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A review of *Beudanticeras* Hitzel, 1902 (Cretaceous Ammonitida), and its occurrence in the Cottonwood District of Northern California

Una revisión de Beudanticeras Hitzel, 1902 (Ammonitida del Cretácico), y su presencia en el Distrito de Cottonwood en el norte de California

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Abstract

Beudanticeras Hitzel is a distinctive but relatively rare Upper Albian (Cretaceous) ammonite that has been reported from the southeast France and the Cottonwood District of northern California coastal ranges. In both iterations of the Treatise (Wright, 1957 and 1996), it has been placed in the Desmoceratidae even though the type species has none of its characteristics. We classify it as the sole genus in the Family Beudanticeratidae Breistroffer, 1953 (*nomen translatum* herein, *ex* Beudanticeratinae Breistroffer, 1953) which is characterized by its discoidal shape, narrow umbilicus with an angulate shoulder, sickle-shaped ornamentation, and strongly asymmetrically bifid L. Most discoidal ammonites identified as "*Beudanticeras*" have features characteristic of the Desmoceratidae, such as, constrictions and trifid L, and are classified in *Roberticeras,* new genus. *Beudanticeras* and *Cleoniceras* are similar with respect to shell shape and strongly asymmetrically bifid suture but significantly different with respect to ornament, and shell shape. Four species are assigned to *Beudanticeras*: *B. beudanti* (Brongniart, 1822) and *B. sphaerotum* (Seeley, 1866) from Europe, *B. haydeni* (Gabb, 1864) from California, and *B. sutherlandbrowni* (McLearn, 1972) from British Columbia. *B. haydeni* (Gabb, 1864), based on a specimen from the Cottonwood district, occurs only in uppermost Albian strata, and can be distinguished from the similar *B. beudanti* by differences of degree in the umbilicus and ornament.

Keywords: Albian, ammonites, biostratigraphy, California, Cretaceous.

Resumen

Beudanticeras Hitzel es una ammonite del Albiano Superior (Cretácico) muy característico, pero relativamente escaso que ha sido reportado en el sureste de Francia y el distrito de Cottonwood en las cordilleras costeras del norte de California. En las dos versiones del Treatise (Wright, 1957 y 1996), se ha ubicado este género en Desmoceratidae a pesar de que la especie tipo no tiene ninguna de sus características. Nosotros lo clasificamos como el único género de la Familia Beudanticeratidae Breistroffer, 1953 (nomen translatum, ex Beudanticeratinae Breistroffer, 1953), que se caracteriza por su forma discoidal, ombligo angosto con pared angulada, ornamentación en forma de hoz y sutura L bífida fuertemente asimétrica. La mayoría de los ammonites discoidales identificados como "Beudanticeras" tienen rasgos característicos de Desmoceratidae, como constricciones y L trífida, y aquí se clasifican como el nuevo género Roberticeras. Beudanticeras y Cleoniceras son similares con respecto a la forma de la concha y la sutura bífida fuertemente asimétrica, pero significativamente diferentes con respecto a la ornamentación y la forma de la concha. Se asignan cuatro especies a Beudanticeras: B. beudanti (Brongniart, 1822) y B. sphaerotum (Seeley, 1866) de Europa, B. haydeni (Gabb, 1864) de California y B. sutherlandbrowni (McLearn, 1972) de Columbia Británica. B. haydeni (Gabb, 1864) está basado en un espécimen del distrito de Cottonwood, estando solo presente en los estratos de la parte más alta del Albiano superior y puede distinguirse de la especie similar B. beudanti por diferencias en la región umbilical y la ornamentación.

Palabras clave: *Albiano, ammonites, bioestratigrafía, California, Cretácico.*

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1. Introduction

In the Treatise classification (Wright, 1996), the Beudanticeratinae, a subfamily of Desmoceratidae, is broadly characterized to encompass varied morphologies of presumed affinity. The diagnostic characteristics of the type species of *Beudanticeras, B. beudanti,* we believe excludes it from the Desmoceratidae. Below we support this exclusion, suggest a different classification, and discuss the implications of this change. The systematic part reviews the species we assign to *Beudanticeras* Hitzel, 1902, the sole genus in the Family Beudanticeratidae.

The *Beudanticeras haydeni* studied herein were collected near the junction of Huling Creek and North Fork of Cottonwood Creek, near Ono, Shasta Co, California (Figure 1).

2. Systematic paleontology

Conventions. Dimensions are given in millimeters: D = diameter; W = whorl breadth; H = whorl height; U = umbilicus. We follow the descriptive categories established by Rodda and Murphy (2022).

Specimens examined are housed in the following collections:

UCLA University of California, Los Angeles (Now at CASG).

CASG California Academy of Sciences, Geology Collection.

CS Clarence Schuchman at CASG

GSC Geological Survey of Canada

LACMIP Los Angeles County Museum, Invertebrate Paleontology Collection.

MNHNP Muséum National d'Histoire Naturelle de Paris

UCMP University of California, Berkeley, Museum of Paleontology

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

Order Ammonitida Zittel, 1884
Suborder Ammonitina Hyatt, 1889
Superfamily Desmoceratoidea Zittel, 1895
Family Beudanticeratidae Breistroffer, 1953
(*nomen translatum* herein, *ex* Beudanticeratinae Breistroffer, 1953)

Diagnosis. Same as for *Beudanticeras*.

Genus *Beudanticeras* Hitzel, 1902

Synonomy

1902 *Beudanticeras* Hitzel, p. 875.
1923 *Beudanticeras,* Hitzel, 1905 (sic), Spath, p. 49 (pars).
1932 *Beudanticeras* Hitzel, 1902, Seitz, p. 392 (pars).
1960 *Beudanticeras* Hitzel, 1905 (sic), Murphy and Rodda, p. 851.
1979 *Beudanticeras* Hitzel, 1902, Scholz, p. 68.
1988 *Rapidoplacenticeras* Alabushev, p. 110.

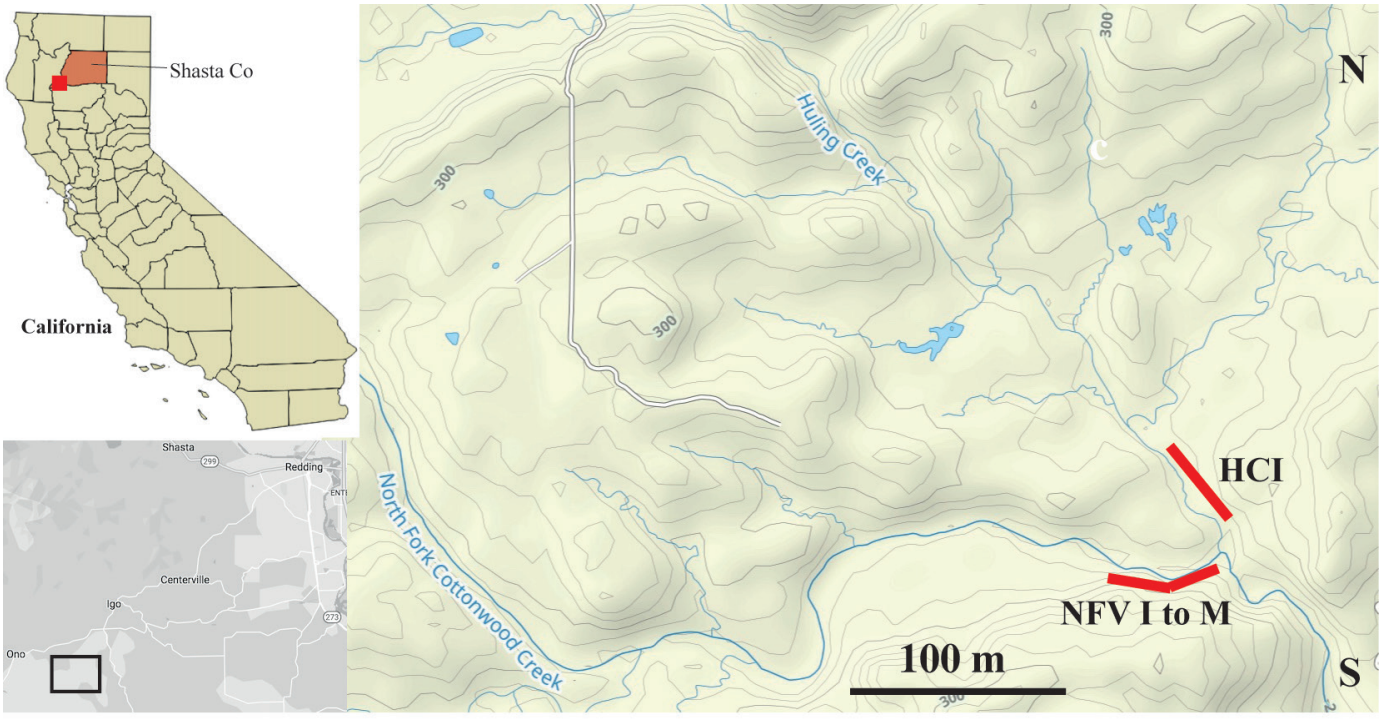

Figure 1. Map of the studied area, with location of the sections that yielded *Beudanticeras haydeni* (Gabb, 1864).

1993 *Beaudanticeras* Hintzel, 1905 (sic), Kennedy, p. 235.

2002 *Beudanticeras* Hitzel, 1905 (sic), Riccardi and Medina, p. 299 (pars).

Type species. *Ammonites beudanti* Brongniart, 1822 (in Cuvier and Brongniart, p. 95, 99, 394) by original designation and tautonomy.

Generic diagnosis. Involute, discoidal, gradumbilicate shells with falcoid growth lines, ornament of ribs on the outer flank, and a suture line with broad, strongly asymmetrical bifid L with E shorter than L.

Discussion. *Beudanticeras* has long been associated with the Desmoceratidae, an assignment that needs to be changed, because the diagnostic characteristics of the type species, *B. beudanti,* (lack of constrictions, suture with strongly asymmetrically bifid L, gradumbilicate shell) excludes it from the Desmoceratidae. We propose to consider *Beudanticeras* as the sole genus of Beudanticeratidae

Beudanticeras Hitzel as emended by Spath (1923) is based on a specimen in the collection of the Muséum National d'Histoire Naturelle, Paris (MNHN-F-J07792), from Rochers de Fiz, Haute-Savoie, France designated as the lectotype by Spath (1923, p. 49; Kennedy, 1993, p. 237). Examination of the figure of the lectotype (Kennedy, 1993, fig. 2) and other specimens from the type region in the Delamette Collection at the Muséum d'Histoire Naturelle, Geneva and the Muséum d'Histoire Naturelle, Paris shows that the lectotype and remaining specimens have neither the constrictions nor collars typical of desmoceratids. Only a single specimen in the Geneva collection shows a constriction and that specimen shows only one on one side of the specimen (the feature on this specimen is regarded as an aberrant variant unrelated to the genetics of the Desmoceratidae). The umbilical edge is acutely rounded or angular and the umbilical wall steep, but not perpendicular to the flank. The ornamentation of most specimens is confined to spaced, crescent-shaped ribs on the outer flank that do not cross the venter. Falcoid growth lines rather than sigmoidal or biconvex ones typical of desmoceratids are present, a distinctive suture line with an asymmetrically bifid L as opposed to the trifid L in typical desmoceratids (Jacob, 1908, fig. 14; Spath, 1923, fig. 12c; Seitz, 1932, fig. 1; Wright, 1957, fig. L482-2c), and an E shorter than L. To our knowledge, the ontogenetic development of the suture line of *B. beudanti* has been reported only by Jacob (1908, fig. 10) and Schindewolf (1966, Figs. 383, 384). In both cases, the specimens used by these authors are not correctly identified. The suture figured by Jacob (1908, fig. 10) has been drawn on an unidentified ammonite from La Balme de Rencurel (Isère, France). The age of this condensed level is lower Albian to basal middle Albian (Breistroffer, 1931) and the ammonite used by Jacob should be assigned to some species of the new genus described below. The material figured by Schindewolf, 1966) comes from the condensed Albian of Escragnolles. The age of Escragnolles material is lower to basal upper Albian but *B. beudanti* has never been reported from Escragnolles, even in the very detailed study of Gebhard (1979). A suture drawn from a juvenile specimen of *B. beudanti* from Entrèves-en-Bauge (Savoie, France), with a whorl height of 7 mm (Figure 2a), clearly shows that L is more strongly asymmetrical than the L of Jacob's figure at a similar size.

Two of us accepted Spath's (1923, p. 50) interpretation of this genus (Murphy and Rodda, 1960) and we all feel his analysis of its history, particularly Jacob's (1908) misidentification of the type species, *Beudanticeras beudanti* (Brongniart) is correct. However, most of the taxa he has placed in the genus are distinct from *Beudanticeras* and should be assigned elsewhere.

Two types of discoidal conchs have traditionally been assigned to *Beudanticeras*: Those without constrictions and with an elaborate suture with a bifid, strongly asymmetrical L that undercuts E, and those with constrictions and with a simpler suture with a trifid, weakly asymmetrical L that does not undercut E. These forms are considered here as convergent with regard to shell shape and, in some cases, suture pattern. We regard the presence or absence of constrictions as an important and relatively common indicator of taxonomic affinity, whereas, gradumbilicate is a relatively rare condition in ammmonites. None of the constricted types has that kind of umbilicus. The first kind, exemplified by *B. beudanti*, ranges from early to late Upper Albian. The latter by "*Beudanticeras*" (of authors) ranges from just above the base of Lower Albian to early Middle Albian (Casey, 1961, Owen, 1988, Kennedy, 2000). As interpreted in the literature, the Upper Albian and the Lower-Middle Albian *Beudanticeras* are separated by a significant morphological and stratigraphical gap (Robert *et al.*, 2001, Robert, 2002, Bulot, 2010).

The Lower-basal Middle Albian morphologies with rounded umbilical shoulder, presence of constrictions at some stage in the ontogeny, a wider venter and a simpler suture, with no overlap, and with lower saddles that were previously assigned to the genus, are here placed within the new genus *Roberticeras*, type species *Ammonites dupinianus* d'Orbigny, 1841, p. 276, pl. 81, figs 6-8 (see Appendix 2). This genus is named after Emmanuel Robert (University of Lyon, France) who first adressed that issue.

The new genus *Roberticeras* is classified as a member of the new desmoceratid subfamily Uhligellinae (see Appendix 2), which includes ammonites with constrictions, and with a simpler suture line characterized by a symmetrical to feebly asymmetrical trifid L. This subfamily also includes the genera *Zuercherella* Casey, 1954; *Uhligella* Jacob, 1907; and *Pseudorbulites* Casey, 1961.

We assign to the new genus the following taxa:

Beudanticeras albense Breistroffer, 1947;

Beudanticeras ambajabense Collignon, 1963;

Beudanticeras ampanihense Collignon, 1963;

Beudanticeras arduennense Breistroffer, 1947;

Beudanticeras caseyi Collignon, 1963;
Ammonites cesticulatus d'Orbigny, 1841;
Ammonites dupinianus d'Orbigny, 1841, p. 276, pl. 81, figs 6, 8;
Desmoceras Dupinianum var. *Africana* – Pervinquière, 1907;
Beudanticeras (*Beudanticeras*) *dupinianum evolutum* Casey, 1961;
Beudanticeras dupinianum percostata Collignon, 1963;
Beudanticeras dupiniforme Collignon, 1963;
Beudanticeras hirtzi Collignon, 1950;
Beudanticeras hourcqi Collignon, 1949;
Beudanticeras komihevitraense Collignon, 1950;
Ammonites laevigatus J. de C. Sowerby, 1827;
Beudanticeras newtoni Casey, 1961;
Ammonites parandieri d'Orbigny, 1841;
Beudanticeras perchoisense Destombes, 1979;
Beudanticeras rectisulcatum Collignon, 1936;
Beudanticeras revoili Pervinquière, 1907;
Beudanticeras Sanctae-Crucis Bonarelli, 1921;
Beudanticeras subrotundum Collignon, 1963.

The synonymies given by Riccardi and Medina (2002), based on morphological resemblances between taxa that mostly come from condensed levels, are to be reconsidered. This stock is very probably polyphyletic and is needs further investigation and revision. The characteristics enumerated above separate *Beudanticeras* from all described taxa, for example *Brewericeras* Casey (Murphy and Rodda, 1960, p. 851). In particular, *Cleoniceras* is similar in gerontic shell shape, has an asymmetrically bifid suture, and smooth venter with ribs that do not cross the venter as in *Beudanticeras*. However, these differences are offset or insignificant when the details are reviewed. The ornamentation in *Cleoniceras* is weak on the middle flank and strong on the inner and outer flanks with well-developed bullae near the umbilical edge in the immature ontogenetic stages. The gerontic specimens of both taxa are smooth. The umbilicus meets the flank wall at an obtuse angle rather than a right angle as in *Beudanticeras.*

D'Orbigny's (1842, pl. 84) rendition of the suture line of *Cleoniceras cleon*, which was reproduced by Wright (1957, p. L393, fig. 2) has a narrow, symmetrically trifid L. However, Jacob (1908, p. 57, fig. 44, reproduced in Spath, 1923, p. 92, fig. 19) figures a different L for *C. cleon*, as does Casey (1966, p. 556, fig. 211). In both the latter cases, the L is broad, complexly incised, and markedly bifid. Spath (1923, p. 92) regards this type of suture as a convergent character that occurs in a number of unrelated genera. However, as mentioned above, this does not have to be the case and he gives no evidence for this interpretation. Although it can be described as bifid, it does not resemble the suture of *Beudanticeras beudanti* or *B. haydeni*.

The suture line in oxyconic ammonites that arise out of clades with more equant whorl shapes compensate for the loss of shell strength accompanying the change in several ways. Some have stretched the existing suture to cover a broader area, others have added lobes, and some have just developed more complex patterns in the existing elements. Because the problem is the same for this kind of change in shell shape, the solution may be similar in unrelated clades and the resulting characters are convergent. Convergence is an interpretation, which may be accurate in some clades, but inappropriate for others. It seems to us that when taxa show several similarities in the morphology of unrelated structures or parts, convergence is the less likely as the number of similarities increases.

In the present case, the differences between the genotypes of the two genera are 1) the depth of the E in *B. beudanti* is about equal to one half of the L, in *C. cleon* E is about equal L; 2) the L undercuts E in B. *beudanti*, but does not in *C. cleon*; 3) *B. beudanti* has no umbilical bullae, whereas *C. cleon* does; 4) *B. beudanti* is gradumbilicate, *C. cleon* umbilicus has a broadly rounded umbilical edge. Ribs when developed in *C. cleon* are sigmoidal, present on the inner flank and may be bullate and may bifurcate at the bullae. In *B. beudanti*, the ribs and are distinctively half-moon shaped and confined to the outer flank. The growth lines in both species are parallel to the margin of the aperture but is sigmoidal in *C. cleon* and falcoid in *B. beudanti*. Neither species consistently has constrictions, although one partial constriction has been observed on one specimen in over 60 of *B. beudanti* in the collection at the Museum of Natural History, Geneva from the type locality, Rochers de Fiz. We see no relation of *Beudanticeras* to other Albian taxa, and it is the sole genus of the Beudanticeratidae.

Alabushev (1988, p. 56) designates *Proplacenticeras sutherlandbrowni* McLearn as the type species of his new genus *Rapidoplacenticeras*. *Proplacenticeras sutherlandbrowni* McLearn is herein considered as a poorly known species of the genus *Beudanticeras* (see below) and consequently, *Rapidoplacenticeras* is a junior synonym of the genus *Beudanticeras*.

Beudanticeras flindersi (McCoy, 1865, p. 334), figured by Etheridge (1892, p. 494, pl. 30, fig. 2, and Whitehouse, 1928, pl. 25, figure 3), from Coolibah, Hughenden, Queensland, Autralia, ?Wallumbilla Formation, and *Beudanticeras mitchelli* (Etheridge, 1872, p. 345, pl. 3, fig. 1, lateral and aperture views) [refigured by Etheridge Jr., 1892, pl. 30, figs 1, 2 and by Whitehouse, 1928, pl. 25, fig. 2 (lectotype)], from Hughenden, Queensland, Autralia, ?Allaru Mudstone, respectively 150 and 128 mm in diameter, shows sigmoidal ribs that seem to be associated with shallow constrictions and low whorl section. Day (1968, unpublished) has claimed that both *Beudanticeras flindersi* and *Beudanticeras mitchelli* are contemporaneous with *Boliteceras daintreei*, which occurs in the Lower Albian, while McKenzie gives a middle Albian age. *B. mitchelli* is probably a junior synonym of *B. flindersi* and is very probably not related to the genus *Beudanticeras*. The holotype of

Beudanticeras flindersi (McCoy, 1865) (n° P.2185, Museums Victoria Collections, Australia), from the base of Walker's Table Mountain, West Bank, Flinders Range, Queensland, is a specimen about 145 mm in diameter, comprising the phragmocone and a 180° sector of body chamber (D: 108 – H: 54 (.50) – W: 36 (.33) – U: 23 (.21) – W/H: .66). The inner whorls almost smooth, with almost inconspicuous fine ribbing on the flanks when the shell is preserved. Constrictions may occur on the adult but are inconspicuous. Fine, almost inconspicuous biconcave ribs can be observed on the body chamber. This specimen seems to differ from *Boliteceras daintreei* only by its more compressed whorl section and by its feebler ornament. According to Day (1968, unpublished thesis), *Desmoceras* (?) sp. in Whitehouse (1928, p. 200, pl. 26, fig. l) is a juvenile of *B. flindersi*.

At present we assign only four species to the genus: *B. beudanti* Brongniart, *B. haydeni* Gabb and *B. sphaerotum* (Seeley 1866), and *B. sutherlandbrowni* (McLearn, 1972). *B. sphaerotum* we retain as a species provisionally on the basis of Spath's (1923, p. 54) statement that some consistent differences exist between the population from Hunstanton and those from Folkstone. Seitz (1932) also reached this conclusion, although he included much more in the genus than we would admit. Scholz (1979, p. 68) prefers to unite *B. beudanti* and *B. sphaerotum*.

Thus restricted the genus ranges through The *Dipoloceras cristatum* Zone to the *Mortoniceras* (*Mortoniceras*) *inflatum* Zone in western Europe. Scholz (1979) reports it also from the *Mortoniceras* (*Mortoniceras*) *fallax* Zone of Hungary.

In California, well-dated *B. haydeni* occur in the *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone and the *Mortoniceras* (*Subschloenbachia*) *perinflatum* Zone in the Dry Creek section (Murphy and Rodda, 1996; Amédro and Robaszinsky, 2005) and possibly in the *Mortoniceras* (*Mortoniceras*) *fallax* Zone, into the interval that also yields *Stoliczkaia dispar* var. *notha*.

Beudanticeras haydeni (Gabb, 1864)
Figures 2b, 3a-c, 4a-f, 5a-d, 6a-c, 7a-d, 8

Synonymy.

1864 *Ammonites haydeni* Gabb, p. 62, pl. 10, fig. 8.
1910 *Desmoceras haydeni* (Gabb); Grabau and Shimer, p. 171, fig. 1419.
1938 *Beudanticeras haydeni* (Gabb); Anderson, p. 190 (pars), non pl. 48, figs. 2, 3 (= *Brewericeras hulenense* Anderson 1938).
Non 1943 *Desmoceras haydeni* Gabb; Hanna and Hertlein, p. 168, fig. 61-8 (= *Brewericeras hulenense* Anderson, 1938).
1956 *Beudanticeras haydeni* (Gabb); Murphy, p. 2119, fig. 6.
1958 *Beudanticeras haydeni* (Gabb); Anderson, p. 212 (pars), non pl. 8, figs. 1 (= *Brewericeras hulenense* Anderson, 1938).
1960 *Beudanticeras haydeni* (Gabb); Murphy and Rodda, p. 851, pl. 104, fig. 4; pl. 105, figs. 1, 2.
1996 *Beudanticeras haydeni* (Gabb); Murphy and Rodda, p. 244-245, fig. 5 (A).

Holotype. UCMP 14973, *Ammonites haydeni* Gabb (1864, pl. 10, fig. 8), North Fork of Cottonwood Creek. This specimen was known only from the original drawing by Gabb and is herein figured for the first time (Figures 2b, 3a–c).

N°	D	H	W	U	W/H
UCMP14973	95.0	54.0 (.57)	24.0 (.25)	15.0 (.16)	0.44

The specimen has an estimated diameter of 105 mm, comprising the phragmocone and a 30° sector of body chamber. It is preserved as an internal mold retaining some parts of aragonitic shell. The coiling is involute (U/D = 0.16), the whorl section is compressed (W/H = 0.44), and sub-elliptical with of maximum of width at the inner third of the flanks. The flanks are slightly convex, converging to a narrowly convex venter. The umbilical wall is low, vertical and slightly concave. The umbilical shoulder is sharp to extremely narrowly rounded. There is no visible ornamentation. It can be seen that the suture figured by Gabb (1864, pl. 10, fig. 8c) and reproduced herein (Figure 2b), which has been drawn from a poorly preserved suture line with overlapping septa, is wrong. The external and lateral saddles are closer to each other and the first auxiliary lobe is not so deep.

Material examined. All California specimens recorded here are from the Upper-Chickabally Member of the Budden Canyon Formation of the Cottonwood District (Murphy *et al.*, 1969).

CASG60892, from NFV-M, is a fragment of a juvenile, about 18 mm in diameter, with parts of the shell preserved (Figure 4a, b). At this stage of growth, the whorl section is compressed (W/H = 0.6), subtriangular, with a maximum width just above the umbilical edge, flattened flanks converging to a narrow convex venter. The coiling is involute, the umbilicus comprises about 16% of the diameter. The umbilical wall is deep and vertical, the umbilical shoulder is narrowly rounded. The ornament, almost inconspicuous, is made of fine, straight, prorsiradiate striae arising on the umbilical shoulder, that are projected backward at mid-flank and then forward on the outer third of the flanks and across the venter.

CASG78582 (CS2001) (Figure 5a-d) is a very well preserved juvenile phragmocone preserved as an internal mold retaining very thin parts of shell. It shows the characteristic ribbing pattern of the species, with fine, growth striae and crescent-shaped riblets on the outer part of the flanks. The internal whorls of LACM IP 9859 are identical.

N°	D	H	W	U	W/H
CASG78582	55.0	29.0 (.53)	14.0 (.25)	8.0 (.15)	0.48

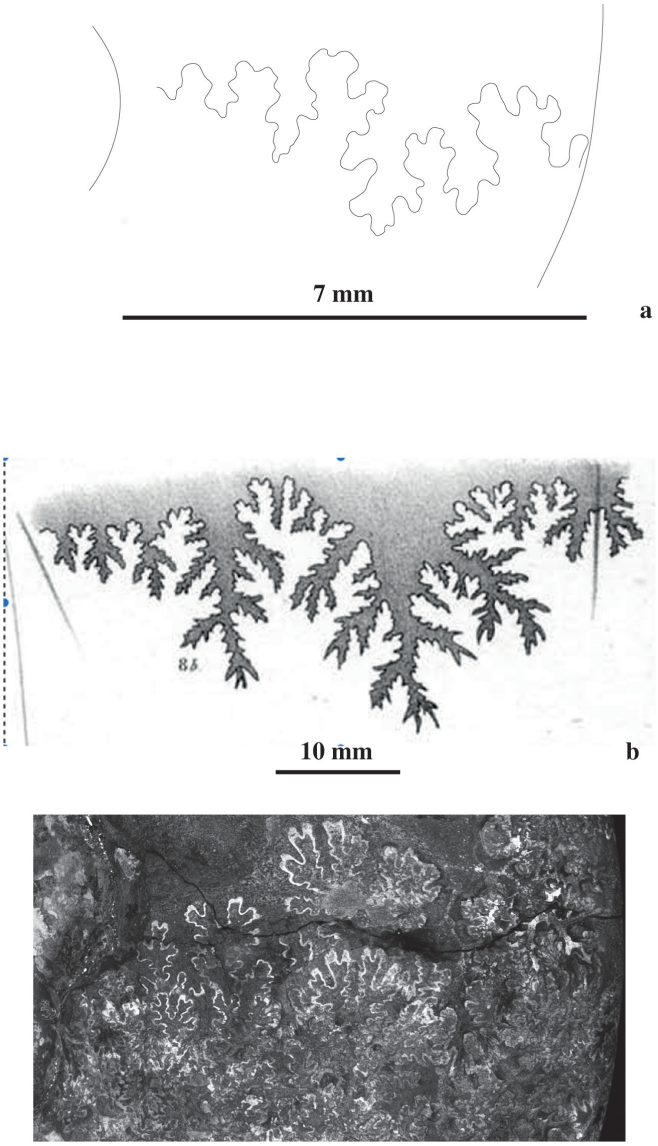

Figure 2. a, suture line of *Beudanticeras beudanti* (Brongniart, 1822), upper Albian of Entrèves-en-Bauges, Savoie, France. b, suture line of Beudanticeras haydeni (Gabb, 1864), uppermost Albian of California, the original drawing of Gabb (1964) and a photography of the same suture.

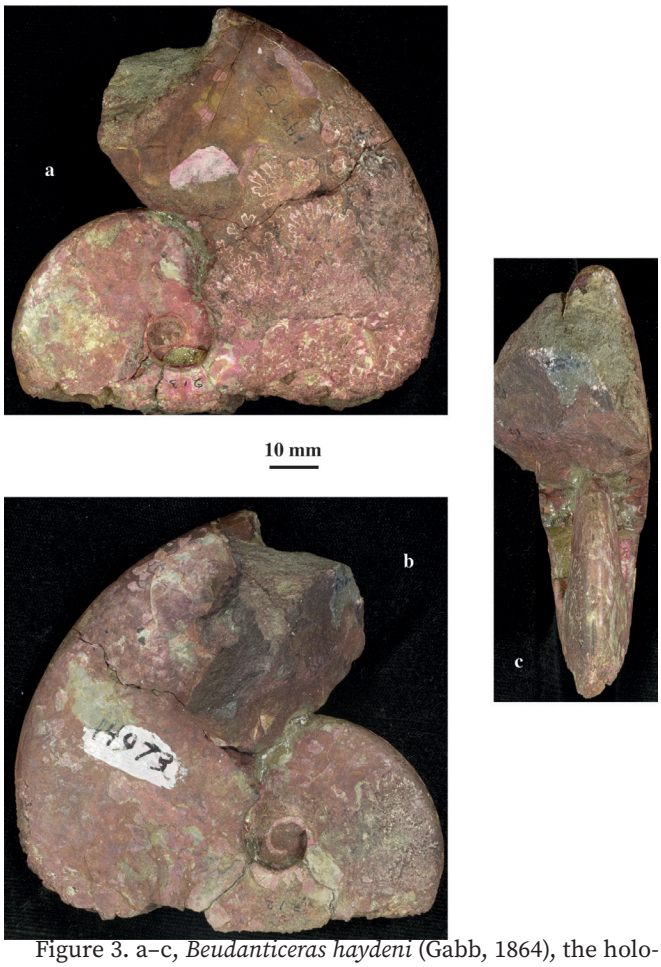

Figure 3. a–c, *Beudanticeras haydeni* (Gabb, 1864), the holotype, figured by Gabb (1864, pl. 10, fig. 8) as Ammonites haydeni, UCMP.14973, upper Albian of North Fork Cottonwood Creek, Shasta Co, California.

CASG78583 (CS1004 from NFV-K) (Figure 4f) is an incomplete juvenile phragmocone, about 65 mm in diameter, preserved as a slightly crushed internal mold with some remains of shell, showing vertical, slightly concave umbilical wall, sharp umbilical edge and flattened flanks. The ornamentation is of numerous, almost inconspicuous, fine striae.

CASG65042.01, from an unknown locality, is a fragment showing the whorl section with feebly convex flanks and narrow rounded venter (Figure 6a, b).

CASG78584 (NFV-K 86-2 below marker bed 3), (Figure 7a, b) is a distorted fragment of an internal mold, with an estimated diameter of 90 mm. There are also some large, poorly preserved fragments from NF V-K.86.2, with an estimated diameter of more than 200 mm seem to bear coarse, low sigmoidal ribs close to the aperture.

CASG78585 (CS1003) (Figure 8) is a well preserved phragmocone, about 100 mm in diameter, surrounded by a piece of crushed body chamber, for a total estimated diameter of 160 mm. The crescent-shaped ribs are well expressed on the outer part of the flanks of the phragmocone. We should note a spectacular broadening of the umbilicus on the last incomplete whorl and that in some specimens the umbilical spiral is distorted.

CASG78586 (CS 2006) (Figure 6c), from Huling Creek, 85 mm in diameter, clearly shows the angular umbilical edge.

CASG78587 (NFV I-3) is a well-preserved fragment showing the crescent shaped ribs on the upper half of the flanks rising from inconspicuous fine straight, prorsiradiate ribs on the inner half of the flanks. There are fine striae on the shell between ribs.

CASG78588 (NFVI 90-6 west chine) is a distorted fragment showing the narrow ventral area.

There are an additional ten poorly preserved fragments from the Schuchman collection at CASG.

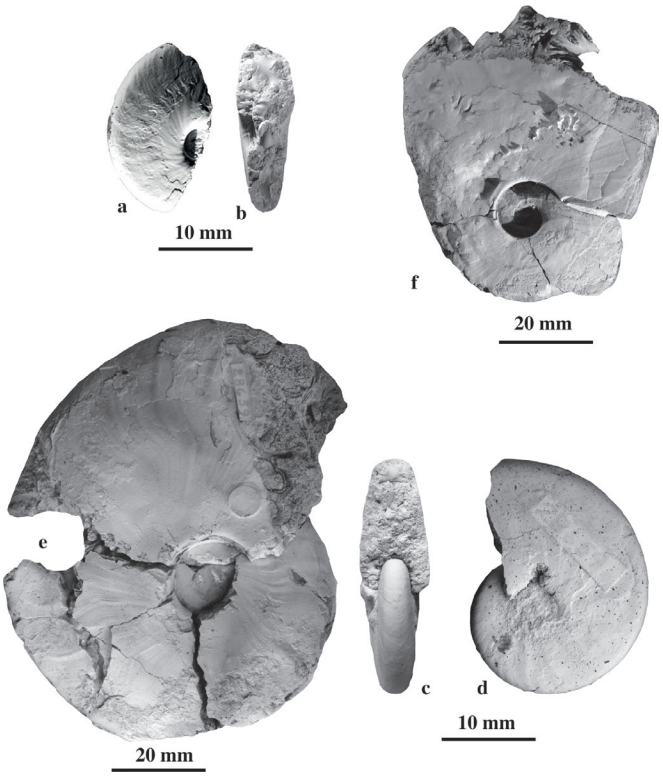

Figure 4. *Beudanticeras haydeni* (Gabb, 1864). a, b, CASG60892, NFV; c-e, LACMIP.9859; f, CASG78583.

LACMIP 9859, from loc. LACMIP 22901 (=UCLA 3467), in lowest conglomerate of the Bald Hills Member on the North Fork of Cottonwood Creek. The specimen, figured by Murphy and Rodda (1960, pl. 105, figs 1, 2), and refigured herein (Figure 4c–e), is a complete phragmocone, 82 mm in diameter, that shows the characteristic ribbing patterns and the extremely narrowly rounded umbilical shoulder on a piece of preserved body chamber.

N°	D	H	W	U	W/H
LACMIP9859	82.0	44.0 (.54)	21.0 (.26)	8.5 (.10)	0.48

LACMIP 9860, from locality LACMIP 22900 b (=UCLA 2900), Chickabally Member; Huling Creek. In conglomeratic sandstone, first sandstone downstream from junction with east fork of Huling Creek. (Murphy and Rodda, 1960, pl. 104, fig. 4) (herein refigured (Figure 7c, d), is a 90° sector of an adult phragmocone, with an estimated diameter of 105 mm that shows the suture line (Figure 7).

N°	D	H	W	U	W/H
LACMIP9860	25.0	14.0 (.56)	7.0 (.28)	? (?)	0.50

In summary, *B. haydeni* is characterized by juvenile stages with narrowly rounded umbilical shoulder and numerous prorsiradiate, falciform striae on the flanks and on the venter, by subadult stages with sharp, angular umbilical shoulder, vertical umbilical wall and sickle-shaped ribs on the outer flanks. The adult stages are not well-known but show a spectacular broadening of the umbilicus.

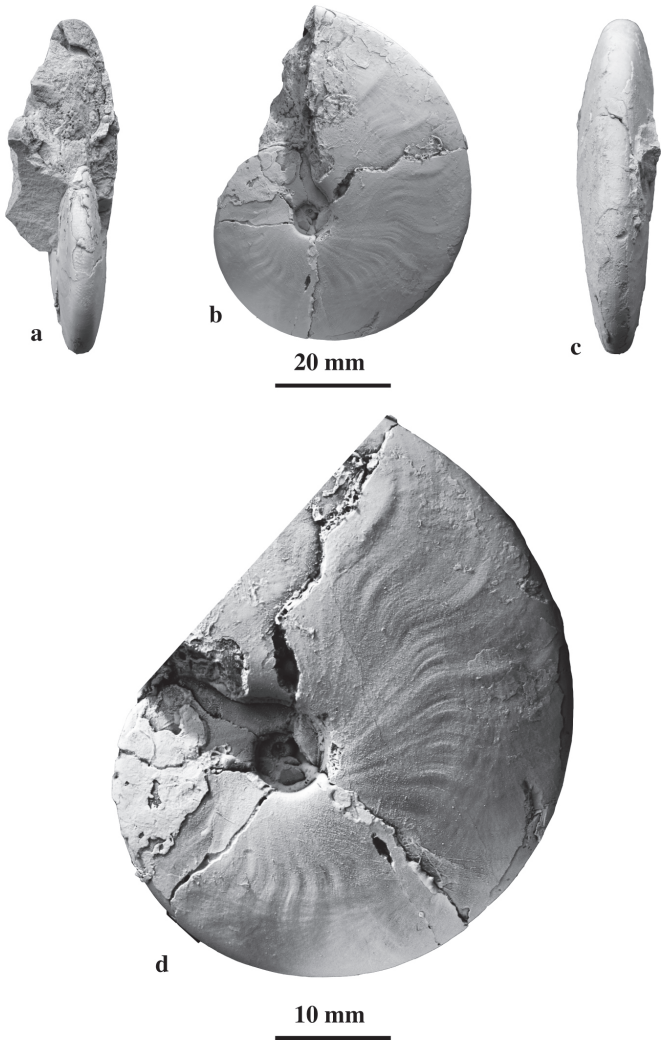

Figure 5. *Beudanticeras haydeni* (Gabb, 1864). a-d, CASG78582 (CS2001).

Discussion. *Beudanticeras* has been misinterpreted by Anderson (1938 and 1958). As pointed out by Murphy & Rodda (1960, p. 851), the specimens figured by Anderson (1938, pl. 8, figs. 3; 1958, pl. 8, fig.1) are small specimens of *Brewericeras hulenense* (Anderson).

Proplacenticeras sutherlandbrowni McLearn (1972, p. 56, pl. 8, figs. 3A, B) is poorly known. (This posthumous work was prepared for publication by J. A. Jeletzky from a nearly complete MS.) Only the Holotype is illustrated, and both its locality and age are in doubt. The figured specimen is a half whorl of an adult phragmocone with a compressed, high, oval, whorl section having maximum width at mid-flank. The slightly convex flanks converge to a narrowly rounded venter. The umbilical wall is high, steep, with a narrowly rounded, almost angular umbilical shoulder. No ornamentation is visible. The highly indented and interlocking suture line shown in the photograph is similar to the suture of *Beudanticeras beudanti* as figured by Spath (1923, p. 51, text-fig. 12c), with wide and deep asymmetrical lateral

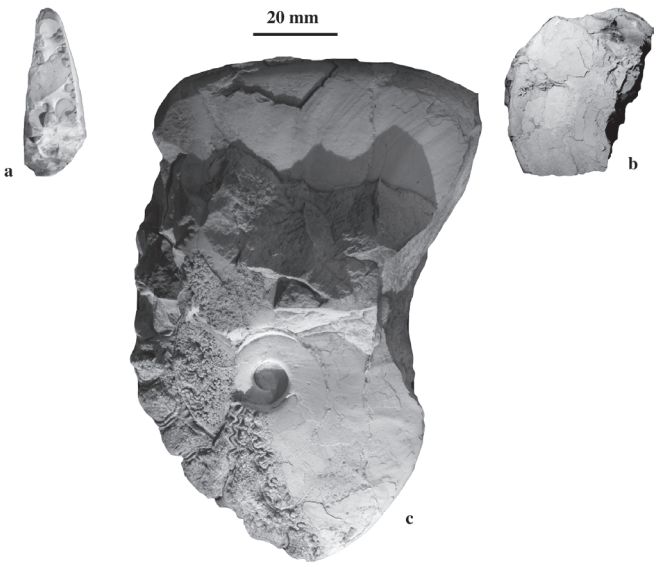

Figure 6. *Beudanticeras haydeni* (Gabb, 1864). a, b, CASG78582; c, CASG78586 (CS.2006), from Huling Creek.

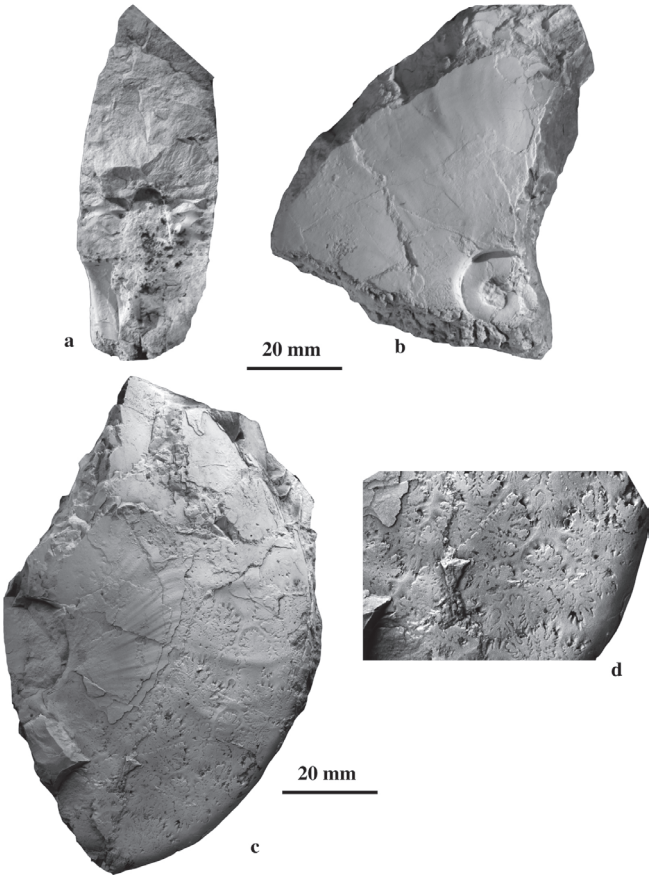

Figure 7. *Beudanticeras haydeni* (Gabb, 1864). a, b, CASG78584 from NFV-K.86-2; c, d, LACMIP.9860, from Huling Creek.

lobe, undercutting the external saddle. McLearn (1972, p.57) notes that 'this species is not a true *Proplacenticeras* and may be a new genus'. But, as Jeletzky notes on p. 56, "In the MS explanation of Pl. VIII, figs. 3a, b, McLearn has crossed out the generic name *Proplacenticeras* and replaced it by *Beudanticeras*." McLearn (1972, p. 56-57) notes that "most" specimens collected for this paper are from a high level in the Sandstone Member of the Haida Formation, at localities A11 and A15 (p. 7). These "Localities" includes several hundred feet of undescribed section for which a few ammonites are listed, including *P. sutherlandbrowni*, and two informal species of *Mortoniceras* similar to *M. pricei* (McLearn, 1972, p. 70-71, pls. 24-27). The age of the Haida specimens, and the Holotype is probably equivalent to the *Mortoniceras* (*M.*) *pricei* or *M.* (*M.*) *inflatum* Zone, the lower part of the Upper Albian, which would make *P. sutherlandbrowni* older than *B. haydeni*, though they are morphologically very close.

It should be noted that the material described as *Rapidoplacenticeras sutherlandbrowni* (McLearn, 1972) by Alabushev (1988, p. 56) from the Upper Albian-Lower Cenomanian of north-east Russia, comes from a higher stratigraphic level. It differs from the Canadian species by its narrower umbilicus, its more compressed and triangular whorl section, its flattened flanks and its more complex saddle L/E which is characteristic of the Placenticeratidae. The specimen described and figured as *Rapidoplacenticeras sutherlandbrowni* (McLearn, 1972) by Alabushev (1988, p. 56 pars, fig. 1, 2), Alabushev and Alabusheva (1988, p. 28, pl. 2, fig. 9); Alabushev and Wiedmann (1994, fig. 4H) and Alabushev (1995, p. 134, figs 11E-I) is placed within the genus *Proplacenticeras* Spath, 1926 (Jagt-Yazikova, 2011) and is renamed here *Proplacenticeras alabushevi nov. nom.* (holotype: specimen number.2060/4 in Alabushev (1988, fig. 1) (Zoobank Identification number: urn:lsid:zoobank.org:act:96B27619-6E26-4B89-8EFC-640EC229D19F).

Comparison of the Californian specimens with the holotype of *Beudanticeras beudanti* from Montagne de Fiz, France is difficult because of the distortion of the French specimen and its preservation as an internal mold. The specimen figured by Spath (1923, pl. 2, fig. 4), and the material from Entrèves-en Bauges herein figured (Figure 9a-h) are better standards for comparison. We earlier maintained the separation of *B. beudanti* and *B. haydeni* on the basis of a slightly more rounded venter and more numerous peripheral ribs in *B. haydeni*. With more material, it is evident that *B. beudanti* differs from *B. haydeni* in several respects:

The ribs that are less numerous in *B. beudanti* and not sickle-shaped as in *B. haydeni* and flexuous in *B. beudanti*;

The ornament that disappears earlier in the ontogeny in *B. beudanti*;

The sharp, angular, umbilical shoulder and the vertical wall in *B. haydeni* as opposed to the inclined umbilical wall and acutely rounded umbilical shoulder in *B. beudanti*, especially in the subadult stages;

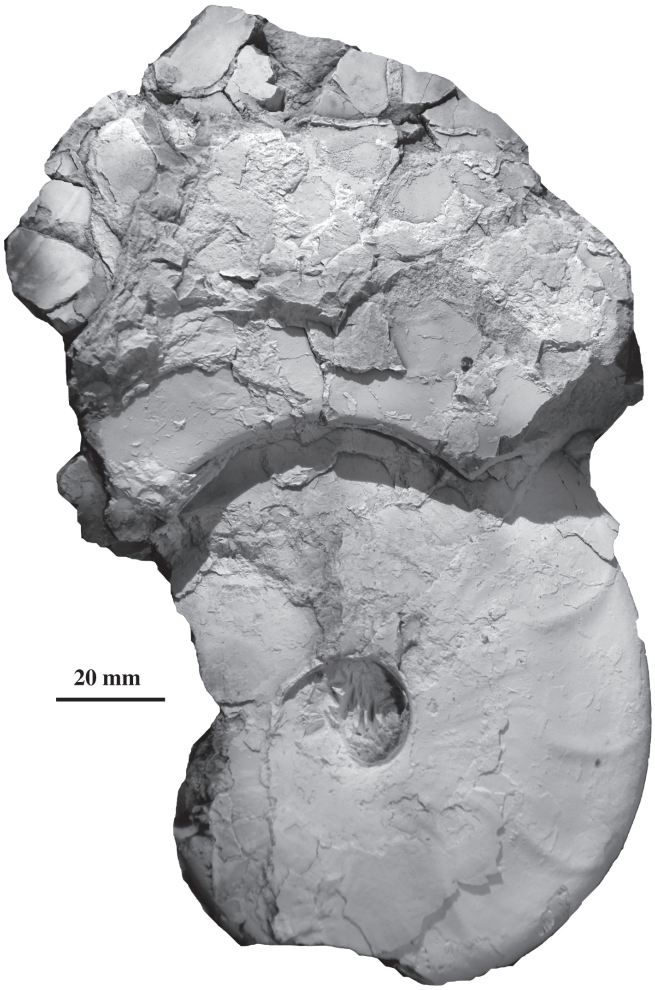

Figure 8. *Beudanticeras haydeni* (Gabb, 1864). CASG78585 (CS.1003)

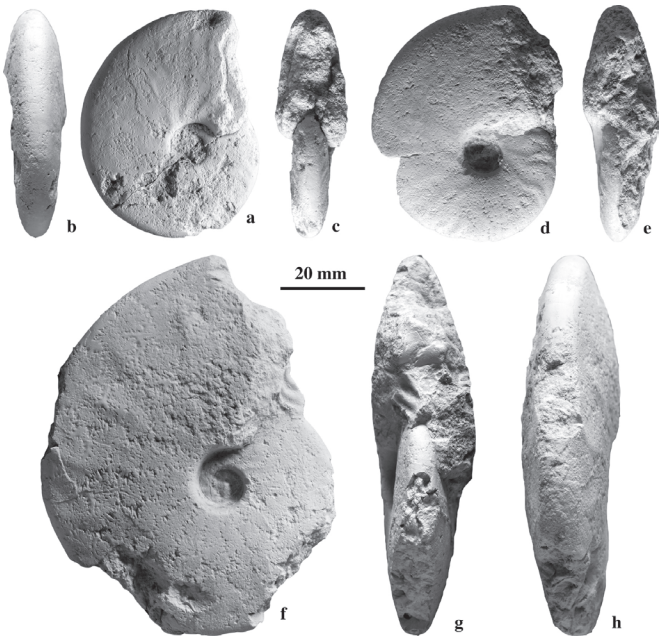

Figure 9. *Beudanticeras beudanti* (Brongniart, 1822). a-c, UJF-ID.15254. d, e, UJF-ID.15255. f-h, UJF-ID.15256. All from the upper Albian of Entrèves-en -Bauges, Savoie, France.

These differences support the separation of the two species.

B. beudanti is known from the Upper Albian of Europe (*Dipoloceras cristatum, Mortoniceras pricei* and *Mortoniceras inflatum* zones). Kennedy and Hancock (1976, p. v-8, v-9) record it from the lower three subzones of the upper Albian (*cristatum, orbignyi,* and *varicosum* Subzones) in England and northern France. It has been reported with certainty from the Upper Albian of England and France by numerous authors, Hungary (Szives, 2007), Italy (Wiedmann and Dieni, 1968), Morocco (Robert and Latil personal data) and Iran (Seyed-Emami and Immel, 1995 and 1996). The presence of the species in Germany (Gümbel, 1888), Switzerland (Tajika *et al.*, 2017), and Crimea (Milaschevich, 1877) needs to be confirmed. The only one report of *B. beudanti* from the uppermost Albian (Scholz, 1979) needs confirmation. Breistroffer (1947, p. 54) remarks that *Beudanticeras* is one of the genera that completely disappears before the 'Vraconnian' [Post *Mortoniceras* (*Mortoniceras*) *inflatum* Zone], but he qualifies that statement paranthetically by saying "at least in Europe".

Distribution. *Beudanticeras haydeni* ranges through approximately the upper half of the Upper Albian (in the North Fork section from NF V-I through most of NFV-M), or from the *Mortoniceras* (*Subschloenbachia*) *rostratum* Zone into the *Mortoniceras* (*Subschloenbachia*) *perinflatum* Zone. It should be noted that in Dry Creek section Amédro and Robaszynski (2005, Fig. 5) indicate that *B. haydeni* extends from well below Marker Bed 1, with no definite lowest occurrence indicated, up to a little below Marker Bed 6, definitely above *M. perinflatum*, but *B. haydeni* has never been reported below Marker Bed 1. Moreover, the presence in the *Mortoniceras* (*Mortoniceras*) *fallax* Zone, into the interval that also yields *Stoliczkaia dispar* var. *notha* is not fully documented.

The specimen figured by Murphy & Rodda (1960, pl. 10, fig. 4), and herein refigured (Figure 7c, d) was assigned to the Middle Albian by Murphy and Rodda (1960, p. 851), which is a mistake. This specimen comes from UCLA locality 2900: Chickabally Member; Huling Creek. In conglomeratic sandstone, first sandstone downstream from junction with east fork of Huling Creek. The age of this locality is without question uppermost Albian.

Appendix 1: Synonymy of other species assigned to the genus Beudanticeras.

Beudanticeras beudanti (Brongniart, 1822)
(Figures 2a, 9a–h)

We include here only the figured specimens in the literature that could be assigned to *Beudanticeras beudanti*.

The other citations have been removed (see Klein and Vašíček, 2011).

1822 *Ammonites Beudanti* Brongniart, p. 95, 99, 394, pl. 7, fig. 2.
1847 *Ammonites Beudanti* Brongniart Quenstedt, p. 222, pl. 17, fig. 10.
?1877 *Haploceras Beudanti* (Brongniart); Milaschevich, p. 116, pl. I, fig. 4, 5.
?1888 *Desmoceras Beudanti* (Brongniart); Gümbel, pl. 437, fig. 2.
1913 *Desmoceras Beudanti* Brong. var. *Jacobi* Heim, p. 286.
1923 *Beudanticeras beudanti* (Brongniart); Spath, p. 49, pl. 2, fig. 4a-d, text-fig. 12a-c.
?1923 *Beudanticeras beudanti* var. *ibiciformis* Spath, p. 51, pl. 2, fig. 4e, f
1932 *Beudanticeras beudanti* (Brongniart); Seitz, p. 409, 410, pl. 17, fig. 3 (=specimen Quenstedt, 1847, pl. 17, fig. 10)
1961 *Beudanticeras beudanti* (Brongniart); Casey, text-fig. 46a-c (=Spath, 1923, pl. II, fig. 4a, b, text-fig. 12c)
?1967 *Beudanticeras beudanti* (Brongniart); Collignon, p. 15, pl. 3, fig. 1.
1967 *Beudanticeras beudanti* (Brongniart); Cox *et al.*, pl. 63, fig. 4.
?1968 *Beudanticeras beudanti* (Brongn.); Wiedmann and Dieni, p. 128, pl. 11, fig. 10.
?1979 *Beudanticeras beudanti* (Brongniart); Scholz, p. 68, pl. 13, fig. 1, 6; text-fig. 21.
?1980 *Beudanticeras beudanti* (Brongniart); Thomel, p. 124, fig. 247
?1983 *Beudanticeras beudanti*; Van Diggelen, text-fig. 26
1988 *Beudanticeras beudanti* (Brongniart); Owen, fig. 43F (=Casey, 1961, text-fig. 46c)
1993 *Beaudanticeras beaudanti* (Brongniart)(sic); Kennedy, p. 233, text-figs. 1-2.
1995 *Beudanticeras beudanti* (Brongniart); Seyed-Emami and Immel, p. 388, fig. 30.
1996 *Beudanticeras* (*Beudanticeras*) *beudanti* (Brongniart); Wright *et al.*, p. 81, fig. 62: 1a, 1b, 1c (=Casey, 1961, text-fig. 46a-c).
1996 *Beudanticeras beudanti* (Brongniart); Seyed-Emami and Immel, p. 11, pl. 1, fig. 4-7; ?pl. 2, fig. 4; pl. 6, fig. 5, 6.
1997 *Beudanticeras beudanti* (Brongniart); Delamette *et al.*, pl. 14, fig. 8, pl. 18, fig. 3, pl. 38, fig. 4.
2007 *Beudanticeras* (*Beudanticeras*) *beudanti* (Brongniart); Szives, p. 54, 97, pl. 1, fig. 8; pl. 19, fig. 1; pl. 21, fig. 1; pl. 25, fig. 2, 6 only.
2008 *Beudanticeras beudanti* (Brongniart); Joly and Delamette, fig. 8A.
2010 *Beudanticeras* (*Beudanticeras*) *beudanti* (Brongniart); Matrion, p. 128, fig. 96B-E.
2011 *Beudanticeras beudanti* (Brongniart); Klein and Vašíček, p. 124.
?2017 *Beudanticeras* cf. *beudanti* (Brongniart); Tajika *et al.*, p. 32, figs X-AA, AL, AM.

Lectotype. MNHN-F-J07792, the specimen designated by Spath (1923, p.49), from Rochers des Fiz, Haute-Savoie, France, refigured by Kennedy (1993, fig. 2).

Beudanticeras sphaerotum (Seeley, 1866)

1866 *Ammonites sphaerotus* Seeley, p. 175.
1923 *Beudanticeras sphaerotum* (Seeley); Spath, p. 53, pl. 3, fig. 1.
1932 *Beudanticeras sphaerotum* (Seeley); Seitz, p. 409, 410, text-fig. 1b.

Holotype. The specimen figured by Spath (1923), pl. 3, fig. 1, from the Red Chalk of Hunstanton, England, Sedgwick Museum.

Beudanticeras sutherlandbrowni (McLearn, 1972)

1972 *Proplacenticeras sutherlandbrowni* McLearn; p. 56, pl. 8, fig. 3.
1988 *Rapidoplacenticeras sutherlandbrowni* (McLearn, 1972); Alabushev, p. 56 pars.
Not 1988 *Rapidoplacenticeras sutherlandbrowni* (McLearn, 1972); Alabushev, figs 1, 2.
Not 1988 *Rapidoplacenticeras sutherlandbrowni* (McLearn, 1972); Alabushev and Alabusheva, p. 28, pl. 2, fig. 9.
Not 1994. *Rapidoplacenticeras sutherlandbrowni* (McLearn, 1972), Alabushev and Wiedmann, fig. 4H.

Holotype. The specimen figured by McLearn (1972, pl. 8, fig. 3) from Fleury Island?, GSC 21227. The species very probably occurs in the Lower Sandstone Member of the Haida Formation in Bearskin Bay, Queen Charlotte Islands, Canada, above the base of the Upper Albian.

Appendix 2: Supraspecific classification of the new subfamily Uhligellinae.

Family Desmoceratidae Zittel, 1895
Subfamily Uhligellinae nov. subfamily

Zoobank identification number. urn:lsid:zoobank.org:act:748CA7CB-7B89-4358-8863-3E0DA5C7B315

Diagnosis. Desmoceratids with constrictions, and with a simple suture line characterized by a symmetrical to feebly asymmetrical trifid L. The subfamily Uhligellinae, as herein understood, is probably polyphyletic and brings together the genera *Zuercherella* Casey, 1954, *Uhligella* Jacob, 1907, *Pseudorbulites* Casey, 1961, *Grantziceras* Imlay, 1961, *Roberticeras* Latil, Murphy and Rodda, 2023, *Leconteites* Casey, 1954, *Brewericeras* Casey, 1954, and provisionally *Boliteceras* Whitehouse, 1928 and *Cophinoceras* Whitehouse, 1928 [see discussion above and Latil, Murphy and Rodda (this volume)].

Genus *Uhligella* Jacob, 1907

Type species. *Desmoceras clansayense* Jacob, 1905, p. 403, by the subsequent designation of Kilian, 1907, p. 63.

Diagnosis. Modified after Wright (1996): Whorl section broadest near umbilical edge; constrictions irregular and shallow; early whorls with sinuous, rounded main ribs distinctly raised into umbilical bullae, with several intercalated ribs; outer whorls smooth.

Genus *Zuercherella* Casey, 1954
(= *Corteziceras* Etayo Serna, 1979, p. 27; type species *C. cortezi* by original designation)

Type species. *Desmoceras zuercheri* Jacob, 1906, p. 9, by the original designation of Casey, 1954, p. 112.

Diagnosis. Medium-sized high-whorled shell with oval or subquadrate whorl-section, venter narrowly rounded; constrictions shallow, sinuous; between the constrictions are several ribs. Main ribs begin slightly above or at the umbilical rim; intercalatory ribs occur only in the upper half of the flanks. Outer whorls appear to be feebly ornamented based on a single specimen.

Genus *Pseudorbulites* Casey, 1961

Type species. *Uhligella convergens* Jacob, 1908, p. 29; pl. 2, figs. 24–26, by the original designation of Casey, 1961, p. 145.

Diagnosis. Stout section and funnel-shaped umbilicus; involute coiling; few, feeble constrictions; narrowly rounded venter.

Genus *Grantziceras* Imlay, 1961

Type species. *Beudanticeras* (*Grantziceras*) *multiconstrictum* Imlay, 1960, by the original designation of Imlay, 1961, p. 56.

Diagnosis. Large-sized ammonites with numerous, regularly spaced, falciform constrictions, broadly bunded striae on the flanks, and a scaphitoid body chamber.

Genus *Roberticeras* nov. gen.

Zoobank identification number. urn:lsid:zoobank.org:act:BB8E77ED-4AFA-4395-9BFD-CAFB453898F9

Type species. *Ammonites dupinianus* d'Orbigny, 1841, p. 276, pl. 81, figs 6–8.

Diagnosis. Rounded umbilical shoulder; presence of constrictions at some stage in the ontogeny, venter rounded; simple suture, with no overlap, and with lower saddles.

Genus *Leconteites* Casey, 1954
[= *Puzosigella* Casey, 1954; *Vnigriceras* Saveliev, 1973; *V.* (*Astrodiscus*) Saveliev, 1973]

Type species. *Desmoceras lecontei* Anderson, 1902, p. 95, by the original designation of Casey, 1954, p. 110.

Diagnosis. Modified after Wright (1996): Umbilical shoulder sharply rounded to angular; primary ribs sinuous, arising singly on umbilical wall or in twos or threes from umbilical bullae, projected towards venter, weakening or disappearing at venter; secondaries branching or intercalated at midflanks; constrictions, if present, with or without collars. Suture finely or coarsely frilled.

Genus *Brewericeras* Casey, 1954

Type species. *Ammonites breweri* Gabb, 1864, p. 62, by the original designation of Casey, 1954, p. 112.

Diagnosis. Modified after Wright (1996): whorl section compressed; coiling eccentric; lack of umbilical tubercles and paired ribs, rarity of constrictions; narrow stems to saddles of suture. A derivative of *Leconteites*.

? Genus *Boliteceras* Whitehouse, 1928

Type species. *Ammonites daintreei* R. Etheridge, 1872, p. 346, pl. 24 part., by the original designation.

Diagnosis. Involute, with funnel-shaped umbilicus; and inflated whorl section, with broad, shallow, sinuous constrictions, fine, feeble ribs and broadly rounded venter. The suture, not figured, is said to have wide-stemmed saddles and regularly trifid first lateral lobe.

? Genus *Cophinoceras* Whitehouse, 1928
(= *Beudantiella* Breistroffer, 1947, p. 99)

Type species. *Cophinoceras ogilviei* Whitehouse, 1928, p. 205, pl. 26, fig. 4, by the original designation.

Diagnosis. Elliptical whorl section, narrow funnel shape umbilicus, straight prorsiradiate primary ribs (constrictions covered by the test), each pair of such ribs being separated by 8-12 short straight intercalatories. The suture is said to have wide-stemmed saddles and regularly trifid first lateral lobe.

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