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Coniacian (Upper Cretaceous) ammonites from the North Cantabrian Basin (Cantabria, northern Spain)

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ABSTRACT:

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A small Coniacian ammonite fauna is described from the North Cantabrian Cretaceous Basin (Cantabria, northern Spain). 11 species, belonging to nine genera, are treated. These are *Gaudryceras mite*, *Forresteria* (*Forresteria*) *alluaudi*, *Peroniceras* (*Peroniceras*) *westphalicum*, *P.* (*P.*) *subtricarinatum*, *P.* (*P.*) cf. *lepeei*, *Puzosia* (*P.*) *muelleri*, *Tetragonites epigonum*, *Tissotioides haplophyllum*, *Tongoboryceras* cf. *canali* and *Scaphites* cf. *kieslingswaldensis*. *Yabeiceras manasoaense* is described for the first time from Europe. The poor fauna does not permit any refined stratigraphic subdivision, but the general distribution pattern fits that observed in other areas. An Early Coniacian age is suggested for the assemblage. Biogeographically, the fauna presumably reflects intermediate conditions between the Tethys and the Boreal.

Key words: Coniacian, Spain, Ammonites, Stratigraphy, Palaeobiogeography.

INTRODUCTION

The Coniacian ammonite fauna of the Basco Cantabrian Basin (northern Spain) has been treated palaeontologically to some extent over the last decades (KARRENBERG 1936, WIEDMANN 1960, 1964; MARTÍNEZ 1982, SANTAMARIA 1992, 1995). Additionally, several faunas were figured in connnection with stratigraphic investigations (WIEDMANN & KAUFFMAN 1978, WIEDMANN 1979a, KÜCHLER & ERNST 1989, KÜCHLER 1998). The North Cantabrian Basin (Cantabria, northern Spain), however, was never considered, and only limited information on the Coniacian ammonites from the area can be obtained from the literature. MENGAUD (1920) was the first to record Coniacian ammonites from the area around Santander. Additional informations were given by WILMSEN *& al*. (1996) and WIESE (1997). Even though Coniacian strata are well exposed in coastal sections, ammonites are extremely rare. The material for this work derived mainly from the localities Trasvia, Tagle, Liencres (Playa de Portio) and the city of Santander (Text-fig. 1). A simplified lithologic column and lateral correlation between the localities (with the exception of the Santander section) is given in Text-fig. 2. As the successions consist of extremely hard, partly silicified, nodular limestones, the few ammonites are extremely difficult to extract. Furthermore, most of the material is only incompletely preserved, and details of the ornament are missing. In 10 years of collecting, only less than 20 specimen have been collected, mostly from the Lower and Middle Coniacian. The scope of this paper will be to describe this small ammonite fauna. Additionally, some limited comments on the stratigraphic and palaeobiogeographic significance, are given.

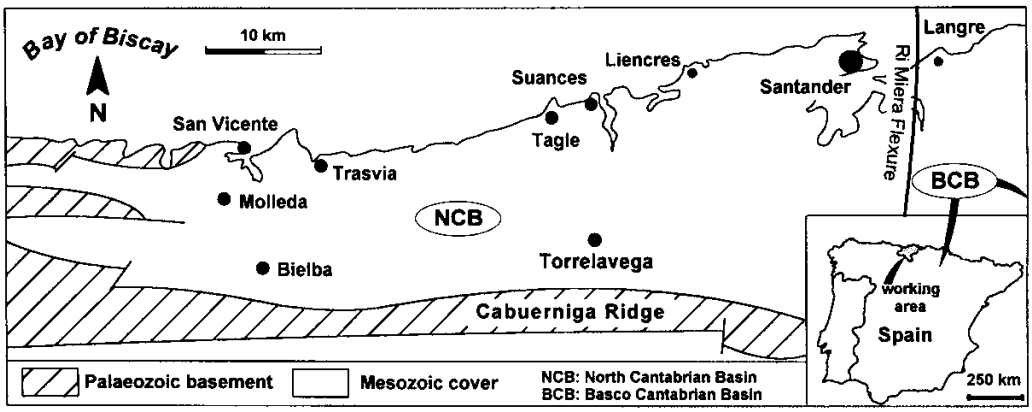

Fig. 1. Geographic/geologic overview of the working area in Cantabria (northern Spain)

GEOLOGICAL SETTING

The E-W trending North Cantabrian Basin (NCB) developed as an intra-shelf basin due to block movements at the northern margin of the Iberian microcontinent during Valanginian times (PUJALTE 1981). In the North, it was delimited by a palaeo-high, today located in the Bay of Biscay. Its southern border was the Cabuerniga High. Towards the east, separated by the N-S trending Rio Miera Flexure, it graded - progressively deepening - into the Basco Cantabrian Basin (BCB; Text-fig. 1) (for a detailed summary of the depositional history, with comprehensive bibliography, see WILMSEN 1997 and WIESE 1997). As can be seen from Text-fig. 1, the treated localities are positioned in an E-W direction. Consequently, the successions of Trasvia represent the shallowest environments, whereas the exposures around Liencres were deposited in deeper settings.

Today, Upper Cretaceous successions are widely exposed in coastal outcrops between the Asturian border in the west and Santander, the Cantabrian capital, in the east. Details of the Upper Cretaceous strata were given by GARCÍA-MONDEJAR & PUJALTE 1982, HEREDIA & *al*. 1990, WILMSEN *& al*. (1996), WILMSEN (1997) and WIESE (1997). A sequence stratigraphic framework for the NCB was presented by WIESE & WILMSEN (1999).

LITHOLOGY AND SEQUENCE STRATIGRAPHY
(Text-fig. 2, Text-fig. 3)

The Coniacian strata were deposited on a mixed carbonate/siliciclastic ramp with varying influx of siliciclastics (WILMSEN *& al*. 1996). After a period of relative sea-level highstand during the Late Turonian, the Coniacian stage reflects a period of regression (WIESE 1997). More distal sediments are represented by (nodular) and thouroughly bioturbated marl/limestone alternations (e.g. Liencres) that grade, *via* sponge-bearing, silty and thickly bedded limestones, into (nodular) glauconitic/glauconititic successions of the on-swell or more proximal environments (e.g. Trasvia). Within the treated interval, two 3rd order cycles, DS Tu/Co and DS Co 1 of WIESE & WILMSEN (1999) can be observed. DS Co 1 is terminated by a major hardground (SB Co 2: *Micraster* Hardground; Text-fig. 3), which marks the uppermost limit of the investigated interval.

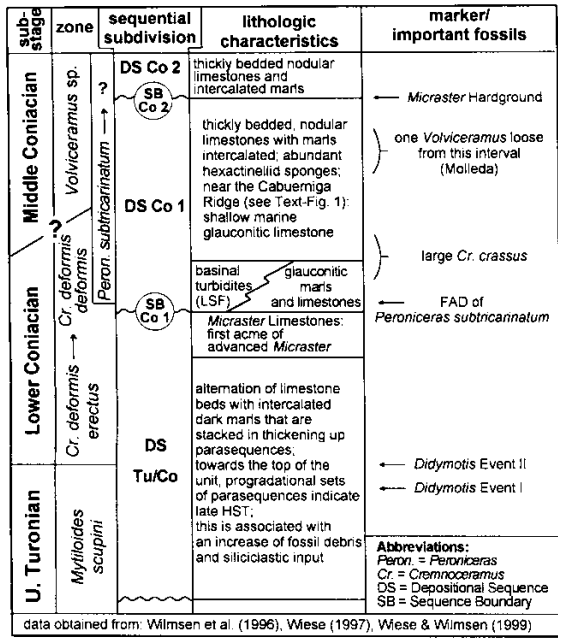

Fig. 2. Stratigraphical subdivision (bio-, event and sequence stratigraphy) of the Upper Turonian to Lower Coniacian in the North Cantabrian Basin (northern Spain)

BIOSTRATIGRAPHY

Biostratigraphic subdivison of the Coniacian in the working area is poor, due to the scarceness of index-fossils (WIESE 1997). The base of the Coniacian is defined by the FAD of *Cremnoceramus deformis erectus* (MEEK) [WALASZCZYK & WOOD 1998 showed that *Cremnoceramus rotundatus* (*sensu* TRÖGER *non*

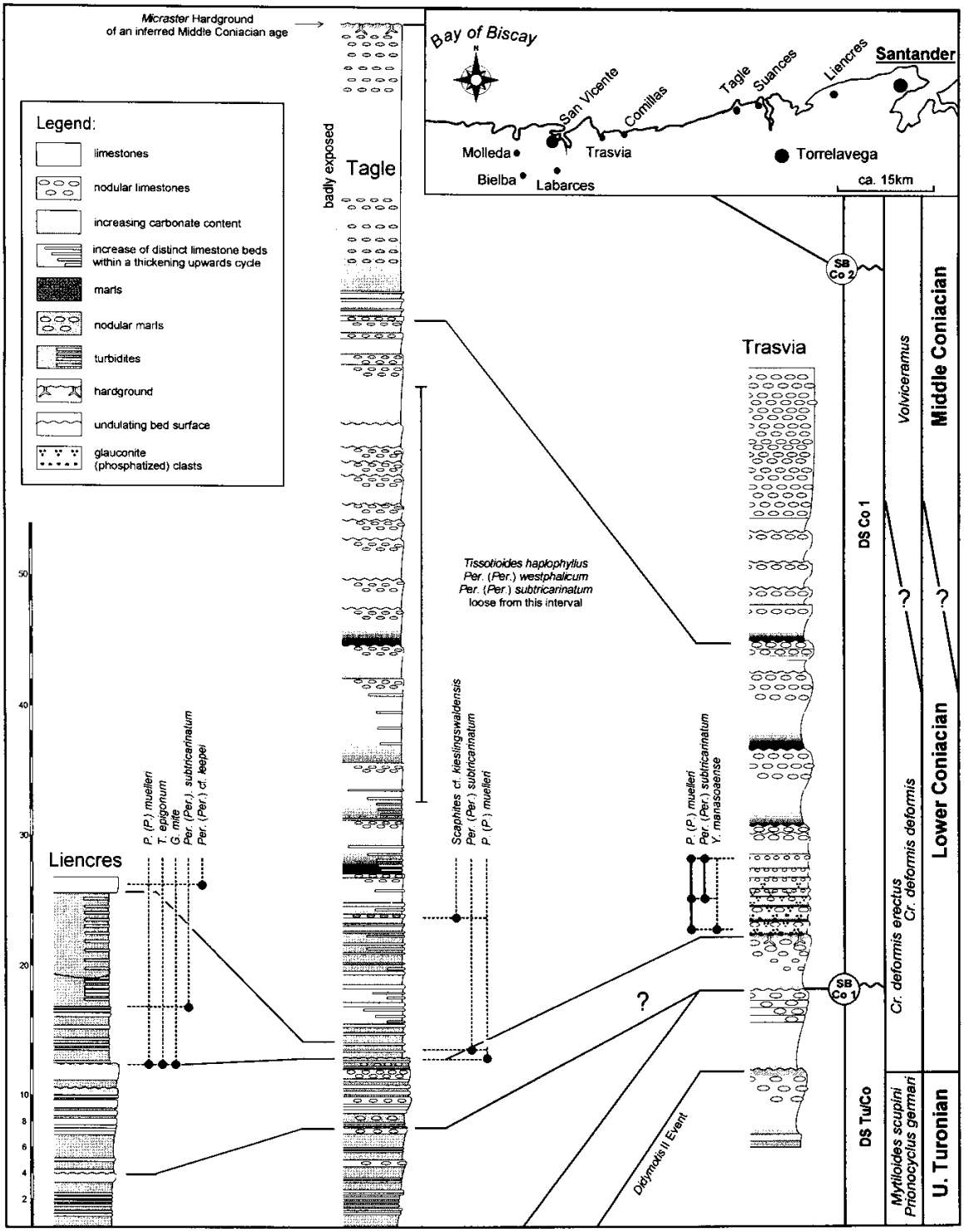

Fig. 3. Lithology and lateral correlation of the Upper Turonian to Lower Coniacian strata of the North Cantabrian Basin, with location of ammonite-bearing beds

FIEGE), the index-taxon for the base of the Coniacian (KAUFFMAN *& al*. 1996), is synonymous with *Cremnoceramus erectus* (MEEK), which itself is now considered to be a subspecies of *Cremnoceramus deformis* by the above authors]. However, due to the rarity of inoceramids in the studied interval, the entry of the marker taxon cannot be exactly located, and consequently the *Didymotis* II Event (Text-fig. 2) is used as a proxy for the boundary. The true position of the base of the stage must be located somewhere above this latter datum (see also discussion *in* WIESE 1999). The Lower Coniacian of the NCB can be subdivided by representatives of the *Cremnoceramus deformis* lineage (here: *Cr. deformis erectus*, *Cr. deformis deformis*). Very rare occurrences of *Cremnoceramus crassus* can be used to identify the upper Lower Coniacian (Text-fig. 2). The presence of the Middle Coniacian in the NCB is indicated by the very rare finds of *Volviceramus*, but it is absolutely impossible to determine the exact position of the Lower/Middle Coniacian boundary. Taking the evolutionary development of *Cremnoceramus* in the Lower Coniacian into consideration, this boundary must be located well above the first intra-Coniacian sequence boundary (SB Co1, Text-fig. 2). As SB Co 2, the *Micraster* Hardground, is inferred to fall within the range of *Volviceramus*, it must be interpreted as Middle Coniacian in age. Based on its inferred middle Mid-Coniacian age, it was interpreted as the Spanish expression of the Ilsede tectonic phase of STILLE (1924) by WIESE & WILMSEN (1999). The relation of the local stratigraphy to ammonite stratigraphic frameworks is disussed in the chapter on stratigraphical implications.

SYSTEMATIC PALAEONTOLOGY

All figured specimens, if not other stated, are registered and housed in the Naturkundemuseum Berlin (MB.C.). Abbreviations used in the text are as follows: D: diameter, Wh: whorl height, Wb: whorl breadth, U: Umbilicus)

Order Ammonoidea ZITTEL, 1884
Suborder Lytoceratina HYATT, 1889
Superfamily Tetragonitaceae HYATT, 1900
Family Gaudryceratidae SPATH, 1927
Genus *Gaudryceras* DE GROSSOUVRE, 1894

TYPE SPECIES: *Ammonites mitis* HAUER, 1866, by designation of BOULE, LEMOINE & THÉVENIN (1906).

Gaudryceras mite (HAUER, 1866) (Pl. 1, Fig. 1)

1866 *Ammonites mitis* HAUER, p. 305, Pl. 2, Figs 3-4
1883 *Ammonites glaneggensis* REDTENBACHER, p. 119, Pl. 27, Fig. 3
1979 *Gaudryceras mite* (HAUER); KENNEDY & SUMMESBERGER, p. 74, Pl. 1, Fig. 1; Pl. 2, Figs 1-2; Text-fig. 1; with synonymy
1979 *Gaudryceras glaneggense* (REDTENBACHER); KENNEDY & SUMMESBERGER, Pl. 3, Figs 1a-b; Pl. 4, Figs 1a-b; with synonymy
1979 *Gaudryceras denseplicatum* (JIMBO); KENNEDY & KLINGER, Pl. 5, Figs 1-2; Pl. 6, Fig. 2; Pl. 7, Fig. 1; with synonymy
1979 *Gaudryceras mite* (HAUER); SUMMESBERGER, Pl. 1, Fig. 1
1984 *Gaudryceras* aff. *mite* (HAUER); SZÁSZ, Pl. 2, Fig. 5; Pl. 3, Fig. 2
1984 *Gaudryceras* aff. *varagurense* (KOSSMAT); SZÁSZ, Pl. 2, Figs 4, 6, 7
1987 *Gaudryceras denseplicatum* JIMBO; POYARKOVA, Pl. 24, Fig. 1
1995 *Gaudryceras mite* (HAUER); KENNEDY, BILOTTE & MELCHIOR, Pl. 1, Figs 20-21
1996 *Gaudryceras glaneggense* (HAUER); WILMSEN, WIESE & ERNST, p. 362, Pl. 2, Fig 3
1996 *Gaudryceras mite* (HAUER); SUMMESBERGER & KENNEDY, Pl. 1, Figs 1-4; with synonymy

TYPE: Holotype, by monotypy, is the original of HAUER (1866, p. 305, Pl. 2, Figs 3, 4), housed in the Geologische Bundesanstalt Wien, Collection no. 1866/01/3, possibly from the Turonian part of the Gosau Group of Austria (see SUMMESBERGER & KENNEDY 1996, pp. 112, 114).

MATERIAL: 2 specimens; one composite mould from excavations in the city of Santander, Middle Coniacian, M. DIAZ-ISA collection, Santander (cast of the original, MB.C.2778); MB.C.2779 from the Lower Coniacian of Playa de Portio near Liencres.

DESCRIPTION: Coiling comparatively evolute. Whorl section compressed and oval with a moderate to narrowly arched venter. The flanks are smoothly rounded with the greatest breadth in the upper third of the flank. MB.C.2779, which is a fragment of one third of a whorl, represents an intermediate ontogenetic state. Its entire surface is densely ornamented with flexuous striae that arise in the umbilical area. In the upper third of the flank, secondaries and even tertiaries can intercalate. With increasing maturity, represented by MB.C.2778 [D: approx. 160 mm

(100%); Wh: approx. 69 mm (43%), U: approx. 55 mm (35%)], flexuous and plicate ribs develop parallel to the striae and cross the venter with a well developed sinus. The figured specimen (Pl. 1, Fig. 1) shows progressive narrowing of ornament with size, thus indicating the specimen to be an adult.

DISCUSSION: *Gaudryceras mite* is well known from Spain. It was figured by WIEDMANN (1962, Pl. 9, Figs 2, 6) as *Gaudryceras vascogoticum* WIEDMANN, which was treated by KENNEDY & SUMMESBERGER (1979) as a synonym of *G. glaneggense* (REDTENBACHER). *G. glaneggense* was considered to be separable from *Gaudryceras mite* (HAUER) by its broad ribbing, while *G. mite* was considered to have only fine lirae throughout ontogenetic development (see discussion *in* KENNEDY & KLINGER 1979). However, to judge from the material figured in the literature, the young whorls of *G. glaneggense* and *G. mite* are virtually indistinguishable. The development of broad ribbing occurs at different stages in ontogeny (and therefore with different size) and with different strength. It, therefore, appears that both species actually represent one single variable species. Consequently, SUMMESBERGER & KENNEDY (1996) regarded *G. glaneggense* as a synonym of *G. mite*. This view is followed here. At the moment it is not clear, to what extent the numerous species of *Gaudryceras* from Japan and Sakhalin (e. g. HIRANO 1975, 1979; JIMBO 1894; MATSUMOTO & YOSHIDA 1979; MATSUMOTO & MOROZUMI 1980; MATSUMOTO 1984; MATSUMOTO & TOSHIMITSU 1995; ZONOVA *& al*. 1993) are valid species or synonyms of *G. mite*.

OCCURRENCE: *G. mite* is known from the Turonian to Maastrichtian. It shows worldwide distribution.

Family Tetragonitidae HYATT, 1900
Genus Tetragonites KOSSMAT, 1895

TYPE SPECIES: *Ammonites timotheanus* PICTET 1847, p. 295, Pl. 2, Fig 6; Pl. 3, Figs 1-2

Tetragonites epigonum KOSSMAT, 1895
(Pl. 1, Figs 2-3)

1895 *Lytoceras* (*Tetragonites*) *epigonum* KOSSMAT, Pl. 17 (3), Figs 4-5 & 10.
1977 *Tetragonites* cf. *epigonus* KOSSMAT; KENNEDY & KLINGER, p. 165, Figs 7 e-g, 9a-c; with synonymy
1983 *Tetragonites rouvillei* (DE GROSSOUVRE); COLLIGNON, p. 168.
? 1981 *Tetragonites* (*Epigoniceras*) n. sp.? (aff. *T.* (*E.*) *epigonum*) KOSSMAT; SZÁSZ, Pl. 1, Figs 10a-c
1995 *Tetragonites epigonus* KOSSMAT; KENNEDY, BILOTTE & MELCHIOR, Pl. 1, Figs 6-8, 11-13; Pl. 2, Figs 5-6; Pl. 3, Figs 13-14; Text-fig. 9.

TYPE: Lectotype is the original of KOSSMAT [1895, Pl. 17(3), Fig. 4], designated by KENNEDY & KLINGER (1977).

MATERIAL: One specimen (MB.C.2780) from Playa de Portio near Liencres, Lower Coniacian.

DESCRIPTION: One fragment that covers approximately two thirds of a whorl. The umbilical wall is almost vertical or directed slightly outwards. Whorl section almost rectangular, slightly compressed with broadly rounded venter and very slightly concave flank. The greatest breadth is at the umbilical shoulder, which is comparatively narrowly rounded. The mould is devoid of ornament but at the most proximal part remnants of a marked constriction can be recognized.

DISCUSSION: Though not uncommon in other parts of the world, *T. epigonum* is a rare species in the European Coniacian. It is absent from the ammonite fauna of Westphalia in northern Germany (KAPLAN & KENNEDY 1994) and large parts of France (KENNEDY 1984). Rare occurrences, however, are reported from the Corbières, southern France (KENNEDY *& al*. 1995). From Romania, SZÁSZ (1981) figured *Tetragonites* sp. and *Tetragonites* (*Epigoniceras*) n. sp.? (aff. *T.* (*E.*) *epigonum* KOSSMAT). Although obviously diagenetically compressed, the latter specimen still shows the typical subrectangular whorl section of *Tetragonites*, and it may well be a *T. epigonum*.

Other than in the Cenomanian, where the genus shows worldwide distribution, Turonian and Coniacian occurrences of the genus in northern and central Europe are extremely rare. It should be emphasized that *Tetragonites* is not uncommon in the Turonian of the NCB: albeit found only in scattered occurrences (e. g. Liencres, Molleda, Trasvia), it is an invariable component of the fauna of more distal settings (WIESE 1995). This single occurrence extends the range of *Tetragonites* in the NCB into the Coniacian. As the genus shows latitudinal controlled distribution pattern at least during Turonian

and Coniacian times, its occurrence in the NCB suggests some southerly influence.

OCCURRENCE: *Tetragonites epigonum* is a widespread species, albeit unknown from most parts of the Boreal Realm in the Turonian and Coniacian. It is recorded from Turonian to Campanian strata from France, Spain, Romania (?), Angola, South Africa, Madagascar, India, Japan and the Far East of Russia as well as from British Columbia, Patagonia and Antarctica.

Suborder Ammonitina HYATT, 1889
Superfamily Desmoceratacea ZITTEL, 1895
Family Desmoceratidae ZITTEL, 1895
Subfamily Puzosiinae SPATH, 1922
Genus *Puzosia* BAYLE, 1878

TYPE SPECIES: *Ammonites planulatus* SOWERBY (1927, p. 134, Pl. 570)

Puzosia (*Puzosia*) *muelleri* DE GROSSOUVRE, 1894
(Pl. 1, Fig. 4)

1894 *Puzosia Mülleri* DE GROSSOUVRE, p. 172.
1979 *Puzosia curvatisulcata* (CHATWIN & WITHERS); WRIGHT, p. 308, Pl. 4; p. 323, Pl. 7.
1994 *Puzosia* (*Puzosia*) *muelleri* (DE GROSSOUVRE); KAPLAN & KENNEDY, Pl. 1, Figs 1-3; Pl. 2, Figs 1, 6; Pl. 3; with synonymy.

TYPE: Lectotype is the original of SCHLÜTER (1872, p. 40, Pl. 11, Figs 12-13), subsequently designated by KAPLAN & KENNEDY (1994) and refigured there on Plate 1, Figure 2.

MATERIAL: 4 badly preserved fragments of internal moulds that do not permit measurements (MB.C.2781 from Playa de Portio, Liencres; MB.C.2782 from Playa de Tagle, MB.C.2783 and MB.C.2784 from Trasvia).

DESCRIPTION: Evolute, with steep umbilical wall leading into a shallow umbilicus. Whorl section compressed with the greatest breadth midflank, narrowly arched venter and rounded umbilical shoulders. On the steinkern, periodic, slightly sinuous constrictions occur, approximately 4-5 in MB.C.2782. Even though the material is badly preserved, it appears that dense, prorsiradiate ribs develop midflank, or a bit further downflank, and project forward as they cross the venter.

DISCUSSION: KAPLAN & KENNEDY (1994) figured and discussed *P.* (*P.*) *muelleri* from the Coniacian of Westphalia. Although badly preserved, the material from the NCB seems to fit this species concept. In particular, the ribs that develop just below midflank differentiate the specimens from *Mesopuzosia* MATSUMOTO, 1988, which has ribbing that starts at the umbilical wall.

OCCURRENCE: *P.* (*P.*) *muelleri* is known from the Upper Turonian and Coniacian of northern Germany. The records from the Lower Coniacian of northern Spain are new.

Family Pachydiscidae SPATH, 1922
Genus *Tongoboryceras* HOUŠA, 1967

TYPE SPECIES: *Lewesiceras tongoboryense* COLLIGNON 1952, p. 23, Pl. 2, Fig. 3.

Tongoboryceras cf. *canali* (DE GROSSOUVRE, 1894)
(Pl. 2, Figs 1-2)

1894. *Pachydiscus canali* DE GROSSOUVRE; p. 195, Pl. 38, Fig. 2
1995. *Tongoboryceras canali* (DE GROSSOUVRE); KENNEDY, BILOTTE & MELCHIOR, Pl. 10, Figs 13-15; Text-fig. 17; with synonymy.

TYPE: Holotype by original designation is the specimen figured by DE GROSSOUVRE (1894, p. 195, Pl. 38, Fig. 2), refigured in KENNEDY *& al*. (1995, p. 399, Text-fig. 17).

MATERIAL: 1 internal mould (MB.C.2785) from the Lower Coniacian of the City of Santander. The associated inoceramids (*Cremnoceramus deformis deformis*, *Cremnoceramus crassus*) indicate an unequivocal Early Coniacian age.

DESCRIPTION: The specimen is obliquely deformed, and measurements are possible only to a limited extent. Approximately half of the last whorl preserved is non-septate, the rest belongs to the septate phragmocone. Coiling moderately involute with the last whorl covering approximately 2/3 of the preceding. Where measuring was possible, the deep umbilicus with steep, outward inclined wall, is approximately 35% of the diameter, which must have been at least 75 mm. The

umbilical shoulders are rounded. The whorl section is very depressed and almost ovale. The greatest whorl breadth must have been, both in costal and intercostal position, near the umbilical shoulders. Due to the very depressed whorls, the convex flanks are reduced to a minimum, and they grade, via a gently curved ventral shoulder, into the broadly rounded venter.

In the upper part of the umbilical wall, faint primary ribs give rise to well developed and very elongated bullae. From these arise one or, in younger growth stage, pairs of strong, initially slightly rursi- to rectiradiate, later recti- to slightly prorsiradiate, well elevated ribs, which project only weakly forward when crossing the venter. There are 10 to 11 primaries per half whorl. In the upper part of the flank, secondaries begin to intercalate. Secondaries and primaries cross the venter in uniform strength and in the same direction. On some primaries, weak ventrolateral bullae can be felt rather than seen. With increasing size, the number of ribs decreases and the strength of individual ribs seem to increase. The suture lines, due to the bad mode of preservation, are only weakly visible.

DISCUSSION: The described specimen is, mainly based on the depressed whorl section and ribs that cross the venter without a sinus, referred to *Tongoboryceras*. However, the constrictions that are typical of this genus are absent, but this may be due to the poor preservation. Even though the suture of *Nowakites* can be similar to that of *Tongoboryceras* (e. g. SUMMESBERGER 1979), the former genus is generally characterized by a compressed rather than a depressed whorl section and by ribs that project markedly forward on the venter. On the basis of the general shape, the specimen is questionably considered to show affinities with *Tongoboryceras canali* (DE GROSSOUVRE 1894). KENNEDY *& al*. (1995) commented on previous taxonomic problems concerning this species.

KÜCHLER (1998, Pl. 13, Figs 7, 8) figured as *Eupachydiscus isculensis* a specimen from the Middle Coniacian *margae* Zone of Zuazu, Basque country of northern Spain, that is very similar to that decribed here. This may well be a *Tongoboryceras* rather than an *Eupachydiscus*.

OCCURRENCE: *Tongoboryceras canali* is known from the (Lower) Coniacian of France, Spain and Romania.

Superfamily Acanthocerataceae DE GROSSOUVRE, 1894
Family Collignoniceratidae WRIGHT & WRIGHT, 1951
Subfamily Barroisiceratinae BASSE, 1947
Genus *Forresteria* REESIDE, 1932
Subgenus *Forresteria* REESIDE, 1932

TYPE SPECIES: *Barroisiceras* (*Forresteria*) *forresteri*, REESIDE, 1932, p. 17, Pl. 5, Figs 2-7, designated by WRIGHT (1957, p. L432).

Forresteria (*Forresteria*) *alluaudi* (BOULE, LEMOINE & THÉVENIN, 1907)
(Pl. 2. Figs 3-4)

1907. *Acanthoceras* (*Prionotropis*) *alluaudi* BOULE, LEMOINE & THÉVENIN, p. 12, pl. 1, Figs 6-7; Text-fig. 17.
1983. *Forresteria* (*Forresteria*) *alluaudi* (BOULE, LEMOINE & THÉVENIN); KENNEDY, WRIGHT & KLINGER, Figs 5-9, 10a-b, 11-14, 15a-b, 16-31, 33, 34, 35c-e, 40d-e; with synonymy.
1991. *Forresteria* (*Forresteria*) *alluaudi* (BOULE, LEMOINE & THÉVENIN); KENNEDY & COBBAN, p. 23, Pl. 4, Figs 1-11; with synonymy.
1997. *Forresteria petrocoriense* (COQUAND); WIESE, p. 90, Pl. 7, Figs 1-2.

TYPE: Holotype is the specimen figured by BOULE & *al*. (1907, Pl. 1, Fig. 7; Text-fig. 17), designated by KENNEDY & *al*. (1983).

MATERIAL: A rubber cast of a composite mould (MB.C.2786), loose from excavations in Lower Coniacian successions in the city of Santander (the original is in the collection of M. DIAZ-ISA, Santander). As no strata higher than the *deformis deformis* Zone were excavated, the find must derive approximately from this interval, as is also shown by the co-occurrence of abundant *Micraster*, which are indicative of the so-called *Micraster* Limestone of the *deformis deformis* Zone in neighbouring localities (cf. WIESE 1997).

DESCRIPTION: The specimen is slightly deformed and has an approximate diameter of 95-100 mm. Parts of the venter are missing due to corrosion. Coiling involute (umbilicus: ca. 22 % at a diameter of 85 mm). Compressed whorl with a fastigate venter. Greatest breadth midflank. The flanks are only weakly rounded. The umbilical shoulder is comparatively narrowly arched and the umbilical walls are steep. Prominent bullate tubercles (6-8 per whorl) at the umbilical shoulder nor-

mally give rise to single ribs. In early ontogenetic stages, they are slightly concave in the lowermost part of the flank, in later growth stages are they recti- to slightly prorsiradiate. Individual ribs vary in development: some are pronounced with well developed umbilical bullae, other are only feebly developed. In rare cases, pairs of ribs start at the umbilical bullae, of which one rib is prominent, the other weaker developed. Mid-lateral tubercles occur on each rib at approximately mid-flank, where the whorl is broadest. At these tubercles or slightly higher up the flank, secondaries can start to intercalate. Each rib, primary and secondary, ends in markedly clavate ventrolateral tubercles (ca. 14-16 per whorl). Locally, fine striae parallel to the main ribs are preserved, suggesting that the entire surface was additionally ornamented by striae. A well developed row of clavi is present in the siphonal area Even though the specimen is corroded, it appears that the ribs become broader and less pronounced with increasing size, and the ventrolateral clavi become less distinct.

DISCUSSION: KENNEDY *& al*. (1983) and KENNEDY (1984) presented an extensive discussion of the differences between the two subgenera *Forresteria* (*Forresteria*) and *Forresteria* (*Harleites*). *Harleites* was considered to differ from *Forresteria* by the "smaller size, fusion of mediolateral and umbilical tubercles, and early loss of siphonal clavi leaving a flat or concave venter on the bodychamber, on the latter parts of which the ventral clavi may also disappear" (KENNEDY *& al*. 1983, p. 263). In fact, specimens of *Forresteria* (*Harleites*) of a size comparable to the specimen described here, as figured *in* KENNEDY (1984), show either the fusion of the umbilical and lateral tubercles (DE GROSSOUVRE 1894, Pl. 2, Fig. 1) or a reduction of ornamentation and a flattened venter. The Spanish specimen still shows well developed umbilical, lateral and ventrolateral tubercles as well as the siphonal clavi at a size of 80-90 mm. Therefore, it is referred to the subgenus *Forresteria* (*Forresteria*). As pointed out by KENNEDY *& al*. (1983), *Forresteria* (*Forresteria*) appears to be restricted to the Coniacian of Africa, South and Middle America, Japan and parts of the Western Interior Seaway of the USA. Rare occurrences are reported from France. *Forresteria* (*Harleites*), however, occurs preferentially in Europe (Germany, France, Czech Republic), in South America (Colombia, Peru) and, doubtfully, in Madagascar and Japan, thus showing clear geographic separation of the two subgenera.

The specimen described here seems best referred to *Forresteria* (*Forresteria*) *alluaudi* (BOULE, LEMOINE & THÉVENIN, 1907) as figured by KENNEDY *& al*. (1983). It can be readily distinguished from all other species of *Forresteria* (*Forresteria*) by its distinct mode of ornamentation, characterized by the constant midflank position of the lateral tubercle throughout all growth stages (for discussion see KENNEDY *& al*. 1983, KENNEDY & COBBAN 1991), even though there can be similarities with *F*. (*F*.) *peruana* (BRÜGGEN, 1910) in some specimens.

KENNEDY & COBBAN (1991) reported *Forresteria* (*Forresteria*) *alluaudi* from the Middle Coniacian of the USA. The North American specimens occur associated with *Scaphites ventricosus* and *Cremnoceramus deformis*, indicating a rather a late Early Coniacian age (KAUFFMAN *& al*. 1996). From the Gosau (Austria), TRÖGER & SUMMESBERGER (1994) reported numerous specimens of *Forresteria* (*Forresteria*) *alluaudi* togehter with *Cremnoceramus crassus* that are interpreted as Early Coniacian in age. From France, a single specimen was recorded from the *Peroniceras tridorsatum* Zone (KENNEDY 1984), which also falls into the *deformis deformis* Zone (KAPLAN & KENNEDY 1994) and, therefore, into the Lower Coniacian. The find from Santander is derived from the same stratigraphic interval in the Lower Coniacian. No other ammonites were collected from this interval. However, in time-equivalent successions in the Playa de Portio section near Liencres (Text-fig. 1), *Peroniceras subtricarinatum*, *Cr. deformis deformis* and abundant *Micraster* ex gr. *cortestudinarium* occur, thus indicating an equivalent of the north German *deformis deformis* Zone.

From Japan, North East and Far East Russia (Sakhalin), *Forresteria* (*Forresteria*) *alluaudi* is interpreted to be indicative of a Middle Coniacian age (TOSHIMITSU *& al*. 1995, ZONOVA & YAZYKOVA 1999). As, however, the associated index-inoceramid *I. uwajimensis* is endemic for the areas, a detailed stratigraphic comparison of the find levels is not possible due to palaeobiogeographic barriers.

OCCURRENCE: In Europe, the species is known to occur in France, Spain and Austria. The are records from the US Western Interior, Mexico, Peru, Colombia, Zululand and Madagascar. It is also known from Japan, North East and Far East Russia.

Genus *Yabeiceras* TOKUNAGA & SHIMIZU, 1926

TYPE SPECIES: *Yabeiceras orientale* TOKUNAGA & SHIMIZU, 1926, Pl. 22, Fig 7; Pl. 27, Fig. 1, by original designation.

Yabeiceras manasoaense COLLIGNON, 1965
(Pl. 2, Fig. 5)

1965. *Yabeiceras manasoaense* COLLIGNON; p. 84, Pl. 452, Fig. 1839.
1971. *Yabeiceras manasoaense* COLLIGNON; MATSUMOTO, p. 144, Pl. 24, Fig. 2.
1976. *Yabeiceras manasoaense* COLLIGNON; KLINGER, KENNEDY & SIESSER, p. 163, Fig. 1; p. 164, Fig. 2; p. 165, Fig. 3.
1983. *Yabeiceras manasoaense* COLLIGNON; KENNEDY, WRIGHT & KLINGER; p. 312, Figs 47a-b; p. 320, Figs 51a-c.
1983. *Yabeiceras* aff. *manasoaense* COLLIGNON; KENNEDY, WRIGHT & KLINGER, p. 316, Fig. 49.

TYPE: Holotype, by original designation, is the original of COLLIGNON (1965, Pl. 452, Fig. 1893), from the Coniacian of Manasoa, Madagascar.

MATERIAL: 1 composite mould (MB.C.2787) from bed 103 of Trasvia, Lower Coniacian.

DESCRIPTION: The specimen is strongly corroded and slightly deformed. Coiling is very evolute with less than 20% of the previous whorl covered. Approximate dimensions (as far as measurable): D: 95 mm, Wh: 25 mm, Wb: 35mm, U: 40 mm (42%). Whorl section depressed (reniform), with very reduced flanks and the greatest breadth in both intercostal and costal section at the ventral shoulder. The ventral shoulder is narrowly arched and the venter is broadly rounded. Remnants of a faint, smooth midventral ridge can be felt rather than seen.

In the earliest growth stage visible, prorsiradiate, simple and comparatively widely spaced, low ribs arise in the umbilical area. They become progressively broader up-flank and end in strong, broad and slightly clavate tubercles at the ventrolateral shoulder. Even though the mould is very corroded, it seems that there are 8-9 tubercles half whorl. The ribs, if visible at all, are only weakly developed. With increasing size, the ribs weaken and prominent, clavate tubercles dominate over the ribbing. The suture line is not visible, due to the mode of preservation.

DISCUSSION: The very distinct mode of coiling and ornamentation in later growth stages makes *Yabeiceras* readily distinguishable from all contemporaneous ammonite genera. *Yabeiceras* seems to be an extremely rare genus, as only some 30 specimens are recorded in the literature (see KENNEDY & *al*. 1983). This paucity of material contrasts with an excessive taxonomic splitting into 12 species, some of which are based only on single finds. The small number of specimens permits neither the recognition of dimorphism nor the determination of the extent of intraspecific variation The described species may actually, as already indicated by MATSUMOTO & *al*. (1964), be only an expression of a few, albeit highly variable forms. In respect of the mode of coiling and tuberculation, the Spanish specimen shows the closest affinities to *Y. manasoaense* COLLIGNON as figured by COLLIGNON (1965) from Madagascar and by KLINGER & *al*. (1976) from Zululand. The find of *Yabeiceras manasoaense* from northern Spain is interesting, as it is the first record of the species in Europe. However, from Romania, SZÁSZ (1981) figured *Yabeiceras* sp. (aff. *Yabeiceras orientale* TOKUNAGA & SHIMIZU) from the Lower Coniacian of Caugagia. This specimen may actually be a *Yabeiceras*, and it shows good accordance with the specimen of *Y. orientale* figured by KENNEDY & *al*. (1983, p. 306, Fig. 44) from Hokkaido, Japan. It thus appears that the genus may be comparatively widespread, albeit extremely rare.

OCCURRENCE: *Yabeiceras manasoaense* COLLIGNON is known to occur in the Coniacian of Japan, Madagascar, Zululand (South Africa), Romania and northern Spain.

Subfamily Peroniceratinae HYATT, 1900
Genus *Peroniceras* DE GROSSOUVRE, 1894
Subgenus *Peroniceras* DE GROSSOUVRE, 1894

TYPE SPECIES: *Peroniceras moureti* DE GROSSOUVRE, 1894, p. 100, Pl. 11, Fig. 4

Peroniceras (*Peroniceras*) cf. *lepeei* (FALLOT, 1885)
(Pl. 2, Figs 6-7)

1885. *Ammonites* (*Schloenbachia*) *L`Epeei* FALLOT, Pl. 1, Fig. 2
1920. *Peroniceras L`Epeei* (FALLOT); DESIO, p. 208, Pl. 12, Figs 6-7; Pl. 14, Fig. 6
1984. *Peroniceras* (*Peroniceras*) aff. *lepeei* (FALLOT); KENNEDY, Pl. 16, Figs 4-5
1991. *Peroniceras* (*Peroniceras*) *lepeei* (FALLOT); KENNEDY & COBBAN, p. 39, Text-fig. 15

1995. *Peroniceras* (*Peroniceras*) *lepeei* (FALLOT); KENNEDY, BILOTTE & MELCHIOR, Pl. 21, Fig. 13

TYPE: Holotype by monotypy is the original of FALLOT (1885, Pl. 1, Fig. 2), in the collections of the Laboratoire de Géologie of the Faculté de Sciences in Grenoble.

MATERIAL: 1 very worn fragment (MB.C. 2788) from the Lower Coniacian of Playa de Portio, Liencres.

DESCRIPTION: The fragment represents approximately one third of a whorl of a compressed and evolute ammonite with a suboval whorl section and the greatest whorl breadth approximately at mid-flank. The venter is fastigate with a prominent siphonal keel and two weakly developed margial keels. At the smoothly rounded umbilical shoulders, primary ribs (ca 8 per half whorl) develop that become stronger in the lowermost part of the flank, without developing any bullae. In the lower third of the whorl, secondaries start to intercalate irregularly, and each rib, secondary and primary, ends in weakly clavate tubercles.

DISCUSSION: The specimen strongly resembles *Peroniceras* (*Peroniceras*) *lepeei* as figured by KENNEDY (1984). KENNEDY stated that *P. leepei* differed from other species of *Peroniceras* in the absence of umbilical bullae and the dominance of the mid-ventral keel over the marginal keels, characters that are also found in the present specimen. However, *Peroniceras* (*Peroniceras*) *lepeei* is considered to lack intercalatories and it differs in this respect from the specimen described here. Additionally, *Peroniceras* (*Peroniceras*) *lepeei* has 18 to 20 ribs per half whorl, thus significantly outnumbering those of the present specimen (8 per half whorl). The high number of ribs can also be found in a specimen that was figured as *Peroniceras* (*Peroniceras*) aff. *lepeei* by KENNEDY (1986, Pl. 16, figs 4-5). As, however, there are more similarities with *Peroniceras* (*Peroniceras*) *lepeei* than with other taxa, the fragment described here is tentatively considered to be closely related to this species.

OCCURRENCE: *Peroniceras* (*Peroniceras*) *lepeei* is a very rare species. It occurs in the *tridorsatum* Zone of France and Italy and in the Austin Chalk of Texas (USA). There are records from Zululand and South Africa. The Spanish specimen comes from the *subtricarinatum* Zone of presumed Early Coniacian age.

Peroniceras (*Peroniceras*) *subtricarinatum* (D'ORBIGNY, 1850) (Pl. 3, Fig. 1)

1841. *Ammonites tricarinatus* D'ORBIGNY, p. 307, Pl. 91, Figs 1-2.
1850. *Ammonites subtricarinatus* D'ORBIGNY, p. 212
1920. *Peroniceras subtricarinatum* D'ORBIGNY; MENGAUD, p. 267.
1984. *Peroniceras* (*Peroniceras*) *subtricarinatum* (D'ORBIGNY); KLINGER & KENNEDY, p. 157, Figs 19a-b, d-e, Pl. 20-23; with synonymy.
1989. *Peroniceras subtricarinatum* D'ORBIGNY; KÜCHLER & ERNST; p. 189, Pl. 3, Fig. 1.
1994. *Peroniceras* (*Peroniceras*) *subtricarinatum* (D'ORBIGNY); KAPLAN & KENNEDY, p. 114, Pl. 23; p. 116, Pl. 24; p. 118, Pl. 25; with additional synonymy.
1995. *Peroniceras* (*Peroniceras*) *subtricarinatum* (D`ORBIGNY); KENNEDY, BILOTTE & MELCHIOR, Pl. 20, Figs 3-5, 9, 11, 12; Text-fig. 23).
1997. *Peroniceras subtricarinatum* (D`ORBIGNY); WIESE, p. 90, Pl. 7, Fig. 3.
1998. *Peroniceras* (*Peroniceras*) *subtricarinatum* (D`ORBIGNY); KÜCHLER, Pl. 12, Fig. 4.

TYPE: Lectotype is specimen no. 7183 from the D`ORBIGNY Collection (MNHP) (D'ORBIGNY, 1841, p. 91, Fig. 2; Pl. 20, Figs 3-5) by designation of KLINGER & KENNEDY (1984).

MATERIAL: 4 specimens, MB.C.2789 (Lower Coniacian of Liencres), MB.C.2790 (Lower Coniacian of Playa de Tagle), MB.C.2791, MB.C.2792 (Lower Coniacian of Trasvia)

DESCRIPTION: Coiling very evolute and serpenticone. In specimen MB.C.2791 (D: 150 mm, Wh: 28 mm), the umbilicus is 66 % of the diameter. The umbilicus is shallow with moderately rounded umbilical shoulders. Whorl section oval to subrounded, with the greatest whorl breadth in costal/intercostal section at the umbilical shoulder. The venter is tricarinate, with the siphonal keel separated from the lateral keels by distinct grooves. Bullate, umbilicolateral tubercles give rise to rectior slightly rursiradiate ribs that can develop secondaries at approximately midflank. Both primaries and secondaries end in ventrolateral, clavate tubercles. With increasing size, both rows of tubercles become less distinct. Suture lines are not preserved.

DISCUSSION: KENNEDY (1984) and KAPLAN & KENNEDY (1994) gave adequate descriptions of this

well known species and nothing new can be added. It has already been described from the working area (Trasvia) by MENGAUD (1920). *P. subtricarinatum* is the most common species in the Lower and Middle Coniacian of the NCB. This fits the observation from the Basco Cantabrian Basin, where this species also is more common than any other representative of the genus *Peroniceras* (KÜCHLER 1998).

OCCURRENCE: *P. subtricarinatum* shows a wide distribution and is obviously not restricted to any palaeobiogeographic realm. It is reported from the Lower and Middle Coniacian of northern Germany, the Czech Republic, Switzerland, France, northern Spain, northern Africa, South Africa, Madagascar, and Mexico.

Peroniceras (*Peroniceras*) *westphalicum* STROMBECK, 1859
(Pl. 3, Fig. 2)

1859. *Ammonites westphalicus* STROMBECK, p. 56.
1963. *Peroniceras westphalicum* (SCHLÜTER); RADWAŃSKA, Pl. 5, Fig. 1.
1984. *Peroniceras* (*Peroniceras*) *westphalicum* (STROMBECK); KENNEDY, Pl. 14, Fig. 5; Pl. 15, Figs 1-3, 6-7; with synonymy.
?1988. *Peroniceras* sp. aff. *westphalicum* (STROMBECK); THOMÉL, Pl. 1, Fig. 5.
1994. *Peroniceras* (*Peroniceras*) *westphalicum* (STROMBECK); KAPLAN & KENNEDY, Pl. 20, Figs 1, 4, 5, 7; Pl. 21, Figs 2-3, 6; Pl. 22, Fig. 1; Pl. 26; Pl. 27, Figs 1, 3-5; Pl. 43, Figs 1-2; with additional synonymy.

TYPE: The original of STROMBECK (1859, p. 56), which may have been lost (cf. KENNEDY 1984).

MATERIAL: 2 specimens, MB.C.2793 & MB.C.2794, loose from Tagle. As it comes from an interval where only sediments of the higher DS Co 1 are exposed, a late Early or early Mid-Coniacian age must be inferred.

DESCRIPTION: Coiling is evolute, the umbilicus is shallow with gently curved umbilical shoulders. In MB.C.2793 (D: approx. 220 mm, Wh: approx. 54 mm, Wb in intercostal section 42 mm), the umbilicus comprises approximately 50% of the diametre (110 mm). Whorl section compressed and suboval, with the greatest breadth in the lower third, above the umbilical shoulder. The venter is fastigate to tricarinate. In MB.C.2794, which represents middle growth stage, a well developed siphonal keel is separated from the two lateral, less pronounced keels by a groove. In the larger specimen, MB.C.2793, the lateral and the siphonal keels tend to be almost equal in strenght, although the latter is still more elavated. Simple recti- to slightly prorsiradiate ribs (ca. 15-16 ribs per half whorl) arise from weakly developed bullae at the umbilical shoulder. In the upper third of the flank, most ribs start to develop secondaries, and each rib ends ventrolaterally in a clavate tubercle. In later growth stages, the main ribs weaken in the upper third of the flank, at the branching point to the secondaries. The latter that are then only weakly developed.

DISCUSSION: The species has been comprehensively discussed (KLINGER & KENNEDY 1984, KENNEDY 1984, KAPLAN & KENNEDY 1994). Due to its significant mode of ribbing (primaries that develop secondaries in the upper third of the flank with each rib ending in clavate ventrolateral tubercles) and its degree of involution, it can be easily distinguished from contemporaneous species of *Peroniceras*.

OCCURRENCE: In the working area, the species was found loosely well above SB Co 1 at Tagle. It is most likely of a terminal Early Coniacian age, although early Mid-Coniacian cannot be excluded. Further records are from Germany, the Czech Republic, France, northern Spain, Italy, South Africa, Madagascar, Texas, New Mexico and Wyoming.

Family Tissotiidae HYATT, 1900
Genus *Tissotioides* REYMENT, 1958

TYPE SPECIES: *Ammonites haplophyllus* REDTENBACHER, 1873, p. 100, Pl. 23, Fig. 1; original designation by REYMENT (1958, p. 48)

Tissotioides haplophyllus (REDTENBACHER, 1873)
(Pl. 4, Fig. 1)

1873. *Ammonites haplophyllus* REDTENBACHER, p. 100, Pl. 23, Fig. 1.
1984. *Tissotioides* (*Tissotioides*) *haplophyllus* (REDTENBACHER); KENNEDY, p. 124, Pl. 28, Figs 2-3; p. 128, Pl. 29, Figs 3-4; with synonymy.
1995. *Tissotioides* (*Tissotioides*) *haplophyllus* (REDTENBACHER); KENNEDY, BILOTTE & MELCHIOR, Pl. 24, Figs 3-4; Text-fig. 27.

1995. *Tissotioides* (*Tissotioides*) *haplophyllus* (REDTENBACHER); SANTAMARIA, Pl. 6, Fig. 8
1998. *Tissotioides* (*Tissotioides*) *haplophyllus* (REDTENBACHER); KÜCHLER, Pl. 13, Figs 1-2

TYPE: Holotype by monotypy is the original of REDTENBACHER (1873, Pl. 23, Fig. 1).

MATERIAL: 1 specimen, MB.C.2795, from the talus of Tagle. The find position and the general lithology of the fallen block indicates a position well above SB Co 1 but below SB Co 2.

DESCRIPTION: One side is slightly abraded by marine erosion, the other is moderately well preserved. Coiling moderately involute [D: ca. 125 mm (100%), Wh: 49 mm (39%), Wb in intercostal section: 32 mm (26%), U: 34 mm (27%)] with greatest breadth at the umbilical shoulders. In younger growth stages, the umbilical shoulder is narrowly arched and the umbilical walls are steep. Later, the umbilical shoulder becomes broadly rounded, thus giving the shell almost a trapezoid shape. In this specimen, 6 massive, nodose tubercles arise in the umbilicolateral area. In younger ontogenetic stages, the tubercles arise at the umbilical shoulder; in later stages, they arise from a position slightly higher upflank and become increasingly bullate and reduced in strength. Each tubercle gives rise to a single or pairs of broad and shallow, slightly prorsiradiate ribs. Between the tubercles, broad and less distinct ribs can be intercalated, starting in the umbilicolateral area. Each rib ends in a row of well developed clavi that rim the ventrolateral shoulder. The venter is tabulate. At a diametre of 94 mm, a row of shallow and small siphonal clavi, smaller than the ventrolateral clavi, can be observed. Suture lines are not visible

DISCUSSION: *Tissotioides haplophyllus* differs from other Tissotiidae in its almost tabulate venter, the weakly developed siphonal clavi and the mode of tuberculation, which makes it readily distinguishable from other contemporaneous species. It is well known from the Basco Cantabrian Basin of northern Spain (WIEDMANN 1979b, SANTAMARIA & MARTÍNEZ 1993, SANTAMARIA 1995, KÜCHLER 1998).

OCCURRENCE: *T.* (*T.*) *haplophyllus* is known from the Middle Coniacian of Austria, France and northern Spain. In Spain, it is known from the Lower Coniacian. The find position of this specimen suggests a terminal Early or an early Mid- Coniacian age.

Suborder Ancyloceratinae WIEDMANN, 1960
Superfamily Scaphitaceae GILL, 1871
Family Scaphitidae GILL, 1871
Genus *Scaphites* PARKINSON, 1811

TYPE SPECIES: *Scaphites equalis* SOWERBY, 1813, p. 33, Pl. 18, Figs 1-3, subsequently designated by MEEK (1876).

Scaphites cf. *kieslingswaldensis* LANGENHAN & GRUNDEY, 1891
(Pl. 1, Fig. 5)

1891. *Scaphites kieslingswaldensis* LANGENHAN & GRUNDEY, p. 9, Pl. 1, Fig. 1.
1987. *Scaphites kieslingswaldensis kieslingswaldensis* LANGENHAN & GRUNDEY; KAPLAN, KENNEDY & WRIGHT, p. 35, Pl. 4, Figs 3-6; p. 37, Pl. 5, Figs 1-5; with synonymy.
1991. *Scaphites kieslingswaldensis kieslingswaldensis* LANGENHAN & GRUNDEY; KENNEDY & CHRISTENSEN, Pl. 3, Fig. 2; Pl. 4, Figs 2, 6; Pl. 5, Fig. 1.
1994. *Scaphites kieslingswaldensis kieslingswaldensis* LANGENHAN & GRUNDEY; KAPLAN & KENNEDY, p. 149, Pl. 40, Figs 9-14; p. 151, Pl. 41, Figs 1-13.

TYPE: Holotype by monotypy is the original of LANGENHAN & GRUNDEY (1891, p. 9, Pl. 1, Fig. 1) from the Coniacian of Kieslingswalda.

MATERIAL: 1 specimen, MB.C.2796, from the Lower Coniacian, Playa de Tagle.

DESCRIPTION: The specimen is a small scaphitid (length: 38 mm). The spire is densely ornamented with simple ribs that split at the umbilical shoulder into two to three, finer secondaries. At the beginning of the shaft, the main ribs strengthen, and ventrolateral tubercles develop. As the ribs, the ventrolateral tubercles become progressively thicker towards mid-shaft, where very elongated bullae develop at the umbilical area. They give rise to the main ribs. Towards the hook, the ornament weakens, and on the hook, which is only partially preserved, the ventrolateral tubercles are reduced to a minimum or even absent. There are no umbilicolateral bullae on the hook.

DISCUSSION: As pointed out repeatedly (KENNEDY 1984, KAPLAN & KENNEDY 1994), the European stock of Coniacian scaphitids is represented by morphologically highly variable species. Even though the Spanish specimen is smaller than the average size of

microconchs of *S. kieslingswaldensis* (42 to 63 mm; KAPLAN & KENNEDY 1994), the general mode of develoment of ornament seems to fit this species.

OCCURRENCE: *S. kieslingswaldensis* occurs in the Upper Turonian and Coniacian of Germany and in the Coniacian of the Czech Republic, northern Spain, Austria, Poland and Madagascar.

STRATIGRAPHICAL IMPLICATIONS

The poor ammonite record does not permit a refined stratigraphical subdivision of the interval investigated comparable with that established by KÜCHLER (1998) for the Barranca (Navarra, northern Spain). However, some more general statements are possible.

In the Santander area, the Turonian/Coniacian boundary interval, defined by means of inoceramids, lacks stratigraphically significant ammonites, a situation known from other European Cretaceous basins (e.g. KENNEDY 1984, ČECH 1989, KAPLAN & KENNEDY 1994, KÜCHLER 1998). The oldest Coniacian ammonites from the working area, *P. subtricarinatum* and *F.* (*F.*) *alluaudi*, occur alongside *Cr. deformis deformis* and large *Cr.* ex gr. *crassus*, thus suggesting, on the basis of inoceramid stratigraphy, a late Early Coniacian age (Liencres section; Text-figs 1, 3). This fits data from other parts of Spain and northern Germany (KAPLAN & KENNEDY 1994, KÜCHLER 1998), where the FAD (first appearance datum) of *P. subtricarinatum* is located well within the *deformis deformis* Zone. Around Trasvia, where the section is less expanded, *Cremnoceramus crassus* occurs together with *P. subtricarinatum* above SB Co1, suggesting a terminal Early Coniacian age for the transgressive sediments of DS Co 1 (Text-fig. 2).

P. subtricarinatum is the most abundant species in the working area, as it is in Navarra (Basco Cantabrian Basin, northern Spain; KÜCHLER 1998). On the other hand, *P.* (*P.*) *tridorsatum*, previously used by some authors to define the base of the Middle Coniacian (e. g. KAPLAN & KENNEDY 1994, 1996; SANTAMARIA 1992; SANTAMARIA & MARTÍNEZ 1993), is rare to absent. KÜCHLER (1998) therefore suggested that the *Peroniceras tridorsatum* Zone should be abandoned in favour of a *Peroniceras subtricarinatum* Zone, the base of which falls within the *deformis deformis* Zone. The *subtricarinatum* Zone characterizes the upper part of the Lower Coniacian in Navarra, a situation also valid for the Santander area. In Navarra, KÜCHLER & ERNST (1989) and KÜCHLER (1998) defined the base of the Middle Coniacian with the FAD of *Gauthiericeras margae* (Pl. 4, Fig. 2), the index ammonite of the succeeding *margae* Zone. However, KAPLAN & KENNEDY (1994, 1996) used the FAD of *G. margae* to define the base of the Upper Coniacian in Westphalia, as was done by SANTAMARIA (1992) and SANTAMARIA & MARTÍNEZ (1993) for the Basco-Cantabrian Basin. As the FAD of *G. margae* approximates that of the inoceramid genus *Volviceramus*, the internationally accepted marker-taxon for the base of the Middle Coniacian (KAUFFMAN *& al.* 1996), the latter interpretation cannot be followed.

No *G. margae* has so far been collected in the exposures investigated, and it appears that most of the fauna [*Peroniceras* (*Peroniceras*) *subtricarinatum*, *P.* (*P.*) cf. *lepeei*, *Gaudryceras mite*, *Tetragonites epigonum*, *Puzosia* (*Puzosia*) *muelleri*, *Forresteria* (*Forresteria*) *alluaudi*, *Yabeiceras manasoaense*, *S.* cf. *kieslingswaldensis*] is, therefore, of an Early Coniacian age.

Peroniceras (*P.*) *westphalicum* and *Tissotioides haplophyllus* were collected, without any other biostratigraphically significant fossils, loose from an interval well above SB Co1. It is impossible to determine whether these are terminal Early or already early Mid-Coniacian in age. In Spain, *Tissotioides haplophyllus* was recorded in numbers from the Burgos area by SANTAMARIA (1992), and rarely from the Barranca (KÜCHLER 1998). Its occurrence is always restricted to the upper part of the *subtricarinatum* Zone, which equates with the *Metatissotia ewaldi* Zone of SANTAMARIA (1992), inferred to be of an Early Coniacian age. A similar stratigraphic position of *Tissotioides haplophyllus* can be observed in France (KENNEDY 1984, KENNEDY *& al.* 1995), where the species is always associated with peroniceratids below the FAD of *Gauthiericeras*. If these stratigraphic data were also valid for the Santander area, the base of the Middle Coniacian could be located well above SB Co1 in the latter region, somewhere in the higher parts of DS Co1. On the other hand, TRÖGER & SUMMESBERGER (1994) recorded *T. haplophyllus* to occur togehter with *Volviceramus koeneni* (MÜLLER) in the Austrian Gosau (locality Schmolnauer Alpe 1a), indicative for a Middle Coniacian age. As neither *G. margae* nor *Volviceramus* have been found in the ammonite loclalities treated here, the exact position of the Lower/Middle Coniacian boundary still remains unclear.

PALAEOBIOGEOGRAPHY

The few ammonites collected do not permit detailed palaeobiogeographic statements. However, the following features should be mentioned. Beside the cosmopolitian peroniceratids, the fauna from Santander yielded several taxa that are unknown [*Forresteria* (*F.*) *alluaudi*, *Yabeiceras manasoaense*, *Tetragonites epigonum*, *Tissotioides haplophyllus*] or rare (*Gaudryceras mite*) in northern Germany. This may indicate that these two areas belonged to different faunal provinces. Towards France and Spain, the character of the ammonite assemblages changes gradually, as indicated by the progressive appearance of the taxa mentioned above (KENNEDY 1984, KÜCHLER & ERNST 1989, KENNEDY *& al*. 1995, KÜCHLER 1998). In Austria, numerous *F.* (*F.*) *alluaudi* occur in Coniacian successions of the Gosau (Northern Calcareous Alps), together with *Metatissotia*, *Tissotioides*, *Tetragonites*, *Pseudophyllites* and peroniceratids (TRÖGER & SUMMESBERGER 1994). This faunal assemblage seems to be suggestive for more southern influence, which makes sense when considering the much more southerly palaeogeographic position of the Northern Calacareous Alps during Coniacian times (it should, however, also be mentioned that the associated inoceramid assemblages show a more northern character, thus indicating a mingling of Boreal and Tethyan taxa in the latter area).

Interpreting the few faunal data from the Santander area palaeobiogreographically, it appears that the faunal assemblage may be indicative for the Northern Transitional Subprovince of ERNST *& al*. (1996). The occurrences of *Forresteria* (*F.*) *alluaudi* and *Yabeiceras manasoaense* may indicate a weak E-W-directed faunal exchange between the Indo-Pacific area and the NCB.

CONCLUSIONS

Even though only a small total number of specimens was collected, the number of taxa is comparatively high. Most of the fauna was collected from thoroughly bioturbated sediments, where even the calcitic shelled organisms are only fragmentarily preserved. This seems to suggest that the rarity of ammonites is rather the expression of unfavorable preservation conditions than true rarity of ammonites. The entire fauna is interpreted to be of an Early Coniacian age. It cannot be excluded that the highest finds from Tagle may have come from the basal Middle Coniacian, but there is no evidence for it. The ammonite assemblage seems to reflect a mingling of Boreal and Tethyan elements.

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PLATE 1

1 – MB.C.2778; *Gaudryceras mite* (HAUER); cast (original in the M. Díaz collection, Santander), loose from the Lower Coniacian of the City of Santander

2-3 – MB.C.2780; *Tetragonites epigonum* KOSSMAT, Lower Coniacian of the Playa de Portio section, Liencres

4 – MB.C.2782; *Puzosia* (*Puzosia*) *muelleri* (DE GROSSOUVRE), Lower Coniacian of Trasvia

5 – MB.C.2796; *Scaphites* cf. *kieslingswaldensis* LANGENHAN & GRUNDEY, Lower Coniacian of Playa de Tagle

All figures × 0.85

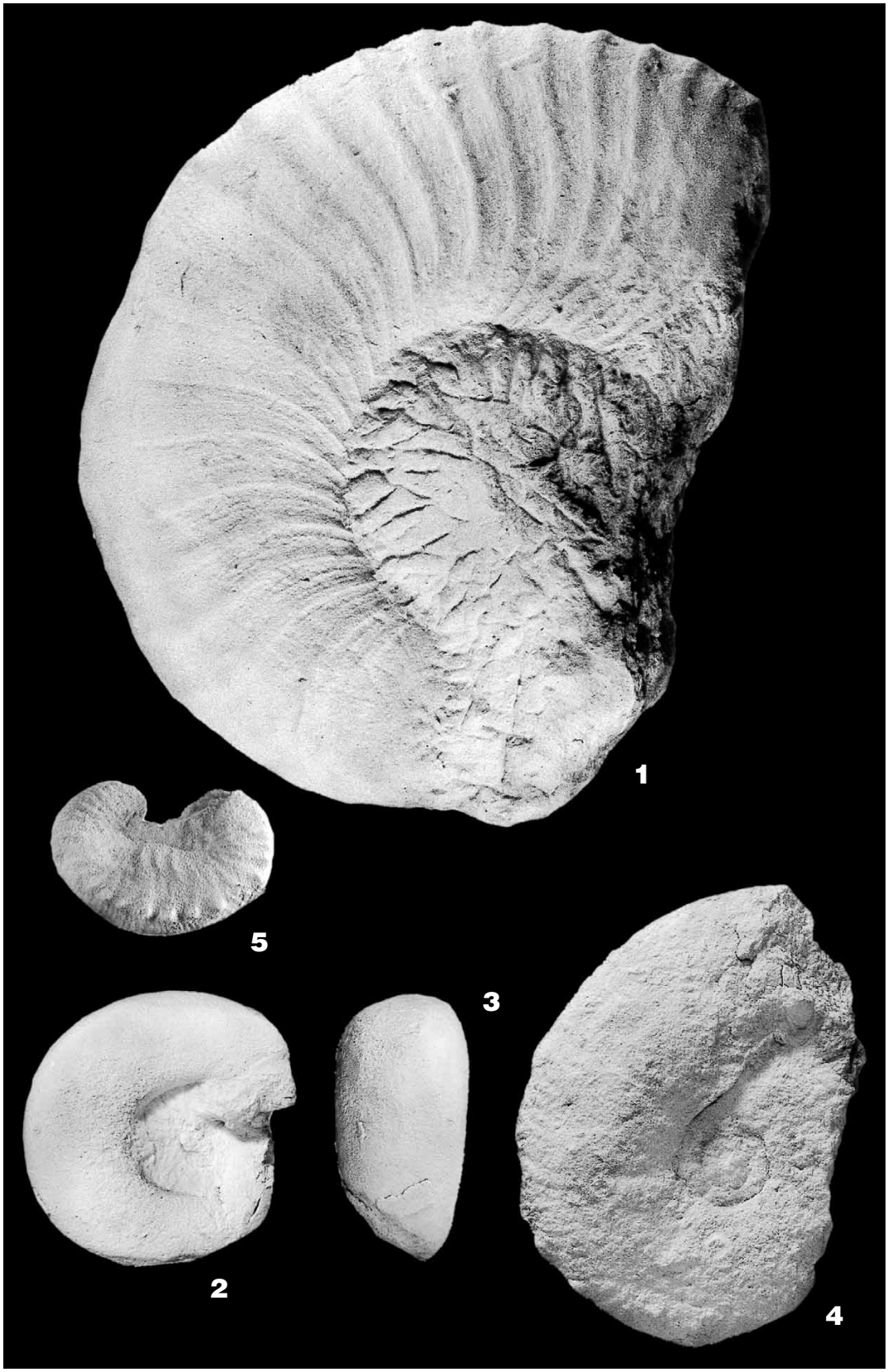
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PLATE 2

1-2 – MB.C.2785; *Tongoboryceras* cf. *canali* (DE GROSSOUVRE), Lower Coniacian of the City of Santander

3-4 – MB.C.2786; *Forresteria* (*Forresteria*) *alluaudi* (BOULE, LEMOINE & THÉVENIN); cast (original in the M. DÍAZ collection, Santander), loose from ther Lower Coniacian of the City of Santander

5 – MB.C.2787; *Yabeiceras manasoaense* COLLIGNON, Lower Coniacian of Trasvia

6-7 – MB.C.2788; *Peroniceras* (*Peroniceras*) cf. *lepeei* (FALLOT), Lower Coniacian of Playa de Portio, Liencres

All figures × 0.85

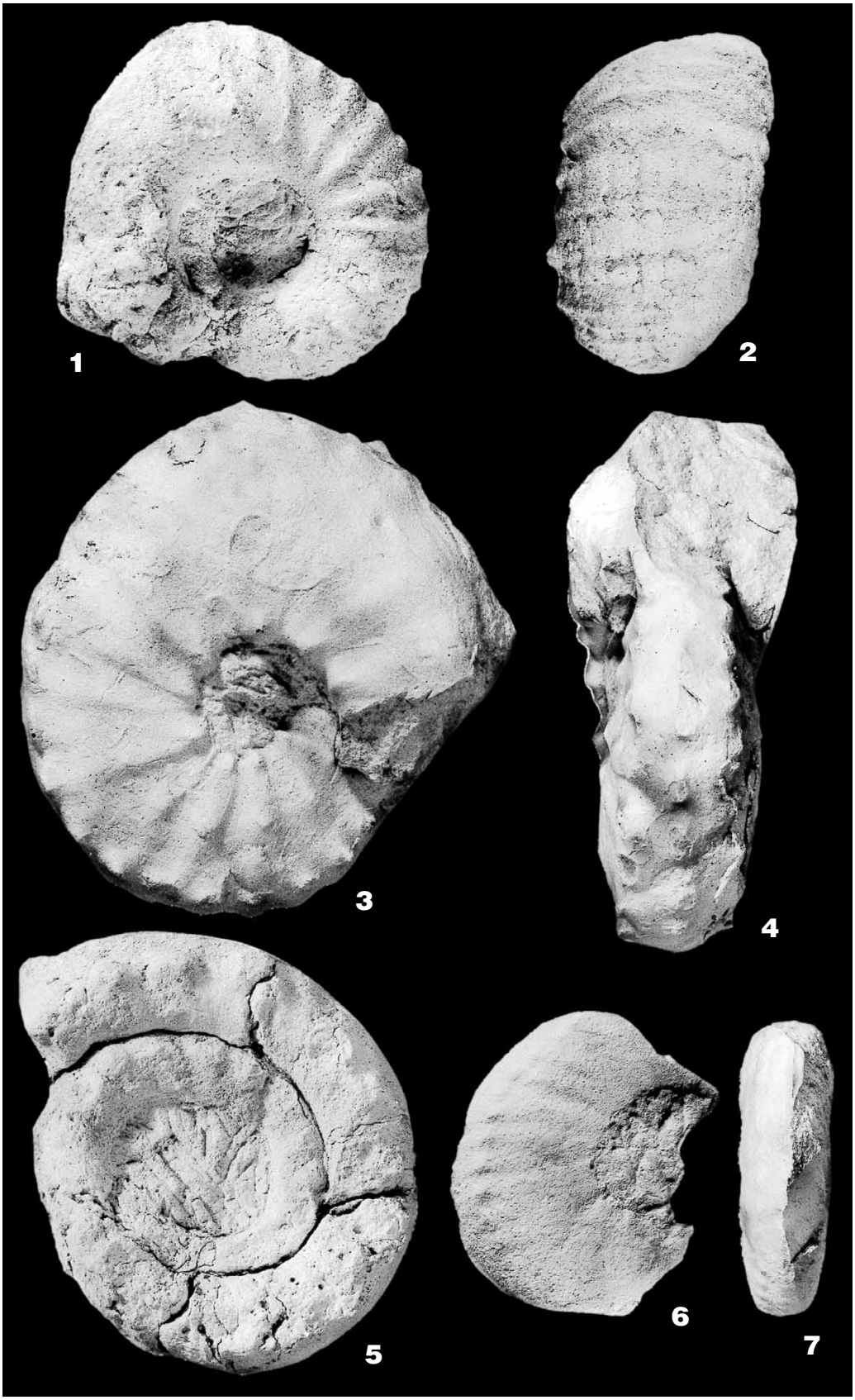
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PLATE 3

1 – MB.C.2791; *Peroniceras* (*Peroniceras*) *subtricarinatum* (D'ORBIGNY), Lower Coniacian of Trasvia; × 0.85

2 – MB.C.2793; *Peroniceras* (*Peroniceras*) *westphalicum* (STROMBECK), loose from Tagle, presumably Lower Coniacian or lowermost Middle Coniacian; app. × 0.5

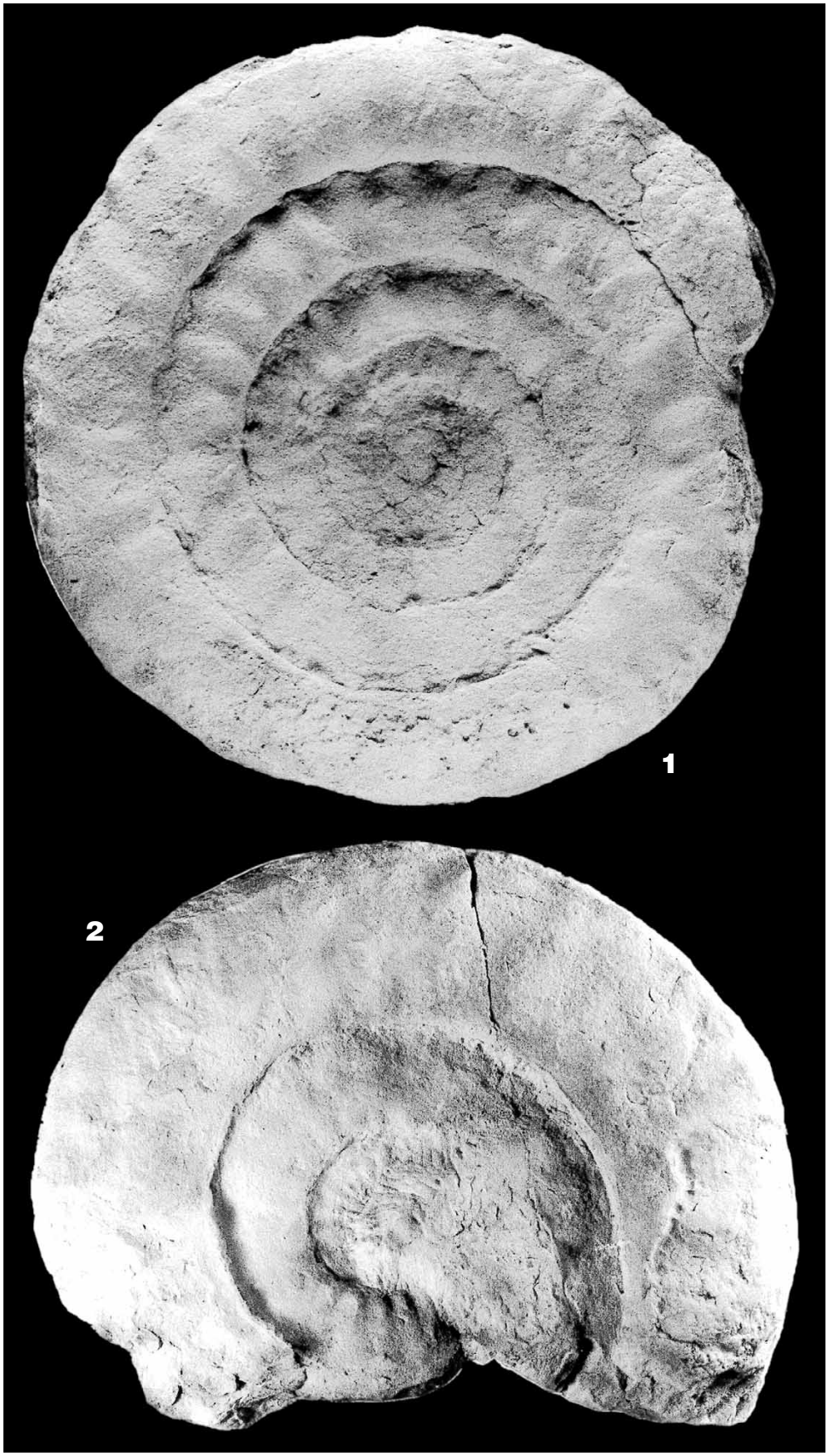
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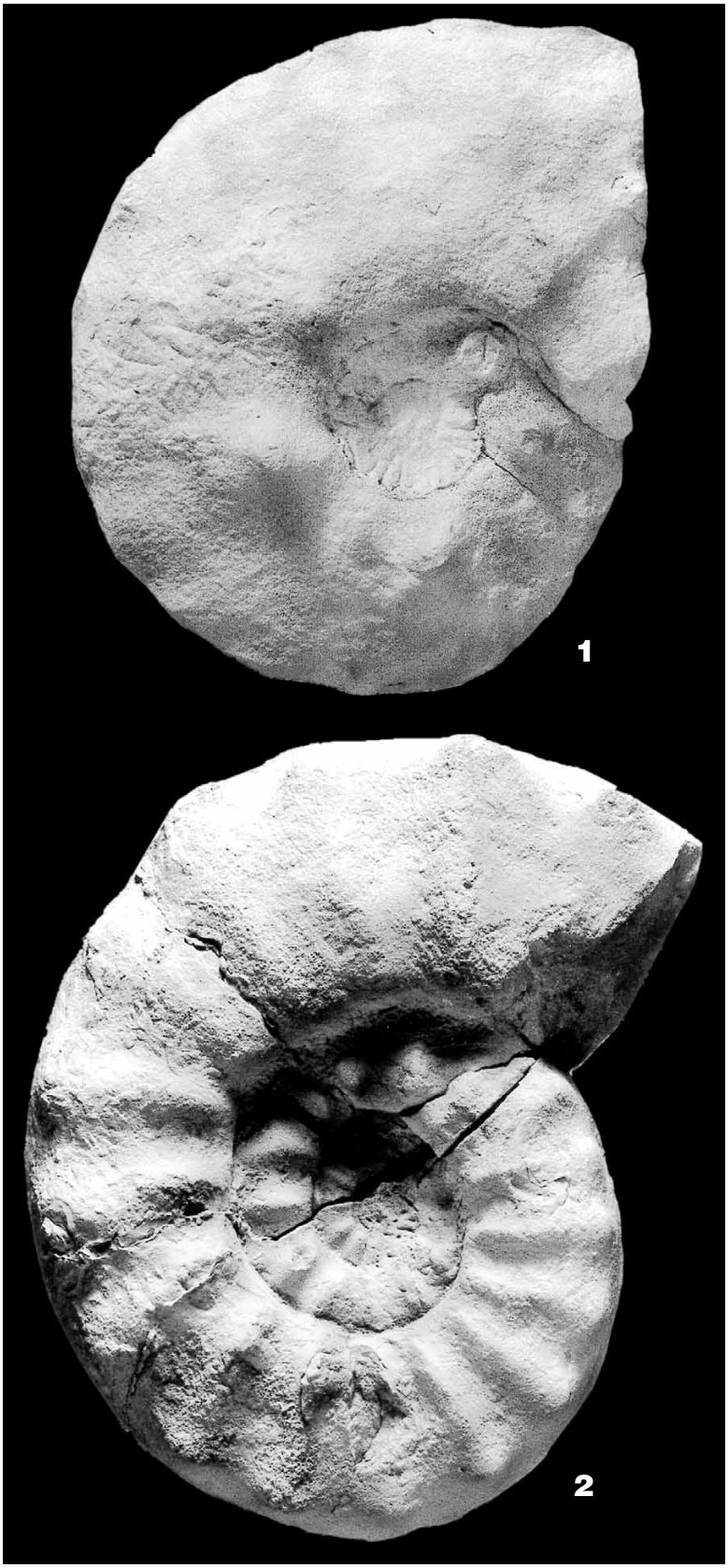
PLATE 4

1 – MB.C.2795; *Tissotioides* (*Tissotioides*) *haplophyllus* (REDTENBACHER), loose from Playa de Tagle, presumably Lower Coniacian or lowermost Middle Coniacian; × 0.85

2 – *Gauthiericeras margae* (SCHLÜTER), the index-ammonite for the base of the middle Coniacian, from the Villanueva section (Basco Cantabrian Basin; see SANTAMARIA & MARTÍNEZ 1993 for locality details); × 0.85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