only compressed and discoidal forms having extremely reduced sculpture. *P. caseyi* sp. nov. was listed previously (MATSUMOTO, 1954; MATSUMOTO & KANMERA, 1964) as *Engonoceras* aff. *stolleyi* (BÖHM), an attribution corrected by MATSUMOTO *et alii* (1980, p. 334). Since CASEY (1961) revised the genus there have been no further contributions regarding the content and systematics of the taxon; however four new species have been described. Most recently BULOT (2010, p. 171) discussed the species assigned of *Platiknemiceras*. He considers the genus to be restricted to *P. bassei, P. hachourii*, and *P. flexuosum*. BULOT (2010) transfers back to *Knemiceras* some of the species that CASEY (1961) referred

to *Platiknemiceras* (*P. gracile, P. subcomplicatum*, and *P. deserti*). Unfortunately, BULOT (2010) did not consider the other five species (*P. caseyi, P. colombiana, P. julieni, P. sequanense*, and *P. valencianum*) of the genus so his revision is not complete. For the moment this genus is considered to be polyphyletic for it is based on morphological features common to all.

[Engonoceratidae gen. et sp. nov. HENDERSON, 1973 = *Borissiakoceras* sp. (STILWELL & GALLAGHER, 2009, p. 881)]

This tiny specimen is reported from the Albian of New Zealand (HENDERSON, 1973, p. 106). The specimen is not strongly evolute (two whorls are visible) atypical for Engonoceratidae. Nor is the suture is typical of Engonoceratidae: therefore the generic assignment is not supported. KENNEDY & KLINGER (1979, p. 116) had already referred it to *Borissiakoceras*, but without further analysis. This was provided by STILWELL & GALLAGHER (2009) who also assigned it to *Borissiakoceras*. However poor preservation and a limited number of specimens do not permit a more precise distinction.

Geographical and stratigraphical distribution of Engonoceratidae

The mean generic range of Jurassic/Cretaceous ammonites is 7.3 myr per ammonite genus (WARD & SIGNOR, 1983). Engonoceratid genera have longer ranges. The longevity of most of the genera is remarkable: seven genera existed for more than 10 myr (*Engonoceras, Glottoceras, Knemiceras, Metengonoceras, Parengonoceras, Platiknemiceras*, and *Protengonoceras*). Only two genera (*Hypengonoceras* and *Neolobites*) had shorter ranges (4 myr) than the average mean generic range. Originally the Engonoceratidae were said to have appeared during the Barremian (ROMAN, 1938, p. 486), but later works did not support this view. Now it is widely accepted that engonoceratids appeared in the latest Aptian-earliest Albian (ARNOULD-SAGET, 1956; COLLIGNON, 1981; BULOT, 2010) in shallow marine platform environments of the southern Tethys (Algeria) and migrated to the peri-Tethyan territories (CASEY, 1957; DESTOMBES, 1965). It is noteworthy that G. SCOTT (1940b, p. 1066) had already speculated that some engonoceratids possibly were present in the Aptian of Texas, an observation supported by KENNEDY *et alii* (2004) when revising the original collection of Ferdinand RÖMER, that included an *Engonoceras* sp. from the ?Upper Aptian of Texas. Obviously, the adaptive radiation of the group was rapid during the Early Albian, for its genera played an important role in the faunas of the Peruvian Basin (South America) and the Western Interior Sea (USA). During Middle and Late Albian times the group occupied the Far East and Australian provinces (Australia, Borneo, India, Japan, Madagascar and South Africa).

In the Cenomanian it successfully invaded some portions of the Boreal Realm (Mowry Sea, Canada) for it became ubiquitous in temperate watery environments everywhere in palaeolatitudes up to the 60 degrees where it co-occurs with Boreal ammonites (IBA, 2009). In the Mowry Sea the adaptive radiation of engonoceratid ammonites was so successful that the invader *Metengonoceras* displaced the endemic *Neogastroplites* from its original morphoplace (YACOBUCCI, 2004) as recorded by changes in its morphotypes (SCHLUTER, 2000). The taxon became extinct during the Cenomanian. The last surviving species of the engonoceratids are reported from the latest Cenomanian of Texas (KENNEDY *et alii*, 1981), Niger and Nigeria (MEISTER *et alii*, 1992, 1994; COURVILLE *et alii*, 1998) and the southern Mediterranean (MEISTER & ABDALLAH, 2005; COURVILLE, 2007; ALY *et alii*, 2008). Table 1 summarizes the stratigraphical ranges of engonoceratid genera. Although FURON (1935) reported a *Metengonoceras dumbli* from the Early Turonian of Niger, this dating is not supported by the detailed biostratigraphical study of MEISTER *et alii* (1992), which showed that *M. dumbli* ranges only to the latest Cenomanian in Niger. The general climate warming of the mid-Cretaceous combined with an increase in subtropical upper ocean temperature (PUCÉAT *et alii*, 2003), may have helped the radiation of engonoceratids along ancient continental shelf seas. Changes in sea level may be an additional favourable factor. The highest relative sea level documented occurred during the Mesozoic (MONNET *et alii*, 2003a). These fluctuations may have been accompanied by changes in the oceanic circulation that aided in increasing productivity and opened new ecological niches, which together resulted in a decline of provincialism in epicontinental seas. Some of these factors may have contributed to a general decline of ammonoid diversity (MONNET *et alii*, 2003a, p. 395). However, the well documented decrease in the richness of ammonoid species significantly pre-dates the spread of anoxic deposits (MONNET *et alii*, 2003b) and surely contributed to the dramatic changes of shallow water habitats that were preferred by engonoceratids, that in the end may have led to their extinction. "Suddenly" raised sea levels would have reduced the number of barriers between those epicontinental and shallow water habitats and endemic centres in which engonoceratids lived.

Mode of life and ecology of Engonoceratidae

Based on our recent knowledge, all engonoceratid genera preferred shallow marine environments, and some (*Knemiceras* and *Neolobites*) occupied extremely shallow (tidal, lagoonal) milieux. However, it took a long time to

arrive at this conclusion, which began seventy years ago.

ECOLOGY AND FACIES DEPENDENCY OF ENGONOCERATIDAE

G. SCOTT (1940a) was among the first to discuss the growing importance of palaeoecology, pointing out that only oxyconic ammonites (as *Engonoceras* and *Oxytropidoceras*) are numerous in the epineritic area of the Cretaceous of Texas (Western Interior Sea, USA) where echinoids, oysters, and thick-shelled gastropods abundant. G. SCOTT (1940a) estimated the epineritic zone to occupy water depths of 40 to 180 metres, which corresponds well with the lower limit of the euphotic zone. G. SCOTT (1940b, p. 1066) considered that the group preferred shallow water and platform facies: "*Knemiceras, Engonoceras* and *Oxytropidoceras* appear to have had their greatest development in the broad, shallow, clear seas of Texas". The habitat-dependency of ammonites was also analyzed by BATT (1991) for the Cenomanian-Turonian ammonites of the Western Interior. It became obvious that most ammonites are not restricted to a particular depth or facies, although compressed and discoidal forms (e.g. the Engonoceratidae) tended to occur in environments where the depth was less than 50 to 100 metres (YACOBUCCI, 2003). KAUFFMAN (1984) also analyzed thoroughly the Western Interior basin, its endemism and faunal provinces concluding that during the Cretaceous the maximum depth of thebasin was never greater than 200-500 metres with a significant area covered by less than a 50 metres. This shallow, warm, trophic environment offered excellent conditions for speciation among many ammonites (including engonoceratids) thus creating an endemic centre (YOUNG, 1972). Based on his extensive research on bivalves, KAUFFMAN (1973) defined a Western Interior Endemic Centre (WIEC). Later KAUFFMAN *et alii* (1993) enlarged the scope of the WIEC to include other molluscs emphasizing that the WIEC was a very important pool of genetic variability and speciation for many molluscs. This direct link between the water depth and the blossoming of the engonoceratids is remarkable. Its validity supported by WESTERMANN (1990, 1996) who from a theoretical standpoint pointed out the special ecological needs of engonoceratids and that they preferred shallow (30-50 metres) water. Ecology of the South American Engonoceratidae was first discussed by RENZ (1970, p. 1022) concluding that the South American Engonoceratidae lived on a subsiding carbonate platform. GEYER (1995a) also recognized the importance of engonoceratids in shallow marine facies: "Knemiceratinae (*Knemiceras, Platiknemiceras, Parengonoceras*) represent important ammonoid "pioneer" genera for mid-Cretaceous transgressive facies: they occur frequently near the base of marine, often glauconitic sediments overlying a continental clastic succession in their Tethyan (s.l.) realm." Engonoceratids frequently occur in glauconitic sediments. *Parengonoceras duboisi* and *Knemiceras saadense* are present in the glauconitic sand/ sandstone of Salazac (Gard, France: BREISTROFFER, 1940; LATIL, 1989) and in the latest Albian glauconitic limestone of Pénzesgyor (Bakony Mts. Hungary; BUJTOR, 1990a, 1990b), furthermore *Parengonoceras attenuatum spinosum* of WRIGHT (1963) from the Early Albian of Bathurst Island (Australia) is found in a glauconite sand. KENNEDY *et alii* (1981) reported an engonoceratid (*Metengonoceras dumbli*) from the Late Cenomanian of stable Europe (Angers, NW France), also in a glauconitic sand. AMIREH (1997) noted a *Knemiceras* from a glauconite bed in the Albian of Jordan. CANÉROT & COLLIGNON (1981) described *Parengonoceras caneroti* from a lignitic deltaic series of latest Albian age at Castellon (Spain). This occurrence also supports the shallow water dependency of engonoceratids. Although ACCARIE & DELAMETTE (1991) considered engonoceratid ammonites to be indicative of a neritic environment they did not discuss their shallow water dependency.

SHALLOW MARINE SPECIALIST *KNEMICERAS* AND *NEOLOBITES*

It became obvious very early on, that the presence of some engonoceratids may be indicative of certain environments. HYATT (1903, p. 148) called attention to the ostreid and bryozoid encrustations of *Knemiceras syriacum* shells. More recently REYMENT (2008) too discussed shell encrustations on *Knemiceras* found in fluvial, deltaic, littoral or sublittoral facies. The encrustation may have occurred during postmortem drifting, rather than during life in natural habitats. However, KENNEDY & COBBAN (1976) and PAGE (1996) found that the postmortem dispersal of ammonoids is rather the exception than the rule. This finding is very probably applicable to *Knemiceras*. Accepted as a generalization, nekroplanktonic dispersal on a large scale must be abandoned; a *Knemiceras* from the Albian of Jordan with oyster encrustation (REYMENT, 2008) makes very likely the probability of a shallow water habitat. HAILE (1955) pointed out that the *Knemoceras* [sic!] beds are linked to basal conglomerate in Borneo. CANÉROT *et alii* (1986) remarked that various species of *Knemiceras* occur in a littoral facies of the southern Atlas Mountains, Africa. GEYER *et alii* (1997) report *Knemiceras* from a delta-influenced carbonate ramp in the Albian of Sinai (Egypt), again supporting the conclusion that many occurrences of *Knemiceras* are coincident with the early stages of transgressive systems tracts. KRASSILOV & SHUKLINA (2008) report *Knemiceras* from intercalated non-marine-shallow marine beds of Middle Albian age in Israel. *Knemiceras uhligi* from the Albian of

Oman occurs in a shallow marine (average depth 35 metres) epicontinental sea, which might not have been more than 80 metres deep (IMMENHAUSER *et alii*, 2000, p. 223). But (ABDALLAH & MEMMI, 1994; ZOUAGHI *et alii*, 2009) report that Late Albian 'Knemiceras beds' in Tunisia involve a unique range of ecological needs. ARNOULD-SAGET (1956) began the attempts to explain the ecology of the highly variable *Knemiceras*. She postulated that as *Knemiceras* lived in a stable environment in the neritic zone at the margin of the old Saharan mainland where there was no deposition of detritus or perturbation, so conditions there were optimum for the rapid expansion of its population, and the stress that would have hindered adaptation did not exist. Consequently, the genetic potential and variability of *Knemiceras* was wasted in useless polymorphism. ARNOULD-SAGET (1956) said that the mode of life of *Knemiceras* species was more benthic than neritic. She outlined a completely opposing view of the mode of life and habitats of *Knemiceras* and other engonoceratids. REYMENT & KENNEDY (1991) proposed that the great variability of shell form and ornamentation can be explained by their inhabintance of a shallow and labile (= epicontinental) environment. Recently SHIRAZI (2008) reported *Knemiceras* from the euphotic, shallow marine deposits of Late Albian age in the Zagros Mountain (SW Iran). Again it is the only ammonite found in that shallow marine environment. The shallow water dependency of *Knemiceras* is supported by the frequent presence of *Knemiceras* on shallow marine platforms (ABDALLAH & MEMMI, 1994) and in fluvial-lagoonal deposits with dinosaur remnants (BENTON *et alii*, 2000). Generally, *Knemiceras* is the only ammonite in shallow water environments of the Arabian Plate (BULOT, 2010). Dinosaur experts also remark that during Cenomanian times the fragmented dinosaur remains found in continental and deltaic facies followed by lagoonal and coastal plain deposits topped by marine limestones containing the first truly marine animals such as *Neolobites* (NOVAS *et alii*, 2005, p. 168). WIESE & SCHULZE (2005) noted that where *Neolobites* occurs in great abundance, it is on shallow-marine shelves. *Neolobites* is always linked to transgression and/or flooding periods in South-America (JAILLARD & ARNAUD-VANNEAU, 1993, p. 600). Distribution of Cenomanian carbonate platforms and *Neolobites* occurrences are correlated to a fine degree in northern Africa and the Americas (JAILLARD & ARNAUD-VANNEAU, 1993). The possible shallow marine dependency of Engonoceratidae is strongly supprted by BULOT (2007) who considers *Neolobites* as the endemic and intra-shelf taxon of the group. That *Neolobites* is a Cenomanian intra-shelf (e.g. shallow marine) taxon is strong support for the same mode of life for its predecessor, the Albian engonoceratids; however the *Neolobites* in Bolivia (BRANISA, 1968; JAILLARD & SEMPERE, 1992) does not support its endemism at the genus level.

EXPLANATION OF PIONEERISM OF ENGONOCERATID AMMONITES

With regard to the dispersal of Ammonoidea, SHIGETA (1993) analyzed the post-hatching early life of 71 selected Cretaceous species of Ammonoidea. He concluded (based on density calculations of the shells), that at the hatching stage most of them were floaters with a positive buoyancy, strongly suggestive of a planktonic mode of life, thus permitting the rapid migration of all Cretaceous Ammonoidea. But positive buoyancy cannot explain the shallow water dependency of all engonoceratids, a relationship strengthened by GONZÁLEZ-LEÓN's (1988) report of well preserved and abundant engonoceratid fauna (*Parengonoceras, Protengonoceras, Engonoceras pierdenalis, E. stolleyi*, and *E. uddeni*) from the Middle Albian open shelf of Lampazos, Sonora (Mexico). COLLIGNON (1981) offered an interesting working hypothesis to explain the connection between the distribution of engonoceratids and the depth of seas in which they occur. He noted that thin forms [of engonoceratids] are found in the western regions and the thickest in eastern areas. This difference would suggest some regional control in the depth of the seas. But recent knowledge of the geographical and facies distribution of engonoceratids, negates this idea. Thin forms are found in the Far East (*Platiknemiceras caseyi* in the Early Albian of Japan (MATSUMOTO *et alii*, 1980).

Some Upper Albian ammonoid habitats in southeastern France were reviewed by REBOULET *et alii* (2005). But this work did not discussed the habitats of the engonoceratids, although engonoceratids occur in that region (cf. BREISTROFFER, 1940; LATIL, 1989). Based on the available data engonoceratids certainly lived in the neritic and epipelagic domain of REBOULET *et alii* (2005) occupying extremely shallow marine habitats. But we have more evidence for the connection between transgression and the rapid distribution of engonoceratids. The "pioneerism" of engonoceratids *sensu* GEYER (1995a) is linked to their shallow water habitancy, for the colonizing populations of engonoceratids were able to occupy rapidly the new areas of shallow water formed by transgressive seas, and thus to inhabit pristine ecological niches. The invasion of engonoceratids into the Peruvian province (ROBERT & BULOT, 2004) is closely linked to a transgression. In Early Albian times, the stem-engonoceratids which originated at the southern margin of the Tethys invaded the Peruvian Basin using shallow water seaways. A similar event occurred during the Cenomanian. COURVILLE (2007) following up on earlier works noted that the Cenomanian shallow water seaway between the southern margin of the Tethys and South America (Saharan seaway), *Metengonoceras* migrated southward during latest Ceno-

manian times (COURVILLE, 2007, fig. 1). FURON (1935) and MEISTER *et alii* (1992) had already reported this southward advance on the Late Cenomanian deposits of Niger. The appearance of *M. oliveirai* in Sergipe, Brazil (BRITO, 1967, 1986; SIMONE, 1994) substantiates this southward migration of the seaway.

Phylogeny

ROMAN (1938, p. 510) attempted to erect a phylogeny of Engonoceratidae, proposing that the first engonoceratid was the Aptian *Protengonoceras* with no direct link to other engonoceratids. The first Albian engonoceratid genus was *Engonoceras* and its offsprings were *Metengonoceras, Parengonoceras, Hoplitoides, Knemiceras, Neolobites*, and *Placenticeras*. WRIGHT (1952) suggested that in all probability, the Engonoceratidae were derived directly from the Parahoplitidae. CASEY (1957, p. 39) proposed that if the pseudoceratitic development of the Albian species is indeed the expression of a development from the deshayesitid lineage, then the superfamily name Placenticeratoidea of HYATT (1900, p. 584) would be applicable. Summarizing the earlier results, CASEY (1960, p. 208) concluded: "origin of the Engonoceratidae has never been settled." Since that statement, there has been no significant development concerning the origin of the engonoceratids. Almost forty years later, the situation is unaltered from the state that KENNEDY *et alii* (1998a, p. 1) remarked: "evolutionary origin of the group is uncertain". Recently LEHMANN & MURPHY (2001) outlined a phylogenetic chart for Engonoceratidae proposing that the most possible ancestor was *Knemiceras* (LEHMANN & MURPHY, 2001, fig. 2) with a questioned relation between *Parengonoceras/Hypengonoceras* and the rest of the group. So uncertainty remains an open field for investigation.

Speculation on the origin of Engonoceratidae and its possible parahoplitid origin now is strengthened by new results on the ecology of *Parahoplites*. LEHMANN *et alii* (2009, p. 904) report *Parahoplites* from a lagoonal environment in north-central Tunisia. In addition to the shallow marine habitat of *Parahoplites*, BULOT *et alii* (2005) proposed that the relationship of the mode of life of the Acanthohoplitinae to the water surface (incl. *Parahoplites*) supports the probability of a relationship. The similarities of the environments of *Parahoplites* and Engonoceratidae furnish a plausible explanation for the origin of the Engonoceratidae.

Recently, ROBERT & BULOT (2004) and LATIL (2008) placed the Engonoceratidae in the superfamily Pulchelliatoidea based on morphological analogies. However, the ecological data on Pulchelliidae *sensu stricto* do not fully support this lineage. Recently BARRAGÁN-MANZO *et alii* (2004) proposed a nektobenthic mode of life for the Pulchelliidae. If the Engonoceratidae is in fact derived from the Pulchelliidae, then their differences in modes of life and palaeoenvironments require an explanation. Other data (BARRAGÁN-MANZO *et alii*, 2008) also refer to neritic platform environment with an abundant pulchelliid fauna. Very recently BULOT (2010) rejected the pulchelliatoid origin for the Engonoceratidae.

A search for the evolutionary driving force behind the genesis of the Engonoceratidae suggests that the global oceanic anoxic event offers a plausible explanation. Dramatic changes in the pelagic ecosystem may have been triggered by the long anoxic event (OAE 1b) and progressively increased ecological pressure on those ammonite populations inhabiting shallow marine and platform environments. They were forced to occupy pristine extremely shallow ecological niches, previously unused. The evolution of the supposed parahoplitid ancestors continued apace and the first Engonoceratidae (*Knemiceras, Platiknemiceras, Parengonoceras*, and *Protengonoceras*) appeared in the latest Aptian-earliest Albian times in the shallow water environments of one or all three large shelves in North Africa, the proto-Gulf of Mexico, and the Caribbean Province.

The origin of Engonoceratidae is almost certainly polyphyletic as indicated by the remarkable differences between the sutures of *Parengonoceras - Hypengonoceras* and those of the remainder of the group, along with the apparently contemporaneous occurrences of these species in shallow marine environments in both Americas and North Africa. However, the enigma of the systematic position of *Hypengonoceras*, the most problematic genus of the Engonoceratidae may also be the result of a polyphyletic origin. KENNEDY & WRIGHT (1983, p. 868) suggested that *Hypengonoceras* may be an off-shoot of an early Late Albian placenticeratid, but as seems more probable, CASEY (1960, p. 208) proposed that *Hypengonoceras* was derived from *Parengonoceras* or some allied members of the Engonoceratidae. This uncertainty of origin is shown in Fig. 11 by the discrete tracing of possible lineages. The most probable course of evolution was from ?*Parahoplites* to *Protengonoceras*. Evolution from *Protengonoceras* toward *Engonoceras* (or from *Engonoceras* toward *Protengonoceras* proposed by LEHMANN & MURPHY, 2001) and *Metengonoceras* and ultimately *Neolobites* is reasonable based on shell morphology and the simplification of suture over time. Lately, BULOT (2010, p. 169) supports this concept assembles these genera into a phylogenetic lineage. The other lineage is more speculative; however ROBERT & BULOT (2004) suggested that the South American Engonoceratidae had a platiknemiceratid origin. But this is not a solution applicable to the other species, for a direct lineage from *Parengonoceras* to *Hypengonoceras* is feasible. Many have speculated on the existence of a direct phylogenetic connection between the Engonoce-

ratidae and the Placenticeratidae (SPATH, 1930, p. 390; ARKELL *et alii*, 1957, p. L109), but CASEY (1960, p. 208) and KLINGER & KENNEDY (1989, p. 365) negated the possibility that the Engonoceratidae was the direct ancestor of the Placenticeratidae. Therefore the proposed phylogenetic connection with *Hypengonoceras* as an offshoot of an early placenticeratid (KENNEDY & WRIGHT, 1983) must be abandoned (Fig. 11). Today's opinion: the Engonoceratidae became extinct without descendants in latest Cenomanian times in the Western Interior Province (USA). However the dating of the end of the Cenomanian is debated by R.W. SCOTT *et alii* (2009), as is the closing of the Saharan seaway (Niger and Nigeria).

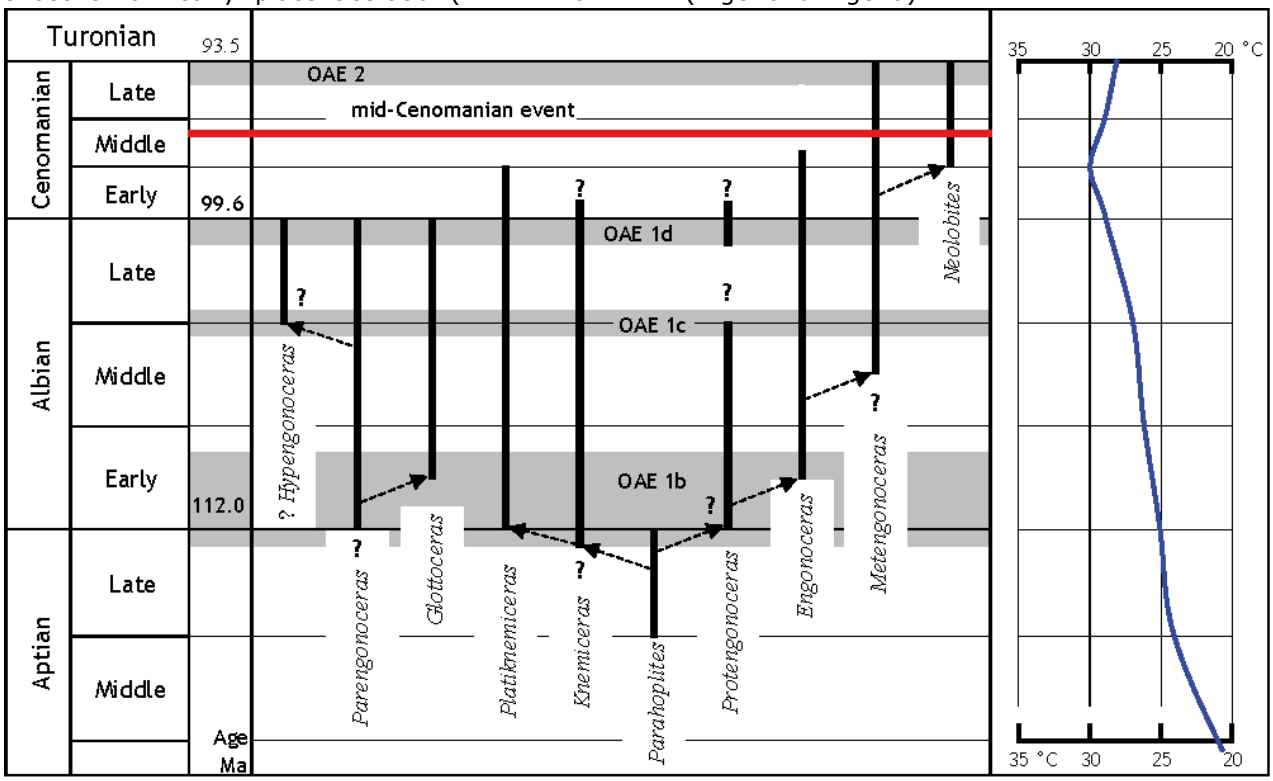


Figure 11: Stratigraphical distribution of engonoceratid genera and supposed phylogeny of Engonoceratidae. Data from ROMAN (1938), CASEY (1960, 1961), KLINGER & KENNEDY (1989), WRIGHT *et alii* (1996), ROBERT & BULOT (2004). Cretaceous time-scale after GRADSTEIN *et alii* (2004). OAE 1b-d dating from TAKASHIMA *et alii* (2006), OAE 2 dating from BRALOWER *et alii* (1999). Seawater temperature curve from PUCÉAT *et alii* (2003).

Homoeomorphy

The apparent similarities between the engonoceratid and ceratitid suture lines tempted palaeontologists to speculate on the cause of the repetition of similar structures (cf. SMITH, 1914, p. 30 on the *Neolobites* suture line). Recently KLUG *et alii* (2005) analyzed the ecology and immigration patterns of approximately 500 specimens of ceratitid Ammonoidea found in strata of the Late Anisian to Early Ladinian age in Germany. Their study was based on the morphological variability of ammonoid shells. The Germanic Basin was the site of a shallow sea during most of the Anisian and Ladinian (KLUG *et alii*, 2005, p. 19). It was occupied repeatedly by incursions of ammonoids, crinoids and brachiopods coincident with intervals of high sea level. After each of these immigrations new species of *Ceratites* evolved (KLUG *et alii*, 2005, p. 25) just as we had seen among Cretaceous engonoceratids in the Peruvian Basin and in the Western Interior Sea (USA). Cretaceous species of the engonoceratids exhibit remarkable morphological convergence very likely that of the Triassic species used in the ecological analysis of KLUG *et alii* (2005). The repetition of suture lines, external shell morphologies, together with records of a shallow marine habitat, successive migrations, and successful adaptation in both Middle Triassic and mid-Cretaceous forms suggest that this pattern is a very successful ammonoid eco-morphotype in shallow marine habitats. This conclusion is supported by the morphological convergences of the Triassic *Ceratites nodosus nodosus* (KLUG *et alii*, 2005, fig. 4) and the Cretaceous *Knemiceras syriacum* (BUCH, 1848, figs. 2-3).

Other morphological convergences occur (Fig. 12) among the Triassic *Discoceratites semipartitus* (KLUG *et alii*, 2005, fig. 4), the Albian-Cenomanian *Metengonoceras teigenense* (COBBAN & KENNEDY, 1989, pl. 2, figs. 1-2) and the Maastrichtian *Sphenodiscus pleurisepta* (IFRIM *et alii*, 2005, fig. 7a-b). The Triassic scheme of colonization followed by speciation follows the same pattern as that of engonoceratids during the Albian. The endemic centres in the Americas were rapidly colonized by engonoceratids, followed by speciation (ROBERT &

BULOT, 2004). This suggests that the repetition of the Triassic eco-morphotype in the engonoceratids was caused by their occupation of nearly identical ecological niches and habitats.

Another interesting convergence is that of the engonoceratids and another group of Ammonoidea, the Maastrichtian sphenodiscids. IFRIM *et alii* (2005) reported several species of *Sphenodiscus* (*S. lobatus* and *S. pleurisepta*) from the Maastrichtian of La Popa Basin, Mexico, a shallow water coastal deposit. The oxyconic *Sphenodiscus* was well adapted to continuous swimming with excellent acceleration skills (JACOBS & CHAMBERLAIN, 1996, p. 211). Shell morphology, suture lines and palaeoenvironments of these sphenodiscid ammonites surprisingly repeat that of the Albian-Cenomanian engonoceratids. IFRIM *et alii* (2005, p. 62) concluded: "sphenodiscid-dominated faunas […] are thus clearly related to bathymetry, i.e. the shallow-water assemblages are very low in diversity and represent specialization to an environment in which ammonoids could not easily survive". It seems obvious that during ammonoid evolution, the combination of shallow water habitats, the oxy- and/or platyconic, brevidome shell morphology and simplified, *Ceratites*-like sutures occurred at least three times, one of them the Albian-Cenomanian engonoceratids. In all cases, this pattern was associated with successful migration, colonization and speciation. This set of characters is summarized in Fig. 12.

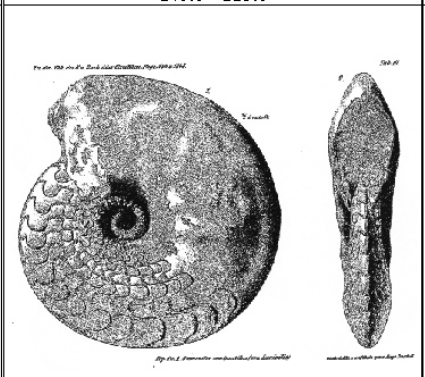
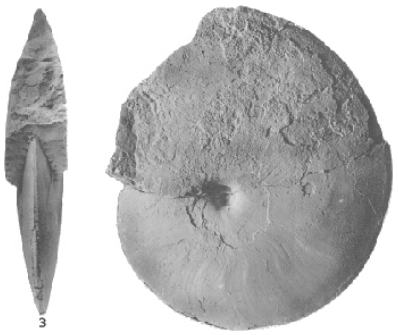
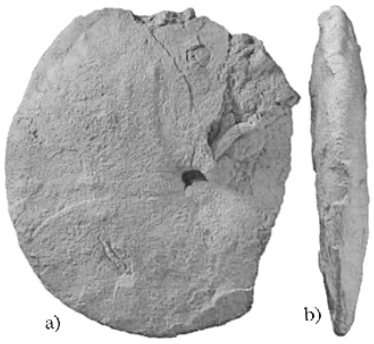
Series	Middle Triassic	Lower Cretaceous	Upper Cretaceous
Stage	Anisian - Ladinian	Upper Albian - Lower Cenomanian	Maastrichtian
Age (Ma)	245.0 - 228.0	112.0 - 93.5	70.6 - 65.5
Shell form			
Species	*Discoceratites semipartitus*	*Metengonoceras teigenense*	*Sphenodiscus pleurisepta*
Mode of life	nektonic, active swimmer	nektonic, active swimmer	nektonic, active swimmer
Environment	shallow marine	shallow marine	shallow marine, coastal environment
Reference	Buch, 1848; Klug *et alii*, 2005	Cobban & Kennedy, 1989	Ifrim *et alii*, 2005

Figure 12: Strong similarities in shell shapes among certain ammonoid taxa. Repeated eco-morphotype pattern among Mesozoic Ammonoidea. The proposed eco-morphotype comprises a set of features consists of nektonic, active swimmer mode of life in shallow marine settings, simplified and ceratitic suture and involute, oxycone-platycone shell form. Mesozoic time-scale after GRADSTEIN *et alii*, 2004.

Conclusion

Engonoceratid ammonites are important time indicators of chronostratigraphic time in strata of shallow marine origin ranging in age from the ?latest Aptian times to the youngest of Cenomanian formations. Where they occur in the Tethyan Faunal Realm, they are excellent indicators of a shallow water environment. Today engonoceratids play an important role in correlation, biostratigraphy and ecological studies, but trhey are limited in distribution to temperate water. Engonoceratids are a versatile, and successful group of Cretaceous Ammonoidea, ecological pioneers that were successful in occupying previously inaccessible pristine ecological niches. The range of suture lines, shell form, all is response to a shallow water habitat created a morphological pattern that proved successful not only for the engonoceratids, but also for other Mesozoic Ammonoidea.

Appendix

Revision of *Engonoceras duboisi* LATIL, 1989

Engoncoeras duboisi LATIL, 1989, is known only from 2 localities and represented by a handful specimen. New specimen from Hungary led the present author for thorough morphological analysis, which resulted the below revision of the species.

Parengonoceras duboisi (LATIL, 1989)

(Figs. 13A-B - 14 - 15)

- v 1989 *Engonoceras duboisi* sp. nov. LATIL: p. 56, pl. 2, figs. 1-3.
- 1989 *Engonoceras* sp. cf. *E. duboisi* sp. nov. LATIL: p. 57, pl. 2, fig. 4.
- v 1990a *Engonoceras duboisi* LATIL; BUJTOR: p. 11, pl. 1, figs. 1-4.
- v 2007 *Engonoceras duboisi* LATIL; SZIVES *et alii*: p. 101, pl. 15, figs. 1, 4.

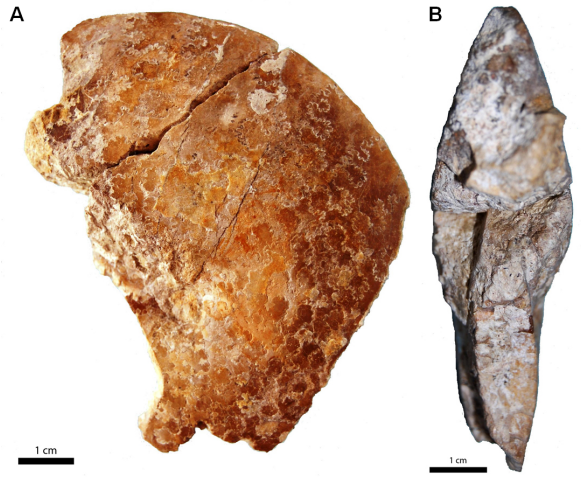


Figure 13: *Parengonoceras duboisi* (LATIL, 1989) from the latest Albian (*Stoliczkaia dispar* Zone) of Tilos forest (Bakony Mts. Pénzesgyor, Veszprém County, Hungary). Specimen NHNM M2010.760.1. A.) lateral view, B.) dorsal view.

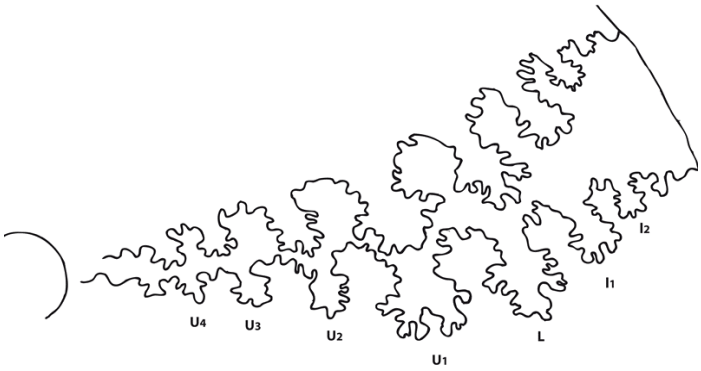
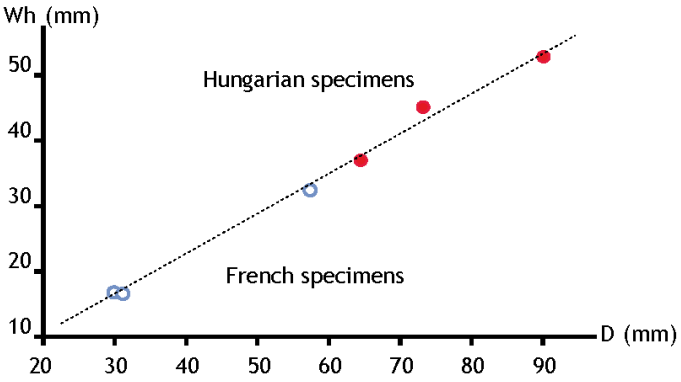


Figure 14: Suture line of *Parengonoceras duboisi* (LATIL, 1989) at whorl height of 51 mm. Specimen HNHM M2010.760.1.

Material. Three internal moulds from the Late Albian (*Stoliczkaia dispar* Zone) of Tilos forest (Pénzesgyor, Bakony Mts, Hungary) and three worn internal moulds from the Late Albian (*Stoliczkaia dispar* Zone) of Salazac, Gard (France).

Occurrence. LATIL (1989) reported it from the latest Albian of Salazac, Gard (France). BUJTOR (1990a) described it from Hungary (Tilos Forest, Bakony Mts.). SZIVES *et alii* (2007) copied the figures of BUJTOR (1990a). New collection by the present author from the Tilos Forest (Bakony Mts., Hungary) yielded a single specimen described here for the first time supporting the distribution of the species for the latest Albian of France and Hungary. The new record of the Late Albian *P. duboisi* from the Bakony Mts. is important as a connector between the rich and diverse western and less well known eastern Tethyan *Parengonoceras* species during the Albian. It suggests a southern Tethyan migration route because the fact that the Alcapa Tectonic Unit (which also includes the Bakony Mts.) was part of the Apulia microplate bordered by the southern edge of the Penninic Ocean (CSONTOS & VÖRÖS, 2004). The revealed third specimen of *P. duboisi* from Hungary refers to the rarity of this species in the Bakony Mts, Hungary: 1:10,000 (Z. Evanics pers. comm.).

Description. Medium sized incomplete but shelly phragmocones and internal moulds. Coiling is typical of the Engonoceratidae. The conch is discoidal and strongly involute and oxycone (Fig. 13). Last whorl embraces the previous ones. The umbilicus is small and shallow. Umbilical wall is low and the umbilical shoulder is gently rounded. Flanks converge and are almost unsculptured. The cross section is lanceolate. Venter is smooth and narrow. Finer or stronger prorsiradiate falcoid ribs arise at midflank, which end at the ventro-lateral shoulders. Six fine and falcoid ribs are on the last quarter of whorl; ribs end at fine tubercles on ventral shoulder. Body chamber is not preserved. Suture line (Fig. 14) is typical for *Parengonoceras* showing two adventive lobes. Suture is characterized by pincer-like and finely incised lobes and saddles. Pincer-like saddles are irregular polyphillic. Lobes are also incised irregularly.



	D	Wb	Wh	U
HNHM 00-000	90	-	52.9	8.3
EC 24-10323	73	22	45	9
EC 24-864	64	18	37	5
GEPI-1348	57.5	14.5	32.5	5.8
GEPI-1346	31	7.5	16.8	4.3
GEPI-1347	30	8.5	17	-

Figure 15: Size distribution of Hungarian (solid) and French (open) specimens of *Parengonoceras duboisi* (LATIL, 1989).

Remarks. *P. duboisi* is most similar to *P. elegans* RENZ and *Platiknemiceras hachourii* (DUBOURDIEU). The Early Albian *Platiknemiceras hachourii* has a slightly more slender cross-section, and the striae on the lower flanks are finer in *P. duboisi* and the suture is less frilled than on *P. hachourii*. The extreme reduction of ornamentation in *P. duboisi* is also not present in *P. hachourii*. The ornamentation is typical of *Parengonoceras* as is the diameter and whorl height ratios (Fig. 15). *P. duboisi* is most similar to *P. elegans* RENZ in its shell ornamentation.

The small, ventrolateral falcoid ribs of *P. elegans* (RENZ, 1970, pl. 3, fig. 1a-c) are comparable with *P. duboisi*. However *P. duboisi* shows fewer ribs per whorl than *P. elegans*. The superficially similar *Engonoceras* and *Parengonoceras* species are clearly distinguished from each other based on suture lines - if present. Normally the saddles of *Engonoceras* are all entire except that the outermost, which is bifid (WRIGHT *et alii*, 1996, p. 130). The present species show only frilled saddles in all stages in the specimens. All saddles of the holotype are incised, mostly bifid (LATIL, 1989, pl. 2, figs. 2-3) being worn specimens, therefore the frilled suture is not well preserved, however there are no entire saddles at any stage. The Hungarian specimens are well preserved, partly shelly specimens with well observable suture revealing more incised saddles. Biometry of the French and Hungarian specimens refers the same species (Fig. 15), too. Based on the well developed and frilled saddles and lacking entire saddles at any stage, this species is convincingly placed into *Parengonoceras*. Recently the uncertainty of the systematic position of *P. duboisi* is also referred by BULOT (2010, p. 169) excluding it from the genus *Engonoceras*. This conclusion is supported here.

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