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A REVIEW OF THE IDENTITY AND BIOSTRATIGRAPHY OF CENOMANIAN "LARGER" BENTHIC FORAMINIFERA: PART 2 – THE ORDER LOFTUSIIDA (EXCLUDING THE SUBORDER ORBITOLININA)

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Abstract. The Loftusiida ("loftusiids" herein) is an order of "larger" benthic foraminifera (LBF) that are common in the Cretaceous neritic carbonate successions of Neotethys. They are encountered in suitable rocks in a broad belt centred around the Mediterranean region and the Arabian Plate but some taxa are found in Central America and the Himalayas. To improve their stratigraphic utility, the identities and distribution of 25 species (excluding those from the Suborder Orbitolinina) are critically reviewed based on published records, these taxa having at least possible occurrences in Cenomanian strata. It is shown that misidentifications have mistakenly overextended the ranges of some taxa, although there are indeed species that have long ranges. This suggests that some loftusiids formed part of a group of environmentally tolerant LBF that were able to recover from palaeoceanographic events such as widespread anoxia or eustatic sea-level change. Some other taxa have short ranges within the Cenomanian that mark them out as potential species to be used, alongside species from other LBF groups, in the development of a biozonation/bioevent scheme for Cenomanian LBF. As with almost all mid-Cretaceous LBF, work on taxonomy/identity of loftusiids is an ongoing task requiring access to pristine material, including topotypes.

Keywords: Foraminifera, Biostratigraphy, Cenomanian, Neotethys, Cretaceous

INTRODUCTION & RATIONALE

The rationale for this paper – part 2 of a series – has previously been discussed by Simmons & Bidgood (2023), Bidgood et al. (2024) and by Simmons et al. (2024b), the latter paper being part 1 of this series.

This paper covers the loftusiid taxonomic grouping, and is the second of an intended series of papers which presents results from a similar process applied to those remaining larger benthic foraminifera (LBF) which have also been recorded from the Cenomanian, including (in summary) the previously evaluated planispiral taxa (Simmons & Bidgood, 2023). In part, this builds on that study (itself built on foundations from pioneering studies such as Henson, 1948a, b, c; Hamoui & Saint-Marc, 1970; Schroeder & Neumann, 1985 and others). The following parts are complete/planned:

Part 1: the nezzazatoids (Simmons et al., 2024b)

Part 2: the loftusiids (excluding the orbitolininids) (this paper)

Part 3: the orbitolinids (see also Bidgood et al., 2024)

Part 4: the textularinids, involutinids and miliolinids

Part 5: the alveolinids

Part 6: the soritids

A seventh part will summarise the findings of the previous six papers in terms of the biostratigraphic utility of Cenomanian LBF, their distribution in time and space, and possible controlling factors.

The full rationale need not be repeated here but is summarised as:

- A summary assessment of the diagnostic features providing the identity of most Cenomanian loftusiid LBF genera and species.
- A critical assessment of the stratigraphic range of those taxa, giving most weight to those records for which the identity has a high probability and the age-calibration is well-founded.

The 25 taxa discussed herein are (in alphabetical order):

Buccicrenata ex gr. *subgoodlandensis* (Vanderpool, 1933)
Charentia cuvillieri Neumann, 1965
Conorbinella? *libanica* (Saint-Marc, 1973)
Cuneolina compressa Schlagintweit, 1988
Cuneolina ex gr. *pavonia* d'Orbigny, 1846
Cyclolina cretacea d'Orbigny, 1846
Cyclopsinella neumannae Cherchi, 1980
Dictyopsella charentensis Loeblich & Tappan, 1985
Dicyclina qatarensis Henson, 1948b
Dicyclina sampoi Cherchi & Schroeder, 1990b
Dicyclina schlumbergeri Munier-Chalmas, 1887
Dicyclina simplex Cherchi & Schroeder, 1990a
Hemicyclammina whitei (Henson, 1948c)
Mangashtia viennoti Henson, 1948c
Moncharmontia apenninica (De Castro, 1966)
Moncharmontia compressa (De Castro, 1966)
Neodubrovnikella turonica (Said & Kenawy, 1957)
Pseudochoffatella algeriana Peybernès et al., 1988

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Pseudocyclammina rugosa (d'Orbigny, 1850)
Pseudocyclammina sarvakensis Schlagintweit & Yazdi-Moghadam, 2023
Pseudotextulariella brevicamerata Schlagintweit & Yazdi-Moghadam, 2023
Pseudotextulariella cretosa (Cushman, 1932)
Reisella ramonensis Hamaoui, 1963
Reticulinella reicheli (Cuvillier et al., 1969)
Spirocyclina atlasica Saint-Marc & Rahhali, 1982

As with review articles of this type a difficult question concerns which taxa to include and which to exclude. Our first-level filter is to include those "larger" benthic foraminiferal taxa with a known or suspected presence in strata of Cenomanian age. This is based on our search of the (extensive) literature and our knowledge through experience of studying Cenomanian microfaunas ourselves.

Our second-level filter is to include taxa which are predominantly studied in thin section because they occur in indurated carbonate sediments common throughout the Neotethyan and Caribbean realms at this time, or are required to be studied in thin section because their identity is based on internal structural components and not simply external shape and features. Not all of these are "larger" benthic foraminifera in the strict sense of test complexity and hosting communities of algal and diatom symbionts (e.g., Hohenegger, 2011), but do form part of distinctive assemblages of foraminifera as studied in thin-section.

A note on higher (supra-generic) classification

As discussed by Simmons & Bidgood (2023) and Simmons et al. (2024b), the supra-generic classification of LBF is, and remains, a work in progress and the validity of the schema such as Kaminski (2014), the last major supra-generic assessment of agglutinating foraminifera, while currently practical, is open to constant amendment. The purpose of this paper (and its associated companion papers) is not higher-level taxonomy, but rather a practical tool for the identification of Cenomanian LBF at species level with the purposes of improving knowledge of their biostratigraphical and paleogeographical distribution.

To that end, our use of supra-generic levels of classification (Family, Superfamily, etc.) herein is merely for structural organisation of the paper and does not endorse or reject any particular classification scheme. The supra-generic organisation herein follows that suggested in Hayward et al. (2025); the World Register of Marine Species ("WoRMS") database at www.marinespecies.org, it being the most recent and "state of the art" at the time of writing (unless otherwise noted). It must be emphasised that WoRMS is a dynamic database subject to improvement over time, thus bearing in mind that the suprageneric information reported herein may differ from those displayed in future versions. Where there is a more up-to-date diagnosis of each supra-generic taxon mentioned herein other than that of the naming authority, we have suggested a reference which contains such a diagnosis.

Loftusiids, and treatment of individual loftusiid species

Herein, we use the informal term "loftusiids" *sensu* "of the Order Loftusiida", to include those taxa listed above within genera placed within the Order Loftusiida Kaminski & Mikhalevich in Kaminski (2004) (see also Kaminski, 2014).

The Order Loftusiida is a large agglutinating foraminiferal order containing several Suborders and diverse lower levels of suprageneric classification. One of these Suborders is the Orbitolinina Kaminski 2004 which contains many genera and species recorded in Cenomanian strata. Such members of this distinctive Suborder are not included in this part of the article series and will be treated separately in a later part (see also Bidgood et al., 2024).

The remaining loftusiid taxa considered here are a small subset (25 taxa) of representatives of four further long-ranging Suborders of the Order Loftusiida (excluding the Orbitolinina as above). Foraminifera in the Order Loftusiida are morphologically defined as…

> *Test free or attached, multilocular, coiled in early stage, later may uncoil; wall agglutinated with organic, microgranular, or calcitic cement; with advanced forms possessing a bilamellar wall differentiated into an imperforate outer layer, and a thicker inner layer that is perforate, alveolar, or forms internal partitions.*
>
> Kaminski & Mikhalevich in Kaminski (2004; p.249).

… and thus encompass a large variable range of coiling modes, chamber arrangements, internal structures and wall textures. Consequently, an illustration of the characteristics of "typical" loftusiids as a group (as in Simmons et al., 2024b; Fig. 1 for the nezzazatoids) is not practical.

Some partial determination keys exist in the literature (e.g., Hottinger, 1967, 1978, 2006; Septfontaine, 1988; Whittaker et al., 1998).

A summary of the main diagnostic features of the loftusiid genera discussed herein is shown in Table 1.

Each loftusiid taxon will be discussed relatively briefly in terms of taxonomic identity and published age ranges in order of general taxonomic grouping. Those taxa previously included in the informal "planispirals" grouping, previously discussed more extensively in Simmons & Bidgood (2023), here contain summaries of identity and stratigraphic criteria mostly taken from that publication, although updated asneeded and with synonymy lists now provided. In addition to representative illustrations of the individual taxa, one or

Table 1. Basic structure of loftusiid supra-generic classification and genera (with descriptions) included in this study.

Suborder – Superfamily – Family – Subfamily	**Genera included herein with description**
LOFTUSIINA **HAPLPHRAGMIOIDEA** **CYCLAMMINIDAE** **BUCCICRENATINAE…………**	***Buccicrenata*** – planispiral, compressed, involute in early stage, later tending to uncoil (rectilinear/uniserial), wall and septa alveolar. Aperture terminal, an elongated or zig-zag slit.
HEMICYCLAMMININAE…….	***Hemicyclammina*** – broadly lenticular, planispiral, wall alveolar but with solid, pointed septa which do not reach the outer wall of the previous whorl, does not uncoil and the aperture is slit-like. ***Pseudocyclammina*** – planispiral (rarely streptospiral in early stage), subspherical to flattened, later uncoiling, wall coarsely agglutinated with coarse subepidermal network continuing onto the septa, possibly with a few irregular pillars in median plane of test. Thick and massive septa perforated by large openings, aperture areal and cribrate.
PSEUDOCHOFFATELLINAE…	***Pseudochoffatella*** – large, discoidal with nearly parallel sides, microspheric form an early planispiral stage of about two whorls followed by peneropliform stage of about seven chambers, and then by up to eighteen or more cyclic or annular chambers, megalospheric test with large subspherical initial chamber constricted in two unequal parts, followed by a peneropliform stage, adult flabelliform but not attaining either a reniform or cyclic stage; wall agglutinated, thin imperforate epidermal layer of microgranular calcite with included quartz grains, and subepidermal polygonal meshwork of beams, rafters and joists or intercalary order beams; aperture multiple, a series of irregularly arranged openings on the apertural face.
LOFTUSOIDEA **SPIROCYCLINIDAE…………………**	***Reissella*** – involute planispiral in early stage, later tending to uncoil and flare, a subepidermal mesh formed by long primary and short secondary exoskeletal beams connected by rafters that do not extend completely into the chamber lumen. Aperture areal, elliptical on a short neck, surrounded by numerous secondary pores over most of the apertural face. ***Spirocyclina*** – large, flattened, planispiral but slightly asymmetrical, increasing rapidly to peneropliform and (rarely) uncoiled and rectilinear. Chambers low and broad, strongly arcuate with a coarse subepidermal network. Endoskeletal septulae or beams and rafters subdividing chambers into rectangular secondary chamberlets, reduced to pillars or protuberances in the central parts. Aperture multiple, two rows of pores parallel to coiling plane.
LOFTUSIIDAE………………………..	***Reticulinella*** – spherical to ovoid, planispiral involute, wall microgranular calcareous, reticulate subepidermal network with a series of radial and transverse partitions that do not extend to the previous septum leaving a narrow preseptal canal at the base of the septum. Apertures multiple, a row of small round openings near the septum base.
BIOKOVININA **BIOKOVINOIDEA** **CHARENTIIDAE……………………..**	***Charentia*** – relatively thick-walled but thin septa, planispiral, lenticular to subglobular with a tendency to uncoil (compressed rectilinear) in the last 1 or 2 chambers (rarely 4). Chambers slightly longer than high in equatorial sections. Aperture areal, arch near base of face, later triangular, later extending as a slit up the apertural face, terminal in uncoiled chambers. ***Moncharmontia*** – relatively thick-walled (with a canaliculate inner layer) with thick septa, planispiral, involute,

	broadly rounded, chambers relatively equidimensional in equatorial sections. Aperture areal and multiple, a single arched row of openings, later more numerous and irregularly distributed.
BIOKOVINIDAE……………………...	***Neodubrovnikella*** – subspherical proloculus followed by slightly compressed lenticular planispiral (slightly asymmetrical in early stage) to peneropliform internally undivided chambers with a subacute periphery. Aperture terminal, composed of a single row of openings. An agglutinated isomorph of the well-known porcellaneous genus *Peneroplis* except *Neodubrovnikella* may not be perfectly planispiral.
CYCLOLININA **CYCLOLINOIDEA** **CYCLOLINIDAE** **CYCLOLININAE…………………..**	***Cyclolina*** – large (up to 6mm diameter), increasing thickness towards periphery, wall calcareous microgranular. Chambers open, no interior subdivisions. Aperture multiple, scattered in many rows on the apertural face.
CYCLOPSINELLINAE……...........	***Cyclopsinella*** – large (up to 10mm), early planispiral in microspheric form, rapidly peneropliform, reniform, then cyclic, wall calcareous, microgranular. Chambers open, unsubdivided except in late growth stage, with one or more endoskeletal pillars which may bifurcate and re-fuse which can (apparently) appear as two chamber layers in thin sections. ***Mangashtia*** – numerous cyclic or annular chambers. Numerous subcylindrical or beam-shaped pillars in the central part of the chamber which are aligned between chambers. Aperture multiple openings in a row in the middle of the apertural face.
ATAXOPHRAGMIINA **ATAXOPHRAGMIOIDEA** **CUNEOLINIDAE** **CUNEOLININAE…………………..**	***Cuneolina*** – compressed, conical to flabelliform, early stage planispiral, followed by broad, low, biserial chambers, interiors subdivided into nearly rectangular chamberlets by radial and horizontal partitions. Aperture a row of pores at the base of the septal face. ***Pseudotextulariella*** – conical, initially trochospiral/triserial, becoming biserial, broad, low chambers subdivided by beams and rafters of one to several orders, up to six tiers of chamberlets per chamber. Wall finely agglutinated, aperture interiomarginal, a low opening at the base of the flattened apertural face.
DICYCLINIDAE……………………	***Dicyclina*** – wall pseudokeriothecal-like, flattened to slightly undulating, initial stage inflated, later chambers annular, alternately added on two sides of the test, interior subdivided by numerous thin radial partitions and aligned from chamber to chamber. Apertures round pores at the periphery.
DICTYOPSELLIDAE………………	***Dictyopsella*** – low trochospiral, plano- or concavo-convex or patelliform with an evolute spiral side and involute umbilical side. Crescentic chambers on spiral side, subtriangular on umbilical side. Interior of chambers subdivided by numerous radial and intercalary beams of varied length, the longest extending nearly to the umbilical region and which are interconnected by (transverse) rafters which produce a characteristic “mesh-like” subepidermal network. ***Conorbinella*** – low trochospiral, plano- or concavo-convex or patelliform with an evolute spiral side and involute umbilical side. Crescentic chambers on spiral side, subtriangular on umbilical side. Interior of chambers subdivided by numerous radial beams of varied length, the longest extending nearly to the umbilical region.

two suitable source references for good images are also provided.

The vast majority of these representative images are adapted from published sources and are often of type material. The sources are detailed in each caption. Characteristic and/or discriminatory taxonomic features are indicated by arrows and annotations. Frequently the images are resized to better fit the figure frame. The scale bars in each figure are approximate and for *guidance only* to show an approximate, relative size and should not be used for calculating measured dimensions (please refer to the original source material to do this).

The ages attributed in the synonymy lists (strictly speaking these are *chresonymy* lists as in a list of usage *sensu* Smith & Smith, 1972) are the ages as documented in each reference, otherwise it is the age of the sampled section (as stated) or the age assigned to the specific, illustrated specimen. Age attribution is mostly taken on trust, unless there is evidence to the contrary (either within the publication or published elsewhere). Ages stated imply an undifferentiated age unless stated otherwise. Thus a "Cenomanian" age attribution implies the age of a particular occurrence can be determined no better than to a generalised stage level. It does not imply, unless otherwise stated, that the taxon ranges throughout the stage. The location given is reported as the applicable country stated in the publication at the time of publication, except when more specific regional locations can be determined (e.g., Iran or Iranian Zagros; Türkiye or western Taurides, Türkiye etc.).

Identifications are considered plausible, unless indicated otherwise. A "?" indicates a doubtful identification (e.g. some features key to identification are not visible). "*Non*" indicates a clear misidentification with an alternative identification expressed if possible.

Comments in square brackets are our assessment of the most likely identity or otherwise of specimen(s) assigned a "*non*" status in the listings, or cases where we emend (for example) an age assignment.

The subsequent systematic section is followed by a discussion of the findings of our critical review of the 25 taxa involved, with a focus on stratigraphic ranges, bioevents, and the potential for biozonation and correlation.

SYSTEMATICS

Phylum **FORAMINIFERA** d'Orbigny 1826
Class **GLOBOTHALAMANA** Pawlowski, Holzmann & Tyska 2013
Subclass **TEXTULARIANA** Mikhalevich 1980
Order **LOFTUSIIDA** Kaminski & Mikhalevich in Kaminski 2004 (diagnosis *sensu* Kaminski, 2014)
Suborder **LOFTUSIINA** Kaminski & Mikhalevich in Kaminski 2004 (diagnosis *sensu* Kaminski, 2014)
Superfamily **HAPLOPHRAGMIOIDEA** Eimer & Fickert 1899 (diagnosis *sensu* Kaminski, 2014)
Family **CYCLAMMINIDAE** Marie 1941 (diagnosis *sensu* Loeblich & Tappan, 1987)
Subfamily **BUCCICRENATINAE** Loeblich & Tappan 1985 (diagnosis *sensu* Loeblich & Tappan, 1987)
Genus ***Buccicrenata*** Loeblich & Tappan 1949 (see Table 1 for diagnosis)

Buccicrenata is an involute planispiral form with rapidly enlarging chambers that also frequently uncoils rapidly. Debate about the nature of the wall and septa of *Buccicrenata* - whether they are, or are not, alveolar - is not yet fully resolved, although the alveolar nature of the wall seems reasonably well established (see Loeblich & Tappan, 1985; Simmons & Bidgood, 2023). The alveolar nature of the septa in *Buccicrenata* (if and when unequivocally proven) separates it from *Everticyclammina* Redmond. *Buccicrenata* is also very similar to *Pseudocyclammina* Yabe & Hanzawa, although the former genus has a single, sinuous slit-like aperture compared with cribrate in the latter and typically somewhat thicker walls. Nevertheless, the two apertural types are hard to discern when observed in oblique/random thin-sections. In addition, and marking another distinction from *Pseudocyclammina*), "*…the septal base thickened against the previous whorl, and may form a continuous imperforate basal layer with solid triangular chomata-like mounds at the position of the septa*" (Loeblich & Tappan, 1985, p. 98). The two genera can also be distinguished by predominantly reniform chambers and a distinctive lobate periphery in *Buccicrenata* (see Simmons & Bidgood, 2023 and species key chart therein). Nonetheless, in much illustrated material in the literature it is often hard to judge the nature of aperture and the alveolar nature of the wall and septa, thus making it difficult to separate possible *Buccicrenata* from *Everticyclammina*, *Pseudocyclammina*, *Ammobaculites* and *Lituola* species, to name but a few.

Buccicrenata ex gr. *subgoodlandensis* (Vanderpool, 1933)

Figure 1

T 1933 *Ammobaculites subgoodlandensis* Vanderpool, p. 407, pl. 49, figs. 1-3; Albian, Oklahoma, USA.
1944 *Ammobaculites subgoodlandensis* – Lozo, p. 540, pl. 1, figs. 2-3, pl. 4, fig. 1, text-figs. 15A-G; Albian, Texas, USA.
1949 *Buccicrenata subgoodlandensis* – Loeblich & Tappan, p. 253, pl. 47, figs. 5-15b; Albian, Texas & Oklahoma, USA.
1953a *Pseudocyclammina hedbergi* n. sp. – Maync, p. 101, pl. 16, figs. 1-8; early Aptian-middle Albian, Venezuela & Florida, USA.
1954 *Buccicrenata subgoodlandensis* – Frizzell, p. 66, pl. 4, fig. 8; Albian, Texas, USA.
1956 *Pseudocyclammina hedbergi* Maync – Cuvillier, pl. 20, fig. 2; Aptian, Pyrenees, France.

? 1964 *Pseudocyclammina hedbergi* – Bozorgnia & Banafti, pl. 72, fig. 2; pl. 83, fig. 2; Aptian-Albian, central Iran.

1965 *Pseudocyclammina* cf. *rugosa* (d'Orbigny) – Hamaoui, p. 19, pl. 1, fig. 11; pl. 5, figs. 6-8; pl. 10, fig. 6; Cenomanian, Israel.

1965 *Pseudocyclammina hedbergi* – Gollesstaneh, p. 130-132, pl. 3, figs. 1-4; Valanginian – Aptian; Iranian Zagros.

1966 *Buccicrenata libyca* n. sp. – Gohrbandt, p. 67, pl. 1, figs. 11-16; middle – late Cenomanian, Libya.

1966 *Pseudocyclammina* aff. *hedbergi* – Banner, pl. 3, figs. 5a-5b; early Cenomanian, offshore Abu Dhabi. [*fide* Banner & Highton, 1990]

1967 *Pseudocyclammina* cf. *rugosa* – Arkin & Hamaoui, pl. 2, fig. 3; Cenomanian, Israel.

1969 *Pseudocyclammina rugosa* – Sampò, pl. 39, figs. 6-8. Albian, Iranian Zagros.

1970 *Pseudocyclammina* aff. *hedbergi* – Banner, pl. 5, figs. 7-7a; early Cenomanian, offshore Abu Dhabi. [*fide* Banner & Highton, 1990).

1974 *Pseudocyclammina rugosa* – Radoičić, pl. 5, figs. 1-3; Cenomanian, Serbia.

? 1974 *Pseudocyclammina* cf. *rugosa* – Moullade & Peybernès, pl. 3, figs. 2, 5; late Albian, Spain.

1975 *Everticyclammina virguliana* (Koechlin) – Gušić, pl. 5, fig. 2; pl. 6, figs. 3-4; pl. 7, figs. 1-3; pl. 8, figs. 1-5; pl. 9, figs. 1-5; pl. 10, figs. 2,4; "late Aptian – early Albian" (now thought to be late Aptian (Gušić, pers. comm., 1987)), Croatia.

1976 *Pseudocyclammina rugosa* – Kalantari, pl. 10, figs. 13-14; Aptian, Iranian Zagros.

1976 *Pseudocyclammina* cf. *rugosa* – Kalantari, pl. 22, figs. 17-18, 25; Cenomanian, Iranian Zagros.

1978 *Pseudocyclammina hedbergi* – Berthou & Schroeder, pl. 8, figs. 3-5; late Albian, Portugal.

1980 *Everticyclammina hedbergi* – Arnaud-Vanneau, p. 489, fig. 178; pl. 40, fig. 5; pl. 63, figs. 3-4; pl. 65, fig. 1; early Aptian (total range given as Barremian – early Aptian), France.

? 1982 *Pseudocyclammina hedbergi* – Altıner & Decrouez, pl. 5, figs. 1-2; early Aptian, Türkiye [alveolar wall not clear].

? 1984 *Everticyclammina hedbergi* – Chiocchini et al., pl. 1, fig. 20; early Aptian, Central Italy [alveolar wall not clear].

1985a *Buccicrenata subgoodlandensis* – Loeblich & Tappan, p. 100, pl. 2, figs. 4-10; Early Cretaceous [= Albian], Texas, USA.

1987 *Buccicrenata subgoodlandensis* – Simmons & Hart, pl. 10.5, fig. 1; Albian, Oman Mountains.

1987 *Buccicrenata hedbergi* – Simmons & Hart, pl. 10.4, figs. 2-3; Valanginian – Hauterivian, Oman Mountains.

? 1987 *Buccicrenata? rugosa* – Simmons & Hart, pl. 10.5, fig. 4; Cenomanian, Oman Mountains [one of us (FS) has also seen similar material from the middle Cenomanian of Oman (unpublished data)].

1988 *Everticyclammina hedbergi* – Sartorio & Venturini, p. 92, lower fig.; Neocomian (total range given as Berriasian-early Cenomanian), Italy.

1987 *Buccicrenata subgoodlandensis* – Loeblich & Tappan, p. 99, pl. 96, figs. 1-9; Albian, Oklahoma, USA

1990 *Pseudocyclammina hedbergi* – Weidich & Al Harithi, p. 603, pl. 2, figs. 1-2; pl. 3, fig. 7; pl. 4, figs. 16-18; Cenomanian (total range given as Albian – Cenomanian), Jordan.

1990 *Buccicrenata hedbergi* – Simmons, p. 84, pls. 3.25-3.28; Valanginian-Aptian (and described as ranging into the Cenomanian), Oman Mountains.

1991 *Buccicrenata hedbergi* – Schlagintweit, pl. 10, figs. 1-4; late Aptian, Austrian Alps.

? 1992 *Buccicrenata hedbergi* – Granier, pl. 2, fig. 2; Barremian – early Aptian, Senegal [alveolar wall not clear].

1994 *Buccicrenata hedbergi* – Simmons, pl. 9.4, fig. 2; Valanginian – ?Hauterivian, Oman Mountains.

1994 *Pseudocyclammina lituus* – Shakib, pl. 7.3, fig. 6; Hauterivian, Iranian Zagros.

Non 1994 *Pseudocyclammina hedbergi* – Bodrogi et al., pl. 12, fig. 17; pl. 13, fig. 1; Early Cretaceous, Hungary [wall appears to be simple, non-alveolar]

? 1995 *Buccicrenata hedbergi* – Arnaud-Vanneau & Sliter, p. 550, pl. 1, fig. 5; ?late Aptian-early Albian, mid-Pacific Ocean [alveolar wall not clear].

Non 1997 *Ammobaculites subgoodlandensis* – Ismail & Soliman, p. 166, pl. 1, fig. 5; Coniacian, Egypt [indeterminate external view, but very unlikely to be this species].

? 1997 *Buccicrenata subgoodlandensis* – Ayyad et al., p. 146, fig. 5b-c; early Cenomanian, Egypt.

1998 *Everticyclammina hedbergi* – Omaña-Pulido & Pantoja-Alor, p. 69, fig. 6 (1-2); early Aptian, Mexico.

1999 *Pseudocyclammina hedbergi* – Scott & Finch, fig. 4D, E; middle-late Albian, Honduras.

2001 *Buccicrenata subgoodlandensis* – BouDagher-Fadel, p. 168-169, pl. 1, figs. 5-7; Albian, Oklahoma, USA and early Cenomanian, offshore Abu Dhabi.

2001 *Buccicrenata hedbergi* – BouDagher-Fadel, p. 169, pl. 1, figs. 3-4; middle Albian, Venezuela.

2007 *Everticyclammina hedbergi* – Schroeder et al., pl. I, figs. 8-9; late Aptian, Switzerland.

2011 *Buccicrenata subgoodlandensis* – Filkorn & Scott, p. 185, fig. 4.7-4.8; late Albian, Mexico.

Non 2011 *Everticyclammina hedbergi* – Roozbahani, pl. 1, fig. 1; Early Cretaceous, central Iran [possibly not a foraminifera].

Non 2013 *Everticyclammina hedbergi* (Gorbachik, 1968) (sic) – Nozaripour et al., pl. 1, fig. 4; Albian-Cenomanian, Iranian Zagros [indeterminate, but very unlikely].

? 2013 *Buccicrenata libyca* Gohrbandt – Shahin & Elbaz, pl. 1, fig. 34; Cenomanian, Sinai, Egypt.

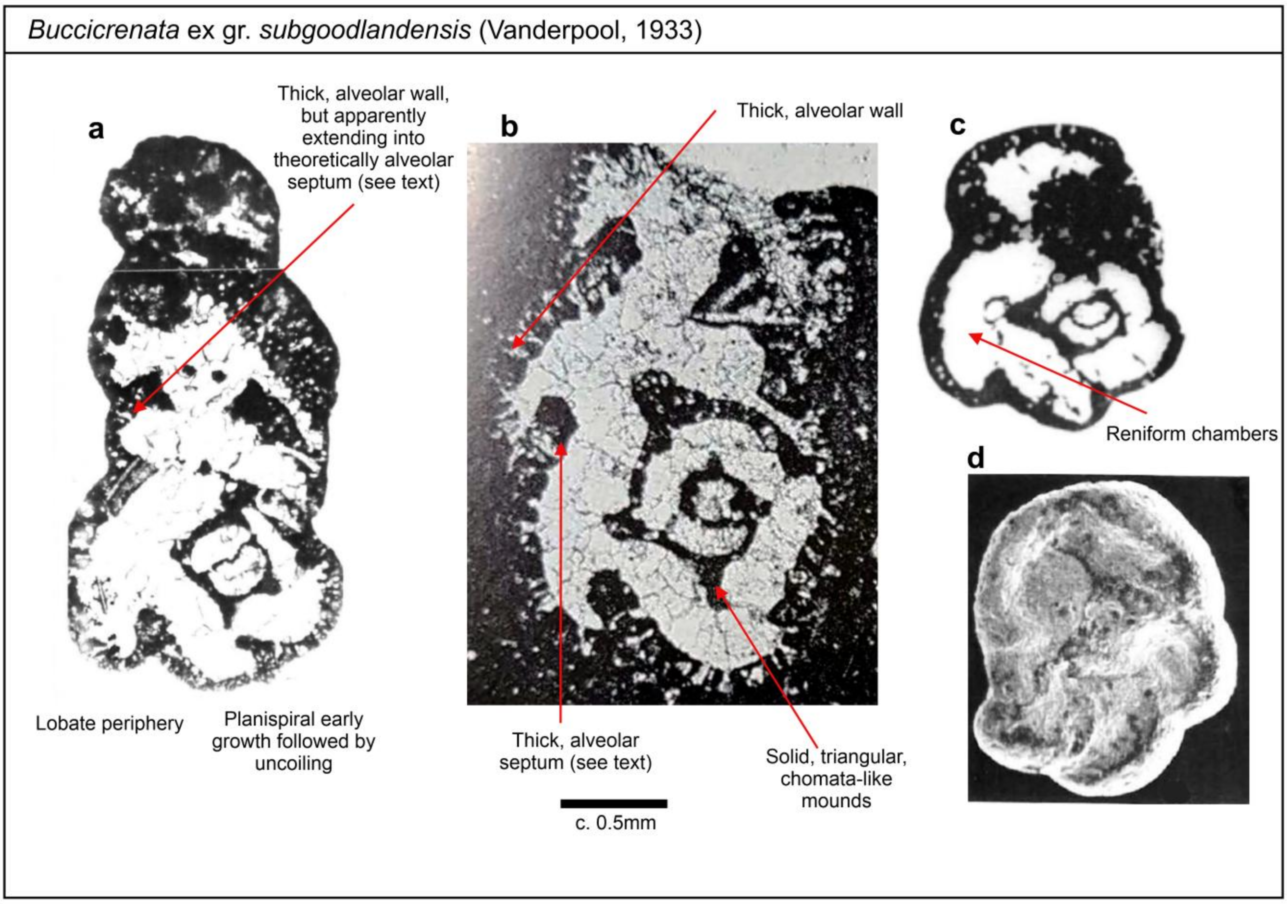


Fig. 1. Representative illustrations of *Buccicrenata* ex gr. *subgoodlandensis*: **a.** Uncoiled equatorial section, Loeblich & Tappan (1985a, pl. 2, fig. 7, Texas); **b.** Uncoiled equatorial section, Gušić (1975, pl. VII, fig. 1 (as *Everticyclammina virguliana*), late Aptian, Croatia); **c.** Equatorial section, Loeblich & Tappan (1985a, pl. 2, fig. 5, Texas); **d.** External view, Loeblich & Tappan (1985, pl. 2, fig. 9, Texas).

? 2014 *Everticyclammina hedbergi* – Khodashenas et al., fig. 3J (mislabelled 3I in caption); Barremian – Aptian, north-east Iran.

? 2015 *Buccicrenata hedbergi* – Maksoud, p. 110, pl. 34, figs. A-H; pl. 35, figs. A-H; Barremian – early Aptian, Lebanon. [alveolar wall is not clear; NB this reference includes *two* plate 34s and plate 35s].

2015 *Everticyclammina hedbergi* – Babazadeh & Dehej, fig. 6f-g; late Barremian-Aptian, central Iran.

? 2017 *Pseudocyclammina hedbergi* Yokoyama (sic) – Yavari et al., fig. 3F; late Aptian-early Albian, Iranian Zagros [alveolar wall not clear].

? 2017 *Pseudocyclammina* sp. – BouDagher-Fadel et al., fig. 9(8); Aptian, Tibet.

2018 *Buccicrenata* aff. *hedbergi* – Andrade, pl. M1, fig. 5; Cenomanian, Portugal.

2018 *Buccicrenata hedbergi* – BouDagher-Fadel, pl. 5.6, fig. 16; middle Albian, Venezuela.

? 2018 *Pseudocyclammina rugosa* – Andrade, pl. M1, figs. 3-4, 6; Cenomanian, Portugal.

2018 *Buccicrenata hedbergi* – Luger, p. 59, pl. 3, figs. 7, 9-10; pl. 4, figs. 1-6; early Aptian – middle Cenomanian, Somalia.

2019 *Pseudocyclammina* sp. – Özkan & Altıner, fig. 9(11); Cenomanian, Turkish Arabian Plate.

Non 2020 *Everticyclammina* cf. *hedbergi* – Abedpour et al., pl. 1, fig. k; Neocomian-Barremian, Iranian Zagros [= biserial foraminifera].

? 2021 *Buccicrenata* cf. *hedbergi* – Suciu et al., fig. 6H; Barremian (reworked into younger sedimentary rocks), Romania [alveolar wall not clear].

2023 *Buccicrenata hedbergi* – Solak & Taslı, fig. 9A-B; late Aptian, Türkiye.

2023 *Buccicrenata* ex gr. *subgoodlandensis* – Simmons & Bidgood, p. 79, fig. 29; Early Cretaceous-latest? Cenomanian, global review.

Non 2023 *Pseudocyclammina hedbergi* – Ghafor et al., pl. 5, fig. c; late Albian – early Cenomanian, southern Iraq [indeterminate but no trace of alveolar wall].

Reference Images: Loeblich & Tappan (1985a) pl. 2, figs. 4-10; Arnaud-Vanneau (1980); pl. 63, figs 3-4.

Taxonomy/Identity: Although BouDagher-Fadel (2001) suggested that *B. hedbergi*, *B. subgoodlandensis*, and *B. libyca* could be separated, herein we follow Simmons & Bidgood (2023) and combine them in a single “ex. gr.” status taxon (*B.* ex. gr. *subgoodlandensis*). This seems an adequate approach to naming typically reniform *Buccicrenata* with a tendency to uncoil, with 4-5 chambers in the last whorl, wall thickness 0.11 – 0.23 mm, and a typical equatorial diameter of the coiled part of between 0.60 and 2.48 mm.

There are several poorly known Early Cretaceous species assigned to *Buccicrenata*, including *Buccicrenata condensa* Dulub 1972, *Buccicrenata irregularis* (Dragastan, 1989), *Buccicrenata italica* Dieni & Massari, 1966, *Buccicrenata maynci* Dragastan, 2011 and *Buccicrenata tuberosa* Fuchs, 1971. *B. condensa* belongs in a different genus – either *Choffatella* (BouDagher-Fadel, 2001) or *Stomatostoecha* (Olszewska, 2010). *B. italica* lacks long, low depressed chambers in its planispire (BouDagher-Fadel, 2001) so may be a distinct taxon. The other Early Cretaceous species of *Buccicrenata* in the literature excluding *B.* ex. gr. *subgoodlandensis* remain in a poor state of knowledge. *B. irregularis* and *B. maynci* appear to be a simple lituolids with non-alveolar walls (see illustrations in Dragastan, 2011), but more research is needed. The nature of the wall of *B. tuberosa* is impossible to determine from the type illustrations.

Confident Stratigraphic Range: Valanginian – undifferentiated middle/late Cenomanian, locally common enough in suitable facies to have local biozone (= biofacies) potential (e.g. Ayyad et al., 1997).

Uncertain Stratigraphic Range: not applicable.

Using a broad concept of the taxon as herein, stratigraphic range is long with records as old as Valanginian (Gollestaneh, 1965; Simmons & Hart, 1987; Simmons, 1994). The suggestion that it might be as old as Berriasian (Sartorio & Venturini, 1988) is unproven. The association of *B. libyca* with *Praealveolina tenuis* Reichel in Libya supports an undifferentiated middle-late Cenomanian youngest age. It seems to be especially common in the Aptian and Albian.

Although difficult to judge based on the single specimen presented, the Coniacian record of Ismail & Soliman (1997) can be discounted.

The notion that *Buccicrenata* occurs in the Cenozoic (*Buccicrenata caunettensis* Massieux, 1973) is unproven based on the type material of this species that does not permit confirmation of the alveolar wall. Thus, there appear to be no confirmed records of the genus younger than Cenomanian.

Geographic Distribution: Within its total range, *B.* ex. gr. *subgoodlandensis* has a very wide palaeogeographic distribution (see records above), being known from Mexico, Honduras, Venezuela and the southern USA within the Caribbean province, across the circum-Mediterranean to the Arabian Plate and Somalia. It is also possibly known from the guyots of the Pacific. Another possible record occurs in Senegal. It has been reported (as *B. hedbergi*) from the Albian of Tibet (Marcoux et al., 1987; BouDagher-Fadel et al., 2017) but not illustrated. By the Cenomanian, the geographic range had contracted somewhat, but still included a belt of occurrences from Iberia to Somalia (see also Simmons & Bidgood, 2023).

Subfamily **HEMICYCLAMMININAE** Banner 1966 (diagnosis *sensu* Loeblich & Tappan, 1987)

Genus ***Hemicyclammina*** Maync 1953b (see Table 1 for diagnosis)

Hemicyclammina whitei (Henson, 1948c)
Figure 2

T 1948c *Cyclammina whitei* n. sp. – Henson, p. 13-14, pl. 13, figs. 3, 12-14; latest Albian, Qatar (also reported from the Albian of Iraq).

1953b *Hemicyclammina sigali* n. sp. – Maync, p. 148-149, figs 1-5; middle Cenomanian, Algeria.

1965 *Hemicyclammina sigali* – Hamaoui, pl.1, fig. 7; pl. 6, fig. 10; pl. 15, fig. 9; Cenomanian, Israel.

1965 *Hemicyclammina* nov. sp.? – Hamaoui, pl. 5, figs. 1-3; Cenomanian, Israel.

? 1965 *Haplophragmoides difformis* n. sp. – Hamaoui, p. 17, pl. 6, fig. 9, non pl. 3, figs. 5-8; Cenomanian, Israel.

1966 *Hemicyclammina whitei* – Banner, pl. 2, figs. 4a, b, 5; latest Albian, Qatar.

1966 *Hemicyclammina sigali* – Banner, pl. 12, figs. 3a; pl. 13, figs. 1-6; early – middle Cenomanian, offshore Abu Dhabi (non pl. 12, fig, 3b from the Aptian of offshore Abu Dhabi – possibly an ancestral non-alveolar form).

1967 *Hemicyclammina sigali* – Arkin & Hamaoui, pl. 1, figs 17-18 (?), pl. 2, fig. 1; Cenomanian, Israel.

1969 *Hemicyclammina sigali* – Sampò, pl. 39, figs. 1-5; pl. 40, fig. 2; pl. 41, fig. 1; Albian-Cenomanian, Iranian Zagros.

1970 *Hemicyclammina whitei* – Banner, pl. 10, figs. 1-2; late Albian, Qatar.

1970 *Hemicyclammina sigali* – Banner, pl. 10, figs. 3-8; early Cenomanian, offshore Abu Dhabi.

1973 *Hemicyclammina sigali* – Berthou, pl. 11, figs. 1-3; late Cenomanian, Portugal.

? 1973 *Charentia granulosa* n. sp. – Kerdany & Eissa in Kerdany et al., p. 93, pl. 1, figs. 19-26; late Cenomanian, Egypt.

? 1974 *Hemicyclammina sigali* – Bignot & Poisson, pl. 3, figs. 1-4; Cenomanian, Türkiye.

? 1974 *Ismailia neumannae* n. sp. – El-Dakkak, p. 173 175, pl. 1, figs. 1-5; Cenomanian, Sinai, Egypt.

1974 *Hemicyclammina sigali* – Saint-Marc, p. 212-214, pl. 1, figs. 1-6; middle Albian-late Cenomanian, Lebanon (reported range to base Albian).

1974 *Hemicyclammina sigali* – Radoičić, pl. 8, fig. 1?, pl. 9, fig. 1; Cenomanian, Serbia-Kosovo.

? 1975 *Sinainella aegyptiaca* n. sp. – El-Dakkak, p. 107 110, pl. 1, figs. 1-7; Cenomanian, Sinai, Egypt.

1976 *Hemicyclammina sigali* – Kalantari, pl. 19, fig. 4; pl. 22, fig. 16; early Cenomanian, Iranian Zagros.

? 1978 *Charentia hasaensis* n. sp. – Basha, p. 75, pl. 1, figs. 9-12; late Cenomanian, Jordan.

? 1978 *Charentia rummanensis* n. sp. – Basha, p. 76, pl. 2, figs. 1-6; late Cenomanian, Jordan.

? 1978 *Lituola hasaensis* n. sp. – Basha, p. 79, pl. 3, figs. 7-9; late Cenomanian, Jordan.

? 1979 *Ammobaculites difformis* – Hamaoui, p. 338-340, fig. 1f, non fig. 1a-e; Cenomanian, Israel.

1981 *Hemicyclammina sigali* – Saint-Marc, pl. 1, fig. 1; Albian-Cenomanian, Lebanon.

? 1985 *Hemicyclammina* sp. – Bilotte, p. 355, pl. 4, fig. 10; Cenomanian, Pyrenees.

1987 *Hemicyclammina sigali* – Shakib, pl. 23, figs. 14-16; Albian, Iranian Zagros.

1987 *Hemicyclammina sigali* – Simmons & Hart, pl. 10.4, fig. 7; Albian-?early Cenomanian, Oman Mountains.

1988 *Hemicyclammina sigali* – Sartorio & Venturini, p. 106; early Cenomanian, Iranian Zagros (reported range Albian – Cenomanian).

1988 *Hemicyclammina sigali* – Berthou & Bengtson, pl. 5e-g; pl. 6e-f, i; Cenomanian, Sergipe Basin, Brazil.

1990 *Hemicyclammina sigali* – Weidich & Al Harithi, p. 602-603; pl. 2, figs. 8-11; pl. 4, figs. 2-3, 7-9, 12-13; latest Albian – Cenomanian, Jordan.

1990 *Hemicyclammina* n. sp.? Hamaoui – Weidich & Al Harithi, p. 603; pl. 4, figs. 21-22; latest Albian – Cenomanian, Jordan.

1990 *Pseudocyclammina* aff. *massiliensis* Maync – Weidich & Al-Harithi, p. 604, pl. 4, fig. 1; latest Albian – Cenomanian, Jordan.

1990 *Haplophragmoides*? *difformis* Hamaoui – Weidich & Al-Harithi, p. 599, pl. 4, fig. 6; latest Albian – Cenomanian, Jordan.

? 1990 *Haplophragmoides* sp. 2 – Weidich & Al-Harithi, p. 599, pl. 4, fig. 14; latest Albian – Cenomanian, Jordan.

1992 *Hemicyclammina sigali* – Kalantari, pl. 78; Albian, Iranian Zagros.

? 1993 *Ismailia neumannae* – Al-Rifaiy et al., pl. 1, fig. 3; late Cenomanian, Jordan.

? 1993 *Hemicyclammina evoluta* Hamaoui – Al-Rifaiy et al., pl. 1, fig. 4; late Cenomanian, Jordan.

? 1993 *Hemicyclammina sigali* – Al-Rifaiy et al., pl. 1, fig. 5; late Cenomanian, Jordan.

? 1993 *Everticyclammina whitei* – Hewaidy & Al-Hitimi, p. 476-477; pl. 3, figs. 9-10; Cenomanian, Qatar.

? 1995 *Pseudonummoloculina* sp. – Dimitrova, p. 81, pl. 1, fig. 4; early Cenomanian, Bulgaria.

1996 *Hemicyclammina sigali* – Andreu et al., pl. 1, fig. 3; early Cenomanian, Morocco.

1998 *Hemicyclammina sigali* – Whittaker et al., p. 40, pl. 59, figs. 3-9; pl. 60, fig. 1; Albian, southern Iraq & offshore Abu Dhabi.

1998 *Hemicyclammina whitei* – Whittaker et al., p. 40-41, pl. 12, figs. 1-2; pl. 60, figs. 2-7; pl. 61, figs. 1-3; early Cenomanian (= latest Albian), Qatar and Albian, southern Iraq.

1998 *Charentia cuvillieri* – El-Sheikh & Hewaidy, pl. 1, fig. 8; late Cenomanian, Egypt.

2005 *Hemicyclammina sigali* – Hart et al., fig. 6f-g; late Cenomanian, Portugal.

2008 *Hemicyclammina* sp. – Ahmadi et al., pl. 2, fig. 6; early-middle Albian, Iranian Zagros.

2009 *Hemicyclammina sigali* – Shirazi et al., pl. 1, fig. 9; early Albian, Iranian Zagros.

2010 *Hemicyclammina whitei* – Forbes et al., fig. 6.7d-e; Albian – early Cenomanian, Oman.

? 2010 *Hemicyclammina sigali* – Schroeder et al., fig. 11(6); early Albian, Iranian Zagros.

Non 2011 *Hemicyclammina sigali* – Roozbahani, pl. 2, fig. 4; Albian, central Iran [= simple planispiral form].

2011 *Hemicyclammina sigali* – Shirazi et al., pl. 2, figs. 11-12; Albian, Iranian Zagros.

? 2012 *Hemicyclammina sigali* – Ghanem et al., fig. 6b/non 12, 14; early Albian, Syria (range shown as Aptian – Cenomanian).

2013 *Hemicyclammina sigali* – Omaña et al., pl. 1, fig. 1; pl. 4, fig. 1; undifferentiated middle – late Cenomanian, Mexico.

? 2013 *Hemicyclammina sigali* – Ghanem & Kuss, fig. 10/27; early Albian, Syria (range shown as Albian-middle Cenomanian).

? 2015 *Hemicyclammina sigali* – Moosavizadeh et al., fig. 12m; early Albian, Iranian Zagros.

? 2016 *Hemicyclammina sigali* – Hosseini et al., fig. 14j-l; Barremian, Iranian Zagros.

Non 2016 *Hemicyclammina* sp. – Ghaseminia et al, fig. 4k; Albian, Iranian Zagros [= simple planispiral form].

Non 2017 *Hemicyclammina sigali* – Ahmadi et al., pl. 1, fig. 10. [= simple planispiral form].

2018 *Hemicyclammina sigali* – BouDagher-Fadel, fig. 5.4; pl. 5.6, figs. 12-13; Albian, southern Iraq.

2018 *Hemicyclammina whitei* – BouDagher Fadel, pl. 5.6, figs. 14-15; Aptian-Albian (= latest Albian), Qatar.

2018 *Hemicyclammina sigali* – Luger, p. 60, pl. 3, fig. 11; Albian, Somalia.

2019 *Hemicyclammina sigali* – Omaña et al., fig. 9e; undifferentiated middle-late Cenomanian, Mexico.

? 2019 *Hemicyclammina sigali* – Shirzade et al., pl. 1, figs. 6, 7; Aptian, Iranian Zagros [lacks alveolar wall].

2020 *Hemicyclammina sigali* – Haftlang et al., fig. 15c; pl. 1, fig. 6; late Albian, Iranian Zagros.

2020 *Hemicyclammina sigali* – Afghah et al., fig. 5a; Albian, Iranian Zagros.

2020 *Hemicyclammina sigali* Maync – Keshavarzi et al., pl. 1, fig. a; pl. 2, fig. h; Albian, Iranian Zagros.

? 2020 *Hemicyclammina sigali* – Moosavizadeh et al., fig. 8h; late Aptian-early Albian, Iranian Zagros.

2021 *Hemicyclammina sigali* – Gholamalian & Fanati Rashidi, pl. 3, fig. 17; Cenomanian, Iranian Zagros.

? 2021 *Nezzazata* sp. – Dehghanian & Afghah, fig. 8/5; middle Cenomanian, Iranian Zagros.

? 2021 *Ismailia neumannae* – Shahin & El Baz, fig. 4(2-3); early Cenomanian, Egypt.

2021 *Hemicyclammina sigali* – Shapourikia et al., pl. 9e, j; Cenomanian, Iranian Zagros.

2021 *Hemicyclammina sigali* – Arampour et al., fig. 3g; late Albian, Iranian Zagros.

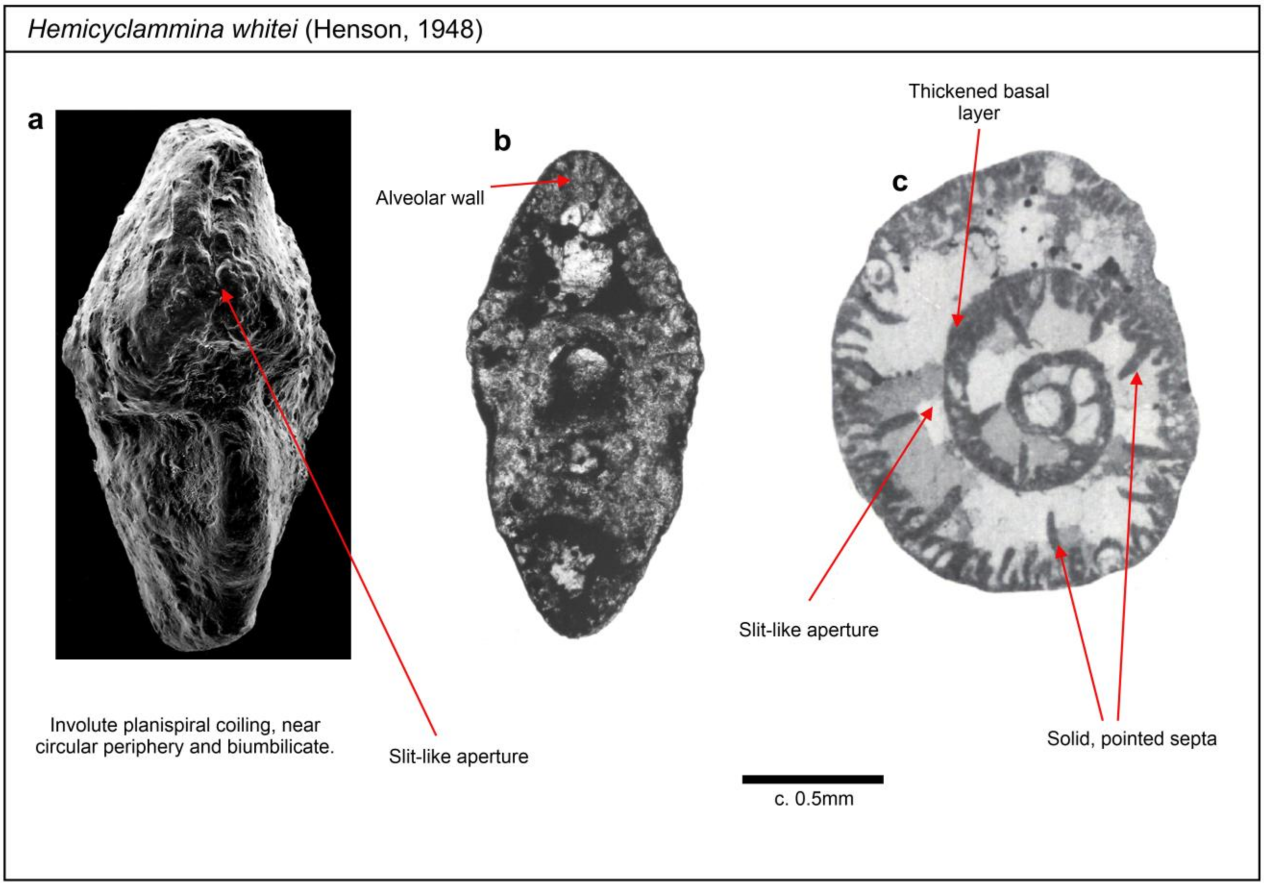


Fig. 2. Representative illustrations of *Hemicyclammina whitei*: **a.** Axial view, Whittaker et al. (1998, pl. 12, fig. 1a, Qatar - see also Simmons & Bidgood, 2022, fig. 1a); **b.** Axial section, Whittaker et al. (1998, pl. 59, fig. 8, U.A.E. - see also Simmons & Bidgood, 2022, fig. 3c); **c.** Equatorial section, Simmons & Bidgood (2022, fig. 3a, Abu Dhabi) (Reproduced after Simmons & Bidgood, 2023).

2021 *Hemicyclammina sigali* – Keshavarzi et al., fig. 6a; Albian, Iranian Zagros.
2022 *Hemicyclammina sigali* – Keshavarzi et al., fig. 7a, ?9a; Albian, Iranian Zagros.
2022 *Hemicyclammina whitei* – Simmons & Bidgood, p. 28, figs. 1-4; Albian-Cenomanian, global review.
2023 *Hemicyclammina whitei* – Simmons & Bidgood, p. 86, fig. 35; early Albian-intra-late Cenomanian, global review.
2024 *Hemicyclammina sigali* – Arampour et al., fig. 7g; Albian, Iranian Zagros.

Reference Images: Simmons & Bidgood (2022) figs. 1-4.

Taxonomy/Identity: Simmons & Bidgood (2022) carried out a thorough investigation of this species, commonly recorded in the literature as its junior synonym, *H. sigali* Maync. *Hemicyclammina* is an involute planispiral genus with an alveolar wall but solid, pointed septa which extend only part way into the chamber lumen in equatorial sections. The otherwise similar genus *Everticyclammina* has septa projecting from both the outer and inner chamber wall (Banner & Highton, 1990). The solid ("semi-" or "hemi-") thin septa serve to distinguish the genus from *Buccicrenata* which has alveolar septa which are continuous outgrowths of the alveolar chamber wall. *Pseudocyclammina* is also similar but in addition to alveolar septa also has multiple apertures compared to the single slit of *Hemicyclammina*.

The Late Cretaceous (mostly Coniacian – Campanian) species *Hemicyclammina chalmasi* (= *Dictyopsella chalmasi* Schlumberger, 1900) differs from *H. whitei* by virtue of a thicker, coarsely agglutinating wall, and a larger test with chambers increasing in height to produce a peneropliform test. The exoskeleton is particularly well developed in *H. chalmasi* with long beams and less pronounced rafters. Excellent illustrations of this species are provided by Schlagintweit & Wagreich (2004) and Albrich et al. (2015). A possible Paleocene form of *Hemicyclammina*, *Hemicyclammina plana* (= *Alveolophragmium planum* Bykova, 1939) is poorly known (Simmons & Bidgood, 2022).

Confident Stratigraphic Range: early Albian – intra-late Cenomanian (common throughout).

Uncertain Stratigraphic Range: not applicable.

A frequently encountered species in suitable Albian – Cenomanian facies.

Hart et al. (2005) recorded *H. sigali* (= *H. whitei*) from strata in Portugal confidently assigned to the *guerangeri* and *geslinianum* ammonite zones of the late

Cenomanian, following earlier records by Berthou (1973); Lauverjat (1976) and Crosaz-Galletti (1979). Saint-Marc (1981) reported the species from latest Cenomanian strata in Lebanon with the ammonites *Eucalycoceras palaestinense* (Blackenhorn) and *Protacanthoceras angolaense* (Spath) and the planktonic foraminifera *Helvetoglobotruncana praehelvetica* (Trujillo) and *Whiteinella* spp. These records confer an upper range age limit of intra-late Cenomanian.

Pre-Albian records appear to be consistently smaller in size compared with *H. whitei* and are more likely an ancestral form "*Hemicyclammina*? sp." (e.g., illustrated as *H. sigali* from the Barremian of the Iranian Zagros by Hosseini et al. (2016) and the Aptian of offshore Abu Dhabi by Banner (1966; pl. 12, fig., 3b) and Iran by Shirzade et al. (2019) although the alveolar nature of the wall is not demonstrated). A similar, slight larger (0.3 mm diameter) specimen has been illustrated by Özkan & Altıner (2019) from the early Aptian of south-east Türkiye (Arabian Plate) as "*Hemicyclammina*? sp.".

Although sometimes used as a biozonal marker (e.g. Arampour et al., 2021; Rahbarman et al., 2024), this reflects biofacies and is of very limited correlative value.

Geographic Distribution: Very widespread. Throughout the Caribbean, central Atlantic (Brazil, Morocco, Iberia) and Neotethys as far east as Oman and Somalia and possibly (unconfirmed) further east in Tibet. Potential ancestral records are located on the Arabian Plate (see Simmons & Bidgood, 2022, 2023).

Genus ***Pseudocyclammina*** Yabe & Hanzawa 1926 (see Table 1 for diagnosis)

The inclusion of *Pseudocyclammina* in this subfamily/family does not follow Hayward et al. (2025) and the "WoRMS" database as discussed below.

Pseudocyclammina is a planispiral, agglutinated genus with coarse alveolar walls and septa that would appear to be relatively uncontroversial in terms of its higher classification but instead has become something rather more problematic. First proposed by Yabe & Hanzawa (1926) with the type species *Cyclammina lituus* Yokoyama, 1890 from the Late Jurassic – Early Cretaceous of Japan, it was said to differ from *Cyclammina* in having a cribrate rather than slit-like aperture and also having a tendency to uncoil.

No higher classification was proposed until Maync (1952) placed the genus in the Lituolidae family, Choffatellinae subfamily (and assigning d'Orbigny's 1850 species – *Lituola rugosa* to *Pseudocyclammina*). Loeblich & Tappan (1987) reassigned the Choffatellinae to the family Cyclamminidae Marie, superfamily Loftusiacea Brady.

However, almost contemporaneously, Septfontaine (1988) tentatively assigned *Pseudocyclammina* to a new family – the Hauraniidae; new subfamily Amijiellinae, both within the superfamily Lituolacea. This was done primarily upon the basis of the "…*progressive appearance of pillars in the '*Pseudocyclammina' *gr.* parvula/muluchensis/Anchispirocyclina *lineage and in* Alveosepta *during the Upper Jurassic*…" (Septfontaine, 1988; p. 237; caption to figure 4). Loeblich & Tappan's (1987; p. 102) genus description also included the phrase "…*may have a few irregular pillars in a narrow zone*…". Septfontaine (1988) also noted in the same caption that *Pseudocyclammina* "*appears as polyphyletic*" (written as "…*probably polyphyletic*" on p. 244). He went on to state that more research was needed, especially for Cretaceous taxa. Although illustrating several taxa in the Hauraniidae photographically, *Pseudocyclammina* was not one of them, and only a simple "cartoon-like" sketch was provided.

Despite Septfontaine's evident uncertainty, several of his new families including the Hauraniidae were re-assigned to a new suborder – the Orbitolinina – by Kaminski (2004) and maintained by him later (Kaminski, 2014) and also to the present day in the WoRMS world foraminifera database (Hayward et al., 2025). It was also a position followed, without discussion, by Simmons & Bidgood (2023). This new suborder was defined in full by Kaminski (2004; p. 251) as "*Test trochospiral or conical, later stage may have reduced number of chambers per whorl, or may become uniserial and rectilinear; chamber interior of advanced taxa subdivided by vertical or horizontal exoskeletal partitions or both, by radial or transverse partitions, or with interseptal pillars*." Kaminski's re-assignment was presumably made on the basis that other genera in the Hauraniidae/Amijiellinae better fit the new subordinal criteria and *Pseudocyclammina* (although never firmly assigned to the family/subfamily by Septfontaine) was "swept up" with the others.

With the exception of "interseptal pillars" – which have not been conclusively proven in the genus (in an extensive treatment of exo- and endoskeletal structures, Hottinger, 1967, did not mention pillars in connection with any *Pseudocyclammina* species except *P. muluchensis* n. sp. which is now assigned to *Streptocyclammina* Hottinger; see also Septfontaine, 1988, and see below) – none of the other subordinal characteristics of the Orbitolinina apply to what we know as *Pseudocyclammina*. It is difficult to envisage an obvious connection between the alveolar, planispiral *Pseudocyclammina* and, say, members of the family Orbitolinidae including "classic" internally-complex, uniserial cyclic/annular conical genera such as *Orbitolina*, for example (see Bidgood et al., 2024).

Moreover, we have seen no conclusive evidence for the presence of pillars in our studied Cenomanian material (e.g., Schlagintweit & Yazdi-Moghadam, 2023; see also Simmons & Bidgood, 2023) and, despite what may have been observed in Late Jurassic material and followed by us previously, we prefer to include (for the present paper) at least Cenomanian members of *Pseudocyclammina* within the Cyclamminidae herein, together with the morphologically similar genera

Buccicrenata and *Hemicyclammina* (see also Albrich et al., 2015, p. 255).

Pseudocyclammina is a distinctive subspherical to somewhat axially compressed, planispiral (sometimes uncoiling) genus, with relatively thick, obviously alveolar, chamber walls and septa. In the mid-Cretaceous, *Buccicrenata* is the most likely confusion genus (see *Buccicrenata* ex. gr. *subgoodlandensis* herein), but can be distinguished by its single aperture, whilst that of *Pseudocyclammina* is cribrate. *Pseudocyclammina* typically lacks the rapidly enlarging chambers and lobate equatorial profile of *Buccicrenata*. The alveoles are broad and less crowded than in *Choffatella* and similar genera.

*Pseudocyclammin*a is a commonly encountered and arguably diverse genus in Jurassic – Early Cretaceous sediments of Neotethys (e.g. Hottinger, 1967; Banner, 1970; Whittaker et al., 1998) but is relatively uncommon in Cenomanian sediments with only two species known: *Pseudocyclammina rugosa* (d'Orbigny, 1850) and *Pseudocyclammina sarvakensis* Schlagintweit & Yazdi-Moghadam, 2023. Confusion taxa include the typically Late Jurassic – Early Cretaceous *Pseudocyclammina lituus* (Yokoyama, 1890) and the Late Cretaceous *Pseudocyclammina sphaeroidea* Gendrot, 1968 and *Pseudocyclammina massiliensis* Maync, 1959. *P. sarvakensis* is distinguished from all previously described *Pseudocyclammina* species by the relatively larger number of chambers (14-16) in the final whorl, and has not been observed to uncoil. *P. rugosa* is relatively large (0.8 – 4.3 mm in external diameter of the coiled portion according to Maync (1959a) although illustrations in Maync (1952, 1959) indicate maximum diameter, including uncoiled to be 4.78 – 6.0 mm) and this, together with a large chamber height, strongly curved thick septa, a rounded periphery, a relatively large axial thickness (0.7-2.3 mm) (a diameter: hickness ratio 1 – 1.9, typically 1.4) and 5-7 chambers in the last whorl serve to distinguish it from other species of *Pseudocyclammina* and indeed *Buccicrenata*. A summary of the characteristics of the five *Pseudocyclammina* species mentioned above is shown in Table 2 and the two exclusively Cenomanian species are discussed below.

We have not considered in further detail the debate between describing the wall of *Pseudocyclammina* as "alveolar" (Schlagintweit & Yazdi-Moghadam, 2023; Simmons & Bidgood, 2023 and as used herein) or "labyrinthic" (Gendrot, 1968; Maync, 1952, 1959) or a combination of both (Banner, 1966, 1970). Hottinger (2006) provided separate definitions (but not illustrations) for both kinds of structure/texture, but these are not unequivocal. Gušić (1975) also provided a discussion, distinguishing *Everticyclammina* from *Pseudocyclammina* claiming that the former genus is the only one to show an "alveolar exoskeleton" (p. 15) and the latter a "subepidermal meshwork type" (p. 13). He went on to say (p. 15) that "*It is unclear whether Pseudocyclammina rugosa… possesses an alveolar rather than subepidermal meshwork exoskeleton…*" leading to more uncertainty in the terminology and raising the question of any significant difference between the terms. The terms used by the various authors above seem to be those of personal preference and further examination of type materials from many taxa would be required to provide clarification, which is beyond the scope of this work.

Pseudocyclammina rugosa (d'Orbigny, 1850)

Figure 3

1850 (1847 MS) *Lituola rugosa* d'Orbigny, vol. 2, p. 185, limited description with no illustration; middle – late Cenomanian, western France.

1952 *Pseudocyclammina rugosa* (d'Orbigny) – Maync, pl. 12, figs. 6-10; middle – late Cenomanian, western France.

1959 *Pseudocyclammina rugosa* – Maync, p. 187, pl. 1, figs. 10-15; middle – late Cenomanian, western France.

Non 1965 *Pseudocyclammina* cf. *rugosa* – Hamaoui, p. 19-20; pl. 1, fig. 11, pl. 5, figs. 6-8, pl. 10, fig. 6; Cenomanian, Israel [= *Buccicrenata* ex gr. *subgoodlandensis*].

? 1967 *Pseudocyclammina* cf. *rugosa* – Bismuth et al., pl. XII, figs. 18-20; Cenomanian, Tunisia [small, with unclear identity].

Non 1967 *Pseudocyclammina* cf. *rugosa* – Arkin & Hamaoui, pl. 2, fig. 3; Cenomanian, Israel [= *Buccicrenata* ex gr. *subgoodlandensis*].

Non 1969 *Pseudocyclammina rugosa* – Sampò, pl. XXXIX, figs. 6-8; Albian, Iranian Zagros [=*B.* ex gr. *subgoodlandensis*].

1973 *Pseudocyclammina rugosa* – Bilotte, pl. III, fig. 15; latest Albian-Cenomanian, Pyrenees.

? 1973 *Pseudocyclammina rugosa* – Berthou, pl. 1, figs. 1, 1a-c; early-middle Cenomanian, Portugal [? =*B.* ex gr. *subgoodlandensis* or unconfirmed].

1974 *Pseudocyclammina rugosa* – Neumann et al., pl. 6, fig. 4; middle – late Cenomanian, western France.

? 1974 *Pseudocyclammina* cf. *rugosa* – Moullade & Peybernès, pl. 3, figs. 2, 5; late Albian, Spain [? = *Buccicrenata* ex gr. *subgoodlandensis*].

Non 1976 *Pseudocyclammina rugosa* – Kalantari, pl. 10, figs. 13-14; Aptian, Iranian Zagros [=*B.* ex gr. *subgoodlandensis*].

Non 1976 *Pseudocyclammina* cf. *rugosa* – Kalantari, pl. 22, figs. 17-18, 25; Cenomanian, Iranian Zagros [=*B.* ex gr. *subgoodlandensis*].

1985 *Pseudocyclammina rugosa* – Bilotte, p. 355, pl. 4, fig. 8; middle – late Cenomanian (total range indicated as Albian – Cenomanian), French Pyrenees.

1986 *Pseudocyclammina rugosa* – Ben Youssef & Peybernès, pl. fig. 18; middle – late Albian, Tunisia.

? 1987 *Buccicrenata? rugosa* – Simmons & Hart, pl. 10.5, fig. 4; early Cenomanian, Oman [not clear, ?=*B.* ex gr. *subgoodlandensis;* one of us (FS) has also seen similar material from the middle Cenomanian of Oman

Table 2. Comparison of morphological characteristics between 5 species of the genus *Pseudocyclammina*. Note: estimates of stratigraphic ranges of these comparative taxa are not based on exhaustive assessment of occurrences in the literature, except *P. rugosa* and *P. sarvakensis* as discussed herein. They have been assessed only from the type descriptions and more recent general summaries (e.g., Bassoullet, 1997; Velić, 2007; Albrich et al., 2015).

CHARACTERISTIC	*PSEUDOCYCLAMMINA LITUUS*	*PSEUDOCYCLAMMINA RUGOSA*	*PSEUDOCYCLAMMINA SARVAKENSIS*	*PSEUDOCYCLAMMINA SPHAEROIDEA*	*PSEUDOCYCLAMMINA MASSILIENSIS*
Original description & provenance	As *Cyclammina lituus*; Yokoyama (1890), Tithonian-Berriasian, Japan	As *Lituola rugosa*; d'Orbigny (1850), Cenomanian, France	Schlagintweit & Yazdi-Moghadam (2023 ☼), Cenomanian, Iranian Zagros	Gendrot (1968), late Santonian, France	Maync (1959 ☼), Santonian, France
Basic image (reference source of image shown thus ☼)					
Other significant illustrative descriptions	Maync (1959 ☼); Kaever (1967); Hottinger (1967); Gušić (1975); Kobayashi & Vuks (2006)	Maync (1952 ☼, 1959)	N/A	Chiocchini et al. (2012); Albrich et al. (2015 ☼); Frijia et al. (2015); Arriaga et al. (2016)	Boix et al. (2011)
Wall	Agglutinated, alveolar	Agglutinated, alveolar	Agglutinated, alveolar	Agglutinated, alveolar (labyrinthic)	Agglutinated, alveolar
Overall shape	Axially compressed, often uncoiling	Axially compressed, often uncoiling	Subspherical, moderately compressed axially, no uncoiling observed	Subspherical, slightly compressed axially, flaring but only occasionally uncoiling	Axially compressed, often uncoiling
Dimensions (mm) (De = diameter equatorial; Da = diameter axial; Dp = diameter proloculus)	De = 1.0-2.7 (*sometimes 3.5+) Da = 0.8-1.8 Dp = 0.24-0.26	De = 3.1-4.3 Da = 0.7-2.3	De = 1.35 Dp = 0.11-0.30	De = 0.60-1.1 ** Da = 0.40-0.42 Dp = 0.10	De = 1.2-2.3 Da = 0.4-0.8
Chambers per whorl (first whorl = W_1, second whorl = W_2 etc.)	W_F = 7-12 c. 3 uncoiled	W_F = 5-7 c. 2-3 uncoiled	W_F = 14-16	W_F = 10-12 in smaller forms, 13-14 in larger forms ** c. 1-2 uncoiled	W_F = 5-7 2-3 uncoiled
No. of whorls	c. 2.5-3.5	c. 2	c. 2.5-3.5	c. 2.5-3.0 **	c. 1.5-2
Foramina diameter (µm)	50		20-35		
Stratigraphic Range (see caption)	Oxfordian – Aptian (Gušić, 1975; Bassoullet, 1997)	Albian –Cenomanian	Middle – late Cenomanian	Turonian –Campanian (Velić, 2007; Albrich et al., 2015; Arriaga et al., 2016; Solak et al., 2020)	Middle Coniacian – Campanian (Velić, 2007; Boix et al., 2011 ; Schlagintweit & Yazdi-Moghadam, 2023)
Commens	(*) = Whittaker et al. (1998)			Note: Not the same as the similarly named *Pseudocyclammina sphaeroidalis* Hottinger, 1967 from the Late Jurassic of Morocco (**) Albrich et al. (2015)	

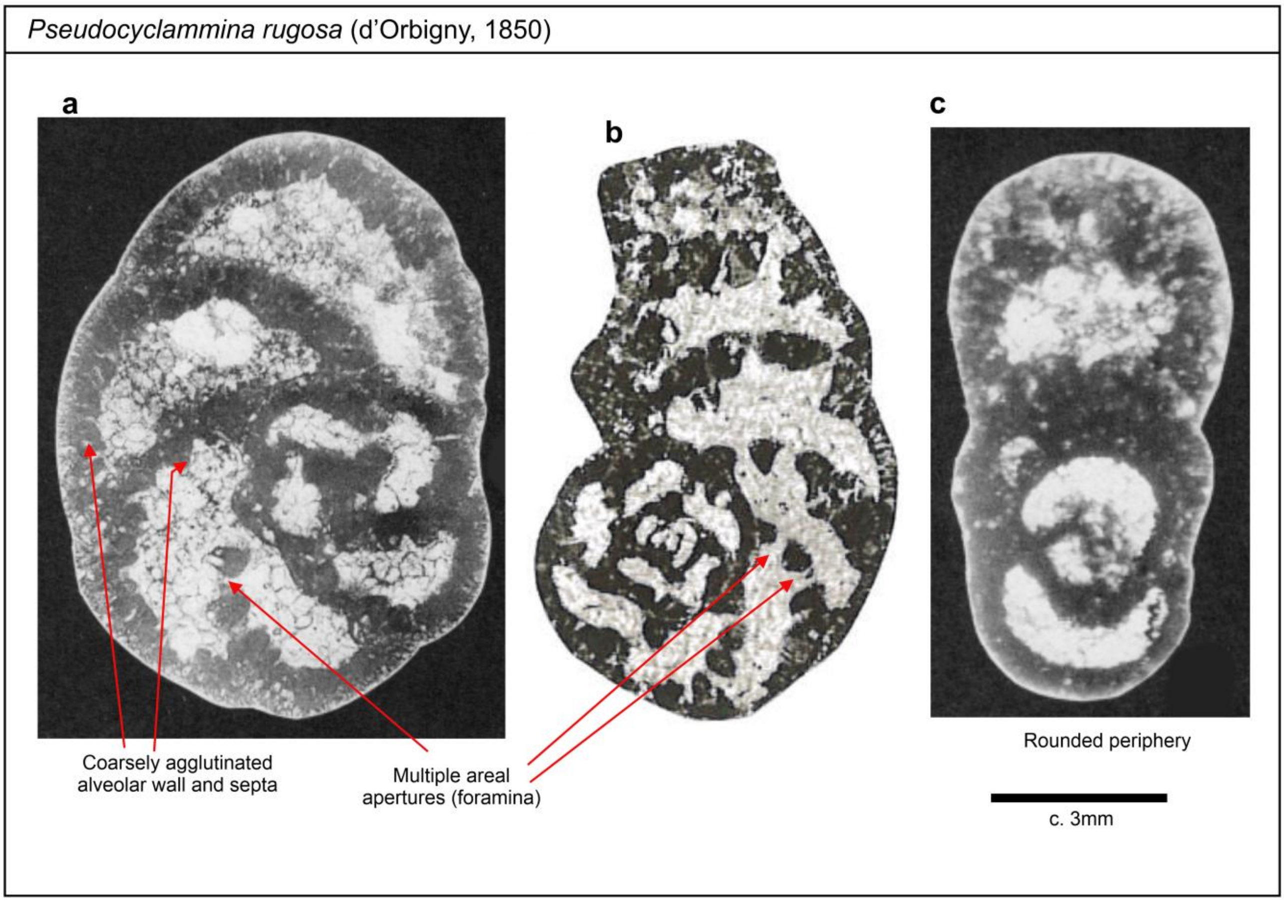


Fig. 3. Representative illustrations of *Pseudocyclammina rugosa*: **a.** Equatorial section, Maync (1952, pl. 12, fig. 9, France); **b.** Equatorial section of uncoiled specimen, Maync (1959, pl. 1, fig. 14, France); **c.** Axial section, Maync (1952, pl. 12, fig. 8, France). (After Simmons & Bidgood, 2023).

(unpublished data)].

Non 1993 *Pseudocyclammina rugosa* – Ettachfini, p. 120, pl. 1, figs. 7-11; Cenomanian, Morocco [=*Ammobaculites/Lituola*, *B.* ex gr. *subgoodlandensis* or indeterminate].

Non 2003 *Pseudocyclammina rugosa* – Aguilero-Franco, pl. 1, fig. 7; Cenomanian, Mexico [prob.=*Ammobaculites* sp., no obvious alveolar wall].

Non 2004 *Pseudocyclammina rugosa* – Ettachfini & Andreu, fig. 7E; Cenomanian, Morocco [=*Ammobaculites/Lituola*, *B.* ex gr. *subgoodlandensis* or indeterminate].

Non 2006 *Pseudocyclammina rugosa* – Ettachfini, pl. 13, fig. 10; late Cenomanian, Morocco [=*Ammobaculites/Lituola*, *B.* ex gr. *subgoodlandensis* or indeterminate].

Non 2012 *Pseudocyclammina rugosa* – Omaña et al., fig. 5(8); middle-late Cenomanian, Mexico [prob. =*Ammobaculites/Lituola* sp.].

Non 2013 *Pseudocyclammina rugosa* – Boavida; pl. 1, fig. 1; Cenomanian, Portugal [?=*B.* ex gr. *subgoodlandensis* or unconfirmed].

Non 2013 *Pseudocyclammina rugosa* – Omaña et al., pl. 5, fig. 10; middle-late Cenomanian, Mexico [prob.=*Ammobaculites/Lituola* sp.].

? 2014 *Pseudocyclammina rugosa* – Danelian et al., fig. 9(3-6); Cenomanian, Armenia [small and unclear identity].

Non 2014 *Pseudocyclammina rugosa* – Afghah & Haghighi, pl. 3, fig. 3; Aptian, Iranian Zagros [=*Ammobaculites* sp. or *Lituola* sp.].

2018 *Pseudocyclammina rugosa* – BouDagher-Fadel, pl. 5.6 (7) middle – late Cenomanian, western France.

? 2018 *Pseudocyclammina rugosa* – Andrade, pl. M1, figs. 3,4,6; pl. M5, fig. 7; Cenomanian, Portugal [?=*B.* ex gr. *subgoodlandensis* or unconfirmed].

Non 2018 *Pseudocyclammina rugosa* – Omidi et al., pl. 2, fig. 5; Cenomanian, Iranian Zagros [=*P. sarvakensis*].

? 2020 *Pseudocyclammina rugosa* – Simmons et al., fig. 9.1; middle Cenomanian, Turkish Arabian Plate.

Non 2022 *Pseudocyclammina rugose* (sic.) – Esfandyari et al., fig. 23l; Cenomanian-Turonian, Iranian Zagros [=*P. sarvakensis*].

2023 *Pseudocyclammina rugosa* – Simmons Bidgood, p. 82, fig. 31; Albian – latest? Cenomanian, global review.

Non 2023 *Pseudocyclammina rugosa* – Abtahiyan et al., fig. 6b; late Barremian – early Aptian, Iranian Zagros [indeterminate, but not *P. rugosa*, possibly *B.* ex gr. *subgoodlandensis*].

Reference Images: Maync (1952), Pl. 12, figs. 6-10, p. 50 and Maync (1959), Pl. 1, figs. 10-15.

Taxonomy/Identity: The typical Cenomanian representative of *Pseudocyclammina* is *P. rugosa*, that despite illustration by Maync (1952, 1959) remains poorly known. *Lituola rugosa* was introduced by d'Orbigny (1850) with a very limited description in a list of Cenomanian foraminifera from France, and there is no illustration. Maync (1952, 1959) illustrated topotype specimens from the Cenomanian of Charente, France (see also BouDagher-Fadel et al., 2017) and discussed elements of the taxonomy (including his justification for placing the species in *Pseudocyclammina*) and differences with similar taxa. Since then, the species has quite frequently been reported from Albian – Cenomanian sediments of Neotethys and the Caribbean (Mexico), but seldom illustrated and often not convincingly. Confusion with *Buccicrenata* ex gr. *subgoodlandensis* is common and in many random sections the species are difficult to distinguish from one another, leading to uncertainties in stratigraphic and geographic distribution (see discussion below).

P. rugosa appears to be relatively large (0.8 – 4.3 mm in external diameter of the coiled whorl according to Maync (1959) although illustrations in Maync (1952, 1959) indicate maximum diameter, including uncoiled to be 4.78 – 6.0 mm) and this, together with a large chamber height, strongly curved thick septa, a rounded periphery, a relatively large axial thickness (0.7-2.3 mm) (diameter: thickness ratio 1 – 1.9mm, typically 1.4) and 5-7 chambers in the last whorl serve to distinguish it from other species of *Pseudocyclammina* (Table 2) and indeed *Buccicrenata*. Wall thickness in *P. rugosa* is 0.17 – 0.50 mm. 2-3 uncoiled final chambers can occur in both *P. rugosa* and *B.* ex. gr. *subgoodlandensis*.

Confident Stratigraphic Range: middle Albian – undifferentiated middle – late Cenomanian.

Uncertain Stratigraphic Range: early Albian.

Neumann et al. (1974) indicated that at its type locality, the species has an undifferentiated middle – late Cenomanian range. Rey et al. (1977), Decrouez (1978), Saint-Marc (1981), and Berthou (1984) suggested that across Neotethys, this species ranges throughout the Albian and Cenomanian (see also Crosaz-Galletti, 1979), but in practice, despite many published occurrences, there are very few records of this species that have both plausible illustrations and precise biostratigraphic calibration. There are no illustrated, unequivocally late Cenomanian records, only those from undifferentiated Cenomanian, or middle – late Cenomanian strata. The oldest confidently illustrated records come from the middle – late Albian of Tunisa (Ben Youssef & Peybernès, 1986).

Illustrated records from the Aptian or older (e.g., Kalantari, 1976; Afghah & Haghighi, 2014; Abtahiyan et al., 2023 from the Iranian Zagros) are not this species (that of Afghah & Haghighi, 2014 = *Ammobaculites* sp. or *Lituola* sp.), and unillustrated records from Aptian and older strata (e.g., Abu Zied, 2007; Habibnia et al., 2010; Mansouri-Daneshvar et al., 2015; Afghah et al., 2016) should be treated with caution. An unillustrated report from the Coniacian – Maastrichtian of Spain (Gräfe, 2005) should most likely be regarded as erroneous.

Restriction of its range to the early Cenomanian (Velić, 2007) reflects local facies control.

Geographic Distribution: Western Mediterranean – ?Arabian Plate within Neotethys.

As can be understood from the limited number of confirmed records mentioned above, the paleogeographic distribution of this species is hard to determine. Confirmed records are limited to the type area in western France, the Pyrenees, Tunisia and possibly Oman and southern Türkiye. Unpublished reports, if confirmed, might extend this distribution, but despite quite numerous records it remains unproven as occurring in Mexico.

Pseudocyclammina sarvakensis Schlagintweit & Yazdi-Moghadam, 2023

Figure 4

1969 *Cyclammina* sp. (?) – Sampò, pl. XLV, fig. 2; Cenomanian, Iranian Zagros.
2018 *Pseudocyclammina rugosa* – Omidi et al., pl. 2, fig. 5; Cenomanian, Iranian Zagros.
2022 *Pseudocyclammina rugose* (sic.) – Esfandyari et al., fig. 23l; Cenomanian, Iranian Zagros.
T 2023 *Pseudocyclammina sarvakensis* n. sp. – Schlagintweit & Yazdi-Moghadam, p. 7, fig. 4a-g; undifferentiated middle-late Cenomanian, Iranian Zagros.
2023 *Pseudocyclammina sarvakensis* – Simmons & Bidgood, p. 84, fig. 33; middle-late Cenomanian, global review.

Reference Images: Schlagintweit & Yazdi-Moghadam (2023), fig. 4a-g, p. 7.

Taxonomy/Identity: A very recently described species from the Sarvak Formation of the Iranian Zagros (Schlagintweit & Yazdi-Moghadam, 2023), *P. sarvakensis* is distinguished from all previously described *Pseudocyclammina* species by the relatively larger number of chambers (14-16) in the final whorl (Table 2). Sampò (1969) illustrated a *Pseudocyclammina* from the Cenomanian of the Iranian Zagros as "*Cyclammina* sp. (?)". This relatively small form (external diameter 1.2 mm) with numerous chambers in the final whorl (in an approximately similar manner to the Late Cretaceous species *Pseudocyclammina sphaeroidea* Gendrot, see, for example, Schlagintweit, 1992) has been occasionally illustrated as *P. rugosa* in other publications on the Cenomanian Sarvak Formation of the Iranian Zagros. In addition, *P. sarvakensis* is larger than *P. sphaeroidea* and has not yet been observed to uncoil.

Confident Stratigraphic Range: undifferentiated middle – late Cenomanian.

Uncertain Stratigraphic Range: not applicable.

Schlagintweit & Yazdi-Moghadam (2023) recorded

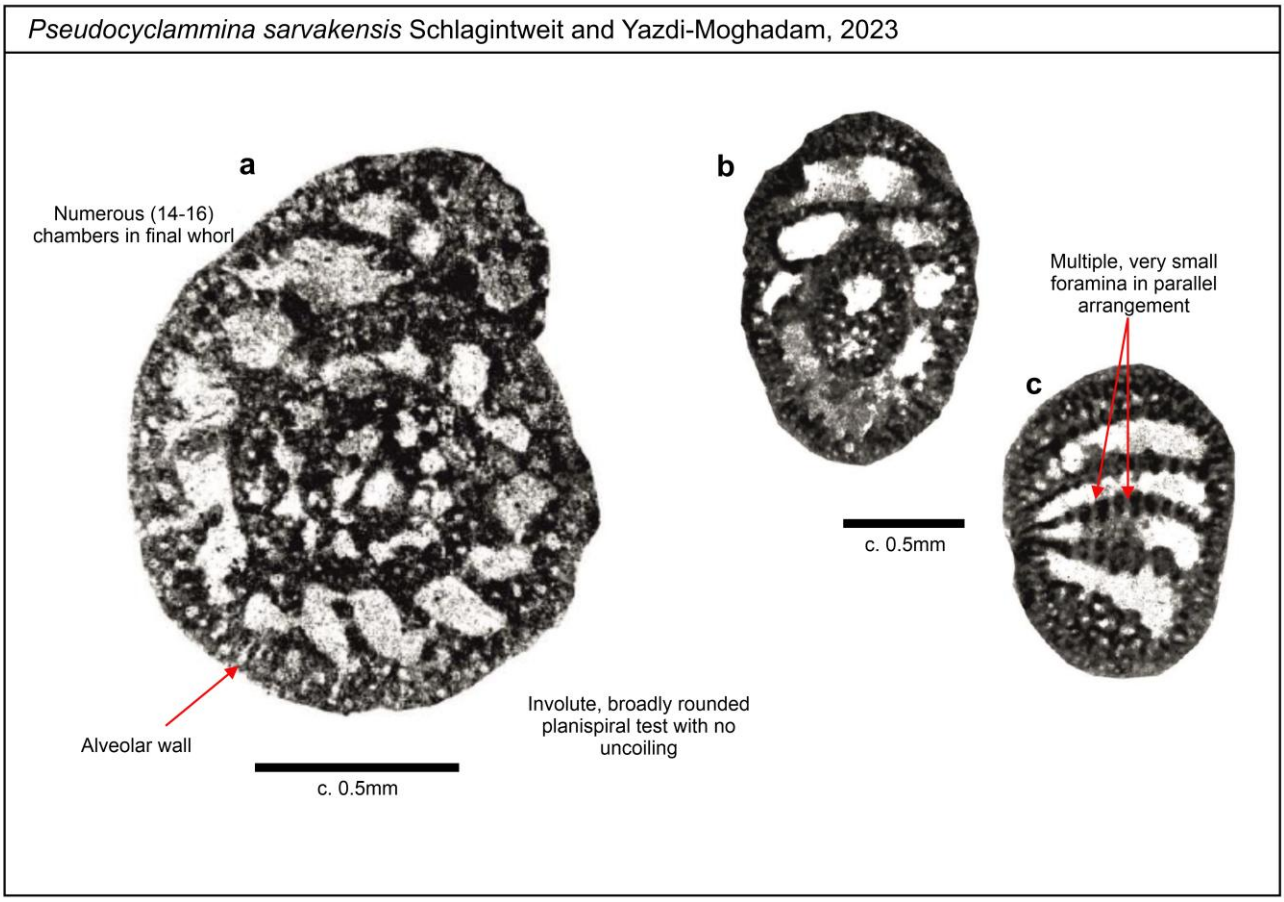


Fig. 4. Representative illustrations of *Pseudocyclammina sarvakensis*: **a.** Equatorial section, Schlagintweit & Yazdi-Moghadam (2023, fig. 4b, Iran, holotype); **b.** Subaxial section, Ibid. (2023, fig. 4d, Iran); **c.** Oblique tangential section, Ibid. (2023, fig. 4f, Iran). (After Simmons & Bidgood, 2023).

P. sarvakensis from the lowermost part of their middle – late Cenomanian interval of the Sarvak Formation of SW Iran. Omidi et al.'s (2018) records of *P. rugosa* (= *P. sarvakensis*) come from the mid – upper parts of their Cenomanian interval. Esfandyari et al. (2022) recorded *P. rugose* (sic) (= *P. sarvakensis* see above) from the Sarvak Formation but with no precise age indication given.

Geographic Distribution: Arabian Plate.

All confirmed occurrences occur in the Zagros region of Iran only (see references above).

Subfamily **PSEUDOCHOFFATELLININAE** Loeblich & Tappan, 1985a (diagnosis *sensu* Loeblich & Tappan, 1987)

Genus ***Pseudochoffatella*** Deloffre, 1961 (see Table 1 for diagnosis)

Pseudochoffatella algeriana Peybernès et al., 1988
Figure 5

1984 "*Pseudochoffatella*" n. sp. Peybernès et al., pl. 1, figs. 10-12; Cenomanian, Algeria.

T 1988 *Pseudochoffatella algeriana* n. sp. Peybernès et al., text-fig. 2, pl. 1, figs. 1-11; upper Cenomanian, Algeria.

Reference Images: Peybernès et al. (1988) text fig. 2, pl. 1, figs. 1-11.

Taxonomy/Identity: First described from the upper Cenomanian of Algeria by Peybernès et al. (1988) having been first identified as a new taxon by Peybernès et al. (1984; see also Peybernès et al., 1986), this species differs from the more commonly recorded Aptian-Albian species *P. cuvillieri* Deloffre, 1961, and the more recently described Barremian? – Aptian *P. minima* Schlagintweit et al., 2020, in having a larger test (up to 16 mm diameter in microspheric forms) and a more discoidal rather than reniform test shape. Schlagintweit et al. (2020) provides useful comparative data.

It superficially resembles other thin, discoidal generic forms discussed herein such as *Cyclolina*, *Cyclopsinella*, *Mangashtia* and *Dicyclina* but differs in possessing a (small) post-embryonic peneropliform stage and a "…*Choffatelliform hypodermis with polygonal subepidermal network*" (Peybernès et al. (1988, p. 458 translated from original).

Confident Stratigraphic Range: not applicable.

Uncertain Stratigraphic Range: late Cenomanian.

Although described as occurring in the late Cenomanian in the only detailed report of this species (Peybernès et al., 1988), this age assignment is based on

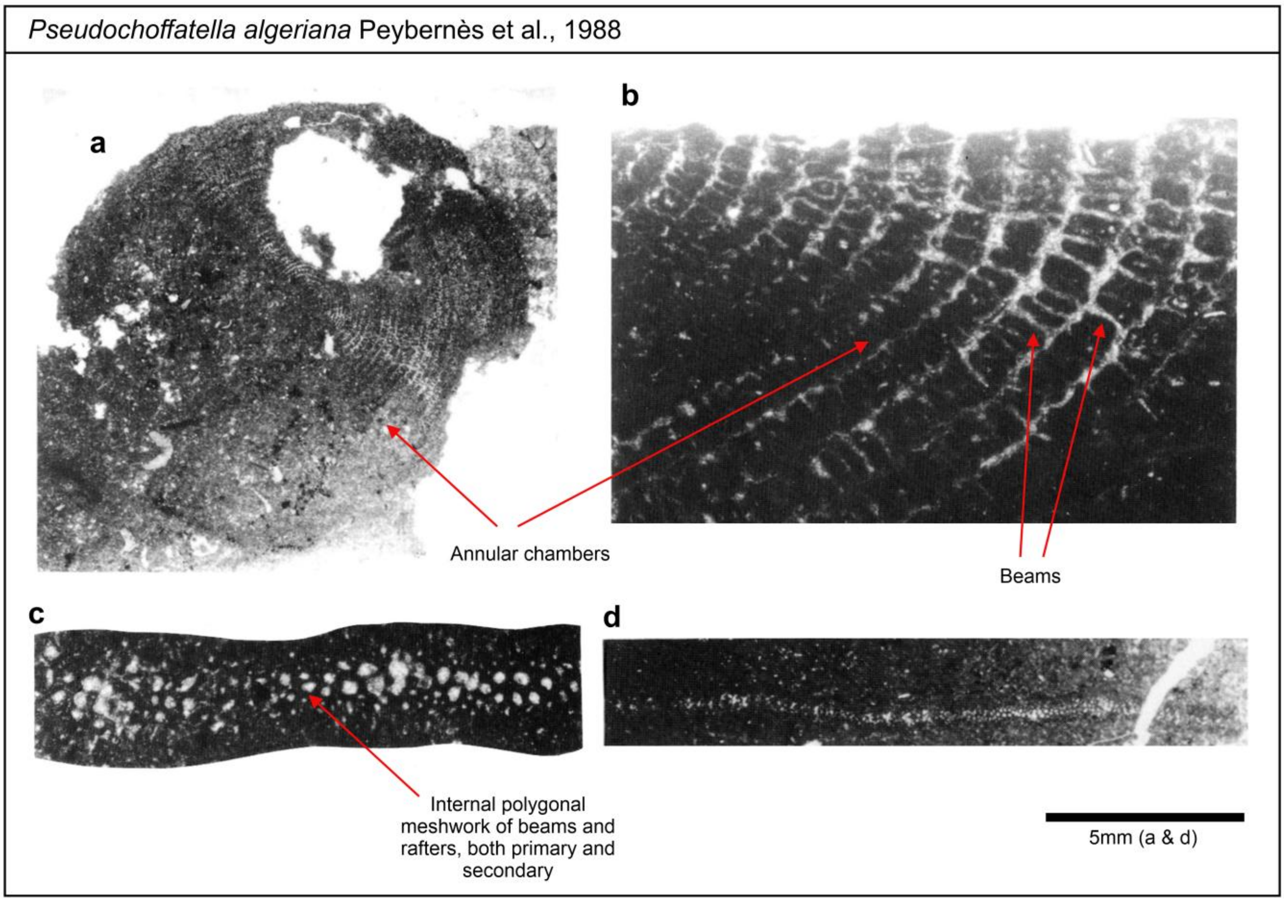


Fig. 5. Representative illustrations of *Pseudochoffatella algeriana*: **a.** Subequatorial view, (Peybernès et al., 1988, pl. 1, fig. 1, holotype, Algeria); **b.** Subequatorial view, Peybernès et al., 1988, pl. 1, fig. 8, Algeria); **c.** Subaxial view (Peybernès et al., 1988, pl. 1, fig. 6, Algeria); **d.** Subaxial view (Peybernès et al., 1988, pl. 1, fig. 5, Algeria).

co-occurrence with *Pseudorhapydionina dubia* (De Castro, 1965). Simmons & Bidgood (2023) noted that *P. dubia* has a long range within the Cenomanian, at least as old as middle Cenomanian, if not older.

Geographic Distribution: This species has so far only been reported from Algeria.

Superfamily **LOFTUSOIDEA** Brady 1884 (diagnosis *sensu* Loeblich & Tappan, 1987)
Family **SPIROCYCLINIDAE** Munier-Chalmas 1887 (diagnosis *sensu* Loeblich & Tappan, 1987)
Genus ***Reissella*** Hamaoui 1963 (see Table 1 for diagnosis)

Reissella ramonensis **Hamaoui, 1963**
Figure 6

T 1963 *Reissella ramonensis* n. gen, n. sp. – Hamaoui, p. 62, pl. 1, figs. 1-13, text-fig. 1; late Cenomanian, Israel.
? 1965 *Reissella ramonensis* – Hamaoui, pl. 13, figs. 8-9; Cenomanian, Israel.
1966 *Reissella ramonensis* – Hamaoui, pl. 5, fig. 8; Cenomanian, Israel.
Non 1966 *Reisella ramonensis* – Hamaoui, pl. 3, fig. 6. [prob.=*Pseudorhipidionina casertana* (De Castro, 1965)].
Non 1970 *Reissella ramonensis* – Hamaoui & Saint-Marc, pl. 40, fig. 8. [probably=*P. casertana*].
2023 *Reisella ramonensis* – Simmons & Bidgood, p. 88, fig. 37; late Cenomanian, global review.

Reference Images: Hamaoui (1963) pl. 1 (1-13), fig. 1.

Taxonomy/Identity: This small but internally complex taxon has an uncertain suprageneric status as the nature of its wall has yet to be unequivocally determined as originally porcelaneous or agglutinated. Similarities with the soritid *Pseudorhipidionina casertana* (De Castro, 1965) are clearly evident but subtle differences occur, although these may be difficult to determine in all but pristine, well-oriented thin-sections. De Castro (1981) and De Castro in Schroeder & Neumann (1985) remarked on the similarity between *P. casertana* and *R. ramonensis* with the former lacking the “rafters” element of the polygonal subepidermal network. *P. casertana* also appears to have a greater tendency to fully uncoil compared with *R. ramonensis*. For the present it appears that *R. ramonensis* is a possibly agglutinated isomorph of *P. casertana* (see Simmons & Bidgood, 2023, and the species key chart therein for a more extensive discussion), but an unequivocal clarification of its status

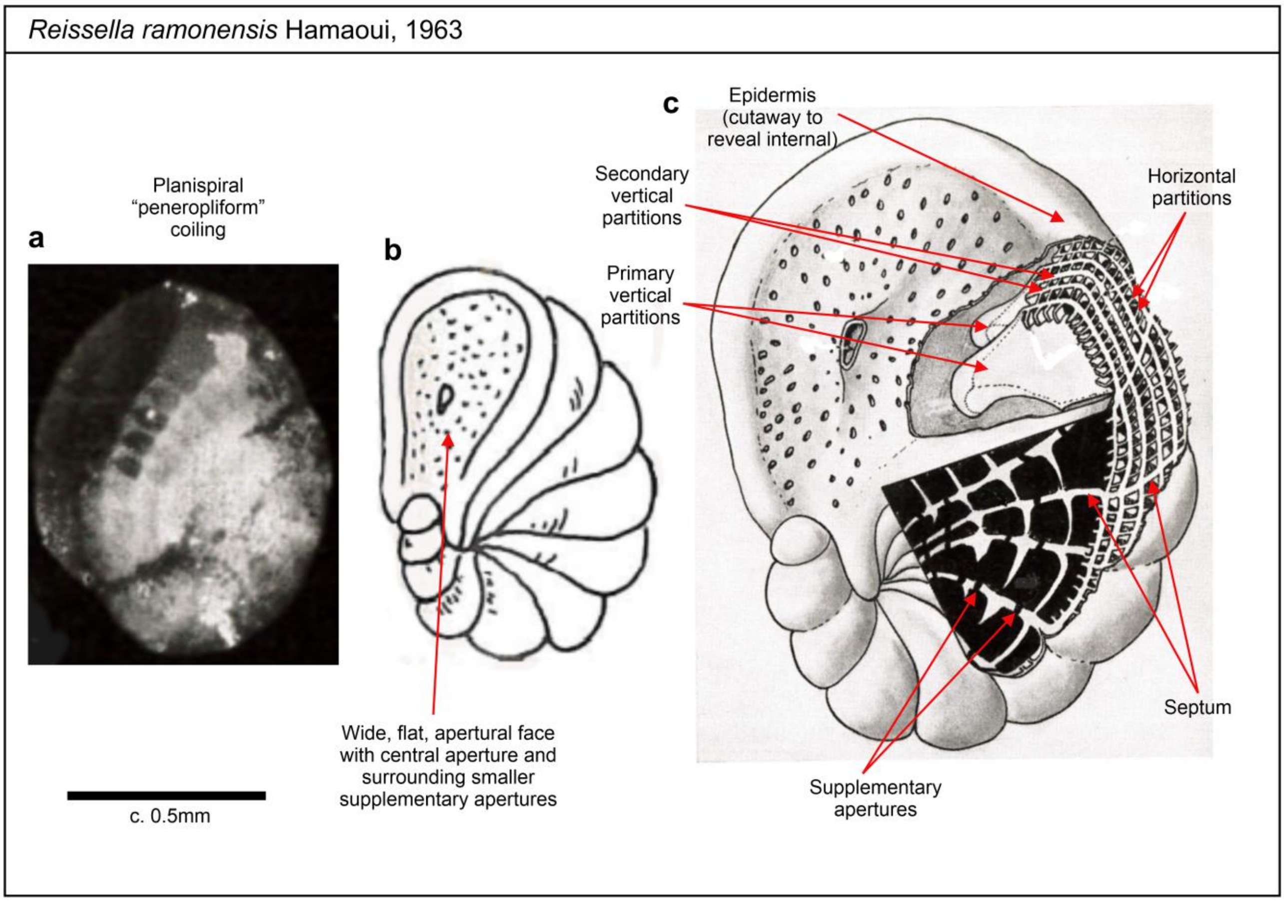


Fig. 6. Representative illustrations of *Reissella ramonensis*: **a.** Exterior view, (Hamaoui 1963, pl. 1, fig. 3, holotype, Israel); **b.** Exterior view (schematic), (Hamaoui 1963, pl. 1, fig. 11, Israel); **c.** Enlarged cutaway exterior view showing internal features (Hamaoui 1963, text fig. 1, Israel) (Reproduced after Simmons & Bidgood, 2023).

awaits more material for study.

Confident Stratigraphic Range: late Cenomanian.

Uncertain Stratigraphic Range: not applicable.

Limited records of this taxon from Israel (illustrated) and from Crete (unillustrated; Leppig, 1976) have so far been noted in late Cenomanian or undifferentiated Cenomanian-Turonian strata respectively. A record of *Reissella* sp. from the Albian of Türkiye (Solak et al., 2021) is not this species but could be an ancestral form of *R. ramonensis* or the *Pseudorhipidionina* group (see Simmons & Bidgood, 2023). A view that *R. ramonensis* occurs in the Turonian (Lipson-Benitah, 2009) has been discounted by Simmons & Bidgood (2023).

Geographic Distribution: Very limited distribution in Central Neotethys; Israel and (unconfirmed) Crete (see Simmons & Bidgood, 2023).

Genus ***Spirocyclina*** Munier-Chalmas 1887 (see Table 1 for diagnosis).

Spirocyclina atlasica Saint-Marc & Rahhali, 1982
Figure 7

T 1982 *Spirocyclina atlasica* – Saint-Marc & Rahhali, p. 134, pls. 1-2; late Cenomanian, Moroccan Atlas.
1984 *Spirocyclina atlasica* – Dufaure et al., pl. 1, figs. 8-12; late Cenomanian, Libya.
1993 *Spirocyclina atlasica* – Ettachfini, pl. 2, figs. 3-7; late Cenomanian, Morocco.
1998 *Spirocyclina atlasica* – Charrière et al., fig. 4(5); fig. 7(1-5); late Cenomanian, Morocco.
2006 *Spirocyclina atlasica* – Ettachfini, pl. 13, figs, 1-9; late Cenomanian, Morocco.
? 2017 *Coxites zubairensis* – Boukhary et al., p. 4; fig.1; late Cenomanian-early Turonian, Eastern Desert, Egypt.
2023 *Spirocyclina atlasica* – Simmons & Bidgood, p. 90, fig. 39; late Cenomanian, Western North Africa.

Reference Images: Saint-Marc & Rahhali (1982) pls. 1-2.

Taxonomy/Identity: The dramatically flattened (more so than in *Reissella ramonensis*) peneropliform coiling style of this species is characteristic (see Simmons & Bidgood, 2023, and the species key chart therein for more information). The generic characteristic is a double row of pores in the apertural face (which can increase to three rows in the final stage).

Confident Stratigraphic Range: late Cenomanian.

Uncertain Stratigraphic Range: not applicable.

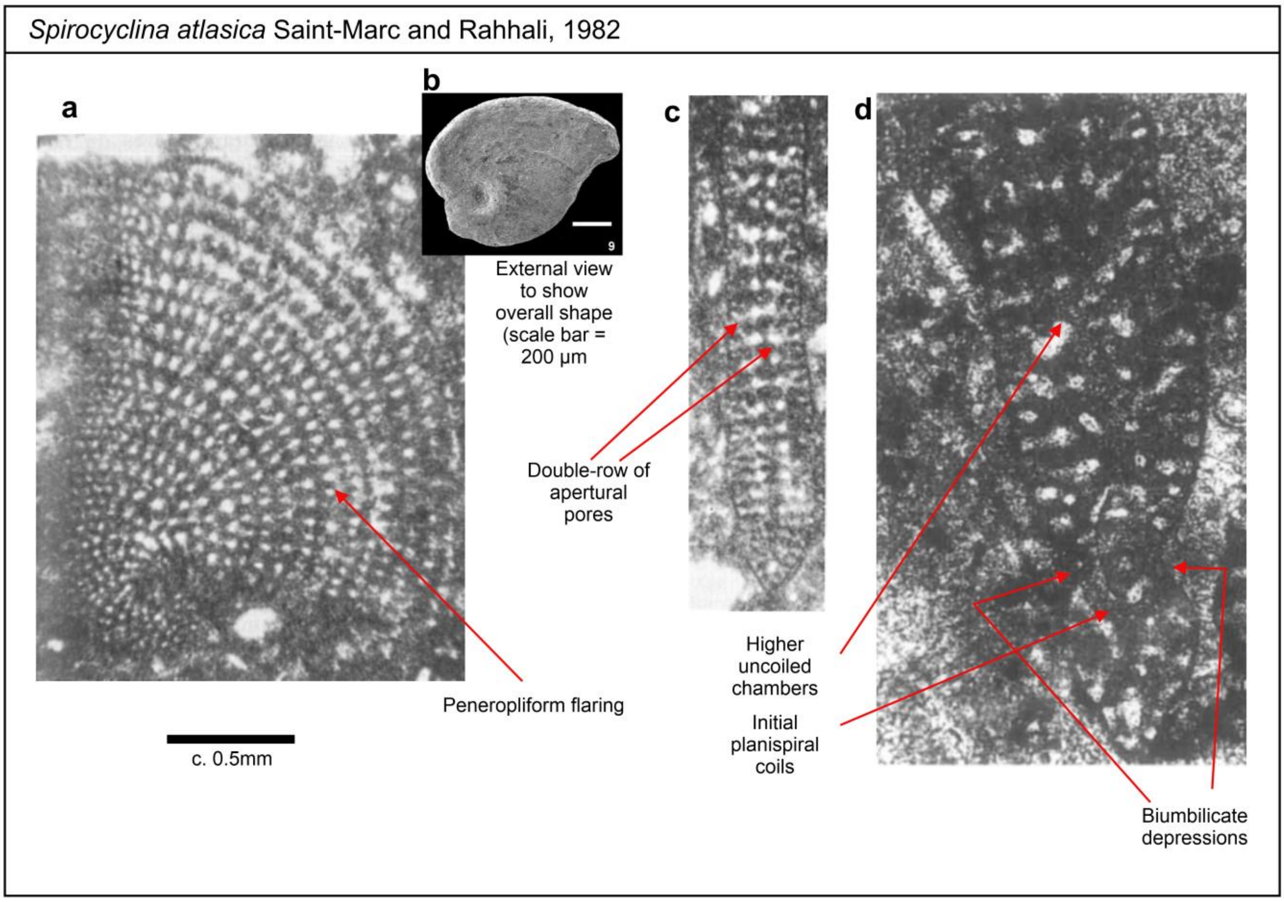


Fig. 7. Representative illustrations of *Spirocyclina atlasica*: **a.** Equatorial section, Saint-Marc & Rahhali (1982, pl. 2, fig. 1, Morocco); **b.** External View, Etachfini (2006, pl. 13, fig. 9, Morocco); **c.** Subaxial section, Saint Marc & Rahhali (1982, pl. 2, fig. 8, Morocco); **d.** Axial section, Charrière et al. (1998, fig. 7(1), Morocco) (Reproduced after Simmons & Bidgood, 2023).

The genus is long-ranging (Kimmeridgian-Santonian; Maync, 1959) but not previously recorded from the Cenomanian until this species was described from the late Cenomanian of the Moroccan Atlas (Saint-Marc & Rahhali, 1982). Almost all records are from Morocco although a plausibly illustrated record also occurs in Libya (Dufaure et al., 1984). The record of *Spirocyclina* sp. from the late Cenomanian of SE France (Rineau et al., 2021) is probably better referred to as *Pseudorhapydionina dubia* (De Castro).

Geographic Distribution: Limited distribution in North Africa (Morocco and Libya; see Simmons & Bidgood, 2023).

Family **LOFTUSIIDAE** Brady 1884 (diagnosis *sensu* Loeblich & Tappan, 1987)
Genus ***Reticulinella*** Cuvillier, Bonnefous, Hamaoui & Tixier in Bonnefous et al. 1970 (see Table 1 for diagnosis).

Reticulinella reicheli (Cuvillier et al., 1969)
Figure 8

? 1915 *Loftusia libyca* nom. nud. – Parona, p. 25; Cenomanian, Libya [probably associated with *Praealveolina fide* Gohrbandt, 1966].

T 1969 *Reticulina reicheli* gen. et sp. nov. – Cuvillier et al., p. 209-224, pls. 1–3, 8–16, text-figs. 1–10, 12; “late Cenomanian – Turonian, possibly Senonian”, Sirte Basin, Libya [most likely Cenomanian] and ??Maastrichtian, Algeria.

1970 *Reticulinella reicheli* nom. subst. pro *Reticulina* Cuvillier et al., 1969 – Bonnefous et al., p. 39.

1970 *Reticulinella reicheli* – Deloffre & Hamaoui, fig. 5A; Late Cretaceous, Libya.

1972 *Ovalveolina ovum* (d’Orbigny) – Barr & Weegar, pl. 4, fig. 8; [*fide* Hamaoui, 1973]; Cenomanian, Libya [Cenomanian age is based on identification of *O. ovum*, but see discussion below].

1973 *Reticulinella reicheli* – Hamaoui, pl. 3, figs. 1-3; pl. 6, figs. 4-7; Late Cretaceous, Libya.

Non 1976 *Reticulinella* cf. *reicheli* – Luperto-Sinni, p. 323-324, pl. 45, figs. 7-16; Senonian, southern Italy [=*Reticulinella fleuryi* Cvetko et al., *fide* Schlagintweit et al., 2024a].

Non 1978 *Reticulinella* cf. *reicheli* – Luperto-Sinni & Richetti, pl. 50, figs. 1-4; Senonian, southern Italy [=*Reticulinella fleuryi* Cvetko et al., *fide* Schlagintweit et

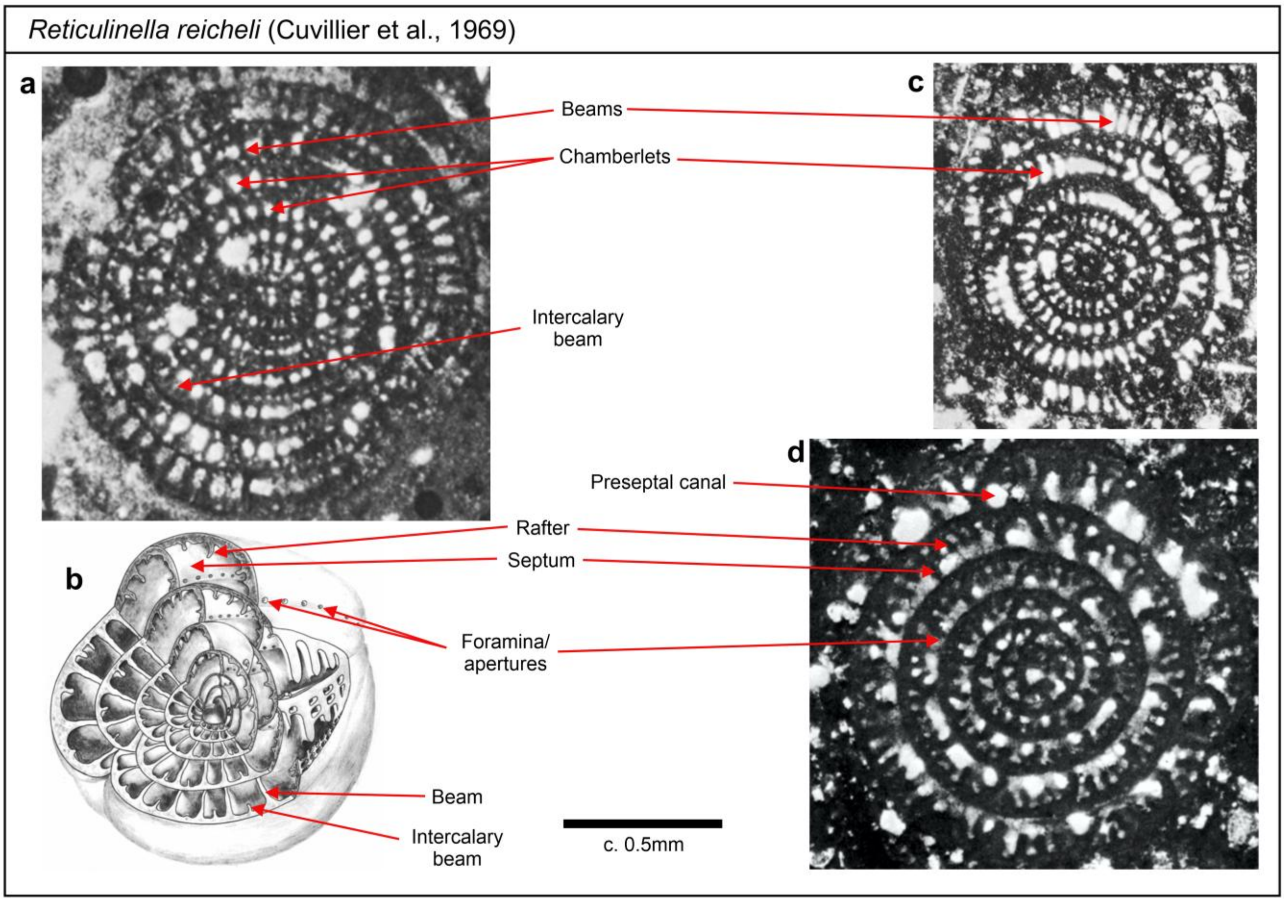


Fig. 8. Representative illustrations of *Reticulinella reicheli*: **a.** Axial section, Cuvillier et al. (1969, pl. 8, fig. 4, late? Cenomanian, Libya); **b.** Schematic reconstruction based on holotype, Cuvillier et al. (1969, fig. 2, Libya); **c.** Tangential section, Cuvillier et al. (1969, pl. 12, fig. 1, late? Cenomanian, Libya); **d.** Equatorial section with *possible* microspheric embryo, Cuvillier et al. (1969, pl. 10, fig. 1, late? Cenomanian, Libya).

al., 2024a].

1985 *Reticulinella reicheli* – Hamaoui in Schroeder & Neumann, p. 41-42, pl. 17, figs. 1-6; late Cenomanian-?Maastrichtian, global review [see discussion below].

Non 1990 *Reticulinella* cf. *reicheli* – Gušić & Jelaska, pl. 14, figs. 4-5; Campanian, Croatia [=*Reticulinella fleuryi* Cvetko et al., *fide* Cvetko Tešović et al., 2001].

Non 2012 *Reticulinella reicheli* – Orabi et al., fig. 3G; Cenomanian, Egypt [=probably an alveolinid, *fide* Schlagintweit et al., 2024a].

Non 2017 *Reticulina reicheli* – Ahmadi et al., pl. 1, fig. 1; late Albian – Cenomanian, Iranian Zagros [indeterminate (possibly a cuneolinid?), but not *R. reicheli*].

2018 *Reticulinella reicheli* – BouDagher-Fadel, pl. 5.4, fig. 3; Cenomanian-Turonian, Libya.

Non 2019 *Reticulinella reicheli* – Kiarostami et al., pl. 2, fig. l; Cenomanian, Iranian Zagros, [= *Rabanitina*, probably a new species, research ongoing].

Non 2021 *Reticulinella reicheli* – Yazdi-Moghadam & Schlagintweit, fig. 2H; middle – late Cenomanian, Iranian Zagros, [= *Rabanitina*, probably a new species, research ongoing].

Non 2021 *Reticulinella reicheli* – Dousti-Mohajer et al., pl. 3, fig. c; late Cenomanian, Iranian Zagros [probably not a foraminifera].

Non 2021 *Rabanitina basraensis* – Dousti-Mohajer et al., pl. 1, fig. k; late Cenomanian, Iranian Zagros, [considered by Simmons et al., 2024b to be *Reticulinella reicheli* but is probably a new species of *Rabanitina*, reasearch ongoing].

Non 2021 *Reticulinella reicheli* – Dehghanian & Afghah, fig. 8.7; late Cenomanian, Iranian Zagros, [= *Rabanitina*, probably a new species, research ongoing].

Non 2024a *Reticulinella reicheli* – Schlagintweit et al., p. 232-235, figs. 2-3; middle-late Cenomanian, Iranian Zagros, [= *Rabanitina*, probably a new species, research ongoing].

Reference Images: Cuvillier et al., pls. 1-3, 8-16, text-figs. 1-10, 12.

Taxonomy/Identity: Superficially, *Reticulinella* is a homeomorph of globular porcellaneous-walled alveolinids (e.g. *Ovalveolina*), although in addition to the fundamental nature of the wall, the subepidermal reticulate wall structure is distinct. Some aspects of higher taxonomy remain equivocal. Described as "*microgranulaire, calcaire imperforé avec de très rares éléments agglutinés*" by Hamaoui in Schroeder &

Neumann (1985) (= Order Lituolida), it is assigned to the Order Loftusiida ("*possessing a bilamellar wall differentiated into an imperforate outer layer, and a thicker inner layer that is perforate*" by Kaminski (2014).

R. reicheli is spherical to ovoid, planispiral involute, wall microgranular calcareous, with a reticulate subepidermal network with a series of radial and transverse partitions ("beams" and "rafters" *sensu* Hottinger, 2006) that are discussed below. Apertures multiple, a row of small round openings near the septum base (see Cuvillier et al., 1969 and Hamaoui in Schroeder & Neumann, 1985 for excellent descriptions and illustrations).

The terms "radial" and "transverse" to describe chamber partitions have been used somewhat inconsistently in the literature when describing *Reticulinella* and similar genera (e.g., see the type descriptions for the taxa included in Table 3). Hottinger (2006) clarified many aspects of LBF morphological terminology. "Radial" partitions run in the direction of growth and are referred to by Hottinger (2006) as "beams". Herein we use the term "beam" to point to a shell element that extends vertically from the base to the roof of a chamber and thus occupies the entire chamber height. Given the objective difficulties in defining this skeletal element in some Loftusiida, this definition does not distinguish whether a "beam" is a primary or secondary chamber partition. In *Reticulinella* they run (in the direction of growth) from one septum towards the next septum, but do not quite reach it, leaving a "preseptal passage". In some LBF, beam-like structures run between and parallel to the main beams but do not occupy the full chamber height (sometimes called "intercalary beams"; see Figure 7b). Transverse partitions on the other hand run parallel with the primary septa and perpendicular to "beams" in the roof of the chamber. They are minor structures compared with "beams" and are termed "rafters" (Hottinger, 2006). They run across the entire width of the chamber (roof).

In axial sections *Reticulinella* resembles *Ovalveolina ovum* (see comments below and compare Schroeder & Neumann, 1985; pl. 17, fig. 2 with text fig. 10) and *Barkerina* Frizzell & Schwartz 1950 (although that genus has no subepidermal network). *Rabanitina* Smout, 1956 is superficially similar but with a distinctive trochospiral initial stage.

There are three species of *Reticulinella* currently recognised: *R. reicheli, Reticulinella kaeveri* Cherchi, Radoičić & Schroeder, 1989 and *Reticulinella fleuryi* Cvetko, Gušić & Schroeder, 1997. *R. kaeveri* and *R. fleuryi* are only known from Turonian and younger strata and are smaller, with fewer whorls and lack a genuinely reticulate wall structure. For example, *R. kaeveri* lacks rafters (Arriaga et al., 2016). In this respect they probably merit removal from the genus *Reticulinella* (see Schlagintweit et al., 2023a for a discussion of *R. kaeveri*). They may have a closer affinity with the Barremian form *Praereticulinella cuvillieri* Deloffre & Hamaoui, 1970. There is also an approximately homeomorphic Late Cretaceous form, *Cuneospirella samnitica* Cherchi, Schroeder & Ruberti 2009. The morphological differences between all these taxa and *Barkerina barkerensis* Frizzel & Schwartz, 1950 and *O. ovum* is summarised in Table 3 and Table 4.

Confident Stratigraphic Range: not applicable.

Uncertain Stratigraphic Range: late Cenomanian – Maastrichtian.

The type material is from Libya (Lidam Formation) and Algeria (Cuvillier et al., 1969). The Algerian material is assigned a Maastrichtian age, but no supporting data is provided. Since location details are scant, this statement cannot be checked. On the other hand, the Lidam Formation of Libya (the primary location of type material) was considered by the authors as late Cenomanian? – Turonian, possibly younger. Most literature (e.g., Hassan & Kendall, 2014; Hallet & Lowes, 2016; Gumati, 2022) assigns the Lidam Formation to the Cenomanian, although definitive proof is lacking. Arguments that *Ovalveolina ovum* is present (Barr & Weegar, 1972; Hallet & Lowes, 2016) are most likely misidentifications of *R. reicheli* (Hamaoui, 1973) creating circular reasoning for the age of *R. reicheli* in the Lidam Formation. Nonetheless, on a regional basis the Lidam Formation seems most likely to be Cenomanian.

Based on the type description, a range of late Cenomanian – Maastrichtian is given and repeated without substantiation by Arnaud et al. (1981) and Hamaoui in Schroeder & Neumann (1985). Records from the middle – late Cenomanian part of the Sarvak Formation of the Iranian Zagros (Kiarostami et al., 2019; Dehghanian & Afghah, 2021; Yazdi-Moghadam & Schlagintweit, 2021; Schlagintweit et al., 2024) are considered to represent a new species of *Rabanitina*, research into which is ongoing. Its presence in the (late) Cenomanian, although likely, must be considered uncertain in the absence of unequivocal calibration. Older (e.g., Orabi et al., 2012; Gheiasvand et al., 2021 – Aptian) and younger records (e.g., Cvetko et al., 1997; Velić, 2007; Benmansour, 2023) are not supported by plausible illustration. Cvetko et al. (1997) and Cvetko Tešović et al. (2001) in discussions of the genus *Reticulinella* commented that *R. reicheli* is *"most abundant in the Middle Campanian*". No substantiation for this statement is provided, although Velić (2007) also commented on the presence of the species in the Campanian.

Geographic Distribution: Southern Neotethys, specifically North Africa. Records from the post-Cenomanian in areas such as the Adriatic are doubted to be this species.

Suborder **BIOKOVININA** Kaminski 2004 (diagnosis *sensu* Kaminski, 2014)

Superfamily **BIOKOVINOIDEA** Gušić 1977 (diagnosis *sensu* Loeblich & Tappan, 1987)

Family **CHARENTIIDAE** Loeblich & Tappan 1985a (diagnosis *sensu* Loeblich & Tappan, 1987)

Table 3. Comparison between the genus *Reticulinella* and morphologically similar but (mainly) unrelated genera.

Genus	Description / Differences from *Reticulinella*	Family/Superfamily/Suborder
Reticulinella Cuvillier et al. 1969 (* originally named *Reticulina*; renamed in Bonnefous et al., 1970)	– Spherical to ovoid, planispiral involute, wall microgranular calcareous, reticulate subepidermal network in roof of chamber with a series of radial (i.e., running in direction of growth) and transverse (i.e., running parallel to septa) partitions that do not extend to the previous septum leaving a narrow preseptal canal at the base of the septum into which the apertures open. Apertures multiple, a row of small round openings near the septum base. Overall morphology is similar to *Ovalveolina* (except the wall structure and which lacks transverse partitions).	**Loftusiidae** Agglutinated with imperforate outer and alveolar inner layer. Large, planispiral with elongate coiling axis. Chambers with interior beams and rafters and endoskeletal pillars. Aperture multiple.
Praereticulinella Deloffre & Hamaoui, 1970	– No preseptal canal at base of chamber (as in *Reticulinella* – the main structural difference between the two genera), instead a preseptal "tunnel" at the top of each chamber – Frequent "oblique lamellae" (rare in *Reticulinella*) – Frequent "horizontal lamellae" found in roof and base of chambers (rare in *Reticulinella* and in roof only) – Transverse partitions never exceed 4 per chamber (up to 6 in *Reticulinella*) – 11-18 chambers in first whorl (6-10 in *Reticulinella*) with growth rate increasing in adult stage – Septa wavy and thicker at base between adult chambers and thinned in contact with the chamber roof (not seen in *Reticulinella*), similar to the dicyclinids	
Barkerina Frizzel & Schwartz, 1950	– Somewhat more laterally compressed and umbilicate cf. *Reticulinella* – Only primary septation present with transverse partitions (i.e. no reticulate subepidermal network)	**?Nezzazatidae** Trochospiral or may become planispiral, median plate (may be digitate) in each chamber (not unequivocally proven in *Barkerina* hence "?"). Wall probably agglutinated, calcareous and imperforate. Aperture interiomarginal or areal, singular or multiple.
Cuneospirella Cherchi et al., 2009	– Only early stage is planispiral, bulbous/subglobular and strongly biumbilicate. Later stage rectilinear, biserial – Transverse partitions increase in number with growth and subdivide chambers into regular, higher-than-broad chamberlets with an arched preseptal passage	**?Spiroplectamminidae** Agglutinated (see Kaminski, 2004), but wall in *Cuneospirella* is calcareous microgranular hence "?"
Ovalveolina Reichel, 1936	– Only possesses partitions running in direction of growth with no transverse partitions, i.e., lacks the reticulate sub-epidermal network of *Reticulinella*	**Alveolinidae** Group of porcellaneous foraminifera (i.e., not microgranular)

Table 4. Comparison of morphological characteristics between 7 taxa of the genus *Reticulinella* or taxa of similar appearance. Note: estimates of stratigraphic ranges of these comparative taxa are not based on exhaustive assessment of occurrences in the literature, except *R. reicheli* as discussed herein. They have been assessed only from the type descriptions and more recent general summaries (e.g., Cvetko et al., 1997; Schlagintweit et al., 2023a, 2024a for the *Reticulinella* species and Hamaoui, 1973; Schroeder & Neumann, 1985 for other taxa) and should be treated with caution.

CHARACTERISTIC	*RETICULINELLA REICHELI*	*RETICULINELLA FLEURYI*	*RETICULINELLA ? KAEVERI*	*PRAERETICULINELLA* (e.g. *P. cuvillieri*)	*BARKERINA* (e.g. *B. barkerensis*)	*CUNEOSPIRELLA* (e.g. *C. samnitica*)	*OVALVEOLINA* (e.g. *O. ovum*)
Original description & provenance	Cuvillier et al. (1969), Lidam Formation of Sirte Basin, Libya; “attributed to Cenomanian-Turonian, probably lower Senonian” (subsurface core A1-104B)	Cvetko et al. (1997), Pučišća and upper Gornji Humac Formations, Brač Island, Croatia; lower-middle Campanian (outcrop)	Cherchi et al. (1989), Poćuta, Western Serbia; Turonian (outcrop)	Deloffre & Hamaoui (1970), Orgaña “cut”, Segre River, Spain; Barremian (outcrop)	Frizzel & Schwartz (1950), Walnut Clay unit, Texas, USA; late Albian (outcrop)	Cherchi et al. (2009), Matese sequences, Central Italy; Santonian (outcrop)	Reichel (1936), Ile Madame, France; Cenomanian-Turonian (outcrop)
Other significant illustrative descriptions	Hamaoui in Schroeder & Neumann (1985); Schlagintweit et al. (2024a)	Schlagintweit et al. (2024a)	Schlagintweit et al. (2023a)		Hamaoui (1973)		Neumann & Fourcade in Schroeder & Neumann (1985)
Higher taxonomy (Fam.)	Loftusiidae				Barkerinidae	?Spiroplectamminidae	Alveolinidae
Wall	Microgranular/agglutinated, calcareous						Porcellaneous
Overall shape	Globular	Globular to slightly fusiform, (** occasional tendency to uncoil)	Globular	Globular	Subglobular (slightly laterally compressed globular)	Subglobular followed by uncoiled biserial	Globular
Genus characteristics & differences cf. *Reticulinella*	Spherical to ovoid, planispiral involute, wall microgranular calcareous, reticulate subepidermal network in roof of chamber with a series of radial (in direction of growth) and transverse (parallel to septa) partitions (herein termed “beams” and “rafters” sensu Hottinger, 2006, respectively) that extend from one septum towards the next septum, but not quite reaching it, leaving a narrow preseptal passage at the base of the septum into which the apertures open. Apertures multiple, a row of small round openings near the septum base. Overall morphology is similar to *Ovalveolina* (except the latter genus has a porcellaneous wall structure and lacks transverse partitions = “rafters”).			No preseptal canal at base of chamber (as in *Reticulinella*), instead a preseptal “tunnel” at the top of each chamber; Frequent “oblique lamellae” (rare in *Reticulinella*); Frequent “horizontal lamellae” found in roof and base of chambers (rare in *Reticulinella* and in roof only); Transverse partitions (“rafters”) never exceed 4 per chamber (up to 6 in *Reticulinella*); 11-18 chambers in first whorl (6-10 in *Reticulinella*) with growth rate increasing in adult stage; Septa wavy and thickened at base between adult chambers and thinned in contact with the chamber roof (not seen in *Reticulinella*), similar to the dicyclinids	Somewhat more laterally compressed and umbilicate cf. *Reticulinella*; Only primary septation present with radial (i.e. “beams” herein, incorrectly described as “transverse”) partitions (i.e. no “rafters” therefore no reticulate subepidermal network)	Only early stage is planispiral, bulbous/subglobular and strongly biumbilicate. Later stage rectilinear, biserial; Partitions (“beams” herein) increase in number with growth and subdivide chambers into regular, higher-than-broad chamberlets with an arched preseptal passage. No transverse partitions (“rafters”)	Only possesses partitions running in direction of growth with no transverse partitions, i.e., lacks the reticulate sub-epidermal network of *Reticulinella*

Dimensions (mm) (De = diameter equatorial; Da = diameter axial; Dp = diameter proloculus)	De = 0.61-1.60 (**0.54-1.45) Da = 0.60-1.60 (*1.15) Dp = 0.075-0.10 (** =0.14-0.2)	De = 0.29-0.46 (** up to 0.57) Da = 0.34-0.38 (** 0.30-0.40) Dp = 0.07-0.13 (** 0.06-0.10)	* De = 0.39 (max 0.47) (*** 0.2-0.42) Da = 0.32 (*** 0.19-0.31) Dp = 0.05-0.07 (*** 0.03-0.07)				
Chambers per whorl (first whorl = W_1, second whorl = W_2 etc.)	W_1 = 6-7; W_2 = 8; W_3 = 10; W_4 = 11; W_5 = 12	W_3 = 12-15 (final whorl) (** c.12)	* W_3 = 14-16 (final whorl) (*** 9-15)				
Length of chambers per whorl (mm) (first whorl = W_1, second whorl = W_2 etc.)	W_1 = 0.05; W_2 = 0.065-0.075; W_3 = 0.10; W_4 = 0.12-0.16; W_5 = 0.15-0.17; W_6 = 0.20-0.25						
Height of chambers per whorl (mm) (first whorl = W_1, second whorl = W_2 etc.)	* W_1 = 0.025-0.05 W_{12} = 0.15	W_1 = 0.03 W_3 = 0.05-0.06	* W_1 = 0.03 W_3 = 0.05				
No. of whorls	>12* (** 5)	3 (**2)	* 3 (*** 2-3)				
No. of “primary transverse partitions” [sensu Cvetko et al. (1997) but “beams” herein] in last chamber	* c. 20	c. 14 (** c.13-14)	* c. 10-12				
“Secondary transverse partitions” [sensu Cvetko et al. (1997) but “rafters” herein]	* Well developed	Slightly developed	* Slightly developed				
Stratigraphic Range (see caption)	Cenomanian	Middle Coniacian-late Maastrichtian	Upper middle – ?lower late Turonian	Barremian	Albian - ?Cenomanian/ Turonian	Santonian (?late Turonian ancestor)	Middle-late Cenomanian
Comments	* No data given in type description and/or data from Cvetko et al. (1997) ** Data from Schlagintweit et al. (2024a; Iran)	** Data from Schlagintweit et al. (2024a)	* No data given in type description and/or data from Cvetko et al. (1997) *** Data from Schlagintweit et al. (2023a; Iran)				

Genus ***Charentia*** Neumann 1965 (see Table 1 for diagnosis)

Charentia cuvillieri **Neumann, 1965**

Figure 9

? 1956 *Cribrostomoides paralens* n. sp. – Omara, p. 887, pl. 103, figs. 1-3; text figs. 3-3, 4d, 4e; Cenomanian, Egypt – *fide* Loeblich & Tappan (1985; assigned to *Charentia*) [examination of the types has so far been unable to demonstrate that this species is the (senior) synonym of *C. cuvillieri*].

T 1965 *Charentia cuvillieri* n. gen., n. sp. – Neumann, p. 93-95, pl. 2, figs. 6-12; middle Cenomanian, France.

1965 *Haplophragmoides greigi* (Henson) – Hofker, p. 185, pl. 2, figs. 1—7, pl. 3 figs. 1—3; late Aptian-early Albian, Spain.

1965 *Haplophragmoides persica* n. sp. – Gollesstaneh, p. 149, pl. 13, figs. 1-5; pl. 14, figs. 1-7; Barremian-Aptian, Iranian Zagros (*fide* Schlagintweit, 2014).

1966 *Hemicyclammina praesigali* n. sp. – Banner, p. 216; Aptian-Albian, Spain (*fide* Loeblich & Tappan, 1985).

1967 *Charentia cuvillieri* – Hottinger, pl. 9, figs. 1-4; Cenomanian, Spain.

1968 *Tonasia evoluta* n. gen., n. sp. – Gorbachik, p. 8-9, pl. 2, figs. 1-5; Berriasian, Crimea.

? 1973 *Charentia cuvillieri* – Kerdany et al., p. 93, pl. 1, figs. 9-12; Cenomanian, Gulf of Suez [non-diagnostic external views only].

? 1973 *Charentia cuvillieri* – Berthou, pl. 1, figs 2, 2a; early Cenomanian, Portugal.

1974 *Charentia cuvillieri* – Saint-Marc, p. 214, pl. I, figs. 9-11; middle Albian, Lebanon (total range reported as middle – late Albian).

1974 *Charentia kosovica* n. sp. – Radoičić, p. 143, pl. XII, figs. 1-5; late Cenomanian, Kosovo (*fide* Rey et al., 1977).

1976 *Navarella*? sp. – Luperto Sinni, pl. 46, fig. 4; Late Cretaceous, southern Italy.

1977 *Charentia cuvillieri* – Rey et al., pl. 3, figs. 11-14; late Albian, Portugal.

? 1978 *Mayncina hasaensis* n. sp. Basha, p. 77, pl. 2, figs. 7-11; late Cenomanian, Jordan.

1979 *Charentia cuvillieri*- Rey et al., pl. XV, figs. 11-15; late Albian, Portugal.

1980 *Charentia cuvillieri* – Arnaud-Vanneau, p. 353, pl. 50, figs. 5-7, 10-11; pl. 76, figs. 7-11; text fig. 124; Barremian-early Aptian, French Jura.

? 1983 *Charentia cuvillieri* – Hassanien & Sigal, pl. 1, figs. 11-12; Cenomanian, Egypt [indeterminate illustration].

1984 *Charentia cuvillieri* – Arnaud-Vanneau & Darsac, pl. 2, figs. 19, 24; Barremian – early Aptian; French Jura.

1984 *Charentia cuvillieri* – Canerot, pl. 2, fig. 2; early Cretaceous, Spain.

1984 *Charentia cuvillieri* – Dufaure et al., pl. 1, figs. 1-7; Cenomanian, southern Libya.

1985a *Charentia cuvillieri* – Loeblich & Tappan, p. 96, pl. 3, figs. 1-13; middle Cenomanian, France.

1985 *Charentia cuvillieri* – Arnaud-Vanneau in Schroeder & Neumann, p. 17-18, pl. 3, figs. 1, (“holotype”), 2-11; middle Cenomanian, France.

1985 *Nummoloculina*? sp. – Weidich, pl. 3, fig. 8; early – middle Cenomanian, Austria.

1986 Lituolidae aff. *Navarella* sp. – Bouyx & Villain, fig. 7k; Late Cretaceous, Afghanistan.

1987 *Charentia cuvillieri* – Arnaud-Vanneau et al., fig. A 25 (19, 24); Barremian – early Aptian, French Jura.

1987 *Charentia cuvillieri* – Loeblich & Tappan, p. 89, pl. 78, figs. 1-10; middle Cenomanian, France.

1987 *Charentia evoluta* (Gorbachik) – Loeblich & Tappan, p. 89, pl. 79, figs. 1-3; Valanginian, Crimea.

1988 *Charentia cuvillieri* – Bucur, pl. I, figs. 18-19; Berriasian – Hauterivian, Romania.

1988 *Charentia cuvillieri* – Bucur & Cociuba – pl. I, fig. 29; Early Cretaceous Romania.

? 1989 *Charentia cuvillieri* – Cherif et al., pl. 1, figs. 11-12; middle Cenomanian – middle Turonian, Egypt [indeterminate external views only].

Non 1990 *Charentia* cf. *cuvillieri* – Weidich & Al-Harithi, p. 602, pl. 4, figs. 25-27; middle Albian, Jordan. [indeterminate but probably not *Charentia*].

1991 *Charentia* sp. - Altıner, pl. 4, figs. 5-7; late Kimmeridgian, northern Türkiye.

1991 *Charentia cuvillieri* – Altıner, pl. 7, fig. 18; Berriasian?, northern Türkiye.

1991 *Charentia cuvillieri* – Schlagintweit, p. 34, Pl. 9, fig. 6-9, Aptian, Austria.

1991 *Charentia cuvillieri* – Schlagintweit & Weidich, pl. 2, fig. 2; late Albian – middle Cenomanian, Austria.

1992 *Lituola*? sp. – Schlagintweit, p. 331, pl. 1, figs. 6-8; middle Coniacian, Austria.

1994 *Charentia cuvillieri* – Bodrogi et al., pl. 13, fig. 9 & 11; Early Cretaceous, Austria & Hungary.

1994 *Charentia cuvillieri* – Chiocchini et al., pl. 31, figs. 26-29; Berriasian – Valanginian, central Italy.

1995 *Charentia* cf. *cuvillieri* – Abdallah et al., fig. 19(8); Cenomanian, Tunisia.

1995 *Nummofallotia apula* Luperto-Sinni – Abdallah et al., fig. 19(7); Cenomanian, Tunisia.

1996 *Charentia evoluta* – Bucur et al. pl. 1, figs. 9-10, Tithonian, Sicily.

? 1996 *Charentia* aff. *cuvillieri* – Kirmaci et al., pl. 4, fig. 12; Barremian – early Aptian, north-west Türkiye.

1998 *Charentia cuvillieri* – Cherchi et al., pl. IV; figs. 3 & 5; early Aptian, Yemen.

Non 1998 *Charentia cuvillieri* – El-Sheikh & Hewaidy, pl. 1, fig. 8; late Cenomanian, Egypt [= *Hemicyclammina whitei* (Henson)].

1999 *Charentia cuvillieri* – Schlagintweit & Ebli, p. 398, pl. 5, figs. 1-3; late Tithonian – early Valanginian.

Non 2000 *Charentia cuvillieri* – Aguilera-Franco, p. 164; late Cenomanian, southern Mexico [septa appear too thick and chambers too numerous].

2004 *Charentia cuvillieri* – Ivanova & Kołodziej, fig. 1 (A); Berriasian – Valanginian, Polish Carpathians.

2004 *Charentia cuvillieri* – Ettachfini & Andreu, fig. 7H; late Cenomanian, Morocco.

2004 *Charentia cuvillieri* – Neagu & Cîrnaru, p. 281, pl. 2, figs. 15-18; pl.4, figs. 13-14; early Aptian, Romania.

2005 *Charentia cuvillieri* – Krobicki & Olszewska, p. 220, fig. 3D; reworked, Polish Carpathians.

2005 *Charentia cuvillieri* – Schlagintweit & Wagreich, p. 117, pl. 1, fig. 6; early Cenomanian, Austria.

2005 *Charentia* cf. *cuvillieri* – Lukeneder & Schlagintweit, fig. 4(1); Hauterivian, Austria.

2006 *Charentia cuvillieri* – Albrich et al., pl. 3, fig. 5; early Valanginian, Spain.

2006 *Charentia evoluta* – Kobayashi & Vuks, fig. 4(27-32); Tithonian-Berriasian, Japan.

2006 *Charentia cuvillieri* – Ettachfini, pl. 16, figs. 7-9; late Cenomanian, Morocco.

? 2006 *Melathrokerion spirialis* Gorbachik – Kobayashi & Vuks, fig. 4(35-45); Tithonian-Berriasian, Japan.

2007 *Charentia cuvillieri* – Schroeder et al., pl. 1, figs. 4-5; late Aptian, Switzerland.

2007 *Charentia evoluta* – Krajewski & Olszewska, p. 299, figs. 5g-h; late Kimmeridgian-Valanginian, Crimea.

? 2007 *Melathrokerion spirialis* – Krajewski & Olszewska, p. 299, figs. 5i; late Tithonian -Valanginian, Crimea.

2008 *Charentia* cf. *cuvillieri* – Hosseini & Conrad, pl. 5, fig. F; Berriasian, Iranian Zagros.

2008 *Charentia cuvillieri* – Sudar et al., fig. 4 (3) pars; fig. 9 (1); late Barremian – early Aptian, Serbia.

2009 *Charentia* cf. *cuvillieri* Neumann – Villalonga, p. 100, pl. 4, figs. 7, 9; Campanian, Spain.

? 2009 *Charentia cuvillieri* – Ismail et al., p. 401, pl. 1, figs. 4-5; Cenomanian, Eastern Desert, Egypt [indeterminate external views only].

2010 *Charentia cuvillieri* – Carevic et al., fig. 5 (9-11); late Barremian – early Aptian, Serbia.

2010 *Charentia cuvillieri* – Ivanova & Kołodziej, p. 9, pl. 3, fig. 5-10; reworked, Polish Carpathians.

2010 *Charentia* sp. – Jamalian et al., fig. 11n-o; Neocomian, Iranian Zagros.

2010 *Charentia cuvillieri* – Schroeder et al., fig. 11(8); early Aptian, Iranian Zagros.

Non 2012 *Charentia* cf. *cuvillieri* – Abyat et al., pl. 1, fig. E; Neocomian, Iranian Zagros [uncertain, but lacks the chroma and thin septa of *Charentia*].

2012 *Charentia cuvillieri* – Chiocchini et al., pl. 174; late Berriasian -early Valanginian, central Italy.

? 2012 *Charentia cuvillieri* – Lazar et al., pl. II, fig. 1; pl. III, fig. 5; Aptian, Romania.

? 2012 *Charentia cuvillieri* – Rami et al., p. 67, fig. 6 (7); Barremian – Aptian, central Iran.

? 2012 *Charentia cuvillieri* – Ghanem et al., fig. 6d (26); early Cenomanian, Syria.

2013 *Charentia cuvillieri* – Carevic et al., figs. 14 C-D; fig. 16 B; Barremian – early Aptian, Serbia.

2013 *Charentia cuvillieri* – Hfaiedh et al., fig. 12J; late Aptian, Tunisia.

? 2013 *Charentia cuvillieri* – Shahin & Elbaz, p. 266, pl. 1, fig. 30; Cenomanian, Egypt [indeterminate external view only].

? 2013 *Charentia cuvillieri* – Ghanem & Kuss, fig. 8(12, 16, 17); early Aptian, Syria.

2014 *Charentia cuvillieri* – Kobayashi & Wernli, p. 72, pl. III, figs. 11-21; Berriasian – Valanginian, Japan.

2014 *Daxia cenomana* Cuvillier & Szakall – Danelian et al., fig. 9(2); Cenomanian, Armenia.

2014 *Charentia* sp. – Bucur et al., pl. 5A; Berriasian – Valanginian, Romania.

? 2014 *Charentia cuvillieri* – Khodashenas et al., fig. 3P; Barremian, north-east Iran.

2015 *Charentia cuvillieri* – Maksoud, p. 134-138, pl. 39, figs. A-S; late Barremian – early Aptian, Lebanon.

2015 *Charentia evoluta* – Pleş et al., fig. 3m-n; Kimmeridgian?-Tithonian; Romania.

2015 *Vidalina radoicicae* Cherchi & Schroeder – Brčic, pl. 5.6c; late Cenomanian, Croatia.

? 2015 *Charentia cuvillieri* – Babazadeh & Dehej, fig. 6j-k, fig. 7o-p; Early Cretaceous, central Iran.

? 2015 *Charentia* cf. *evoluta* – Rahiminejad & Hassani, fig. 6P (*non* M); Cenomanian, central Iran.

2016 *Charentia cuvillieri* – Schlagintweit et al., fig. 6E-F; late Aptian, Spain.

? 2016 *Charentia* cf. *cuvillieri* – Rahiminejad & Hassani, fig. 3b; Aptian, central Iran.

Non 2016 *Charentia* cf. *cuvillieri* – Afghah et al., pl. 2, fig. 3; Barremian, Iranian Zagros [indeterminate planispiral form, but chambers too numerous and septa too thick for *Charentia*].

? 2017 *Charentia* sp. – Gutierrez-Alejandro et al., fig. 8A, D; Barremian, Mexico.

2018 *Charentia cuvillieri* – Luger, p. 57, pl. 1, fig. 10, pl. 10, figs. 3, 6, 8; Albian (also reported from early Cenomanian), Somalia.

? 2018 *Charentia cuvillieri* – Andrade, pl. M8, fig. 5; Cenomanian, Portugal.

? 2018 *Charentia* cf. *cuvillieri* – Rostami et al., pl. 2i; Valanginian, Persian Gulf.

2019 *Charentia cuvillieri* – Bucur et al., fig. 15a; late Barremian – early Aptian, central Iran.

2019 *Charentia cuvillieri* – Özkan & Altıner, fig. 5 (16-18); early Aptian, Turkish Arabian Plate.

2020 *Charentia cuvillieri* – Kaya, pl. D, figs. D-F; Cenomanian, Tajik Basin, Central Asia.

2020 *Charentia cuvillieri* – Simmons et al., figs. 9.5-9.6; middle Cenomanian, Turkish Arabian Plate.

2020 *Charentia cuvillieri* – Bucur et al., fig. 8A; Berriasian, Serbia.

2020 *Charentia cuvillieri* – Al-Mamory & Al-Dulaimi, pl. B, fig. 5; Albian, northern Iraq.

2020 *Charentia cuvillieri* – Gheiasvand et al., fig. 9F; late Barremian – Aptian, central Iran.

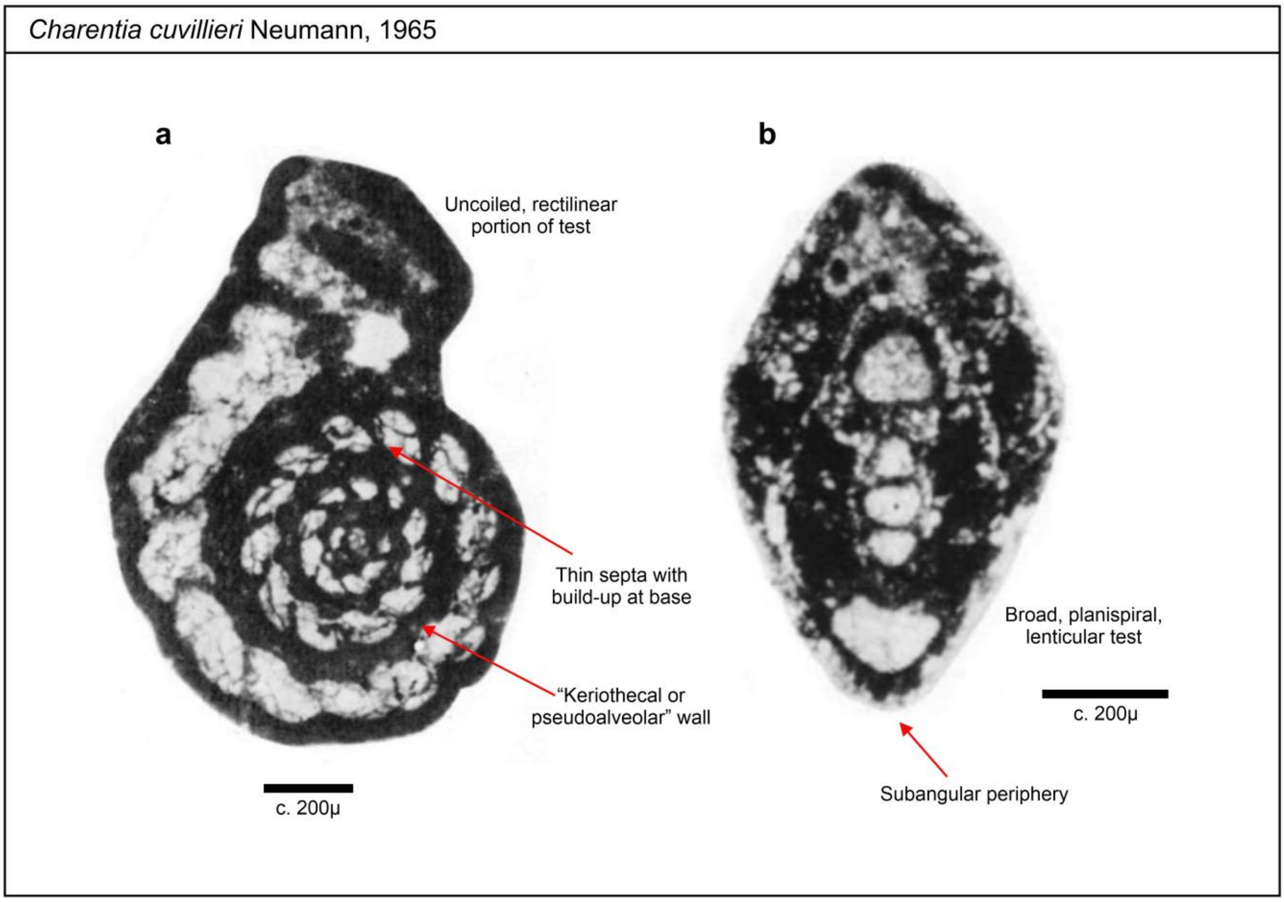


Fig. 9. Representative illustrations of *Charentia cuvillieri*: **a.** Equatorial section, Neumann (1965, holotype, pl. 2, fig. 1c, France); **b.** Axial section, Schroeder & Neumann (1985, pl. 3, fig. 3, France) (Reproduced after Simmons & Bidgood, 2023).

2020 *Navarella* sp. – Sha et al., fig. 9c; Campanian, Western Tibet.
2020 *Charentia cuvillieri* – Randazzo et al., fig. 12L; reworked, Sicily.
? 2021 *Charentia cuvillieri* – Al-Hassani & Al-Dulaimi, pl. A, fig. 3; Berriasian, southern Iraq.
2022 *Charentia cuvillieri* – Andronache et al., fig. 4I-L; Berriasian – Valanginian, Romania.
2022 *Charentia cuvillieri* – Hassani, fig. 8(1); early Aptian, central Iran.
Non 2022 *Charentia cuvillieri* – Khazaal & Shakir, pl. 2B; Berriasian – Valanginian, southern Iraq [indeterminate planispiral form – too many small chambers for *C. cuvillieri*].
2023 *Charentia cuvillieri* – Simmons & Bidgood, p. 70, fig. 21; Late Jurassic – late Cenomanian, global review.
2024b *Charentia cuvillieri* – Schlagintweit et al., fig. 4K; reworked, Slovenia.
2024 *Charentia cuvillieri* – Skupien et al., fig. 6D; Tithonian – Berriasian, Czech Republic.
2024 *Charentia cuvillieri* – Sun & Schlagintweit, fig. 5; late Barremian – early Aptian, Iran.
2024 *Charentia* cf. *cuvillieri* – Sun & Schlagintweit; fig. 4; Campanian, Tarim Basin & Croatia.
2025 *Charentia cuvillieri* – Schlagintweit et al., fig. 5(6, 10-12, 15); Cenomanian, Tarim Basin, China.

Reference Images: Arnaud-Vanneau in Schroeder & Neumann (1985) pl. 3. See also Loeblich & Tappan (1985) pl. 3 and Maksoud (2015) pl. 41.

Taxonomy/Identity: This is one of the most widely reported (and illustrated) LBF from the Late Jurassic – Cretaceous of Neotethys. The characteristics and history of this broadly lenticular, planispiral to uncoiling, pseudokeriothecal-walled and widely recorded species are summarised by Arnaud-Vanneau in Schroeder & Neumann (1985), Simmons & Bidgood (2023) and Sun & Schlagintweit (2024). Chomata-like wall thickenings below the apertural foramen of earlier chambers characterize *Charentia*, along with thin septa. The species (and genus) has similarities with several other taxa and one of its peculiarities is the variation of the shape of the aperture throughout ontogeny from a triangular arch to a three-pronged opening to a larger vertical part to eventually a narrow slit along the apertural face (see Hassanien & Sigal, 1983; Luger, 2018).

Everticyclammina greigi (Henson) is superficially similar but readily distinguishable by its alveolar wall. The genus *Comaliamma* Loeblich & Tappan is also similar but has simple, rather than canaliculate walls and septa. The similar Maastrichtian genus *Navarella* Ciry & Rat is mainly streptospirally coiled (before uncoiling) and with a broadly-rounded periphery.

Arnaud-Vanneau in Schroeder & Neumann (1985) recognised two morphotypes of *C. cuvillieri* – a large form (1.2 – 1.4mm diameter) and a small form (0.78 – 0.83mm diameter). The two forms also appear to have different stratigraphic ranges: small forms from around the Jurassic/Cretaceous boundary (where they are often referred to as *Charentia evoluta* (Gorbachik) and possibly *Melathrokerion spirialis* Gorbachik), and the large forms from the Cenomanian – Campanian. However, Schlagintweit & Wagreich (2005; p. 117) state that these smaller morphotypes "*can hardly be distinguished from* C. cuvillieri". An even smaller form – *Charentia nana* (Arnaud-Vanneau, 1980) with a diameter between 0.365 – 0.480mm has been described, although a pseudokeriothecal wall structure for this form remains to be demonstrated. Herein the species is treated *sensu lato* that includes small forms in the Late Jurassic and Early Cretaceous, and larger forms known from the Late Cretaceous.

Cribrostomoides paralens Omara from the Cenomanian of Egypt (Omara, 1956) is a possible (senior) synonym, as suggested by Loeblich & Tappan (1985a). The authors have observed CT-scan images of the type specimens of *C. paralens* (generated by the Natural History Museum, London) but did not observe convincing evidence of either a pseudokeriothecal wall or the characteristic aperture forms.

Other ostensibly Cenomanian taxa referred to *Charentia* include *C. kosovica* Radoičić (a likely synonym of *C. cuvillieri*) and *C. granulosa* Kerdany & Eissa, *C. hasaensis* Basha and *C. rummanensis* Basha, but their relationship to *C. cuvillieri* (either morphotype) or even to the genus is debatable and requires re-examination of all type material. Synonymy with *Hemicyclammina whitei* (Henson) cannot be excluded. Some older species assigned to *Charentia* – *Charentia arabica* Tobolina et al. in Kuznetsova et al., 1996 and *Charentia atlasica* Fares 1975 remain poorly known precluding meaningful comment.

Confident Stratigraphic Range: late Kimmeridgian – Campanian. Common throughout the Early Cretaceous – Cenomanian.

Uncertain Stratigraphic Range: not applicable.

Using a *sensu lato* concept of this species means that it is reported with a very long stratigraphic range. The oldest records are from the late Kimmeridgian of Crimea (Krajewski & Olszewska, 2007) and northern Türkiye (Altıner, 1991), and the youngest from the Campanian of the Tarim Basin and Spain (Sun & Schlagintweit, 2024). There are plentiful records from the Berriasian – Cenomanian.

The use of *C. cuvillieri* as a biozonal marker (e.g. for the Berriasian – Al-Hassani and Al-Dulaimi, 2021) is inappropriate, except at the most local level. The species, especially when treated *sensu lato*, is long ranging.

Geographic Distribution: Throughout its entire stratigraphic range this species is widespread across the northern and southern margins of Neotethys with records as far east as Japan, the Tarim Basin, the Tajik Basin and Tibet. Only records from the Caribbean (Mexico) are uncertain. Within the Cenomanian most records are from the circum-Mediterranean and the Arabian Plate, although a new record (Schlagintweit et al., 2025) demonstrates occurrence in the Tarim Basin, China.

Genus ***Moncharmontia*** De Castro 1967 (see Table 1 for diagnosis)

Moncharmontia apenninica (De Castro, 1966)

Figure 10

T 1966 *Neoendothyra apenninica* De Castro, p. 328, pls. I-III (*non* pl. III, figs. 4-8), text figs. 5-6; Turonian-Senonian, Italy.

1967 *Moncharmontia apenninica* De Castro *nom. nov*., p. 475.

1967 *Neoendothyra apenninica* – Bignot & Guernet, p. 264-265, pl. 1, figs. 8-11; early Senonian, Greece.

1970 *Moncharmontia apenninica* – Fleury, pl. 2, fig. 4; Senonian, Greece.

1974 *Montcharmontia apenninica* (sic) – Bignot & Poisson, pl. III, fig. 6; Cenomanian, Turkish Taurides.

1976 *Moncharmontia apenninica* – Luperto-Sinni, pl. 48, figs. 6-7; Senonian, Italy.

1977 *Moncharmontia apenninica* – Chiocchini & Mancinelli, p. 133, pl. XL, fig. 1; pl. XLI, fig. 1; Senonian, central Italy.

1978 *Moncharmontia apenninica* – Luperto-Sinni & Ricchetti, pl. 45, figs. 6-7; Late Cretaceous, Italy.

1982 *Montcharmontia apenninica apenninica* (sic) - Altıner & Decrouez, pl. 7, fig. 7; Senonian, Turkish Taurides.

1985 *Moncharmontia apenninica* – Bilotte, p. 369, pl. 5, fig. 1; late Cenomanian, Pyrenees.

1988 *Moncharmontia apenninica* – Drobne et al., pl. 24, figs. 6, 7 [= *Fleuryana adriatica* De Castro et al. *fide* De Castro et al., 1994].

? 1988 *Moncharmontia apenninica* – Sartorio & Venturini, p. 119; early Senonian, Italy [= *Fleuryana adriatica* De Castro et al. *fide* De Castro et al., 1994].

1989 *Moncharmontia apenninica* – Drobne et al., pl.3, figs. 10, 11, 12 [= *F. adriatica fide* De Castro et al., 1994].

1989 *Moncharmontia apenninica* – Molinari- Paganelli & Tilia Zuccari, Fig. 15 [= *F. adriatica fide* De Castro et al., 1994].

1990 *Moncharmontia* ex gr. *apenninica* – Gušić & Jelaska, pl. 14, figs. 10-11 (*non* fig. 9); Campanian, Croatia.

1990 *Moncharmontia apenninica* – Sribar & Plenicar, pl. 5, fig. 4; Coniacian – early Santonian, Slovenia.

1992 *Moncharmontia apenninica* – Schlagintweit, p. 334, pl. 1, figs. 10-12, text fig. 1; late Turonian – Santonian,

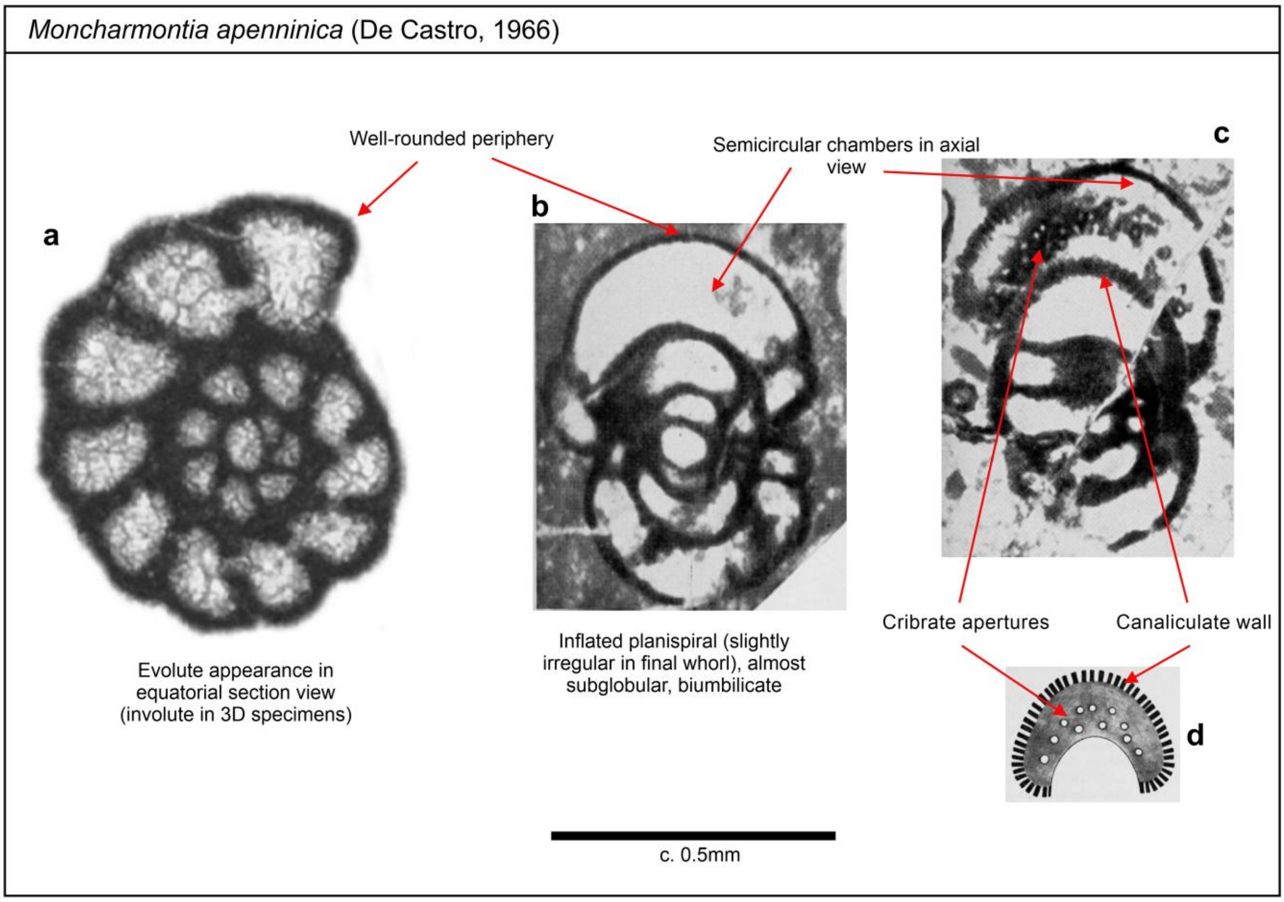


Fig. 10. Representative illustrations of *Moncharmontia apenninica*: **a** Equatorial section, Arriaga et al. (2016, fig. 5(3), Italy); **b** Axial section, De Castro (1966, pl. III, fig. 9, Italy); **c** Subaxial section, De Castro (1966, pl. 2, fig. 1, Italy); **d** Apertural face, De Castro (1966, fig. 6B) (Modified after Simmons & Bidgood, 2023).

Austria.

1992 *Moncharmontia apenninica* – Foglia, pl. 3, figs. 8, 11; late Turonian – early Senonian, southern Italy.

1994 *Moncharmontia apenninica* – Chiocchini et al., pl. XXII, figs. 16-19; early Senonian; central Italy.

1994 *Moncharmontia apenninica* – Ramirez del Pozo & Martin-Chivelet, pl. 1, fig. 5; Late Cretaceous, Spain.

1998 *Moncharmontia apenninica* – Koch et al., pl. 2, fig. 7; Turonian, Slovenia [age in part based on occurrence of *M. apenninica*].

? 2000 *Moncharmontia apenninica* – Benedetti et al., fig. 53; early Senonian, north-east Italy.

Non 2000 *Moncharmontia apenninica* – Aguilera-Franco, p. 165; middle – late Cenomanian, Mexico [indeterminate, but number of chambers far too numerous].

2001 *Moncharmontia apenninica* – Cvetko Tešović et al., fig. 7 (G-I); Campanian, Croatia.

2003 *Moncharmontia apenninica* – Polavder, fig. 4(12); early Campanian, Serbia.

? 2003 *Moncharmontia apenninica* – Korbar & Husinec, p. 177, pl. 2, fig. 1; Turonian – ?Coniacian; Croatia.

Non 2003 *Moncharmontia apenninica* – Aguilera-Franco, pl. 1, fig. 4 ; Cenomanian, Mexico [= *Biconcava bentori*].

Non 2004 *Moncharmontia* aff. *apenninica* – Ettachfini & Andreu, fig. 8D; late Cenomanian, Morocco [=*Biconcava bentori*].

2005 *Montcharmontia apenninica* (sic) – Vaziri et al., pl. 2, figs. 14-15; Santonian – Campanian/Maastrichtian?, central Iran.

Non 2006 *Moncharmontia* aff. *apenninica* – Ettachfini, pl. 16, fig. 10; late Cenomanian, Morocco [=*Biconcava bentori*].

2008 *Moncharmontia apenninica* – Chiocchini et al., p. 123, pl. XXIX, fig. 3; pl. XXX, fig. 1; late Turonian – Santonian, central Italy.

2008 *Moncharmontia apenninica* – Frijia & Parente, fig. 4i; Turonian, southern Italy.

2008 *Moncharmontia apenninica* – Checconi et al., pl. 1, figs. 4-7; Coniacian – early Campanian, southern Italy.

? 2008 *Moncharmontia apenninica* – Schlüter, fig. 2.3d; Campanian, southern Italy.

? 2008 *Moncharmontia apenninica* – Schlüter et al., fig. 3d; Campanian, southern Italy.

2011 *Montcharmontia apenninica* (sic) – Vaziri, pl. 2, figs. N-O; Santonian – Campanian/Maastrichtian?, central Iran.

2011 *Moncharmontia apenninica* – Jez et al., fig. 7(d, f); Coniacian-Santonian, Slovenia.

2012 *Moncharmontia apenninica* – Chiocchini et al., pl. 130, figs. 1-12; Coniacian-Santonian (range shown to begin in late Turonian), Central Italy.

2012 *Moncharmontia apenninica* – Rahimpour-Bonab et al., fig. 8(N-O); Turonian, Iranian Zagros [age in part based on presence of *M. apenninica*].

Non 2012 *Moncharmontia apenninica* – Ghanem et al., fig. 6d (11, 19); early Cenomanian, Syria [=*M. compressa*].

2013 *Moncharmontia apenninica* – Rahimpour-Bonab et al., fig. 8(Q); Turonian, Iranian Zagros [age in part based on presence of *M. apenninica*].

? 2013 *Moncharmontia apenninica* – Shahin & Elbaz, p. 270; pl. 1, figs 32-33; Cenomanian, Egypt [indeterminate external views only].

2014a *Moncharmontia apenninica* – Omidvar et al., pl.1, figs. R-S; Turonian, Iranian Zagros [age in part based on presence of *M. apenninica*].

2014b *Moncharmontia apenninica* – Omidvar et al., fig. 4(4-6); Turonian, Iranian Zagros [age in part based on presence of *M. apenninica*].

2015 *Moncharmontia apenninica* – Frijia et al., fig. 8(H-I); Turonian-Campanian, Italy.

2015 *Moncharmontia apenninica* – Solak et al., fig. 9F-G; Coniacian – Santonian, Turkish Taurides.

2016 *Moncharmontia apenninica* – Arriaga et al., p. 14, fig. 5; Turonian, southern Italy.

2017 *Moncharmontia apenninica* – Solak et al., fig. 11(A-B); late Campanian, Turkish Taurides.

2017 *Moncharmontia apenninica* – Koç, fig. 10(A1-3); age uncertain in text and figure caption, Turkish Taurides.

? 2018 *Moncharmontia apenninica* – Omidi et al., pl. 2, fig. 4; Turonian, Iranian Zagros [age in part based on the presence of *M. apenninica*].

2019 *Montcharmontia apenninica* (sic) – Özkan & Altıner, fig. 9(19-23); Turonian [=?Cenomanian *fide* Simmons et al., 2020], Turkish Arabian Plate.

2019 *Moncharmontia apenninica* – Solak et al., fig. 10(A-B); late Campanian, Turkish Taurides.

? 2019 *Moncharmontia apenninica* – Le Goff et al., fig. 5C; Campanian, Albania.

2020 *Moncharmontia apenninica* – Solak et al., fig. 14(F-G); Turonian, Turkish Taurides.

2020 *Moncharmontia apenninica* – Sinanoğlu et al., pl. 1, figs. 8-9; Maastrichtian, Türkiye.

2021 *Moncharmontia apenninica* – Sinanoğlu, pl. 1, fig. 8; Maastrichtian, Türkiye.

2021 *Moncharmontia apenninica* – Bagherpour et al., fig. 12e-f; Turonian, Iranian Zagros (age in part based on the presence of *M. apenninica*, but independently supported by strontium isotope values; forms intermediate to *M. compressa*).

2021 *Moncharmontia apenninica* – Schlagintweit & Yazdi-Moghadam, p. 22, pl. 1, figs. A-L; middle – late Cenomanian, Iranian Zagros.

2021 *Moncharmontia apenninica* – Yazdi-Moghadam & Schlagintweit, fig. 2G; middle – late Cenomanian, Iranian Zagros.

2021 *Moncharmontia apenninica* – Dousti-Mohajer et al., pl. 1, fig. l; late Cenomanian; Iranian Zagros.

2021 *Montcharmontia apenninica* (sic) – Özkan, fig. 11 (21-22); Campanian, Turkish Arabian Plate.

2023 *Moncharmontia apenninica* – Simmons & Bidgood, p. 75, fig. 25; upper middle Cenomanian-Maastrichtian, global review.

? 2023a *Moncharmontia apenninica* – Mehrabi et al., fig. 11M; Santonian (?), Persian Gulf.

2023b *Moncharmontia apenninica* – Mehrabi et al., fig. 6Q; Turonian, Iranian Zagros.

2024 *Moncharmontia apenninica* – Consorti et al., fig. 3L, P; early – middle Campanian, Italy.

2024 *Moncharmontia apenninica* – Křížová et al., fig. 4a-b; early – middle Turonian, north-east Italy.

2024 *Moncharmontia apenninica* – Solak & Taslı, p. 6, fig. 2E-H; late Campanian, Turkish Taurides.

Reference Images: De Castro (1966), figs. 5-6, pls. I-V (not pl. III, figs. 4-8).

Taxonomy/Identity: De Castro's original description (1966) is comprehensive (see also Arriaga et al., 2016; Simmons & Bidgood, 2023, and the species key chart therein). *M. apenninica* differs from *M. compressa* (De Castro) in being larger, less compressed (almost subglobular) and with a larger proloculus. Cvetko Tešović et al. (2001) have provided a comprehensive biometric analysis between the two species.

Moncharmontia is very similar to *Fleuryana* De Castro et al. 1994, with the only substantial difference being the nature of the aperture which is cribrate in *Moncharmontia*, but single, slit-like and basal in *Fleuryana*. *Fleuryana gediki* Solak et al. 2020 is very similar to *M. apenninica*, but in addition to apertural differences, *F. gediki* has slightly fewer chambers in the final whorl and thinner walls. Differences are discussed by Solak & Taslı (2024). Species of *Fleuryana* are only known from Turonian and younger strata.

Confident Stratigraphic Range: middle Cenomanian – Maastrichtian. Scarce in the Cenomanian and Maastrichtian.

Uncertain Stratigraphic Range: not applicable.

Commonly considered to be not older than Turonian (e.g. Chiocchini & Mancinelli, 1977; Omidvar et al., 2014a, b; Frijia et al., 2015; Solak et al., 2015, 2019; Arriaga et al., 2016; Solak & Taslı, 2024), plausible specimens occurring together with middle-late Cenomanian taxa (e.g., *Chrysalidina gradata* d'Orbigny, 1839, *Cisalveolina fraasi* (Gümbel, 1872) and *Simplalveolina simplex* (Reichel, 1936)) clearly indicate the species can be as old as (middle) Cenomanian. These have been recorded (illustrated) in the Turkish Taurides (Bignot & Poisson, 1974) and the Iranian Zagros (Schlagintweit & Yazdi-Moghadam, 2021; Dousti-Mohajer et al., 2021).

Unillustrated/unverifiable records attributed to Cenomanian strata also occur in Mexico (e.g., Aguillera-Franco, 2000; Omaña et al. 2012, 2013), Egypt (Shahin & Elbaz, 2013) and Oman (Piuz & Meister, 2013).

It is probable that some Turonian records may have that age attributed by "circular reasoning" and that a Cenomanian age might not be excluded (e.g., Özkan & Altıner, 2019, from Türkiye).

See Schlagintweit & Yazdi-Moghadam (2021), Simmons & Bidgood (2023) and Solak & Taslı (2024) for a more extensive discussion on stratigraphic range. The species is often used as a biozonal marker (e.g. for Turonian strata in the Iranian Zagros (Omidvar et al., 2014b); Turonian and younger strata in Italy (De Castro, 1991)), but now that the species is confidently known from the Cenomanian (at least on the Arabian Plate and Türkiye) and to be long-ranging, such assessments should be treated with care.

Geographic Distribution: In post-Cenomanian strata, the species is widespread within Neotethys, with many records from the northern Mediterranean, as far north as Austria. There are also records from the Arabian Plate (Zagros) and Central Iran. Cenomanian records are limited but include the Iranian Zagros and Türkiye. Records from Mexico are unproven.

***Moncharmontia compressa* (De Castro, 1966)**
Figure 11

T 1966 *Neoendothyra apenninica compressa* De Castro, p. 20, pl. III, figs. 4-8; Turonian-Senonian, Italy.
1967 *Moncharmontia compressa* De Castro *nom. nov*., p. 475.
1970 *Moncharmontia apenninica compressa* – Fleury, pl. 2, figs. 2-3; Senonian, Greece.
? 1972 *Moncharmontia apenninica compressa* – Bignot, pl. 16, figs. 6-8; Senonian, Croatia [= *Fleuryana adriatica* De Castro et al. *fide* De Castro et al., 1994].
? 1978 *Moncharmontia* (?) cf. *apenninica compressa* – Berthou & Schroeder, pl. 9, fig. 2; late Albian, Portugal [hard to determine if this is *Moncharmontia* in the random sections presented].
1982 *Montcharmontia apenninica compressa* (sic) - Altıner & Decrouez, pl. 7, fig. 8; Senonian, Turkish Taurides.
1985 *Moncharmontia apenninica* – Bilotte, p. 369, pl. 15, fig. 9; late Santonian, Pyrenees.
1994 *Moncharmontia compressa* – Chiocchini et al., pl. 23, figs. 2-3, 10; early Senonian, central Italy.
2001 *Moncharmontia compressa* – Cvetko Tešović et al., fig. 7(N); Coniacian-Campanian, Croatia.
2006 *Moncharmontia compressa* – Taslı et al., fig. 7(J-K); Coniacian-Santonian, Türkiye.
2006 *Moncharmontia apenninica* – Sari, pl. 6.3, figs. 4?, 5, 6?; late Cenomanian – Turonian; Turkish Taurides [late Cenomanian age judged as plausible].
2008 *Moncharmontia apenninica* – Schlüter, fig. 2.3k; Campanian, southern Italy.
2008 *Moncharmontia apenninica* – Schlüter et al., fig. 3k; Campanian, southern Italy.
2009 *Moncharmontia apenninica-compressa* – Sari et al., pl. 4, figs. 4-?5; Turonian-Coniacian, Turkish Taurides.
2011 *Moncharmontia compressa* – Jez et al., fig. 7g; Coniacian-Santonian, Slovenia.
? 2012 *Moncharmontia* cf. *compressa* – Korbar et al., fig. 5M, Turonian, Croatia [age partly based on presence of *M. compressa*].
? 2012 *Moncharmontia apenninica* – Ghanem et al., fig. 6d (11, 19); early Cenomanian, Syria.
? 2017 *Moncharmontia*(?) sp. – Solak et al., fig. 8(M-N); middle – late Cenomanian, Turkish Taurides [or =*Biconcava bentori*].
? 2020 *Fleuryana adriatica* De Castro et al. 1994 – Solak et al., fig. 14(A-E); Turonian, Turkish Taurides.
2021 *Moncharmontia compressa* – Sinanoğlu, pl. 1, fig. 9; Maastrichtian, Türkiye.
2023 *Moncharmontia compressa* – Simmons & Bidgood, p. 77, fig. 27; early Cenomanian?-Maastrichtian, global review.

Reference Images: Taslı et al. (2006) fig. 7(J-K).

Taxonomy/Identity: A smaller and more laterally-compressed *Moncharmontia* species compared with *M. apenninica* and with only a single row of apertural openings. Cvetko Tešović et al. (2001) have provided a comprehensive biometric analysis between the two species, although in random thin-sections separation is difficult and there are forms that appear intermediate between the two.

It is very similar to the genus *Fleuryana*, especially *F. adriatica* De Castro, which has a single aperture, rather than multiple apertural openings. Records of *F. adriatica* from the Turonian of Türkiye by Solak et al. (2020), are virtually indistinguishable from *M. compressa*. *F. adriatica* is also long-ranging and further work is needed to establish the degree of separation of these two taxa. Differences are discussed by Solak & Taslı (2024).

Simmons & Bidgood (2023) further discuss the differences between the two *Moncharmontia* species and between them and their two *Fleuryana* counterparts.

Confident Stratigraphic Range: Turonian – Maastrichtian (scarce in the Maastrichtian).

Uncertain Stratigraphic Range: late Cenomanian.

Commonly regarded as Turonian and younger (e.g., Chiocchini & Mancinelli, 1977). Most plausible, illustrated records of *M. compressa* are from Turonian and younger (up to Maastrichtian) strata. Cenomanian records are either poorly/equivocally illustrated or not illustrated at all, with the possible exception of that by Sari (2006). The late Albian record of Berthou & Schroeder (1978) is very doubtful, as is the early Cenomanian record of Ghanem et al. (2012). A possible middle – late Cenomanian record (Solak et al., 2017) as "*Moncharmontia*(?) sp." is unconfirmed. Unillustrated records from the Cenomanian include those from the Natih Formation of Oman by Piuz & Meister (2013) and

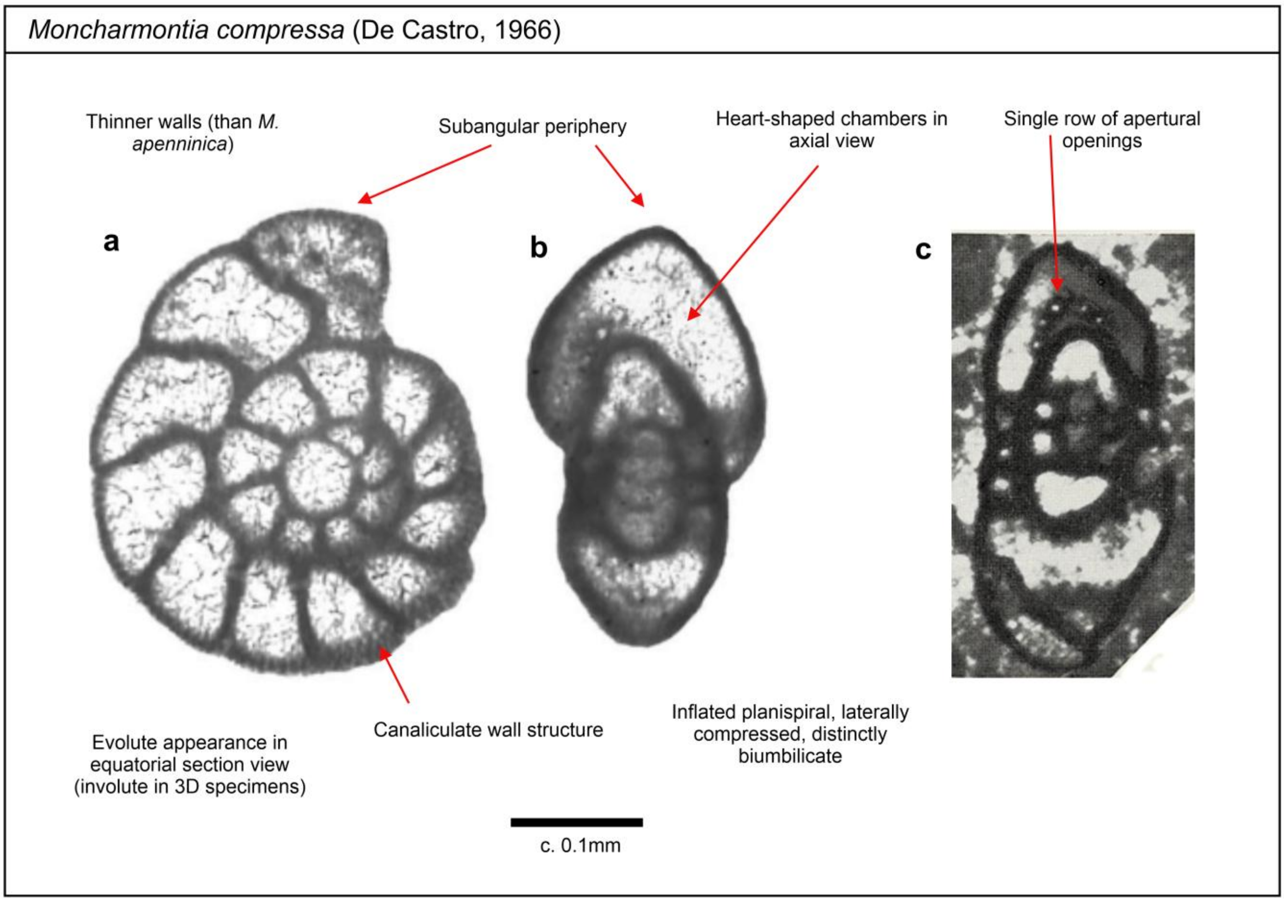


Fig. 11. Representative illustrations of *Moncharmontia compressa*: **a.** Equatorial section, Taslı et al. (2006, fig. 7(J), Turkey); **b.** Axial section, Taslı et al. (2006, fig. 7(K), Turkey); **c.** Subaxial section, De Castro (1966, pl. 3, fig. 8, Italy) (Modified after Simmons & Bidgood, 2023).

Piuz et al. (2014).

Geographic Distribution: This species is known from the Mediterranean region (Italy, Adriatic, Türkiye, Pyrenees) in the post-Cenomanian (although not the Arabian Plate?). In the Cenomanian records are doubtful, but the most probable is from the Turkish Taurides.

Family **BIOKOVINIDAE** Gušić 1977 (diagnosis *sensu* Loeblich & Tappan, 1987)
Genus ***Neodubrovnikella*** Schlagintweit & Rashidi 2018 (see Table 1 for diagnosis)

Neodubrovnikella turonica (Said & Kenawy, 1957)
Figure 12

T 1957 *Peneroplis turonicus* n. sp. Said & Kenawy, p. 82, pl. 13, figs. 14a–c, 16a–c; Turonian (now considered Cenomanian *fide* Schlagintweit & Yazdi-Moghadam, 2022), Egypt.
Non 1973 *Peneroplis turonicus* – Kerdany et al., pl. 1, fig. 16-18; Cenomanian, Egypt [= *Biconcava bentori* Hamaoui *fide* Hamaoui in Schroeder & Neumann, 1985].
1974 *Peneroplis* cf. *turonicus* – Saint-Marc, p. 235, pl. 8, figs. 5–9; middle-late Cenomanian, Lebanon (Turonian age discounted *fide* Schlagintweit & Yazdi-Moghadam, 2022).
1974 Foraminifer F-50 – Radoičić, pl. 6, figs. 5-6; early Turonian (now considered Cenomanian *fide* Schlagintweit & Yazdi-Moghadam, 2022), Serbia.
1976 *Peneroplis* cf. *turonicus* – Charvet et al., pl. 7, figs. 2-3; late early – late Cenomanian, Greece.
1981 *Peneroplis* cf. *turonicus* – Saint-Marc, pl. 4, figs. 11–12; middle-late Cenomanian, Lebanon (Turonian age discounted).
1989 *Merlingia* cf. *cretacea* (sic) Hamaoui & Saint-Marc – Kuss & Malchus, text-figs. 48-49; Cenomanian, Egypt.
1990 *Pseudolituonella reicheli* Marie – Šribar & Pleničar, pl. 2, fig. 8; middle – late Cenomanian, Slovenia.
1994 *Peneroplis* cf. *turonicus* -Velić & Vlahović, pl. 5, figs. 1-4; middle-late Cenomanian, Croatia.
2004 *Peneroplis* cf. *turonicus* – Chiocchini et al., pl. 6, fig. 6; late Cenomanian, southern Italy.
2006 *Peneroplis* cf. *turonicus* – Ettachfini, pl. 15, figs. 1-2; late Cenomanian, Morocco.
2006 *Pseudolituonella reicheli* – Taslı et al., Fig. 6 D; middle – late Cenomanian, Turkish Taurides.
2012 ?*Peneroplis* cf. *turonicus* – Chiocchini et al., pl. 109, fig. 1 (pars), 2–8; late Cenomanian, southern Italy.

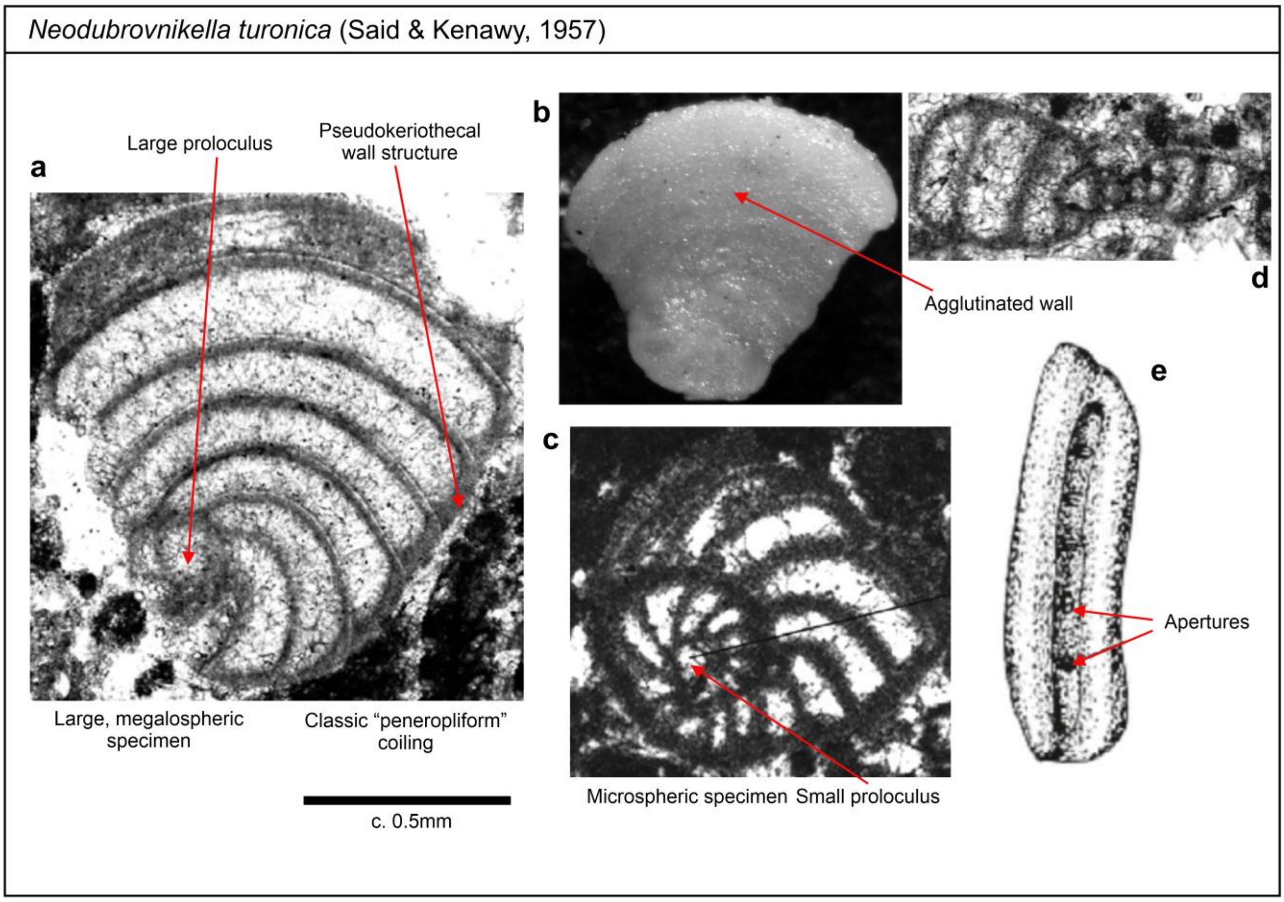


Fig. 12. Representative illustrations of *Neodubrovnikella turonica*: **a.** Equatorial section, Schlagintweit & Yazdi-Moghadam (2022, fig. 4(E), Iran); **b.** Re-illustration of holotype, Schlagintweit & Yazdi-Moghadam (2022, fig. 4 (A), Egypt); **c.** Equatorial section, Schlagintweit & Yazdi-Moghadam (2022, fig. 6(B), Croatia); **d.** Axial section, Schlagintweit & Yazdi-Moghadam (2022, fig. 6(C), Kosovo); **e.** Apertural face, Said & Kenawy (1957, holotype, pl. 13, fig. 14c, Egypt) (Reproduced after Simmons & Bidgood, 2023).

2013 *Pseudolituonella reicheli* – Al-Dulaimi et al., fig. 9/8; late Cenomanian, Southern Iraq.

? 2013 *Peneroplis parvus* De Castro – Ghanem & Kuss, fig. 14(10); late Cenomanian, Syria.

Non 2013 *Peneroblis* cf. *turonicus* (sic) – Shahin & Elbaz, p. 278, pl. 3, fig. 3; Cenomanian, Egypt [= *Peneroplis parvus*].

2016 *Peneroplis turonicus* – Assadi et al., fig. 6 a5; middle – late Cenomanian, Iranian Zagros.

2018 *Peneroplis parvus* – Omidi et al., pl. 4, fig. 8; middle – late Cenomanian, Iranian Zagros.

2020 *Peneroplis turonicus* – Solak et al., ?fig. 6M, fig. 10S–T, ?fig. 13I; late Cenomanian, Western Taurides, Türkiye.

2021 *Pseudolituonella reicheli* – Dousti-Mohajer et al., pl. 1i; middle – late Cenomanian, Iranian Zagros.

2021 *Peneroplis planatus* (Fichtel and Moll) – Brčić et al., fig. 9i; late Cenomanian, Croatia.

2021 “*Peneroplis*” *turonicus* – Consorti & Schlagintweit, fig. 2H; late Cenomanian, Albania-Kosova.

? 2021 *Peneroplis* sp. – Solak, pl. 2E; middle – late Cenomanian, Turkish Taurides.

? 2021 *Peneroplis turonicus* – Dousti-Mohajer et al., pl. 3a; middle – late Cenomanian, Iranian Zagros.

2022 *Neodubrovnikella turonica* – Schlagintweit & Yazdi-Moghadam, p. 4, figs. 3A; 4A-F, 5-6; upper early – late Cenomanian, southern Neotethys.

Non 2022 *Peneroplis turonicus* – Esfandyari et al., fig. 25j; Cenomanian – early Turonian, Iranian Zagros [= *Pseudolituonella reicheli*].

2023 *Neodubrovnikella turonica* – Simmons & Bidgood, p. 70, fig. 19; (upper early?) middle-late Cenomanian, global review.

2023 *Neodubrovnikella turonica* – Xu et al., fig. 3c, Cenomanian, Iranian Zagros.

Non 2023 *Peneroplis turonicus* – Moghaddam et al., fig. 5v; Cenomanian – early Turonian, Iranian Zagros [= *Pseudolituonella reicheli*].

2024 *Peneroplis turonicus* – Moghaddam et al., fig. 2l; Cenomanian, Iranian Zagros.

2024 *Neodubrovnikella turonica* – Křížová et al., fig. 4r-s; late Cenomanian, north-east Italy.

Reference Images: Schlagintweit & Yazdi-Moghadam (2022) p. 4, figs. 3A; 4A-F, 5-6.

Taxonomy/Identity: The taxonomic status of this species and its identity has recently been reviewed by Schlagintweit & Yazdi-Moghadam (2022) who recognised that this is in fact an agglutinated taxon with a pseudokeriothecal wall, not a species of the porcellaneous genus *Peneroplis* (indeed also not Turonian). It was assigned to the genus *Neodubrovkinella,* the only other species of which, *Neodubrovnikella maastrichtiana* Schlagintweit & Rashidi, is Maastrichtian (Schlagintweit & Rashidi, 2018; Schlagintweit & Yazdi-Moghadam, 2022). See also Simmons & Bidgood (2023).

It is similar to *Peneroplis parvus* De Castro and appears to be an agglutinated isomorph of this miliolid genus (see also *Peneroplis cairensis* Chiocchini, 2008). *N. turonica* is smaller (c. 0.25-0.8 mm) and with fewer chambers in the last whorl (7-8) than *P. parvus* and *P. cairensis* (Chiocchini, 2008). *Peneroplis* is also always planispiral whereas *N. turonica* is frequently not perfectly planispiral.

It is also often confused in the literature with *Pseudolituonella reicheli* Marie which has a much-reduced coiled part, a cylindrical rather than flattened uncoiled portion, and apertures that are cribrate, rather than in a row as in *N. turonica*.

Confident Stratigraphic Range: middle-late Cenomanian.

Uncertain Stratigraphic Range: upper early Cenomanian.

Originally regarded as being restricted to the Turonian (hence the name), a re-assessment of the age of the type specimens from Egypt by Schlagintweit & Yazdi-Moghadam (2022), together with a review of other ostensibly Turonian records, indicates that this species is in fact restricted to the (middle-late) Cenomanian (see also Velić, 2007). Records in the upper part of the early Cenomanian are based on illustrated but uncertainly age-calibrated records (Charvet et al., 1976), or unillustrated records (Decrouez, 1975), from Greece (and see also Schlagintweit & Yazdi-Moghadam, 2022, for records from the Iranian Zagros).

Geographic Distribution: Throughout Neotethys, from Morocco to Iran (see Schlagintweit & Yazdi-Moghadam, 2022).

Suborder **CYCLOLININA** Mikhalevich 1992 (diagnosis *sensu* Kaminski, 2014)
Superfamily **CYCLOLINOIDEA** Loeblich & Tappan 1964 (diagnosis *sensu* Loeblich & Tappan, 1987)
Family **CYCLOLINIDAE** Loeblich & Tappan 1964 (diagnosis *sensu* Loeblich & Tappan, 1987)
Subfamily **CYCLOLININAE** Loeblich & Tappan 1964 (diagnosis *sensu* Loeblich & Tappan, 1987)
Genus ***Cyclolina*** d'Orbigny 1846 (see Table 1 for diagnosis)

Cyclolina cretacea d'Orbigny, 1846

Figure 13

T 1846 *Cyclolina cretacea* n. sp. – d'Orbigny, p.139; pl. 21, fig. 22-25; Turonian (now regarded as middle Cenomanian – Moreau, 1976), western France.
1919 *Cyclolina cretacea* – Douvillé, p. 1131; text-fig. 2; Cenomanian, western France.
1949 *Cyclolina cretacea* – Cuvillier & Szakall, p. 11; pl. 2, fig. 15; pl. 13, fig. 11; Cenomanian, western France.
1964 *Cyclolina cretacea* – Loeblich & Tappan, p. C301-C302; text-fig. 207 (1a-b); middle Cenomanian, western France.
1964 *Cyclolina cretacea* – Neumann, p. 49-52; pl. 1, fig. 1-4; text-fig. 1; Cenomanian, western France.
1967 *Cyclolina cretacea* – Neumann, p. 128-132; pl. 15, fig. 1-3; text-fig. 78-79; Cenomanian, western France.
? 1978 *Cyclolina* cf. *cretacea* – Berthou & Schroeder, pl. 9, fig. 2; latest Albian, Portugal.
1985 *Cyclolina cretacea* – Cherchi in Schoeder & Neumann, p. 18-19, pl. 4, figs. 1-11; middle Cenomanian, western France.
1987 *Cyclolina cretacea* – Loeblich & Tappan, p. 94, pl. 86, figs. 1-8; middle Cenomanian, western France.
Non 2011 *Cyclolina* aff. *cretacea* – Boix et al., p. 816, fig. 10a-d; Coniacian, Spanish Pyrenees [most likely a new species].

Reference Images: Schroeder & Neumann (1985) pl. 4, figs. 1-11.

Taxonomy/Identity: This species was comprehensively reviewed by Cherchi in Schroeder & Neumann (1985). No further taxonomic study has been carried out since then.

The genus *Cyclolina* was introduced by d'Orbigny (1846), with the species *Cyclolina cretacea* its type by monotypy. It is a simple, large (up to 6.7 mm) discoidal, microgranular/finely agglutinating form, increasing in thickness towards the periphery. Adult chambers are cyclic, with concentric sutures slightly depressed, and a simple interior with no internal partitions. A multiple aperture of rounded pores is scattered in many rows over the apertural face. Three ontogenetic stages are recognised: (i) a central embryonic apparatus consisting of a protoconch and a deuteroconch. The maximum inner diameter of the protoconch varies between 0.08 and 0.1 mm. In equatorial section, the deuteroconch is crescent-shaped; its diameter varies between 0.1 and 0.12 mm; (ii) the embryonic apparatus is followed by a rectilinear series of 4-5 undivided sickle-shaped chambers; (iii) 40-55 undivided annular chambers, of which the height and thickness increase during ontogeny (description after Cherchi in Schroeder & Neumann, 1985; Loeblich & Tappan, 1987).

Confusion with the soritid genera *Broeckina* Munier-Chalmas, 1882 and *Pastrikella* Cherchi, Radoičić & Schroeder, 1976 is possible in random sections, although suggestions that some illustrations of *C. cretacea* from western France (Neumann, 1964, 1967) are of these genera (Cherchi et al., 1976) is rejected (Saint-Marc, 1977; Cherchi in Schroeder & Neumann, 1985). It may also be confused with *Balkhania* Mamontova/

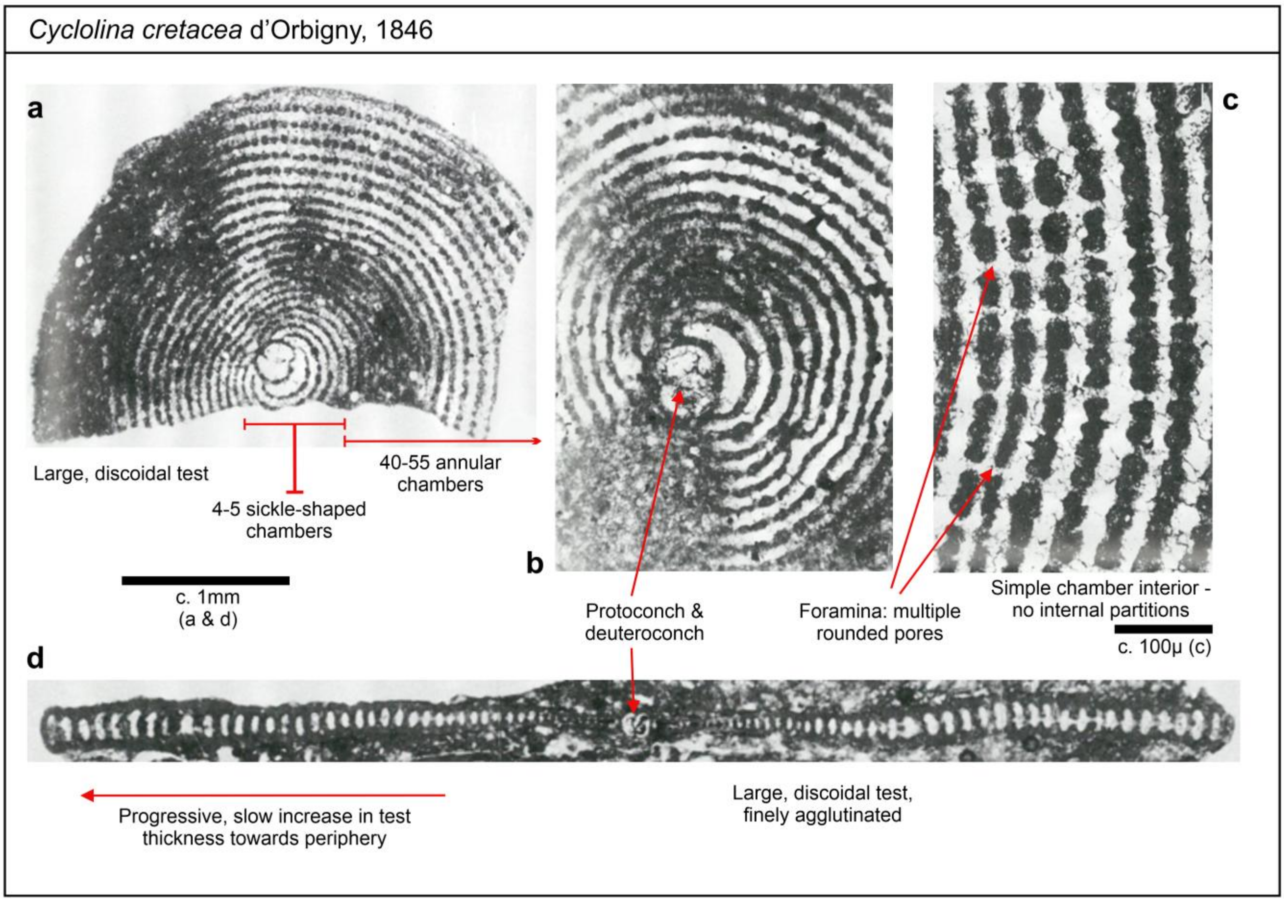


Fig. 13. Representative illustrations of *Cyclolina cretacea*: **a.** Partial equatorial section, Schroeder & Neumann (1985, pl. 4, fig. 1, France); **b.** Partial equatorial section, Schroeder & Neumann (1985, pl. 4, fig. 5, France); **c.** Partial equatorial section, Schroeder & Neumann (1985, pl. 4, fig. 7, France); **d.** Axial section, Schroeder & Neumann (1985, pl. 4, fig. 10, France).

Neobalkhania Cherchi, Radoičić & Schroeder, where the subepidermal network is often not well discernible.

Confident Stratigraphic Range: middle Cenomanian.

Uncertain Stratigraphic Range: latest Albian and early and late Cenomanian.

The only reliable illustrated records of this species are those pertaining to the type and nearby localities in western France as illustrated and documented by Cherchi in Schoeder & Neumann (1985). These are middle Cenomanian, and Schroeder & Neumann (1985) thus restricted the range of the species to the middle Cenomanian. Saint-Marc (1966) mentioned the species (not illustrated) from Landes in western France in association with *Praealveolina tenuis*, thus undifferentiated middle – late Cenomanian. Calonge et al. (2002) reported (not illustrated) the species from Spain in association with *Praealveolina iberica*, thus possibly early Cenomanian. It was reported (not illustrated) from Albian/Cenomanian transition beds of Portugal (Berthou, 1973; Berthou & Lauverjat, 1979) but restricted to the latest Albian by Berthou & Schroeder (1978) who illustrated an uncertain “cf.” form. A report from the late Cenomanian – ?early Turonian of Kuwait (El-Naggar & Al-Rifaiy, 1973) is not supported by a convincing illustration.

Boix et al. (2011) illustrated an "aff." form, probably a new species (larger than *C. cretacea* from the type locality), from the Coniacian – Santonian of Spain. One of us (LC) has observed similar forms in the similar aged Ilam Formation of the Iranian Zagros. Very small forms (up to an equatorial diameter of 1.10 mm) of *Cyclolina* sp. were found by Taslı & Solak (2019) in the late Albian of the Turkish Taurides.

Geographic Distribution: Confirmed occurrences are restricted to France but this species has been reported (though unconfirmed) more widely. It was reported, but not illustrated from Croatia (Sakač, 1970; Magas et al., 1999), Greece (Zambetakis-Lekkas et al., 1995) and the Iranian Zagros (e.g., Omidvar et al., 2014a, b; Rikhtegarzadeh et al., 2016; Asghari et al., 2022).

Subfamily **CYCLOPSINELLINAE** Loeblich & Tappan 1984 (diagnosis *sensu* Loeblich & Tappan, 1987)
Genus ***Cyclopsinella*** Galloway 1933 (see Table 1 for diagnosis)

Cyclopsinella neumannae Cherchi, 1980

Figure 14

? 1948c *Zekritia langhami* n. gen., n. sp. – Henson, p. 95, pl. 11, fig. 7; "Turonian" (possibly Cenomanian), Qatar.
? 1964 *Cyclolina* sp. – Bozorgnia & Banafti, pl. LXXXII; fig. 1; Cenomanian, central Iran.
1964 *Cyclopsinella steinmanni* (Munier-Chalmas) – Neumann, p. 51-52; pl. 1, fig. 5; pl. 2, fig. 1-3, 5-8 ; middle Cenomanian (after Moreau, 1976), western France.
1967 *Cyclopsinella steinmanni* – Neumann, p. 162-164; pl. 27, fig. 1-5; middle Cenomanian (after Moreau, 1976), western France.
T 1980 *Cyclopsinella neumannae* n. sp. – Cherchi, p. 74-79; pl. 1, fig. 1-4; pl. 2, fig. 1-4; pl. 3, fig. 1-4; middle Cenomanian (after Moreau, 1976), Western France.
1985 *Cyclopsinella neumannae* – Cherchi in Schroeder & Neumann, p. 19-21, pl. 5, figs. 1-6; middle Cenomanian (after Moreau, 1976), western France.
1987 *Cyclopsinella steinmanni* – Loeblich & Tappan, pl. 87, figs, 2-4; middle Cenomanian (after Moreau, 1976), western France.
? 1998 *Zekritia langhami* – Whittaker et al., p. 87-88, pl. 107, figs. 5-6; "Turonian" (possibly Cenomanian), Qatar.
? 2018 *Zekritia langhami* – BouDagher-Fadel, pl. 5.22, fig. 1; "Turonian" (possibly Cenomanian), Qatar.

Reference Images: Schroeder & Neumann (1985) pl. 5, figs. 1-6.

Taxonomy/Identity: The genus *Cyclopsinella* was introduced by Galloway (1933) with *Cyclopsina steinmanni* Munier-Chalmas, 1887 as described from the Santonian of southern France and northern Spain as the type species (known to range to the late Maastrichtian – see Schlagintweit (2020) for a review). It is a large, discoidal, microgranular/finely agglutinating form, that in the macrospheric generation has a protoconch and deuteroconch followed by numerous cyclic chambers. Later chambers have endoskeletal pillars arising from a median position on the chamber floor to extend radially from one septum the next, and may bifurcate and fuse to give an irregular appearance in thin-section and a misleading false appearance of two layers of chambers. Multiple apertures are present in a double row of pores. *Mangashtia* Henson, 1948c (emended Fourcade et al., 1997) is similar but the pillars are in the form of beams and only a single row of apertural pores are present.

Specimens described as *C. steinmanni* from the middle Cenomanian of western France (Neumann, 1964, 1967) formed the basis of the introduction of *Cyclopsinella neumannae* by Cherchi (1980) and further documented by Cherchi in Schroeder & Neumann (1985), which was the last taxonomic discussion of this species.

Specimens of *C. neumannae* are typically 4 – 6 mm in diameter (max. 6.6 mm), with test thickness increasing towards the periphery to c. 0.3 mm. Four ontogenetic stages are known: (i) a central embryonic apparatus, formed of a protoconch and deuteroconch. The protoconch, with a diameter between 0.078 and 0.092 mm, is ellipsoidal or more rarely subspherical; (ii) the embryo is followed laterally by a series of 4 undivided sickle-shaped chambers; (iii) there follows a series of 15-20 annular undivided annular chambers; (iv) The last ontogenetic stage is characterized by annular chambers, divided in the equatorial plane. This dividing partition is interrupted by large holes which are, in the first half of this stage, frequent, and connected by stolons that are sometimes a little oblique.

C. steinmanni is distinguished from *C. neumannae* by the larger dimensions of the test (6 – 7 mm in diameter) and of the embryonic apparatus (protoconch: 0.15 mm; deuteroconch: 0.2 mm). It lacks sickle-shaped chambers following the embryo. *Cyclopsinella roselli* described from the Campanian of Spain (Villalonga et al., 2019) is probably a synonym of *C. steinmanni* (Schlagintweit, 2020).

Zekritia langhami described as a new genus and species by Henson (1948c) from the Turonian (possibly Cenomanian on regional grounds – Le Blanc, 2015; Bromhead et al., 2022) is a possible synonym (Gendrot, 1964; Fourcade et al., 1997; Schlagintweit, 2020), but description is limited to a single thin-section specimen and crucial features cannot be seen (Whittaker et al, 1998) although the cyclopsinellid structure of the pillars (Hottinger, 2006, p. 12) can be seen. *Zekritia* and *Z. langhami* are effectively taxa of uncertain status (Loeblich & Tappan, 1987). Probably mistakenly, BouDagher-Fadel (2018) considered *Zekritia* a soritid.

Confident Stratigraphic Range: middle Cenomanian.

Uncertain Stratigraphic Range: late Cenomanian. The only confirmed record is the type description from the middle Cenomanian of France (Cherchi, 1980; Cherchi in Schroeder & Neumann, 1985; age after Moreau, 1976). The species has been recorded (as "cf.") but not illustrated from the late Cenomanian of Morocco (Ettachfini & Andreu, 2004) and *Cyclopsinella* sp. has been recorded from the late Cenomanian of Kuwait, although an illustration (pl. 6, fig. 13) is most likely not this genus (El-Naggar & Al-Rifaiy, 1973). These same authors also report but do not illustrate *Zekritia* from the Mishrif Formation of Kuwait, occurring alongside *Praealveolina*, *Cisalveolina*, etc. Thus, most likely late Cenomanian. An illustration of "*Cyclolina* sp." from the undifferentiated Cenomanian of central Iran (Bozorgnia & Banafti, 1964) may be this species. As noted above, *Z. langhami* might be a synonym, and the stratigraphic position of its type occurrence (from the Mishrif Formation of Qatar) suggests a late Cenomanian or possibly early Turonian age (Le Blanc, 2015, Bromhead et al., 2022; Simmons et al., 2024a).

Geographic Distribution: Confirmed occurrences are restricted to France but this species has been reported (though unconfirmed) ranging as far eastwards as Qatar and central Iran.

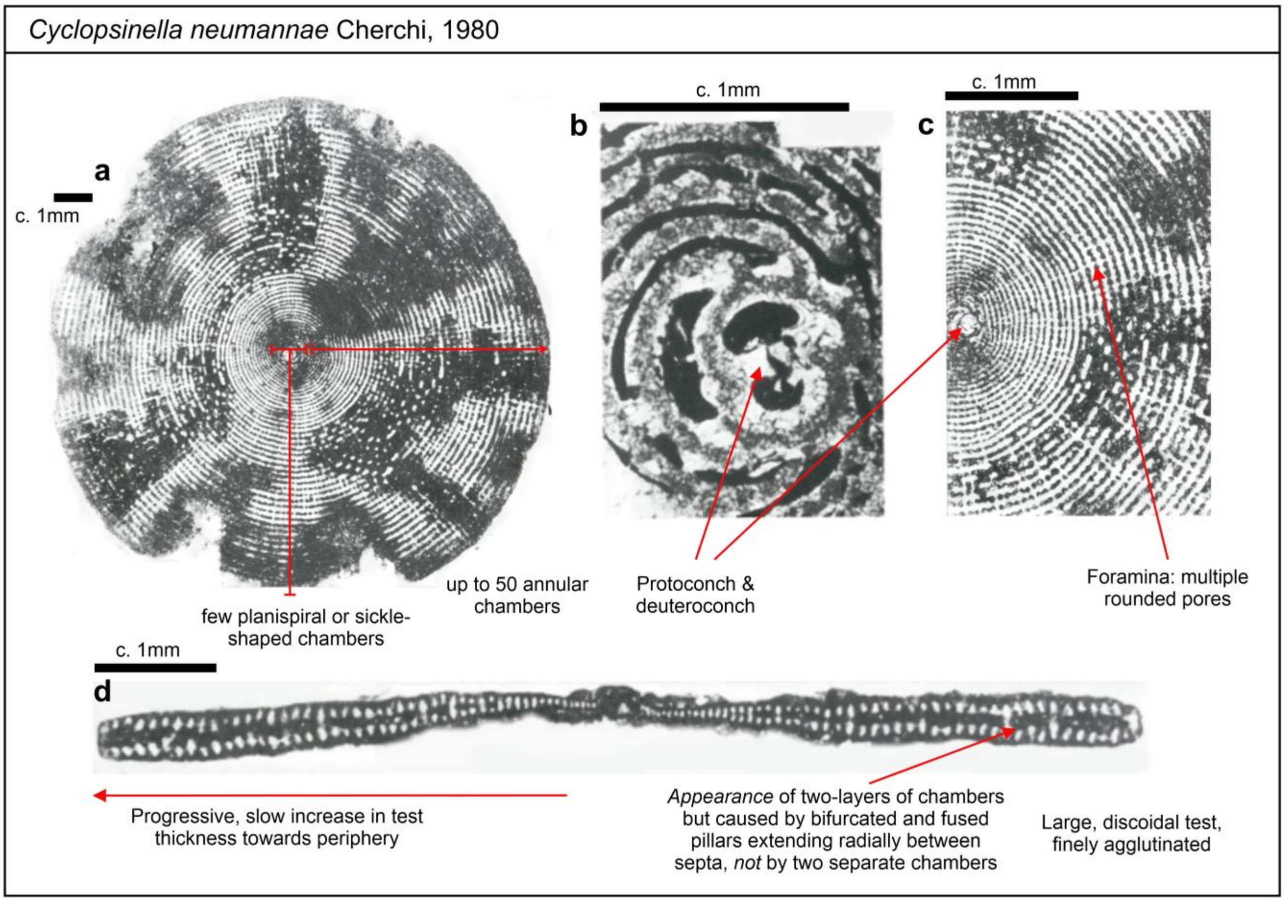


Fig. 14. Representative illustrations of *Cyclopsinella neumannae*: **a.** Equatorial section, Schroeder & Neumann (1985, pl. 5, fig. 1, France); **b.** Partial equatorial section, Schroeder & Neumann (1985, pl. 5, fig. 6, France); **c.** Partial equatorial section, Schroeder & Neumann (1985, pl. 5, fig. 5, France); **d.** Axial section, Schroeder & Neumann (1985, pl. 5, fig. 4, France).

Genus ***Mangashtia*** Henson 1948c (see Table 1 for diagnosis)

Mangashtia viennoti Henson, 1948c
Figure 15

T 1948c *Mangashtia viennoti* n. gen, n. sp. Henson, p. 94-95, pl. XII, figs. 16-21; Cenomanian-Turonian, Iranian Zagros.

Non 1965 *Mangashtia viennoti* – Gollestaneh, p. 344-348, pl. 104, figs. 1–2; pl. 105, figs. 1-6; pl. 106, figs. 1-5; pl. 107, figs. 1-8; late Oxfordian-Kimmeridgian, Iranian Zagros. [=*Levantinella egyptiensis* Fourcade et al. 1997].

Non 1996 *Mangashtia viennoti* – Hughes, pl. 1 (pars); Kimmeridgian, Saudi Arabia. [= *Levantinella egyptiensis*].

1997 *Mangashtia viennoti* – Fourcade et al., p. 183, figs. 5–6, 7.1–7.6; late Cenomanian? – Turonian, Iranian Zagros.

1998 *Mangashtia viennoti* – Whittaker et al., p. 48–49, pl. 71, figs. 1–4; late Cenomanian, Iranian Zagros. Explanation for the late Cenomanian age attribution is not given.

Non 2004a *Mangashtia viennoti* – Hughes, fig. 26 (8). Kimmeridgian, Saudi Arabia. [= *Levantinella egyptiensis*].

2013 *Mangashtia viennoti* – Rahimpour-Bonab et al., fig. 8T; Turonian, Iranian Zagros.

2014a *Biplanata peneropliphormis* (sic) Hamaoui & Saint-Marc – Omidvar et al., pl. 1(I); Cenomanian-Turonian, Iranian Zagros.

2014b *Mangashtia viennoti* – Omidvar et al., fig. 4.1; Turonian, Iranian Zagros.

? 2014 *Mangashtia viennoti* – Afghah & Fadaei, labelled fig. 8g, but referring to fig. 9g; late Cenomanian, Iranian Zagros. [Effectively indeterminate, but possibly a fragment of *Biplanata peneropliformis* Hamaoui & Saint-Marc].

Non 2016 *Mangashtia viennoti* – Rikhtegarzadeh et al., pl. 1, fig. 13; Cenomanian, Iranian Zagros. [Indeterminate biserial foraminifera].

? 2017 *Mangashtia viennoti* – Jamalpour et al., pl. 2, fig. h. Cenomanian, Iranian Zagros. [Effectively indeterminate but might be a fragment of *Biplanata peneropliformis*].

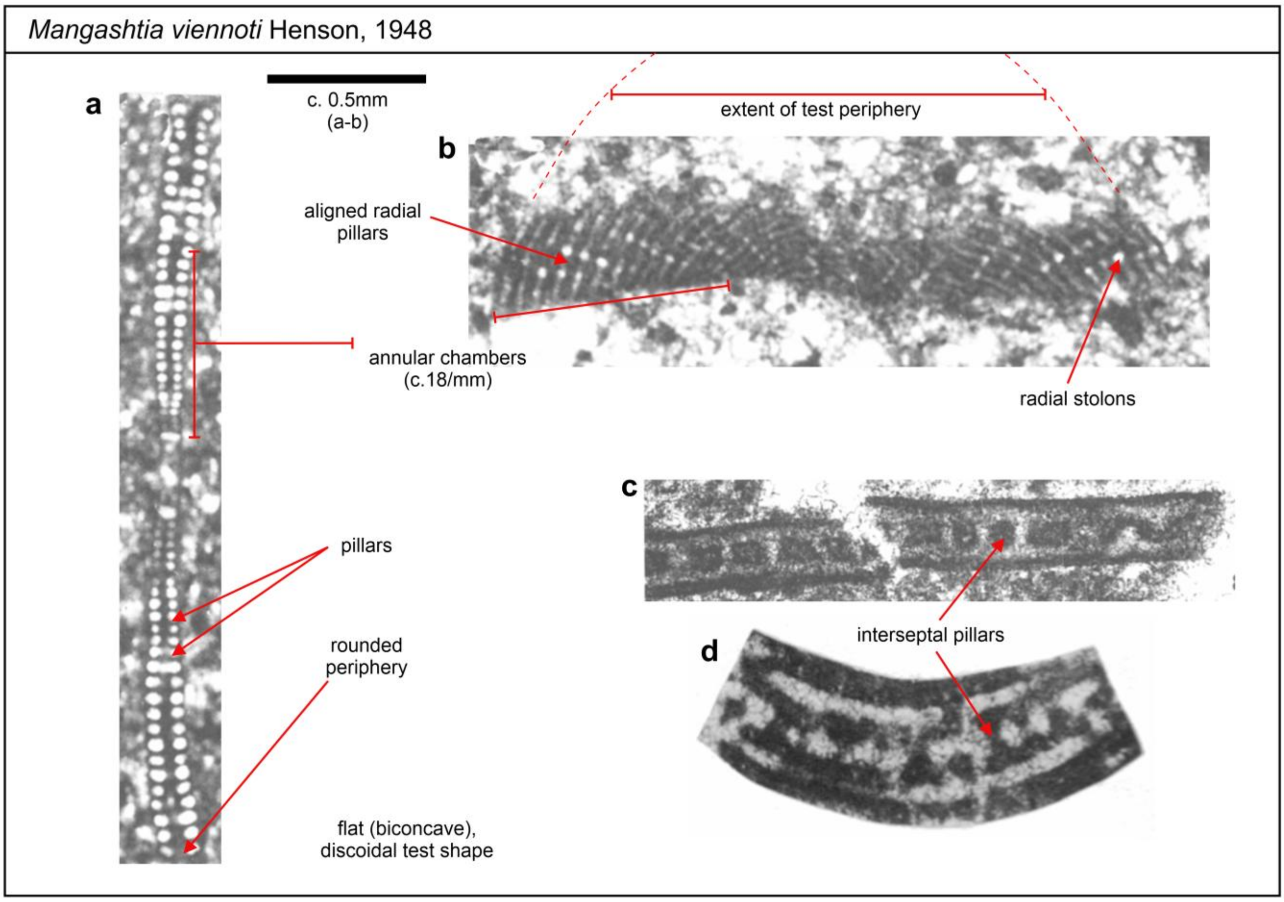


Fig. 15. Representative illustrations of *Mangashtia viennoti*: **a.** Subaxial section, Fourcade et al. (1997, fig. 6(5), Iran); **b.** Subequatorial section, Fourcade et al. (1997, fig. 5(4), Iran); **c.** Transverse section, Fourcade et al. (1997, fig. 6(8), Iran); **d.** Slightly oblique equatorial section, Henson (1948c, pl. XI, fig. 20, Iran).

2018 *Mangashtia viennoti* – BouDagher-Fadel, p. 306-307; pl. 5.1, fig. 14; pl. 5.9, fig. 5. Cenomanian-Turonian, Iranian Zagros.

Non 2019a *Mangashtia viennoti* – Ghalandari et al., Pl. 1, fig. G; Jurassic, Persian Gulf. [= indeterminate, but not *M. viennoti*].

Non 2019b *Mangashtia viennoti* – Ghalandari et al., text-fig. 7C; Jurassic, Persian Gulf. [= indeterminate, but not *M. viennoti*].

? 2019 *Biplanata peneropliformis* Hamaoui & Saint-Marc – Kiarostami et al., pl. 2, fig. j; Santonian [erroneous label, probably Cenomanian], Iranian Zagros.

? 2021 *Mangashtia viennoti* – Bagherpour et al., fig. 12k; Turonian, Iranian Zagros.

? 2021 *Mangashtia viennoti* – Dousti-Mohajer et al., pl. 1, fig. h; early Turonian, Iranian Zagros.

2021 *Cycledomia iranica* (Henson) – Dousti-Mohajer et al., fig. 3l ; early Turonian, Iranian Zagros.

2022 *Cycledomia iranica* – Esfandyari et al., fig. 25b ; late Cenomanian?, Iranian Zagros.

Non 2022 *Mangashtia viennoti* – Dousti-Mohajer et al., fig. 5c; late Cenomanian, Iranian Zagros. [= *Biplanata peneropliformis*].

2023a *Mangashtia viennoti* – Schlagintweit et al., p. 8, figs. 2E, 4A, C-F, 6, 7E-I; middle – ?late Turonian, Iranian Zagros. [Probably can be restricted to mostly middle Turonian – Simmons et al., 2024a, b].

Non 2023a *Mangashtia viennoti* – Mehrabi et al., fig. 11(O); Santonian; Persian Gulf. [= new taxon to be described, Schlagintweit et al., 2024c].

Non 2024 *Mangashtia viennoti* – Moghaddam et al., fig. 2h; Cenomanian, Iranian Zagros. [= *Biplanata peneropliformis*].

Reference Images: Fourcade et al. (1997); Schlagintweit et al. (2023a).

Taxonomy/Identity: First described from rather fragmentary material by Henson (1948c) from "Cenomanian-Turonian" limestones of the Izeh Zone of the Iranian Zagros, a detailed emended illustrated diagnosis for *Mangashtia* and the type species *Mangashtia viennoti* was published by Fourcade et al. (1997).

The test is compressed, discoidal with numerous annular chambers. Apertures are multiple, aligned in one row in the middle of the apertural face. The axes of the stolons are radial. Numerous subcylindrical or elongated pillars that are perpendicular to the septa are present in the central zone of the chambers. Pillars are aligned from one chamber to the next. The marginal zone of the chamber is not internally subdivided. The embryo of the megalospheric form consists of a globular proloculus with a simple wall.

Originally listed by Loeblich and Tappan (1987) in their "genera of uncertain status", they noted that the genus is "unrecognisable" because many of the essential characters were not described by Henson (1948c). Fourcade et al. (1997) revised the genus based on the study of new topotype material, as well as specimens preserved in the F.R.S. Henson & Associates Collection housed in the Natural History Museum (London) and placed the genus in the subfamily Cyclopsinellinae. Critically, they recognised that *Mangashtia* lacks an initial planispiral stage as suggested by Henson (1948c).

Mangashtia differs from *Cyclopsinella* in the nature of the internal structure (pillars in the form of beams) and in its apertural characteristics (a single row of pores rather than a double row). Occasionally the Cenomanian species *Pastrikella balkanica* Cherchi, Radoičić & Schroeder has been confused with *Mangashtia* (Cherchi et al., 1976), but it lacks pillars.

Fourcade et al. (1984) introduced *Mangashtia*? *egyptensis* for a form from the Late Jurassic of Egypt. Later (Fourcade et al., 1997), this was taken as the type species of the new genus *Levantinella*. Although similar in some random sections to *Mangashtia, Levantinella* is peneropliform and compressed axially. A simple proloculus followed by a planispiral evolute stage and a later uniserial stage. Chambers contain internal structures in the form of "pillars" in the shape of a zigzag blade situated in the median plane of the chamber. In the marginal zone of the chamber, this pilaroid structure forms intercalating digitations between two apertures of the same row, but it never reaches the lateral wall. Subepidermal partitions are absent. Apertures are aligned in rows that alternate from one side of the equatorial plane to the other. Thus, *Levantinella* differs from *Mangashtia* in the presence of a planispiral stage and in the presence of multiple apertures in alternating rows. *L. egyptensis* is the identity of the taxon described from the Jurassic but ascribed to *M. viennoti* (e.g., Gollesstaneh, 1965; Hughes, 1996, 2004a, b).

The taxonomy of this species has undergone a relatively complex pathway and was once proposed to be the possible senior synonym of *Biplanata peneropliformis* (Whittaker et al., 1998) but Schlagintweit et al. (2023a) and Simmons & Bidgood (2023) disagreed with that opinion and regard the two species as distinctly separate, although certain views in random thin-sections do show superficial similarities (see Schlagintweit et al., 2023a, for comparative illustrations). Nevertheless, records in the literature where the two species have been mistaken for one another occur and which has complicated evaluation of *M. viennoti*'s stratigraphic distribution. *Mangashtia* has many annular chambers and *Biplanata* is entirely planispiral (and later uncoiled). The periphery of *B. peneropliformis* is also much more angular than that of *M. viennoti* and the test thickens towards the periphery. Fourcade et al. (1997) suggested a clear stratigraphic separation of the occurrence of *B. peneropliformis* (Cenomanian) and *M. viennoti* (Turonian) in their studied section from the Iranian Zagros.

Confident Stratigraphic Range: early to middle Turonian.

Uncertain Stratigraphic Range: late Cenomanian, Coniacian – Santonian.

First described from the undifferentiated "Cenomanian-Turonian" Sarvak Formation of Iran by Henson (1948c), a detailed emended description by Fourcade et al. (1997) somewhat refined the range as late Cenomanian? – Turonian. The biostratigraphy of the Sarvak Formation (and its regional equivalents) has long been debated (Omidvar et al., 2014a, b; Bromhead et al. 2022; Schlagintweit et al., 2023a; Hosseini et al., 2024; Simmons et al., 2024a). Nevertheless, the youngest Sarvak Formation, where preserved, is early – middle Turonian. However, this is not commonly preserved in many areas due to a tectonic/eustatic-induced sea level fall in the middle Turonian (Schlagintweit et al., 2023a; Simmons et al., 2024a). Schlagintweit et al. (2023a) concluded that, with correct identification of *M. viennoti*, it is possible to equate the range of *M. viennoti* with the Wynd (1965) assemblage zone (biofacies) 29, and which is "most likely Turonian" (Wynd, 1965) or intra-Turonian (i.e. no younger than middle Turonian in age (Simmons et al., 2024a) and represents the youngest preserved Sarvak Formation. Schlagintweit et al. (2023a) defined a *Reticulinella*? – *Mangashtia* foraminiferal association (Zone 29b) in recognition of this.

Purported records of *M. viennoti* from the Cenomanian part of the Sarvak Formation or its regional equivalents (often unverified by illustration) should mostly be treated with caution (e.g., Afghah & Fadaei, 2014 illustration indeterminate; Jamalpour et al., 2017 illustration indeterminate; Dousti-Mohajer et al., 2022 and Moghaddam et al., 2024 illustrated but incorrectly identified). An exception is the record of "*Cycledomia iranica*" by Esfandyari et al. (2022). This is, in fact, a specimen of *M. viennoti*. Unfortunately, there is no clear definition of where in the Sarvak Formation this specimen was recovered from, but much of the associated fauna is late Cenomanian. Whittaker et al. (1998) regarded the types of *M. viennoti* as being of late Cenomanian age but gave no explanation for their reasoning. Records of "*Mangashtia* sp." from the probable late Cenomanian Mishrif Formation of Kuwait (El-Naggar & Al-Rifaiy, 1973) are not this genus, and are possibly *Cycledomia*.

Records from sediments younger than Turonian are also doubtful (e.g., from the Santonian of the Persian Gulf – Ilam Formation – by Mehrabi et al., 2023a, illustrated but identification doubted – Schlagintweit et al. 2024c). Abdolahi et al. (2024) reported but did not illustrate *M. viennoti* from the Turonian uppermost Sarvak Formation and the overlying Santonian Ilam

Formation in a well from the Dezful Embayment of the Iranian Zagros.

Geographic Distribution: Restricted to the Arabian Plate/Zagros region. The species is apparently absent from the circum-Mediterranean region (e.g., Velić 2007; Chiocchini et al., 2012; Frijia et al., 2015; Schlagintweit et al., 2023a).

Suborder **ATAXOPHRAGMIINA** Fursenko 1958 (diagnosis *sensu* Kaminski, 2014)
Superfamily **ATAXOPHRAGMIOIDEA** Schwager 1877 (diagnosis *sensu* Loeblich & Tappan, 1987)
Family **CUNEOLINIDAE** Saidova 1981 (diagnosis *sensu* Loeblich & Tappan, 1987)
Subfamily **CUNEOLININAE** Saidova 1981 (diagnosis *sensu* Loeblich & Tappan, 1987)
Genus ***Cuneolina*** d'Orbigny 1839 (see Table 1 for diagnosis)

Cuneolina compressa Schlagintweit, 1988

Figure 16

1976 *Cuneolina* sp. – Luperto Sinni, pl. 30, fig. 4; Senonian, Italy.
T 1988 *Cuneolina pavonia compressa* n. sp. – Schlagintweit, p. 25, pl. 1, figs. 1-11; late Turonian or Coniacian, Germany (Northern Calcareous Alps).
2025 *Cuneolina compressa* – Schlagintweit et al., p.253, figs. 50-52; Cenomanian, SW China (Tarim Basin).

Reference Images: Schlagintweit (1988); Schlagintweit et al. (2025).

Taxonomy/Identity: The name refers to the reduced test thickness (= strong compression in the plane of biseriality) compared to the type-species *C. pavonia* and other species. With a comparably thin wall, fine septa and radial partitions, as well as the rudimentary character of the partitions, *C. compressa* can be regarded a primitive species of the genus *Cuneolina* differentiating it from all other species described. Some similarities exist to *Vercorsella* (ex *Cuneolina) tenuis* (Velić & Gušić, 1973), a taxon from the Valanginian of Croatia (see Velić, 2007) and Albania (Schlagintweit et al., 2008).

C. compressa was originally described as a subspecies by Schlagintweit (1988) because of a smaller size and thickness compared to *C. pavonia*. It is now elevated to a full species (see also the WoRMS catalogue – Hayward et al., 2025).

Confident Stratigraphic Range: Cenomanian – Coniacian.

Uncertain Stratigraphic Range: not applicable.

Geographic Distribution: So far recorded (with illustrations) only from its type-locality in southern Bavaria (Northern Calcareous Alps, Germany), from Italy and from far to the east in southwestern China (Tarim Basin). Velić (2007, p. 18) reported the species without illustration from the late Turonian of Croatia.

Cuneolina ex gr. *pavonia* d'Orbigny, 1846

Figure 17

1839 *Cuneolina pavonia* n. sp. – d'Orbigny, p. 151; *Nomen nudem* – no description.
T 1846 *Cuneolina pavonia* – d'Orbigny, p.253, figs. 50-52; Turonian (reinterpreted as Cenomanian), western France.
1850 *Cuneolina conica* n. sp. – d'Orbigny, p. 186; Turonian (reinterpreted as Cenomanian), western France.
1900 *Cuneolina conica* – Schlumberger, p. 461-462, pl 8, figs. 8-10; Turonian (reinterpreted as Cenomanian), western France.
1947 *Cuneolina walteri* n. sp. – Cushman & Applin, p. 30, pl. 10, figs 4-5; middle Cenomanian, Florida
1948b *Cuneolina pavonia* var. *parva* var. nov. – Henson, pp. 624-627, pl. XIV, figs. 1-6; pl. XVII, figs. 7-12; pl. XVIII, figs. 12-14; Santonian (variously reinterpreted as Albian or Turonian), Egypt.
1961 "Cuneolinas" – Cuvillier, pl. XLII, fig. 1 ; "Lower Senonian", Aquitaine, France.
1962 *Cuneolina pavonia parva* – Sartoni & Crescenti, p. 278-279, pl. 31, fig. 2; pl. 32; pl. 47, figs. 4-6 ; Albian – intra-Late Cretaceous, southern Italy.
1964 *Cuneolina pavonia* – Loeblich & Tappan, figs. 193/1-2; Cenomanian, western France.
1964 *Cuneolina sp.* – Bozorgnia & Banafti, pl. LXXVII, fig. 2; late Albian – Cenomanian, central Iran.
1964 *Cuneolina sp.* – Bozorgnia & Banafti, pl. LXXX, fig. 2; Cenomanian, Iranian Zagros.
1964 *Cuneolina* cf. *hensoni* – Bozorgnia & Banafti, pl. LXXIX, fig. 1; Cenomanian, Iranian Zagros.
? 1965 *Cuneolina pavonia parva* – Gollesstaneh, p. 165-166, pl. 24, figs. 1-4 ; Early Cretaceous (precise age uncertain), Iranian Zagros.
1965 *Cuneolina walteri* – Applin & Applin, pl. 2, figs. 1-2; middle Cenomanian, Florida.
1967 *Cuneolina conica* – Bismuth et al., pl. 12, fig. 8; Cenomanian, Tunisia.
1967 *Cuneolina pavonia* – Neumann, pl. 53, fig. 1; Cenomanian, western France.
1968 *Cuneolina conica* – Gendrot, p. 676-677, pl. 4, fig. 16; Santonian, southern France.
1968 *Cuneolina pavonia* – Gendrot, p. 676-677, pl. 4, figs. 17-19; Santonian, southern France.
1969 *Cuneolina* sp. – Sampò, pl. XXXVII, fig. 16; pl. XLII, figs. 13, 17; Aptian, Cenomanian, Iranian Zagros.
1973 *Cuneolina pavonia-parva* – Berthou, p. 2, fig. 3; late Cenomanian, Portugal.
1974 *Cuneolina pavonia* – Saint-Marc, p. 220, pl. 2, fig. 1 ; Albian – Turonian, Lebanon.
1974 *Cuneolina* gr. *pavonia* – Bignot & Poisson, pl. 1, fig. 1; pl. 2, fig. 1; Cenomanian, Turkish Taurides.
? 1976 *Iraqia simplex* Henson – Kalantari, pl. 15, fig. 10; Albian, Iranian Zagros.
1976 *Cuneolina* cf. *pavonia* – Kalantari, pl. 18; pl. 22, fig. 5; Cenomanian, Iranian Zagros.

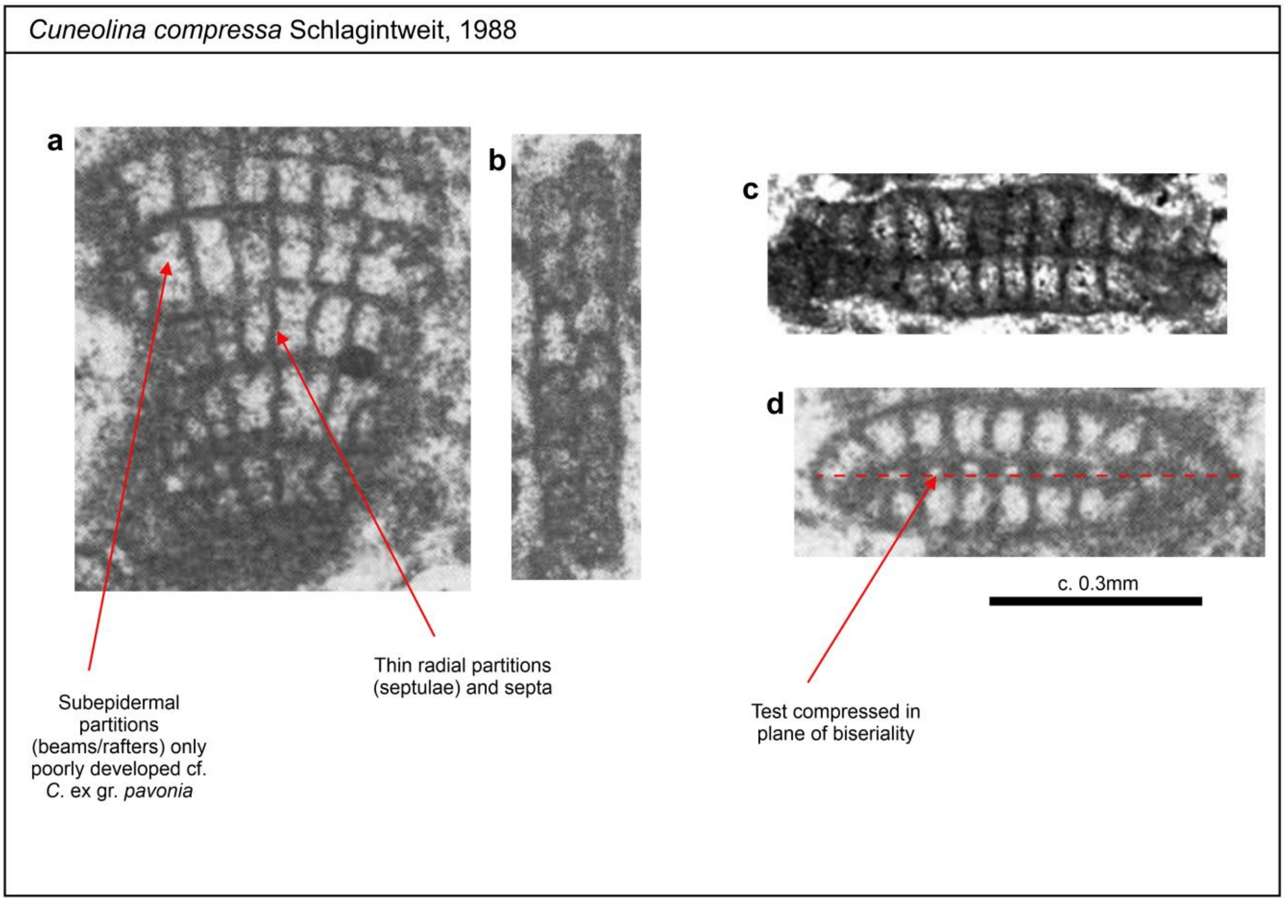


Fig. 16. Representative illustrations of *Cuneolina compressa*: **a.** Median section, Schlagintweit (1988, pl. 1, fig. 1, Germany); **b.** Axial section, Schlagintweit (1988, pl. 1, fig. 7, Germany); **c.** Transverse section, Schlagintweit et al. (2025, fig. 5(8), NW China); **d.** Transverse section, Schlagintweit (1988, pl. 1, fig. 9, Germany).

1976 *Cuneolina* gr. *pavonia* – Decrouez, p. 79-82, pl. 14, figs. 3-4, pl. 17, figs. 1, 5; Late Cretaceous, Greece [*fide* Cvetko Tešović et al., 2001]

1977 *Cuneolina pavonia* – Rey et al., p. 381, pl. 3, figs. 8-9; late Albian, Portugal.

1977 *Cuneolina pavonia parva* – Velić, pl. 29, figs. 1-3, 5; early Albian, Croatia.

1977 *Cuneolina pavonia* – Velić, pl. 29, figs. 4, 6-7; early Albian, Croatia.

1977 *Cuneolina* ex. gr. *pavonia parva* – Velić, pl. 31, figs. 2-4; late Albian, Croatia.

1978 *Cuneolina* gr. *pavonia* – Decrouez, pl. 1, figs. 2-3; early – late Cenomanian, Greece.

1978 *Cuneolina* sp. – Luperto Sinni & Richetti, pl. 46, figs. 1-11; Santonian – Maastrichtian, southern Italy.

1979 *Cuneolina pavonia parva* Sartoni & Crescenti [sic] – Bachmann & Risch, pl. 8, figs. 7-9; early Cenomanian, Greece.

1981 *Cuneolina pavonia* – Bismuth et al., pl. 1, figs. 7-8; late Cenomanian, Tunisia.

1981 *Cuneolina pavonia* – Saint-Marc, pl. 1, fig. 4; Albian – Turonian, Lebanon.

1982 *Cuneolina* gr. *pavonia* – Altıner & Decrouez, pl. 3, figs. 13-14; Aptian – Cenomanian, Turkish Taurides.

1982 *Cuneolina pavonia* – Mouty & Saint-Marc, pl. 1, fig. 9; latest Aptian – Cenomanian, Syria.

1984 *Cuneolina* gr. *pavonia* – Chiocchini et al., pl. 5, figs. 1-3; mid-Cretaceous, Italy.

1985 *Cuneolina conica* – Bilotte, pl. 5, fig. 3; Cenomanian, French Pyrenees.

1985 *Cuneolina gr. pavonia-parva* – Bilotte, pl. 5, fig. 4; late Cenomanian, French Pyrenees.

1988 *Cuneolina* gr. *pavonia* – Kuss & Schlagintweit, p. 83, pl. 18, fig. 5; pl. 20, figs. 9-10; latest Aptian – early Cenomanian, Sinai, Egypt.

1988 *Cuneolina pavonia* – Sartorio & Venturini, p. 109, 112, 113; Albian-Santonian; Italy.

1988 *Cuneolina pavonia* – Sartorio & Crescenti, p.113; "Lower Senonian", southern Italy.

1990 *Cuneolina pavonia* – Weidich & Al-Harithi, p. 604, pl. 3, fig. 6; pl. 4, fig. 24; late Albian – Cenomanian, Jordan.

1990 *Cuneolina pavonia* – Šribar & Pleničar, pl. 4, fig. 5; late Turonian, Slovenia.

1991 *Cuneolina pavonia parva* – Schlagintweit, p. 36, pl. 11, figs. 13-16; late Aptian – early Albian, Austria.

1991 *Cuneolina walteri* – Scott & Gonzalez-Leon, p. 58, fig. 5O; Albian, Mexico.

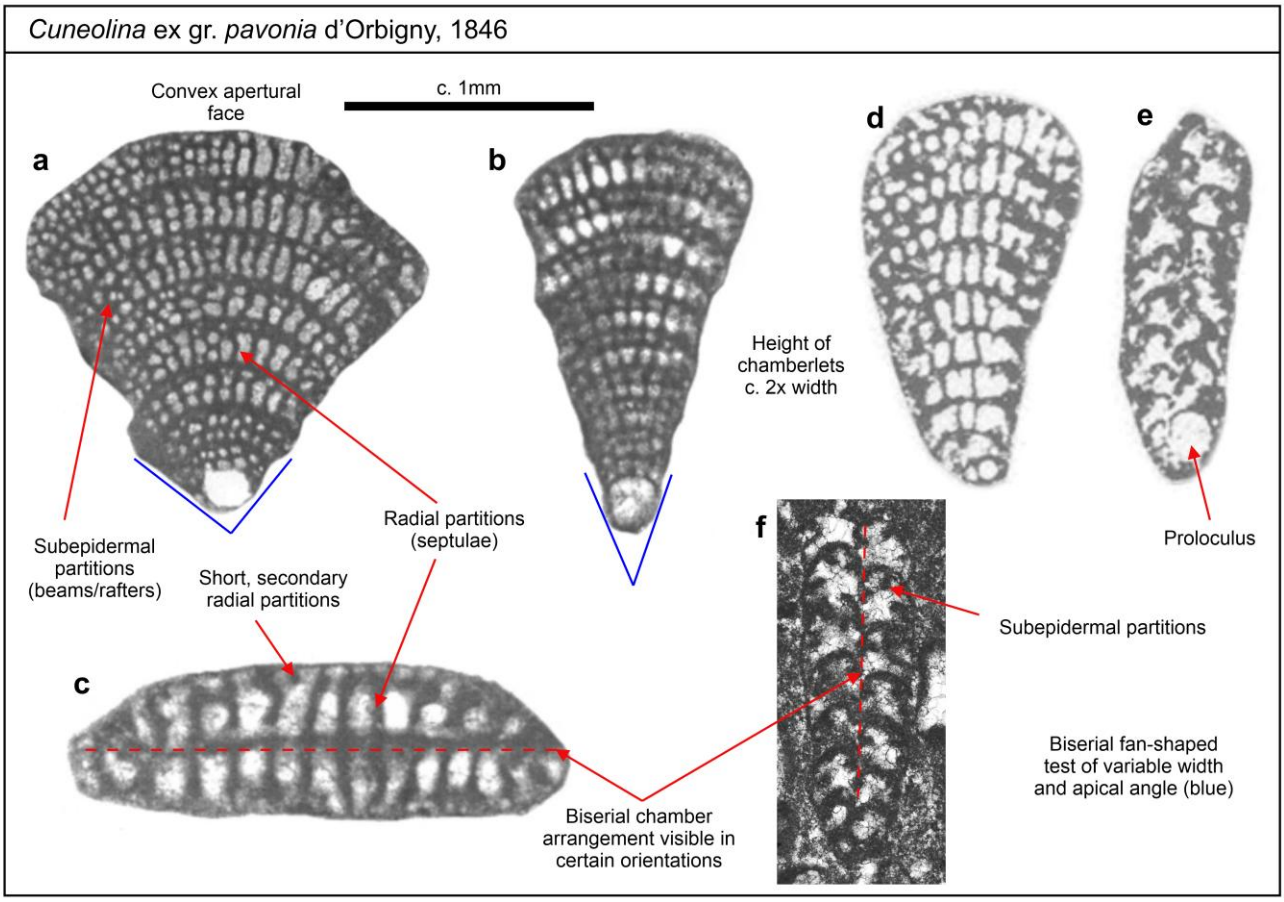


Fig. 17. Representative illustrations of *Cuneolina* ex gr. *pavonia*: **a.** Subequatorial section, Whittaker et al. (1998, pl. 45, fig. 8, Egypt); **b.** Subequatorial section, Whittaker et al. (1998 pl. 46, fig. 2, Egypt); **c.** Parallel section (normal to radius), Whittaker et al. (1998, pl. 46, fig. 4, Egypt; see text for discussion on Whittaker et al.'s ages); **d.** Subequatorial section, Schlagintweit (1992, pl. 2, fig. 1, late Turonian or Coniacian, Austria); **e.** Axial section, Schlagintweit (1992, pl. 2, fig. 2, late Turonian or Coniacian, Austria); **f.** Axial section, Ali Alibrahim personal image (unpublished, middle Turonian, Jordan).

1992 *Cuneolina* ex gr. *pavonia* – Schlagintweit, p. 336-337, text-fig. 6; pl. 2, figs. 1-6; Cenomanian – Coniacian, Austria. Demonstrates the initial chambers are planispiral rather than trochospiral.
1993 *Cuneolina pavonia* – Grötsch et al., fig. 5B-E; late Albian, Slovenia.
1995 *Cuneolina* sp. cf. *C. pavonia* – Arnaud-Vanneau & Sliter, p. 554, pl.4, figs. 1-5; late Albian, Mid-Pacific seamounts.
1995 *Cuneolina parva* – Arnaud-Vanneau & Sliter, p.554, pl, 5, figs. 6-9; late Albian, Mid-Pacific seamounts.
1998 *Cuneolina pavonia parva* – Whittaker et al., p. 28-29; pl. 4, figs. 1-2; pl. 45, figs. 7-8; pl. 46, figs. 1-6; Type material of Henson (1948b) of uncertain age (see text), Egypt.
1999 *Cuneolina walteri* – Scott & Finch, fig. 4A-C; late Albian, Honduras.
2000 *Cuneolina pavonia* – Aguilera-Franco, p. 160; middle – late Cenomanian, Mexico.
2000 *Cuneolina conica* – Aguilera-Franco, p. 161; middle – late Cenomanian, Mexico.
2000 *Cuneolina pavonia* – Benedetti et al., fig. 54; Late Cretaceous, Montenegro.
2001 *Cuneolina pavonia* – Cvetko Tešović et al., p. 601-602, fig. 6B-C; Campanian, Brac Island, Croatia.
2004 *Cuneolina* gr. *pavonia* – Menegatti, p. 2/24-2/25, pl. 7, fig. 5; pl. 8, figs. 2-3, 6; pl. 9, fig. 5; Cenomanian, Dubai.
? 2005 *Cuneolina pavoni* [sic] – Vaziri et al., pl. 2, figs 5-7; Campanian – Maastrichtian, central Iran. [Fragmentary specimens].
2006 *Cuneolina pavonia* – Husinec & Sokač, fig. 9 H-L; Albian, Croatia.
2006 *Cuneolina pavonia* – Taslı et al., fig. 6L; middle – late Cenomanian, Turkish Taurides.
2009 *Cuneolina pavonia* – Sari et al., pl. 3, fig. 7; middle Cenomanian – Coniacian, Turkish Taurides.
? 2009 *Cuneolina pavonia* – Shirazi et al., pl. 1, figs. 10-11; Albian – Cenomanian, Iranian Zagros [Fragmentary specimens].
? 2009 *Nakkadyia awadi* n. gen, n. sp. – Ismail et al., 402-403; text-fig. 4; pl. 3, figs. 1-5; pl. 4, figs. 2-4; Cenomanian, Egypt.

2010 *Cuneolina pavonia* – Spalluto & Caffau, fig. 13A-B; Albian – Cenomanian, southern Italy.

Non 2011 *Cuneolina pavonia* – Shirazi et al., pl. 2, fig. 16; Albian, Iranian Zagros. [=Indeterminate textulariid].

2011 *Cuneolina parva* – Filkorn & Scott, p. 186, figs. 4.9-4.12; late Albian, Mexico.

? 2011 *Cuneolina pavonia* – Roozbahani, pl. 1, fig. 11; Albian, central Iran. Indeterminate fragment.

? 2011 *Cuneolina walteri* – Roozbahani, pl. 2, fig. 3; Albian, central Iran. Indeterminate fragment.

2012 *Cuneolina pavonia* – Ghanem et al., fig. 6c/3, 8, 11; fig. 6d/1-2 ; Albian – Cenomanian, Syria.

2012 *Cuneolina pavonia* – Chiocchini et al., pl. 96; middle Cenomanian, southern Italy.

2012 *Cuneolina* sp. 1 – Chiocchini et al., pl. 82; early Cenomanian, southern Italy.

2012 *Cuneolina pavonia* – Orabi et al., fig. 5A, C; late Cenomanian, Egypt.

2012 *Cuneolina parva* – Orabi et al., fig. 5B; late Cenomanian, Egypt.

2012 *Cuneolina cylindrica* Henson – Orabi et al., fig.5 E; late Cenomanian, Egypt. [May be an oblique and/or partial section].

2012 *Cuneolina pavonia* – Spalluto, fig. 4a; Albian – Cenomanian, southern Italy.

2013 *Cuneolina parva* – Ghanem & Kuss, fig. 10/13; fig. 12/13; Albian – Cenomanian, Syria.

2013 *Cuneolina pavonia* – Ghanem & Kuss, fig. 11/2-4; Albian – Cenomanian, Syria.

2013 *Dicyclina* sp. – Ghanem & Kuss, fig. 12/30; Albian – Cenomanian, Syria.

2013 *Cuneolina pavonia* – Omaña et al., pl. 1, fig. 2; pl. 5, fig. 5; late Cenomanian, Mexico.

? 2013 *Cuneolina* aff. *C. parva* – Hfaiedh et al., fig. 12/L-N; Aptian, Tunisia.

2013 *Cuneolina hensoni* – Shanin & Elbaz, pl. 1, fig. 44; late Cenomanian, Sinai.

2013 *Cuneolina pavonia* – Shanin & Elbaz, pl. 1, figs. 45-46; late Cenomanian, Sinai.

2014b *Cuneolina pavonia* – Omidvar et al., fig. 4/3; late Cenomanian – intra-middle Turonian (as interpreted following Simmons et al., 2024a), Iranian Zagros.

2014 *Dicyclina schlumbergeri* – Afghah et al., Fig. 11F; early Cenomanian(?), Iranian Zagros.

2015 *Cuneolina conica* – Albrich et al., fig. 13 H, O; fig. 14 C-D; Campanian, Spain.

2015 *Cuneolina pavonia* – Solak et al., fig. 9A; Cenomanian – Coniacian, Turkish Taurides.

2016 *Cuneolina pavonia* – Rikhtegarzadeh et al., pl. 3, fig. 1; Cenomanian, Iranian Zagros.

Non 2016 *Cuneolina pavonia* – Ghaseminia et al., fig. 4L; Cenomanian, Iranian Zagros. [Indeterminate textulariid].

2017 *Cuneolina pavonia* – Ahmadi et al., pl. 1, fig. 11; Albian – Cenomanian (probably late Albian – early Cenomanian), Iranian Zagros.

2017 *Cuneolina pavonia* – BouDagher-Fadel et al., fig. 11/8-10; Albian – early Cenomanian, Tibet.

2017 *Cuneolina pavonia* – Hamedanian et al., pl. 1/F; Aptian, Iranian Zagros.

? 2017 *Cuneolina* gr. *pavonia* – Koç, fig. 6/G1-2; Aptian, Turkish Taurides.

2018 *Cuneolina pavonia* – Luger, p. 66-67, pl. 6, figs. 1, 2, 5; late Albian – Early Cenomanian, Somalia.

2019 *Cuneolina pavonia* – Omaña et al., p. 709, fig. 10a-b, middle – late Cenomanian, Mexico.

2019 *Cuneolina parva* – Omaña et al., p. 709-711, fig. 10c-f; middle – late Cenomanian, Mexico.

? 2019 *Cuneolina pavonia* – Kiarostami et al., pl. 1K; Cenomanian, Iranian Zagros.

2019 *Cuneolina pavonia* – Saeedi Razavi et al., pl. 2, fig. 10; Cenomanian, Iranian Zagros.

2019 *Cuneolina pavonia* – Solak et al., fig., 8R-T; fig. 10T; middle – late Cenomanian, late Campanian, Turkish Taurides.

2019 *Cuneolina pavonia* – Taslı & Solak, fig. 10/5; late Albian, Turkish Taurides.

2019 *Cuneolina* ex gr. *pavonia* – Özkan & Altıner, fig. 9/14; early – middle Cenomanian (as interpreted by Simmons et al., 2020), south-eastern Türkiye.

2020 *Cuneolina* sp. – Haftlang et al., fig. 2/24; Santonian, Iranian Zagros.

? 2020 *Cuneolina pavonia* – Randazzo et al., fig. 9R; Albian – Cenomanian, Sicily.

2020 *Cuneolina pavonia* – Solak et al., fig. 6T?; fig. 11N-O; fig. 14S; Albian?, late Cenomanian – Turonian, Turkish Taurides.

2021 *Cuneolina parva* – Solak et al., p. 678, figs. 5.1-5.3; Albian, Turkish Taurides.

2021 *Cuneolina pavonia* – Sinanoglu, p. 276-277, pl. 1, figs. 15-16; Maastrichtian, southern Türkiye.

2021 *Cuneolina pavonia* – Saedi Razavi et al., pl. 1, fig. 8; late Cenomanian (as interpreted herein), Iranian Zagros.

2021 *Cuneolina* sp. – Özkan, fig. 11/13; Campanian, southeast Türkiye.

2021 *Cuneolina pavonia* – Dousti-Mohajer et al., pl. 1j; Cenomanian, Iranian Zagros.

? 2021*Cuneolina pavonia* – Nagm et al., fig. 4E; late Cenomanian, Egypt.

2021 *Cuneolina parva* – Solak, pl. 2A-C; middle – late Cenomanian, Turkish Taurides.

2021 *Cuneolina pavonia* – Solak, pl. 3E-F; late Cenomanian, Turkish Taurides.

2021 *Cuneolina pavonia* – Gholamalian & Fanati Rashidi, pl. 3, fig. 1; Cenomanian, Iranian Zagros.

2021 *Dicyclina schlumbergeri* – Radmacher et al., pl. 1, figs. 8-9; Albian-Santonian Guatemala.

Non 2022 *Cuneolina pavonia* – Esfandyari et al., fig. 25c; Cenomanian, Iranian Zagros. [Probably *Praetaberina bingstani*].

? 2022 *Cuneolina pavonia* – Dousti-Mohajer et al., fig. 4l; Cenomanian, Iranian Zagros. [Test is possibly annular, thus suggesting *Dicyclina*].

2023 *Cuneolina* gr. *C. pavonia* – Solak & Taslı, fig. 10C, K; late Aptian – Albian, Turkish Taurides.

2025 *Cuneolina pavonia* – Salmouna et al., fig. 15D; Turonian, Tunisia.
2025 *Cuneolina pavonia* (?*parva*) – Messaoud et al., fig. 8 (f-g); Turonian, Jordan.

Reference Images: Schlagintweit (1992); Whittaker et al. (1998).

Taxonomy/Identity: As noted by Scott & Gonzalez-Leon (1991), discrimination among the species of *Cuneolina* (currently composed of 16 accepted species; WoRMS.org – Hayward et al., 2025) is difficult because many were defined by exterior features and the corresponding features or internal features are not known in the same detail for each species. Furthermore, thin-sections usually reveal only partial sections through the specimens.

As can be understood from the long synonymy list (which is only partial and does not include unillustrated records of which there are many), relatively large fan-shaped cuneolinids are common components of Cretaceous Neotethyan carbonate sediments. They are known from Central America (e.g., Filkorn & Scott, 2011), the peri-Mediterranean (e.g. Solak & Taslı, 2023), the Middle East (e.g., Saint-Marc, 1974), Tibet (e.g., BouDagher-Fadel et al., 2017), and guyots in the Pacific (e.g., Arnaud-Vanneau & Sliter, 1995). These have been described under a variety of names such as *Cuneolina pavonia* d'Orbigny (the type species of *Cuneolina*), *Cuneolina parva* Henson and *Cuneolina conica* d'Orbigny. Some authors maintain that separate species can be distinguished (e.g. Arnaud-Vanneau & Sliter, 1995; Ghanem & Kuss, 2013), others place them into synonymy (with C. *pavonia* the senior synonym) (e.g. Saint-Marc, 1974; Luger, 2018), and there are advocates to use a "group" concept (e.g. Altıner & Decrouez, 1982; Simmons & Hart, 1987; Kuss & Schlagintweit, 1988; Schlagintweit, 1992; Solak & Taslı, 2023). Pending a full taxonomic review and evaluation of intra-specific variation, we feel that use of "*Cuneolina* ex gr. *pavonia*" is the best solution for the moment and includes a group of similar taxa that are hard to separate from one another in many thin-sections. This includes *C. pavonia*, *C. parva*, *C. conica*, and *Cuneolina walteri* Cushman & Applin. This grouping does not include *Cuneolina compressa* Schlagintweit, 1988 that is smaller, with a thinner wall, and with finer septa and radial partitions.

The following description by Kuss & Schlagintweit (1988) is a useful summary of the concept of "*Cuneolina* ex gr. *pavonia*": "*...represents a highly developed flabelliform* Cuneolina *with a convex base [apertural face]. The primary chambers of the test are divided by radial partitions into chamberlets, forming narrow rectangular shapes with a height approximately twice width. Secondary subepidermal partitions (both horizontal and vertical) are developed. Unilocular proloculus large, measuring about 0.11 mm in diameter. Size (in mm): height: 0.75 – 2.0 mm; thickness 0.27 – 0.3 mm. The angle of inclination [apical angle] of the test varies too greatly to use the width of individual tests as a characteristic measurement*."

A description of *C. conica* is similar (Albrich et al., 2015): "*Fan-shaped shell, biserially arranged, with low and broad chambers occupying an opening angle [apical angle] of about 70º. The number of chambers is about 20. The shell varies from 0.7mm to 1.2 mm in length. The exoskeleton consists of well-developed beams and rafters. The number of beams per chamber can reach about 20 in the last chamber*".

C. pavonia was mentioned by d'Orbigny in 1839 and a description subsequently provided by him in 1846 based on material from Ile Madam, France. Although originally considered as Turonian by d'Orbigny, Loeblich & Tappan (1964) regarded the types as Cenomanian. Schlumberger (1900) subsequently described the species from the Santonian of Spain.

C. parva was originally described as a subspecies (because of a smaller size) of *C. pavonia* by Henson (1948b) but has often been regarded as a species in its own right (e.g. Arnaud-Vanneau & Sliter, 1995). It was first described from Egypt from a section considered to be Santonian, but subsequently regarded as Albian (Arnaud-Vanneau & Sliter, 1995) or Turonian (Whittaker et al., 1998).

C. walteri was described from the middle Cenomanian of Florida (Cushman & Applin, 1947; Applin & Applin, 1965), with a supposed relatively small size: Length up to 1.00 mm; breadth up to 1.40 mm; thickness 0.30 mm. The indistinct sutures are said to be a distinguishing feature, and it has a markedly flaring test. Nonetheless, Filkorn & Scott (2011) regarded it as synonymous with *C. parva* (see also Omaña et al., 2019), in turn noting that this is hardly distinguishable from *C. pavonia*.

The Early Cretaceous species *Cuneolina hensoni* Dalbiez, 1958 is similar to *C.* ex gr. *pavonia* but has a much coarser internal structure with broad rectangular, almost square chamberlets. There are a number of other Cretaceous species of cuneolinids. These include *Cuneolina axinoides* Arnaud-Vanneau, 1980; *Vercorsella arenata* Arnaud-Vanneau, 1980; *Scythiolina camposaurii* (Sartoni & Crescenti, 1962); *Vercorsella laurentii* (Sartoni & Crescenti, 1962); *Vercorsella scarsellai* (De Castro, 1963); and *Cuneolina sliteri* Arnaud-Vanneau & Premoli-Silva, 1995 and other species assigned to *Scythiolina* Neagu 1997 and *Histerolina* Neagu 1997. All are smaller and less flabelliform than *C.* ex gr. *pavonia*, and with fewer radial partitions and typically no or few secondary subepidermal partitions. Those assigned to *Vercorsella* have a slit-like aperture including the earliest species, *V. halleinensis* Schlagintweit & Gawlick, 2005 from the late Tithonian – early Berriasian of Austria, also recorded by Hosseini & Conrad (2008) from the Berriasian of Iran. The poorly-known Late Cretaceous *Cuneolina cylindrica* Henson, 1948b is characterised by an acute apical angle leading to a narrow, cylindrical test shape.

Random sections of *C.* ex gr. *pavonia* can be confused with the discoidal genus *Dicyclina* (see separate species entries) that has annular chambers. As mentioned by Brönnimann et al. (1983), *Dicyclina* represents a more specialized form and is regarded as the final stage in the evolution of a flabelliform *Cuneolina. Nakkadyia awadi* introduced by Ismail et al. (2009) from the Cenomanian of Egypt might be an intermediate form between *Cuneolina* and *Dicyclina* (and is considered as a taxon of uncertain status by WoRMS.org – Hayward et al., 2025). Given that it is not truly annular (i.e. it is said to be fan-shaped) it is tentatively regarded as a synonym of *Cuneolina* ex gr. *pavonia* pending further research. As noted by Schlagintweit (1992) and Cvetko Tešović et al. (2001) the embryonic apparatus of advanced *Cuneolina* ex gr. *pavonia* comprises a globular eccentric proloculus surrounded by low and wide chambers (i.e. with a subembryonic zone similar to that of *Dicyclina schlumbergeri*). However, that of *D. schlumbergeri* is larger and more complex. Axial sections also have a similarity in the nature of septa and subepidermal partitions.

Confident Stratigraphic Range: Aptian – Maastrichtian. Common records throughout this range.

Uncertain Stratigraphic Range: not applicable.

The long range of *C.* ex gr. *pavonia* is well established. Sartoni & Crescenti (1962) introduced a biozone of *Cuneolina pavonia parva* for the Albian – Cenomanian and of *Cuneolina pavonia parva* and *Dicyclina schlumbergeri* for the Turonian – Senonian (intra-Late Campanian) period of the southern Apennines, Italy. However, according to Chiocchini et al. (2012) the range of *Cuneolina pavonia* in the Apennines is restricted to within the late Cenomanian. The oldest specimens of *C.* ex gr. *pavonia* appear to be Aptian (Altıner & Decrouez, 1982; Mouty & Saint-Marc, 1982; Kuss & Schlagintweit, 1988, Schlagintweit et al., 2016; Solak & Taslı, 2023 and – possibly – Gollesstaneh, 1965 and Koç, 2017) and the taxon has long been regarded as long-ranging throughout the mid-Cretaceous and into the upper part of the Late Cretaceous (Saint-Marc, 1974; Velić, 2007). Barremian records (e.g. Soklić, 2019) are not confirmed by illustration. It appears to range throughout the Late Cretaceous to the Maastrichtian (Caus & Cornella, 1983; Sinanoğlu et al., 2020), giving a total long range of Aptian – Maastrichtian.

Locally, the inception or extinction of *C.* ex gr. *pavonia* may have stratigraphic significance (e.g. Aguilero-Franco, 2000, 2003), but given the long range of the taxon these will be facies-controlled events.

Geographic Distribution: Very widespread from the Caribbean/Central America region (including mid-Pacific seamounts), and through Neotethys as far east as Somalia and Tibet.

Genus ***Pseudotextulariella*** Barnard in Barnard & Banner, 1953 (see Table 1 for diagnosis)

Pseudotextulariella cretosa **(Cushman, 1932)**

Figure 18

T 1932 *Textulariella cretosa* n. sp. **–** Cushman, p. 97-98; pl. 11, figs. 17-19; Cretaceous, southern England.

1937 *Textulariella cretosa* – Cushman, p. 61, pl. 6, figs. 26-28; Cretaceous, southern England.

1948 *Textulariella cretosa* – Williams-Mitchell, p. 97, pl. 8, fig. 1; early Cenomanian (*Schloenbachia varians* Zone), southern England.

1953 *Pseudotextulariella cretosa* (Cushman) – Barnard in Barnard & Banner, p. 198-199; fig. 6B-I; early Cenomanian (*Schloenbachia varians* Zone), southern England.

1963 *Pseudotextulariella cretosa* – Barnard, p. 48-51, pl. 7, figs. 1-6, 8; text-figs. 6a-d, 7a-f, 8a-c; early Cenomanian (*Schloenbachia varians* Zone), southern England.

1964 *Pseudotextulariella cretosa* – Loeblich & Tappan, fig. 202 (3-4); Cenomanian, southern England.

1965 *Pseudotextulariella cretosa* – Charollais & Brönnimann, pl. 2, figs. a-b; pl. 3, figs. a-b; early Cenomanian (*Schloenbachia varians* Zone), southern England.

1966 *Pseudotextulariella cretosa* – Grönhagen & Luterbacher, text-figs. 1-3; Cenomanian, Swiss Jura.

1966 *Pseudotextulariella cretosa* – Brönnimann, pl. 3, figs. 1-2, 5; early Cenomanian (*Schloenbachia varians* Zone), southern England.

Non 1972 *Pseudotextulariella* sp. cf. *P. cretosa* – El-Naggar & Al-Rifaiy, fig. 5 (3-4); middle – late Cenomanian, Kuwait [simple biserial form].

1972 *Pseudotextulariella cretosa* – Gawor-Biedowa, p. 34-35, pl. 3, figs. 4a-b; Cenomanian, Poland.

? 1975 *Pseudotextulariella cretosa* – Heller, pl. 2, fig. 1; Cenomanian, Poland [poor external view only].

1977 *Pseudotextulariella cretosa* – Carter & Hart, p. 23-24, pl. 2, fig. 12; early – middle Cenomanian, southern England.

1980 *Pseudotextulariella cretosa* – Frieg, p. 238, pl. 2, figs. 12-13; early – middle Cenomanian, northern Germany.

1983 *Pseudotextulariella cretosa* – Peryt, p. 438, pl. 21, fig. 6; early – middle Cenomanian, Poland.

? 1983 *Pseudotextulariella cf. cretosa* – Schroeder & Willems, pl. 4, fig. 6; Cenomanian, northern Spain [indeterminate].

? 1985 *Pseudotextulariella cretosa* – Weidich, pl. 4, fig. 2; early – middle Cenomanian, southern Germany [indeterminate].

1987 *Pseudotextulariella cretosa* – Leary, p. 75, pl. 13, figs. 1-3; late Cenomanian, North Sea.

1989 *Pseudotextulariella cretosa* – Hart et al., pl. 7.2; figs. 11-12; intra-early – middle Cenomanian, southern England.

1989 *Pseudotextulariella cretosa* – Frieg, text-fig. 2, pl. 1, figs. 1-2, 4-11; intra-late Albian – intra-early Cenomanian, northern Germany.

1990 *Pseudotextulariella cretosa* – Hart et al., figs. 3, l, o; intra-early – middle Cenomanian, southern England.
1991 *Pseudotextulariella cretosa* – Packer, pl. 2, fig. 13; Cenomanian, Denmark.
? 1993 *Pseudotextulariella cretosa* – Al-Rifaiy et al., pl. 1, fig. 8; late Cenomanian, Jordan [external view only].
1993 *Pseudotextulariella cretosa* – Witte et al., pl. 2, figs. 8-9; middle Cenomanian, Netherlands.
1996 *Pseudotextulariella cretosa* – Mitchell, pl. 1, figs. 9-10; early – middle Cenomanian, northern England.
? 1996 *Pseudotextulariella cretosa* – Zghal et al., pl. 1, figs. 9-10; middle Albian (range given as middle – late Albian), Tunisia [uncertain external view only].
1998 *Pseudotextulariella cretosa* – Mitchel & Carr, pl. 4, fig. 4; intra-early – middle Cenomanian, southern England.
2000 *Pseudotextulariella cretosa* – Herngreen et al., pl. 3, fig. 82; middle Cenomanian, The Netherlands.
2002 *Pseudotextulariella* sp. – Császár, pl. 4, figs. 3-4; late Albian – early Cenomanian, Hungary [age is based on the presence of the genus].
2002 *Pseudotextulariella cretosa* – Bucur & Baltres, p. 83-84, pl. 3, figs. 1-10, pl. 4, figs. 1-8; early Cenomanian, Dobrogea, Romania.
Non 2013 *Pseudotextulariella cretosa* – Shahin & Elbaz, pl. 2, figs 1-2; Cenomanian, Sinai, Egypt [lacks complexity of internal architecture].
2021 *Pseudotextulariella cretosa* – Besen et al., p. 424, fig. 8s; undifferentiated late Albian – (middle) Turonian, northern Germany.
2023 *Pseudotextulariella cretosa* – Schlagintweit & Yazdi-Moghadam, fig. 5m-n [specimens illustrated by Brönnimann, 1966].

Reference Images: Brönnimann (1966).

Taxonomy/Identity: This species was introduced by Cushman (1932) as *Textulariella cretosa* with a limited description from the Cretaceous Chalk of southern England. It was adopted by Barnard (in Barnard & Banner, 1953) as the type species for his new genus *Pseudotextulariella*. Further information was given by Barnard (1963), Charollais & Brönnimann (1965), Frieg (1989), Bucur & Baltres (2002), and Schlagintweit & Yazdi-Moghadam (2023).

Pseudotextulariella is subconical, early stage triserial (no trochospiral initial stage e.g., Loeblich & Tappan, 1987), later biserial with chambers subdivided by vertical and horizontal partitions (beans and rafters). The aperture is interiomarginal. A small embryo is present in a form called *Pseudotextulariella* sp. by Dufaure et al. (1984). Although probably of this genus, this specimen seems to fit with neither the morphology of *P. cretosa* or *Pseudotextulariella brevicamerata* Schlagintweit & Yazdi-Moghadam, 2023 (see also *Pseudotextulariella* sp. illustrated by Solak et al., 2020). An embryo is also possibly visible in the illustrations of *P. cretosa* by Grönhagen & Luterbacher (1966, fig. 2b).

P. cretosa is a distinctively large (up to 1.75 mm in test height and maximum diameter) and complex species with multiple orders of rafters (see Table 1 of Schlagintweit & Yazdi-Moghadam, 2023). Only two orders of beams appear to be present. However, some specimens are quite small – see Gawor-Biedowa (1972) who recorded dimensions of around 0.6 – 0.9 mm. Frieg (1989) considered that both simple, smaller, microspheric, and more complex, larger, macrospheric forms occurred. *P. brevicamerata* (see below) and Valanginian *Pseudotextulariella courtionensis* Bronnimann, 1966 are smaller and only have one order of rafters and reduced height of chamber lumen.

Other supposed species of *Pseudotextulariella* – *Pseudotextulariella salevensis* Charollais, Brönnimann & Zaninetti, 1966, *Pseudotextulariella scarsellai* De Castro, 1963, *Pseudotextulariella subalpina* Arnaud-Vanneau, 1980 and “*Pseudotextulariella barnardi*” Gollesstaneh, 1965 – can be assigned to other genera (see WoRMS online catalogue, Hayward et al., 2025; Schlagintweit, 2014). *Pseudotextulariella* sp. 1 of Chiocchini et al. (1994) from the late Cenomanian of Italy, is a simple biserial form, without the architectural complexity of the genus.

The holotype of *P. cretosa* (external view) has been re-illustrated by Smithsonian National Museum of Natural History (https://collections.nmnh.si.edu/search/paleo/?ark=ark:/65665/3aaf1d197dc954c1680875acc55800236).
https://www.marinespecies.org/aphia.php?p=taxdetails&id=1045991

Confident Stratigraphic Range: Intra-late Albian – late Cenomanian (common in suitable facies within the intra-early – middle Cenomanian).

Uncertain Stratigraphic Range: middle Albian, Turonian – Coniacian.

A species whose range is highly facies-dependent. Supposedly (according to Barnard, 1963) the type specimens are from the Lower Chalk at Charing, Kent, England (early Cenomanian, *Schloenbachia varians* Zone). Williams-Mitchell (1948) and Barnard & Banner (1953) considered the species a useful marker for this zone. In more recent research, Wilkinson & Hopson (2011) recognised the inception of *P. cretosa* as indicating foraminiferal Zone 9 of Carter & Hart (1977), UKB3 of Hart et al. (1989) and BGS 2 of Wilkinson (2011) which indicates a level close to the base of the *dixoni* Zone or high in the *mantelli* zone. Carter & Hart (1977) remarked that it “*occurs in large numbers in the lower levels of the Cenomanian*” but showed that the inception (base of their Zone 9) is intra-early Cenomanian (see also Hart et al., 1989).

Outside of chalk facies, the species is known from open marine marly facies of the intra-late Albian (Frieg, 1989; Besen et al., 2021) and has been reported from the latest Albian of Switzerland by Grönhagen & Luterbacher (1966) but not illustrated. Magniez-Jannin (1983)

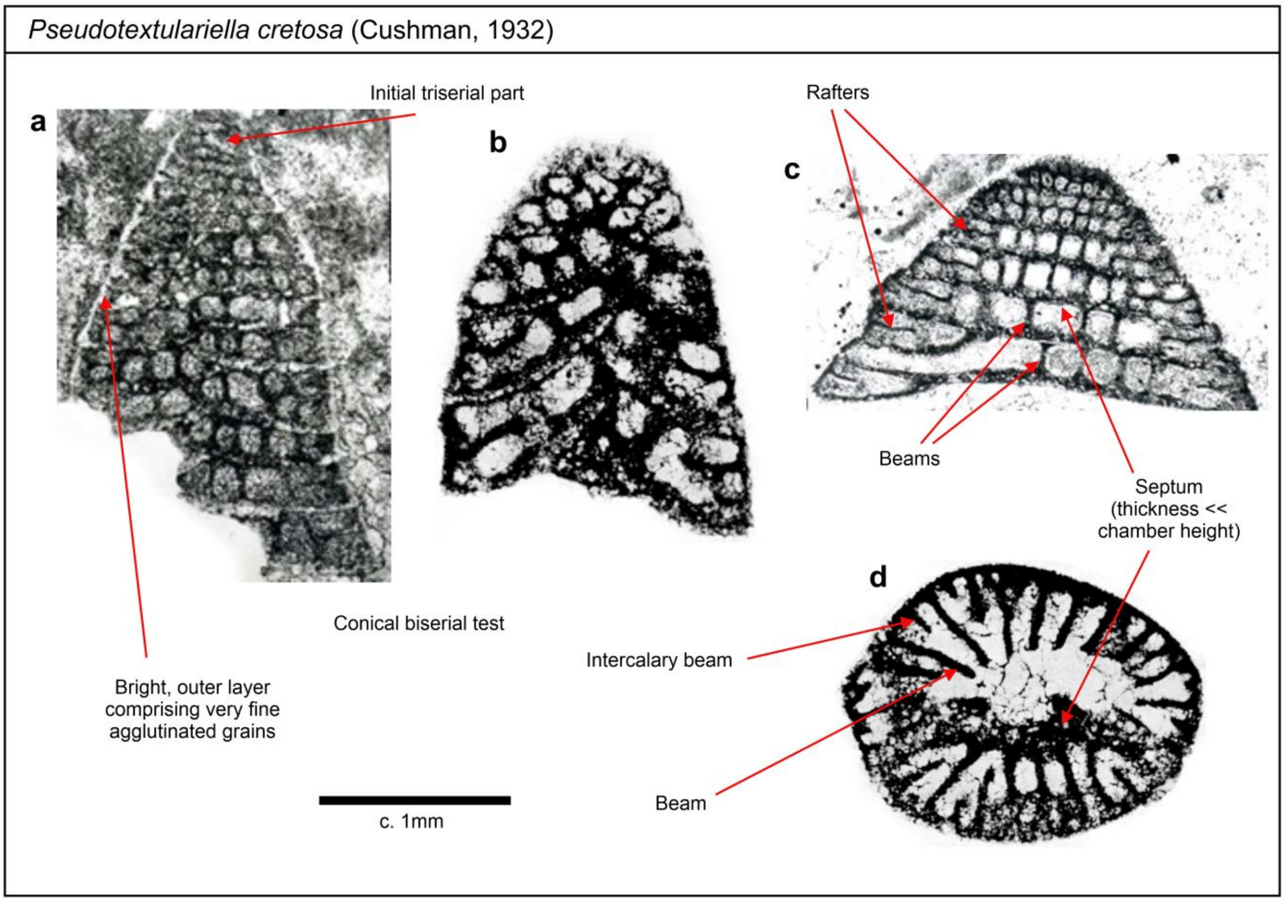


Fig. 18. Representative illustrations of *Pseudotextulariella cretosa*: **a.** Axial section, Bucur & Baltres (2002, pl. 3, fig. 1, Romania); **b.** Near axial section, Brönnimann (1966, pl. 3, fig. 1, southern England); **c.** Oblique tangential section, Bucur & Baltres (2002, pl. 3, fig. 9, Romania); **d.** Transversal section, Brönnimann (1966, pl. 3, fig. 2, southern England).

reported it from the late Albian of northern France.

P. cretosa is said to range up to the near top middle Cenomanian of northern France (Amédro et al., 1978) but is not illustrated. Besen et al. (2021) reported it from the middle Turonian and further extended the range to the Coniacian (Besen et al., 2023) but without illustration. Reported but not illustrated from the late Cenomanian of the Czech Republic (Cech et al., 2005; Zitt et al., 2010). The last appearance datum is considered a marker horizon for middle Cenomanian in the North Sea (King et al., 1989), but Leary (1987) found rare and small specimens in the late Cenomanian.

Geographic Distribution: The species is mostly known from the marls of the chalk facies from north-west Europe (southern England, northern France, northern Germany, Poland), but has been recorded, if seldom illustrated, from the northern margin of Neotethys in Switzerland (Grönhagen & Luterbacher, 1966; Brönnimann, 1966), northern Spain (Gräfe, 2005), the Czech Republic (Čech et al., 2005; Zitt et al., 2010), Hungary (Görög, 1996; Császár, 2002) and Romania (Bucur & Baltres, 2002). It appears to be absent from the Mediterranean and Arabian Plate, notwithstanding some highly uncertain records (see synonymy list).

Pseudotextulariella brevicamerata Schlagintweit & Yazdi-Moghadam, 2023

Figure 19

1965 Gen. nov. ? cf. *Pseudotextulariell*a sp. – Hamaoui, pl. 7, figs., 15, 17; pl. 12, fig. 2, 4; Cenomanian, Israel.

2014 *Nummoloculina regularis* Philippson – Afghah & Fadaei, fig. 8b; Cenomanian, Iranian Zagros. [N.B. the captions for figures 8 and 9 are transposed, the authors intended to indicate that this is *Orbitolinella depressa* Henson].

T 2023 *Pseudotextulariella brevicamerata* n. sp. – Schlagintweit & Yazdi-Moghadam, p.7-10, figs. 5-a-i, k; middle Cenomanian, Iranian Zagros.

Reference Images: Schlagintweit & Yazdi-Moghadam (2023).

Taxonomy/Identity: This species was first named and comprehensively described by Schlagintweit & Yazdi-Moghadam (2023) and comparison made to *P. cretosa* and *P. courtionensis.* Compared to the type species of the genus, *P. cretosa*, *P. brevicamerata* is a small species (test height up to 0.8 mm; test diameter up to 0.85 mm) with many (20-34) chambers, divided by a

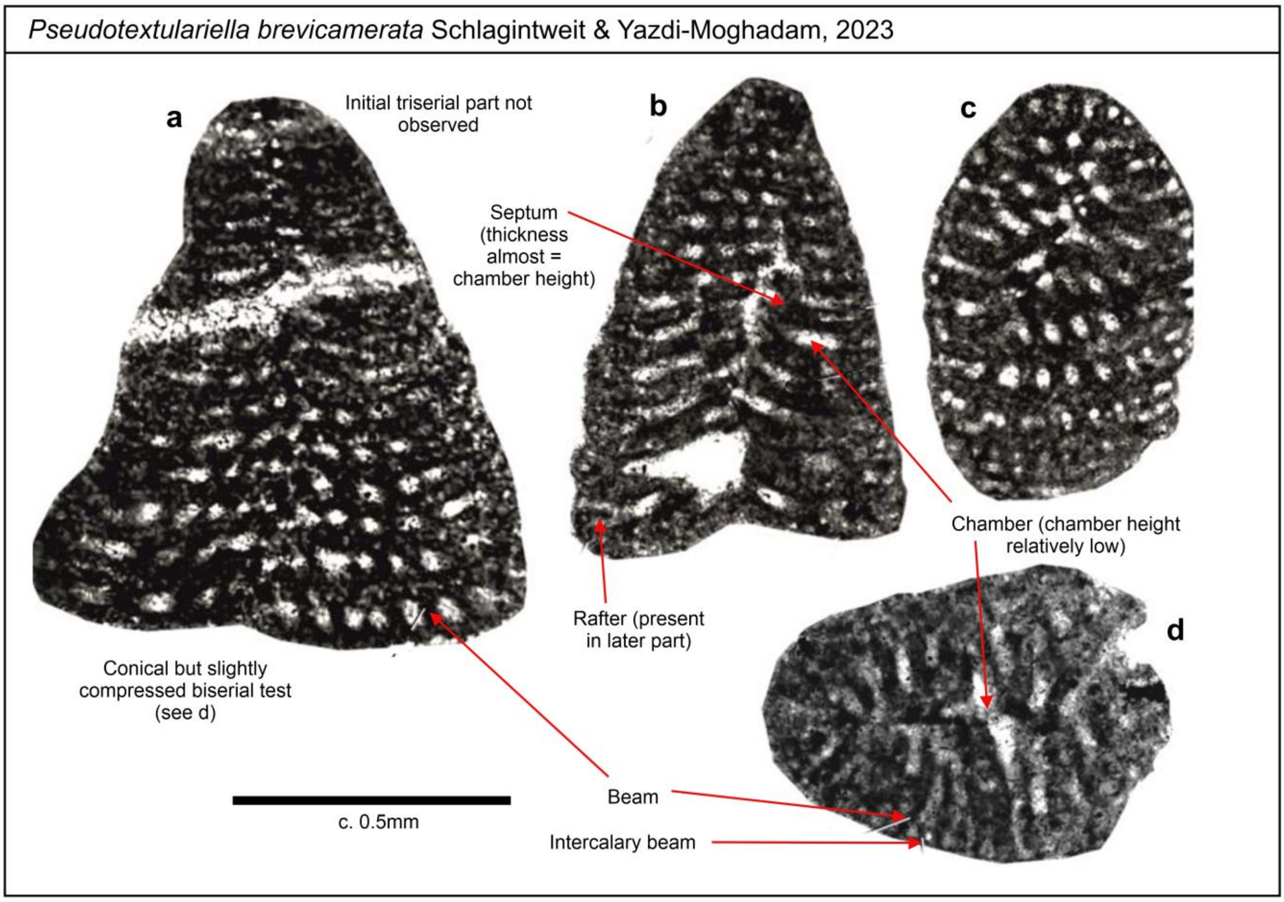


Fig. 19. Representative illustrations of *Pseudotextulariella brevicamerata*: **a.** Subaxial section, Schlagintweit & Yazdi-Moghadam (2023, fig. 5d, Iranian Zagros); **b.** Subaxial section (holotype), Schlagintweit & Yazdi-Moghadam (2023, fig. 5e, Iranian Zagros); **c.** Oblique section, Schlagintweit & Yazdi-Moghadam (2023, fig. 5c, Iranian Zagros); **d.** Fragmentary transverse section, Schlagintweit & Yazdi-Moghadam (2023, fig. 5f, Iranian Zagros).

single order of rafters. Chambers are thus relatively and distinctively reduced in height (25-50 µm). The short initial triserial stage as typical for the genus (Barnard, 1963) has not been observed due to inadequate sections. The biserial chambers are subdivided by both horizontal and vertical (= radial) partitions. It appears that the horizontal partitions (rafters) are not present in the early part but appear later during ontogeny. In contrast, the radial vertical partitions (beams; up to three orders) seem to be present in the early stage.

Like *P. brevicamerata*, *P. courtionensis* also has only one order of rafters appearing in the adult part of the test. With equivalent dimensions (height, diameter) compared with *P. courtionensis*, *P. brevicamerata* has more chambers due to reduced thickness of septa and chamber height (lumen).

Confident Stratigraphic Range: middle Cenomanian (scarce).

Uncertain Stratigraphic Range: not applicable.

This species was only recently described from the middle Cenomanian of the Iranian Zagros (Schlagintweit & Yazdi-Moghadam, 2023). However, it was illustrated as “Gen. nov. ? cf. *Pseudotextulariella* sp.” by Hamaoui (1965) from the undifferentiated Cenomanian of Israel.

Geographic Distribution: So far, only known from the Iranian Zagros and Israel (Arabian Plate, southern Neotethys margin).

Family **DICYCLINIDAE** Loeblich & Tappan 1964 (diagnosis *sensu* Loeblich & Tappan, 1987)

Genus ***Dicyclina*** Munier-Chalmas 1887 (see Table 1 for diagnosis)

Dicyclina is morphologically one of a group of agglutinating genera characterised by a large, flattened disc with an initial embryonic stage (forming the thickest part of the test), followed by a small planispiral stage (or no planispiral stage at all) and finally a post-embryonic stage where the characteristic biseriate chambers are added annularly or cyclically (i.e., *Cyclolina*, *Cyclopsinella*, *Mangashtia* and *Dicyclina*). These are also somewhat reminiscent of porcellaneous forms such as *Broeckina*. *Dicyclina* differs from all the others in that it has a relatively large and complex embryonic apparatus, and that it adds successive annular chambers alternately either side of the median equatorial plane (i.e. in two alternating layers analogous to the term “biserial”). The other annular genera herein add successive single annular chambers across the median plane. Some genera (e.g., *Mangashtia*, *Cyclopsinella*) may give the *appearance* of

2-layers of chambers as their annular chambers have a series of radial pillars or clusters of pillars in the middle of the chambers but these "chambers" therefore do not alternate.

As with all LBF, a descriptive terminology when naming the fossilised parts of the organism's shell is required and variations of these are often used to discriminate between taxa. The nomenclature and characteristics of internal structures are especially important. A comprehensive illustrated glossary of descriptive terms applied to the study of foraminifera in general was provided by Hottinger (2006) which has achieved "standard" status among most workers and is followed here. Members of the Dicyclinidae (which at present includes only the genus *Dicyclina*) display variably complex internal structures and Figure 20 shows, in very generalised schematic form, the broad disposition and identity of these.

Specific variation in *Dicyclina* is based primarily on (a) the nature of the embryonic apparatus (Figure 20 part a); (b) the number and disposition of both the radial ("beams") and transverse ("rafters") elements which together evolve externally to form a subepidermal network beneath the outer test wall (Hottinger, 1978) and (c) the general shape (in axial cross-section) of the primary chamber septa and attachments thereto such as other "rafters" and the annular "groove" or "gutter" running close to the free edge of the septa (Figure 20 part b).

In some cases when dealing with these morphological attributes, the exact nature of these features; their relationship to other features; and their biological function(s) are not clear or are unknown. Theoretically, elongated unclosed (stolons) or tubular closed (canals) spaces serve for protoplasmic flow or differentiation of protoplasmic activity in foraminifera (see e.g. Hottinger & Dreher, 1974). For example, in species of *Dicyclina* (studies of which are challenged in general by a lack of suitable material) both the form and function of the annular "groove" or "gutter" are imperfectly known with some workers (e.g., Schlumberger & Choffat, 1904, and Neumann, 1967) showing the "gutter" as fully enclosed, whereas we believe (see inset image in Figure 20) the "gutter" is open and connected to the foramina and is an active part of the protoplasmic flow system.

Another feature imperfectly known is the nature and position of the radial (i.e., running from the embryonic region in the direction of annular growth) "grooves" or "canals" which lie in between the radial partitions themselves ("beams") and which – although shown herein running immediately below the outer chamber wall (which is removed in our schematic illustration) – could equally be positioned at the lower part of the transverse "rafters".

Meanwhile for the purposes of this article the "naming of parts" is sufficient to provide a useful descriptive framework.

The (generally) large diameter and relative thinness of the *Dicyclina* test, plus the tendency for its post-embryonic disc to undulate, means that specimens in thin section are seldom complete and oriented optimally to display many of the features mentioned above. Moreover, because of the disc-like nature of the test with the embryonic zone at the centre, it is very often difficult to discern on which side of the embryo the sub- and supra-embryonic zones are in fact placed (this is not an issue in conical genera like *Orbitolina*). This makes identification to species level especially challenging in random sections and even important taxonomic elements are sometimes not observed in type material (see *Dicyclina qatarensis* and Table 5 below). In practice, many specimens cannot be identified more definitively than "*Dicyclina* sp.", even when a species name has been attached. Saint-Marc (1974, 1981) did not identify *Dicyclina* beyond generic level in his material from Lebanon, presumably in acknowledgement of this issue.

Furthermore, some transverse sections of species of *Dicyclina* – especially when only fragmentary – resemble fragmentary axial sections of non-discoidal/cyclic genera such as *Cuneolina* (e.g., compare Figure 17 of *C.* ex gr. *pavonia* with Figure 22 of *D. schlumbergeri* herein). Cherchi & Schroeder (1990a) (following Brönnimann et al., 1983 and others) hypothesised that *Dicyclina* had in fact developed from *Cuneolina* by becoming fully annular and based on (p. 330) "…*identical internal chamber structures and a very pronounced initial spiral stage, which was more and more reduced in the course of the phylogenesis*". To this one might add that *Dicyclina* has a larger, more complex embryonic apparatus than even the most advanced *Cuneolina*. In practice, some specimens are best identified as "*Cuneolina*/*Dicyclina* sp." (Simmons et al., 2020; see also discussion in section on *Cuneolina* ex gr. *pavonia* in this paper).

The status of *Dicyclina* taxonomy remains somewhat ambiguous. Schroeder & Neumann (1985) in their extensive treatment of mid-Cretaceous larger foraminifera did not include *Dicyclina* (or *Cuneolina* for that matter) in their work, stating that they are "… *still subject of anatomical and taxonomical problems to be solved.* " *(p. 8). Despite subsequent smaller publications on Dicyclina by Cherchi & Schroeder (1990a, b), and as is clear from the following discussions on the genus and the individual species, these problems have yet to be fully resolved.*

The online WoRMS catalogue of foraminifera records six possible species of *Dicyclina* (Hayward et al., 2025). Of these, *Dicyclina lusitanica* Egger, 1902 belongs in the genus *Anchispirocyclina* (*fide* Hottinger, 1967) and *Dicyclina aegyptiaca* Hewaidy, 1993 lacks sufficient internal description to distinguish it as a *Dicyclina* and to separate it from possible synonyms (thus a *taxon inquirendum* pending further study of type material). In any case, it (and the associated "*Dicyclina* sp. A") were described from Maastrichtian strata and are thus outside

Table. 5. Characteristic features of four broadly defined Cenomanian species of *Dicyclina* herein: *D. schlumbergeri*, *D. qatarensis*, *D. simplex* and *D. sampoi*.

CHARACTERISTIC	***D. SCHLUMBERGERI***	***D. QATARENSIS***	***D. SIMPLEX***	***D. SAMPOI***
Original description & provenance	Munier-Chalmas (1877), Senonian of Dep. Bouches-du-Rhône, France (outcrop). Type material lost	Henson (1948b), Cenomanian of Qatar (subsurface)	Cherchi & Schroeder (1990a), middle Cenomanian of Île Madame, France (outcrop)	Cherchi & Schroeder (1990b), middle-late Cenomanian of Tang-e-Benori, Iran (outcrop)
Overall shape	Flat (undulating), thin discoidal	Flat (undulating), thin discoidal	Flat (undulating), rel. thick discoidal	Flat (undulating), thin discoidal
Dimensions	Neotype material of Gendrot (1968) from Coniacian of France, designated by Cherchi & Schroeder (1990a): Test Diameter: 10.7mm Thickness 0.33mm Embryo Diameter: 0.65-0.95mm	Test Diameter: max 6mm	Test Diameter: 1.32-3.0mm Thickness 0.27-0.35mm Embryo Diameter: 0.30-0.38mm	Test Diameter: 2.40-6.80mm Thickness 0.16-0.30mm Embryo Diameter: 0.30-0.61mm
Annular chambers / mm	Slightly less than that of *D. qatarensis** (i.e. c.7)**	8	Not stated	8-9
Radial features (“beams”) / quadrant	Less than half of *D. qatarensis** (i.e. c.40-50)***	c. 100	Not stated	Not stated
Transverse features (“rafters”)	Present on chamber roof and inner part of septa	Uncertain	Present on chamber roof and inner part of septa	Present on chamber roof only (****)
Embryo	Irregular ellipsoid or globular	Not observed	Globular or reniform	Irregular broad ellipsoid
Sub-embryonic zone	Subdivided by septula forming an “alveolar layer”	Not observed	Drop-shaped, subdivided by septula	Smaller diameter and less vaulted than Supra-EZ but same kind of subdivision
Supra-embryonic zone	Well-developed subepidermal chamberlets	Not observed	Incomplete layer of chamberlets in eccentric position relative to test axis (i.e., an initial spiral)	Relatively thin, thin septulae (chamberlets sl. higher than wide) and minute secondary chamberlets
Septa shape	C-shaped	Unclear	Unclear	Hook-shaped
Comments	* According to remarks by Henson (1948b). (No dimensions were provided by Gendrot (1968) for the Neotype designated by Cherchi & Schroeder, 1990a) ** 5-7/mm according to Cvetko Tešović et al., 2001; p. 602) *** Specimens illustrated by Schlagintweit & Rashidi (2018) show approx. 20-?25/quadrant.			**** Although some illustrations show rafters occurring on the inner septal wall (see text) so this feature may not be species-diagnostic.

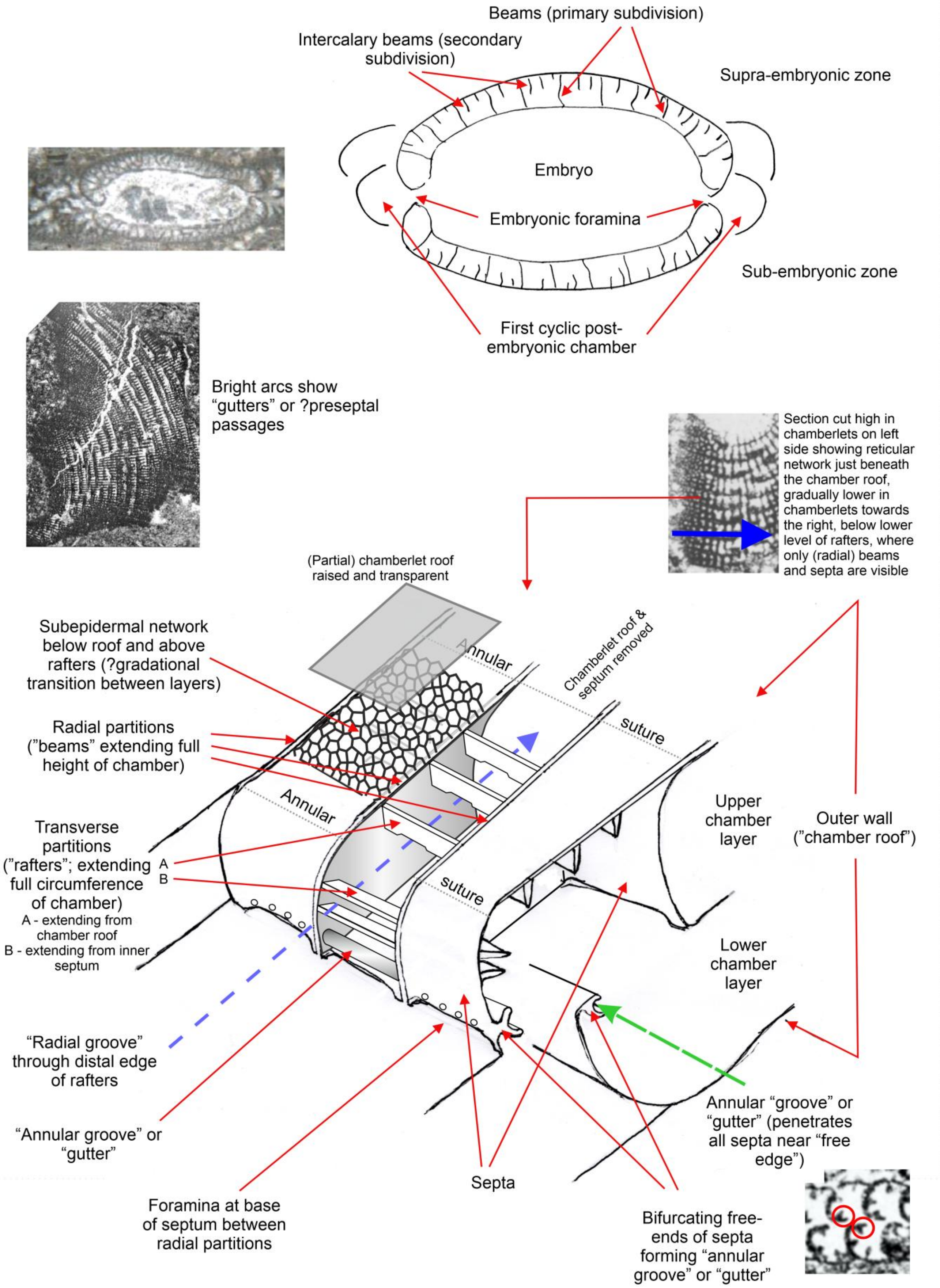


Fig. 20. Broad disposition of internal morphological features of *Dicyclina* (schematic view, conceptual only; the relative proportions between elements are estimated. See text for details).

the focus of this paper. Therefore, four species of *Dicyclina* are included herein: *Dicyclina schlumbergeri* Munier-Chalmas 1887 (the type species of the genus); *D. qatarensis* Henson 1948b; *D. simplex* Cherchi & Schroeder 1990a and *D. sampoi* Cherchi & Schroeder 1990b. They are distinguished from one another by a combination of overall size (diameter), embryonic apparatus size and complexity (i.e., the presence/absence of secondary chamberlets in the supra- or sub-embryonic zones), and whether transverse subepidermal partitions (in this case, "rafters") are limited to the inside of the peripheral chamber wall or also occur on the septa (as shown in Figure 20b). The numbers of (a) annular chambers per mm radius and (b) radial partitions ("beams") per quadrant are also used. Overall chamber shape in axial section may also be useful, at least for distinguishing *D. simplex* from other taxa (Figure 21). *D. qatarensis* is probably the most poorly described/defined and Cherchi & Schroeder (1990b) regarded it as (p. 210) "*… a badly defined and unrecognisable species*" citing a lack of a megalospheric embryo visible in the type material. It is also excluded from general discussions of Middle East *Dicyclina* by Schlagintweit & Rashidi (2018) and Schlagintweit & Yazdi-Moghadam (2021). The species as can currently be best understood is further discussed below.

On the other hand, *D. schlumbergeri* is a very widely-reported taxon over a long stratigraphic interval (late Albian-Maastrichtian – but see discussion below) and it is likely that this has been used as a "bucket" term for dicyclinids found in random orientations that are technically indeterminate at species level if using "best practice". This emphasises the need for deliberate or fortuitously good, oriented sections, ideally displaying the embryonic apparatus, septa, and sub-epidermal partitions which show both genus *and* species characteristics before arriving at a specific determination (Frijia et al., 2015).

Prior to 1990 and the introduction of *D. simplex* and *D. sampoi* (Cherchi & Schroeder, 1990a, b), almost all records of *Dicyclina*, if assigned to a species, were assigned to *D. schlumbergeri*. Cherchi & Schroeder (1990a, b) challenged this paradigm implying that there was an evolutionary plexus from *D. simplex* (e.g. Cenomanian) to *D. schlumbergeri* (e.g. Coniacian and younger) with *D. sampoi* (e.g. Cenomanian) forming a separate Arabian Plate evolutionary lineage. *D. simplex* has a relatively simple embryonic apparatus and *D. schlumbergeri* a complex one, thus Cherchi & Schroeder (1990a) envisaged an evolution plexus of embryonic apparatus development similar to that seen in the Orbitolininae (e.g. Schroeder, 1975; Schroeder et al., 2010). That *D. sampoi* has a complex embryonic apparatus and occurs in the Cenomanian suggests it belongs to a separate lineage according to Cherchi & Schroeder (1990b). Although many authors have ignored or were unaware of this (i.e. continuing to use *D. schlumbergeri* as a *sensu lato* term), the large number of records of *Dicyclina* published since 1990 allow the hypothesis of Cherchi & Schroeder (1990a, b) to be tested.

In summary (see discussion of each of the four species of *Dicyclina* below), the phylogeny of *Dicyclina* is a little more complex than envisaged by Cherchi & Schroeder (1990a, b) and some subsequent workers. All validated records of *Dicyclina* in Coniacian – Maastrichtian strata are *D. schlumbergeri* with *D. simplex* restricted to the Cenomanian and *D. sampoi* to the Cenomanian – ?Turonian. However, *D. schlumbergeri* is also known from the middle – late Cenomanian of Mexico only. Thus, it appears that independent lineages of *Dicyclina* with a complex embryo appeared in the Cenomanian in both Mexico (*D. schlumbergeri*) and the Arabian Plate (*D. sampoi*). By Coniacian times, *D. schlumbergeri* had replaced *D. sampoi* or a repetitive form of evolution had occurred. The relationship to *D. simplex* is unclear.

The morphological details "above" of the differences between the four species are discussed in the individual species treatments and summarised in Table 5 and (excluding *D. qatarensis*) in Figure 21.

As a genus, *Dicyclina* is widely known from Neotethys (as far east as the Arabian Plate) and the Caribbean in rocks ranging in age from supposedly Albian to Maastrichtian (e.g. Cherchi & Schroeder, 1990a, b). Within this review we have been unable to confirm any Albian records of *Dicyclina* and even early Cenomanian records are doubtful. Such specimens may have been confused with *Cuneolina*. Omaña et al. (2019) state that *D. schlumbergeri* is very common in the Albian and Cenomanian strata of Mexico but offer no clear-cut evidence of Albian occurrences. Rey et al. (1977) report but do not illustrate *Dicyclina* sp. from the late Albian of Portugal. Saint-Marc (1974, 1978) places the inception of *Dicyclina* in the middle Cenomanian in Lebanon, although in his 1981 work the Neotethyan inception of the genus occurs within the early Cenomanian. Herein we consider *Dicyclina* to be a middle Cenomanian – Maastrichtian genus, at least in terms of confident records of its occurrence.

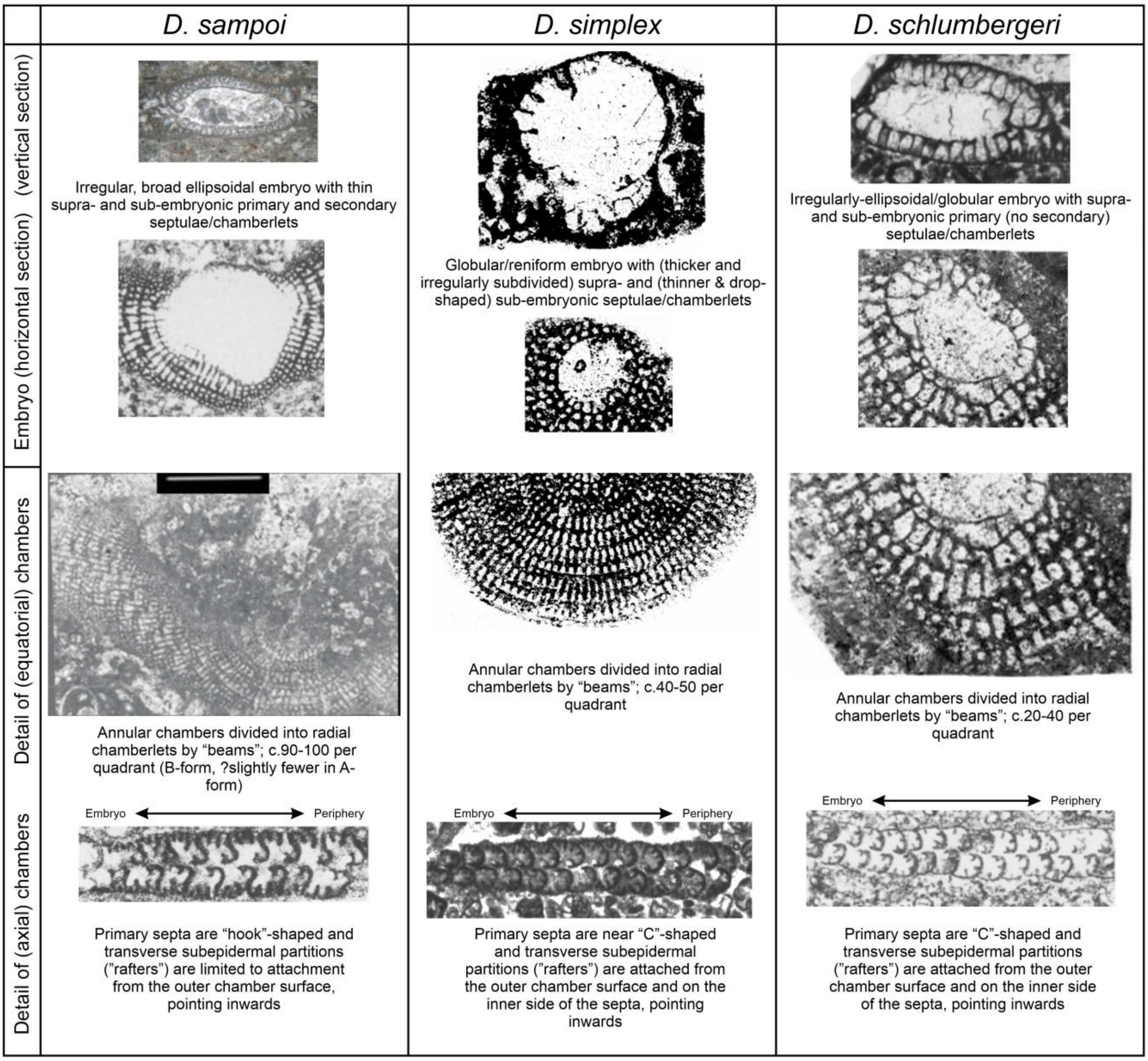
Biozonations utilising *Dicyclina* (e.g. Wynd, 1965; Taslı et al., 2006; Omidvar et al., 2014b; Haftlang et al., 2020; Omidi et al., 2018) are typically recognising a local biofacies, rather than a chronostratigraphically significant discrete range.

***Dicyclina schlumbergeri* Munier-Chalmas, 1877**

Figure 22

T 1877 *Dicyclina schlumbergeri* n. gen., n. sp. Munier-Chalmas, p. 30-31; Senonian, southern France (type material lost) [probably Coniacian – Santonian see Gendrot, 1968].

1904 *Dicyclina schlumbergeri* – Schlumberger & Choffat, p. 148-149, text-figs. 1-2; Senonian, southern France [probably Coniacian – Santonian see Gendrot,



Irregular, broad ellipsoidal embryo with thin supra- and sub-embryonic primary and secondary septulae/chamberlets

Globular/reniform embryo with (thicker and irregularly subdivided) supra- and (thinner & drop-shaped) sub-embryonic septulae/chamberlets

Irregularly-ellipsoidal/globular embryo with supra- and sub-embryonic primary (no secondary) septulae/chamberlets

Annular chambers divided into radial chamberlets by “beams”; c.90-100 per quadrant (B-form, ?slightly fewer in A-form)

Annular chambers divided into radial chamberlets by “beams”; c.40-50 per quadrant

Annular chambers divided into radial chamberlets by “beams”; c.20-40 per quadrant

Primary septa are “hook”-shaped and transverse subepidermal partitions (”rafters”) are limited to attachment from the outer chamber surface, pointing inwards

Primary septa are near “C”-shaped and transverse subepidermal partitions (”rafters”) are attached from the outer chamber surface and on the inner side of the septa, pointing inwards

Primary septa are “C”-shaped and transverse subepidermal partitions (”rafters”) are attached from the outer chamber surface and on the inner side of the septa, pointing inwards

Fig. 21. Differentiation between *D. sampoi*, *D. simplex* and *D. schlumbergeri* based on differences in embryonic apparatus, radial annular chamberlets and axial sections. (*D. qatarensis* not included as no embryonic apparatus has been observed in the few verified specimens illustrated). Note that in axial sections of *D. simplex* and *D. schlumbergeri* the chambers are overlapping at the outer margins (relating to the curved septa) providing a useful distinguishing feature in comparison to *D. sampoi*.

1968].

? 1948b *Dicyclina schlumbergeri* – Henson, pl. XIV, fig. 9; Maastrichtian, Qatar & Iraq [fragment only].

? 1956 *Dicyclina schlumbergeri* – Bonet, p. 406-7, pls. 5-7; Cenomanian, Mexico [fragments only].

? 1961 *Dicyclina* cf. *qatarensis* – Hamaoui, pl. 1, figs. 2-6; Cenomanian, Israel.

Non L 1964 *Dicyclina schlumbergeri* – Loeblich & Tappan, p. C303, fig. 209 (1a-1b); middle Cenomanian, France [lectotype invalid *fide* Cherchi & Schroeder, 1990a = *D. simplex*].

? 1966 *Dicyclina schlumbergeri* – Luperto Sinni, pl. 13, fig. 3; Santonian?, southern Italy [= *Dicyclina* sp.].

? 1967 *Dicyclina schlumbergeri* – Luperto Sinni, p. 176-177, pl. 10, fig. 1; pl. 13, fig. 1; late Cenomanian – Santonian, southern Italy [= *Dicyclina* sp.].

1967 *Dicyclina* cf. *schlumbergeri* – Neumann, pl. 55, fig. 3; pl. 56, figs. 1-2; early Senonian, southern France.

Non 1967 *Dicyclina schlumbergeri* – Neumann, pl. 55, fig. 2; Cenomanian, western France [from the type locality/strata of *D. simplex*].

? 1967 *Dicyclina schlumbergeri* – Neumann, pl. 55, fig. 1; Santonian, Spain [= *Dicyclina* sp.].

1968 *Dicyclina schlumbergeri* – Gendrot, p. 677-678, pl. V, figs. 14-16; Coniacian – Santonian, southern France. [fig. 15 designated as a Neotype by Cherchi & Schroeder, 1990a].

? 1970 *Dicyclina* sp. – Hamaoui & Saint-Marc, pl. 40, fig. 14; late Cenomanian, Lebanon.

1976 *Dicyclina schlumbergeri* – Luperto-Sinni, p. 308-309, pl. 33, figs. 1-6; pl. 34, figs. 1; Senonian, southern Italy.

1978 *Dicyclina schlumbergeri* – Luperto-Sinni & Richetti, pl. 47, figs. 1-7; pl. 48, figs. 1-6; pl. 49, figs. 1-6; Santonian – Maastrichtian, southern Italy.

? 1984 *Dicyclina schlumbergeri* – Bilotte, pl. 5, fig. 2; middle Cenomanian, Pyrenees [= *Dicyclina* sp.].

1984 *Dicyclina schlumbergeri* – Bilotte, pl. 15, fig. 2; early Campanian, Pyrenees.

? 1984 *Dicyclina schlumbergeri* – Bilotte, pl. 25, fig. 5; Maastrichtian, Pyrenees [= *Dicyclina* sp.].

? 1987 *Dicyclina schlumbergeri* – Simmons & Hart, pl. 10.4, fig. 5; middle-late Cenomanian, Oman [= *D. simplex* or *D. schlumbergeri*, possibly *Cuneolina* ex. gr. *pavonia*].

? 1987 *Dicyclina schlumbergeri* – Al-Rifaiy & Cherif, pl. II, fig. 11; Turonian, Jordan [=*Dicyclina* sp.].

1987 *Dicyclina schlumbergeri* – Loeblich & Tappan, pl. 157, fig. 7 (non 8-10); Senonian, France.

Non 1987 *Dicyclina schlumbergeri* – Loeblich & Tappan, pl. 157, figs. 8-10; Cenomanian, France [*fide* Cherchi & Schroeder, 1990a = *D. simplex*].

? 1988 *Dicyclina schlumbergeri* – Sartorio & Venturini, p. 114 lower image, p. 115 upper image, p. 121; Senonian, southern Italy.

? 1988 *Dicyclina schlumbergeri* – Sartorio & Venturini, p. 115 lower image; upper Senonian, Tunisia.

Non 1989 *Dicyclina schlumbergeri* – Rosales-Dominguez, fig. 11B; Albian-early Cenomanian; southwest USA [= *Cuneolina* sp.].

? 1990 *Dicyclina schlumbergeri* – Šribar & Pleničar, pl. 4, fig. 4; late Turonian, southwest Slovenia [indeterminate fragment].

N 1990a *Dicyclina schlumbergeri* – Cherchi & Schroeder, figs. 5-11; Coniacian, France & Sardinia.

? 1992 *Dicyclina schlumbergeri* – Kalantari, pl. 77; Cenomanian, Iranian Zagros [= *Dicyclina* sp.].

1994 *Dicyclina schlumbergeri* – Chiocchini et al., pl. 23, fig. 16; Senonian, central Italy.

Non 1998 *Dicyclina schlumbergeri* – Charrière et al., fig. 4 (3a, 6); late Cenomanian, Morocco [= *D. simplex*].

2000 *Dicyclina schlumbergeri* – Aguilera-Franco, p. 161; middle-late Cenomanian, southern Mexico.

2001 *Dicyclina schlumbergeri* – Cvetko Tešović et al., p. 602, fig. 6D-H; Campanian, Brač Island, Croatia.

? 2003 *Dicyclina schlumbergeri* – Polavder, fig. 5 (17-18); Santonian-Campanian, former Yugoslavia [= *Dicyclina* sp.].

Non 2004 *Dicyclina schlumbergeri* – Khosrow Tehrani & Afghah, pl. 2, fig. 4 [=*Broeckinella arabica* Henson *fide* Schlagintweit & Rashidi, 2016].

? 2005 *Dicyclina schlumbergeri* – Vaziri et al., pl. 2, fig. 4; Santonian-Maastrichtian, central Iran [indeterminate fragment].

? 2006 *Dicyclina schlumbergeri* – Taslı et al., fig. 7U; Coniacian-Santonian, southern Türkiye [= *Dicyclina* sp.].

2007 *Dicyclina schlumbergeri* – Velić, pl. 23, figs. 1-4; Santonian-Campanian, Adriatic platform.

? 2008 *Dicyclina schlumbergeri* – Schlüter et al., fig. 3E; late Campanian, southern Italy [= *Dicyclina* sp.].

Non 2008 *Dicyclina schlumbergeri* – Khosrow Tehrani et al., pl. 1, fig. 6 [=*Broeckinella arabica* Henson *fide* Schlagintweit & Rashidi, 2016].

? 2008 *Dicyclina schlumbergeri* – Ahmadi et al., pl. 3, fig. 1; Cenomanian, Iranian Zagros [best considered as *Dicyclina* sp.].

Non 2009 *Dicyclina schlumbergeri* – Sari et al., pl. 3, figs. 8-9; age uncertain, reworked, Turkish Taurides [= *D. simplex fide* Schlagintweit & Rashidi, 2018].

? 2010 *Dicyclina* sp. – Cavin et al., fig. 9F; late Cenomanian-middle Turonian, Morocco. [image captioned as *Dicyclina* sp. but referred to as *D. schlumbergeri* in text (p. 405)].

Non 2011 *Dicyclina schlumbergeri* – Vaziri, fig. 2D, F; Santonian-Maastrichtian, central Iran [most likely *Cuneolina* sp.].

2011 *Dicyclina schlumbergeri* – Khosrotehrani et al., pl. 1, fig. C; Santonian, Iranian Zagros.

? 2011 *Dicyclina schlumbergeri* – Amer, pl. 19, fig. 1; Cenomanian, western Iraq [best considered as *Dicyclina* sp.].

2012 *Dicyclina schlumbergeri* – Chiocchini et al., pl. 134, figs. 1-8; Santonian, central Italy.

Non 2012 *Dicyclina schlumbergeri* – Rahimpour-Bonab et al., fig. 8G; Cenomanian – Turonian, Iranian Zagros [= *D. sampoi*].

? 2012 *Dicyclina shlumbergeri* [sic] – Kiarostami et al., pl. 2, fig. 10; Cenomanian, Iranian Zagros [= *Dicyclina* sp.].

? 2012 *Dicyclina schlumbergeri* – Omaña et al., fig. 5(1); late Cenomanian, Mexico [= *Dicyclina/Cuneolina* sp.].

Non 2013 *Dicyclina schlumbergeri* – Rahimpour-Bonab et al., fig. 8U; Turonian [?], Iranian Zagros [= *D. sampoi*].

? 2013 *Dicyclina schlumbergeri* – Al-Dulaimi et al., fig. 10(1); late Cenomanian; southern Iraq [= *Dicyclina* sp.].

2013 *Dicyclina schlumbergeri* – Omaña et al., pl. 1, figs. 2, 4; pl. 4, figs. 2, 4; late Cenomanian, Mexico.

? 2013 *Dicyclina schlumbergeri* – Shahin & Elbaz, p. 276, pl. 2, figs. 3-4; late Cenomanian, Egypt [= *Dicyclina/Cuneolina* sp.].

? 2014a *Dicyclina schlumbergeri* – Omidvar et al., pl. 2, fig. P; Cenomanian, Iranian Zagros [= *Dicyclina* sp.].

Non 2014b *Dicyclina schlumbergeri* – Omidvar et al., fig. 3(10); Cenomanian-Turonian, Iranian Zagros. [=*D. sampoi* Cherchi & Schroeder *fide* Schlagintweit & Rashidi, 2018].

Non 2014 *Dicyclina schlumbergeri* – Afghah et al., fig. 11(f); early Cenomanian, Iranian Zagros [= *Cuneolina* ex. gr. *pavonia*].

Non 2014 *Dicyclina schlumbergeri* – Afghah & Yaghmour, pl. 2, fig.3; pl. 3, fig. 2; Maastrichtian, Iranian

Zagros [perhaps *Dicyclina* sp., but embryonic apparatus too simple to be *D. schlumbergeri*].

? 2014 *Dicyclina schlumbergeri* – Shahin & Elbaz, fig. 6/6; late Cenomanian, Egypt [= *Dicyclina* sp.].

? 2015 *Dicyclina schlumbergeri* – Frijia et al., fig. 9C; Coniacian-Campanian, central Italy [= *Dicyclina* sp.].

Non 2015 *Dicyclina schlumbergeri* – Babazadeh & Dehej, fig. 7 (i, j, k); early Albian, central Iran. [=*Balkanica balkhanica* Mamontova *fide* Schlagintweit, 2024].

Non 2016 *Dicyclina schlumbergeri* – Ghaseminia et al., fig. 4E; Coniacian – Santonian, Iranian Zagros [indeterminate fragment that cannot be assigned to a genus].

Non 2016 *Dicyclina schlumbergeri* – Kazemzadeh & Loftpoor, pl. 2, fig. 6; Cenomanian, Iranian Zagros [indeterminate fragment, but unlikely to be *Dicyclina* sp.].

? 2016 *Dicyclina schlumbergeri* – Rikhtegarzadeh et al., pl. 1, figs. 3-5; Cenomanian, Iranian Zagros. [= *Dicyclina/Cuneolina* sp.].

? 2016 *Dicyclina schlumbergeri* – Dehghani et al., pl. 2, fig. 7; Campanian-Maastrichtian, Iranian Zagros [= *Dicyclina* sp.].

? 2016 *Dicyclina schlumbergeri* – Assadi et al., fig. 6(b2); Cenomanian-Turonian, Iranian Zagros [indeterminate fragment].

? 2017 *Dicyclina schlumbergeri* – Consorti et al., fig. 3A; late Santonian? – middle Campanian, Italy [= *Dicyclina* sp.].

? 2017 *Dicyclina schlumbergeri* – Rikhtegarzadeh et al., pl. 1, fig. 3; Cenomanian, Iranian Zagros [axial section that may be *D. simplex* or *D. schlumbergeri*].

? 2017 *Dicyclina schlumbergeri* – Koç, fig. 10D; Santonian-early Campanian, central Taurides, Türkiye [= *Dicyclina* sp.].

? 2017 *Dicyclina schlumbergeri* [sic] – Jamalpour et al., pl. 2d; Cenomanian, Iranian Zagros [= *Dicyclina* sp.].

2018 *Dicyclina schlumbergeri* – Schlagintweit & Rashidi, fig. 7a-f; late Maastrichtian, Iranian Zagros.

Non 2019 *Dicyclina schlumbergeri* – Saedi Razavi et al., pl. 1, fig. 3; Cenomanian, Iranian Zagros [= *D. sampoi*].

Non 2018 *Dicyclina schlumbergeri* – Omidi et al., pl. 2, fig. 9; Cenomanian, Iranian Zagros [= *D. simplex*].

2019 *Dicyclina schlumbergeri* – Omaña et al., p. 711, fig. 10 (g-j); middle-late Cenomanian, Mexico.

? 2019 *Dicyclina schlumbergeri* – Özkan & Altıner, fig. 9 (1-2); Cenomanian, southeast Türkiye [= *Dicyclina* sp.].

Non 2019 *Dicyclina schlumbergeri* – Alloul, fig. III.9C; Cenomanian, southwest Algeria. [=*D. qatarensis*].

2019 *Dicyclina schlumbergeri* – Villalonga et al., p. 29, pl. 12(a-f); middle Campanian, Spanish Pyrenees.

? 2020 *Dicyclina schlumbergeri* – Sinanoğlu et al., pl. 1, fig. 19; Maastrichtian, Turkish Arabian Plate [axial section only].

? 2020 *Dicyclina schlumbergeri* – Consorti, fig. 3B; Late Cretaceous, central Italy [= *Dicyclina* sp.].

? 2020 *Cuneolina pavonia* d'Orbigny – Solak et al., fig. 11N; late Cenomanian, western Taurides, Türkiye [probably best regarded as *Dicyclina/Cuneolina* sp.].

? 2020 *Dicyclina schlumbergeri* – Fabbi et al., fig. 5 (l, n); Santonian, Italy [= *Dicyclina* sp.].

2021 *Dicyclina schlumbergeri* – Bagherpour et al., fig. 12h; Coniacian-Santonian, Iranian Zagros.

Non 2021 *Dicyclina schlumbergeri* – Gholamalian & Fanati Rashidi, pl. 3, figs 4-5; Cenomanian, Iranian Zagros [= indeterminate foraminifera, not *Dicyclina*].

? 2021 *Dicyclina schlumbergeri* – Saedi Razavi et al., pl. 1, fig. 3; Cenomanian, Iranian Zagros [axial section of *D. simplex* or *D. schlumbergeri*].

2021 *Dicyclina schlumbergeri* – Özkan, fig. 11(12); Campanian, Turkish Arabian Plate.

? 2021 *Dicyclina schlumbergeri* – Sinanoğlu, p. 277, pl. 1, fig. 19; Maastrichtian, Turkish Arabian Plate.

? 2021 *Dicyclina schlumbergeri* – Dousti-Mohajer et al., pl. 2, fig. u; Cenomanian, Iranian Zagros [= *Dicyclina* sp.].

Non 2021 *Dicyclina schlumbergeri* – Radmacher et al., pl. 1, figs. 8 (cf.), 9; Albian-Santonian, Guatemala [= *Cuneolina pavonia*].

? 2021 *Dicyclina schlumbergeri* – Shapourikia et al., fig. 8f; Turonian [?], Iranian Zagros [= *Dicyclina/Cuneolina* sp.].

? 2022 *Dicyclina schlumbergeri* – Dousti-Mohajer et al., fig. 4k; Cenomanian, Iranian Zagros [= *Dicyclina* sp.].

? 2022 *Dicyclina shlumbergri* (sic) – Al-Dulaimi et al., pl. 1D; middle-late Cenomanian, southern Iraq [effectively indeterminate].

? 2022 *Dicyclina* cf. *schlumbergeri* – Ghanbarloo et al., fig. 4k; ?fig. 6d; Maastrichtian, Iranian Zagros [= *Dicyclina* sp.].

? 2022 *Dicyclina schlumbergeri* – Esfandyari et al., fig. 25a; Cenomanian-Turonian, Iranian Zagros [= *Dicyclina* sp.].

2023a *Dicyclina schlumbergeri* – Mehrabi et al., fig. 11 (C-D); Santonian, Persian Gulf.

? 2023b *Dicyclina schlumbergeri* – Mehrabi et al., fig. 6(R); Turonian, Iranian Zagros [= *Dicyclina* sp.].

? 2023b *Dicyclina schlumbergeri* – Schlagintweit et al., fig. 3E, H, L; Campanian, Croatia [= *Dicyclina* sp.].

Non 2023 *Dicyclina schlumbergeri* – Al-Salihi & Ibrahim, pl. 1, fig. E, pl. 3, fig. f; middle – late Cenomanian, southern Iraq [? = *D. sampoi* and *D. qatarensis*].

? 2024 *Dicyclina schlumbergeri* – Božović et al., fig. 3(c); Turonian – Santonian, Montenegro [= *Dicyclina* sp.].

Reference Images: Luperto-Sinni & Richetti (1978), pl. 47, figs. 1-7; pl. 48, figs. 1-6; pl. 49, figs. 1-6; Cvetko Tešović et al., (2001) figs. 6D-H; Schlagintweit & Rashidi (2018) fig. 7a-f; Villalonga et al. (2019) pl. 12, figs. a-f.

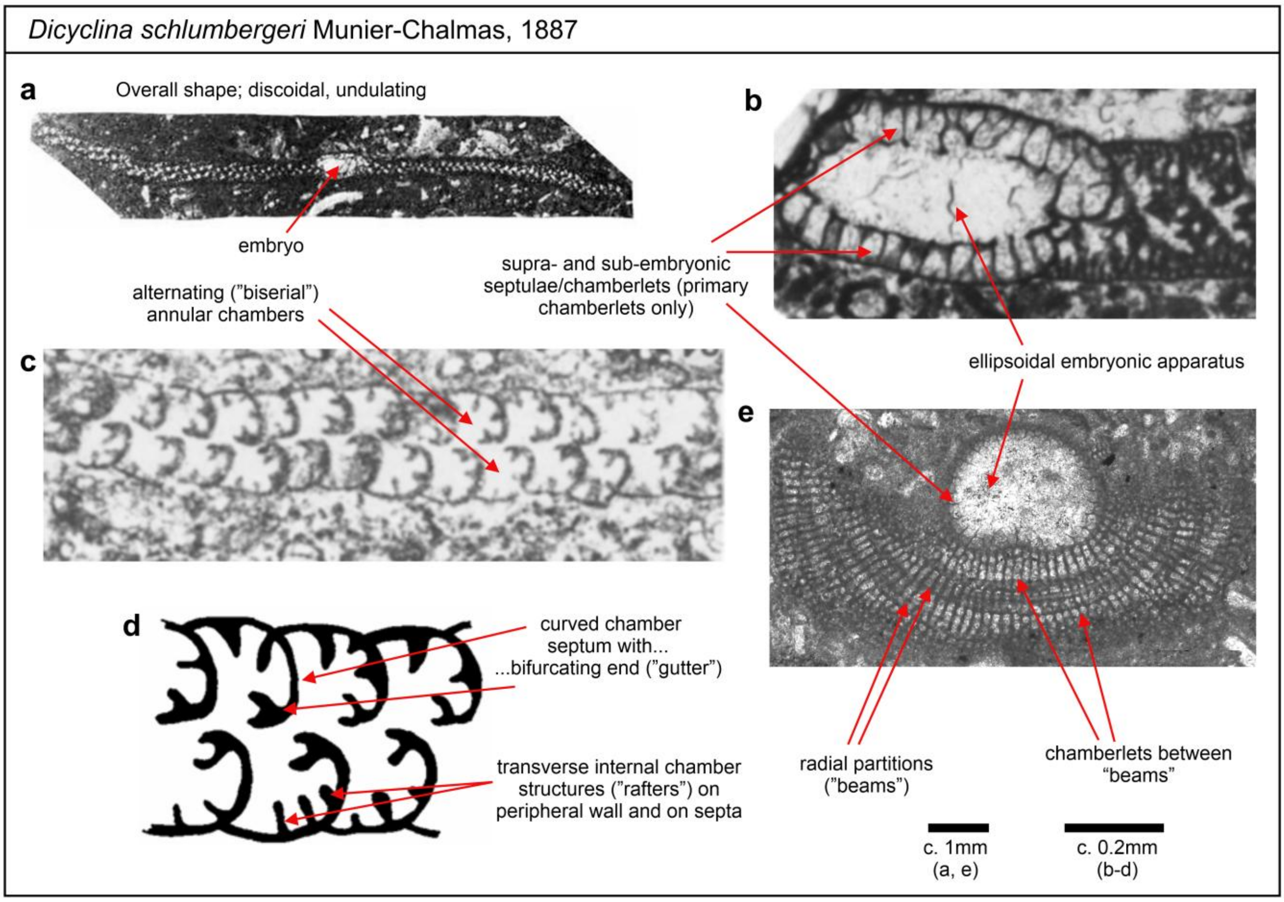


Fig. 22. Representative illustrations of *Dicyclina schlumbergeri*: **a.** Axial section, Gendrot (1968, pl. V, fig. 15, France); **b.** Axial section through embryo, Cvetko Tešović et al. (2001, fig. 6H, Campanian, Croatia); **c.** Axial section through post-embryonic chambers, Cherchi & Schroeder (1990b, fig. 24, Sardinia); **d.** Schematic view of **b**, Cherchi & Schroeder (1990b, fig. 10b); **e.** Oblique equatorial section through embryo and initial annular chambers, Schlagintweit & Rashidi (2018, fig. 7a, Maastrichtian, Iranian Zagros).

Taxonomy/Identity: First described from the Senonian of the Étang de Berre, Bouches-du-Rhône province of France by Munier-Chalmas (1877), the original types of *D. schlumbergeri* are said to be lost (Cherchi & Schroeder, 1990a). The species was later recorded from the Île Madame, Charente-Maritime department by Schlumberger & Choffat (1904) from which population Loeblich & Tappan (1964) designated a lectotype. This, however, is not valid according to Cherchi & Schroeder (1990a) because the specimen does not come from the type locality, nor, in fact, does it belong to *D. schlumbergeri* (it is *D. simplex*).

Cherchi & Schroeder (1990a) chose a neotype based on an axial section previously illustrated by Gendrot (1968) from the Coniacian of the Étang de Berre locality.

Cvetko Tešović et al. (2001) noted that specimens of *D. schlumbergeri* from the Campanian of Croatia indicated a value of 5-7 annular chambers per mm of radius (see also Table 5). They also described the structure of the embryonic apparatus, situated in the centre of the test, noting that is composed of an irregular ellipsoidal or globular embryonic chamber followed by a subembryonic zone. The upper part of the embryonic chamber shows a well-developed layer of subepidermal chambers (chamberlets), which are sometimes subdivided by very short septula. The dimensions of the embryonic apparatus range from 0.82 – 1.2 mm, which is larger than type material from the Coniacian of France: 0.65 – 0.95 mm (Cherchi & Schroeder, 1990a). Thus, they speculated this was a consequence of the phylogenetic evolution of *D. schlumbergeri* during the Late Cretaceous.

Following Cherchi & Schroeder (1990a), Cvetko Tešović et al. (2001) noted that the wall of *D. schlumbergeri* can display a pseudokeriothecal texture. The fine size of these features led them to believe that these served to facilitate exchange of gases rather than house algal symbionts. The features are most likely (or similar to) the "egg holder" structures of Hottinger (2006; fig. 40) which facilitate gas-exchange of the housed symbiont and thus are not mutually exclusive.

Specimens from the late Maastrichtian of the Iranian Zagros by Schlagintweit & Rashidi (2018; fig. 7a, b & e) show that the approximate number of radial elements per quadrant of *D. schlumbergeri* is approximately 20-?25. These are useful biometric data not mentioned in the type descriptions, and confirm the qualitative assessment of differences between *D. schlumbergeri* and *D. qatarensis* by Henson (1948b), the former species having lower annular and radial element densities than the latter (see below).

D. simplex is smaller than *D. schlumbergeri* and the post-embryonic disc is also, relatively, the thickest of all the *Dicyclina* species. *D. sampoi* has characteristically hook-shaped septa in transverse section (even "S"-shaped in some views) compared with the more curved, "C"-shaped septa of other species, and with subepidermal partitions confined to attachment to the inside of the outer wall and not both the wall and septa like *D. schlumbergeri*. This results in a smoother outline to the wall, without the depressed sutures seen in *D. simplex* and *D. schlumbergeri*. However, there are specimens with the embryonic apparatus of *D. sampoi* that show rafters attached to the septal wall (see Omidvar et al., 2014b; fig. fig. 3.10 and Solak et al. 2020; fig. 10U), thus the clear secondary partitions in the subembryonic zone of the embryonic apparatus of *D. sampoi* may be the best evidence for clear identity since in *D. schlumbergeri* they are absent or, at best, rare. It is probable that (along with the rather convoluted taxonomic history), specimens not clearly showing these features which otherwise distinguish species of *D. qatarensis*, *D. simplex* and *D. sampoi* are often "by default" labelled as *D. schlumbergeri*.

Confident Stratigraphic Range: middle – late Cenomanian (local range in Mexico only); common records from Coniacian – Maastrichtian elsewhere.

Uncertain Stratigraphic Range: Not applicable although Turonian records could be anticipated and exist in unconfirmed records, although we know of none.

Despite the many records of *D. schlumbergeri* in the published literature, only a relatively small proportion are illustrated, and of those only a few can be confidently identified. Therefore, confident assessment of stratigraphic range is based a small amount of material.

The published stratigraphic range of *D. schlumbergeri* is confused by imprecise use of the species name. Prior to the introduction of *D. simplex* and *D. sampoi* by Cherchi & Schroeder (1990a, b) almost all records of *Dicyclina* were assigned to *D. schlumbergeri* and even today the name continues to be applied with a lack of precision. Cherchi & Schroeder (1990a) suggested that as the phylogenetic descendant of *D. simplex, D. schlumbergeri* might be a Coniacian and younger species. This notion has been followed by a number of authors including Cvetko Tešović et al. (2001), Velić (2007), Chiocchini et al. (2012), Schlagintweit & Rashidi (2018) and Schlagintweit & Yazdi-Moghadam (2021). This phenomenon was first hinted at by Henson (1948b) with his separation of *D. qatarensis* (supposedly Cenomanian) and *D. schlumbergeri* (supposedly younger) (see also archive records in Le Blanc, 2015).

This appears to be partially correct (i.e., that verified records from the Mediterranean region and Arabian Plate are Coniacian – Maastrichtian), but there are several verified records from middle – late Cenomanian in Mexico only (Aguilera-Franco, 2000; Omaña et al., 2013, 2019). This suggests the species arose in the Caribbean and then migrated eastwards to the Mediterranean and Arabian Plate where it replaced other *Dicyclina* species by the Coniacian, or that there is a more complex pattern of evolution with homeomorphy and repetition of phylogeny from a *Cuneolina* ancestor. As noted above, Cvetko Tešović et al. (2001) suggested that the embryonic apparatus of *D. schlumbergeri* increases in size through its Coniacian – Maastrichtian evolution.

Geographic Distribution: Validated records of this species have a wide stratigraphic distribution from Mexico, across much of the Mediterranean, and from the Arabian Plate. It is also reported from Florida (Applin & Applin, 1965). Interestingly, the occurrences from Mexico are distinctly older (Cenomanian) than those elsewhere which are Coniacian – Maastrichtian.

Dicyclina qatarensis Henson, 1948b

Figure 23

T 1948b *Dicyclina qatarensis* n. sp. Henson, p. 622, pl. XIV, fig. 8; Cenomanian, Qatar.

Non 1961 *Dicyclina* cf. *qatarensis* – Hamaoui, pl. 1, figs. 2-6; Cenomanian, Israel [?= *D. schlumbergeri*].

1998 *Dicyclina qatarensis* – Whittaker et al., p. 31, pl. 48, figs. 5-7; Cenomanian, Palestine/Israel & Qatar.

2008 *Dicyclina qatarensis* – BouDagher-Fadel, pl. 5.3, figs. 8-9; Cenomanian, Qatar.

? 2008 *Cuneolina* sp. – Ahmadi et al., pl. 2, fig. 3; Cenomanian, Iranian Zagros.

2009 *Dicyclina sampoi* Cherchi & Schroeder – Ismail et al., p. 402, pl. 2, figs. 3, 5, 9 (not 1-2, 4, 6-8, 10-11); late Cenomanian, Egypt.

2013 *Dicyclina qatarensis* – Ghanem & Kuss, fig. 14 (20, 48-50); late Cenomanian, Syria.

? 2014 *Dicyclina schlumbergeri* – Afghah & Fadaei, fig. 7(g); early Cenomanian, Iranian Zagros [fragment illustrated with a high density of radial partitions; precision of age doubtful].

2018 *Dicyclina qatarensis* – BouDagher-Fadel, pl. 5.11, figs. 1-3; pl. 5.12, figs. 8-9; Cenomanian, Qatar.

2018 *Dicyclina qatarensis* – Omidi et al., pl. 2, fig. 10; Turonian [?], Iranian Zagros.

2019 *Dicyclina schlumbergeri* Munier-Chalmas – Alloul, fig. III.9C; Cenomanian, southwest Algeria.

? 2023 *Dicyclina schlumbergeri* – Al-Salihi & Ibrahim, pl. 3, fig. F; middle – late Cenomanian, southern Iraq.

Reference Images: Whittaker et al. (1998) pl. 48, figs. 5-7.

Taxonomy/Identity: The limited illustrated records and the poor-quality type material provide challenges for firm identity of this species. The original type material of Henson (1948b) shows no embryonic chambers and only a limited number of sections (see also Whittaker et al., 1998). Even subsequent illustrations (see synonymy list

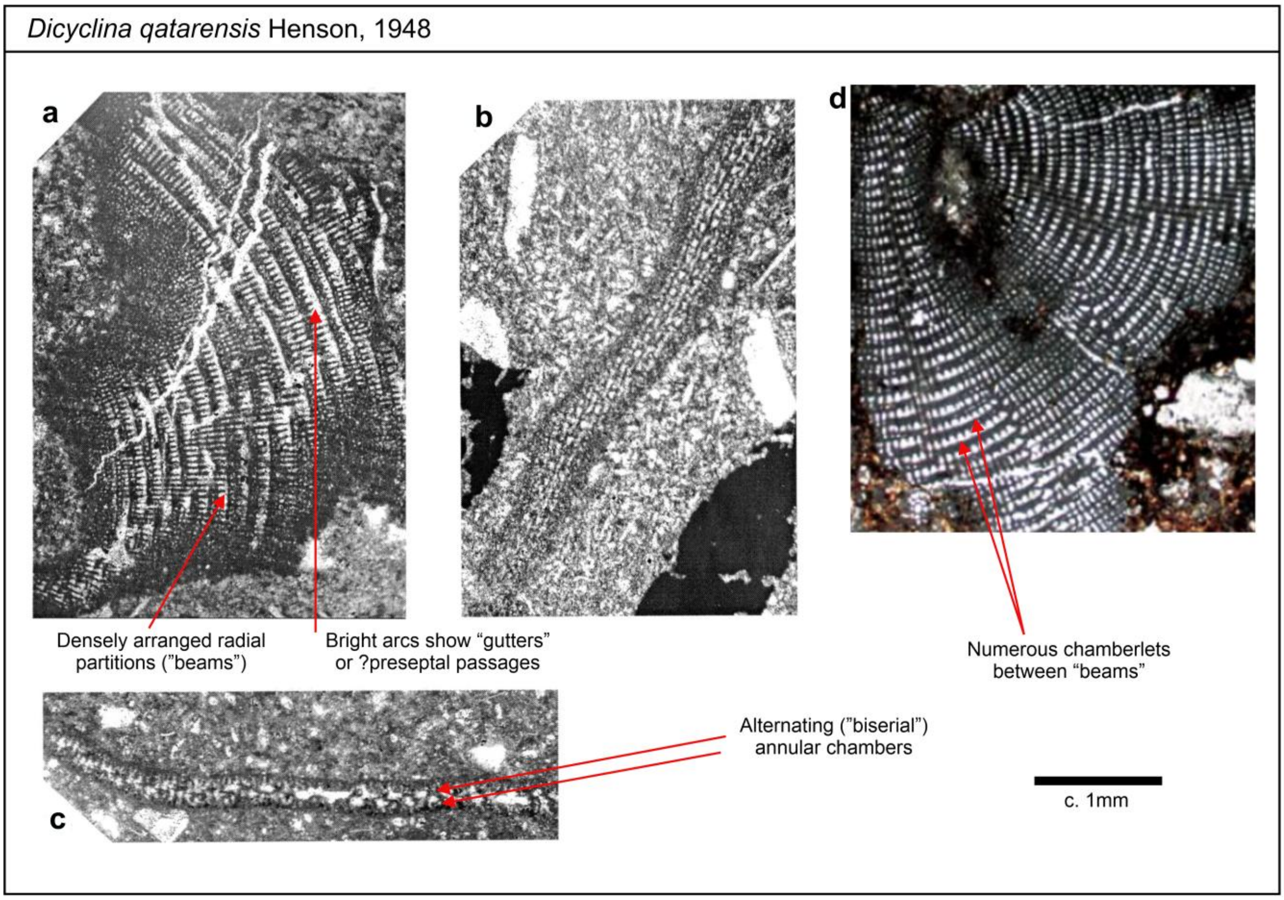


Fig. 23. Representative illustrations of *Dicyclina qatarensis*: **a.** Parallel oblique section, Whittaker et al. (1998, pl. 48, fig. 5, Palestine/Israel); **b.** Subequatorial section (partial), Whittaker et al. (1998, pl. 48, fig. 6, Qatar); **c.** Transverse section, Whittaker et al. (1998, pl. 48, fig. 7, Qatar); **d.** Parallel oblique section, Omidi et al. (2018, fig. 10, Turonian (?), Iranian Zagros).

above) provide only limited additional observations. Cherchi & Schroeder (1990b) regarded it as an "…*unrecognisable species*". Nevertheless, *D. qatarensis* appears distinguishable at least from *D. schlumbergeri* and even *D. simplex* and *D. sampoi* in having a characteristically very large number (c. 100/quadrant) of densely-packed radial partitions ("beams") and chamberlets. It is possible that *D. qatarensis* is a microspheric form of another species of *Dicyclina*, probably *D. sampoi* given that *D. schlumbergeri* appears to be absent from the Cenomanian of Arabia (although is present in younger strata). However, that is impossible to prove without access to populations in which both "taxa" are present. Herein, we retain the use of the name *D. qatarensis* for specimens of *Dicyclina* that have distinctive densely packed radial partitions and chamberlets – however, see for example some illustrations of *D. sampoi* by Ismail et al. (2009) and Figure 24 below.

Hamaoui (1961) stated that his illustrated records of *D*. cf. *qatarensis* (pl. 7, figs. 2-6 therein) "…*strongly resemble Dicyclina qatarensis*…" (p. 13). However, we believe the partial subequatorial oblique section of Hamaoui (1961: pl. 7, fig. 2) does not show the characteristically densely-packed radial partitions (c. 100/quadrant) typical of *D. qatarensis* that it purports to, and that the transverse section (pl. 7, fig. 3) shows chambers very similar to those of *D. schlumbergeri* (see Figure 21b-c herein). If correct, this would be the only record of *D. schlumbergeri* in the Cenomanian from outside Mexico, but on the meagre evidence available, must be regarded as doubtful.

D. qatarensis is sometimes erroneously recorded as *D. qatarica* (e.g., El-Naggar & Al-Rifaiy, 1972, 1973; Al-Salihi & Ibrahim, 2023 and also by Hamoui, 1961 (p. 7), in what must be a *lapsus calami*).

Confident Stratigraphic Range: middle – late Cenomanian.

Uncertain Stratigraphic Range: Turonian.

The types from Qatar (Henson, 1948b) are almost certainly Cenomanian (association with *Praealveolina* reported by Le Blanc, 2015). Other illustrated records of this species are from the middle – late Cenomanian or undifferentiated Cenomanian. The exception is that of Omidi et al. (2018) that is said to be from the Turonian part of the Sarvak Formation of the Iranian Zagros, although proof of this age is not compelling from the data presented. The early Cenomanian record of Afghah &

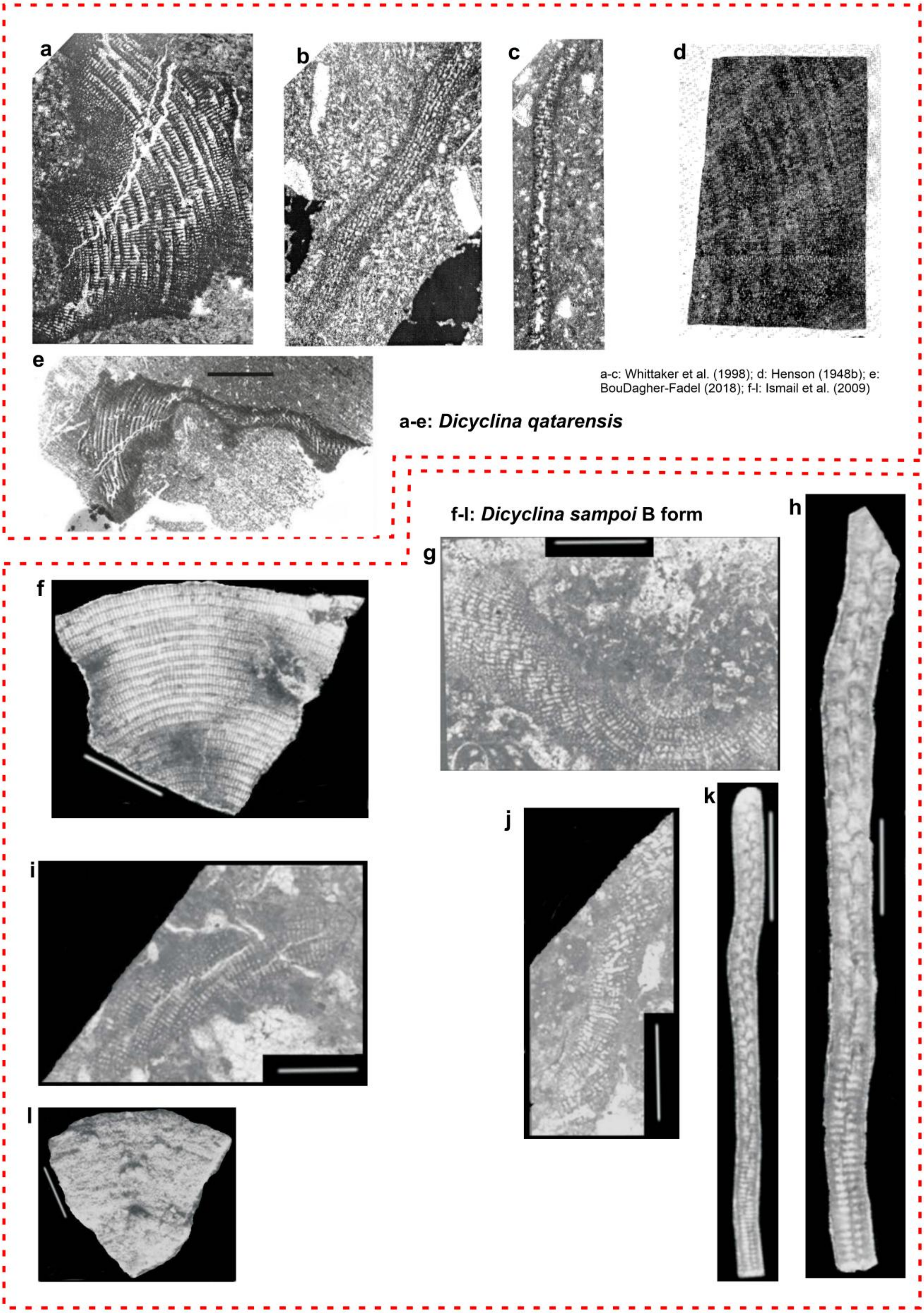


Fig. 24. Comparison between features of *D. qatarensis* (**a-c.** Whittaker et al., 1998; **d.** Henson, 1948b; **e.** BouDagher-Fadel, 2018), and those of *D. sampoi* (B-form) (**f-l.** Ismail et al., 2009). Similarities suggest the two taxa may be synonymous.

Fadaei (2014) is uncertain, at least in terms of identity and very doubtful in terms of age.

Geographic Distribution: This species appears to be restricted to Egypt and the Arabian Plate (Eastern Neotethys). Although the type material was from Qatar, Henson (1948b) also reported the species from Jordan, the Levant region and Iran. In addition, Whittaker et al. (1998) reported it from Iraq, Kuwait and Yemen although it is possible that some of these records are referable to other *Dicyclina* species, especially *D. schlumbergeri*, as Whittaker et al. (1998) report an unexplained age-range for *D. qatarensis* as Turonian-Maastrichtian.

Dicyclina simplex Cherchi & Schroeder, 1990a

Figure 25

1964 *Dicyclina schlumbergeri* – Loeblich & Tappan, p. C303, fig. 209 (1a-1b); middle Cenomanian, France.
1967 *Dicyclina schlumbergeri* – Neumann, pl. 55, fig. 2; middle Cenomanian, western France.
1987 *Dicyclina schlumbergeri* – Loeblich & Tappan, pl. 157, figs. 8-10; middle Cenomanian, western France.
T 1990a *Dicyclina simplex* n. sp. Cherchi & Schroeder, p. 331, figs. 1-4; middle Cenomanian, western France.
1998 *Dicyclina schlumbergeri* – Charrière et al., fig. 4 (3a, 6); late Cenomanian, Morocco.
2009 *Dicyclina schlumbergeri* – Sari et al., pl. 3, figs. 8-9; age uncertain, reworked, Turkish Taurides.
? 2013 *Dicyclina sampoi* – Ghanem & Kuss, fig. 13 (20-21); middle Cenomanian, Syria.
? 2017 *Dicyclina schlumbergeri* – Rikhtegarzadeh et al., pl. 1, fig. 3; Cenomanian, Iranian Zagros [axial section that may be *D. simplex* or *D. schlumbergeri*].
2018 *Dicyclina schlumbergeri* – Omidi et al., pl. 2, fig. 9; Cenomanian, Iranian Zagros.
? 2021 *Dicyclina schlumbergeri* – Saedi Razavi et al., pl. 1, fig. 3; Cenomanian, Iranian Zagros [axial section of *D. simplex* or *D. schlumbergeri*].

Reference Images: Cherchi & Schroeder (1990a), figs. 1-4.

Taxonomy/Identity: *D. simplex*, first described from the middle Cenomanian of France, is the smallest of the *Dicyclina* species (max. diameter c. 3mm). It also has the most spherical and simple embryo compared with *D. schlumbergeri* and *D. sampoi* (the embryo of *D. qatarensis* has not been properly observed). It also has (relatively) the thickest post-embryonic test thickness of all *Dicyclina* species.

Confident Stratigraphic Range: middle – late Cenomanian.

Uncertain Stratigraphic Range: not applicable.

There are relatively few verified records of this species that was introduced by Cherchi & Schroeder (1990a) for material previously assigned to *D. schlumbergeri* from the middle Cenomanian of western France. The only other well dated record is that of Charrière et al. (1998) from the late Cenomanian of Morocco. Others (e.g. Omidi et al., 2018) have an undifferentiated Cenomanian age (but probably middle – late Cenomanian), whilst that of Sari et al. (2009) represents reworked material.

Geographic Distribution: Sporadic distribution, including western France, Morocco, the Turkish Taurides and Iranian Zagros.

Dicyclina sampoi Cherchi & Schroeder, 1990b

Figure 26

? 1965 *Dicyclina* sp – Hamaoui, pl. 13, fig. 12; Cenomanian, Israel.
1969 *Dicyclina* sp. – Sampò, pl. 43, fig. 8 (non pl. 43, fig. 16; ? pl. 43, figs. 7, 9, 14, 15); middle – late Cenomanian, Iranian Zagros.
1988 *Dicyclina* sp. – Sartorio & Venturini, p. 114 (upper fig.); Cenomanian, Iranian Zagros.
T 1990b *Dicyclina sampoi* n. sp. Cherchi & Schroeder, p. 204-210, figs. 10-23; middle-late Cenomanian, Iranian Zagros.
2009 *Dicyclina sampoi* – Ismail et al., p. 402, pl. 2, figs. 1-11 [not 3, 5, 9 =?*D. qatarensis* – see that species herein]; late Cenomanian, Egypt.
2012 *Dicyclina schlumbergeri* – Rahimpour-Bonab et al., fig. 8G; Cenomanian – Turonian, Iranian Zagros.
2013 *Dicyclina schlumbergeri* – Rahimpour-Bonab et al., fig. 8U; Turonian (?), Iranian Zagros.
Non 2013 *Dicyclina sampoi* – Ghanem & Kuss, fig. 13 (20-21); middle Cenomanian, Syria. [=?*D. simplex*].
2014b *Dicyclina schlumbergeri* – Omidvar et al., fig. 3.10; Cenomanian, Iranian Zagros (*fide* Schlagintweit & Rashidi, 2018).
2018 *Dicyclina sampoi* – Schlagintweit & Rashidi, fig. 6; Cenomanian, Iranian Zagros.
? 2018 *Dicyclina sampoi* – Omidi et al., pl. 2, fig. 11; Cenomanian, Iranian Zagros [= *Dicyclina sp.*].
2019 *Dicyclina schlumbergeri* – Saedi Razavi et al., pl. 1, fig. 3; Cenomanian, Iranian Zagros.
2020 *Dicyclina sampoi* – Solak et al., fig. 10U; late Cenomanian, Western Taurides, Türkiye.
? 2021 *Dicyclina sampoi* – Gholamalian & Fanati Rashidi, pl. 3, figs 2-3; Cenomanian, Iranian Zagros [= *Dicyclina* sp.].
? 2023 *Dicyclina schlumbergeri* – Al-Salihi & Ibrahim, pl. 1, fig. E; middle – late Cenomanian, southern Iraq.

Reference Images: Schlagintweit & Rashidi (2018) fig. 6; Solak et al. (2020); fig. 10U.

Taxonomy/Identity: First described from the middle-late Cenomanian of the Iranian Zagros by Cherchi & Schroeder (1990b), based in part upon an illustration of a *Dicyclina* sp. by Sartorio & Venturini (1988), *D. sampoi* differs from other *Dicyclina* species in the characteristically hook-shaped nature of its septa in transverse section (even "S"-shaped in some views, perhaps depending on section orientation) and with subepidermal partitions confined to attachment to the

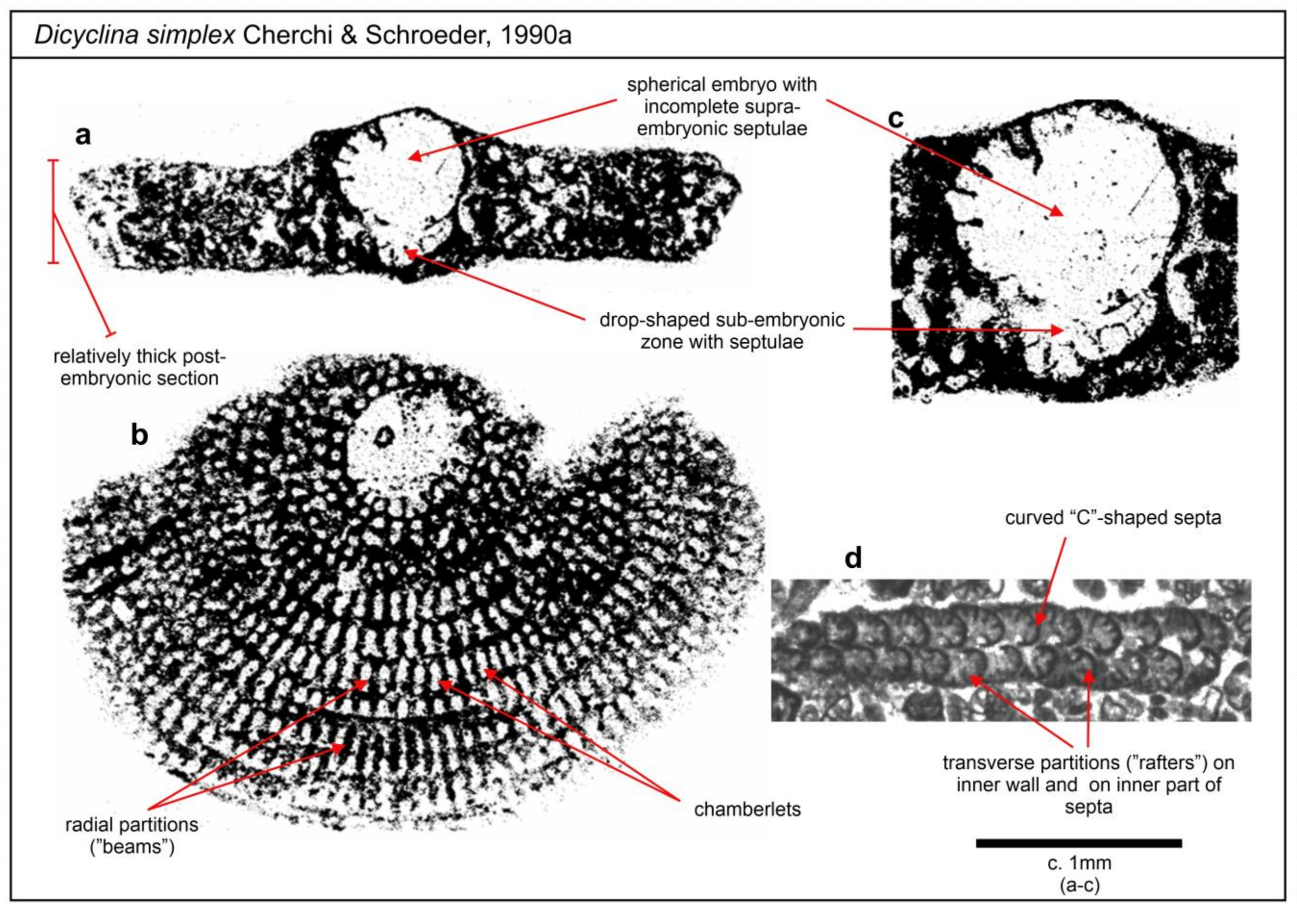


Fig. 25. Representative illustrations of *Dicyclina simplex*: **a** Axial section, Cherchi & Schroeder (1990a, fig. 1, France); **b** Transverse oblique section, Cherchi & Schroeder (1990a, fig. 3, France); **c** Detail of embryo in fig. **a**, Cherchi & Schroeder (1990a, fig. 2, France); **d** Axial section of biserially arranged annular chambers, Sari et al. (2009), pl. 3, fig. 9, age uncertain, Turkish Taurides).

inside of the outer wall and not both the wall and septa like *D. schlumbergeri* (however, see below). It may be difficult to observe but the secondary chamberlets in the upper part of the supra-embryonic zone and the lower part of the sub-embryonic zone are also less well developed in *D. schlumbergeri*.

Cherchi & Schroeder (1990b) stated that "… D. sampoi *cannot be integrated in the evolutionary lineage characterised by* D. simplex *and* D. schlumbergeri…" (1990b, p. 210 as hypothesised by them in 1990a) and conclude that this demonstrates polyphyletic origins of *Dicyclina* species. They suggest a "European" origin for *D. schlumbergeri* and *D. simplex* and a Near and Middle East origin for *D. sampoi*.

Cherchi & Schroeder's types (1990b) show transverse chamber partitions ("rafters") confined to the inner side of the outer wall between the septa and they describe this feature as one of the ways of distinguishing *D. sampoi* from *D. schlumbergeri* (which has rafters on both surfaces). However, some illustrated occurrences of *D. sampoi* appear to also show rafters on the inner part of the septal wall as well as the chamber roof (e.g., see Rahimpour-Bonab et al., 2012, fig. 8G; Rahimpour-Bonab et al., 2013, fig. 8U; Omidvar et al., 2014b, fig. 3(10); Solak et al., 2020, fig. 10U). It is possible, therefore, that that these two species may only be distinguished by their respective supra- and sub-embryonic characteristics.

The specimen of *D. sampoi* illustrated by Ghanem & Kuss (2013) from Syria (especially fig. 13(20)) does not show the characteristic "hook-shaped" septa of *D. sampoi* in transverse view, whilst the embryonic apparatus (fig. 13(21)) seems to fit that of *D. simplex*.

Confident Stratigraphic Range: middle – late Cenomanian (common).

Uncertain Stratigraphic Range: Turonian.

The species was first described (as *Dicyclina* sp.) from probable middle – late Cenomanian of the Iranian Zagros (Sampò, 1969; Cherchi & Schroeder, 1990b). Since then, it has been recorded from the late Cenomanian of the Turkish Taurides (Solak et al., 2020) and Egypt (Ismail et al., 2009). Most records come from the undifferentiated Cenomanian of the Zagros (e.g. Schlagintweit & Rashidi, 2018), although Rahimpour-Bonab et al. (2013) present evidence that it can be found in the Turonian part of the Sarvak Formation in this region. However, the very same specimen illustrated is given an undifferentiated Cenomanian – Turonian age by

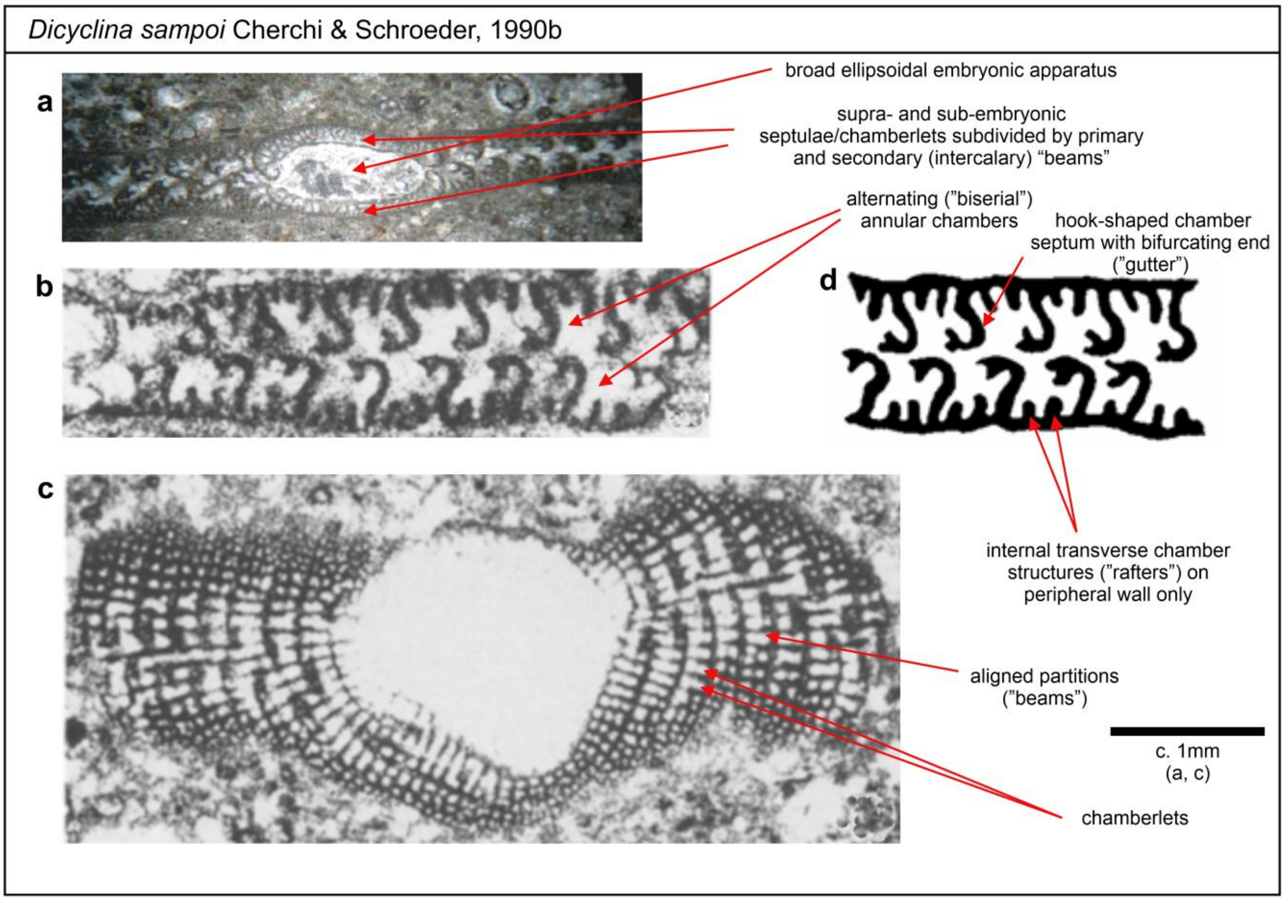


Fig. 26. Representative illustrations of *Dicyclina sampoi*: **a.** Axial section (labelled as *D. schlumbergeri* by Omidvar et al., 2014b – reclassified as *D. sampoi* by Schlagintweit & Rashidi (2018, fig. 6a, Cenomanian, Iranian Zagros); **b.** Detail of **a**, Cherchi & Schroeder (1990b, fig. 13, Iran); **c.** Schematic detail of **b**, Cherchi & Schroeder (1990b, fig. 10a); **d.** Oblique transverse section (partial), Cherchi & Schroeder (1990b, fig. 17, Iran).

Rahimpour-Bonab et al. (2012) and a Cenomanian age by Omidvar et al. (2014b).

Geographic Distribution: The vast majority of verified records of this species come from the Iranian Zagros with a single record from Egypt and a record from the Turkish Taurides.

Family **DICTYOPSELLIDAE** Brönnimann, Zaninetti & Whittaker 1983 (diagnosis *sensu* Loeblich & Tappan, 1987)

Genera ***Dictyopsella*** Munier-Chalmas 1900 and ***Conorbinella*** Poroshina 1976 (see Table 1 for diagnosis)

Unlike other genera discussed above, these two genera are discussed together in this section because of a rather convoluted suprageneric taxonomic history. The genus *Dictyopsella* (type species *Dictyopsella kiliani* Munier-Chalmas in Schlumberger, 1900), with or without its subfamily the Dictyopsellinae which would include *Conorbinella* (type species *Conorbinella azerbaidjanica* Poroshina, 1976), has had a varied history with regard to its higher classification, being placed at different times by different authors in the Trochamminidae, the Barkerinidae, the Ataxophragmiidae, the Remaneicidae and the Dictyopsellidae, and to the superfamilies Orbitolinacea and Loftusiacea (see Loeblich & Tappan, 1985b, for a discussion on this topic). This was due primarily to its internal complexity not being well understood.

Loeblich & Tappan (1985b) transferred the Dictyopsellidae Brönnimann et al. (1983) to the superfamily Loftusiacea and included in it the genera *Dictyopsella*, *Conorbinella* and *Dictyopselloides* n. gen. However, they reverted the Dictyopsellidae family back to within the Ataxaophragmiacea (=Ataxophragmoidea) superfamily in their extensive 1987 treatment – though without an explicit explanation – and included a fourth genus in the family, *Andamookia* Ludbrook, 1966. This position (within the order Loftusiida) was maintained by Kaminski (2014) and the WoRMS foraminiferal database (Hayward et al., 2025).

Dictyopsella is a low conical trochospiral genus which because of its complex internal structure was compared to the externally similar *Coxites*. However, the latter genus has an internal median plate which may bifurcate or digitate, whereas the former genus has many radiating radial partitions (beams) (Loeblich & Tappan, 1985b, 1987).

It is the nature of subepidermal "network" or "mesh" (comprised of radial beams and cross-cutting rafters) that seems, morphologically, to distinguish *Dictyopsella* from the three other genera in the family (note age-ranges taken from Loeblich & Tappan, 1987):

Conorbinella: radial partitions (beams) only [Barremian-Aptian (but possibly as young as Cenomanian – see below)]

Dictyopselloides: radial partitions (beams) with a few incipient rafters in later chambers [Santonian-?Campanian]

Andamookia: radial partitions (beams) with a few transverse rafters [Aptian]

Dictyopsella: radial partitions (beams) as well as intercalary beams extending from the outer wall towards the centre, and shallow secondary cross-cutting partitions (rafters) projecting inwards from upper and lower chamber surfaces forming a full sub-epidermal network [Cenomanian-Maastrichtian]

In some examples of *Dictyopsella*, the "mesh-like" nature of the subepidermal network can obscure the radial nature of the beams near the test surface (see Loeblich & Tappan, 1985b, figs. 1-5 and Figure 27d below).

Dictyopsella charentensis Loeblich & Tappan, 1985b

Figure 27

T 1985b *Dictyopsella charentensis* Loeblich & Tappan, p. 179, pl. 1, figs. 9-11; pl. 2, figs. 1-9; fig.1; Cenomanian, France.

Reference Images: Loeblich & Tappan (1985b), p. 179, fig. 1; pl. 1, figs. 9-11; pl. 2, figs. 1-9. The holotype has been rephotographed and illustrated by the Smithsonian National Museum for Natural History: https://collections.nmnh.si.edu/search/paleo/?ark=ark:/65665/31ddbcd412c514eddaa915bf61c9c7c2d

Taxonomy/Identity: Described by Loeblich & Tappan (1985b, p. 179) as a "small lenticular *Dictyopsella*…" SEM illustrations nevertheless show a typical "discorbid" shape with a subcircular outline and a moderately concave umbilical side. Chambers are typically crescentic and evolute on the spiral side with strongly oblique, depressed sutures and typically subtriangular and involute on the umbilical side with slightly curved and depressed radial sutures. In umbilical view the final chamber occupies up to a third of the test circumference. The subepidermal network is distinct.

D. charentensis differs from the Santonian *D. kiliani* in being smaller, more lenticular, and in having a less extensive subepidermal network and from the Maastrichtian *D. hofkeri* Loeblich & Tappan, 1985b in having a smaller umbilicus and depressed sutures. Another Santonian form, *D. muretae* Hottinger, 1967, has more numerous chambers (8-14 cf. 6-7). *Dictyopsella chalmasi* Schlumberger, 1900 has been shown to belong to the genus *Hemicyclammina* (Caus et al., 1978). *Dictyopsella cuvillieri* Gendrot, 1968 was designated the type species of *Dictyopsellinoides* by Loeblich & Tappan (1985, and re-confirmed by Sun & Schlagintweit, 2024). The early Turonian *Dictyopsella fragilis* Hercogová, 1988 is impossible to assess further due to the lack of detail on the internal structure.

Apart from Loeblich & Tappan's record from France, there seems to be no further mention of this species in the literature concerning other occurrences.

Confident Stratigraphic Range: Cenomanian (undifferentiated).

Uncertain Stratigraphic Range: not applicable.

Geographic Distribution: Western Neotethys (France).

Conorbinella? *libanica* (Saint-Marc, 1973)

Figure 28

T 1973 *Dictyopsella libanica* n. sp. – Saint-Marc, p. 410, pl. 1-2; early Cenomanian, Lebanon.
1974 *Dictyopsella libanica* – Saint-Marc, p.221, pl. 1, figs. 12-18; late Albian, Lebanon.
? 1979 *Dictyopsella* sp. – Velić & Sokač, pl. 3, fig. 8; late Albian, Croatia.
1981 *Dictyopsella libanica* – Saint-Marc, pl. 1, figs. 8-10; late Albian, Lebanon.
? 1985 *Dictyopsella* sp. – Bilotte, pl. 4, fig. 2; Cenomanian, French Pyrenees.
? 1990 *Dobrogelina* ? cf. *angulata* – Bilotte & Pamouktchiev, pl. 1, figs. 5-10; Albian, Bulgaria.
? 2015 *Dictyopsella* cf. *libanica* – Schlagintweit et al., fig. 5h; early-middle Cenomanian, Spain.
? 2021 *Dictyopsella* sp. – Rineau et al., fig. 7k; late Cenomanian, southern France.

Reference Images: Saint-Marc (1973), pl. 1-2, p. 410.

Taxonomy/Identity: First described as *Dictyoconella libanica* from the early Cenomanian of Lebanon by Saint-Marc (1973), he indicated (his new species has a "*system of shallow subepidermal blades*" (i.e., beams herein) with another "*system of blades more or less perpendicular to the previous ones…*" (i.e., rafters herein) which are "*much less well developed*". He went on to state that the combination of these groups of blades constituted "*a sketch of a network*". Furthermore, he distinguished *D. libanica* from all known species of the genus by its "*poorly developed sub-epidermal network*".

However, of Saint-Marc's (1973) 45 illustrations, only one (pl. 1, fig. 1; the holotype) shows hints of a partial "network". This led Loeblich & Tappan (1985b) to conclude that this lack of a distinctive subepidermal mesh justified the species' removal from *Dictyopsella* and suggested that it "may be" a *Conorbinella*, a position we have tentatively followed here. However, the hint of at least a partial network does not therefore exclude assignment to *Dictyopselloides*.

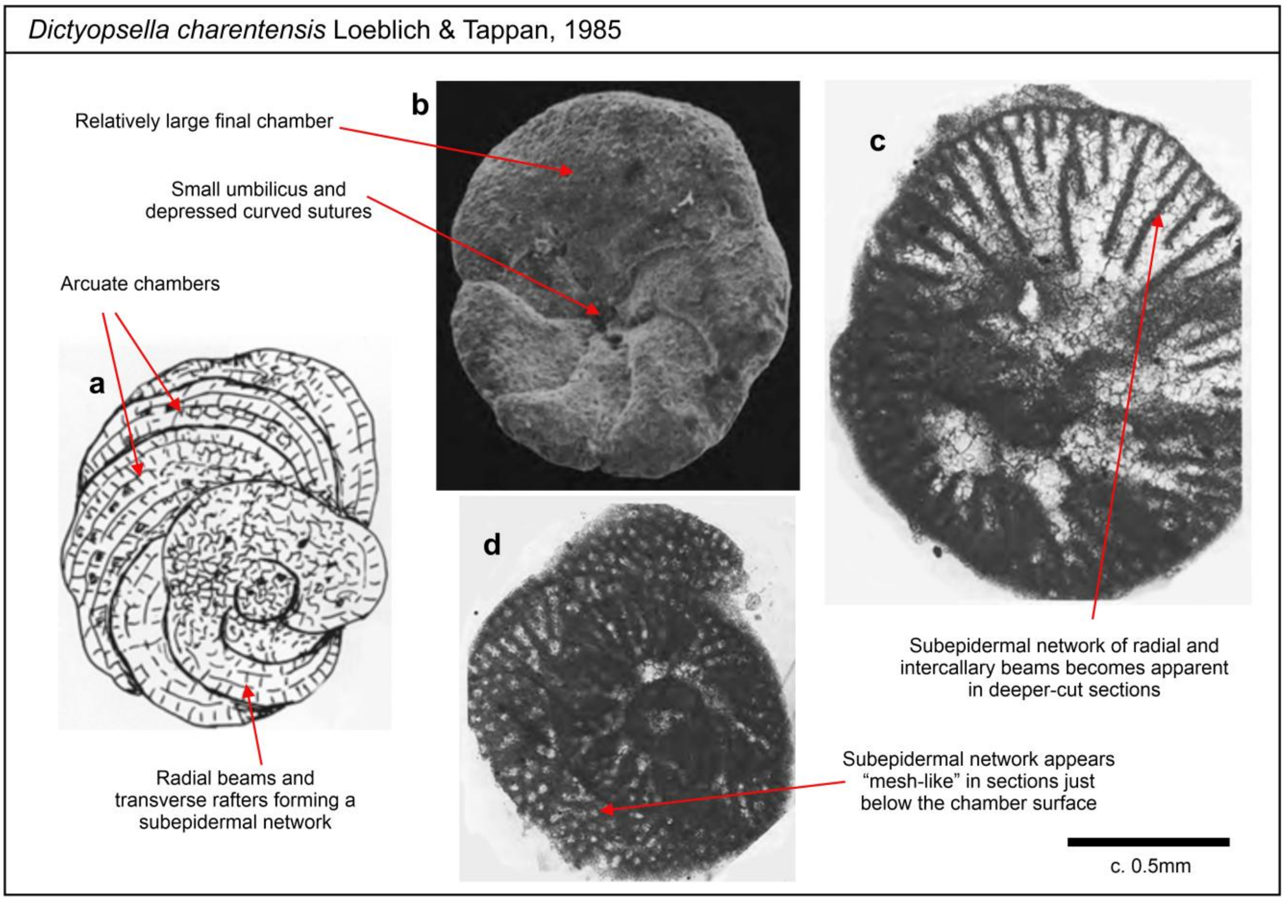


Fig. 27. Representative illustrations of *Dictyopsella charentensis*: **a.** Dorsal view (*camera lucida* drawing), Loeblich & Tappan (1985b, fig. 1, France); **b.** Umbilical view (SEM photograph), Loeblich & Tappan (1985b, pl. 1, fig. 10, France); **c.** Near equatorial section (deep cut), Loeblich & Tappan (1985b, pl. 2, fig. 8, France); **d.** Near equatorial section (shallow cut), Loeblich & Tappan (1985b, pl. 2, fig. 4, France).

Confident Stratigraphic Range: late Albian – middle Cenomanian.

Uncertain Stratigraphic Range: late Cenomanian.

The age range of this species is difficult to assess. Saint-Marc (1973) first recorded his new species from the early Cenomanian of Lebanon but subsequently restricted the species' range to the late Albian (1974b; Table 3; 1981). Schlagintweit et al. (2015) recorded and illustrated a form *Dictyopsella* cf. *libanica* from the early-middle Cenomanian of the Altimira Formation of Spain. That specimen shows radial beams but no signs of rafters and no hint of any "mesh-like" subepidermal network and therefore the identity is questionable

It was recorded (but unillustrated) under the same name from the Mauddud Formation (late Albian-early Cenomanian) of the Northern Arabian Gulf by Awa (1987).

It was also recorded (as *Dictyopsella libanica*) from the middle Cenomanian part of the Villa de Vés Formation of Spain by Vicedo et al. (2011) and from the late Cenomanian part of the Casa Medina Formation of Spain by Caus et al. (2009) but was unillustrated in both cases.

Berthou (1984) reports two taxa named as *Dictyopsella* cf. *kiliani* and *Dictyopsella* cf. *libanica* from the late Cenomanian – early Turonian of Portugal, but no illustration or description is provided (see also Crosaz-Galletti, 1979).

Geographic Distribution: Although not well known or widely recorded, the above references suggest a distribution in Mediterranean Neotethys.

STRATIGRAPHIC RANGE: CONFIDENCE AND UNCERTAINTY

The determination of the stratigraphic range of a species or genus carries a degree of uncertainty. At the very least stratigraphic range assessments can be judged to be confident or uncertain. This is reflected in the text below and are coded by line ornament in Figure 29 to reflect degrees of confidence in our assessments and interpretations. It should be noted that even confident ranges have a degree of uncertainty, with assignment to a substage typically implying the assignment is undifferentiated, unless clearly stated otherwise. In other words, if a taxon is known from the late Cenomanian, but

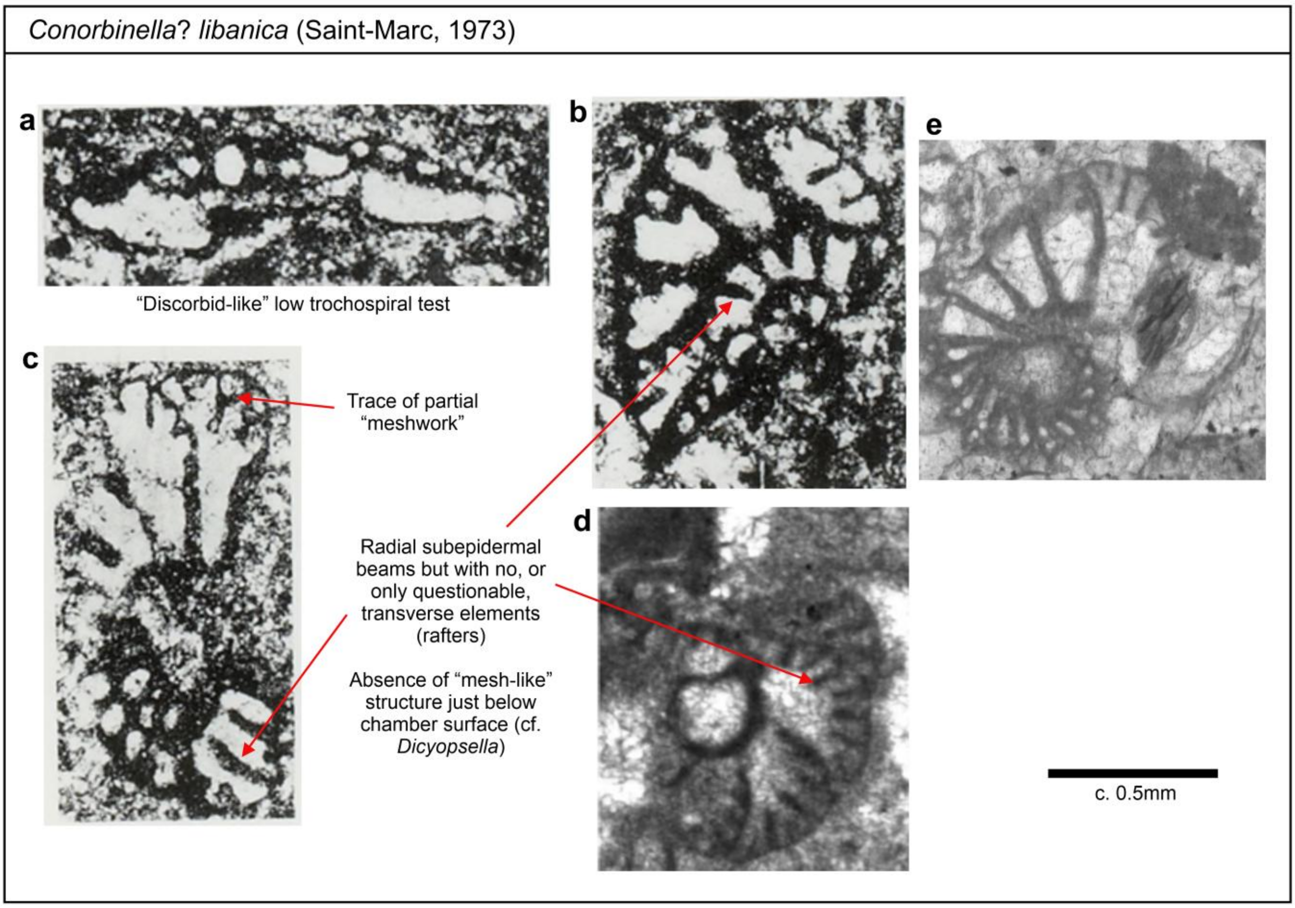


Fig. 28. Representative illustrations of *Conorbinella*? *libanica*: **a.** Near axial view, Saint-Marc (1974, pl. 1, fig. 14, Lebanon); **b.** Subequatorial view, Saint-Marc (1974, pl. 1, fig. 15, Lebanon); **c.** Subequatorial view (holotype), Saint-Marc (1974, pl. 1, fig. 13, Lebanon); **d.** Subequatorial view (as *Dictyopsella* cf. *libanica*), Schlagintweit et al. (2015, fig. 5h, Spain); **e.** Near equatorial view, Schlagintweit (personal collection, Spain).

with no information on where in the late Cenomanian it has an inception or extinction, the range is shown as throughout the stage. To imply anything else would be a false impression of known biostratigraphic precision. Further discussion on the philosophy of certainty in biostratigraphic evaluation can be found in Simmons & Bidgood (2023) and in Simmons et al. (2024b).

In this work we have used three broad categories to depict stratigraphic range confidence:

Confident and common – a wide, solid, green line on range charts.

A relatively large number of (correctly) illustrated records (or if unillustrated, from a generally reliable source) with at least plausible age-control.

Confident but scarce – a narrow, solid, green line on range charts.
At least one, but relatively fewer records but which fit the same criteria as above.

Uncertain – a series of orange "?" on range charts. Occurrences that lie outside of the "confident" ranges that are neither confirmed in terms of identity nor age-control but cannot be completely dismissed (e.g., an illustrated record with poor age-control or an unillustrated record from a generally reliable source with good age control).

As can be readily understood, subjectivity plays a role here, and the boundaries between one category and other are inevitably gradational. Records which exist of named species occurring in rocks outside of these ranges, but which are based on very uncertain (i.e. dubious) identity and/or age control are not shown.

To use *Moncharmontia* herein as an example, both *M. apenninica* and *M. compressa* have been commonly recorded from early-middle Turonian (and younger) strata (many records with identities confirmed by illustration) (= a wide, solid green line on Figure 29), but *M. apenninica* has also occasionally been recorded from middle – late Cenomanian strata (confirmed by illustration of material coming from the Arabian Plate) (= a thin, solid green line on Figure 29). On the other hand, the Cenomanian records of *M. compressa* have a degree of uncertainty regarding identity or have not been illustrated at all. This is represented by a series of orange "?" on Figure 29. We freely acknowledge that these are the results of our own (subjective) assessment of the various data points we have observed and examined and

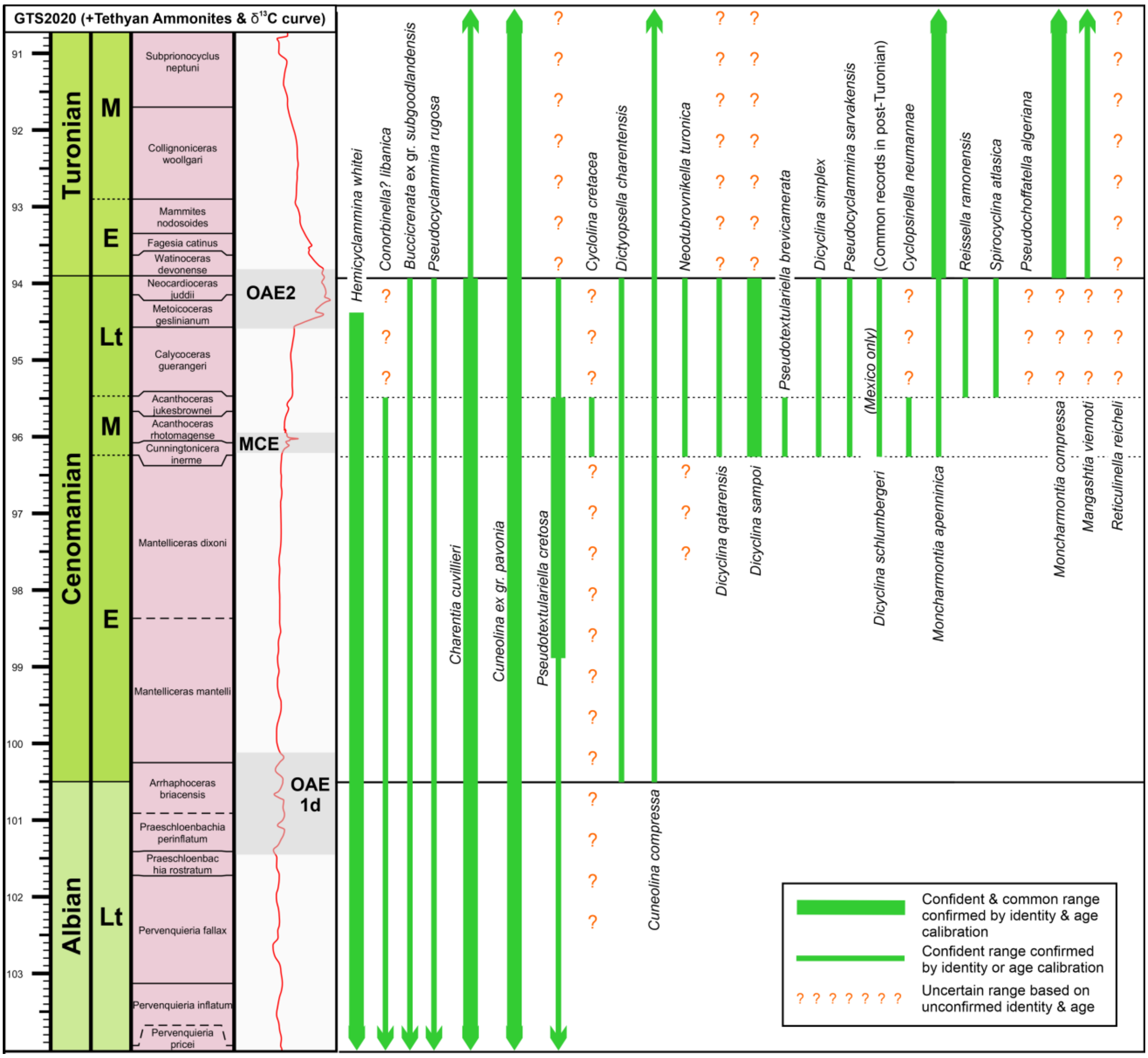


Fig. 29. Stratigraphic ranges of loftusiid taxa with definite and possible occurrence within Cenomanian strata.

agree that others may come to different conclusions.

In addition, and alongside all these factors is the fact that the stratigraphic ranges of benthic fossils such as LBF will vary geographically because of facies control or because of differential biogeographic dispersal of a taxon in time (i.e., due to endemism or depending on paleoceanographic factors). This implies that constructing a composite stratigraphic range for an individual species is dependent on many locational/observation factors which build up from a series of local stratigraphic occurrences. At a local scale, a taxon may have a range very different from its combined global composite range.

DISCUSSION

Figure 29 demonstrates that many mid-Cretaceous loftusiid taxa (i.e. those that might be encountered in Cenomanian strata from Neotethys and excluding the Orbitolinina) are quite long ranging and therefore have limited biostratigraphic utility. Examples include *Buccicrenata* ex gr. *subgoodlandensis*, *Cuneolina* ex. gr. *pavonia* and *Charentia cuvillieri*. This is doubtlessly in part because relatively loose taxonomic concepts are used. Regrettably but inevitably, pragmatism is sometimes required in LBF taxonomy. The nature of some genera is such that identification of the features needed for precise speciation is difficult in random thin-sections, or that possible differences are so slight that it is not yet clear if they are meaningful for taxonomic subdivision. As is shown by the analysis of mid-Cretaceous *Buccicrenata*, the species *B. hedbergi*, *B. subgoodlandensis* and *B. libyca* are hardly distinguishable based on their stated characteristics (see Table 6 below). It thus makes sense to group these taxa using an "ex. gr." formulation, even if that is at the risk of losing stratigraphic resolution.

On the other hand, some taxa have useful short ranges. Whilst there are no taxa restricted to the early Cenomanian, there are a number of taxa that are most likely restricted to the middle and late Cenomanian (e.g.

Dicyclina sampoi, *Dicyclina simplex*, *Reticulinella reicheli*) and some only to the middle Cenomanian (e.g. *Cyclopsinella neumannae*) or late Cenomanian (e.g. *Spirocyclina atlasica*). As with the nezzazatoids (Simmons et al., 2024b), the onset of the middle Cenomanian seems have seen a burst of loftusiid evolution with the inception of several new taxa.

Table. 6. Comparison of mid-Cretaceous *Buccicrenata* species (from Simmons & Bidgood, 2023).

Feature	*B. libyca* Gohrbandt 1966	*B. subgoodlandensis* (Vanderpool, 1933) – data from Loeblich & Tappan (1949, 1985a)	*B. hedbergi* (Maync, 1953a) – data also from Maync (1959)
Number of coiled chambers in final whorl	4 – 4 ½	4 ½ - 5	4-5
Length of uncoiled specimens	2.1 - 2.75 mm	1.27 – 4.73 mm	1.74 – 2.67 mm
Equatorial diameter of coiled part	1.37 – 2.08 mm	0.59 – 2.48 mm	0.8 – 2.00 mm
Axial Diameter	0.51 – 0.63 mm	0.25 – 0.58 mm	0.5 - 0.92 mm
Wall thickness	0.15 – 0.23 mm	0.11 – 0.23 mm	0.11 – 0.18 mm

A number of taxa become extinct at or just before the Cenomanian/Turonian boundary (bearing in mind the limited stratigraphic resolution of the ranges of many taxa that does not permit to precisely say when relative to the Cenomanian/Turonian boundary extinction occurred). This coincides with a well-known extinction event associated with the paleoceanographic perturbation of the Ocean Anoxic Event (OAE) II (Philip & Airaud-Crumiere, 1991; Parente et al., 2008; Orabi et al., 2012; Frijia et al., 2015). Cyclamminids such as *Hemicyclammina whitei*, *Buccicrenata* ex. gr. *subgoodlandensis*, *Pseudocyclammina rugosa* and *Pseudocyclammina sarvakensis* have pre-Turonian last appearance events. The same can be said for dicyclinids such as *Dicyclina sampoi* and *Dicyclina simplex*. Interestingly, representatives of all these genera except *Buccicrenata*, reappear in the younger parts of the Cretaceous. For *Pseudocyclammina* this occurs as soon as the Turonian (*Pseudocyclammina sphaeroidea* – see Albrich et al., 2015; Arriaga et al., 2016), whereas for *Dicyclina* it is in the middle Coniacian (*Dicyclina schlumbergeri* – see Frijia et al., 2015). Clearly the morphology of these genera was well suited to ecological niches in the Late Cretaceous shallow marine seas of Neotethys. However, it is unclear if the genera re-evolved new species from simple, extinction-resilient root stock, or that survivors remained dormant (Ross & Hallock, 2016) in protected shelters of Neotethys uninfluenced by OAE II and associated climatic, sea-level and oceanographic changes.

Some individual species such as *Moncharmontia apenninica*, *Dicyclina schlumbergeri* and *Cuneolina* ex gr. *pavonia* survived the Cenomanian/Turonian extinction event such that they can be found in sediments either side of the boundary, although with some geographic distinction (Schlagintweit & Yazdi-Moghadam, 2021; Simmons & Bidgood, 2023). *M. apenninica* has so far only been found in the Cenomanian of Arabia, whilst *D. schlumbergeri* has only been found in the Cenomanian of Mexico. Such taxa may be r-strategist survivors (e.g., Arriaga, 2016; Schlagintweit & Yazdi-Moghadam, 2021; Consorti et al., 2022; Consorti & Schlagintweit, 2021; Schlagintweit et al., 2023b; Křížová et al., 2024; Simmons et al., 2024b) able to tolerate environmental perturbations and occupy environmental niches available after the extinction events. Other taxa such as *Pseudocyclammina* or *Reticulinella* experienced instead speciation as a consequence of the extinction event, re-appearing during the Turonian under a renewed, better adapted, taxonomic and genetic status.

CONCLUSIONS

We have critically reviewed the available literature (several hundred references) for the loftusiid taxonomic group (i.e., Order Loftusiida, excluding Suborder Orbitolinina), and have likewise critically applied both identity and age criteria for LBF taxa that are present in the Cenomanian. Twenty-five separate Cenomanian LBF loftusiid taxa (including two with “ex gr.” status) have been treated herein. We have constructed a biostratigraphic range chart for these taxa based on our assessment of data points as being confirmed (i.e., with correct or at least plausible identification and age-calibration) which will subsequently form the basis for a more comprehensive Cenomanian biozonation. Whilst some taxa are long-ranging throughout the Cenomanian and adjoining stages, others have restricted ranges within the Cenomanian, providing stratigraphic utility for correlation. It should be borne in mind that as benthic foraminifera are adapted to specific ecological niches, local ranges can (and often will be) more restricted than global composite ranges, providing some local stratigraphic utility if understood to be a biofacies phenomenon rather than a chronostratigraphic one. A number of taxa, either at generic or specific level, survived the end-Cenomanian extinction event, suggesting a certain tolerance to environmental perturbations and an ability, especially for those considered to be r-strategsists, to occupy environmental niches that became available immediately after the extinction event(s).

Many of these loftusiid LBF taxa require further study (and re-examination of type material and/or access to new/additional material) to improve our taxonomic understanding, and the evolutionary and biogeographic relationships between them.

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In order to carry out this review it has been essential to gather literature, some of it quite obscure. In this endeavour we have been greatly assisted by Prof. Johannes Pignatti of the Università degli Studi di Roma “La Sapienza” and by the library of the Geological Society of London. Ali Alibrahim (KAUST, Saudi Arabia) is thanked for supplying images of *Cuneolina* from Jordan. Dr. Blanka Cvetko Tešović (University of Zagreb, Croatia) kindly provided some clarification on occurrences of the genus *Reticulinella*. The manuscript was very helpfully and constructively reviewed by Francois Le Coze (Saint-Étienne, France) and Cemile Solak (Mersin, Türkiye) who we gratefully thank, along with APR journal editor George Pleş. Please note however that the opinions expressed in this paper are those of the authors who are also responsible for any omissions, errors, and other shortcomings.

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