

Palaeobiology and evolutionary context of *Angulithes mermeti*, a streamlined early Late Cretaceous shallow-water nautiloid

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Cretaceous nautiloids are commonly characterized by inflated shells and prolonged stratigraphic ranges. In the Albian, the species of *Angulithes* appeared and compressed, short-lived forms with narrow venters emerged during the Cenomanian age. Based on a new description, the late Cenomanian nautiloid *Angulithes mermeti* is discussed with its palaeobiological background and placed in an evolutionary context of the Cenomanian lineage of *Angulithes*, considering contemporaneous palaeoenvironmental changes and inferred functional traits. *A. mermeti* is characterized by a nearly oxycone shell with sharp venter and narrow umbilicus, a fairly sinuous suture, low inter-septal distances, and an almost dorsal siphuncle. Its palaeobiogeographical occurrence was latitudinally restricted to shallow tropical–subtropical shelf seas with a preferred habitat depth between 5–50 m. Several morphological trends reflected by the Cenomanian species of the genus culminated in the late Cenomanian species *A. mermeti*, i.e., (i) increasing shell compression and sharpening of the venter, (ii) increasing folding of the septa, (iii) reduction of inter-septal distances, and (iv) dorsally directed migration of the siphuncle. The hydrodynamically efficient form was favorable to successfully populate the wide and shallow epicontinental seas that formed during the Cenomanian age. The increasing sutural sinuosity and the dense septal spacing aimed to buttress the shells against shell-breaking predators while the functional reason for the dorsal-directed migration of siphuncle is more elusive; it may have improved the efficiency of the hydrostatic apparatus and its internal position is beneficial in the case of predation, too. The gradual morphological change in the Cenomanian lineage of the genus *Angulithes* provides a well-constrained case study of rapid evolutionary response to major environmental pressure, i.e., the opening of newly available niches in the course of the great early Late Cretaceous transgression, in an otherwise rather bradytelic biotic group.

Key words: Cephalopoda, Nautilida, palaeobiogeography, autecology, functional morphology, evolutionary patterns, Cenomanian, Egypt.

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Introduction

Recent nautilids are iconic externally shelled cephalopods and a well-studied group, today being restricted to a few species populating relatively small relict habitats in deeper waters (e.g., Saunders and Landman 1987; Ward et al. 2016). During the Cretaceous nautiloids were common and both environmentally and palaeobiogeographically much more widespread (e.g., Wiedmann 1960). However, Cretaceous nautiloids are fairly meagre in external shell characters and tend to be rather conservative in terms of evolutionary

change, commonly resulting in prolonged stratigraphical ranges, especially when compared to fast-evolving contemporaneous ammonites (e.g., Ward and Signor 1983). Furthermore, homeomorphies, common in nautiloids in general (e.g., Kummel 1956; Dzik 1984), and taphonomical constraints (often restriction to commonly poorly preserved internal moulds in carbonate facies and/or selective preservation of ribbing; e.g., Wilmsen 2016; Malchyk et al. 2017) complicate the understanding of systematic relationships and the elaboration of comprehensive taxonomical revisions. Furthermore, when evaluating the general shell

forms of Cretaceous nautiloids it is fairly obvious that many representatives of the typical genera such as *Eutrephoceras* Hyatt, 1894, *Paracenoceras* Spath, 1927, *Cymatoceras* Hyatt, 1884 or *Cimomia* Conrad, 1866 are characterized by inflated shells with wide whorl cross-sections and broadly rounded or even flattened venters (e.g., see Kummel 1956; Dzik 1984: text-fig. 71), suggesting, in analogue to ammonites, an overall low hydrodynamic efficiency (e.g., Westermann 1996, 1999; see also Peterman et al. 2019). However, in the latest Early Cretaceous, a genus of compressed forms with predominantly narrow, tapered venters arose, i.e., *Angulithes* de Montfort, 1808, some representatives of which acquired disco- to oxycone shell shapes and were also characterized by fairly short-lived stratigraphical ranges. The scope of the present contribution is a detailed description as well as a taxonomic, autecological, stratigraphical, and palaeobiogeographical discussion of the strongly compressed nautiloid species *Angulithes mermeti* (Coquand, 1862) based on new material from the upper Cenomanian of Egypt. Furthermore, evolutionary trends in Cenomanian species of *Angulithes* are evaluated in the light of contemporaneous palaeoenvironmental changes and inferred functional traits.

Institutional abbreviations.—MMG, Museum für Mineralogie und Geologie, Senckenberg Naturhistorische Sammlungen Dresden, Germany; African (AFK) and Spanish (SpK) Cretaceous sub-collections; EN-WI/WH, collection from Wadi Irkas/Wadi Hawashiya sections, Department of Geology, Al-Azhar University, Assiut, Egypt; MB.C., Museum für Naturkunde, Berlin, Germany.

Other abbreviations.—D, diameter; D_{\max} , maximum diameter; Wb, whorl breadth at D_{\max} ; Wh, whorl height at D_{\max} ; Th, shell inflation; w, whorl expansion; U, umbilical exposure.

Geological setting

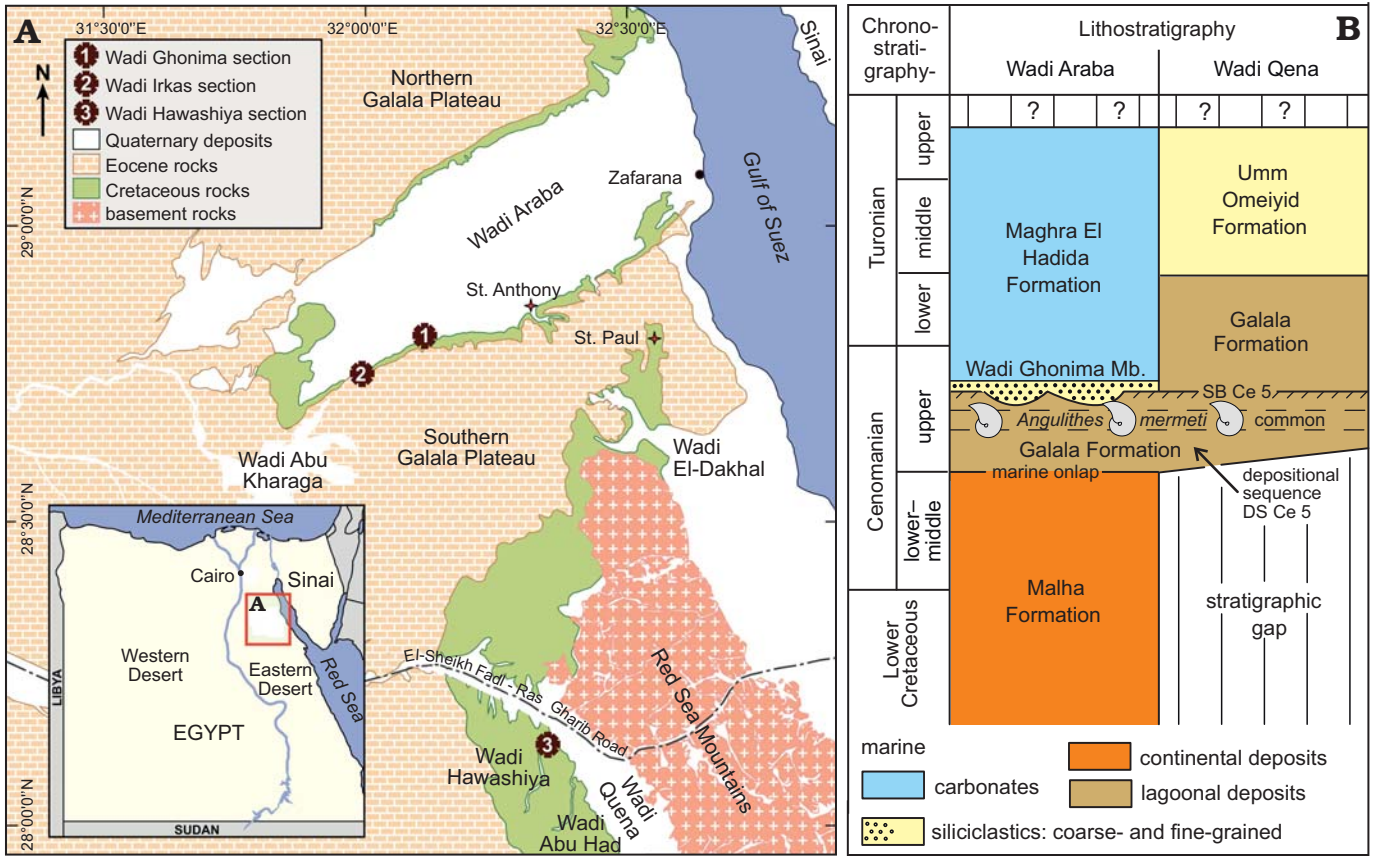
West of the Gulf of Suez, Wadi Araba is the main geomorphological feature represented by a low and wide southwest–northeast-directed valley that dissects the northern part of the Eastern Desert of Egypt into two high and large plateaus, i.e., the Northern and Southern Galala plateaus (Fig. 1A). To the south, Wadi Qena forms a north–northwest–east–southeast-oriented geomorphological element parallel to the Gulf of Suez/Red Sea rift system. The Galala plateaus and the southwestern slopes of Wadi Qena consist of clastic upper Paleozoic–Lower Cretaceous strata and mainly carbonate Upper Cretaceous–Paleogene successions

(Bandel and Kuss 1987; Kuss et al. 2000). At their foothills, lower Upper Cretaceous rocks are well-exposed and widely distributed (Fig. 1A).

Structurally, Said (1962) subdivided the continental platform area of Egypt into two tectonic domains, the unstable shelf in the north and the stable shelf in the south. Most sedimentary exposures in the northern and central parts of the study area are following a NE–SW direction, reflecting the course of the Syrian Arc System (the best-known structural feature in the northern unstable part of the shelf; Said 1990), the tectonic activity of which began during the Early Cretaceous and intensified during the Late Cretaceous (Aal and Lelek 1994; Kuss et al. 2000; Rosenthal et al. 2000). To the south at Wadi Qena (Fig. 1A), the stable shelf area is represented by a nearly horizontal sedimentary cover with less deformation.

During the early Late Cretaceous, the study area was situated at the southern margin of the Neotethys at about 5–10° northern palaeo-latitudes (e.g., Philip and Floquet 2000; Barrier and Vrielynck 2008). In response to the major Cenomanian sea-level rise, a widespread peri-continental shelf sea covered large areas in Sinai and the Eastern Desert during the late Cenomanian. Transgression proceeded from north to south and the facies sequence shows an overall retrogradational stacking (Said 1990; Wilmsen and Nagm 2012, 2013). Marine onlap started in the study area with the mixed siliciclastic to carbonate strata of the Galala Formation, representing an open lagoonal to shallow-marine shelf environment (Wilmsen and Nagm 2012; Fig. 1B). In the northern part of the study area, the Galala Formation comprises the lower upper Cenomanian, being overlain by the offshore strata of the uppermost Cenomanian to Turonian Maghra El Hadida Formation, while the Galala Formation ranges into the Turonian in the southern part (Wadi Qena; Fig. 1B), reflecting the time-transgressive onlap of marine facies belts during the Late Cretaceous transgression. The Galala Formation in Wadi Araba and its lower upper Cenomanian segment in Wadi Qena correspond to the depositional sequence Cenomanian 5 (DS Ce 5) in the Cenomanian standard sequence stratigraphy (Robaszynski et al. 1998; Wilmsen 2003; Fig. 1C). The nautiloids of this study stem from a carbonate-dominated interval in the upper part of the depositional sequence (the *Neolobites* Bioevent of Nagm 2019; Fig. 1B) and were collected from measured sections logged in detail at three sites, i.e., at Wadi Ghonima, Wadi Irkas (acronym EN-WI), and Wadi Hawashiya (acronym EN-WH) (Fig. 1A, C). The lower two thirds of the sections show overall retrogradational facies stacking patterns by means of decreasing siliciclastic content and grain size as well as increasing carbonate contents, reflecting the transgressive systems tract of DS Ce 5 (Fig. 1C). The *Neolobites*

Fig. 1. **A.** Location of the studied sections in Wadi Araba (1, Wadi Ghonima section 28°51'19.00" N, 32°8'48.00" E; 2, Wadi Irkas section 28°49'44.40" N, 32°3'38.70" E) and the northern part of Wadi Qena (3, Wadi Hawashiya section 28°7'51.00" N, 32°22'0.00" E). **B.** Stratigraphical framework of the lower Upper Cretaceous in the study area; the stratigraphical position of the nautiloids described herein is indicated. **C.** Correlation and sequence stratigraphic interpretation of the studied sections; the *Neolobites* Bioevent sensu Nagm (2019) represents the maximum flooding zone (mfz) of depositional sequence DS Ce 5. Abbreviations: HST, highstand systems tract; TST, transgressive systems tract. →



C Stratigraphic correlation chart showing the relationship between the Wadi Ghonima, Wadi Irkas, and Wadi Hawashiya sections. The chart is divided into three columns representing the sections. The Wadi Ghonima section shows the upper Cenomanian Galala Formation (0-80 m) and the Malha Formation (0-10 m). The Wadi Irkas section shows the upper Cenomanian Galala Formation (0-50 m) and the Malha Formation (0-10 m). The Wadi Hawashiya section shows the upper Cenomanian Galala Formation (0-50 m) and the Malha Formation (0-10 m). The Malha Formation is shown as a continental deposit underlying the Galala Formation. A stratigraphic gap is indicated between the Malha Formation and the Galala Formation. The Cenomanian stage is further divided into upper, lower-middle, and lower. The Wadi Ghonima Mb. is characterized by a marine onlap and contains the *Neolobites* Bioevent. The Galala Formation is characterized by lagoon deposits and contains the *Neolobites* Bioevent. The Malha Formation is characterized by continental deposits. The Lower Cretaceous stage is characterized by continental deposits. The Turonian stage is characterized by carbonates and lagoon deposits. The Cenomanian stage is characterized by lagoon deposits and siliciclastics (coarse- and fine-grained).

Legend for Lithology:

- sandstone
- siltstone
- sandy siltstone
- marl
- shaly marl
- silty marl
- dolomite
- limestone
- marly limestone
- sandy limestone
- shale
- sandy shale
- silty shale

Legend for Fossils:

- Angulithes mermeti*
- non-oyster bivalves
- oysters
- gastropods
- ammonites
- echinoids
- bioturbation

Stratigraphic Correlation:

- Wadi Ghonima: 0-80 m (upper Cenomanian Galala Formation), 0-10 m (Malha Fm.)
- Wadi Irkas: 0-50 m (upper Cenomanian Galala Formation), 0-10 m (Malha Fm.)
- Wadi Hawashiya: 0-50 m (upper Cenomanian Galala Formation), 0-10 m (Malha Fm.)

Stratigraphic Correlation:

- Wadi Ghonima Mb. (Cenomanian upper): marine onlap, *Angulithes mermeti* mfz, DS Ce 5
- Galala Formation (Cenomanian upper): lagoon deposits, *Angulithes mermeti* mfz, DS Ce 5
- Malha Formation (Lower Cretaceous): continental deposits, stratigraphic gap

Bioevent marks the maximum flooding zone of the sequence, overlain by highstand deposits that are erosionally truncated along sequence boundary SB Ce 5 (see Wilmsen and Nagm 2012, 2013 and Nagm 2019 for further stratigraphical and sedimentological details).

Material and methods

Herein, we follow the nautiloid classification of Shimansky (1975) with the exception that we regard the genus *Deltoidonautilus* Spath, 1927 as a synonym of *Angulithes* Montfort, 1808 (see also Kummel 1956; Wilmsen 2000). Morphological descriptions and terms are used according to Teichert (1964). Biometrical measurements were obtained using a Vernier Caliper and are also given in mm and percent of maximum diameter (in brackets; Fig. 2, Table 1). The data were also used to plot the shell form of *A. mermeti* in the Westermann morphospace diagram (cf. Ritterbush and Bottjer 2012), commonly used for comparing planispiral ammonoid shells. First, raw values of the key shape parameters of shell inflation (Th), whorl expansion (w), and umbilical exposure (U) are calculated (see Table 2). Scaling followed the procedures given in Ritterbush and Bottjer (2012) and Yacobucci (2018):

$$Th_{\text{scaled}} = (Th_{\text{raw}} - 0.14) / 0.54$$

$$w_{\text{scaled}} = (w_{\text{raw}} - 1.00) / 0.77$$

$$U_{\text{scaled}} = U_{\text{raw}} / 0.52$$

Scaling is necessary in order to bring the values within the range of values for common ammonoids. The scaled values were finally normalized to range from 0 to 1:

$$Th_{\text{norm}} = Th_{\text{scaled}} / (Th_{\text{scaled}} + w_{\text{scaled}} + U_{\text{scaled}})$$

$$w_{\text{norm}} = w_{\text{scaled}} / (Th_{\text{scaled}} + w_{\text{scaled}} + U_{\text{scaled}})$$

$$U_{\text{norm}} = U_{\text{scaled}} / (Th_{\text{scaled}} + w_{\text{scaled}} + U_{\text{scaled}})$$

The normalized values are plotted in the Westermann morphospace diagram (see Yacobucci 2018 for a detailed protocol).

Systematic palaeontology

Order Nautilida Agassiz, 1847

Superfamily Nautiloidea Blainville, 1825

Family Hercoglossidae Spath, 1927

Genus *Angulithes* Montfort, 1808

Type species. *Angulithes triangularis* Montfort, 1808, from the Cenomanian of France.

Angulithes mermeti (Coquand, 1862)

Figs. 3–5, 6A, B, 10A.

1862 *Nautilus Mermeti* H. Coq., Coquand 1862: 166, pl. 2: 1, 2.

1886 *Nautilus Munieri*; Choffat 1886: 1, pl. 1: 2, pl. 2: 1.

1907 *Nautilus Mermeti* Coquand; Pervinquier 1907: 46.

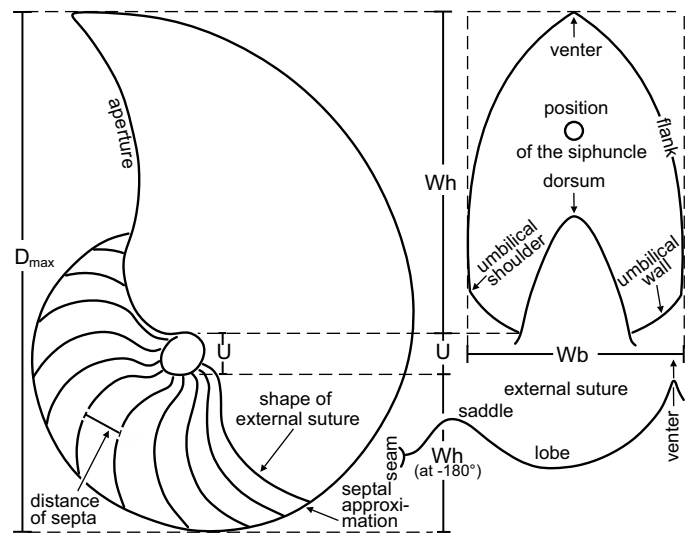


Fig. 2. Shell parameters, suture terminology, and biometric factors of the planispiral nautiloid shell (modified after Wilmsen 2016). Abbreviations: D_{max} , maximum diameter; U, umbilical width at D_{max} ; Wb, whorl breadth at D_{max} ; Wh, whorl height at D_{max} .

- 1910 *Nautilus Mermeti* Coquand; Eck 1910: 11.
 1912 *Nautilus munieri* Choffat; Schlagintweit 1912: 99, pl. 6: 9.
 1914 *Nautilus Mermeti* Coquand; Eck 1914: 183, pl. 9: 1.
 non 1914 *Nautilus Mermeti* Coquand var. *Munieri* Choffat; Eck 1914: 184, pl. 9: 2–4 (= *Angulithes triangularis* Montfort, 1808).
 1956 *Lissoniceras mermeti* (Coquand); Benavides-Cáceres 1956: 435, pl. 40: 1–3.
 1960 *Angulithes (Angulithes) triangularis mermeti* (Coquand); Wiedmann 1960: 188, pl. 22: h; pl. 25: 8, 9; pl. 26: 4; pl. 27: 1, 2; text-figs. 16–20.
 1989 *Angulithes mermeti* (Coquand); Luger and Gröschke 1989: 358.
 1992 *Deltoidonautilus mermeti* (Coquand); Abdel-Gawad et al. 1992: 326, pl. 1: 1.
 2000 *Angulithes mermeti* (Coquand, 1862); Wilmsen 2000: pl. 5: 3; text-fig. 5.
 2002 *Angulithes* sp.; Meister and Rhalmi 2002: 768, pl. 5: 1, 3; text-fig. 13b, c.
 2004 *Angulithes mermeti* (Coquand, 1862); Abdel-Gawad et al. 2004: pl. 1: 1.
 2006 *Angulithes mermeti* (Coquand, 1862); El Qot 2006: 114, pl. 24: 1, 2.
 2006 *Angulithes mermeti* (Coquand); Abdel-Gawad et al. 2006: pl. 3: 4, 7.
 2009 *Angulithes mermeti* (Coquand, 1862); Nagm 2009: 52, text-figs. 5.1A, B, 5.2A.
 2010 *Angulithes* sp.; Cavin et al. 2010: text-fig. 7X.
 2011 *Angulithes mermeti* (Coquand, 1862); Ayoub Hannaa 2011: 205, pl. 21: 1; text-fig. 3.36.
 2012 *Angulithes* sp.; Benyoucef et al. 2012: pl. 1: 1.
 2012 *Angulithes mermeti* (Coquand, 1862); Ayoub Hannaa and Fürsich 2012: 64, text-fig. 7.
 2015 *Angulithes mermeti* (Coquand); Nagm 2015: text-fig. 7D.
 2015 *Angulithes mermeti* (Coquand, 1862); Meister and Piuz 2015: 19, pl. 1: 1–4.
 2017 *Angulithes mermeti* (Coquand, 1862); Meister et al. 2017: 5, pl. 1: 1a, b.
 2019 *Angulithes mermeti* (Coquand, 1862); Nagm 2019: text-fig. 6C.

Material.—Eight internal moulds (listed in Table 1) from the lower upper Cenomanian *Neolobites vibrayeanus* Zone of

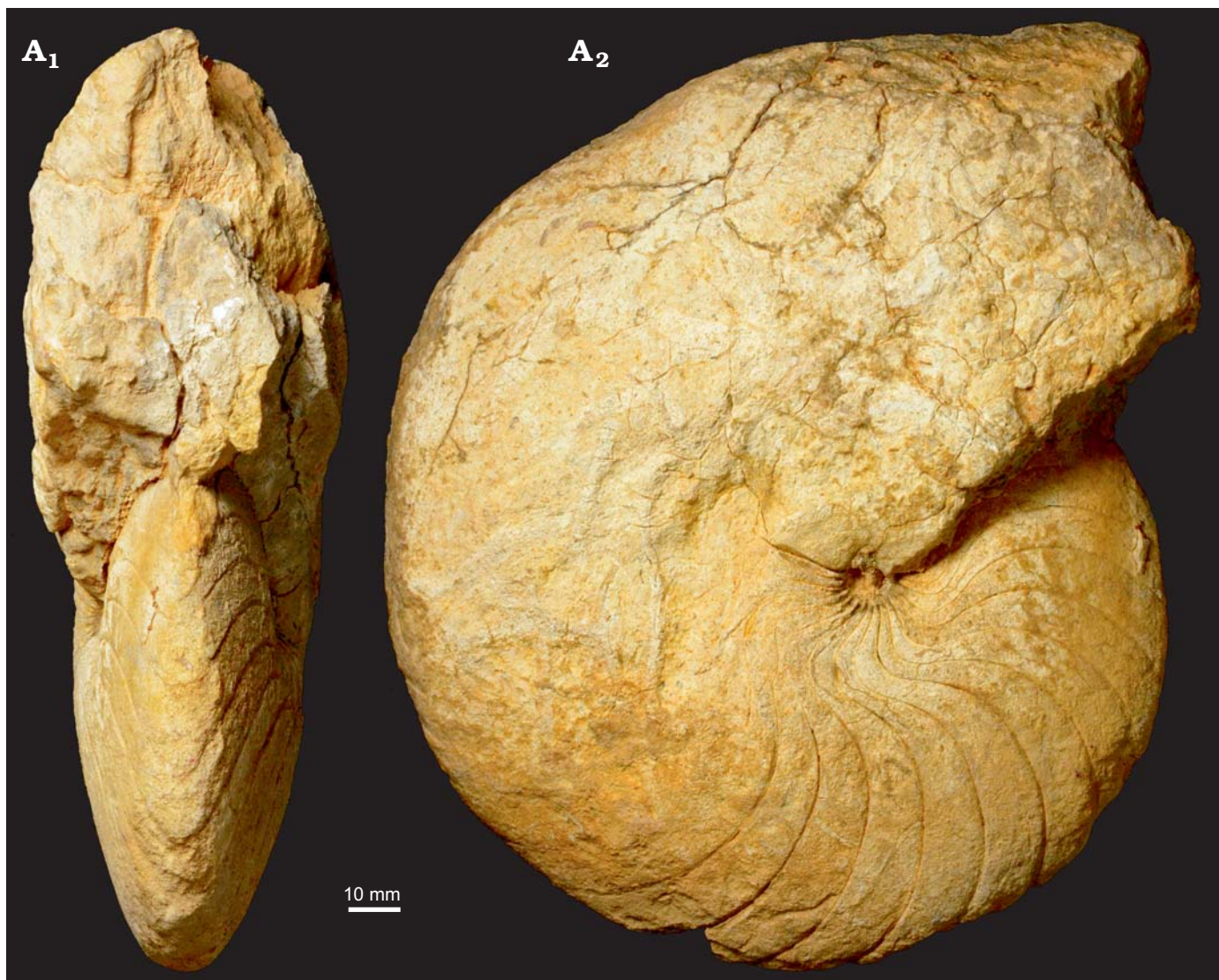


Fig. 3. Hercoglossid nautiloid *Angulithes mermeti* (Coquand, 1862), AFK 225 from the Cenomanian of Wadi Ghonima, Egypt, in apertural (A_1) and lateral (A_2) views.

the Galala Formation in Wadi Araba, north Eastern Desert of Egypt (Wadi Ghonima section, Wadi Irkas section), and northern Wadi Qena (Wadi Hawashiya; see Fig. 1A for location), ranging from complete adult specimens to small septate fragments. AFK 225 (Fig. 3) is an excellently preserved complete adult specimen from Wadi Ghonima, Egypt.

Measurements.—See Table 1.

Description.—Involute, almost oxycone and large-sized nautiloid with strongly compressed whorl cross-section ($Wb/Wh = 0.5-0.6$). The small and shallow umbilicus (5–7% of D_{max}) has a rounded wall with a gradual transition onto the lower flanks where the maximum whorl breadth occurs. From there, the flanks converge to a venter which is acute in juvenile and adolescent stages, becoming very narrowly rounded in the adult stage. Maximum diameter is around 200 mm as indicated by septal approximation, e.g., in AFK 225. Ribbing has not been observed on any part of the internal

moulds. The external suture is rather sinuous with a faint umbilical saddle and a low lobe on the umbilical wall rising to a prominent, knee-like saddle on the lower flank. The mid- and outer flanks are characterized by a wide lateral lobe that rises to a narrowly pointed saddle at the venter. The septal spacing is rather low (8–10 mm at $D = 120$ mm, ~12 mm at $D = 180$ mm), resulting in a high number of septa per whorl (e.g., 14 septa/half a whorl in specimen EN-WI-1 at $D \sim 130$ mm). The siphuncle has a subdorsal position, at about 1/5 of the distance from the dorsum to the venter. The nearly complete and mature specimen AFK 225 suggests that the length of the adult body chamber was relatively short and did not exceed 150° of the last whorl.

Stratigraphic and geographic range.—All specimens described herein from Wadi Araba and Wadi Qena (Eastern Desert, Egypt) are from the lower upper Cenomanian *Neolobites vibrayanus* Zone that is broadly contemporaneous to the *Calycoceras* (*C.*) *naviculare*–*C.* (*Proeucalycoceras*)

Table 1. Measurements (in mm; in brackets % of D_{\max}) of the studied specimens of *Angulithes mermeti* (Coquand, 1862), see also Fig. 2. Abbreviations: D_{\max} , maximum diameter; U, size of umbilicus at D_{\max} ; Wb, whorl breadth at D_{\max} ; Wh, whorl height at D_{\max} ; Wh_{-180° , whorl height at -180° from D_{\max} .

Specimen No.	D_{\max}	Wb	Wh	Wb/Wh	U	$Wh_{-180^\circ} [= D_{\max} - (Wh+U)]$
AFK 202	120.9 (100%)	45.3 (37.5%)	75.2 (62.2%)	0.60	~6 (5.0%)	39.7
AFK 218	—	42.5	72.0	0.59	—	—
AFK 225	180.4 (100%)	61.3 (34.0%)	105.2 (58.3%)	0.58	9.0 (5.0%)	66.2
AFK 272	—	25.9	48.1	0.54	—	—
EN-WI-1	131.6 (100%)	47.0 (35.7%)	76.6 (58.2%)	0.61	~7 (5.3%)	48.0
EN-WI-2	57.3 (100%)	20.0 (34.9%)	33.6 (58.6%)	0.59	~4 (6.9%)	19.7
EN-WI-5	—	39.1	72.2	0.54	—	—
EN-WH-1	113.0 (100%)	33.3 (29.4%)	68.5 (60.6%)	0.49	~6 (5.3%)	38.5
type of Coquand (1862: pl. 2)	~200 (100%)	~57.5 (28.8%)	~121 (60.5%)	0.48	~11 (5.5%)	~68
<i>Nautilus munieri</i> Choffat (1886: pl. 2)	137.6 (100%)	50.2 (36.5%)	83.2 (60.5%)	0.60	~7 (5.1%)	47.4

guerangeri Biozone of the NW European standard biostratigraphy (see Nagm et al. 2010a, b and Nagm and Wilmsen 2012 for details). This stratigraphic range seems to correspond to the records from literature which almost all fall into the late Cenomanian. The palaeogeographic distribution is confined to occurrences south and north of the (western) Neotethys in northern Africa and southern Europe with additional records from Peru and Oman.

Discussion

Taxonomical remarks.—The smooth, strongly compressed, nearly oxycone form with sharp venter, the sinuous external suture line with conspicuous saddles on the lower flank and the venter, the high density of septa, and the subdorsal position of the siphuncle are characteristic features of *Angulithes mermeti* (Coquand, 1862) as described and illustrated in the literature (see synonymies above). The type specimen is from Ténoukla, near Tébassa (northeast Algeria), from the uppermost beds of the “étage rhotomagien” (Coquand 1862: pl. 2: 1, 2), the sutures have been displayed in a simplified, less sinuous pattern as already remarked by Pervinquère (1907), Schlagintweit (1912) and Eck (1914) (see Fig. 6A). This led Choffat (1886) to the erection of a new species when he compared his *Nautilus munieri* (Fig. 7B) to the illustration of Coquand (1862). However, Coquand’s (1862) species has carefully been described and can unequivocally be recognized, and both taxa are contemporaneous. Thus, the two taxa are conspecific and *Nautilus mermeti* Coquand, 1862 has priority over *Nautilus munieri* Choffat, 1886. Nevertheless, the specimens recorded as “*Nautilus Mermeti* Coquand var. *Munieri* Choffat” by Eck (1914: 184, pl. 9: 2–4) correspond to *Angulithes triangularis* Montfort, 1808 based on their more inflated shell form and less sharp venter. Wiedmann (1960), on the other hand, followed yet another taxonomical approach and considered *A. mermeti* and *A. triangularis* as conspecific and regarded the former as a subspecies of the latter. However, *A. triangularis* dif-

fers from *A. mermeti* by its less compressed whorl section ($Wb/Wh = 0.65–0.80$), less sinuous suture, larger inter-septal distances and a more central position of the siphuncle (Fig. 6C, D; see Wilmsen 2000). Furthermore, the two taxa seem to be stratigraphically separate, *A. triangularis* being a typical late early to middle Cenomanian species (e.g., Wilmsen 2000; Debris 2006) while *A. mermeti* is slightly younger (see subchapters on Stratigraphy and Evolutionary trends during the Cenomanian below).

Palaeobiogeography.—*Angulithes mermeti* has been recorded from the upper Cenomanian of southern America (Peru: Schlagintweit 1912; Benavides-Cáceres 1956), Portugal (Choffat 1886; Barroso-Barcenilla et al. 2011; Segura et al. 2014), Spain (Wiedmann 1960, 1964; Barroso-Barcenilla et al. 2017), the Maghreb area (Morocco, Algeria and Tunisia: Coquand 1862; Pervinquère 1907; Meister and Rhalmi 2002; Cavin et al. 2010; Benyoucef et al. 2012; Meister et al. 2017), Egypt (Western Desert: Blanckenhorn 1900; Eastern Desert and Sinai: Eck 1910, 1914; Luger and Gröschke 1989; Abdel-Gawad et al. 1992, 2004, 2006; El Qot 2006; Nagm 2009, 2015, 2019; Ayoub Hanna 2011; Ayoub Hanna and Fürsich 2012) and Oman (Meister and Piuze 2015). This palaeobiogeographical distribution suggests an affinity to tropical–subtropical palaeolatitudes north and south of the palaeo-equator and a general warm-water preference of the species (latitudinal restriction; cf. Fig. 7). The reports from northern Spain are so far the northernmost records of *A. mermeti*, reaching into the Northern Transitional Subprovince of Ernst et al. (1996) which was characterized by a mingling of Boreal and Tethyan faunal elements throughout the Late Cretaceous. Other Late Cretaceous representatives of the genus are also known from the warm-temperate part of the Boreal Realm (e.g., *Angulithes westphalicus* Schlüter, 1872; cf. Wilmsen 2000) but the genus appears to be absent from high palaeo-latitudes.

Autecology of *Angulithes mermeti*.—The smooth shell and streamlined, nearly oxycone form (mean umbilical exposure: 0.054; mean whorl expansion over the last 180° : 1.73; mean overall inflation: 0.34; see Table 2) indicate hydrodynamic efficiency and suggest, analogue to the basic pla-



Fig. 4. Hercoglossid nautiloid *Angulithes mermeti* (Coquand, 1862) from the Cenomanian of Wadi Ghonima, Egypt. **A.** AFK 202 in lateral (A_1 , A_3) and ventral (A_2) views. **B.** AFK 218 in lateral (B_1) and apertural (B_2) views; arrow shows the position of the siphuncle.

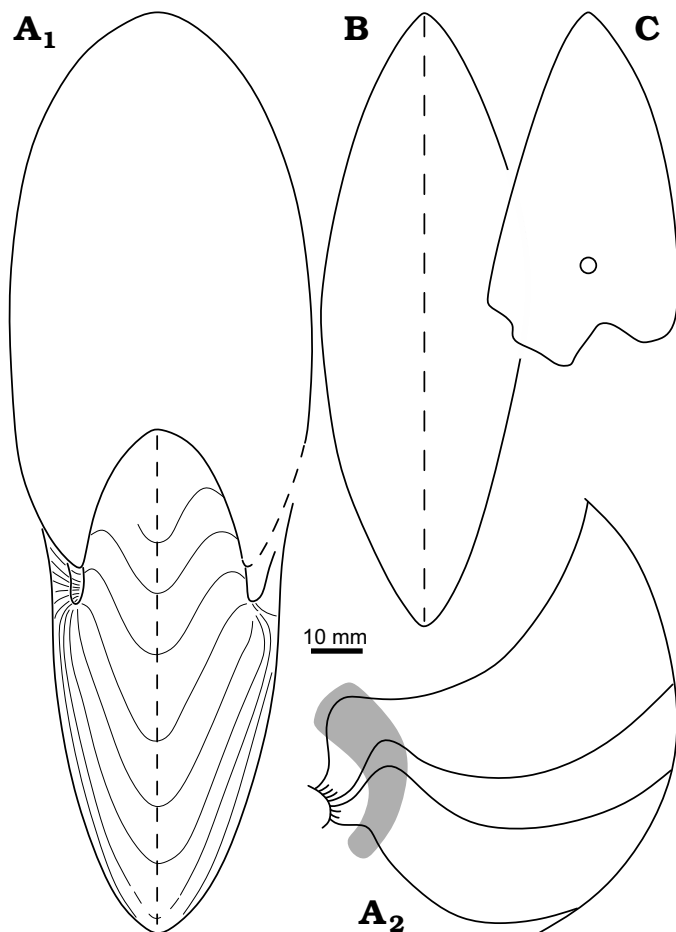


Fig. 5. Cross-sections and external sutures of the hercoglossid nautiloid *Angulithes mermeti* (Coquand, 1862) from the Cenomanian of Wadi Ghonima, Egypt. **A.** AFK 225, shell shape in apertural view (A_1), external sutures (A_2); grey shading indicates position of the umbilical saddle. **B.** AFK 202, shell shape in ventral view. **C.** AFK 218, whorl shape, showing the position of the siphuncle.

nispiral ammonoid shell shapes (Jacobs and Chamberlain 1996; Westermann 1996; Ritterbush and Bottjer 2012; Ritterbush et al. 2014; Lukenender 2015), adaptation for continuous fast swimming combined with excellent acceleration of *A. mermeti*. In the Westermann (1996: fig. 1) morphospace diagram developed for planispiral ammonites (Fig. 8), the oxycone shell form caps the nekton field and *A. mermeti* plots into the nekton field between oxycones and discocones. In direct comparison, *Nautilus pompilius* has a significantly higher shell inflation ratio and a smaller whorl expansion (Fig. 8). Increased acceleration, speed and steering (maneuverability combined with directional stability) by reducing drag is indicated by the smooth shell, small umbilicus, compression of the whorl section, and by the narrowly rounded to acute venter (Chamberlain 1993; Westermann 1996, 1999). According to Ritterbush (2016), such oxycone shells produce minimal drag at larger sizes and/or faster speeds (low drag coefficient of 0.25 compared to 0.7–1.1 in cadicocones and gyrocones, respectively; cf. Chamberlain 1993). In contrast to the limited steering that restricts the

Recent *Nautilus* to demersal bottom feeding (Chamberlain 1992), *A. mermeti* almost certainly was shaped for better hydrodynamic performance and may thus have been able to pursuit small nektonic prey.

Furthermore, the ability for rapid acceleration and sustained fast swimming was certainly beneficial to escape shell-breaking predators (see below). The breviodome shell (body chamber length of about 145° , similar in length to that of the Recent *Nautilus pompilius*) aided in stability and indicates a similar living position and orientation of the aperture ($30 \pm 15^\circ$ from the vertical) as in the modern ecto-cochleates (Fig. 9; Chamberlain 1987; Westermann 1999; Peterman et al. 2019). The compressed form of *A. mermeti* is shared by the co-occurring ammonite *Neolobites vibraveanus* that corresponds to morphotype group 11 of Batt (1989). According to this latter study from the upper Albian to middle Turonian of the Western Interior Seaway (USA), ammonites of this group were almost always associated with nearshore and proximal offshore facies, thus being reliable indicators of relatively shallow conditions (≤ 40 m water depth; Batt 1989). However, the shell shape of *N. vibraveanus* is more platycone due to the high and sub-parallel flanks and the venter is flattened (tabulate) to weakly concave, the sharp umbilical shoulders being ornamented by numerous small clavi (e.g., Wiese and Schulze 2005). This shell form certainly produced considerable drag at the leading edge during backward swimming (cf. Westermann 1996) and was definitely less well optimized (streamlined) for fast locomotion and improved steering (Chamberlain 1993; Westermann 1999).

Based on the carbonate facies of the host strata and palaeogeographical constraints, the habitat of *A. mermeti* was a relatively shallow, wide epicontinental sea and the species sometimes even invaded open-lagoonal environments where

Table 2. Raw values of shell inflation (thickness ratio; $Th = Wb/D_{max}$), whorl expansion rate ($w = Wh/Wh$ at -180°) and umbilical exposure U ($=$ width of umbilicus in % of D_{max}) of *Angulithes mermeti* (Coquand, 1862) for illustration in Westermann morphospace (Fig. 8A); see Table 1 for initial measurements and Ritterbush and Bottjer (2012) and Yacobucci (2018) for methodology. Abbreviations: D_{max} , maximum diameter; U , size of umbilicus at D_{max} ; Wb , whorl breadth at D_{max} ; Wh , whorl height at D_{max} .

Specimen No.	shell inflation (Th)	whorl expansion rate (w)	umbilical exposure (U)
AFK 202	0.37	1.89	0.05
AFK 225	0.34	1.59	0.05
EN-WI-1	0.35	1.60	0.05
EN-WI-2	0.35	1.71	0.07
EN-WH-1	0.29	1.78	0.05
type of Coquand (1862: pl. 2)	0.29	1.78	0.06
<i>Nautilus munieri</i> Choffat (1886: pl. 2)	0.37	1.76	0.05
mean	0.34	1.73	0.054
scaled mean	0.37	0.94	0.104
normalized mean	0.26	0.67	0.07

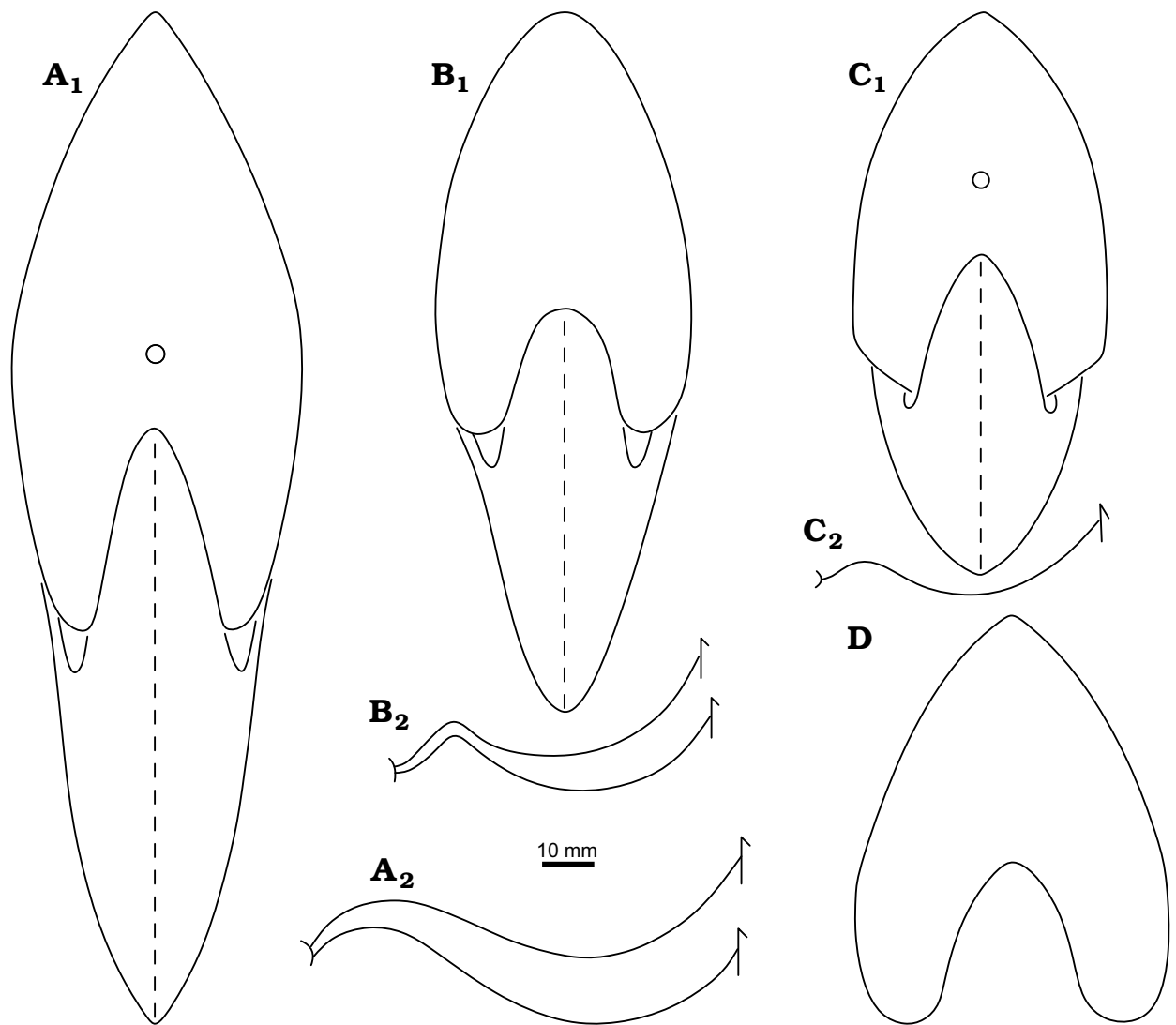


Fig. 6. Shell form (A_1 – C_1), external sutures (A_2 – C_2), and whorl cross-section (D) of selected hercoglossid nautiloids. **A.** *Nautilus mermeti* (Coquand, 1862) from the Cenomanian of Ténoukla near Tébassa, northeast Algeria (after Coquand 1862: pl. 2: 1, 2). **B.** *Nautilus munieri* Choffat, 1886 from the upper Cenomanian of Villa Nova d’Ourem, Portugal (after Choffat 1886: pl. 2: 1). **C.** *Angulithes triangularis* Montfort, 1808 (MB.C.2052) from the lower Sardinero Formation, lower Middle Cenomanian of Langre, Cantabria, northern Spain (after Wilmsen 2000: pl. 1: 2b, pl. 5: 15). **D.** *Nautilus triangularis* Montfort, 1808 from the Cenomanian of Île de Madame, Charente-Maritime, France (after d’Orbigny 1840: pl. 12: 2).

it was recorded from dasycladalean algae-bearing wacke- and floatstone with rudists and corals (Fig. 10; see Wilmsen and Nagm 2012 for facies analysis of the Galala Formation). Wiese and Schulze (2005) also reconstructed a preferential distribution of the co-occurring ammonite *N. vibrayeanus* in shallow-marine shelf settings in predominantly less than 30 m water depth (see also Batt 1989, for inferred palaeobathymetry of ammonites of morphotype group 11). Based on random size distribution of the ammonites and taphonomical observations, Wiese and Schulze (2005: 944) also concluded that the depositional setting corresponds to the original habitat and that post-mortem transport played no role. Nautiloids, on the other hand, are conventionally thought to be prone for significant post-mortem drift (e.g., House 1987). However, extensive post-mortem transport will commonly result in the removal of shells from the fossil record under most geological circumstances (Hewitt 1988)

and the inferred drift shells of *Nautilus pompilius* along the eastern African coast, the classical “smoking gun” for this process, have recently been suggested to rather indicate the existence of a modern, or recently extirpated, living population in the western Indian Ocean (Yacobucci 2018). Furthermore, only those shells at all with relatively high inflation are likely to float for a significant time after death of the animal whereas limited post-mortem buoyancy of compressed shells argues against substantial dispersal by (surface) currents (Yacobucci 2018). We also do not see any evidence of heavy fouling by encrusting epibenthos suggesting prolonged periods of floating (cf. Reymont 2008) and thus conclude that the strata in which *A. mermeti* has been found corresponding to the original habitat of the species. Habitat depth was thus indeed very shallow, in the case of dasycladalean algae-bearing strata the upper, light-saturated parts of the euphotic zone where the species lived

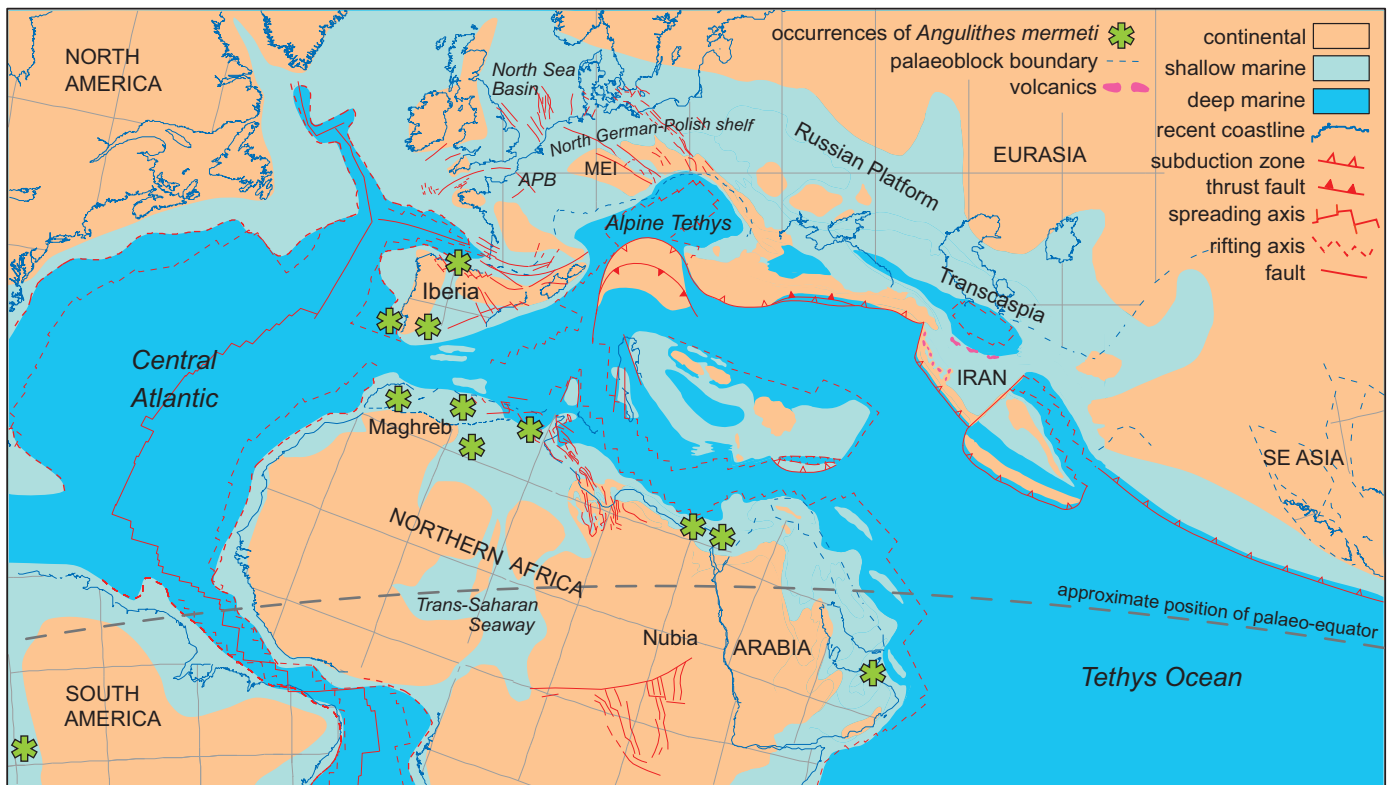


Fig. 7. Palaeobiogeographical distribution of the hercoglossid nautiloid *Angulithes mermeti* (Coquand, 1862). Cenomanian palaeogeographical and plate tectonic situation modified after Barrier and Vrielynck (2008); nautiloid occurrences are indicated by asterisks (see text for literature sources). Abbreviations: APB, Anglo-Paris Basin; MEI, Mid-European Island,

between rudist/coral thickets and above green algae meadows in open lagoons of at a maximum 5–20 m water depth (Fig. 10A–C) (e.g., Liebau 1984). The fact the larger study area was part of a structured, predominantly shallow shelf system (e.g., Bauer et al. 2002; Schulze et al. 2005; Wilmsen and Nagm 2012) argues against significant daily vertical movements of *A. mermeti* (as documented for the Recent *Nautilus*; e.g., Saunders and Ward 1987, see Ward et al. 2016 for a current synopsis) because such regular ascents and descents at the magnitude of the *Nautilus* (between 130–700 m; Dunstan et al. 2011) would have always been associated with extensive horizontal migrations. We thus conclude for a preferred habitat depth of *A. mermeti* between 5–50 m, corresponding to the depth range of the Galala Formation (Wilmsen and Nagm 2012).

Stratigraphy.—Where well-dated, *A. mermeti* has been recorded exclusively from lower upper Cenomanian strata (e.g., Luger and Gröschke 1989; Nagm 2009, 2019; Ayoub-Hannaa and Fürsich 2012; Kennedy and Gale 2015; Meister et al. 2017), often associated with the ammonite *Neolobites vibrayeanus* (d’Orbigny, 1841) that is very widespread in the western Tethyan Realm from northern Africa and Iberia into the Middle East (e.g., Lefranc 1981; Luger and Gröschke 1989; Kennedy and Simmons 1991; Wiese and Schulze 2005; “assemblage faunique à *N. vibrayeanus* [A]” of Meister and Abdallah 2005). *N. vibrayeanus* characterizes the eponymous lower upper Cenomanian ammonite

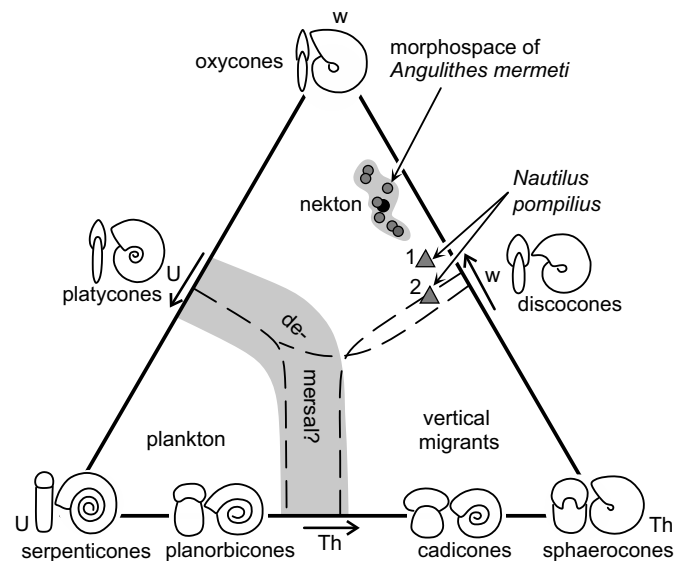


Fig. 8. Westermann morphospace diagram, simplified and modified after Ritterbush et al. (2014), with placement of the hercoglossid nautiloid *Angulithes mermeti* (Coquand, 1862) (see Table 2 for raw data; black circle indicates mean value); for comparison, two specimens of *Nautilus pompilius* Linnaeus, 1758 are plotted in the diagram, too (1, specimen 17 of Tajika et al. 2015; 2, an early Pleistocene specimen from Wani et al. 2008). Abbreviations: Th, shell inflation; U, umbilical exposure; w, whorl expansion.

biozone that is broadly contemporaneous to the *Calycoceras* (*C. naviculare*)/*C. (Proeulacoceras) guerangeri* Biozone of the NW European standard biostratigraphy (Charrière

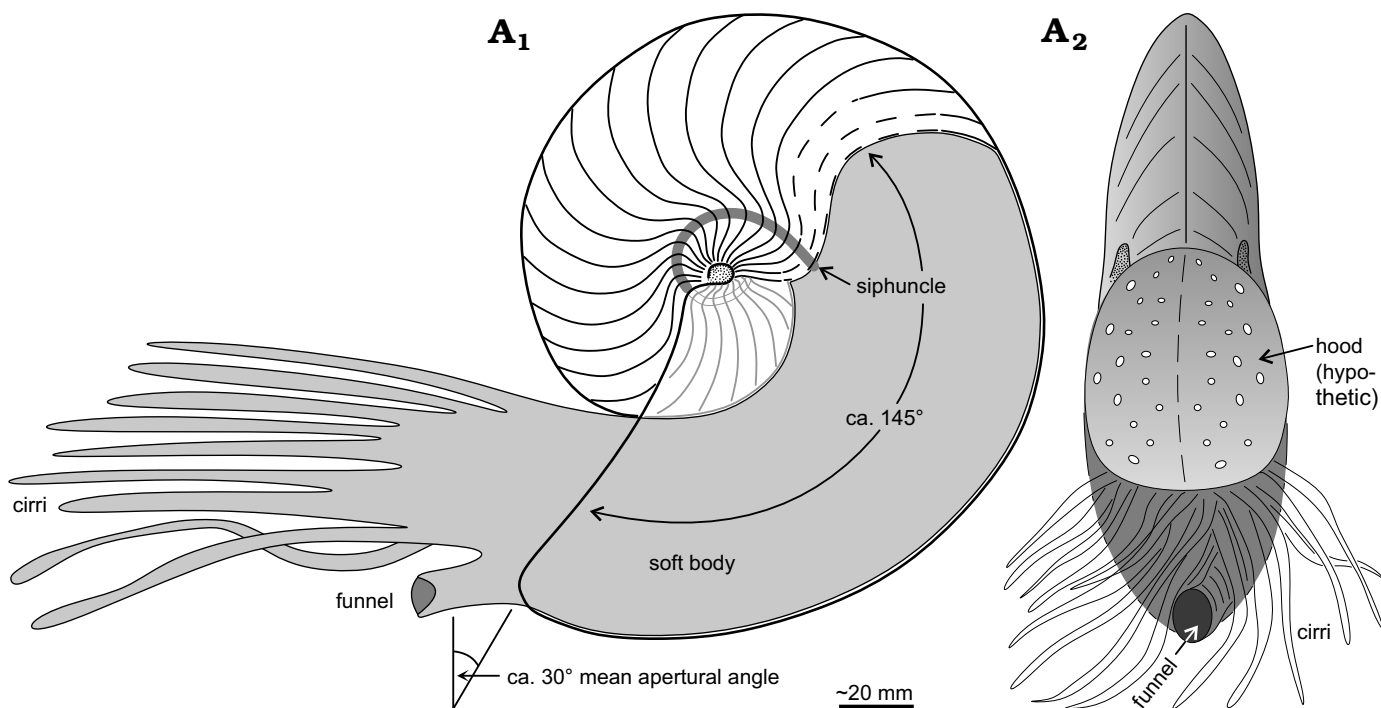


Fig. 9. Reconstruction of the life position of the hercoglossid nautilid *Angulithes mermeti* (Coquand, 1862) in sagittal cross-section (A₁) and apertural view (A₂) (approximately 1/2 of natural size).

et al. 1998; Meister and Rhalmi 2002; Nagm et al. 2010a, b; Nagm and Wilmsen 2012; Meister et al. 2017; Wright and Kennedy 2017). In terms of absolute duration, the early late Cenomanian corresponds to the interval between 95.5–94.5 Ma (Ogg and Hinnov 2012). Thus, the range of *A. mermeti* is rather short, corresponding to about 1 myr of geological time. The common co-occurrence of *A. mermeti* and *N. vibrayeanus* was early recognized (Basse and Choubert 1959; Luger and Gröschke 1989) and the correlatable character of the assemblage has led some authors to define a bioevent, i.e., the *Neolobites* bioevent of Cavin et al. (2010), the cephalopod assemblage 2 of Barroso-Barcenilla et al. (2011), the *Neolobites vibrayeanus* bioevent (A1) of Meister and Piuz (2013), the *N. vibrayeanus*–*A. mermeti* assemblage of Segura et al. (2014) and the *Neolobites* bioevent of Nagm (2019). Based on these records it becomes apparent that this bioevent is related to maximum flooding conditions of Cenomanian depositional sequence DS Ce 5 (see Fig. 1B, C; Wilmsen and Nagm 2013; UZA-2.4 in Segura et al. 2014), forming a maximum flooding bioevent sensu Ernst et al. (1996) and Wilmsen (2012). Such events commonly have an overlapping character and the *Neolobites* bioevent can be correlated from Iberia via northern Africa into the Middle East (Meister et al. 2017; Nagm 2019). For a detailed stratigraphical, palaeontological and sedimentological description of the event, see Nagm (2019).

Evolutionary trends during the Cenomanian.—Starting with the first appearance of the genus *Angulithes* de Montfort, 1808 in the Albian (*A. arcuatus* [Deshayes in Leymerie, 1842]), there are a number of directed morpho-

logical trends reflected by the Cenomanian species of the genus that appear to document gradual evolutionary changes during the course of the stage (c. 100–94 Ma). These have in part already been noted by Wilmsen (2000) and pertain to *A. fleuriausianus* (d’Orbigny, 1840), *A. triangularis* Montfort, 1808, *A. mermeti* (Coquand, 1862) and *Angulithes vascogoticus* Wiedmann, 1960, broadly tracing a chronological sequence characterized by (Fig. 11): (i) an increasing compression of the shell associated with a sharpening of the venter; (ii) an increasing sinuosity of the suture lines; (iii) a reduction of inter-septal distances; (iv) a dorsally directed migration of the siphuncle.

The Cenomanian age witnessed one of the greatest Phanerozoic transgressions (e.g., Hallam 1992) and it is thus very tempting to relate the observed changes in the successive species of *Angulithes* to the concomitant sea-level rise and the expansion of shallow epicontinental seas in the early Late Cretaceous. *A. fleuriausianus* is still very similar to its basic Albian predecessor, *A. arcuatus*, by means of a relatively inflated whorl shape with only slight ventral angling, a low septal sinuosity combined with wide septal spacing and central position of the siphuncle (note that siphuncle position is unknown in *A. arcuatus*). This general similarity to *A. fleuriausianus* (d’Orbigny, 1840) has already been noted in the original description of *Nautilus arcuatus* by Deshayes in Leymerie (1842: 15) and more material is needed to evaluate if the two taxa are in fact conspecific (d’Orbigny’s [1840] species would have priority). Nevertheless, it is quite clear that these two taxa form the basic stock of the morphological development in *Angulithes* during the Cenomanian. In the late early to middle Cenomanian, the more compressed and angu-

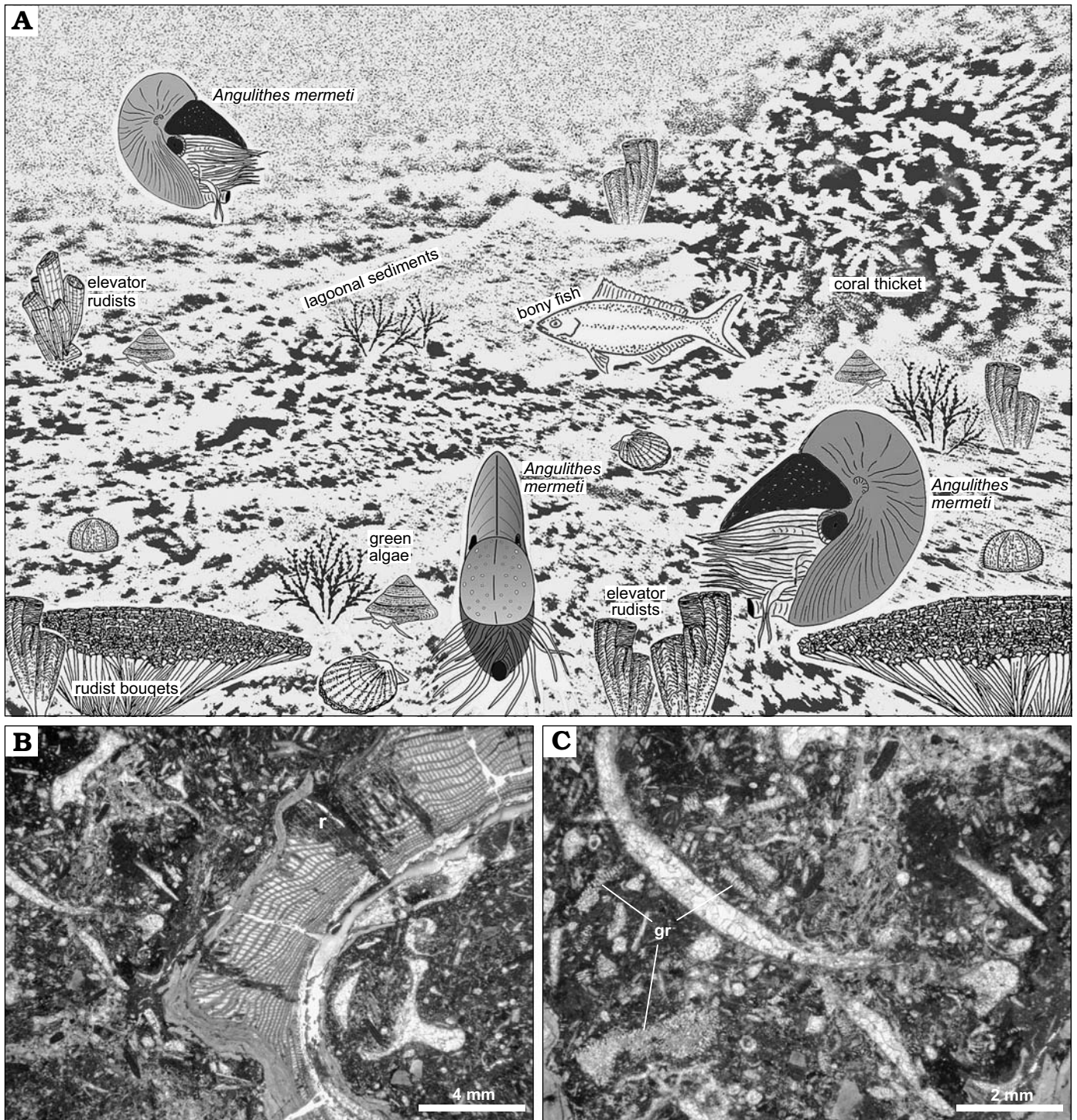


Fig. 10. Palaeoecology of the hercoglossid nautiloid *Angulithes mermeti* (Coquand, 1862). **A.** Reconstruction of *A. mermeti* (Coquand, 1862) in the lagoonal shallow-water environment of the Galala Formation (background after a subaqueous photograph in the property of MW from a lagoonal site in the present-day Red Sea near Hughhada taken in 1999, treated by greyscale-filtering in Photoshop CS2); rudist illustrations from Mitchell (2002). **B.** Bioclastic rudist (r) floatstone, the lagoonal host sediment in which *A. mermeti* has been found in the Wadi Ghonima section (thin-section photomicrograph of sample 080217-18). **C.** Close-up of Fig. 9B showing the bioclastic packstone matrix in detail, including numerous fragments of dasycladalean algae (gr).

lar-ventered *A. triangularis* appeared, also featuring a slightly more dorsally oriented siphuncle and a more sinuous suture. These trends continued into the early late Cenomanian, when *A. mermeti* represents a culmination of these morphological developments. In the late late Cenomanian, *A. vascogoticus*

sustained the septal differentiation by means of a strongly sinuous suture transitional to *Hercoglossa* (Wiedmann 1960) and an almost dorsal siphuncle, but the shell of this species is less compressed compared to *A. mermeti* and the distance of the septa is larger (Fig. 11, Table 3; Wilmsen 2000).

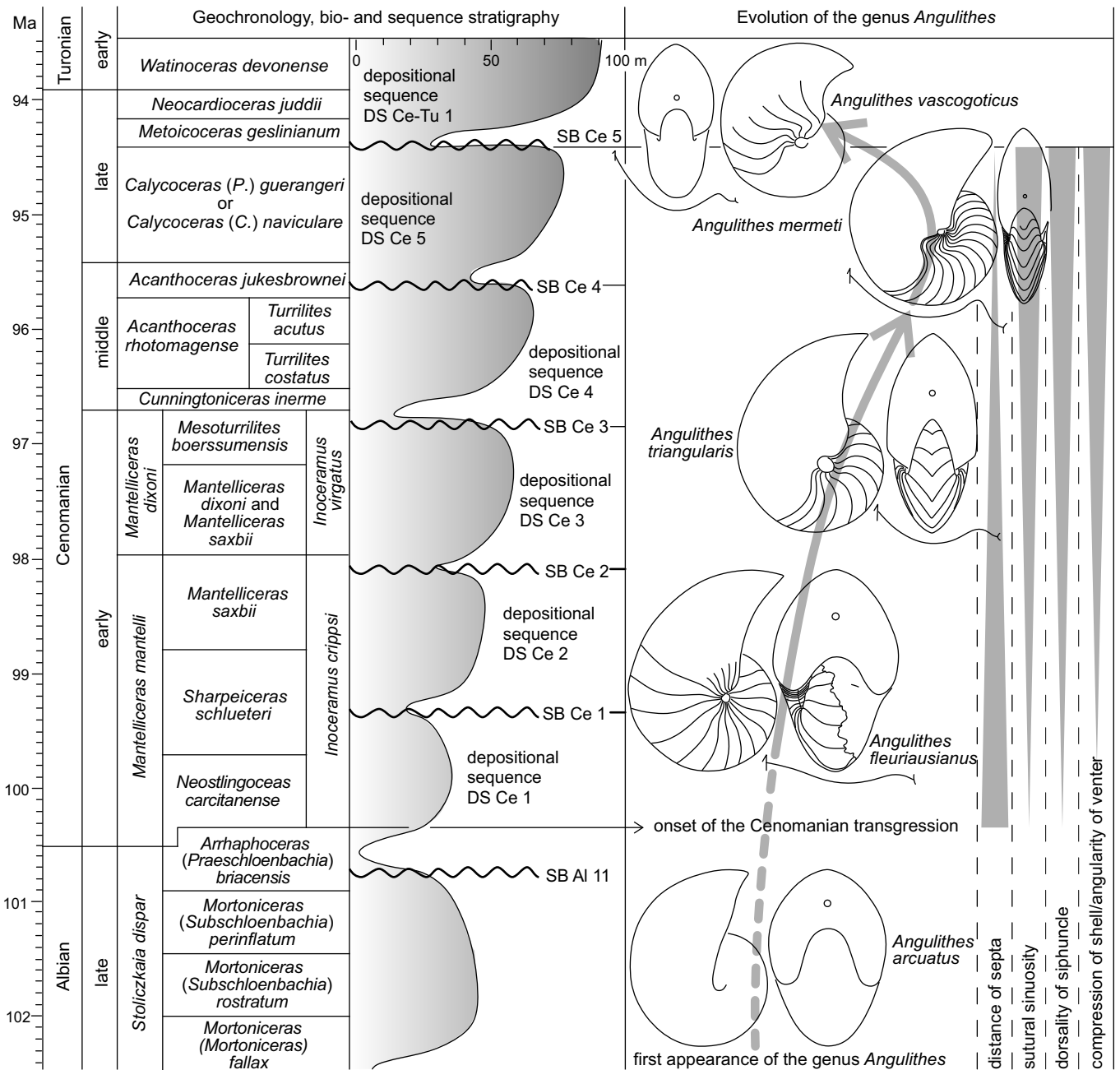


Fig. 11. Geochronology (Ogg and Hinnov 2012), ammonite biostratigraphy (Wright and Kennedy 2017) and sequence stratigraphy (Robaszynski et al. 1998; Wilmsen 2003) of the Cenomanian Stage plotted against evolutionary trends in the hercoglossid nautiloid genus *Angulithes*. See text for further explanations.

The increasingly more compressed forms, culminating in the nearly oxycone shell of *A. mermeti*, certainly reflect improved swimming capabilities and steering (see discussion on autecology of *A. mermeti* above). Such adaptations were necessary to successfully occupy new niches in the wide, shallow epicontinental seas that formed during the early Late Cretaceous and are mirrored by the morphology of many contemporaneous ammonoids found in such settings (e.g., Batt 1989). The increasing sutural sinuosity and the denser spacing of the septa are probably buttressed the shells but a simple relation to increasing water depths falls short of a meaningful explanation given the inferred

shallow habitat depth of *A. mermeti* (see above). The reason for the dorsal-directed migration of siphuncle is likewise not straightforward. Both aspects are detailed below.

An important function of the septa in ectocochleate cephalopods, apart from forming the hydrostatic apparatus, i.e., the phragmocone, is the buttressing of shell against water pressure that may ultimately result in shell implosion (e.g., Westermann 1973). For Cretaceous ammonites, Batt (1991) developed a “Sutural Amplitude Index” (SAI) based on maximum height of sutural elements and the length of the suture that offers a useful proxy for the relative living depth of ammonoids with comparable shell morphologies,

Table 3. Septal distances (in mm, measured at venter) of different Cenomanian species of *Angulithes*.

Species	Diameter (D)	Distance of septa
<i>A. fleuriausianus</i> (d'Orbigny, 1840), early to middle Cenomanian	D = 120 (SpK 206)	c. 20
<i>A. triangularis</i> de Montfort, 1808, late early to middle Cenomanian	D = 130 (SpK 211)	c. 17
<i>A. mermeti</i> (Coquand, 1862), early late Cenomanian	D = 120 (AFK 202)	10–12
<i>A. vascogoticus</i> Wiedmann, latest Cenomanian	D = 125–138 (SpK 214, 216, 223)	c. 18–20

with inferred deeper water dwellers being characterized by higher SAI indices. This observation suggests that a greater septal support for the shell wall under increased hydrostatic pressures is effective against implosion. Even if this relationship was questioned by some authors (e.g., Olóriz and Palmqvist 1995; Daniel et al. 1997; Olóriz et al. 2002), Hassan et al. (2002) demonstrated by means of finite-element analysis of simulated ammonoid septa that the marginal differentiation in fact improved the dispersion of stress in the shell walls. This line of argument was also applied to nautiloids and Westermann and Ward (1980) concluded that septal curvature and thickness in orthocone nautiloids are useful proxies to bathymetry. Following this suggestion, Tintant and Kabamba (1985: 60) also proposed that the shape of the suture line in planispiral nautiloids is an adaptive response to variations in water depth, i.e., a plicate septum improved mechanical resistance to implosion. Studies on Recent nautilids showed that their (in comparison to most ammonites relatively thick) shells implode at a water depth of around 800 m, that the maximum depth range comprises about 100–700 m and that the preferred depth range is between 100–300 m (Hewitt and Westermann 1987; Saunders and Ward 1987; Dunstan et al. 2011; Ward et al. 2016). The suture line of *Nautilus pompilius* is relatively strongly differentiated (see Wani et al. 2008), the external part of which showing similar amplitudes as in *A. mermeti*, but the distance of the septa is relatively high compared to the Cenomanian species (Fig. 12A, B). According to the autecological discussion above, the habitat depth of *A. mermeti* was much shallower than the one of *N. pompilius*, i.e., a relatively shallow, wide epicontinental shelf sea, and considerable vertical migrations were largely excluded. Thus, habitat depth can be omitted as trigger for increasing sutural differentiation and denser septal spacing in *Angulithes*. A similar conclusion has been reached for the sutural differentiation in Jurassic ammonites (e.g., Olóriz et al. 2002; Pérez-Claros 2005).

An interesting explanation for the generally simple septum design in many nautiloids put forward by Westermann (1971) is that wall implosion of the rounded ovate whorls of nautiloids is prevented largely by the vaulted shell-surface design of the walls themselves, the septum functioning mainly against pressure transmitted through the soft body. A deviation from this inflated design to more compressed forms (for the sake of better swimming capabilities and steering) weakens the shell and may necessitate a stronger vaulting and/or denser spacing of the septa even if the habitat depth is relatively shallow. A thickening of the outer shell and septa may fulfill the same function but increases

weight (as does denser septal spacing to some extent) and thus counteracts the need for better swimming skills; in any case, (nearly) neutral buoyancy acts as a constraint on the total weight of the shell.

Another factor influencing the need for increased rigidity of nautiloid shells in shallow waters is the greater stress by shell-breaking predators in such settings compared to deeper waters (Vermeij 1977; Ward 1996; Kelley and Hansen 2001); the complex vertical migration patterns of modern *Nautilus* are also dictated by avoidance of daytime visual predators (e.g., Dunstan et al. 2011). The number of durophagous predators during the Mesozoic Marine Revolution increased significantly from the Early into the Late Cretaceous (Vermeij 1977) and important Cretaceous durophages known to attack ectocochleate cephalopods were mosasaurid lizards and (ptychodontoid) sharks (e.g., Tsujita and Westerman 2001; Kauffman 2004). Considering this, Wilmsen and Yazykova (2003) suggested that the preferential shallow-water distribution of ribbed cymatoceratid nautiloids reflects increased predation pressure, their coarse ornament apparently being defensive in nature (other sculptural defensive elements such as horns and spines that commonly occur in contemporaneous ammonites were obviously missing from the genetic toolkit of Cretaceous nautiloids). Ribbing is unknown in *Angulithes* (only some ventral folds are known from the adult body chambers of *A. vascogoticus*; Wilmsen 2000) and, thus, septal folding and approximation may be the generic evolutionary response in this lineage in order to increase shell resistance against predation. Furthermore, in case of a shell injury, the reduced individual cameral volume due to the approximated septa and the compressed shell may have facilitated survival because only a limited segment of the phragmocone would have been affected. Interestingly, Lemans et al. (2016) proposed that sutural complexity does not really aid in greater resistance to hydrostatic pressure but it seems to enhance resistance of the shell to point loads such as those exerted by pointed-toothed shell-breaking predators (e.g., mosasaurs, ptychodontoid sharks). We thus speculate that the septal folding and approximation in *Angulithes* was predominantly an “act of defense” against predation with the hydrodynamically efficient shell form providing additional means for possible successful escape (according to Vermeij 1977, locomotion may be more important than armor as an anti-predatory measure). We suggest that these adaptations were clues for the successful occupation of the dynamic and perilous shallow-water habitats by *A. mermeti* during the early late Cenomanian that previously were not natural nautiloid territory.

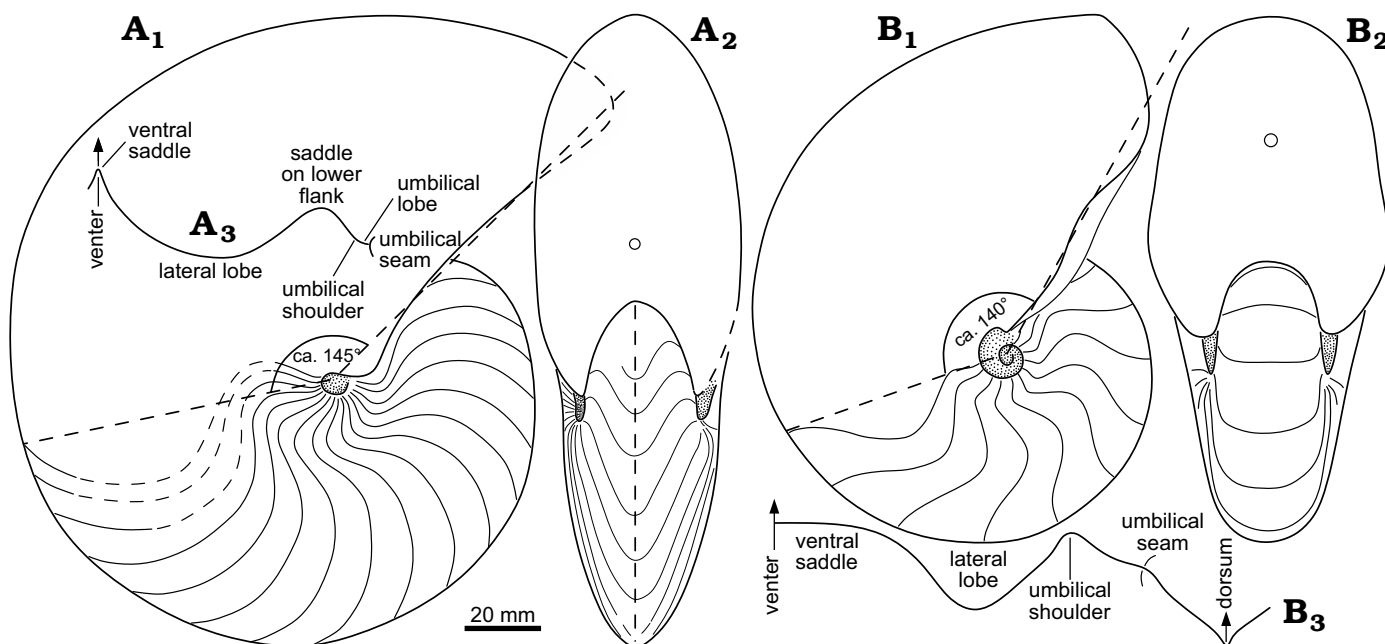


Fig. 12. Comparison of whorl sections, position of siphuncles, sutural sinuosity, and septal spacing of *Angulithes mermeti* (Coquand, 1862) (A) and a specimen illustrated as *Nautilus pompilius* Linnaeus, 1758 in the Treatise (Kummel 1964: fig. 329) (B). A. AFK 225 from the upper Cenomanian of Egypt in lateral (A₁) and apertural (A₂) views; external suture (A₃). B. Specimen from Tagnan (Philippines) at D = 130 mm from the SW Pacific (drawn from an artificial internal mould) (B₁, B₂); suture line (B₃) (modified from Wani et al. 2008).

The functional interpretation for the dorsal-directed migration of the siphuncle is difficult to elucidate. Without going into any detail, Tintant and Kabamba (1985) proposed that the dorsal position of the siphuncle represents an adaptation to a relative deep-water mode of life, facilitating the pumping of cameral liquids necessary for vertical movements. However, as shown above, *A. mermeti* lived in shallow waters, most likely did not migrate vertically and nevertheless developed a fairly dorsal siphuncle; thus, this explanation cannot be applied here. Densely spaced septa and compression of the shell reduce the volume of the chambers, facilitating their emptying/filling by the siphuncle. The dorsal position of the siphuncle, on the other hand, minimizes the arc length relative to a median position and thus reduces siphuncular surface area. However, Chamberlain (1978) and Chamberlain and Moore (1982) have shown that the permeability of the siphuncle of the living *Nautilus* is three times higher than the actual rates of osmotic flow. Thus, the transport capacity of the siphuncular tube is no limiting factor for short-term buoyancy regulations (Kröger 2002) and its dorsal position may therefore fulfill another function in the hydrostatic apparatus of *A. mermeti* (and *A. vascogeticus*). The pellicle, an organic membrane with hydrophilic properties that lines the septal faces and inner shell walls plays an important role in the fluid balance within the chambers and buoyancy changes. In partially emptied chambers, it transports the liquid to the siphuncle by capillary forces, acting as blotting-paper (Ward 1987). The pellicle surface area in *Nautilus* chambers is significantly smaller than in ammonoids (Kröger 2002), suggesting that the direct contact of the cameral liquid with the siphuncle may be more important for (short-term) buoyancy

regulations in nautiloids. This is where the dorsal position of the siphuncle has advantages: in living position, it prevents early decoupling of the cameral liquid and the siphuncle in the last-formed chamber and allows a rapid and nearly complete emptying (Fig. 9); due to the median position of the siphuncle in Recent *Nautilus*, the decoupling already occurs after approximately half of the cameral liquid has been removed (Ward et al. 1981). This late decoupling may be a benefit in the shallow-water habitat and guarantees the maintenance of buoyancy of the relatively heavy shells buttressed by numerous, densely spaced septa. Interestingly, the dorsal siphuncle in Late Devonian clymeniid ammonoids may have served a similar function: in inferred life-position, the dorsal clymeniid siphuncle is located at or near the bottom of the most recently formed chambers, seemingly an ideal location for an effective complete draining of liquid and maintaining buoyancy of the relatively thick-walled (= heavy) shells (Gottobrio and Saunders 2005). Another explanation may be the fact that the internal position provides a better protection of the siphuncular tube in the case of predation that, in conjunction with the low individual cameral volumes (see above), facilitates survival from phragmocone shell injuries.

Conclusions

Cretaceous nautiloids are commonly characterized by inflated shells with broad whorl cross-sections and round or flattened venters. Furthermore, they tend to be rather long-ranging compared to co-occurring ammonites. However, in the Albian, the genus *Angulithes* Montfort, 1808 with

compressed forms and predominantly narrow venters arose, some representatives of which acquired nearly oxycone shell shapes and were also characterized by fairly short-lived stratigraphical ranges. Herein, the strongly compressed nautiloid species *Angulithes mermeti* (Coquand, 1862) is treated in detail and evolutionary trends among Cenomanian species of *Angulithes* are evaluated in the light of contemporaneous palaeoenvironmental changes and inferred functional traits.

Angulithes mermeti is characterized by a compressed, nearly oxycone shell form with a sharp venter and narrow, shallow umbilicus, a fairly sinuous external suture line, a low distance of septa, and a subdorsal position of the siphuncle. The studied nautiloids stem from a carbonate-dominated interval roughly in the middle part of the early late Cenomanian depositional sequence Cenomanian 5 in which they commonly co-occur with the ammonite *Neolobites vibrayanus* (d'Orbigny, 1841), forming the “*Neolobites* Bio-event”. The strata correspond to a maximum flooding interval that can be correlated from Iberia via the southern Tethyan margin along northern Africa into the Middle East; the species has also been reported from South America (Peru). Its latitudinally restricted palaeobiogeographical distribution suggests an affinity to tropical–subtropical warm-water areas. Based on facies and palaeogeography, the environment of *A. mermeti* was a relatively shallow, wide epicontinental sea with a preferred habitat depth between 5–50 m. The smooth shell, small and shallow umbilicus, compression of the whorl section, and the narrowly rounded to acute venter indicate (relative to most other nautiloids) pronounced acceleration, high speed and steerage (maneuverability combined with directional stability) by reducing drag. *A. mermeti* may thus have been able to successfully pursue small nektonic prey in shallow-water areas structured by reefs and shoals. Furthermore, the hydrodynamically efficient shell form was probably beneficial in order to escape shell-breaking predators.

Starting with the appearance of the genus *Angulithes* in the Albian, several gradual morphological changes are reflected by the Cenomanian species of the genus, i.e., *A. fleuriausianus* (d'Orbigny, 1840), *A. triangularis* Montfort, 1808, *A. mermeti* Coquand, 1862 and *A. vascogoticus* Wiedmann, 1960, i.e., (i) an increasing compression of the shell and angulation of the venter, (ii) an increasing folding of the suture, (iii) a reduction of inter-septal distances, and (iv) a dorsally directed migration of the siphuncle. The early late Cenomanian species *A. mermeti* reflects a culmination of these morphological trends. The hydrodynamically efficient form was favourable to successfully occupy new niches in the wide, shallow epicontinental seas that formed during the early Late Cretaceous. The increasing sutural sinuosity and the denser spacing of the septa may be related to the buttressing of the shells. However, in contrast to conventional interpretations, these adaptations are not related to a greater septal support for the shell wall under increased hydrostatic pressures against implosion as evident from the shallow-water habitat of *A. mermeti*. We speculate that the

septal folding and approximation in *Angulithes* aimed at an improved resistance of the shell to point loads such as exerted by (pointed-toothed) shell-breaking predators (e.g., ptychodontoid sharks) which were common in the conquered shallow warm-water habitats. The functional reason for the dorsal-directed migration of siphuncle is more difficult to explain. In living position it prevents early decoupling of the cameral liquid and the siphuncle in the last-formed chambers and allows a nearly complete emptying directly by the siphuncle which may be beneficial for the maintenance of buoyancy. Furthermore, the internal position provides a better protection of the siphuncular tube in the case of predation and non-lethal shell injuries.

The herein presented directed morphological change in the Cenomanian representatives of the genus *Angulithes* provides a well-constrained case study of gradual (Darwinian) evolutionary response in a nautiloid lineage triggered by the opening of newly available niches in the course of the expansion of widespread shallow epeiric seas during the great early Late Cretaceous transgression. It also suggests that strong environmental pressure obviously acting during the Cenomanian age was able to induce rapid evolutionary response in otherwise bradytelic biotic groups such as nautiloids.

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