Systematics, phylogeny and homeomorphy
def 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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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 oxycone 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; Perquiviére, 1907; Sommermeier, 1910; Basse, 1940; Knochel in Knochel 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 Evans, 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 prolocanid 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 ceratid group, naming them as Cretaceous Ceratites (Buch, 1848, p. 30) or “pseudo-ceratites based on an apparent resemblance between the sutures of Triassic ceratids and those of Cretaceous engonoceratids” (Hyatt, 1903; G. Scott, 1940a, 1940b; Kennedy & Cobb, 1976; Rawson, 1981; Kennedy et alii, 1998a). The first engonoceratid ammonite was published by d’Orbigny (1841) as Ammonites Vibrayanus [= Neolobites vibryeanus] 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 Vibrayeanus and Ammonites Robini [= Metatissotia ewaldi and M. robini], these species belong to discrete taxa (Acanthoceroidea) 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). Spåth (1922, 1924) introduced Hypengonoceras, and Parenengonoceras. The last described member of the family is Platiknemeceras (Battaller, 1954).

In the mid 1900’s Chipplonkar (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, Parenengonoceras, Platiknemeceras, 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 Hoplitoidea. 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 Pulchellatoidea, this attribution is not yet widely accepted. KENNEDY et alii (2004), YACOBUCCHI (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 Pulchellatoidea. Most recently, BULOT (2010, p. 169) rejects the pulchelliatoid origin of Engonoceratidae, suggesting that the genus Subpulchellia/Moghareceras 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, Parenengonoceras, Platikнемiceras, 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 DOUVILLE, 1890
Family Engonoceratidae HYATT, 1900
= Knemiceratidae HYATT, 1903, p. 144;
Neolobitinae LUPOV & MIKHAILOV, 1958, p. 125

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

Type species. Glottoceras attenuatum HYATT, 1875, from the Lower Alban 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 crassicostatum SOMMERMEIER, 1910: p. 343, pl. 10, fig. 4; Pl. 11, figs. 1-3.
- Knemiceras gabi 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 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. 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. 49, fig. 1. 

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 zigzagging 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.
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 oligulacae 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 Cragn, 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 Perquiníere, 1907: p. 302, pl. 9, fig. 8.
Engonoceras toussainti Perquiníere, 1907: p. 305, pl. 9, fig. 7a-c.
Sphenodiscus belviderensis var. udeni Cragn, 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).

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. fourtau) 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 seemingly 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 brancai] Staff & Eck, 1908: p. 277, fig. 5 = subspecies of N. vibrayeanus (Meister & Abdallah, 2005, p. 123); =


- *Neolobites fourtau* Pervinquiére, 1907: p. 209, pl. 8, figs. 2-6.


- *Ammonites* *Vibrayeanaus* d’Orbigny, 1841: p. 322, pl. 96, figs. 1-3.

Remarks. Wiese & Schulze (2005) stated that only *N. vibrayeanaus*, *N. fourtau* 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 & Jügnet (1981, p. 24) argued that *N. peroni* is also no more than an intraspecific variety of *N. vibrayeanaus*. 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. vibrayeanaus* and *N. peroni*. Taking into consideration the extreme morphological variety of the populations of *Neolobites*, the present author accepts the opinion of Kennedy & Jügnet (1981) on *N. peroni*, and considers this species an intraspecific variety of *N. vibrayeanaus*. It is possible that *N. fourtau* will also be found to fall into the intraspecific range of *N. vibrayeanaus*, especially taking into consideration the eco-morphological analysis of Wiese & Schulze (2005). The other possibility, that future research will elucidate, is that *N. fourtau* and *N. vibrayeanaus* form two discrete chronospecies, namely *N. fourtau* is older and *N. vibrayeanaus* is younger. The Early Cenomanian *N. bedoti* of Grossouvre (1912, p. 31) has been assigned to Metengonoceras by Kennedy & Jügnet (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 = *Cnemioceras* 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.”

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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 arambourgi* BASSE, 1940: p. 426, pl. 1, fig. 2.
- *Knemiceras collignonii* 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 orientalis* MAHMOUD, 1955: p. 54, pl. 2, figs. 2-7; text-figs. 28-29 = synonym with *K. spathi* (BULOT, 2010)].
Knemiceras (Omaimaceras) rittmanni Mahmoud, 1955: p. 63, pl. 3, fig. 5.

Placenticeras saaharense Peron & Thomas, 1890: p. 19, pl. 16, figs. 3-7.


?Knemiceras sinaticum 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 about 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 quadrutuberculate ornament is unknown in Hypengonoceras. Bifid (e.g. K. compressum, K. subcompressum) or irregular (K. douvilliei, K. iraniensi) 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. douvilliei) 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).

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 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. Adventitious 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 emarginatum* (Cragin, 1893): p. 245. referred by Hyatt (1903, p. 177) is a synonym of *Engonoceras emarginatum* (Hyatt, 1903, p. 157)].
- *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 cannot 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 falcoïd 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.
- 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 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.

Diagnosis. Diagnosis is after KLINGER & KENNEDY (1989, p. 362). "Umbilicus is narrow. The shell compressed, the flanks generally little rounded. Sculpture consists of low falloid 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 foliules; 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.
- 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 quadratuberculate 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.
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* *CAÑÉROT* & *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.
- *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.
- *Parengonoceras elegans* *RENZ*, 1970: p. 1036, pl. 3, fig. 1a-c, 2a-b; pl. 4, fig. 1, 3a-b; text-fig. 4a-g.
- *Placenticeras guadaloupaforme* *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.
- *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 tetranosum* *LISSÓN*, 1925: p. 25, pl. 2, fig. 3= synonym of *P. pernodosum* (*ROBERT* & *BULOT*, 2004, p. 20)].
- [*Knemiceras trinitense* *G. SCOTT*, 1940b: p. 1069, pl. 67, fig. 6; pl. 68, fig. 6 = 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. 1].
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, refugured 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 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.
- *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 & KAMERA, 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.](CG2010_A06)**

**Henderson, 1973**

* Borissiakoceras sp.  
(Stilwell & Gallagher, 2009, p. 881)

This tiny specimen is reported from the Albain of New Zealand (Henderson, 1973, p. 106). The specimen is not strongly evolve (two whors are visible) atypical for Engonoceratidae. Nor is the suture is typical of Engonoceratidae: therefore the generic assignment is not supported. Kennedy & Klingar (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*, *Knemeras*, *Metengonoceras*, *Parenongoceras*, *Platiknemiceras*, and *Protengonoceras*). Only two genera (*Hyponegonoceras* 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 *Neogastropilites* from its original morphospace (Yacoubucci, 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 dumbi* 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. dumbi* 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 (*Knemeras* 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 the basin 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 efforts, 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 natural habitats. However, Engel and Kauffman (1997) reported that many occurrences of *Knemiceras* may 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 post-mortem drifting, rather than during life in natural habitats. However, Kennedy & Cobbán (1976) and Page (1996) found that the post-mortem 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 & Shukhina (2008) report *Knemiceras* from intercalated non-marine-shallow marine beds of Middle Albian age in Israel. *Knemiceras uhi* 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 inhabitance 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 supported 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 Bolivía (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 (Parengonoconceras, Protengonoconceras, Engonoconceras 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-
Engonoceratidae had a platiknemiceratid origin. Latest Aptian–earliest Albian 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 for the Pulchelliidae. If the Engonoceratidae is a 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 (2008) also refer to the systematic position of the Engonoceratidae. Almost certainly polyphyletic as indicated by the remarkable differences between the sutures of Engonoceratidae - 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 Parengonoceras. 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, 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 Engonocer-
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).


**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 (IRIM 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 suture lines 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.

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 nektontic, 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 chron stratigraphic 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 they 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

*Engonoceras 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 allii: 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, Veszprémm 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). BUTOR (1990a) described it from Hungary (Tilos Forest, Bakony Mts.). SZIVES et alii (2007) copied the figures of BUTOR (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 Parengonoceras 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 Pen-
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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**Bibliographic references**

Abdallah H. & Memmi L. (1994).- Sur l’âge des couches à *Knemiceras* de Tunisie méridiona-


Amédro F. (2008).- Support for a Vraconnian Stage between the Alban sensu stricto and the Cenomanian (Cretaceous System).- Carnets de Géologie / Notebooks on Geology, Brest, Memoir 2008/02 (CG2008_M02), 83 p.

Amireh B.S. (1997).- Sedimentology and paleo-geography of the regressive-transgressive


FÖRSTER R. (1975).- Die geologische Entwicklung im südlichen Keltiberikum (Spa-


GEYER O.F. (1995b).- Zur Alb-Cenoman-Transgression im südlichen Keltiberikum (Spa-


KENNEDY W.J. (1988).- Late Cenomanian and Turonian ammonite faunas from northeast


KOSSMAT F. (1895).- Untersuchungen über die Sühindische Kreideformation.- Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients, Wien, Band 9, p. 97-203.


LISSÓN C.I. (1908).- Contribución al conocimiento sobre algunos ammonites del Perú.- Tipografía el Perú, Lima, 22 p.

LISSÓN C.I. (1925).- Algunos fósiles del Perú.- Boletin de la Sociedad Geológica del Perú, Tipografía el Perú, Lima, 22 p.

LOPEZ-HORGUE M., OWEN H.G., ARANBURU A., FERNANDEZ-MENDIOLA P.A. & GARCIA-MONDÉJAR J. (2009).- Early Late Albian (Cretaceous) of


MOUTY M. & GAUTHIER H. (1999).- Mid-Cenomanian ammonites from the coastal chain of Syria. In: HISTON K. (ed.), Cephalopods -


