

A new placenticeratid ammonite from the Albian (Lower Cretaceous) of California and the inferred history of some placenticeratid and engonoceratid ammonites

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With 5 figures

LEHMANN, J. & MURPHY, M. A. (2001): A new placenticeratid ammonite from the Albian (lower Cretaceous) of California and the inferred history of some placenticeratid and engonoceratid ammonites. – N. Jb. Geol. Paläont. Mh., 2001: 343–358; Stuttgart.

Abstract: A new ammonite species from the lower Cretaceous (middle Albian) of California is questionably assigned to *Placenticeras* MEEK, 1876 by its suture line whose lobe frillings are more regularly arranged than in most *Placenticeras* and by its ornamentation and coiling that resemble some *Placenticeras*. The California material shows strong similarities to *Sokolovites* CASEY, 1966, a member of the Gastropplitinae WRIGHT, 1952, and therefore suggests a hoplitid origin for the Placenticeratidae. A review of criteria separating the families Placenticeratidae HYATT, 1900 and Engonoceratidae HYATT, 1900 suggests possible relations between these families.

Zusammenfassung: Eine neue Ammonitenart aus der Unterkreide (Mittleres Alb) von Kalifornien wird mit Vorbehalt zu *Placenticeras* MEEK, 1876 gestellt. Wir interpretieren unser Material als möglicherweise ältesten Vertreter der Gattung und schlagen ihn als Ursprung der Placenticeraten vor. Das Exemplar aus Kalifornien zeigt enge Beziehungen zu *Sokolovites* CASEY, 1966, einem Vertreter der Gastropplitinae WRIGHT, 1952, und legt deshalb einen Ursprung der Placenticeratidae aus den Hoplitiden nahe. Eine Neubewertung der Charakteristika der Placenticeratidae HYATT, 1900 und Engonoceratidae HYATT, 1900 zeigt mögliche Beziehungen zwischen diesen beiden Familien und innerhalb beider Taxa auf, denen einige Merkmale gemeinsam sind.

Introduction

Members of the ammonite family Placenticeratidae HYATT, 1900 are common in Upper Cretaceous strata. However, only the Pacific Realm late Cretaceous *Metaplacenticerat* SPATH, 1926 has been recorded from California. SMITH'S (1900) record of *Placenticerat* from the "Upper Gault" of California is misdated and in fact based on specimens late Late Cretaceous in age (compare ANDERSON 1958, p. 253). The middle Albian specimen described below shares features that are reported from three hoplitacean families, Placenticeratidae HYATT, 1900, Hoplitidae H. DOUVILLÉ, 1890 and Engonoceratidae HYATT, 1900 (WRIGHT 1996), and enlarges the known geographic distribution of the Albian members of this group of ammonites.

In an effort to classify the California specimen from Alkalai Gulch, One Quadrangle, in California (Fig. 1) we have adjusted WRIGHT'S classification (Fig. 2). The combination of criteria used by WRIGHT (1996) to characterize the Placenticeratidae are the degree of involution, the narrow, grooved or flattened venter, inner whorls with little or no ornament, outer whorls with strong ornament, and a suture with much frilled adventive and auxiliary elements. This is believed to contrast with the Engonoceratidae only in suture patterns, which are characterized by numerous simplified adventive and auxiliary elements and the tendency of the early forms to be ornamented. Some authors have been ambivalent about the taxonomic position of the genera in these two families (SPATH 1922, KENNEDY & WRIGHT 1983, KLINGER & KENNEDY 1989, WRIGHT 1996). For example, SPATH erected the genus *Hypengonoceras*, first assigning it to the Engonoceratidae, but later (SPATH 1931) placed it in the Placenticeratidae, without comment. WRIGHT (1996, p. 126) states that "*Hypengonoceras*, despite some resemblance to Engonoceratidae, seems to belong here" [Placenticeratidae]. However, he lists *Hypengonoceras* (p. 130) under the Engonoceratidae. As a further indication of uncertainty, he has queried the family Engonoceratidae. This illustrates the difficulty of assigning taxa in these two families. Our conclusion is that, if the suture line is used as the primary criterion for family assignment, the classification in Fig. 2 is more logical both taxonomically and stratigraphically.

Conventions

We use the suture terminology of WEDEKIND (1916), revised by KULLMANN & WIEDMANN (1970) and the following abbreviations: E = external lobe, A1 = adventive lobe 1, A2 = adventive lobe 2, L = lateral lobe, U = umbilical lobe.

U/D is the ratio of the width of the umbilicus to the diameter.

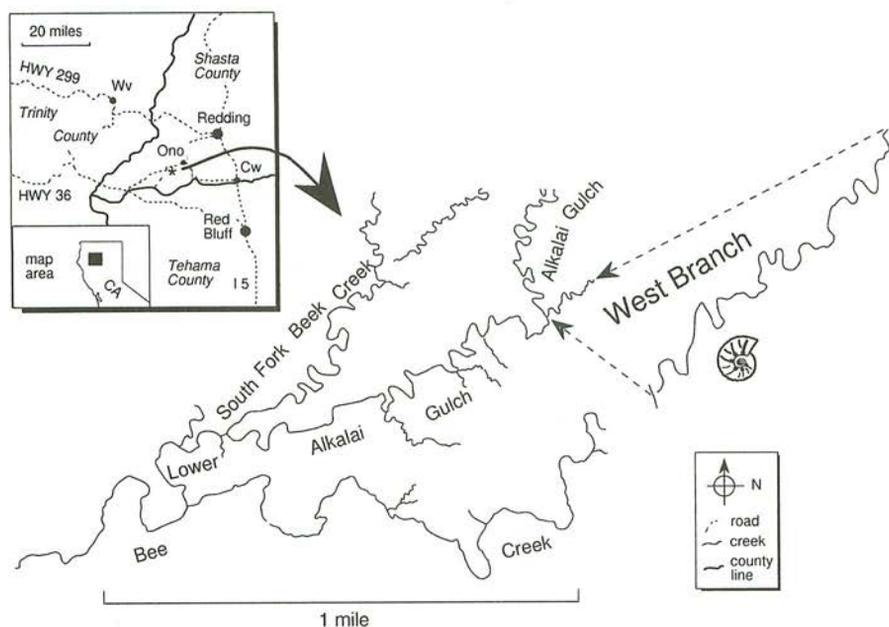


Fig. 1. Map of the Bee Creek area in Northern California, showing the spot at the West Branch where *Placenticeras* ? n. sp. was loosely collected.

Fig. 2. Inferred history of placenticeratid and engonoceratid ammonites and the relationship of that history to relative changes of sea level. Breadth of range lines expresses the morphospace, referring to the morphological variability of taxa. Star indicates the position of the specimen from California described herein. Stage boundaries as in GRADSTEIN et al. (1995), relative change in coastal onlap after HAQ et al. (1987). Remarks: 1. The questionable record of *Knemiceras* in the late Aptian (WRIGHT 1996, p. 130) is based on a determination for a faunal list of the middle Apón Formation, Venezuela, by IMLAY (ROD & MAYNC 1954). The late Aptian age is based on the cooccurrence of the ammonite taxa *Chelonicerias*, *Colombicerias*, *Dufrenoyia* and *Sanmartinoceras*. This specimen is assigned to *Knemiceras* sp. and not figured or described. 2. *Engonoceras* presumably derived from *Knemiceras* by a reduction of saddle complexity (most saddles are entire in *Engonoceras*). 3. *Protengonoceras* evolved from its probable ancestor *Engonoceras*, by reduction of ornament only; a close relationship is therefore assumed. However, the suture of *Pro-*

tengonoceras is unknown (compare BÖHM, 1898, p. 197). 4. The transition *Protengonoceras* - *Metengonoceras* is not characterized by a distinct morphological change, the suture can not be compared (see comment 3). Comparing the suture of *Engonoceras* and *Metengonoceras* however, shows less numerous lobe frillings in most forms of *Metengonoceras*. 5. *Neolobites* is presumably derived from *Metengonoceras* by simplification of lobes; compare diagnosis for *Neolobites* in KENNEDY & JUIGNET (1984, p. 99) who pointed out that its suture shows entire lobes and saddles. The first certain occurrence of *Neolobites* comes from the middle Cenomanian (KENNEDY & JUIGNET 1984, p. 99). 6. *Platknemiceras* is characterized by a strong reduction in ornament. However, we believe that it is very close to *Knemiceras* because of an identical suture (compare WRIGHT 1996, p. 130). 7. The relationship of *Parengonoceras* to the Engonoceratidae is questioned, a tendency in reduction of ornament can be seen too. According to RENZ (1982, p. 44) *Parengonoceras* ranges up into the middle Albian, *Hysteroceas orbigny* Zone, in contrast to WRIGHT (1996, p. 130). 8. *Hypengonoceras* shows a further reduction in ornament in comparison to its supposed ancestor. 9. *Hengestites* evolved maybe directly from *Parengonoceras* lineage that is characterized by a reduction in ornament. The same kind of reduction in the *Parengonoceras*-*Hypengonoceras* transformation is a parallel trend in a separate lineage since several taxa of *Hypengonoceras* (including the type species) show a very simple suture line but the suture of *Hengestites* is complex. *Hengestites* has a very restricted stratigraphic range, it is known from the upper Albian, *Callihoplites* Subzone of the *Mortoniceras inflatum* Zone only (CASEY 1960, p. 205). 10. There are only small differences in suture ontogenesis between *Parengonoceras*, *Hypengonoceras* and placenticeratids. This suggests a possible relation to the placenticeratids, which they resemble in other sutural characteristics. 11. The star represents the position of *Placenticerias* ? n. sp., the arrow indicates the last occurrence of forms previously assigned to *Karamaites* by MIKHAILOVA (1983). 12. The genus *Karamaites* is a synonym of *Placenticerias* after WRIGHT (1996, p. 127), compare discussion by KENNEDY 1986, p. 56. 13. *Placenticerias* ranges from the upper Albian into the upper Campanian (cf. chapter on 'Stratigraphy'). 14. *Metaplacenticerias* derived from *Placenticerias* by the development of a tricarinate venter (mid growth only ?, see WRIGHT 1996, p. 128). 15. *Hoplitoplacenticerias* is separated by the development of prominent ribs. According to LARSON et al. (1997, p. 145) *Hoplitoplacenticerias marroti* (COQUAND, 1859) first occurs in the upper lower Campanian, *Baculites* sp. (smooth) zone of the Western Interior, USA. Note that this is not in contrast to WRIGHT (1996, p. 129) who reports its first appearance from the upper Campanian, because the Treatise divides the Campanian into two substages (WRIGHT, 1996, tab. 1), with a *Hoplitoplacenticerias marroti* zone as the lowermost zone of the upper Campanian, whereas the present paper is following the subdivision of the Campanian into three substages as used by GRADSTEIN et al. (1995) and LARSON et al. (1997), where the equivalent interval lies in the upper lower Campanian. 16. *Sokolovites* is known from the lower Albian of Transcaspa, ? Spitzbergen and Arctic Canada only. 17. *Gastrolites* and *Sokolovites* are different from *Placenticerias* ? n. sp. because of the presence of a hoplitid suture.

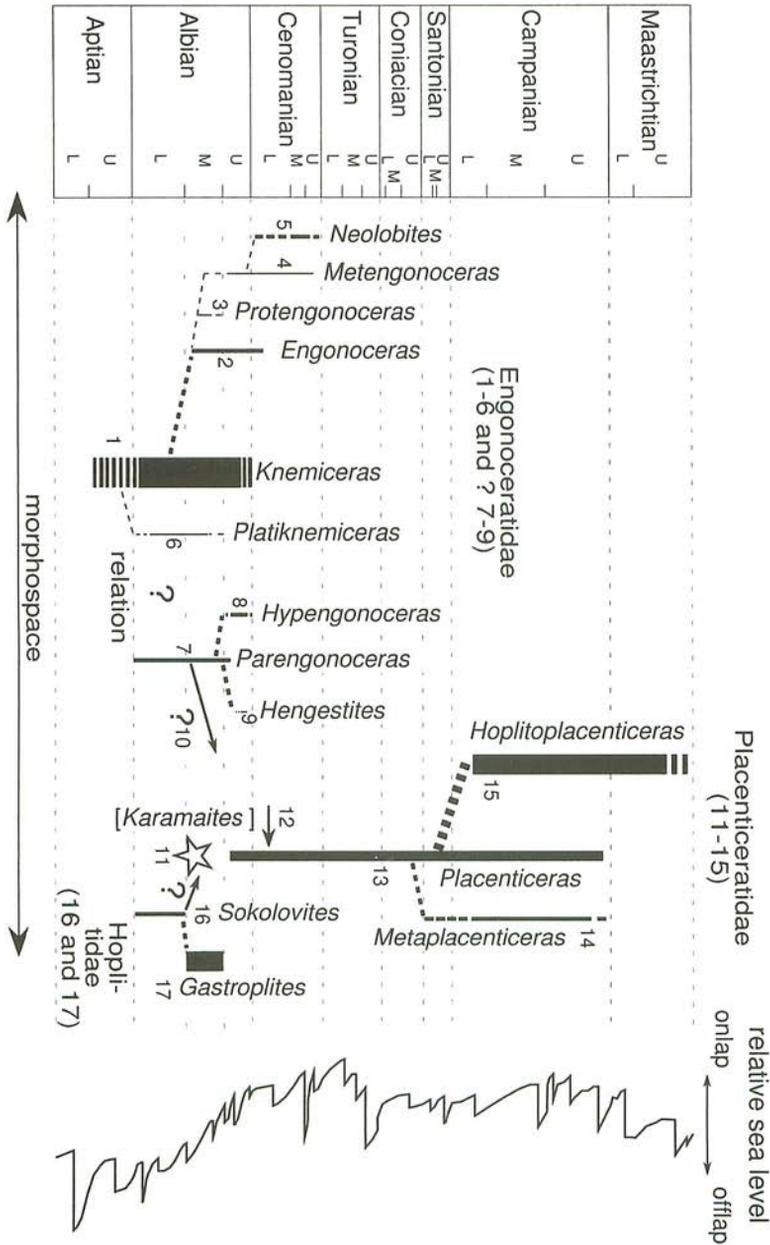


Fig. 2 (Legend see p. 345/346)

Systematic Paleontology

Superfamily Hoplitaceae DOUVILLÉ, 1890

Family Placenticeratidae HYATT, 1900

We agree with other authors (e.g. KLINGER & KENNEDY 1989) that a separation of engonoceratids and placenticeratids is difficult, but that there are strong hints for an origin of placenticeratids in the hoplitids. CASEY (1965, p. 461) and MIRZOYEV (1967, fig. 5) believed that the early placenticeratids such as *Karamaites* were derived from *Semenovites* GLASUNOVA, 1960 and KLINGER & KENNEDY (1989, fig. 8) indicate without comment that *Metaclavites* CASEY, 1965 is the direct ancestor, but both of these hoplitid genera are too high in stratigraphic position to be so considered.

We see strong morphological similarities between our specimen and the hoplitid *Sokolovites* CASEY, 1966, these are a growth stage at which the venter is tabulate, umbilical bullae, branching ribs that cross almost straight over the venter and a wide umbilicus. However, the suture line of *Sokolovites* is hoplitid and our specimen has a placenticeratid suture in which the width/height ratio of the E/L and L is greater than in the Hoplitidae (Fig. 3:2). With respect to *Parengonoceras* and *Hypengonoceras*, both classified in the Engonoceratidae by WRIGHT (1996, p. 130, figs. 100-1, [1c, figured upside down], 101-3), have more complex sutures than is typical for that family. They are also similar to one another, but the suture line of *Hypengonoceras* is more variable and falcoid ribs are present (DE LORIO 1882, KOSSMAT 1895, COLLIGNON 1966, LEWY 1981, KLINGER & KENNEDY 1989). KLINGER & KENNEDY (1989, p. 362) state that "in typical forms [of *Hypengonoceras*] some saddles are little divided and 'pincer like' with bifid folioles, in others as incised as in normal placenticeratid pattern".

The ontogenesis of the engonoceratid suture is unknown for the type genus or any of the other related genera with simple terminations of the saddles. The sutural ontogenesis for *Parengonoceras*, however, has been described by RENZ (1970) who shows that the A1 and A2 lobes of the adult suture both develop from the external saddle of the primary suture. This could constitute a reason for separating *Parengonoceras* from the Placenti-

Fig. 3. *Placenti ceras?* n.sp. from the Budden Canyon Formation, Chicabally Member, float specimen, middle Albian. Bee Creek, Northern California. **1.** Lateral view of plaster cast, made from negative imprint. **2.** Suture line drawn at a whorl height of about 15 mm (a-c, exact position see thin arrow in Fig. 4:1); actual length 15 mm.

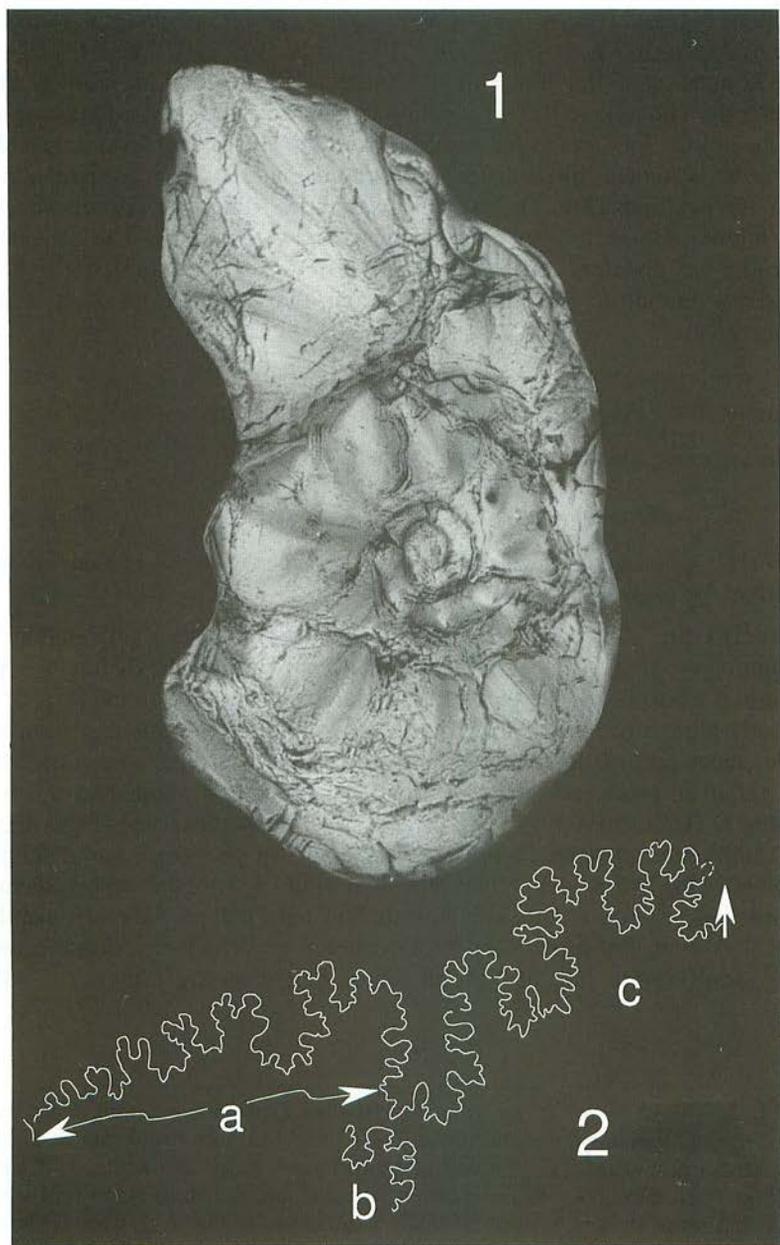


Fig. 3 (Legend see p. 348)

ceratidae because *Placenticerus* ('*Karamaites*') and *Placenticerus* (*Placenticerus*), MIKHAILOVA (1974; 1978; 1983, figs. 105, 107) and MIRZOYEV (1967) show that the lobes in the same adult position develop a little differently. The lobe in the A1 position comes from the flank of the external saddle and the lobe in the A2 position from the crest of the external saddle. As far as is known, these differences are characteristic for sequential stratigraphic positions (Fig. 2), lower to basal upper Albian for *Parengonoceras* and middle Albian to upper Cretaceous for *Placenticerus*. The sequential stratigraphic positions and only small differences in suture ontogenesis suggest a relation to placenticeratids, which they resemble in other sutural characteristics.

Genus *Placenticerus* MEEK, 1876

Type-species: *Ammonites placenta* DEKAY, 1828

Placenticerus ? n. sp. (Figs. 3, 4)

Material: One incomplete specimen; CASG number AGW 94-13 from the west branch of Alkalai Gulch (Fig. 2).

Description: Specimen characterized by prominent ornamentation on phragmocone (Fig. 4:1); umbilical bullae very prominent, distinctly separated to a whorl height of about 20 mm, later ribs without bullae (Fig. 3:1); on early phragmocone (up to 55 mm D) two main ribs branching from one bulla; secondary rib intercalated between main ribs on outer third of flank; ribs radial to prorsiradiate, some flexuous; involution about two thirds at 40 mm D (U/D: 0.19; Fig. 3:1); ventral side poorly preserved (Figs. 4:2 & 4:4) but venter appears flattened on later part of phragmocone at 60 mm D where ribs cross venter undiminished (Fig. 4:2); high whorl section, regarded as primary feature although shell is distorted; partial body chamber (Fig. 4:3) with flat prosinuate plicae covered by prominent, dense growth lines; adult suture line at 15 mm whorl height strongly incised; saddle

Fig. 4. *Placenticerus* ? n. sp. from the Budden Canyon Formation, Chicabally Member, float specimen, middle Albian. Bee Creek, Northern California. 1. Lateral view. Broad arrows refer to positions of ventral views (large arrow Fig. 4:2, small one Fig. 4:4), thin arrow to the position where suture drawings (Fig. 3:2) were taken. 2. Ventral view at position of small broad arrow in Fig. 1. 3. Lateral view of part of mature body chamber. 4. Ventral view at position of large broad arrow in Fig. 1:1.

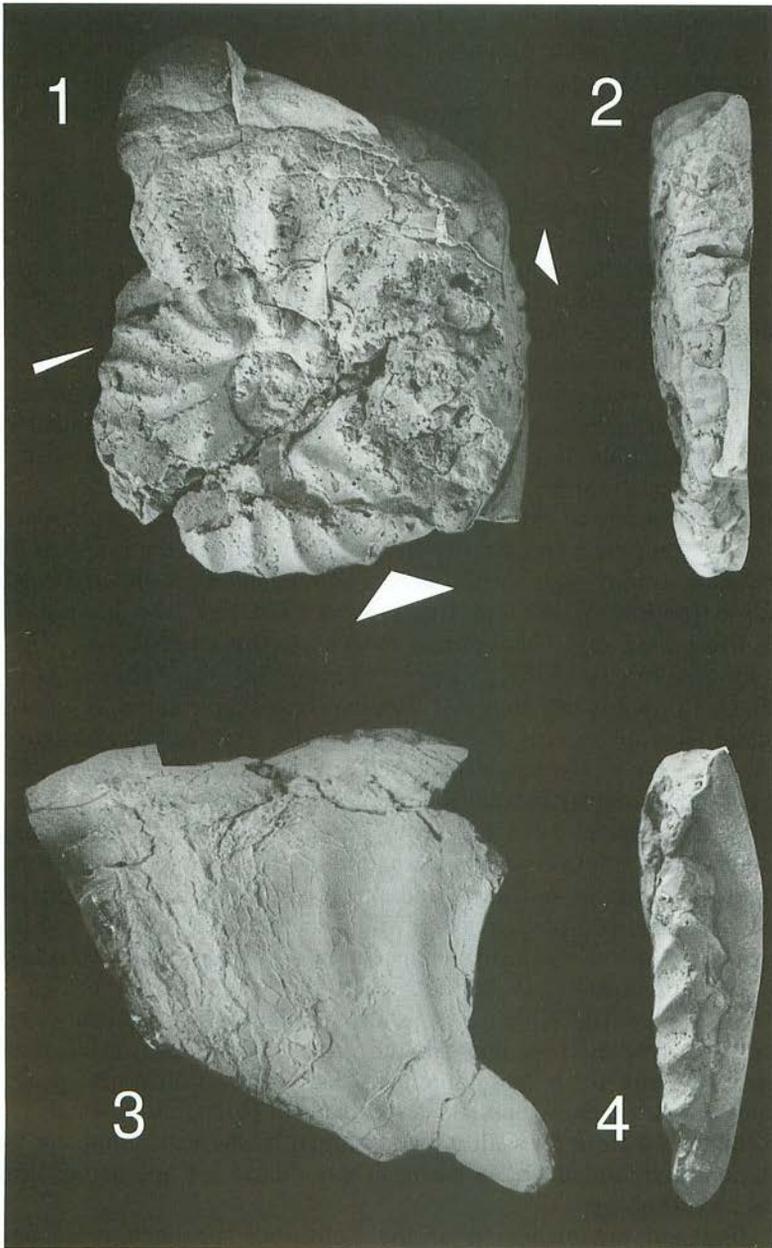


Fig. 4 (Legend see p. 350)

termination mostly with two subdivided folioles; presumed external saddle (see c in Fig. 3:2) broad, with deep incision dividing saddle into smaller part with one major incision and somewhat larger part with two major incisions; deepest and largest lobe interpreted as A1, two additional main lobes inferred to be A2 and L, but ontogenesis unknown.

Comparison: Our specimen shows a placenticeratid suture pattern, with most saddles terminating in two subdivided folioles. The pattern remains the same but becomes smaller towards the umbilicus. This is different in contemporaneous gastroplitids, which show an irregular pattern of lobe and saddle terminations within the same suture line. Ribbing similar to the strong ribbing of *Placenticeras* ? n. sp. occurs in microconchs of the mid Cretaceous *Placenticeras* formerly referred to as *Karamaites*. Contemporaneous mid Cretaceous placenticeratids show a similar pattern of element subdivision of the suture line, with regularly arranged lobe and saddle frillings, in contrast to gastroplitids.

Striking features of the California specimen, an A1 that is the deepest lobe of the suture line and the proportional dominance of the L and A1 lobes in the adult suture occur in the genera *Parengonoceras* and *Hypengonoceras* too ([DE LORIO 1882, pl. 1 pars; RENZ 1970, figs. 3e-i, k, 4e-g, 5d-g, 7c, e; RENZ 1982, fig. 32 for *Parengonoceras*]; [BOULE et al. 1907, fig. 26; COLLIGNON 1963, fig. 1269; 1966, pl. 5; LEWY 1981, fig. 3; KOSSMAT 1895, pl. 20, fig. 8 for *Hypengonoceras*]. However, the simple suture of the engonoceratid *Hypengonoceras*, is easy to distinguish from that of *Placenticeras* ? n. sp. because of the pincer-like saddle terminations that differentiate it from the more complex subdivision of *Placenticeras* ? n. sp..

Some engonoceratids of the genus *Parengonoceras* are similar to our specimen, for example *Parengonoceras zagrosiense* COLLIGNON, 1981 by its comparatively strong ornament and open umbilicus. However, the only known specimen is a phragmocone with a diameter of 170 mm and is not comparable with our much smaller specimen. A further species, *Parengonoceras duplicatum* RENZ, 1970 (RENZ 1970, pl. 5, figs. 1-4; pl. 6, figs. 1-2; pl. 7, fig. 3, pl. 8, fig. 2; figs. 5-6), is also similar up to a diameter of about 50 mm where the shell becomes smooth, but even at the early stage of development, the ribbing is less prominent than in the California specimen. *Hypengonoceras* species, possible descendants of *Parengonoceras*, are clearly distinguished from the California specimen by the less prominent ornamentation, non-falcoid ribs, a narrower umbilicus, and alternating ventro-lateral clavi (Fig. 2).

Coiling and ornamentation of the California specimen is somewhat similar to some forms of the more than 50 taxa that have been described of

another engonoceratid genus, *Knemiceras* BÖHM, 1898. GEYER (1995) and GEYER et al. (1997) claim that most of these taxa could be suppressed. The desirability of amalgamation is also suggested by the demonstration of the great variability in inflation and ornamentation in *Knemiceras* specimens that are believed to represent a single species by REYMENT & KENNEDY (1991). In any case, most of the taxa referred to *Knemiceras* have depressed whorls, a smaller umbilicus, and simple saddles and, in addition to the more simple suture line, they are clearly separated by these characteristics. Only the suture of *Knemiceras* aff. *gabbi* HYATT, 1903 (RENTZ 1970, fig. 10d) shows a more complex pattern. However, in contrast to our specimen, this taxon has less numerous and extended, but not pointed lobe endings.

Our review of these taxa suggests the suture line should be used as the primary criterion for classification within these groups. Therefore, the specimen from California is regarded as a compressed, strongly ribbed early representative of the Placenticeratidae, possibly *Placenticeras*, with distinct bullae on the first part of the phragmocone only.

Stratigraphy

The California specimen was found loose in a stream bed within the ranges of *Cleoniceras susukii* MURPHY & RODDA, 1959 and *Oxytropidoceras packardi* ANDERSON, 1938 and occurs in a faunal association that typically is comprised of *Douvilleiceras*, *Brewericeras*, *Lyelliceras*, *Anagaudryceras*, *Lytoceras*, *Puzosia*, and undetermined heteromorphs (Fig. 4). The west branch of Alkalai Gulch is incised into beds containing this assemblage only and therefore it can not have been washed downstream from another stratigraphic level. POPENOE et al. (1960, p. 1509 and chart 10e) interpreted the *Oxytropidoceras packardi* Assemblage Zone as representing most of the middle Albian. We agree with this interpretation because of its stratigraphic position with relation to the first occurrence of the middle and upper Albian genus *Dipoloceras* (see WRIGHT 1996, p. 140). Furthermore, the genus *Douvilleiceras* occurs through three zones in California (POPENOE et al. 1960, p. 1509) and *Placenticeras* ? n. sp. comes from the upper zone of the three, indicating a high position in the range of the lower and middle Albian genus *Douvilleiceras*. The presence of *Lyelliceras*, probably the middle Albian index form *L. lyelli* from France, suggests that an early middle Albian age is most likely.

Placenticeras ranges from the upper Albian up into the lower Campanian according to WRIGHT (1996, p. 128). However, this taxon ranges at least into the upper Campanian with three species following LARSON et al. (1997, p. 145). One of the latter, *Placenticeras costatum* HYATT, 1903, is recorded in

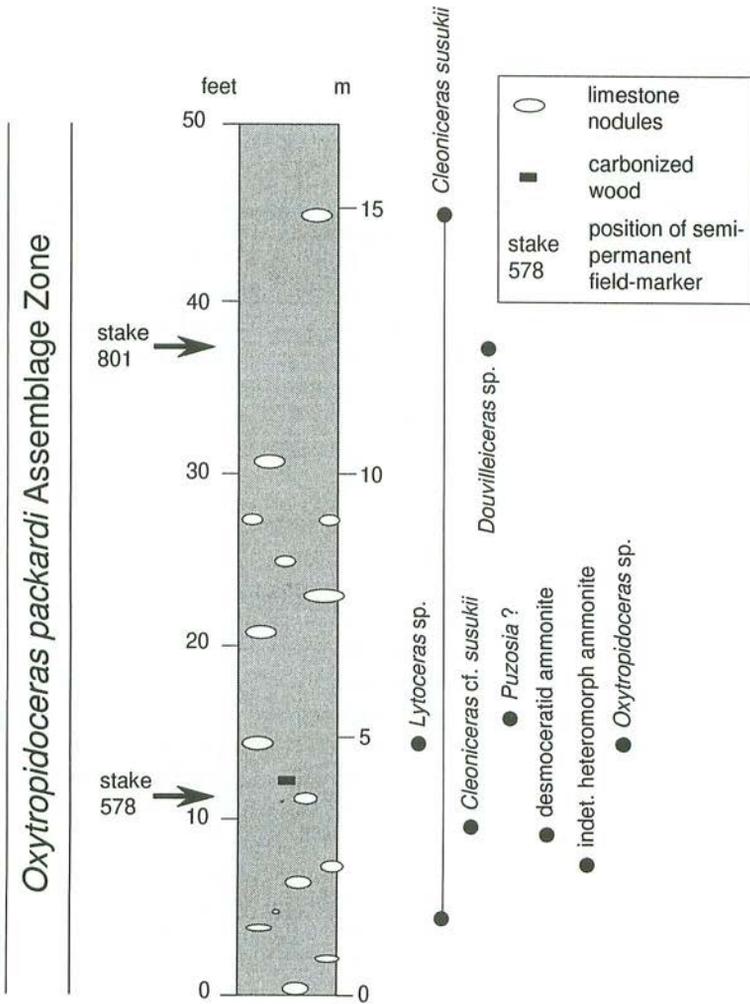


Fig. 5. Profile of the West Branch of Bee Creek, Northern California, where *Placenti-ceras*? n. sp. was collected in float. Additionally to the specimens listed in the figure and that have been collected in situ, *Lyelliceras*, *Brewericeras* and *Anagaudryceras* occur in this interval as well according to float material.

the late upper Campanian, *Baculites reesidei* Zone (KENNEDY et al. 1996, p. 9). The stratigraphical occurrence of the California specimen of *Placenticeras* ? n. sp. therefore could indicate that *Placenticeras* may have appeared in the middle Albian.

Correlation between sea level and evolution

The establishment of new habitats in the middle Cretaceous can be correlated to a general onlap of sea level that started at the end of the Valanginian and reached its maximum during the Albian (HAQ et al. 1987; Fig. 2). This triggered the evolution of the fauna in general and the range chart (Fig. 2) suggests that the increased flooding of shelf areas in the Albian also played a role in the diversification of engonoceratid and placenticeratid ammonites because the main evolutionary steps within those families took place during the Albian. The high increase of morphologic variability found by REYMENT & KENNEDY (1991) in engonoceratid material from Iran fits with this picture as does their interpretation of the shallow, labile epicontinental environment.

Acknowledgments

The material was collected as part of a study of Albian fossils of California sponsored by the National Science Foundation. JL was supported by a grant of the Common University Special Program III of the Federal Republic of Germany and the single states of the Federal Republic provided by the Daad (German Academic Exchange Program). We thank W. A. COBBAN (DENVER) for reviewing an earlier version of this paper, K. PIOLKA (Tübingen) for technical support, W. GERBER (Tübingen) for making the prints and I. LEHMANN (Rheine) for providing rare publications.

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Manuscript received: May 30, 2000.

Revised version accepted by the Tübingen editors: July 4, 2000.

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