Cenomanian ammonites from Santander (Cantabria) and Sopeira (Aragón, southcentral Pyrenees), northern Spain

William J. Kennedy¹ and Michel Bilotte²

Resumen

KENNEDY, W.J. y BILOTTE, M. Ammonites del Cenomaniense de Santander (Cantabria) y de Sopeira (Aragón, Pirineos centro-meridionales), España septentrional. Se describen por primera vez ammonites del Cenomaniense superior (Cretácico) de los alrededores de Santander y de Sopeira (provincia de Huesca), España septentrional. Las siguientes especies están presentes: *Tetragonites subtimotheanus* Wiedmann, 1962, *Calycoceras (Newboldiceras) asiaticum asiaticum* (Jimbo, 1894), *Calycoceras (Newboldiceras) planecostatum* (Kossmat, 1897), *Eucalycoceras pentagonum (Jukes-Browne, 1896), Eucalycoceras jeanneti* Collignon, 1937 y *Thomelites sornayi* (Thomel, 1966). Esta asociación es típica de la parte inferior del Cenomaniense superior de la zona de *Calycoceras (Proeucalycoceras) guerangeri* a excepción de *E. jeanneti*, conocido solamente de Madagascar.

Palabras clave: ammonites, Cretácico, Cenomaniense, Cantabria, Huesca, España.

Abstract

Upper Cenomanian (Cretaceous) ammonites are described for the first time from the environs of Santander (Cantabria) and Sopeira (Aragón, Huesca province) in northern Spain. The following species are present: *Tetragonites subtimotheanus* Wiedmann, 1962, *Calycoceras* (*Newboldiceras*) *asiaticum asiaticum* (Jimbo, 1894), *Calycoceras* (*Newboldiceras*) *planecostatum* (Kossmat, 1897), *Eucalycoceras pentagonum* (Jukes-Browne, 1896), *Eucalycoceras jeanneti* Collignon, 1937, and *Thomelites sornayi* (Thomel, 1966). This assemblage is typical of the lower Upper Cenomanian *Calycoceras* (*Proeucalycoceras*) *guerangeri* Zone, with the exception of *E. jeanneti*, previously known only from Madagascar.

Key words: ammonites, Cretaceous, Cenomanian, Cantabria, Huesca, Spain.

INTRODUCTION

The ammonite faunas described below have two origins (Fig. 1). The first is the material collected by Louis Mengaud in the Santander area of Cantabria during the course of his thesis research (Mengaud, 1920), housed in the collections of the University of Toulouse (UPS). The second is new collections made by one of us (MB) in the Sopeira area of Huesca province in the south-central Pyrenees. Ammonite faunas of this age are sparse; Mengaud's material is revised, while the new material is described for the first time. Both collections are characterised by an association of Eucalycoceras pentagonum (Jukes-Browne, 1896) and Thomelites sornayi (Thomel, 1966), typical of the lower Upper Cenomanian Calycoceras guerangeri Zone of the standard North-West European sequence. Of note is the presence of Eucalycoceras jeanneti Collignon, 1937, previously known only from Madagascar.

UPPER CENOMANIAN AMMONITES FROM THE SAN-TANDER REGION

The Cenomanian ammonites in the Mengaud collection (LM) come from the glauconitic marly limestones that form the cliffs of Tagle between Suances and Ría de la Rabia (W of Comillas). One of them, situated between Suances and La Atalaya de Santa Justa (Mengaud, 1920, fig. 41) is particularly rich. It was termed "Pas du Chat" by Mengaud because of its relative inaccessibility. Mengaud's original determinations were: Acanthoceras rhotomagense, A. Newboldi, A. cf. harpax, A. cf. meridionale var. tuberculata, A. naviculare, A. Barruei, A. Mantelli, A. Villei and Puzosia cf. Gaudemarisi, which he regarded as characteristic of the Rhotomagien, that is to say the upper part of the Cenomanian. Our revised determinations are: Puzosia (P.) mayoriana (d'Orbigny, 1841) (UPS LM 101), Calycoceras (Newboldiceras) asiaticum asiaticum (Jimbo, 1894) (UPS LM106), C. (N.) planecostatum (Kossmat, 1897) (UPS LM103 and LM 109), C. (N.) hippocastanum (J. de C. Sowerby, 1826) (UPS LM108), Thomelites sornayi (Thomel, 1966) (UPS LM 110), and Eucalycoceras jeanneti Collignon, 1937 (UPS LM 1023).

LOWER AND UPPER CENOMANIAN AMMONITES FROM SOPEIRA

The first records of Cenomanian ammonites from the southern flank of the Pyrenees are all from the Sopeira region. Dalloni (1910, 1930) mentioned the discovery of Cenomanian ammonites (*Turrilites costatus, Mantelliceras mantelli*) in the sequence of marls subsequently termed "Marnes de Sopeira" by Souquet (1967) and formally Sopeira marl Formation (Mey *et al.*, 1968). Bilotte & Souquet (1972) recognised Upper Cenomanian faunas in the

¹ Oxford University Museum of Natural History, Parks Road, Oxford OX1 3PW and Department of Earth Sciences, South Parks Road, Oxford OX1 3AN, U. K. jim.kennedy@oum.ox.ac.uk

² Université de Toulouse; Géoscience Environnement Toulouse (GET), 14 avenue E. Belin, 31400 Toulouse and Service Commun d'Étude et de Conservation des Collections Patrimoniales (SCECCP). michel.bilotte@get.obs-mip.fr

conglomerates that overlie the Sopeira marl Formation. Martínez (1982a, b) recognised abundant Lower and Middle Cenomanian ammonite faunas from the Sopeira marl Formation. In the latest study, Caus *et al.* (1993) correlated the abundant benthic and planktonic microfaunas in this transitional platform to basinal sequence.

The three assemblages recognised in the Sopeira marl Formation (Martínez, 1982a, b; Caus *et al.*, 1993) with the original determinations are listed below and in Table 1, which also includes our new records:

Assemblage 1: *Puzosia (P.) subplanulata, Puzosia* sp., *Mantelliceras picteti, Sharpeiceras* sp. aff. *S. florencae, Acompsoceras* sp. aff. *A. renevieri, A.* sp. aff. *A. essendiense.*

Assemblage 2: Hypoturrilites gravesianus, Turrilites (T.) costatus, Puzosia (P.) subplanulata, Puzosia sp., Forbesiceras sp. aff. F. largilliertianus, Mantelliceras saxbii, M. picteti, M. cantianum.

Assemblage 3: Turrilites (T.) scheuchzerianus, Calycoceras paucinodatum, C. sp. gr. C. newboldi, Acanthoceras sp., A. rhotomagense sussexiense, Euomphaloceras cunningtoni.

Assemblages 1 and 2 were assigned to the Lower Cenomanian by Martínez (1982a, b), and assemblage 3 to the Middle Cenomanian.

Our new collections are as follows. From the Sopeira marl Formation at the same general level as assemblages 1 and 2 of Martínez: Sharpeiceras schlueteri Hyatt, 1903 (UPS BS226: Fig. 3.B) and Mantelliceras dixoni Spath, 1926 (UPS BS228; Fig. 3.C). From the upper part of the Sopeira marl Formation: Calycoceras (Newboldiceras) asiaticum asiaticum (Jimbo, 1894) (UPS J0). This species was also collected from the lower part of the Santa Fe Breccia Formation (J6), together with Calycoceras sp. (UPS J4, J5), and Tetragonites subtimotheanus Wiedmann, 1962. The upper part of these breccias yielded Thomelites sornayi (UPS J1, J2, K1-2), and numerous examples of Eucalycoceras pentagonum (UPS J3, J8, J9, BS253). These faunas are placed in Table 1 on the principal formations present in the Sopeira section.

The standard ammonite zonation for the Upper Cenomanian of Western Europe (Wright & Kennedy, 1984) is as follows: *Neocardioceras juddii* Zone (youngest) - *Metoicoceras geslinianum* Zone - *Calycoceras (Proeucalycoceras) gueranger* Zone (oldest).



Fig. 1. Geographic location of the Santander and Sopeira outcrops. Fig. 1. Situación geográfica de los afloramientos de Santander y Sopeira.

The presence of Eucalycoceras pentagonum and Thomelites sornayi date both the Santander and Sopeira assemblages very precisely, to the lower Upper Cenomanian Calycoceras (Proeucalycoceras) guerangeri Zone, which can be recognised across western Europe from southern England and Germany to Haute Normandie, Sarthe, and Provence in France, while we have previously recognised elements of the zonal fauna from Pech de Foix in Ariège (Kennedy et al., 1996). A particularly interesting occurrence in the present fauna is *Eucalvcoceras ieanneti* Collignon, 1937, previously known only from the holotype, from Ankilimanarivo, Madagascar (Fig. 2), a locality that is the source of the type material of *Hourcquiceras* Collignon, 1937, a poorly understood genus of Euomphaloceratinae that also occurs in south India, and only now precisely dated.

SYSTEMATIC PALAEONTOLOGY

Order AMMONOIDEA Hyatt, 1889 Suborder LYTOCERATINA Hyatt, 1889 Superfamily TETRAGONITOIDEA Hyatt, 1900 Family TETRAGONITIDAE Hyatt, 1900

Tetragonites Kossmat, 1895

Type species. Ammonites timotheanus Pictet, 1847: 295, pl. 2, fig. 6; pl. 3, figs. 1, 2, by original designation.

Tetragonites subtimotheanus subtimotheanus Wiedmann, 1962 Fig. 6.K, L

- 1895 Lytoceras (Tetragonites) Timotheanum Mayor; Kossmat: 133 (37), pl. 17 (3), figs. 11, 13
- 1962 Tetragonites subtimotheanus Wiedmann: 31
- 1973 *Tetragonites subtimotheanus subtimotheanus* Wiedmann; Wiedmann: 592, text-fig. 2, pl. 1, fig. 5; pl. 2, fig. 2; pl. 3, figs 1-5; ? pl. 7, fig. 8 (with synonymy)
- 1987 *Tetragonites subtimotheanus maclearni* Wiedmann; Thomel: 16, pl. 2, figs. 5, 6; pl. 3, fig. 2; pl. 4, figs. 1-3, 8-10; pl. 5, figs. 1, 2, 6-8 (with synonymy)

Type. The holotype, by original designation, is the original of Kossmat (1895: 133 [37], pl. 17 [3], figs. 11, 13), from the Utatur Group of south India.

Material. Specimen UPS J10, from the lower Sopeira breccias.

Description and discussion. UPS J10 is a well-preserved composite mould 56.4 mm in diameter. Coiling is involute, the umbilicus deep, with a flattened, outwardinclined umbilical wall and narrowly rounded umbilical shoulder. The whorl section varies from compressed to depressed as a result of *post-mortem* distortion: the original whorl proportions cannot be established. The flanks are flattened, the ventrolateral shoulders broadly rounded, the very broad venter very feebly convex. There are at least six constrictions on the adapertural half whorl; the last four progressively closer together. They are prorsiradiate, straight on the inner flank, flexed feebly forwards and feebly concave on the outer flank, flexed back and convex across the ventrolateral shoulder and feebly concave across the venter. The specimen closely resembles individuals of comparable size and preservation described by Thomel (1987) from southeast France as *Tetragonites subtimotheanus maclearni* Wiedmann, 1973.

Occurrence. Upper Albian to lower Upper Cenomanian, southern England, southeast France, Sopeira (Huesca province, Spain), Crimea, Ukraine, KwaZulu-Natal (South Africa), Madagascar, south India, Alaska and British Columbia.

Superfamily DESMOCERATOIDEA Zittel, 1895 Family DESMOCERATIDAE Zittel, 1895 Subfamily PUZOSIINAE Spath, 1922

Puzosia Bayle, 1878

Type species. Ammonites planulatus J. de C. Sowerby, 1827: 134, pl. 570, fig. 5, *non* Schlotheim, 1820: 59 (= *Ammonites mayorianus* d'Orbigny, 1841: 267, pl. 79, figs. 1-3), by subsequent designation by H. Douvillé (1879: 91).

Puzosia (Puzosia) mayoriana (d'Orbigny, 1841)

- 1841 Ammonites Mayorianus d'Orbigny: 267, pl.79, figs. 1-3
- 1984 *Puzosia* (*Puzosia*) *mayoriana* (d'Orbigny, 1841); Wright & Kennedy: 55, text-figs. 1a, b, 2c, h, m, 3n-r, 4a-c, pl. 3, figs. 1, 2, 4, 6, 9-12; pl. 4, figs. 1, 2, 5-7 (with synonymy)
- 1996 *Puzosia (Puzosia) mayoriana* (d'Orbigny, 1841); Kennedy *et al.*: 312, pl. 39, figs. 4, 5
- 2004 *Puzosia (Puzosia) mayoriana* (d'Orbigny, 1841); Kennedy & Jolkičev: 372, pl. 1, figs. 4-6 (with additional synonymy)
- 2005 *Puzosia* (*P*.) *mayoriana* (Sowerby); Reboulet *et al.*: text-fig. 3a
- 2006 *Puzosia mayoriana* (d'Orbigny, 1841); Kennedy & Juignet *in* Gauthier: 96, pl. 49, fig. 4
- 2007 *Puzosia (Puzosia) mayoriana* (d'Orbigny, 1841); Kennedy & Latil: 460, pl. 1, figs. 1-6; pl. 3, fig. 1
- 2007 *Puzosia* (*Puzosia*) *mayoriana* (d'Orbigny, 1841); Szives: 96, pl. 13, fig. 9; pl. 14, fig. 7; pl. 19, fig. 8; pl. 28, figs. 8, 10, 13
- 2008 *Puzosia* (*Puzosia*) *mayoriana* (d'Orbigny, 1841); Kennedy *et al.*: 37, pl. 8, figs. 15, 16
- 2009 *Puzosia* (*Puzosia*) *mayoriana* (d'Orbigny, 1841); Kennedy & Bilotte: 47, pl. 3, figs. 32, 33, 37-40



Fig. 2. *Eucalycoceras jeanneti* Collignon, 1937. The holotype, the original *Calycoceras (Eucalycoceras) jeanneti* of Collignon (1937: 71, pl. 6, fig. 1), specimen EM 1632 in the École des Mines de Paris collection, currently housed in the collections of the Université de Lyon I-Villeurbanne, from Ankilimanarivo, Madagascar. Scale bar 2 cm.

Fig. 2. Eucalycoceras jeanneti Collignon, 1937. Holotipo, el original Calycoceras (Eucalycoceras) jeanneti de Collignon (1937: 71, pl. 6, fig. 1), ejemplar EM 1632 de la colección École des Mines de Paris, actualmente conservada en las colecciones de la Université de Lyon I-Villeurbanne, procedente de Ankilimanarivo, Madagascar. Escala 2 cm.

Type. The lectotype, by the subsequent designation of Wright & Wright (1951: 35), is BMNH 9381, the original of J. de C. Sowerby (1827: 570, fig. 5), from the Cenomanian Lower Chalk of Hamsey, near Lewes (Sussex, England).

Material. UPS LM 101, from the glauconitic marls of the "Pas du Chat" section, Santander.

Discussion. This well-known species is represented by a large worn individual 150 mm in diameter; it differs in no significant respect from specimens of similar size from southern France figured by Thomel (1992, pl. 13, figs. 1-3) and Kennedy (1994, pl. 5, figs. 8, 9).

Occurrence. Upper Albian to Upper Cenomanian; widespread throughout Europe, Africa, south India, and Japan.

Superfamily ACANTHOCERATOIDEA de Grossouvre, 1894

Calycoceras Hyatt, 1900

(ICZN Generic Name No. 1352)

Type species. By designation under the Plenary Powers (ICZN Opinion No. 557) *Ammonites navicularis* Mantell, 1822: 198, pl. 22, fig. 5 (ICZN Specific Name No. 1633).

Discussion. Calycoceras are the commonest element of the "Pas du Chat" fauna, with 18 individuals, of which most are comparable to the subgenus *Newboldiceras* Thomel, 1972. Unfortunately, all but five are specifically indeterminate.

Calycoceras (Newboldiceras) Thomel, 1972

Type species. By original designation by Thomel (1972: 105), *Acanthoceras newboldi* Kossmat, 1897: 5 (112), which is a junior synonym of *Acanthoceras rhotomagense* var. *asiatica* Jimbo, 1894: 177, pl. 20, fig. 1 (Wright & Kennedy, 1990: 239).

Calycoceras (Newboldiceras) asiaticum asiaticum (Jimbo, 1894)

Fig. 4.D-F; Fig. 6.J

- 1894 *Acanthoceras rhotomagense* var. *asiatica* Jimbo: 177, pl. 20, fig. 1
- 1990 Calycoceras (Newboldiceras) asiaticum asiaticum (Jimbo, 1894); Wright & Kennedy: 239, text-figs.
 87a-c, 88f, 97, 98, pl. 58, fig. 1; pl. 64, figs. 1, 2; pl. 65, figs. 1-3, 5, 7; pl. 72, fig. 3; (with full synonymy)
- 2010 *Calycoceras* (*Newboldiceras*) *asiaticum asiaticum* (Jimbo, 1894); Kennedy & Klinger: 11, figs. 32, 33a-f, 34j-l, p, q, 36-38, 44d, e, h, 57a-f (with additional synonymy)

Formation	Martínez (1982)	This study Assemblages F1 to 4	Horizon
Upper Sopeira breccias		F4 Eucalycoceras pentagonum Thomelites sornayi	lower Upper Cenomanian
Lower Sopeira breccias		Calycoceras sp. F3 Tetragonites subtimotheanus Calycoceras (N.) asiaticum asiaticum	lower Upper to Middle Cenomanian
Sopeira marl	Assemblage 3: Turrilites (T.) scheuchzerianus, Calycoceras paucinodatum, C. sp. gr. C. newboldi, Acanthoceras sp., A. rhotomagense sussexiense, Euomphaloceras cunningtoni	F2 Calycoceras (N.) asiaticum asiaticum	
	Assemblage 2: Hypoturrilites gravesianus, Turrilites (T.) costatus, Puzosia sp., Puzosia (P.) subplanulata, Forbesiceras sp. aff. F. largilliertianus Mantelliceras saxbii, M. picteti, M. cantianum	F1 Mantelliceras dixoni Sharpeiceras schlueteri	Middle to Lower Cenomanian
	Assemblage 1: Puzosia (P.) subplanulata Puzosia sp., Mantelliceras picteti, Sharpeiceras sp. aff. S. florencae, Acompsoceras sp. aff. A. renevieri, A. sp. aff. A. essendiense		

Table 1. Ammonite assemblages in the Sopeira section.

Tabla 1. Asociaciones de ammonites en la serie de Sopeira.



Fig. 3. Sopeira outcrops. A, Sopeira marl Formation with position of ammonites: 1) *Sharpeiceras schlueteri* Hyatt, 1903 (UPS BS 226) also figured in B; 2) *Mantelliceras dixoni* Spath, 1926 (UPS BS 228) also figured in C; 3) indeterminate ammonite also figured in D. All from the Lower Cenomanian assemblage F1. E, outcrop of the F3 assemblage; F, outcrop of the F4 assemblage. G-I, *in situ* ammonites from the F4 assemblage outcrop: G, *Eucalycoceras pentagonum* (Jukes-Browne, 1896); H, I, *Calycoceras* (*Newboldiceras*) sp.

Fig. 3. Afloramientos de Sopeira. A, Formación Marga de Sopeira indicando la posición de los ammonites: 1) *Sharpeiceras schlueteri* Hyatt, 1903 (UPS BS 226) también figurado en B; 2) *Mantelliceras dixoni* Spath, 1926 (UPS BS 228) también figurado en C; 3) ammonites indeterminado también figurado en D. Todos de la asociación F1 del Cenomaniense inferior. E, localización del afloramiento de la asociación F3; F, localización del afloramiento de la asociación F4. G-I, ammonites *in situ* del afloramiento de la asociación F4: G, *Eucalycoceras pentagonum* (Jukes-Browne, 1896); H, I, *Calycoceras (Newboldiceras)* sp.

Type. The holotype by monotypy is the original of Jimbo, 1894: 20, fig. 1, no. 1-105 in the Collections of the Geological Institute, Tokyo University, from the Middle Cenomanian *Trigonia* Sandstone of the Ikushumbets, Hokkaido, Japan.

Material. UPS J6, UPS J0, from Sopeira and UPS LM 106, from Santander.

Description and discussion. UPS J6 (Fig. 6.J) is a wellpreserved juvenile 49 mm in diameter. The umbilicus comprises 30% of the diameter, with a convex wall and broadly rounded umbilical shoulder. The whorl section is depressed, with a costal whorl breadth to height ratio of 1.15, rounded-trapezoidal in intercostal section and polygonal in costal section. Nine bullae perch on the umbilical shoulder of the outer half whorl, and give rise to single straight ribs with, in some cases, a second rib feebly linked to the bulla. There are one or two long or short intercalated ribs. All ribs bear a small rounded-clavate inner ventrolateral tubercle, outer ventrolateral and siphonal clavi, linked across the venter by a strong straight transverse rib.

Specimen UPS J0 (Fig. 4.D-F) is a well-preserved, and 81 mm in diameter. The umbilicus comprises 31% of the diameter. The whorl section is depressed. Nine to ten small umbilical bullae give rise to one or two primary ribs, with short intercalate ribs between the primaries to give a total of 17 ribs per half whorl at the umbilical shoulder. All ribs bear rounded inner ventrolateral tubercles and outer ventrolateral and siphonal clavi, linked across the broad, feebly convex venter by a strong transverse rib. This specimen is close to the holotype of Calycoceras newboldi newboldi (a synonym of asiaticum), as figured by Kossmat (1897, pl. 1 (12), fig. 2; reproduced by Wright & Kennedy, 1990, text-fig. 98). Calycoceras (Newboldiceras) asiaticum asiaticum and C. (N.) asiaticum spinosum (Kossmat, 1897) differ in the much more robust tuberculation of the latter, although there are transitional forms.

Occurrence. Middle and lower Upper Cenomanian, southern England, northern and southern France, Spain, Romania, Bulgaria, Algeria, Tunisia, KwaZulu-Natal (South Africa), Madagascar, south India, and Japan, with possible records from Poland, Israel, and China.

Calycoceras (Newboldiceras) planecostatum (Kossmat, 1897)

Fig. 4.A-C

- 1897 Acanthoceras Newboldi var. planecostata Kossmat: 9 (116), pl. 2 (13), fig. 1
- 1990 *Calycoceras (Newboldiceras) planecostatum* (Kossmat, 1897); Wright & Kennedy: 252, text-figs. 101c-e, pl. 61, figs. 2, 3; pl. 67, figs. 1-4 (with full synonymy)
- 1996 *Calycoceras (Newboldiceras) planecostatum* (Kossmat, 1897); Kennedy *et al.*: 314, pl. 40, fig. 3
- 2010 *Calycoceras (Newboldiceras) planecostatum* (Kossmat, 1897); Kennedy & Klinger: 14, figs 34d, g, h, 35l, p, q, 44f, g, 46-54, 56a-k, 57h (with additional synonymy)

Type. The lectotype, by the subsequent designation of Wright & Kennedy (1990: 252), is number 14842 in the Collections of the Geological Survey of India, the original in Kossmat (1897, pl. 2 [13], fig. 1) (Wright & Kennedy, 1990, text-fig. 101c-e), from the Utatur Group of Odium, south India.

Material. UPS LM 103, UPS LM 109, from Santander and UPS J7, from Sopeira.

Description and discussion. UPS J7 (Fig. 4.C) is a wellpreserved individual with a maximum preserved diameter of 71.5 mm. The umbilicus comprises 20% approximately of the diameter. The original proportions cannot be established as the specimen is partially embedded in matrix, but the umbilical wall is flattened, the umbilical shoulder quite narrowly rounded, the flanks very feebly convex, convergent, the ventrolateral shoulder broadly rounded and the venter flattened. There are four welldeveloped umbilical bullae on the outer half whorl of the specimen, with up to three non-bullate primaries and occasional shorter intercalated ribs between to give 22 ribs per half whorl at the ventrolateral shoulder. All ribs bear outer ventrolateral clavi only, linked across the feebly convex venter by a broad flat-topped rib, the ribs separated by narrower interspaces. The second specimen, UPS LM 109 (Fig. 4.A, B) is typical of the numerous poorly preserved Calycoceras in the fauna, although retaining diagnostic features: crowded variably bullate primary ribs with occasional shorter intercalated ribs, and outer ventrolateral clavi only.

Occurrence. Upper Middle to lower Upper Cenomanian, southern England, Sarthe, Ariège and Provence (France), northern Spain, the Munster Basin (Germany), Iran, KwaZulu-Natal (South Africa), Madagascar, South India, and James Ross Island (Antarctica).

Calycoceras (Newboldiceras) hippocastanum (J. de C. Sowerby, 1826) Fig. 6.D, E

- 1826 Ammonites hippocastanum J. de C. Sowerby: 23 (pars), pl. 514, fig. 2
- 1990 *Calycoceras* (*Newboldiceras*) *hippocastanum* (J. de C. Sowerby, 1826); Wright & Kennedy: 253, text-figs. 107e, i, l, 108a-d, pl. 71, figs. 1-7; pl. 72, figs. 1, 2; pl. 73, fig. 3 (with full synonymy)
- 1992 *Calycoceras* (*Newboldiceras*) *hippocastanum* (J. de C. Sowerby, 1826); Thomel: 111, ?pl. 23, figs. 7, 8; pl. 62, fig. 4; pl. 63, figs. 1-5; pl. 64, figs. 2, 3; pl. 65, figs. 2, 3
- 1994 *Calycoceras (Newboldiceras) hippocastanum* (J. de C. Sowerby, 1826); Kennedy & Juignet: 51, figs. 1b, 20a-d
- 1998 *Calycoceras (Newboldiceras) hippocastanum* (J. de C. Sowerby, 1826); Kaplan *et al.*: 160, pl. 42, figs. 5, 6

Type. The lectotype, by the subsequent designation of Kennedy & Hancock (1970: 474) is GSM 37667 in the collections of the British Geological Survey, Keyworth,



Fig. 4. A-C, *Calycoceras (Newboldiceras) planecostatum* (Kossmat, 1897): A,B, specimen UPS LM 109 (Santander); C, specimen UPS J7 (Sopeira). D-F, *Calycoceras (Newboldiceras) asiaticum asiaticum* (Jimbo, 1894), specimen UPS J0 (Sopeira). G-I, *Eucalycoceras pentagonum* (Jukes-Browne, 1896), specimen UPS J9 (Sopeira). Scale bar 2 cm.

Fig. 4. A-C, *Calycoceras* (*Newboldiceras*) *planecostatum* (Kossmat, 1897): A,B, ejemplar UPS LM 109 (Santander); C, ejemplar UPS J7 (Sopeira). D-F, *Calycoceras* (*Newboldiceras*) *asiaticum* asiaticum (Jimbo, 1894), ejemplar UPS J0 (Sopeira). G-I, *Eucalycoceras pentagonum* (Jukes-Browne, 1896), ejemplar UPS J9 (Sopeira). Escala 2 cm. Nottinghamshire, the original of J. de C. Sowerby (1826, pl. 514, fig. 2) (Wright & Kennedy, 1990, pl. 71, fig. 7), from the lower Upper Cenomanian fauna of Bed C of the Cenomanian Limestone, probably near Humble Point (Devon, England).

Material. Specimen UPS LM 108, from Santander.

Description and discussion. The specimen is 37.5 mm in diameter. Strong, coarse straight prorsiradiate ribs primary ribs bear strong umbilical and inner ventrolateral tubercles, and weaker outer ventrolateral clavi. They are separated by intercalated ribs with outer ventrolateral and siphonal clavi only. This pattern of ribs and tubercles is characteristic of *C*. (*N*.) *hippocastanum*, and corresponds to that of better-preserved juveniles figured by Wright & Kennedy (1990, pl. 71, figs. 1, 2).

Occurrence. Lower Upper Cenomanian Calycoceras guerangeri Zone, southern England, Sarthe and Provence (France), the Munster Basin (Germany), "Pas du Chat" section (Cantabria, northern Spain) and, possibly, Japan.

Thomelites Wright & Kennedy, 1973

Type species. Jeanrogericeras sornayi Thomel, 1966: 431, pl. 11, figs. 1-3, by the original designation of Wright & Kennedy (1973: 231).

Thomelites sornayi (Thomel, 1966)

Fig. 5.A, B, E; Fig. 6.A-C, F-H

- 1966 Protacanthoceras sornayi Thomel: 432, pl. 11, figs. 1-3
- 1990 *Thomelites sornayi* (Thomel, 1966); Wright & Kennedy: 286, text-figs. 107a-d; 125c, g, h, 126a-c, f, 127a-d, pl. 80, fig. 1; pl. 81, figs. 1-6; pl. 82, figs. 1-8; pl. 83, figs. 1-3; pl. 84, figs. 1-7 (with full synonymy)

Type. The holotype, by monotypy is number 178 in the Thomel collection in the Faculté des Sciences, Nice, the original of Thomel (1966: 432, pl. 11, figs. 1-3), from the Upper Cenomanian of Les Lattes (Alpes-Maritimes, France).

Material. Specimens UPS LM110 and UPS LM 12303 from Santander, and UPS J1, UPS J2, UPS K1- K2, from Sopeira.

Description and discussion. The inner whorls are not seen in the present material. On the outer whorl, the whorl section is compressed, the coiling moderately evolute. The ornament of the phragmocone, well-shown by UPS J2 (Fig. 6.A, B) consists of strong umbilical bullae that give rise to pairs of low, coarse, straight ribs, with up to three non-bullate long or short intercalated ribs between. All ribs bear strong outer ventrolateral clavi, linked over the venter by a coarse transverse rib with a weaker siphonal clavus. This ornament extends onto the adapical part of the adult body chamber. Thereafter, the bullae are lost, and the ribs are predominantly long primaries. On the adapertural part of the body chamber the ventral and siphonal clavi are lost, the venter broadens and rounds, and is crossed by coarse transverse ribs. Specimen UPS LM12303 (Fig. 6.F-H) is a complete adult that shows the change in ornament from phragmocone to body chamber well. The fragmentary UPS J1 (Fig. 5.A, B) is very well-preserved and demonstrates the loss on tuberculation on the adapertural part of the body chamber. An adult, UPS LM 110 (Fig. 5.E) bears a close apparent similarity to the specimen of *Eucalycoceras jeanneti* Collignon, 1937 from the "Pas du Chat" (Fig. 5.C, D), but has predominantly long ribs with persistent ventrolateral clavi, and the typical coarse umbilical bullae of *T. sornayi* on the poorly preserved adapical part of the outer whorl.

Thomelites sornayi is comprehensively reviewed by Wright & Kennedy (1990), who discuss differences from other *Thomelites* species.

Occurrence. Upper Cenomanian *Calycoceras guerangeri* Zone, southern England, Sarthe, Anjou, Touraine, Basses-Alpes, and Alpes-Maritimes (France), "Pas du Chat" (Cantabria, northern Spain), and Sergipe (Brazil).

Eucalycoceras Spath, 1923

(ICZN Generic Name no. 1354)

Type species. Ammonites pentagonus Jukes-Browne, 1896: 156, pl. 5, fig. 1, by the original designation of Spath (1923: 144, ICZN Specific name no. 1635).

Eucalycoceras pentagonum (Jukes-Browne, 1896) Fig. 4.G-I; Fig. 6.I

- 1896 Ammonites pentagonus Jukes-Browne: 156, pl. 5, fig. 1
- 1990 *Eucalycoceras pentagonum* (Jukes-Browne, 1896); Wright & Kennedy: 282, text-figs. 89e, 123a, b, pl. 78, figs. 1, 3; pl. 79, figs 1-5 (with full synonymy)
- 1996 *Eucalycoceras pentagonum* (Jukes-Browne, 1896); Kennedy *et al.*: 316, pl. 39, figs. 6, 7; pl. 40, figs. 1, 2, 4 (with additional synonymy)

Type. The holotype, by monotypy, is specimen GSM 5348, in the collections of the British Geological Survey, Keyworth, Nottinghamshire, the original of Jukes-Browne (1896: 156, pl. 5, fig. 1), from the reworked phosphatic fauna of bed C of the Cenomanian Limestone at Humble Point, west of Lyme Regis (Devon, England).

Material. There are four specimens (UPS J3, UPS J9, UPS J8 and UPS BS 253), all from Sopeira.

Description and discussion. Specimens UPS J3 and UPS BS 253 (Fig. 6.1) are well preserved juveniles. Long umbilical bullae give rise to pairs of ribs and additional long ribs intercalate. The ribs are narrow, crowded, feebly prorsiradiate and feebly flexuous. They broaden across the outer flank and ventrolateral shoulder, and all bear delicate inner and outer ventrolateral and siphonal tubercles. Specimen UPS J9 (Fig. 4.G-I) is a complete



Fig. 5. A, B, E, *Thomelites sornayi* (Thomel, 1966): A,B, specimen UPS J1 (Sopeira); E, specimen UPS LM 110 (Santander). C,D, *Eucalycoceras jeanneti* Collignon, 1937, specimen UPS LM 102 (Santander). Scale bar 2 cm. Fig. 5. A, B, E, *Thomelites sornayi* (Thomel, 1966): A,B, ejemplar UPS J1 (Sopeira); E, ejemplar UPS LM 110 (Santander). C,D, *Eucalycoceras jeanneti* Collignon, 1937, ejemplar UPS LM 102 (Santander). Escala 2 cm.

microconch. Phragmocone ornament is as in the previous specimens. On the body chamber the characteristic flat-topped ribs appear, separated by narrow interspaces. The final sector of the body chamber is crushed (Fig. 4.I), but shows well the complete loss of ventrolateral and ventral tuberculation.

Occurrence. The species first appears in the lower Upper Cenomanian *Calycoceras guerangeri* Zone, and extends into the succeeding *Metoicoceras geslinianum* Zone, with records from southern England, Sarthe, Provence and Pech de Foix, Ariège (France), Spain, Portugal, Tadjikistan, Algeria, Tunisia, Madagascar, south India, Japan, and Colorado and New Mexico in the United States.

Eucalycoceras jeanneti Collignon, 1937

Fig. 2; Fig. 5.C, D 1937 *Calycoceras (Eucalycoceras) jeanneti* Collignon: 71, pl. 6, fig. 1

Type. The holotype, by monotypy, is number EM 1632 in the collections of the École des Mines, Paris, currently housed in the collections of the Université de Lyon I-Villeurbanne, from Ankilimanarivo, Madagascar, the original of Collignon (1937, pl. 6, fig. 1). Its dimensions, in millimetres, are as follows: diameter, 115.5 (100%); whorl breadth, 36 (31.2%); whorl height, 43.2 (37.4%); whorl breadth/whorl height, 0.83; umbilical diameter, 39.5 (34.2%).

Material. Specimen UPS LM 102, from Santander.

Description. The holotype (Fig. 2) is a complete adult with a half whorl of body chamber preserved. The inner whorls are damaged, but show bullate, straight, feebly prorsiradiate ribs, with occasional long intercalated ribs. Inner and outer ventrolateral tubercles persist on the phragmocone to an estimated diameter of 70 mm,

REFERENCES

- Bayle, É. 1878. Fossiles principaux des terrains. Explication de la Carte géologique de France 4(1), Atlas: pls. 1-158. Service de la Carte géologique detaillée, Paris.
- Bilotte, M. & Souquet, P. 1972. Les biozones de foraminifères benthiques du Cénomanien pyrénéen. Comptes Rendus de l'Académie des Sciences, Paris, 274: 3352-3355.
- Caus, E., Gómez-Garrido, A., Simó, A. & Soriano, K. 1993. Cenomanian-Turonian platform to basin integrated stratigraphy in the South Pyrenees (Spain). Cretaceous Research, 14: 531-551.
- Collignon, M. 1937. Ammonites cénomaniennes du sud-ouest de Madagascar. Annales Géologiques du Service des Mines, Madagascar, 8: 29-72, pls. 1-11.
- Dalloni, M. 1910. Étude géologique des Pyrénées de l'Aragon. Annales de la Faculté des Sciences de l'Université de Marseille, 19: 1- 444.
- Dalloni, M. 1930. Étude géologique des Pyrénées catalanes. Annales de la Faculté des Sciences de l'Université de Marseille, 26: 1-373.

beyond which the venter is damaged until the beginning of the body chamber at an estimated diameter of 80 mm, where the first few ribs have outer ventrolateral tubercles only, thereafter lost. The body chamber is compressed, with flattened subparallel flanks; the whorl breadth to height ratio is 0.82 at the adapical end, and 0.69 at the adapertural end. The ventrolateral shoulders and venter are broadly rounded. There are 12 umbilical bullae on the adapertural half whorl of the body chamber, weakening on the last few ribs before the aperture. The bullae are small, sharp, and linked to the umbilical seam by a welldeveloped rib. At the adapical end of the body chamber they occasionally give rise to a pair of ribs, thereafter single ribs only. The ribs are narrow, straight and prorsiradiate across the flanks, with one to three long or short intercalated ribs between. All ribs flex forwards, and are feebly concave over the ventrolateral shoulder, strengthening, the ventrolateral clavi lost, the ribs strong, and passing straight across the venter.

Discussion. Although poorly preserved, the present specimen shows the distinctive coiling, rib style, and, so far as can be established, the tuberculation of the holotype and previously only known specimen of *Eucalycoceras jeanneti*.

Occurrence. Upper Cenomanian of Madagascar and the "Pas du Chat" (Cantabria, northern Spain).

ACKNOWLEDGEMENTS

The authors acknowledge the Professor Ricardo Martínez and the Dr. Jaume Gallemí for their highly constructive review of the original manuscript, the technical support of the staff of the Department of Earth Sciences, Oxford, and the Geological Collections, Oxford University Museum of Natural History and Christiane Hester-Cabaré of the laboratory Géosciences Environnement de Toulouse (GET).

- Douvillé, H. 1879. Note accompagnant la présentation de l'Atlas du tome IV de l'explication de la Carte géologique de France de E. Bayle & R. Zeiller. Bulletin de la Société Géologique de France, 3ème série, 7: 91-92.
- Gauthier, H. 2006. Volume 4, Céphalopodes crétacés. *In* Fischer, J.-C. (dir.), "Révision critique de la Paléontologie Française d'Alcide d'Orbigny": 1-662 + 1-28 (Supplément), pls. 1-65 + 1-148, 13bis, 115bis + 2-9. Backhuys, Leiden.
- Grossouvre, A. de 1894. Recherches sur la craie supérieure. 2, Paléontologie. Les ammonites de la craie supérieure. Mémoires du Service de la Carte Géologique détaillée de la France. 1-264, pls. 1-39 (misdated 1893).
- Hyatt, A. 1889. Genesis of the Arietidae. Smithsonian Contributions to Knowledge, 673: xi + 1-239.
- Hyatt, A. 1900. Cephalopoda. *In* Zittel, K.A. von (1896-1900), "Textbook of Palaeontology", transl. Eastman: 502-604. C.R. Macmillan, London and New York.
- Hyatt, A. 1903. Pseudoceratites of the Cretaceous. United States Geological Survey Monograph, 44: 1-351, pls. 1-47.
- Jimbo, K. 1894. Beiträge zur Kenntniss der fauna der Kreideformation von Hokkaido. Paläontologisches Abhandlungen, n. f., 2: 147-194, pls. 17-25.



Fig. 6. A-C, F-H, *Thomelites sornayi* (Thomel, 1966): A, B, specimen UPS J2 (Sopeira); C, specimen UPS K1 (Sopeira); F-H, specimen UPS LM 12303 (Santander). D, E, *Calycoceras (Newboldiceras) hippocastanum* (J. de C. Sowerby, 1826), specimen UPS LM 108 (Santander). I, *Eucalycoceras pentagonum* (Jukes-Browne, 1896), specimen UPS BS 253 (Sopeira). J, *Calycoceras (Newboldiceras) asiaticum asiaticum* (Jimbo, 1894), specimen UPS J6 (Sopeira). K, L, *Tetragonites subtimotheanus* Wiedmann, 1962, specimen UPS J 10 (Sopeira). Scale bar 2 cm. Fig. 6. A-C, F-H, *Thomelites sornayi* (Thomel, 1966): A, B, ejemplar UPS J2 (Sopeira); C, ejemplar UPS K1 (Sopeira); F-H, ejemplar UPS LM 12303 (Santander). D, *E, Calycoceras (Newboldiceras) hippocastanum* (J. de C, Sowerby, 1826), eiemplar UPS LM 108 (Santander). J. *Eucalycoceras pen-*

(Santander). D, E, *Calycoceras (Newboldiceras) hippocastanum* (J. de C. Sowerby, 1826), ejemplar UPS LM 108 (Santander). I, *Eucalycoceras pentagonum* (Jukes-Browne, 1896), ejemplar UPS BS 253 (Sopeira). J, *Calycoceras (Newboldiceras) asiaticum asiaticum* (Jimbo, 1894), ejemplar UPS J6 (Sopeira). K, L, *Tetragonites subtimotheanus* Wiedmann, 1962, ejemplar UPS J 10 (Sopeira). Escala 2 cm.

- Jukes-Browne, A.J. 1896. *In* Jukes-Browne, A.J. & Hill, W., "A delimitation of the Cenomanian:- being a comparison of the corresponding beds in south-western England and western France". Quarterly Journal of the Geological Society of London, 52: 99-178, pl. 5.
- Kaplan, U., Kennedy, W.J., Lehmann, J., & Marcinowski, R. 1998. Stratigraphie und Ammonitenfaunen des westfälischen Cenoman. Geologie und Paläontologie in Westfalen, 51: 1-236, pls. 1-66.
- Kennedy, W.J. 1994. Cenomanian ammonites from Cassis, Bouches-du-Rhône, France. Palaeopelagos, Special Volume 1: 209-254, pls. 1-12.
- Kennedy, W.J. & Bilotte, M. 2009. A revision of the cephalopod fauna of the 'niveau rouge' of the Selva de Bonansa, Huesca Province, northern Spain. Bulletin of the Moscow Society of Naturalists, 84: 39-70, pls. 1-8.
- Kennedy, W.J. & Hancock, J.M. 1970. Ammonites of the genus *Acanthoceras* from the Cenomanian of Rouen, France. Palaeontology, 13: 462-490, pls. 88-97.
- Kennedy, W.J. & Jolkičev, N. 2004. Middle Cenomanian ammonites from the type section of the Sanandinovo Formation of Northern Bulgaria. Acta Geologica Polonica, 54: 369-380, pls. 1-6.
- Kennedy, W.J. & Juignet, P. 1994. A revision of the ammonite faunas of the type Cenomanian. 5. Acanthoceratinae [*Calycoceras (Calycoceras), C. (Gentoniceras)* and *C. (Neboldiceras)*]. Cretaceous Research, 15: 17-57.
- Kennedy, W.J. & Klinger, H.C. 2010. Cretaceous faunas from Zululand and Natal, South Africa. The ammonite subfamily Acanthoceratinae de Grossouvre, 1894. African Natural History, 6: 1-76.
- Kennedy, W.J. & Latil, J.L. 2007. The Upper Albian ammonite sucession in the Montlaux section, Hautes-Alpes, France. Acta Geologica Polonica, 57: 453-478, pls. 1-12.
- Kennedy, W.J., Bilotte, M., & Hansotte, M. 1996. Cenomanian ammonites from Pech de Foix (Ariège, France). Géobios, 29: 307-318, pls. 39-40.
- Kennedy, W.J., Jagt, J.W.M., Amédro, F., & Robaszynski, F. 2008. The late Albian (Mortoniceras fallax Zone) cephalopod fauna from the Braquegnies Formation at Strépy-Thieu, southern Belgium. Geologica Belgica, 11: 35-69, pls. 1-10.
- Kossmat, F. 1895-1898. Untersuchungen über die Sudindische Kreideformation. Beitrage zur Paläontologie und Geologie Österreich-Ungarns und des Orients, 9: 97-203 (1-107), pls. 15-25 (1-11) (1895); 11: 1-46 (108-153), pls. 1-8 (12-19) (1897); 11: 89-152 (154-217), pls. 14-19 (20-25) (1898).
- Mantell, G.A. 1822. The fossils of the South Downs; or illustrations of the geology of Sussex. 1-327, pls. 1-42. Lupton Relfe, London.
- Martínez, R. 1982a. Distribución de los ammonites del Cretácico sudpirenaico. Cuadernos de Geologia Ibérica, 8: 1035-1047.
- Martínez, R. 1982b. Ammonoideos cretácicos del Prepirineo de la provincia de Lleida. Publicaciones de Geología, Universidad Autónoma de Barcelona, 17: 1-197, pls. 1-30.
- Mengaud, L. 1920. Recherches géologiques dans la région cantabrique: 1-370. Thèse Faculté des Sciences, Paris.
- Mey, P.W.H., Nagtegaal, P.J.C., Roberti, K.J. & Hartevelt, J.J.A. 1968. Lithostratigraphic subdivision of posthercynian deposits in the south-central Pyrenees. Leidse Geologische Mededelingen, 41: 221-228.
- Orbigny, A. d'. 1840-1842. Paléontologie française: Terrains crétacés. 1. Céphalopodes: 1-120, pls. 1-30 (1840); 121-430, pls. 31-112 (1841); 431-662, pls. 113-148 (1842). Masson, Paris.
- Pictet, F.J. 1847. Céphalopodes. *In* Pictet, F.J. & Roux, W. (1847-1853), "Description des mollusques fossiles qui se trouvent dans les Grès Verts des environs de Genève": 9-156, pls. 1-15. Imp. J-G. Fick, Genève.

- Reboulet, S., Giraud, F. & Proux, O. 2005. Ammonoid abundance variations related to changes in trophic conditions across the Oceanic Anoxic Event 1d (latest Albian, SE France). Palaios, 20: 121-141.
- Schlotheim, E.F. von. 1820. Die Petrefaktenkunde auf ihrem jetzigen Standpunkle durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier- und Pflanzenreichs der Vorwelt erläutert: lxii + 1-437. Beckersche Buchhandlungen, Gotha.
- Souquet, P. 1967. Le Crétacé supérieur sud-pyrénéen en Catalogne, Aragon et Navarre. 1-530. Thèse, Faculté des Sciences, Université Paul Sabatier, Toulouse.
- Sowerby, J. de C. 1823-1846. The Mineral Conchology of Great Britain (continued), 5: 1-168, pls. 408-503 (1823); 6: 1-250, pl. 504-609 (1829); 7: 1-80, pls. 610-648 (1834-1846, never completed). The author, London.
- Spath, L.F. 1922. On the Senonian ammonite fauna of Pondoland. Transactions of the Royal Society of South Africa, 10: 113-147.
- Spath, L.F. 1923. On the ammonite horizons of the Gault and contiguous deposits. Summary of Progress of the Geological Survey of Great Britain for 1922: 139-149.
- Spath, L.F. 1926. On the zones of the Cenomanian and the uppermost Albian. Proceedings of the Geologists Association, 37: 420-432.
- Szives, O. 2007. Albian Stage. *In* Szives, O. (ed.), "Aptian-Campanian ammonites of Hungary". Geologica Hungarica, Series Palaeontologica, 57: 75-122, pls. 14-28.
- Thomel, G. 1966. Ammonites. *In* Porthault, B., Thomel, G. & Villoutreys, O. de (eds.), "Étude biostratigraphique du Cénomanien du bassin supérieur de l'Esteron (Alpes Maritimes). Le problème de la limite Cénomanien-Turonien dans le sud-est de la France". Bulletin de la Société Géologique de France, (7ème série), 8: 423-439, pls. 8-11.
- Thomel, G. 1972. Les Acanthoceratidae cénomaniens des chaînes subalpines méridionales. Mémoires de la Société Géologique de France (N.S.), 116: 1-204, pls. 1-88.
- Thomel, G. 1987. La famille des Tetragonitidae (Ammonoidea) dans le Cénomanien du sud-est de la France. Annales de Paléontologie (Vertébrés-Invertébrés), 73: 241-272, pls. 1-5.
- Thomel, G. 1992. Ammonites du Cénomanien et du Turonien du Sud-Est de la France. 1: 1- 422, pls. 1-41; 2: 1- 383, pls. 43-130. Editions Serre, Nice.
- Wiedmann, J. 1962. Ammoniten aus der Vascogotischen Kreide (Nordspanien). 1, Phylloceratina, Lytoceratina. Palaeontographica, 118A: 119-237, pls. 8-14.
- Wiedmann, J. 1973. The Albian and Cenomanian Tetragonitidae (Cretaceous Ammonoidea), with special reference to the Circum-Indic species. Eclogae Geologicae Helvetiae, 66: 585-616, pls. 1-8.
- Wright, C.W. & Kennedy, W.J. 1973. Paléontologie systématique. In Juignet, P., Kennedy, W.J. & Wright, C.W., "La limite Cénomanien-Turonien dans la région du Mans (Sarthe): stratigraphie et paléontologie". Annales de Paléontologie (Invertébrés), 59: 207-242, pls. 1-3.
- Wright, C.W. & Kennedy, W.J. 1984. The Ammonoidea of the Lower Chalk. Part 1. Palaeontographical Society Monographs, 137(1), 567: 1-126, pls. 1-40.
- Wright, C.W. & Kennedy, W.J. 1990. The Ammonoidea of the Lower Chalk. Part 3. Palaeontographical Society Monographs, 144(3), 585: 219-294, pls. 56-86.
- Wright, C.W. & Wright, E.V. 1951. A survey of the fossil Cephalopoda of the Chalk of Great Britain: Primarily a nomenclatorial revision of Daniel Sharpe's. Palaeontographical Society Monographs, 104(3), 453: 1-40.
- Zittel, K.A. von. 1895. Grundzüge der Paläontologie (Paläozoologie). viii + 1-971. R. Oldenbourg, Munich & Leipzig.