

# Late Cretaceous nautilids from northern Cantabria, Spain

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## ABSTRACT:

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Nautilids do not occur throughout the Upper Cretaceous succession in northern Cantabria. Although relatively rare, they preferentially occur in condensed transgressive horizons. Nine species belonging to the genera *Angulithes* MONTFORT, 1808, *Eutrephoceras* HYATT, 1894, and *Pseudocnoceras* SPATH, 1927 are recorded. *A. westphalicus* (SCHLÜTER, 1872) and *E. cf. justum* (BLANFORD, 1861) are reported for the first time from the Iberian Peninsula. The diagnosis of *A. vascogoticus* WIEDMANN, 1960 is emended.

The Cenomanian was characterized by a relative abundance of nautilids of the genus *Angulithes* which display a major radiative event, evolving relatively short-lived species. This development was probably related to the "Cenomanian transgression". Compared to co-occurring ammonite faunas, *Angulithes* inhabited deeper and more distal environments. A possible transitional form, connecting the two genera *Angulithes* and *Deltocymatoceras* KUMMEL, 1956 (?Turonian, Coniacian - Santonian), is recorded from the Mid-/Late Cenomanian. The Turonian to Campanian succession is dominated by long-ranging nautilids of the genus *Eutrephoceras*.

**Key words:** Nautilids, Late Cretaceous, Spain, Taxonomy.

## INTRODUCTION

Nautiloids are the least studied Cretaceous cephalopod group and the compiled literature stands in remarkable contrast to that of ammonites and belemnites. Furthermore, systematic studies are suffering from inconsistencies and knowledge is distributed among many different papers. The last comprehensive accounts on post-Triassic nautiloids were presented by KUMMEL (1956), WIEDMANN (1960), and SHIMANSKY (1975), the latter two with a bias to Cretaceous nautiloids.

Apart from papers dealing with limited material (e.g. CALZADA & VIADER 1980, reporting two cymatoceratid genera from the Aptian), Cretaceous nau-

tiloids from the Iberian Peninsula have received little attention since the last synoptic work by WIEDMANN in 1960. In northern Cantabria (Text-fig. 1), fossiliferous Cretaceous rocks are superbly exposed in spectacular coastal sections. In 1990, the Berlin Cretaceous working group started their investigations on the Upper Cretaceous Series, and, during fieldwork, numerous nautilids were collected. However, due to their limited stratigraphic value and sometimes poor preservation, these cephalopods were hitherto not studied. In order to provide a basis for taxonomic, palaeobiogeographic, and palaeoecologic studies, a documentation and systematic description of Late Cretaceous nautilids of northern Cantabria is attempted in this paper.

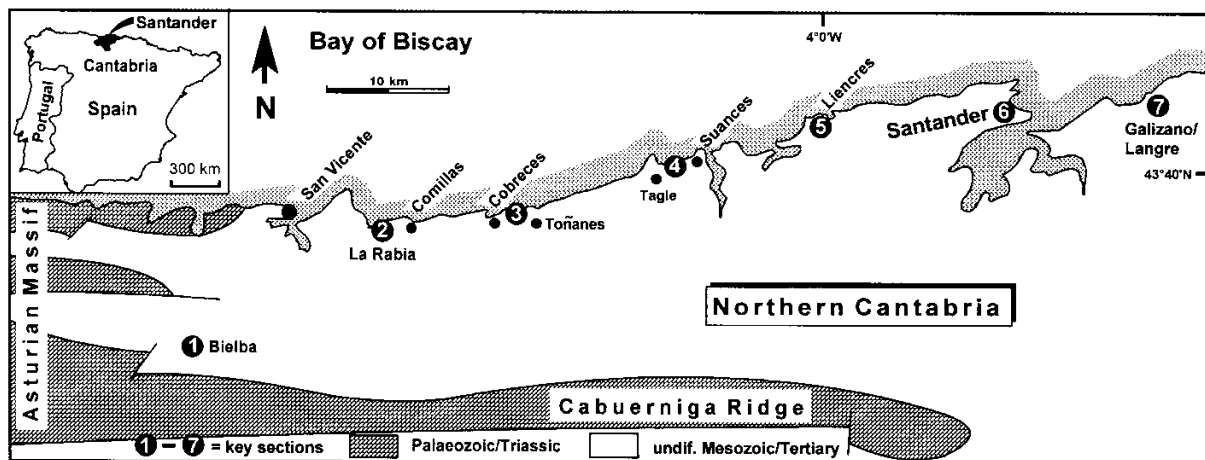


Fig. 1. Locality map of investigated sections in northern Cantabria

## GEOLOGICAL SETTING

During the Mesozoic, numerous basins developed at the North Iberian continental margin in response to rifting and spreading processes in the evolving Biscay Ocean. In northern Cantabria, basin development started in the mid-Valanginian and gave rise to the so-called “North Cantabrian Basin” (WIESE & WILMSEN 1999). During the Late Cretaceous, the North Cantabrian Basin was situated at the northern margin of the Iberian microplate, forming a narrow, E/W elongated intra-shelf basin in which a lithologically variable, ca. 1100 m thick succession of marine, predominantly calcareous sediments accumulated (Text-fig. 2). The sediments record a transgressive/regressive megacycle starting with deltaic siliciclastics at the Albian/Cenomanian boundary (lower Bielba Formation) and ending with prolonged emersion in the (?)Late Maastrichtian (Muñorrodero Formation, Text-fig. 2). Transgressive maxima are recorded in the Late Cenomanian, Mid-/Late Turonian, Mid-Santonian, and Early Campanian. Deposition occurred under a subtropical climate at a palaeo-latitude of 30–40°N and the fauna showed a mingling of Boreal and Tethyan faunal elements to different extents. For this intermediate palaeobiogeographic region, ERNST & *al.* (1996) introduced the term “Northern Transitional Subprovince” in order to define a transitional zone between the Boreal and Tethyan Realm. The depositional history of the North Cantabrian Basin is beyond the scope of this paper and has been discussed elsewhere (WILMSEN & *al.* 1996; WIESE & WILMSEN 1999).

## LITHOSTRATIGRAPHY

The Upper Cretaceous Series of northern Cantabria is subdivided into five formations (GARCIA-MONDÉJAR & PUJALTE 1982) and several (in part informal) lithostratigraphic sub-units (members, beds; WILMSEN & *al.* 1996; Text-fig. 2). The Bielba Formation (uppermost Albian/Lower Cenomanian, 100 to 250 m) comprises deltaic sediments (*siliciclastic member*) and sandy marl and limestone (*transitional member*). The Altamira Formation (Lower to lower Upper Cenomanian, 80 to 140 m) consists of thickly-bedded brownish calcarenites and some intercalated marl. Its terminal bed (Hardground 99, Nivel Ferruginizado) is strongly condensed (it yielded abundant nautilids) and represents a drowning unconformity (WILMSEN 1997). The *Cenomanian marl formation* is an informal lithostratigraphic unit and laterally replaces the Altamira Formation in the eastern parts of the North Cantabrian Basin; it may reach a thickness of more than 100 m. The Altamira Formation as well as the *Cenomanian marl formation* are followed by the thick (>500 m) Turonian to Campanian Sardinero Formation comprising fossiliferous light-grey limestone and dark-grey marl; mainly according to fossil content, several members are recognized (Text-fig. 2). The Sardinero Formation contains several levels where nautilids are relatively abundant. The succeeding Cabo de Lata (sandy limestones) and Muñorrodero (primary dolomites, marl) formations of the Maastrichtian are poorly fossiliferous. They record the progressive infilling of the basin.

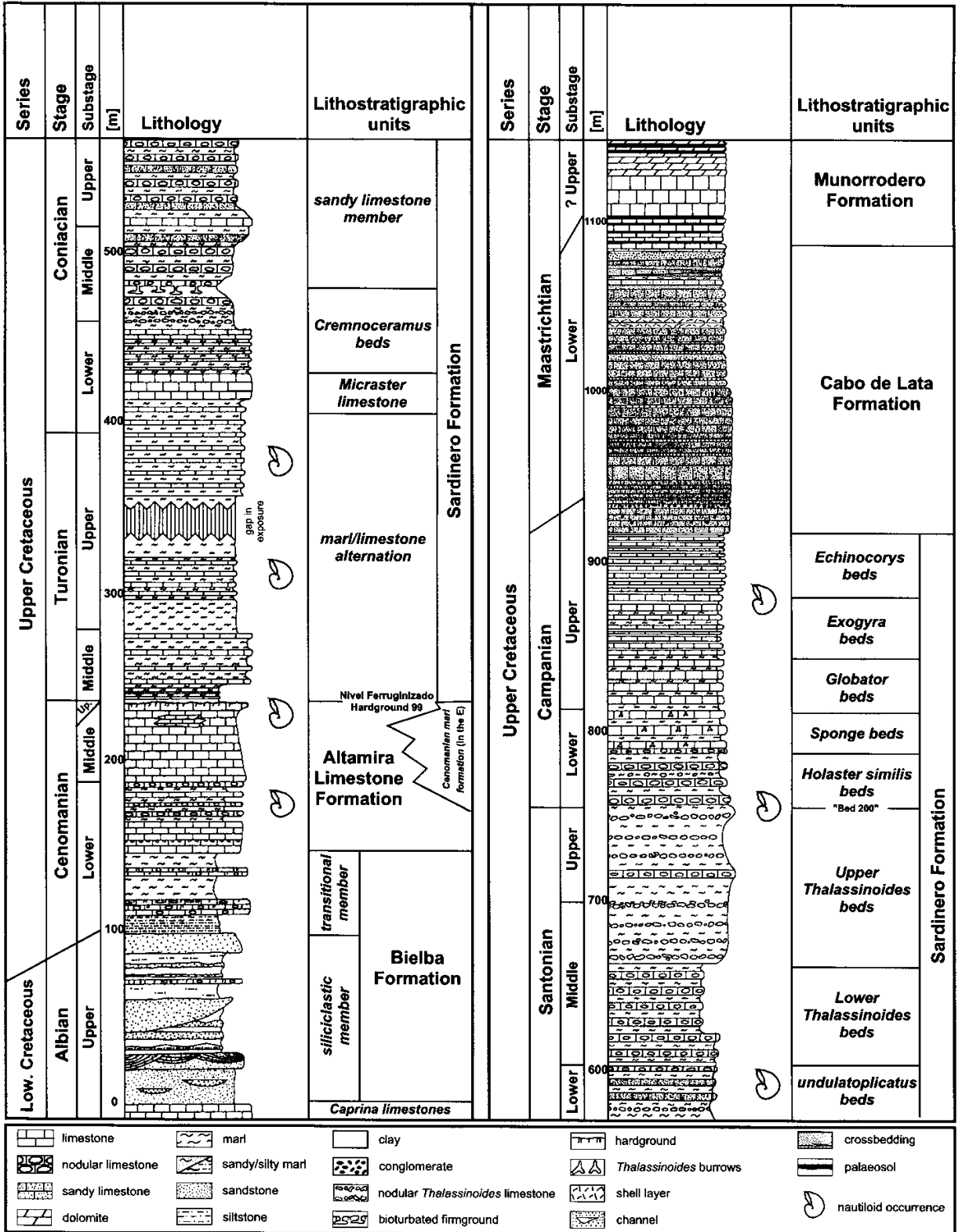


Fig. 2. Lithologic summary log and lithostratigraphic subdivision of the Upper Cretaceous Series in northern Cantabria (derived from sections in the Santander area)

## MATERIAL AND METHODS

The Upper Cretaceous succession was logged and nautilid specimens were collected bed-by-bed at several localities on a 70 km E-W traverse. High resolution integrated stratigraphy including ammonite and inoceramid data, as well as event and sequence stratigraphy, permits a precise dating of the nautilid occurrences. Only a short description of the find localities (cf. Text-fig. 1, Tab. 1) is provided in this paper; detailed maps of all cited localities can be found in BRÜNING (1996), OPPERMAN (1996), WIESE (1997), and WILMSEN (1997).

The preservation of the fauna is moderate, most specimens are internal moulds (e.g. Text-fig. 4). For taxonomic analyses, the shape of the suture is considered the most important feature; dimensions of the shell ( $a$  = maximum height of shell;  $b$  = maximum breadth of last whorl;  $c$  = maximum height of last whorl; all values were obtained using a sliding caliper and are given in mm) and the location of the siphuncle are also of great significance (cf. Text-fig. 3); the ratios of  $b/a$ ,  $c/a$ , and  $b/c$  describe the form of

the shell (for morphological terms see TEICHERT 1964). These features were emphasized in documentation (Pls 1-4); sutures and whorl shapes were compiled in Pl. 5. However, due to poor preservation, a part of the collected material was kept in open nomenclature (cf. BENGTSO 1988) or proved to be undeterminable.

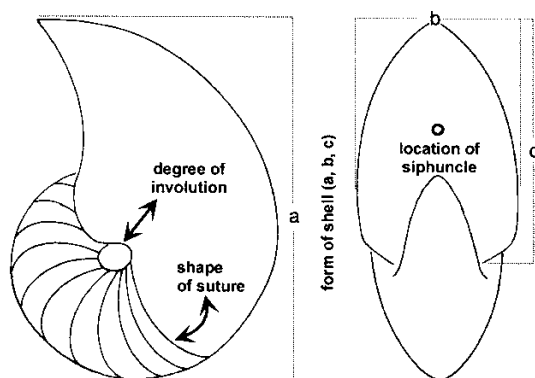


Fig. 3. Criteria used for taxonomic classification

Specimen	Determination	Locality	Lithostratigraphy	Age
PIW99I 1	<i>Angulithes fleuriausianus</i> (D'ORBIGNY, 1840)	Bielba	top of Altamira Limestones	late Mid-Cenomanian
PIW99I 2	<i>Angulithes triangularis</i> MONTFORT, 1808	Tagle	<i>Cenomanian marl formation</i>	late Mid-Cenomanian
PIW99I 3	<i>Angulithes vascogoticus</i> WIEDMANN, 1960	Bielba	Nivel Ferruginizado	Late Cenomanian
PIW99I 4	<i>A. vascogoticus</i> WIEDMANN, 1960	Bielba	Nivel Ferruginizado	Late Cenomanian
PIW99I 5	<i>A. vascogoticus</i> WIEDMANN, 1960	Tagle	<i>Cenomanian marl formation</i>	Late Cenomanian
PIW99I 6	<i>A. vascogoticus</i> WIEDMANN, 1960	Tagle	<i>Cenomanian marl formation</i>	Late Cenomanian
PIW99I 7	<i>A. vascogoticus</i> WIEDMANN, 1960	Mijares (s'Tagle)	<i>Cenomanian marl formation</i>	Late Cenomanian
PIW99I 8	<i>A. cf. vascogoticus</i> WIEDMANN, 1960	Bielba	<i>Cenomanian marl formation</i>	Late Cenomanian
PIW99I 9	<i>Angulithes westphalicus</i> (SCHLÜTER, 1872)	Liencres	<i>Echinocorys beds</i>	Late Campanian
PIW99I 10	<i>Angulithes</i> sp.	Tagle	<i>Cenomanian marl formation</i>	late Mid-Cenomanian
PIW99I 11	(?) transitional form <i>Angulithes</i> MONTFORT, 1808 - <i>Deltocymatoceras</i> KUMMEL, 1956	Liencres	Hardground 99	Mid-/Late Cenomanian
PIW99I 12	<i>Eutrephoceras</i> sp.	Tagle	<i>Cenomanian marl formation</i>	Late Cenomanian
PIW99I 13	<i>Eutrephoceras bouchardianum</i> (D'ORBIGNY, 1840)	Liencres	Sardinero Formation	Late Turonian
PIW99I 14	<i>Eutrephoceras cf. indicum</i> (D'ORBIGNY, 1850)	Liencres	Sardinero Formation	Mid-Turonian
PIW99I 15	<i>Eutrephoceras darupense</i> (SCHLÜTER, 1876)	Liencres	<i>Upper Thalassinoides beds</i>	Late Santonian
PIW99I 16	<i>Eutrephoceras darupense</i> (SCHLÜTER, 1876)	Liencres	<i>Exogyra beds</i>	Late Campanian
PIW99I 17	<i>Eutrephoceras cf. justum</i> (BLANFORD 1861)	Liencres	<i>undulatoplicatus beds</i>	Early Santonian
PIW99I 18	<i>Eutrephoceras cf. darupense</i> (SCHLÜTER, 1876)	Liencres	Sardinero Formation	Late Turonian
PIW99I 19	<i>Eutrephoceras</i> sp.	Liencres	Sardinero Formation	latest Santonian
PIW99I 20	<i>Eutrephoceras</i> sp.	Liencres	Sardinero Formation	latest Santonian
PIW99I 21	<i>Eutrephoceras</i> sp.	Liencres	Sardinero Formation	latest Santonian
PIW99I 22	<i>Pseudocnoceras dorsoplicatus</i> (WIEDMANN, 1960)	Santander	Altamira Limestones	Early Cenomanian
MB.C.2052	<i>Angulithes triangularis</i> MONTFORT, 1808	Langre	<i>Cenomanian marl formation</i>	early Mid-Cenomanian
MB.C.2066	<i>A. vascogoticus</i> WIEDMANN, 1960	La Rabia	Nivel Ferruginizado	Late Cenomanian

Tab. 1. Repository, found locality, lithostratigraphy, and age of Cantabrian nautilids (cf. Text-figs 1, 2)

The material is stored at the institute for Palaeontology of the Bayerische Julius-Maximilians University Würzburg (repository PIW99I). Specimens MB.C.2066 and MB.C.2052 are stored and registered at the Museum für Naturkunde, Humboldt-Universität, Berlin (Tab. 1).

Order Nautilida DE BLAINVILLE, 1825  
 Suborder Nautilina DE BLAINVILLE, 1825  
 Superfamily Nautilaceae DE BLAINVILLE, 1825  
 Family Nautilidae DE BLAINVILLE, 1825

Genus *Angulithes* MONTFORT, 1808

## SYSTEMATIC PALAEOLOGY

Modern work on the taxonomy of post-Triassic nautiloids is limited and somewhat controversial. The most important contributions are the monographs of KUMMEL (1956, 1964 [Treatise]), WIEDMANN (1960), and DZIK (1984); SHIMANSKY (1975) and MATSUMOTO & *al.* (1984b) mainly concentrated on Cretaceous nautiloids. However, there are major disagreements concerning classification at the family and generic level. Whereas the Treatise proposes a subdivision of post-Triassic nautiloids (superfamily Nautilaceae) into six families (*sensu* SPATH 1927), WIEDMANN (1960), SHIMANSKY (1975) and WIEDMANN & SCHNEIDER (1979) strongly argue against a splitting of this group which is generally accepted as a monophyletic unit derived from Late Triassic *Cenoceras* (KUMMEL 1956). Especially the family Cymatoceratidae SPATH, 1927 was regarded as a taxonomic "sink" for sculptured offshoots of the "regular" nautiloid stock (e.g. TINTANT 1993). SHIMANSKY (1975) included most of the cymatoceratid genera in the family Nautilidae (a view that is supported in this study).

However, WIEDMANN himself (1960) proposed in his inclusive subfamily Nautilinae a major reorganisation at the generic and species level (dismissing several genera and erecting numerous subgenera and subspecies), which is not followed here. As "the present understanding of the phylogeny of the Nautilina does not permit the construction of coherent systematics" (DZIK 1984, p. 183), the herein presented taxonomic subdivision is somewhat provisional and largely follows SHIMANSKY (1975). As an exception, the genus *Angulithes* MONTFORT, 1808 (= *Deltoidonautilus* SPATH, 1927) is placed within the Nautilidae (not Hercoglossidae SPATH, 1927), which is consistent with the classification of the Nautilidae by MATSUMOTO in MATSUMOTO & *al.* (1984b, p. 342, Text-fig. 4). According to MATSUMOTO (p. 343), *Angulithes* is a derivative of *Kummelonautilus* MATSUMOTO, 1984 which, in turn, is considered to be ancestral to the extant genus *Nautilus* LINNAEUS, 1758 (TEICHERT & MATSUMOTO 1987).

TYPE SPECIES: *Angulithes triangularis* MONTFORT, 1808 (p. 7).

DIAGNOSIS: Nautiliconic, compressed, rather involute, with slightly convex whorl sides. Whorl section sagittate with narrowly rounded to angular venter and deeply impressed dorsal zone; siphuncle small, located dorso-centrally; suture moderately sinuous with umbilical saddle, broad lateral lobe and narrowly rounded to pointed ventral saddle; shell generally smooth, growth lines may be very pronounced.

REMARKS: The genus name *Angulithes* was not used until 1927, when SPATH (1927, p. 21) revived it and placed it in the family Nautilidae. In the same work, he erected the new genus *Deltoidonautilus*, stating that it strongly resembles *Angulithes* (SPATH 1927, p. 26). It was thought that *Angulithes* was confined to the Cretaceous Period, *Deltoidonautilus* to the Tertiary. However, since there is a continuous record of nautiloids with angular venters and moderately sinuous sutures throughout the Cretaceous to the Eocene and no "stratigraphic taxa" are accepted, *Deltoidonautilus* SPATH, 1927 is placed as a synonym of *Angulithes* (cf. KUMMEL 1953, 1956). Later, KUMMEL (1964, p. K456) changed his mind and placed *Angulithes* as *nom. dub.* in *Deltoidonautilus*. However, *Angulithes* is well defined by its type species *A. triangularis* MONTFORT, 1808 and has, thus, priority over *Deltoidonautilus* (see also WIEDMANN & SCHNEIDER 1979, p. 653; and MATSUMOTO 1983, p. 14).

OCCURRENCE: *Angulithes* occurred from the Early Cretaceous (Albian: *A. arcuatus* [DESHAYES in LEYMERIE, 1842; *Angulithes* sp., KUMMEL 1953) to Oligocene (*A. bakeri* [TEICHERT, 1947]). Cretaceous species of *Angulithes* are mostly known from Europe, but also from India, Peru, Texas, and New Mexico (e.g. KUMMEL 1953, 1956); Tertiary species are nearly global in distribution.

*Angulithes fleuriausianus* (D'ORBIGNY, 1840)  
 (Text-fig. 4; Pl. 1, Fig. 1a/b; Pl. 5, Figs 1, 14)

1840. *Nautilus fleuriausianus* n. sp.; D'ORBIGNY, p. 82, Pl. 15.
- non 1853. *Nautilus fleuriausianus* D'ORBIGNY; SHARPE, p. 16, Pl. 6, Fig. 3.
- non 1876. *Nautilus Fleuriausianus* D'ORBIGNY; SCHLÜTER, p. 169, Pl. 45, Figs 3, 4.
1910. *Nautilus fleuriausianus* D'ORB. var. *indica* STOL.; SPENGLER, p. 143, Pl. 13(28), Fig. 1a/b.
- non 1910. *Nautilus* cf. *fleuriausianus* D'ORBIGNY; SPENGLER, p. 144, Pl. 13(28), Fig. 2a/b.
1956. *Angulithes fleuriausianus* (D'ORBIGNY) 1840; KUMMEL, p. 456, Text-fig. 33/D, E, F.
1960. *Angulithes* (*Angulithes*) *fleuriausianus* (D'ORBIGNY) 1840; WIEDMANN, p. 183, ?Pl. 19, Fig. A; Pl. 20, Figs N, O; Pl. 21, Figs I, L, M; ?Pl. 23, Fig. O; Pl. 26, Figs 1-3; Text-figs 14, 15 (see for extensive synonymy).
1962. *Angulithes fleuriausianus* (D'ORBIGNY); AVNIMELECH & SHORESH, p. 529.
1975. *Deltoidonautilus ?fleuriausianus* (D'ORBIGNY, 1840); SHIMANSKY, p. 138, Pl. 31, Fig. 1.
1994. *Angulithes fleuriausianus* (D'ORBIGNY, 1840); COBBAN & KENNEDY, p. E2, Pl. 1, Figs 6-9; Pl. 2, Figs 1-3.

**MATERIAL:** One internal mould (specimen PIW99I 1) from the road from Bielba to Labarces, ca. 500 km ENE of Bielba; parts of the shell on the inner whorl are preserved (Text-fig. 4).

**DESCRIPTION:** Large, moderately compressed, involute nautilid with broad ovoidal to subtrigonal whorl section ( $a = 170.0$ ;  $b = 95.9$ ;  $c = 96.9$ ;  $b/a = 0.56$ ;  $c/a = 0.57$ ;  $b/c = 0.99$ ), convergent outer flanks and a narrowly rounded venter; the inner flanks are broadly rounded. Maximum breadth of whorl is near the umbilical shoulders. The suture has a small lobe at the umbilical wall, a weakly developed saddle at the umbilical shoulder, a broad, shallow lateral lobe, and a ventral saddle which is only slightly higher than the umbilical one; the siphuncle is located centrally. The specimen is a phragmocone; maximum distance of septa at the venter is 30 mm. Parts of the shell in the umbilical area are preserved and show that the umbilical area was completely closed.

**REMARKS:** *A. fleuriausianus* differs from *A. triangularis* (see below) by having a narrowly rounded venter and a less compressed subtrigonal whorl section. It is also known from the Early Cenomanian (COBBAN & KENNEDY 1994) and, thus, appears earlier than *A. triangularis*. The Cantabrian specimen differs not significantly in dimensions of shell and shape of suture from WIEDMANN'S (1960) Iberian material of *A. fleuriausianus* and is, therefore, assigned to the same species.

One internal mould of an isolated body chamber (PIW99I 10) from bed TE 35 at the "Pas du Chat" section north of Tagle (WILMSEN 1997), herein listed as *Angulithes* sp., might also belong to this species. The large body chamber comprises 1/3 of a complete whorl ( $b \sim 71$  mm;  $c \sim 95$  mm;  $b/c = 0.75$ ) and is moderately compressed with strongly converging outer flanks and a narrowly rounded venter. The diameter of the complete nautilid was  $>210$  mm. The suture is similar to that of *A. fleuriausianus* and it occurs at the same stratigraphic level (late Mid-Cenomanian) like specimen PIW99I 1. However, a specific assignment is not possible due to incomplete preservation.

**OCCURRENCE:** *A. fleuriausianum* is a typical Cenomanian species known from England, France, Spain, Germany, Austria, Tunisia, Israel, India, and New Mexico (e.g. COBBAN & KENNEDY 1994). WIEDMANN (1960) recorded *A. fleuriausianum* from the Coniacian of Iberia. In northern Cantabria, it occurs in upper Middle Cenomanian rocks.



Fig. 4. *Angulithes fleuriausianus* (D'ORBIGNY, 1840); specimen PIW99I 1;  $\times 0.6$

*Angulithes triangularis* MONTFORT, 1808  
(Pl. 1, Figs 2a/b; Pl. 5, Figs 2, 15, 16)

1802. 'Nautilite triangulaire du Hâvre'; MONTFORT, p. 292, Pl. 49, Fig. 2.  
 1808. *Angulithes triangularis*; MONTFORT, p. 7.  
 1840. *Nautilus triangularis* MONTFORT; D'ORBIGNY, p. 79, Pl. 12.  
 1912. *Nautilus munieri* CHOFFAT; SCHLAGINTWEIT, p. 99, Pl. 6, Fig. 9, Text-fig. 3.  
 1915. *Nautilus mermeti* COQUAND var. *munieri* CHOFFAT; ECK, p. 184, Pl. 9, Fig. 3, 4.  
 1951. *Angulithes triangularis* MONTFORT; WRIGHT & WRIGHT, p. 11.  
 1956. *Angulithes triangularis* MONTFORT; KUMMEL, p. 454, Text-fig. 33/C, Pl. 25, Figs 1, 2 and Pl. 26, Figs 1, 2.  
 1960. *Angulithes (Angulithes) triangularis triangularis* MONTFORT - WIEDMANN, p. 186, Pl. 21, Fig. P; Pl. 22, Fig. I (see for extensive synonymy).  
 1962. *Angulithes (?) triangularis* (D'ORBIGNY); AVNIMELECH & SHORESH, p. 530.  
 1997. *Angulithes (Angulithes) triangularis triangularis* (MONTFORT); WILMSEN, p. 104, Pl. 24, Fig. 4a-b.  
 1998. *Angulithes triangularis*; BRETON, p. 13, Pl. 3, Fig. 43.

**MATERIAL:** Two specimens (PIW99I 2 and MB.C.2052) which are complete internal moulds; specimen PIW99I 2 is slightly deformed.

**DESCRIPTION:** Medium-sized, compressed, involute nautilid with triangular whorl section. In juvenile stage with rounded, later with an angular venter formed by strongly converging outer flanks; the dorsal area is deeply impressed. The suture shows a moderately high saddle on the umbilical shoulder, a broad and shallow lateral lobe, and a pointed ventral saddle. The siphuncle is located dorso-centrally. The dimensions of the two specimens are as follows:

Specimen	a	b	c	b/a	c/a	b/c
MB.C.2052	114.4	48.8	74.6	0.43	0.65	0.65
PIW99I 2	145.0	53.5	89.3	0.37	0.62	0.60

Both specimens are adults as indicated by septal crowding.

**REMARKS:** The first description of *A. triangularis* is commonly referred to MONTFORT (1802, 'Nautilite triangulaire du Hâvre'). However, this first description of MONTFORT (1802, p. 292-296, Pl. 49, Fig. 2) did not come up to the rules of international zoologic nomenclature. Therefore, the designation of MONTFORT (1808, p. 7) is regarded as the first valid introduction of the species' and the genus' name.

*A. triangularis* is closely related to *A. vascogoticus* (see below) which has a different suture and whorl section. *A. triangularis* differs from *A. mermeti* (COQUAND, 1862) (comp. Pl. 5, Fig. 3) by its less compressed whorl section and the less sinuous suture. However, WIEDMANN (1960) considered both as conspecific and regarded *A. mermeti* as a subspecies of *A. triangularis*. According to the (limited) Cantabrian material, late Middle Cenomanian representatives of *A. triangularis* are more compressed and have a more sinuous suture, closely resembling the (Late Cenomanian) species *A. mermeti*. However, more material is needed to clarify if *A. mermeti* really falls into intraspecific variation with *A. triangularis*.

Although a rounded venter in adult stage is reported by WIEDMANN (1960), the venters of the two adult specimens from Cantabria are acute.

**OCCURRENCE:** *A. triangularis* was regarded by WIEDMANN (1960) as a Late Cenomanian species. However, in northern Cantabria, it first appears in the early Mid-Cenomanian (MB.C.2052) and it is also reported by BRETON (1998, p. 13) from the "Craie de Rouen" in Normandy, where it is associated with early Mid-Cenomanian ammonites (e.g. *Acanthoceras rhotomagense*). In northern Cantabria, it exclusively occurs in rocks of Middle Cenomanian age. Its range, therefore, includes the Mid- and Late (?) Cenomanian. *A. triangularis* has been recorded from England, France, Spain, northern Africa, Israel and Peru.

*Angulithes vascogoticus* WIEDMANN, 1960

(Pl. 1, Fig. 3a/b; Pl. 2, Figs 1a/b, 2a/b, 3a/b; Pl. 5, Figs 4, 5, 17, 18)

1960. *Angulithes (Angulithes) vascogoticus* n. sp.; WIEDMANN, p. 191, Pl. 27, Fig. 3; Text-figs 22, 23.  
 1997. *Angulithes (Angulithes) triangularis triangularis* (MONTFORT); WILMSEN, p. 104, Pl. 37, Fig. 1a-b.

**MATERIAL:** Seven specimens (PIW99I 3-PIW99I 8, MB.C.2066); specimen PIW99I 3, -5, -6 are complete internal moulds including the body chamber; specimens PIW99I 7 and -8 are incomplete, and specimens PIW99I 4 and MB.C.2066 are septate fragments with parts of the shell preserved.

**EMENDED DIAGNOSIS:** Moderately compressed nautilid with ovoid to triangular whorl section (whorl breadth-to-height ratio between 0.9 and 1.0);

flanks strongly convex with maximum breadth at inner flanks; steep umbilical wall; venter rounded in early ontogenetic stages, later angular, adult body chamber again with rounded venter; suture with deep lobe at the umbilical seam, narrow and pronounced umbilical saddle, broad and deep lateral lobe and pointed external saddle, slightly higher than the umbilical one; siphuncle located dorso-centrally; large fold-like undulations may be present on outer flanks of the phragmocone, rapidly decreasing on inner flanks and not crossing the venter.

**DESCRIPTION:** Moderately compressed, involute nautilids with ovoid to trigonal whorl section (b/a ratio is around 0.55, c/a ratio around 0.60); the venter is rounded up to a diameter of ~50 mm, getting more acute in adult stages. Full grown-ups again develop a rounded venter of the body chamber (Pl. 5, Figs 4, 5). Maximum breadth of whorl in juvenile stage is near the middle of the flanks; in adult stage, it is near the umbilical shoulder; umbilical walls are steep. The whorl breadth-to-height ratio (b/c) is around 0.9 to 1.0.

Dimensions of *A. vascogoticus* WIEDMANN, 1960:

specimen	a	b	c	b/a	c/a	b/c
	[mm]	[mm]	[mm]			
PIW99I 3	126.5	70.0	69.6	0.55	0.55	1.01
PIW99I 4	67.1	35.9	39.8	0.54	0.59	0.90
PIW99I 5	129.2	~70	~74	0.54	0.57	0.95
PIW99I 6	135.4	80.2	86.4	0.59	0.64	0.93
PIW99I 7	110.1	59.5	66.1	0.54	0.60	0.90
PIW99I 8	132.7	73.6	76.5	0.55	0.58	0.96
MB.C.2066	—	38.1	42.5	—	—	0.90

The suture is marked by a lobe at the umbilical seam, a pronounced saddle at the umbilical shoulder (“umbilical knee”), a deep and broad lateral lobe and a pointed ventral saddle which is narrowly rounded in adult stages, reflecting the ontogenetic development of the venter; the suture is getting less sinuous in adult stage. The siphuncle is located dorso-centrally. Internal moulds may show some large fold-like undulations at the venter, decreasing rapidly on the flanks; they seem to be confined to the chambered part of the shell (Pl. 2, Fig. 3). Specimen PIW99I 3 and PIW99I 5-7 are full-grown adults as indicated by septal crowding.

**REMARKS:** The species was erected by WIEDMANN (1960) on the basis of a single phragmocone of a juvenile, the venter of which was rounded in early ontogenetic stage and angular in the more adult stage.

The development of the body chamber was unknown to WIEDMANN. Adult representatives from northern Cantabria show clearly a rounded venter of the body chamber. Furthermore, internal moulds show some fold-like undulations at the venter which decrease rapidly on the flanks. These undulations may reflect a very coarse ribbing, a feature largely unknown in *Angulithes*. It closely resembles the coarse ribbing known in *Anglonautilus* SPATH, 1927 (i.e. *Anglonautilus undulatus* [J. SOWERBY]). This cymatoceratid genus is known from the Early Cretaceous (Aptian) to Cenomanian of Europe (KUMMEL 1956, 1964) and Japan (MATSUMOTO & MIYAUCHI 1983; MATSUMOTO & al. 1984a). Therefore, the original diagnosis of WIEDMANN (1960, p. 191) was emended.

*A. vascogoticus* is closely related to *A. triangularis* with regard to early ontogenetic development of the venter; its main difference is the strongly differentiated suture and the higher b/c-ratio in adult representatives. Due to the highly sinuous suture, *A. vascogoticus* was regarded by WIEDMANN (1960, p. 191) as intermediate to *Hercoglossa* CONRAD, 1866. The suture development from “simple” to complex in Cenomanian *Angulithes* (*fleuriausianus* - *triangularis* - “*mermeti*” - *vascogoticus*) as well as the shift of the siphuncle to a more dorsal position can be regarded as an evolutionary sequence and may be connected with the deepening of the marine environments during the Cenomanian transgression (Text-fig. 5; e.g. TINTANT & KABAMBA 1985). The very thick shells in Cenomanian *Angulithes* (up to 5 mm) may also indicate deep water habitats for representatives of this genus. The diameter values (a) indicate a maximum size of around 130 to 150 mm for adult representatives of *A. vascogoticus*.

The recognition of coarse ribbing in *Angulithes* (also reported by WRIGHT & WRIGHT 1951, and by WIEDMANN 1960) raises the question of familiar affiliations in Mesozoic nautiloids. The phyletic uniformity of the family Cymatoceratidae SPATH, 1927, including all sculptured post-Triassic nautiloids, was repeatedly questioned by WIEDMANN (1960) and WIEDMANN & SCHNEIDER (1979). However, it appears that ribbing was developed several times within the Nautilaceae and the recognition of a “cymatoceratid” taxon strongly depends on preservation (especially of the shell); the family might, therefore, represent a polyphyletic reservoir for sculptured offshoots of the “regular” nautiloid stock (compare also TINTANT 1993, Text-fig. 2b). This assumption is corroborated by a possible transitional form connecting *Angulithes* and *Deltocymatoceras* KUMMEL, 1956 (see below).



**OCCURRENCE:** The holotype was assigned by WIEDMANN (1960, p. 192) to his earliest Turonian zone of *Metoicoceras swallowi* which is a synonym of *M. geslinianum* (KENNEDY & al. 1981; WRIGHT & KENNEDY 1981), a Late Cenomanian index fossil. Therefore, *A. (A.) vascogoticus* is now placed in the Late Cenomanian, which is consistent with the record from northern Cantabria. Here, *A. vascogoticus* occurs frequently in rocks of late *pentagonum* to *geslinianum* zonal age. The species is endemic and was, to my knowledge, so far only recorded from Burgos, northern Spain.

*Angulithes westphalicus* (SCHLÜTER, 1872)  
(Pl. 3, Fig. 1a/b; Pl. 5, Figs 6, 20)

1872. *Nautilus Westphalicus* n. sp.; SCHLÜTER, p. 13.  
1876. *Nautilus Westphalicus* SCHLÜTER; SCHLÜTER, p. 175, Pl. 47, Figs 1, 2.  
1956. *A. westphalicus* (SCHLÜTER) 1872; KUMMEL, p. 457, Text-fig. 33/I.  
1999. *Deltoidonautilus westphalicus* (SCHLÜTER 1872); WITTLER, ROTH & LEGANT, p. 37, Text-figs 51a/b, 52.

**MATERIAL:** One slightly deformed internal mould (PIW99I 9) from Playa de Arnia near Liencres.

**DESCRIPTION:** Large, strongly compressed, involute nautilus with angular venter ( $a = 195$ ;  $b = \sim 65$ ;  $c = \sim 100$ ;  $b/a = 0.33$ ;  $c/a = 0.51$ ;  $b/c = 0.65$ ); maximum whorl breadth is at the umbilical shoulder. The disk-shaped form of specimen PIW99I 9 ( $b/a$  ratio of 0.33) was probably enhanced by compaction. The body chamber is completely preserved and shows an uncrushed peristome. The suture displays a shallow lobe at the umbilical seam, a shallow saddle on umbilical wall and inner flanks, a shallow lateral lobe and rounded ventral saddle; overall "relief" of the suture is low. The position of the siphuncle is unknown. The last septa show slight crowding.

**REMARKS:** *A. westphalicus* is a "Senonian" representative of the continuous line of compressed, involute nautilus with angular venters ranging from the Albian to the Oligocene (KUMMEL 1956). Despite its low relief, the suture is in overall shape very similar to Cenomanian *Angulithes* (e.g. *A. fleuriausianus*). The Cantabrian representative is very similar in dimensions and suture to the specimen figured by SCHLÜTER (1876, Pl. 47, Figs 1, 2) and comparative material collected in Upper Campanian rocks of Poland (Piotrawin quarry, middle Vistula area south

of Kazimierz) and northern Germany (e.g. Ahlten near Hannover). This is the first record of *A. westphalicus* from the Iberian Peninsula.

**OCCURRENCE:** Although there are some records from the Santonian (e.g. WITTLER & al. 1999), *A. westphalicus* is a typical Campanian species occurring in northern Germany, Poland, and Hungary (I. FÖZY, Budapest, in prep.). In Spain it occurs in the Late Campanian (*Bostrychoceras polyplacum* Zone); this time interval seems to represent the peak occurrence of the species.

Possible transitional form between *Angulithes* and *Deltocymatoceras* KUMMEL, 1956  
(Pl. 3, Fig. 2a/b; Pl. 5, Figs 7, 19)

**MATERIAL:** One only poorly preserved specimen (PIW99I 11); parts of the shell are preserved.

**DESCRIPTION:** Large, moderately compressed, very involute nautilus with a bulbous whorl section and a rapid increase of whorl breadth during ontogenesis ( $a = 180.0$ ;  $b = 107.5$ ;  $c = 121.5$ ;  $b/a = 0.60$ ;  $c/a = 0.67$ ;  $b/c = 0.88$ ); the flanks are strongly convex with maximum breadth near the middle, rapidly converging to the venter which is acute (keel-like) in all growth stages. The inner flanks are broadly rounded, grading into a moderately steep inclined umbilical slope. The suture is *Angulithes*-like (very similar to that of *A. triangularis*) with a lobe at the umbilical seam, a saddle on the umbilical shoulder and inner flanks, and a broad lateral lobe and (pointed) ventral saddle. The siphuncle has a position between the center and the dorsum. Coarse growth lines are visible on the shell of the body chamber. The shell is up to 5 mm thick.

**REMARKS:** DZIK (1984) discusses the relationship between *Deltocymatoceras leiotropis* (SCHLÜTER, 1876), known from the Emscher (Coniacian - Santonian) of northern Germany, and *Angulithes triangularis*, stating that the two species do not differ significantly (this was also noticed by MATSUMOTO in MATSUMOTO & MURAMOTO 1983, p. 89). In fact, the suture of *D. leiotropis* is very similar to that of *A. triangularis* and WIEDMANN (1960, p. 149) places *Deltocymatoceras* as a synonym of *Angulithes*. However, since *Deltocymatoceras* has a pronounced keel-like ridge and prominent "cymatoceratid" ribs that bifurcate near the middle of the whorl sides, the maintenance of two genera appears (at this time) justified. However, they should not be placed in differ-

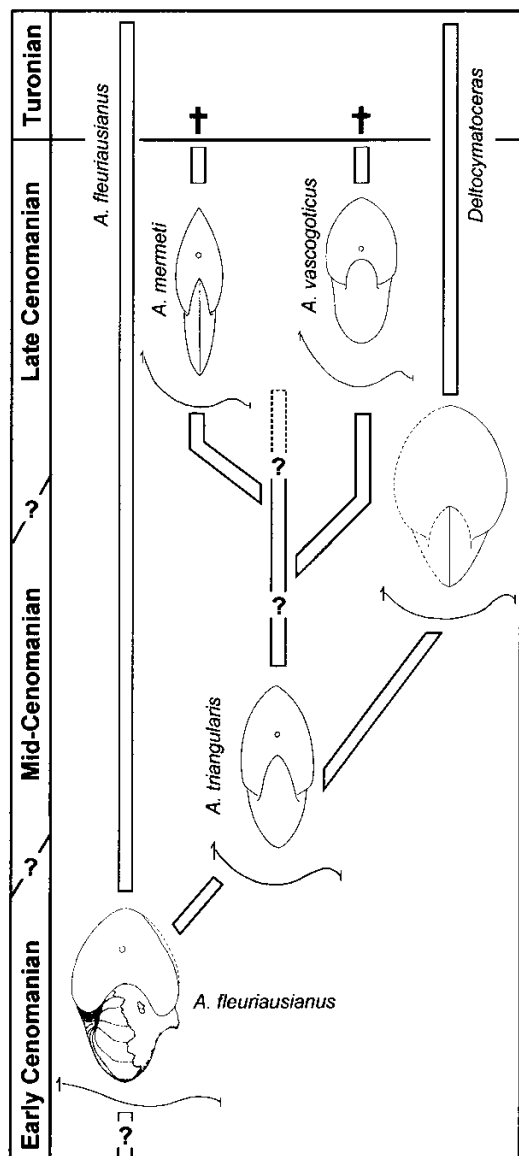


Fig. 5. Proposed phylogenetic relationship in Cenomanian *Angulithes*

ent families. The Cenomanian form described here is intermediate to *Angulithes* and *Deltocymatoceras* in form of shell and type of venter but lacks the cymatoceratid ribs. The genus *Deltocymatoceras* KUMMEL, 1956 may, thus, be regarded as an offshot of *Angulithes*, most probably *A. triangularis* (Text-fig. 5). This hypothesis was also proposed by TINTANT (1993), again questioning the validity of the family Cymatoceratidae. *Deltocymatoceras* was already placed by SHIMANSKY (1975) within the Nautilidae.

OCCURRENCE: Mid- to Late Cenomanian of Liencres.

Genus *Eutrephoceras* HYATT, 1894.

TYPE SPECIES: *Nautilus dekayi* MORTON, 1834 (p. 33, Pl. 8, Fig. 4).

DIAGNOSIS: Shell nautiliconic, typically subglobular depressed to compressed; umbilicus small to occluded, umbilical shoulders low and rounded; venter commonly broadly rounded; siphuncle small, orthochoanitic, circular in cross-section, variable in position, but often located ventro-centrally; suture simple to straight, very shallow saddles and lobes may be developed; shell generally smooth, sometimes sculptured on inner flanks.

OCCURRENCE: *Eutrephoceras* ranges from the Late Jurassic to the Miocene and is global in distribution (KUMMEL 1956).

*Eutrephoceras bouchardianum* (D'ORBIGNY, 1840)  
(Pl. 4, Fig. 1a/b; Pl. 5, Fig. 9, 22)

1840. *Nautilus bouchardianus* n. sp.; D'ORBIGNY, p. 75, Pl. 13.

1956. *Eutrephoceras bouchardianus* (D'ORBIGNY) 1840; KUMMEL, p. 380.

1960. *Eutrephoceras bouchardianum* (D'ORBIGNY) 1840; WIEDMANN, p. 161, Pl. 19, Figs H, I; Pl. 23, Fig. J; Pl. 24, Figs 6-9; Text-fig. 6 (see for synonymy).

1975. *Eutrephoceras bouchardianum* (D'ORBIGNY, 1840); SHIMANSKY, p. 60, Pl. 5, Fig. 2-3; Text-fig. 16-17.

MATERIAL: One internal mould (PIW991 13) from the Ensenada de Madero section near Liencres (*Romaniceras deverianum* event of WIESE 1997).

DESCRIPTION: Depressed, involute nautilid with a rounded whorl section; maximum breadth at the inner flanks ( $a = 104.2$ ;  $b = 73.6$ ;  $c = 63.6$ ;  $b/a = 0.71$ ;  $c/a = 0.61$ ;  $b/c = 1.15$ ). Venter narrowly rounded in juvenile stages, getting more broadly rounded in adult stage; rapid increase in whorl breadth during ontogenesis. The suture is rather straight with shallow umbilical and ventral saddles and a broad lateral lobe. The position of the siphuncle is not exactly known, but it is not located between the dorsum and center of the septum.

REMARKS: This species is very similar to *E. indicum* (see below) which has in adult stage ( $a >$

100 mm) a b/c-ratio of  $\sim 1.0$  (WIEDMANN 1960, p. 160) and a more sinuous suture. It differs from *E. sublaevigatum* (D'ORBIGNY, 1850) by the lack of a median deflection of the ventral saddle and the ontogenetic development of the venter.

**OCCURRENCE:** *E. bouchardianum* is known from the Gault (Lower Cretaceous) of France, Switzerland, and Spain, and the Upper Cretaceous of Russia, India, Madagascar, and Spain (where it occurs in Upper Turonian to Coniacian rocks, WIEDMANN 1960). The Cantabrian specimen is from the Late Turonian zone of *Subprionocyclus neptuni* and *Romaniceras deverianum* (cf. WIESE 1997).

*Eutrephoceras* cf. *indicum* (D'ORBIGNY, 1850)  
(Pl. 4, Fig. 3a/b/c; Pl. 5, Figs 10, 23)

- cf. 1846. *Nautilus sowerbyanus* D'ORBIGNY; D'ORBIGNY, Pl. 4, Figs 1, 2.  
cf. 1850. *Nautilus indicus* n. sp.; D'ORBIGNY, p. 211.  
non 1956. *Eutrephoceras indicum* (SPENGLER) 1910; KUMMEL, p. 382.  
cf. 1960. *Eutrephoceras indicum* (D'ORBIGNY) 1850; WIEDMANN, p. 159, Pl. 21, Fig. G; Pl. 24, Figs 1-4; Text-figs 3-5.

**MATERIAL:** One slightly deformed internal mould (PIW99I 14) without body chamber from bed 102N of WIESE (1997).

**DESCRIPTION:** Very involute nautilid with trigonal whorl section; maximum whorl breadth is close to the umbilical shoulder and the umbilical slope is steep ( $a = 85.6$ ;  $b = 60.5$ ;  $c = 59.4$ ;  $b/a = 0.71$ ;  $c/a = 0.69$ ;  $b/c = 1.02$ ; values refer to the restored whorl section, cf. Pl. 4, Fig. 3c, Pl. 5, Fig. 10). The weakly convex flanks are gradually converging towards the narrowly rounded venter. The suture is contorted due to compaction but shows a saddle at the umbilical shoulder, a lateral lobe and a ventral saddle. The position of the siphuncle is not known.

**REMARKS:** *E. indicum* differs from *E. bouchardianum* by its whorl breadth-to-height ratio, which is around 1.0 in adult representatives (WIEDMANN 1960). It is also very similar to *E. darupense* (see below) which, however, has a much wider whorl section (b/c-ratio generally  $> 1.2$ ). The suture (Pl. 5, Fig. 23) is slightly bent backwards due to deformation of the specimen but in general shape it is very similar to WIEDMANN'S (1960) Text-fig. 5.

However, due to slight deformation, the species is kept in open nomenclature.

**OCCURRENCE:** In Spain, *E. indicum* preferentially occurs in the Middle Turonian *Romaniceras ornatisimum* Zone (WIEDMANN 1960) which is also true for the Cantabrian specimen. *E. indicum* is, furthermore, reported from the "Senonian" of southern India and Chile.

*Eutrephoceras darupense* (SCHLÜTER, 1876)  
(Pl. 2, Figs 5a/b; Pl. 4, Figs 4a/b, 5a/b; Pl. 5, Figs 11, 24-25)

1876. *Nautilus Darupensis*, n. sp.; SCHLÜTER, p. 176, Pl. 49, Figs 4, 5.  
1876. *Nautilus Neubergericus* REDTENBACHER; SCHLÜTER, p. 174, Pl. 48, Figs 3-5.  
1951. *Eutrephoceras* cf. *darupense* (SCHLÜTER); WRIGHT & WRIGHT, p. 11.  
1956. *Eutrephoceras darupensis* (SCHLÜTER) 1876; KUMMEL, p. 381.  
1960. *Eutrephoceras darupense* (SCHLÜTER) 1876; WIEDMANN, p. 157, Pl. 21, Figs C, D; Pl. 23, Figs F, P; Text-fig. 2.  
1996. *Nautilus* sp.; OPPERMANN, Pl. 7, Fig. 4.  
1999. *Eutrephoceras darupense* (SCHLÜTER, 1876); WITTLER, ROTH & LEGANT, p. 37, Text-figs 47a/b, 48.

**MATERIAL:** Three internal moulds; specimen PIW99I 15 is a complete juvenile with crushed body chamber from bed 59 of OPPERMANN (1996), specimen PIW99I 16 is a septate fragment and specimen PIW99I 18 an isolated chamber of a phragmocone.

**DESCRIPTION:** Very involute, depressed nautilid with sub-rectangular whorl section and broadly rounded venter and maximum whorl breadth at inner flanks. The whorls are generally very depressed ( $b/c > 1.2$ ) and show a rapid increase in breadth during ontogenesis; b/a-ratio is around 0.75, c/a-ratio between 0.60 and 0.62. The suture shows a small saddle on the umbilical shoulders, a shallow lateral lobe rising to a ventral saddle which crosses the venter either straightly or may be deflected by a small ventral lobe. The siphuncle is located ventrocentrally to ventrally. Shell parameter of *E. darupense* (SCHLÜTER, 1976):

Specimen	a	b	c	b/a	c/a	b/c
PIW99I 15	$\sim 47.0$	35.2	$\sim 29.0$	0.75	0.62	1.21
PIW99I 16	119.8	$\sim 90.0$	71.6	0.75	0.60	1.25
PIW99I 18	—	71.4	54.1	—	—	1.32

REMARKS: *E. indicum* (D'ORBIGNY, 1850) is a similar species but lacks the ventral lobe; furthermore, it generally has a b/c-ratio of around 1.0. *E. darupense* differs from *E. sublaevigatum* (D'ORBIGNY, 1850) by its more ventral siphuncle and the sub-rectangular whorl section.

Despite its incomplete preservation, the very depressed whorl section of specimen PIW99I 18 with the broadly rounded venter and the ventral siphuncle indicates a close relationship to *E. darupense*. It is placed, with reservation, within this species.

OCCURRENCE: *E. darupense* occurs in the Coniacian to Campanian of northern Germany and the Upper Cretaceous of England and France. In Spain, it was recorded from the Turonian/Coniacian boundary succession and Upper Santonian by WIEDMANN (1960). The Cantabrian specimens are of Late Turonian, latest Santonian and Late Campanian age, respectively.

*Eutrephoceras* cf. *justum* (BLANFORD, 1861)  
(Pl. 4, Fig. 2a/b; Pl. 5, Fig. 12)

- cf. 1861. *Nautilus justus* n. sp.; BLANFORD, p. 22, Taf 10, Fig. 2, 3.  
cf. 1910. *Nautilus justus* BLANFORD; SPENGLER, p. 142, Pl. 14(29), Fig. 3.  
cf. 1956. *Eutrephoceras justus* BLANFORD; KUMMEL, p. 337, Text-fig. 13/F.  
cf. 1960. *Eutrephoceras justum* (BLANFORD) 1861; WIEDMANN, p. 164, Pl. 25, Figs 4, 5; Pl. 26, Figs 5, 6; Text-fig. 7.

MATERIAL: One internal mould (PIW99I 17) from the Playa de Arnia near Liencres (upper *undulato-plicatus* beds, cf. OPPERMANN 1996).

DESCRIPTION: Involute, compressed nautilid with ovoid whorl-section. Maximum breadth of whorls is on middle flanks ( $a = 61.8$ ;  $b = 37.1$ ;  $c = 39.5$ ;  $b/a = 0.60$ ;  $c/a = 0.64$ ;  $b/c = 0.94$ ); whorl section is slightly higher than wide and with broadly rounded venter. The suture appears relatively straight in the umbilical area but is only poorly preserved on the flanks. The position of the siphuncle is not known.

REMARKS: This nautilid shows a very characteristic ovoidal ("egg-shaped") cross-section. It is very similar to *E. merteni* WIEDMANN, 1960. However, maximum whorl breadth in *E. merteni* is on the

inner flanks and b/c-ratio is 1.0 (see WIEDMANN 1960, p. 164-165). The Cantabrian nautilid is, due to its overall similarity to figured specimens (especially SPENGLER 1910, Pl. 14, Fig. 3) with reservation assigned to *E. justum* (BLANFORD, 1861).

OCCURRENCE: *E. justum* is known from the Upper Cretaceous of India. In Cantabria, it occurs in rocks of Early Santonian age.

*Eutrephoceras* sp.

(Pl. 2, Fig. 4a/b; Pl. 5, Figs 8, 21)

MATERIAL: One internal mould (PIW99I 12) from the coast north of Tagle ("Pas du Chat", cf. WILMSEN 1997).

DESCRIPTION: Depressed, involute nautilid with broadly rounded venter and rapid increase in whorl breadth during ontogenesis ( $a = 74.9$ ;  $b = 52.5$ ;  $c = 45.5$ ;  $b/a = 0.70$ ;  $c/a = 0.60$ ;  $b/c = 1.15$ ). Flanks and venter are evenly rounded; whorls are wider than high and nearly circular in outline. The suture is characterized by a weak umbilical saddle, a broad and shallow lateral lobe slightly rising to the external side; at the venter, it is deflected by a shallow lobe. The position of the siphuncle is not known.

REMARKS: Due to the shape of the suture, whorl shape, and the absence of ribs, the specimen is assigned to the genus *Eutrephoceras*. The described species is in its dimensions of shell (e.g. b/a- and c/a-ratios) and suture very similar to *Eutrephoceras sublaevigatum* (D'ORBIGNY, 1850) (compare REDTENBACHER 1873, p. 95, Pl. 22, Fig. 1.; WIEDMANN 1960, p. 165, Pl. 19, Fig. O; Pl. 20, Fig. A; Pl. 23, Fig. L; WIEDMANN & SCHNEIDER 1979, p. 652, Pl. 2, Figs 2, 3; Text-fig. 4a); especially the nearly circular outline of the whorl section fits well with this species. However, due to the poor preservation, as specific determination is not possible.

OCCURRENCE: *Eutrephoceras* sp. was found in Upper Cenomanian rocks at the coast north of Tagle.

Genus *Pseudocenoceras* SPATH, 1927.

TYPE SPECIES: *Nautilus largilliertianus* D'ORBIGNY, 1840 (p. 86, Pl. 18).

DIAGNOSIS: Nautiliconic, involute, strongly com-

pressed; shell generally smooth, rarely with coarse concave ventral folds; whorl section subrectangular with broad and flattened venter and rounded ventral shoulders; flanks flattened, subparallel to weakly convergent; umbilical shoulder rounded, umbilical wall very steep; suture with broad, shallow lateral lobe and ventral saddle, straight across the venter or deflected by small lobe; siphuncle subcentral to dorsal.

REMARKS: *Pseudocnoceras* SPATH, 1927 is a poorly diverse genus of Cretaceous nautilids and includes only 8 species (KUMMEL 1956). It was regarded by WIEDMANN (1960, p. 147) as a subgenus of *Angulithes* and later (WIEDMANN & SCHNEIDER 1979, p. 653) re-established as an independent genus.

OCCURRENCE: The genus is widely distributed in Cretaceous rocks of Europe, northern Africa, and northern America (KUMMEL 1956).

*Pseudocnoceras dorsoplicatus* (WIEDMANN, 1960)  
(Pl. 5, Figs 13, 26)

1853. *Nautilus largilliertianus*; SHARPE, pars, only Pl. 6, Fig. 2.

1897. *Nautilus largilliertianus*? (D'ORBIGNY); PARONA & BONARELLI, Pl. 10, Fig. 6.

1960. *Angulithes (Pseudocnoceras) dorsoplicatus* n. sp.; WIEDMANN, p. 176 (on the basis of figures in SHARPE and PARONA & BONARELLI).

1975. *Pseudocnoceras?* *dorsoplicatum* WIEDMANN; SHIMANSKY, p. 76.

MATERIAL: One fragmentary internal mould (PIW99I 22) from El Piquio in Santander.

DESCRIPTION: Compressed nautilid with subrectangular whorl section ( $a \sim 70$ ;  $b = 36.5$ ;  $c = 41.9$ ;  $b/a = 0.52$ ;  $c/a = 0.60$ ;  $b/c = 0.87$ ) and only weakly impressed dorsal zone. The flanks are subparallel and the ventral shoulders are narrowly rounded; the venter is broad and flattened. The umbilical shoulders are sharp and the umbilical wall is steeply inclined. At the ventral shoulders of the phragmocone, distinct concave folds are developed which rapidly decrease on the flanks. The suture shows a shallow saddle on the umbilical shoulder and inner flanks, a broad and relatively deep lateral lobe rising to an external saddle which is nearly straight across the venter. The siphuncle is located dorsally.

REMARKS: The described specimen differs in no significant respects from *Pseudocnoceras dorsopli-*

*catus* which was erected by WIEDMANN (1960) on the basis of material figured by SHARPE (1853) and PARONA & BONARELLI (1897) as "*Nautilus largilliertianus*". However, it differs from *P. largilliertianum* (D'ORBIGNY, 1840) by its relatively broad venter and the distinct concave folds which are restricted to the chambered part of the shell (but are also well visible on internal moulds). In *P. undulatus* (J. SOWERBY, 1813), these folds occur on the body chamber in later growth stages whereas the phragmocone is smooth; furthermore, this species has a more rounded whorl section and is less compressed.

OCCURRENCE: *P. dorsoplicatus* is known from the Albian of France (Escragnolles) and Lower Cenomanian rocks of England. The Cantabrian specimen is from the Early Cenomanian *Mantelliceras mantelli* Zone of El Piquio at Playa de Sardinero in Santander.

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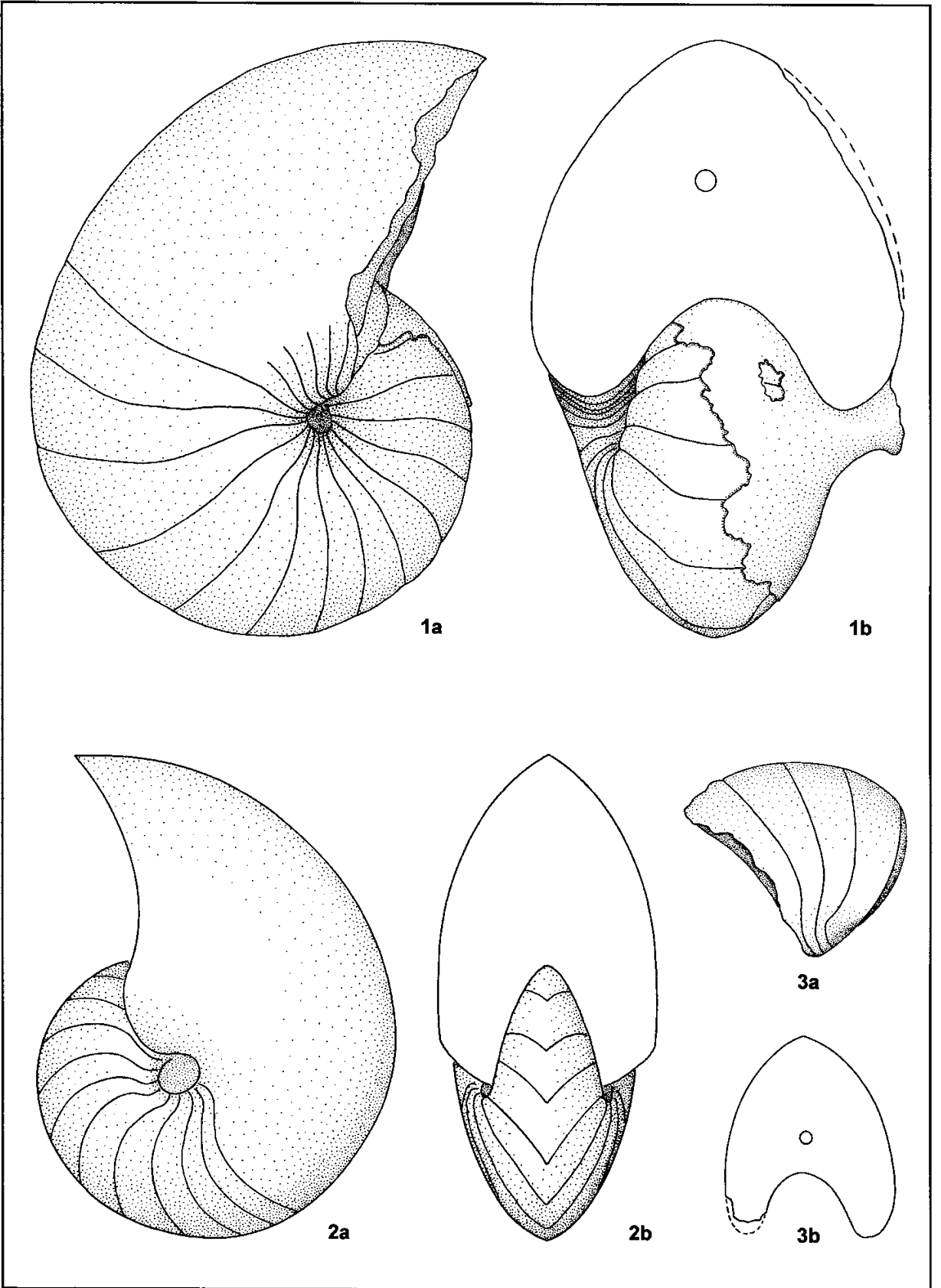
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PLATE 1

- 1 – *Angulithes fleuriausianus* (D'ORBIGNY, 1840); PIW99I 1;  $\times 0.6$ 
  - a – lateral view
  - b – apertural view
- 2 – *Angulithes triangularis* MONTFORT, 1808; MB.C.2052;  $\times 0.75$ 
  - a – lateral view
  - b – apertural view
- 3 – *Angulithes vascogoticus* WIEDMANN, 1960; MB.C.2066;  $\times 0.8$ 
  - a – lateral view
  - b – whorl section





## PLATE 2

- 1 – *Angulithes vascogoticus* WIEDMANN, 1960; PIW99I 3;  $\times 0.65$ 
  - a – lateral view
  - b – ventral view
- 2 – *Angulithes vascogoticus* WIEDMANN, 1960; PIW99I 4;  $\times 0.77$ 
  - a – lateral view
  - b – cross-section and inner whorls
- 3 – *Angulithes vascogoticus* WIEDMANN, 1960; PIW99I 5;  $\times 0.6$ 
  - a – lateral view
  - b – ventral view
- 4 – *Eutrephoceras* sp.; PIW99I 12;  $\times 0.56$ 
  - a – lateral view
  - b – ventral view
- 5 – *Eutrephoceras* cf. *darupense* (SCHLÜTER, 1876); PIW99I 18;  $\times 0.6$ 
  - a – whorl section
  - b – lateral view

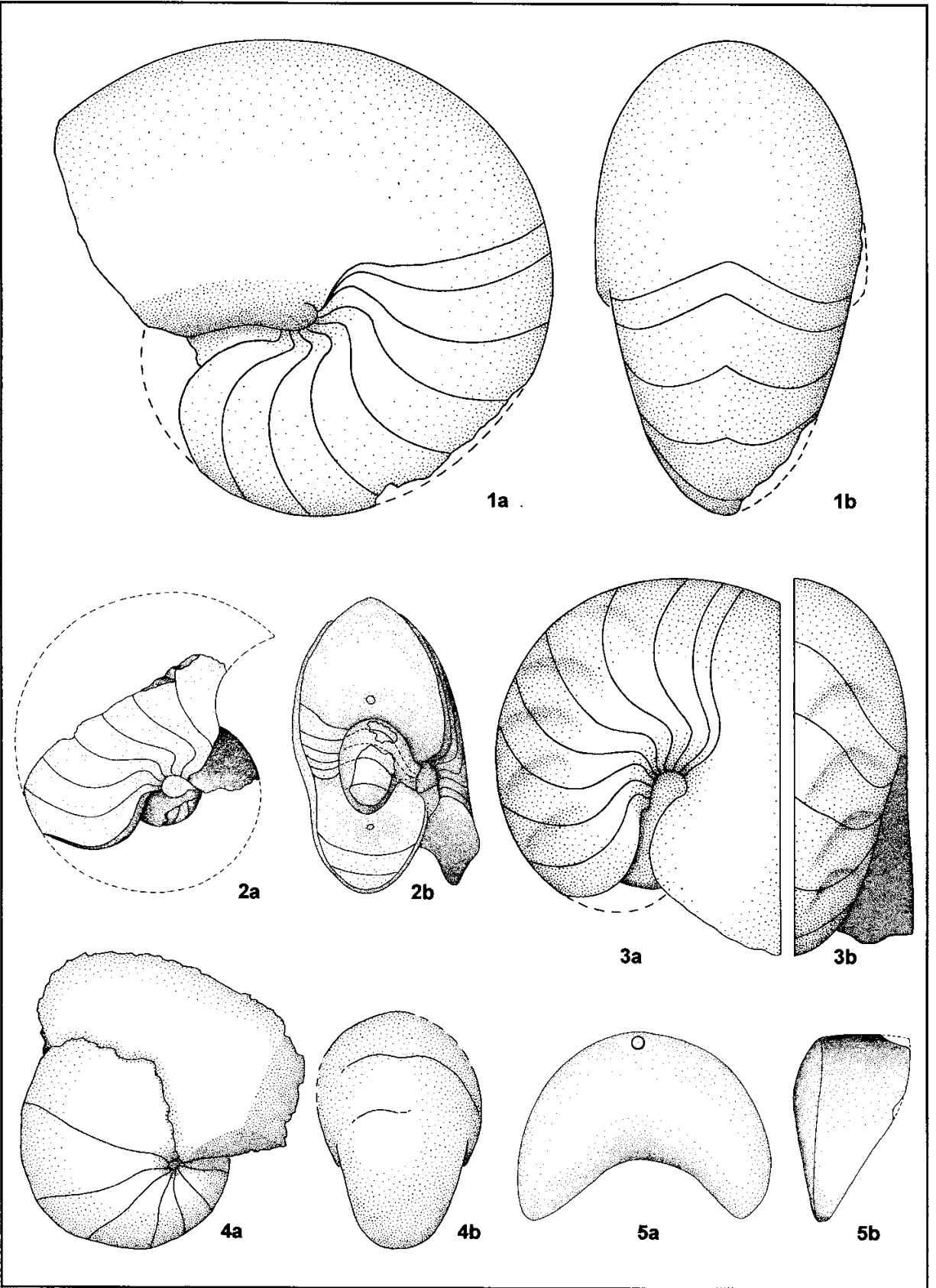
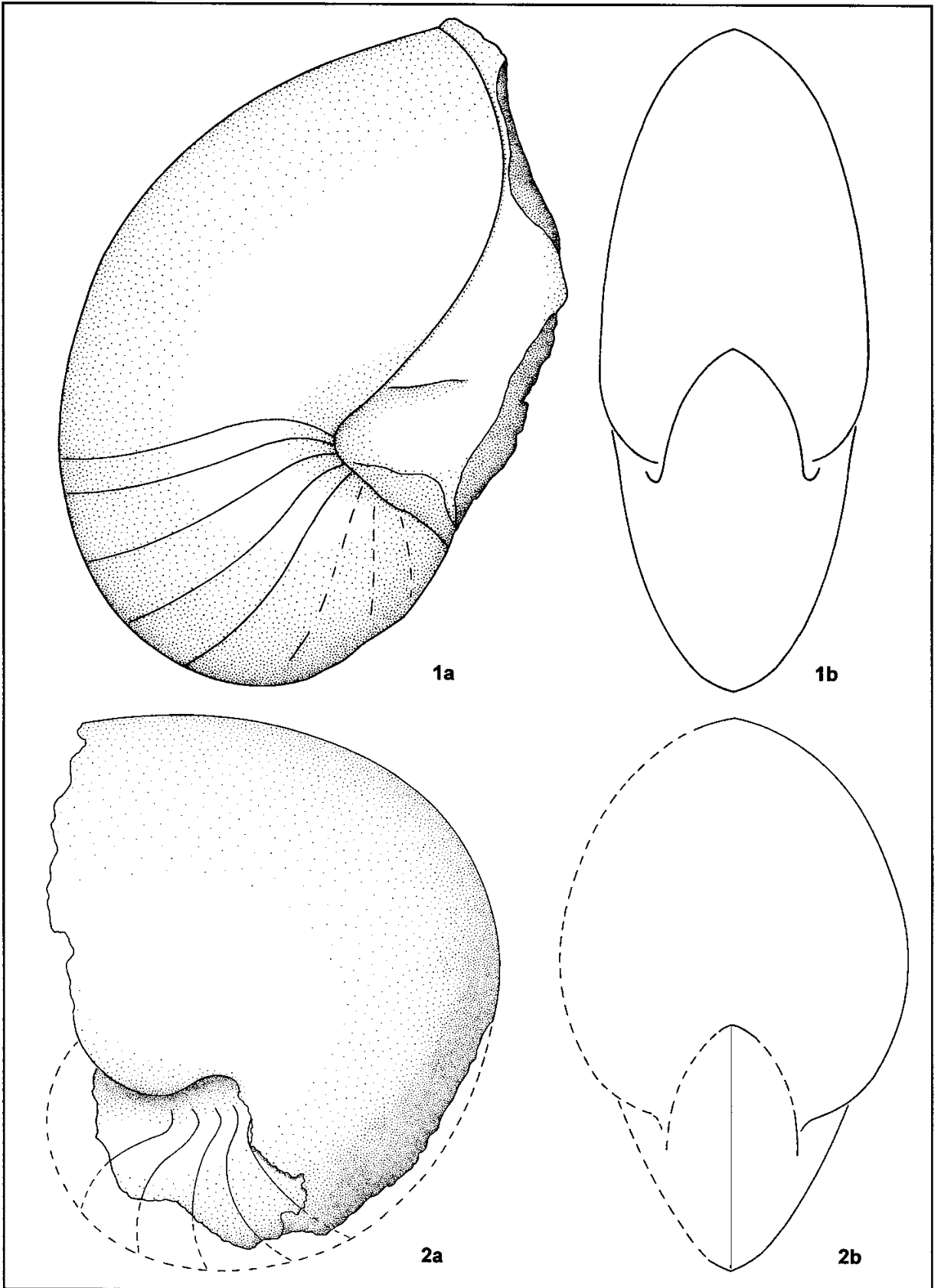


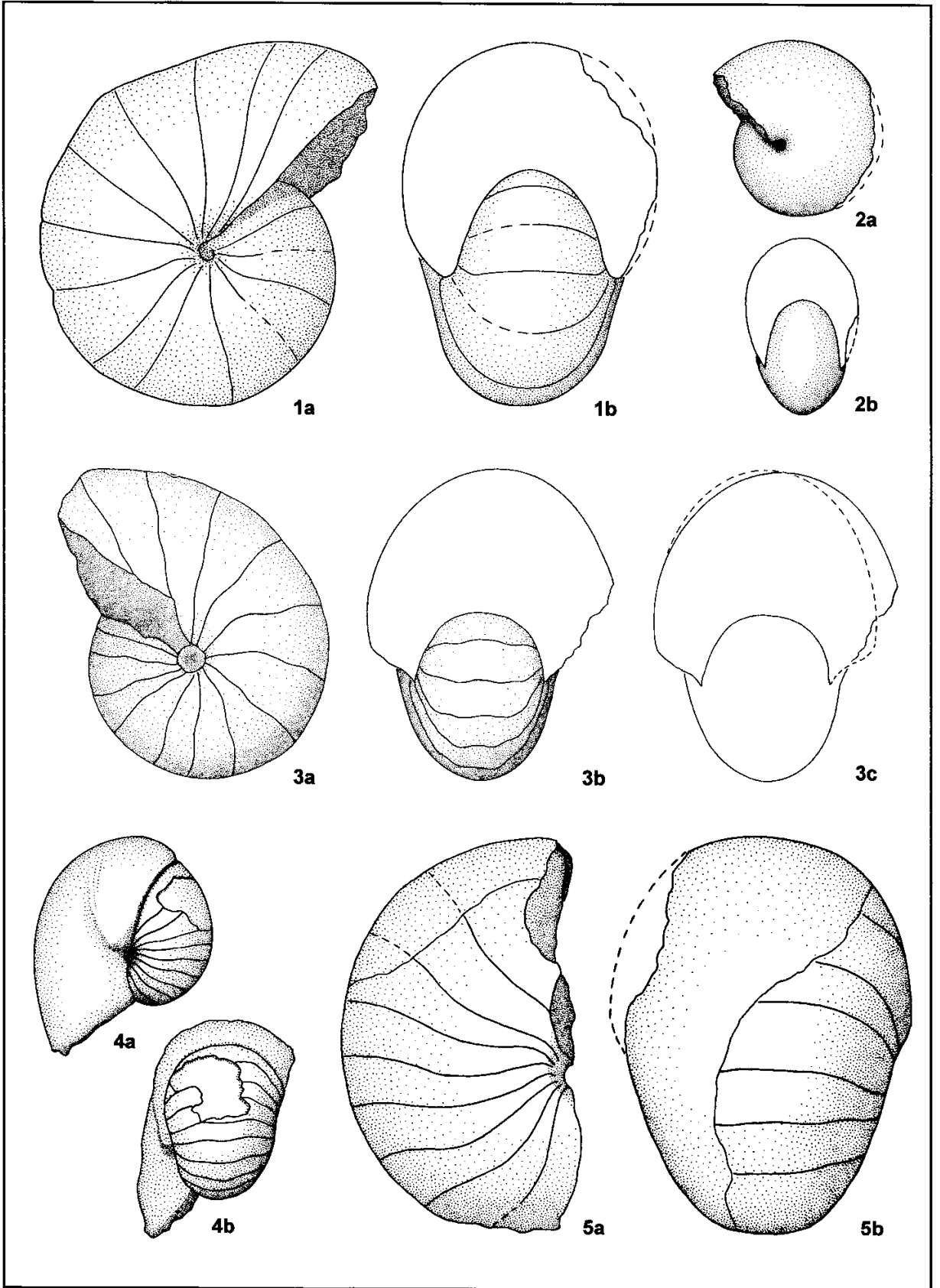
PLATE 3

- 1 – *Angulithes westphalicus* (SCHLÜTER, 1872); PIW99I 9; × 0.6
  - a – lateral view
  - b – cross-section
- 2 – (?) transitional form between *Angulithes* MONTFORT, 1808, and *Deltocymatoceras* KUMMEL, 1956; PIW99I 11; × 0.5
  - a – lateral view
  - b – cross-section (partly reconstructed)



## PLATE 4

- 1 – *Eutrephoceras bouchardianum* (D'ORBIGNY, 1840); PIW99I 13;  $\times 0.67$ 
  - a – lateral view
  - b – apertural view
- 2 – *Eutrephoceras* cf. *justum* (BLANFORD, 1861); PIW99I 17;  $\times 0.5$ 
  - a – lateral view
  - b – apertural view
- 3 – *Eutrephoceras* cf. *indicum* (D'ORBIGNY, 1850); PIW99I 14;  $\times 0.65$ 
  - a – lateral view
  - b – apertural view
  - c – reconstructed whorl section
- 4 – *Eutrephoceras darupense* (SCHLÜTER, 1876); PIW99I 15;  $\times 0.55$ 
  - a – lateral view
  - b – ventral view
- 5 – *Eutrephoceras darupense* (SCHLÜTER, 1876); PIW99I 16;  $\times 0.58$ 
  - a – lateral view
  - b – ventral view



## PLATE 5

Whorl shapes (Figs 1-13) and sutures (Figs 14-25, not to scale; the arrow marks the external side and points towards aperture)

- 1 – *Angulithes fleuriausianus* (D'ORBIGNY, 1840); PIW99I 1;  $\times 0.36$
- 2 – *Angulithes triangularis* MONTFORT, 1808; MB.C.2052;  $\times 0.45$
- 3 – *Angulithes mermeti* (COQUAND, 1862); after WIEDMANN (1960: pl. 22, H);  $\times 0.4$
- 4 – *Angulithes vascogoticus* WIEDMANN, 1960; PIW99I 4 (juvenile);  $\times 0.57$
- 5 – *Angulithes vascogoticus* WIEDMANN, 1960; PIW99I 5 (whorl section of adult body chamber);  $\times 0.45$
- 6 – *Angulithes westphalicus* (SCHLÜTER, 1872) ; PIW99I 9;  $\times 0.33$
- 7 – (?) transitional form between *Angulithes* MONTFORT, 1808, and *Deltocymatoceras* KUMMEL, 1956; PIW99I 11;  $\times 0.26$
- 8 – *Eutrephoceras* sp.; specimen PIW99I 12;  $\times 0.73$
- 9 – *Eutrephoceras bouchardianum* (D'ORBIGNY, 1840) ; PIW99I 13;  $\times 0.52$
- 10 – *Eutrephoceras* cf. *indicum* (D'ORBIGNY, 1850); PIW99I 14;  $\times 0.55$
- 11 – *Eutrephoceras darupense* (SCHLÜTER, 1876); PIW99I 16;  $\times 0.45$
- 12 – *Eutrephoceras* cf. *justum* (BLANFORD, 1861); PIW99I 17;  $\times 0.52$
- 13 – *Pseudocnoceras dorsoplicatus* (WIEDMANN, 1960); PIW99I 22;  $\times 0.75$
- 14 – *Angulithes fleuriausianus* (D'ORBIGNY, 1840); PIW99I 1
- 15 – *Angulithes triangularis* MONTFORT, 1808; MB.C.2052 (early Mid-Cenomanian)
- 16 – *Angulithes triangularis* MONTFORT, 1808; PIW99I 2 (late Mid-Cenomanian)
- 17 – *Angulithes vascogoticus* WIEDMANN, 1960; PIW99I 3
- 18 – *Angulithes vascogoticus* WIEDMANN, 1960; PIW99I 4
- 19 – (?) transitional form between *Angulithes* MONTFORT, 1808, and *Deltocymatoceras* KUMMEL, 1956; PIW99I 11
- 20 – *Angulithes westphalicus* (SCHLÜTER, 1872) ; PIW99I 9
- 21 – *Eutrephoceras* sp.; specimen PIW99I 12
- 22 – *Eutrephoceras bouchardianum* (D'ORBIGNY, 1840) ; PIW99I 13
- 23 – *Eutrephoceras* cf. *indicum* (D'ORBIGNY, 1850); PIW99I 14
- 24 – *Eutrephoceras darupense* (SCHLÜTER, 1876); PIW99I 15
- 25 – *Eutrephoceras darupense* (SCHLÜTER, 1876); PIW99I 16
- 26 – *Pseudocnoceras dorsoplicatus* (WIEDMANN, 1960); PIW99I 22



