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“LARGER” BENTHIC FORAMINIFERA OF THE CENOMANIAN. A REVIEW OF THE IDENTITY AND THE STRATIGRAPHIC AND PALAEOGEOGRAPHIC DISTRIBUTION OF NON-FUSIFORM PLANISPIRAL (OR NEAR-PLANISPIRAL) FORMS

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Abstract A key but challenging task for biostratigraphers is to provide a biozonal/bioevent framework for geological correlation. Species of Larger Benthic Foraminifera (LBF) are important biostratigraphic markers in depositional environments where classical biostratigraphic fossils such as planktonic micro- and macrofossils are rare or absent – e.g., tropical-subtropical shallow water platforms. However, a lack of taxonomic rigour in identifying some LBF species, together with a lack of good age-calibration of their occurrences, has given rise to artificially extended biostratigraphic and paleogeographic ranges for many taxa, diluting their usefulness. In this study, the occurrences of Cenomanian LBF belonging to a “planispiral morphogroup”, both agglutinated and calcareous, have been critically evaluated to determine (i) identity; (ii) stratigraphic range; and (iii) palaeogeographic distribution.

Since the last major review of the group in 1985, a voluminous literature has appeared reporting occurrences and adding new taxa. An extensive review of some 600+ published items on Cenomanian planispiral LBF – mostly published after 1985 – and a critical review of the confidence in species identification and age-calibrations therein, has led us to identify 39 taxa (three in “open” status) which appear to have distinct identity. The vast majority of these records are from Neotethys although some also occur in (or are endemic to) the Caribbean/West Atlantic and the Eastern Pacific. The quality of the published taxonomic data is variable and many published records based on identity can be discounted or termed “unconfirmed”. Likewise, many records (confirmed or otherwise) are poorly age-calibrated due to lack of corroborating biostratigraphy or chemostratigraphy, or by using circular reasoning.

We summarise and illustrate the main defining characteristics of each taxon and their possible confusion species, including new taxa described since the mid-1980s. We publish new, more confident, age-ranges for these taxa – confirmed by identity and/or age-calibration – and identify where published range data may be unreliable. Paleogeographic distribution maps for each taxon are also provided. Particular stratigraphic issues around the Cenomanian-Turonian boundary are observed due to the difficulty of identifying that boundary, or its preservation, in shallow marine carbonate settings.

Although most Cenomanian planispiral LBF are somewhat long-ranging, an increase in diversity throughout the middle – late Cenomanian has shown potential for biostratigraphic resolution to at least substage level using this group. Integration of the planispiral taxa with other LBF morphogroups, after similar treatment, will yield even higher biostratigraphic resolution of Cenomanian LBF and provide a sound basis for biozonation (both local and global), correlation, and age calibration.

Keywords: Foraminifera, Neotethys, Cretaceous, Cenomanian, micropaleontology, biostratigraphy

INTRODUCTION

Biostratigraphy remains a key tool for correlation and palaeoenvironmental determination of most sedimentary rocks (e.g., McGowran, 2005; Jones, 2006; Gradstein et al., 2020). To be effective, biostratigraphers need to know the relative order of bioevents (inceptions, influxes, extinctions, etc.) across a region, and the relative stratigraphic ranges, or (preferably) chronostratigraphically calibrated ranges of individual taxa (Simmons, 2015). This is founded on the ability to determine the *identity* of the various taxa. Correct identification of a taxon requires the clearly visible presence of key diagnostic features (Schlagintweit & Simmons, 2022). It follows that knowing identity allows for the assessment of records in the literature to establish a critical analysis of a taxon’s range.

The informal grouping of “Larger” Benthic Foraminifera (LBF) provides potentially very useful biostratigraphic marker taxa in warm, shallow-water facies across the globe from Paleozoic times until the present day (Simmons & Aretz, 2020). The term “Larger” is often assigned to foraminifera that are not only “large” in size (>1.0mm) but that also – critically – require analysis of their internal structures in thin-section to determine taxonomy and identity (see below). However, some relatively small foraminifera (<1.0mm) also have complex internal structures critical for taxonomy/identity and are also included here.

The last major revision and catalogue of mid-Cretaceous LBF species (for the Neotethyan region) was the monumental work coordinated by Schroeder & Neumann (1985) which involved input from many specialists. Since then, many new taxa and many more occurrence records have been added to the literature and a further review of mid-Cretaceous LBF groups seems necessary.

Taxonomic precision in palaeontology is improving, but very much remains a “work in progress”. This is particu-

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larly true of the LBF, which requires analysis of both external and internal structures to define taxonomic units, with internal features as observed in thin-section often being key. In many cases randomness in the way thin-sections are presented means that – more often than not – such key features may not always be seen (Schlagintweit & Simmons, 2022). Moreover, when new species were first being identified and described, these were often based on imperfect or limited material leading to descriptions that later turned out to be (i) incomplete; (ii) incorrect; or (iii) represent junior synonyms of already described taxa.

This paper forms the first part of an intended series of papers describing the taxonomic status, stratigraphic and paleogeographic distribution of LBF of the Cenomanian stage of the Cretaceous, with a view to improving biostratigraphic resolution and correlation of events within this stage. This article concerns those LBF which predominantly show a planispiral (or nearly so) progressive mode of coiling in a single plane, which may or may not uncoil in later growth (i.e., broadly-speaking, the “flat planispirals”). This grouping does not therefore include forms with a planispiral growth mode around an extended axis leading to fusiform and spherical forms such as the alveolinids, which will be treated in a separate work. This is a grouping of solely morphological convenience and includes representatives from several unrelated families and superfamilies within two orders/suborders of Foraminifera (Table 1). Not all the species treated herein are strictly large or even particularly complex (e.g., the genus *Vidalina* Schlumberger). What they do have in common is that they require observation of internal structure to assure identification, a critical feature of LBF (Hottinger, 2006; BouDagher-Fadel, 2018; Simmons & Aretz, 2020; Schlagintweit & Simmons, 2022).

Taxa identified and discussed herein (in alphabetical order of genus) are:

Biconcava bentori Hamaoui & Saint-Marc, 1970
Biplanata peneropliformis Hamaoui & Saint-Marc, 1970
Buccicrenata ex gr. *subgoodlandensis* (Vanderpool, 1933)
Charentia cuvillieri Neumann, 1965
Daxia cenomana Cuvillier & Szakall, 1949
Demirina meridionalis Özcan, 1994
Deuterospira pseudodaxia Hamaoui, 1965 emend. Hamaoui, 1979
Fleuryana gediki Solak et al., 2020
Hemicyclammina whitei (Henson, 1948)
Mayncina orbignyi (Cuvillier & Szakall, 1949)
Merlingina cretacea Hamaoui 1965 emend. Hamaoui & Saint-Marc, 1970
Moncharmontia apenninica (De Castro, 1966)
Moncharmontia compressa (De Castro, 1966)
Neodubrovnikella turonica (Said & Kenawy, 1957)
Nummofallotia? apula Luperto-Sinni, 1968
Nummoloculinodonta akhdarensis Piuz & Vicedo, 2020
Peneroplis parvus De Castro 1965
Perouvianella peruviana (Steinmann, 1929)
Planinummoloculina gnosi Piuz & Vicedo, 2020
Praetaberina apula Consorti et al., 2015
Praetaberina bingistani (Henson, 1948)
Pseudocyclammina rugosa (d’Orbigny, 1850)
Pseudocyclammina sarvakensis Schlagintweit & Yazdi-Moghadam, 2023
Pseudonummoloculina aurigerica Calvez, 1988
Pseudonummoloculina? ex gr. *heimi* (Bonet 1956, emend. Conkin & Conkin, 1958)
Pseudonummoloculina? cf. *irregularis* (Decrouez & Radoičić, 1977) sensu Chiocchini et al. 2012
Pseudonummoloculina? *regularis* (Philippson, 1887) sensu Chiocchini et al. 2012
Pseudopeneroplis oyonensis Consorti et al., 2018
Pseudorhapydionina chiapanensis Michaud et al., 1984
Pseudorhapydionina dubia (De Castro, 1965)
Pseudorhapydionina laurinensis (De Castro, 1965)
Pseudorhapydionina anglonensis Cherchi & Schroeder, 1986
Pseudorhipidionina ex gr. *casertana-murgiana* sensu De Castro, 1965, 2006
Rajkanella hottingerinaformis Schlagintweit & Rigaud, 2015
Reisella ramonensis Hamaoui, 1963
Scandonea? *phoenissa* Saint-Marc, 1974b
Scandonea? *pumila* Saint-Marc, 1974b
Spirocyclina atlasica Saint-Marc & Rahhali, 1982
Vidalina radoicicae Cherchi & Schroeder, 1986

It can be much debated whether other taxa might be included within this informal grouping, but in truth it would be difficult to decide exactly where the group boundaries might be. We have excluded clearly fusiform and discoidal/annular forms. We have also largely excluded very poorly known taxa known only from their type descriptions. However, such taxa are briefly discussed in the relevant section(s) of other species, where appropriate.

The main morphological diagnostic characteristics of these selected taxa, based on type and emended descriptions and some of our own observations, are tabulated in a Species Key Chart (Appendix). This chart acts as a single reference point on how these taxa can be compared. Potential confusion taxa can be quickly assessed. Wall structure is the first hierarchic feature in this table, but it may be difficult to determine unequivocally in some cases. Thin-section studies reveal often complex internal structures and growth patterns of LBF that are hidden in external views of specimens (see the extensive glossary of internal structures by Hottinger, 2006). These internal views are therefore crucial in the taxonomic separation (identity) of numerous LBF species, genera, and higher taxa. On the other hand, this often makes identification of specimens that are not either well-preserved or where the section has not been favourably oriented difficult, and has resulted in numerous incorrect records in the literature (Schlagintweit & Simmons, 2022).

LBF are common throughout the geological record from Carboniferous times to the present day, especially in shallow tropical seas and carbonate shelves where they can attain rock-forming mass. Most living representatives are symbiotic with various photosymbiotic partners, and much of their complex internal structure (visible in thin-section) has evolved to optimise the foraminifera's ability to host these partners. This is applicable to fossil forms conditional upon the observation of certain morphological features associated with such behaviour (see Consorti et al., 2000 and references therein). For an extensive and very readable description of these organisms in the modern seas and their photosymbiotic relationships see Hohenegger (2011).

In evolutionary terms LBF are considered to mostly display characteristics of "*K-strategists*" (Hallock, 1985; Hottinger, 2007) – usually associated with habitation within stable environments. This promotes longer individual life-spans, increasing evolutionary size ("Cope's rule"), increasing complexity, and delayed reproduction. However, the trimorphic life-cycle of LBF (see below) allows LBF to become "*r-strategists*" when subject to ecological stress (Harney et al., 1998). These are short-lived forms which with successive asexual generations (as opposed to alternation of sexual/asexual generations) can rapidly build population density and potentially survive major extinction events (see also Consorti & Rishidi, 2018).

It should be noted that this is not a "monographic" treatment of this group. There are no extensive synonymy lists for the taxa included. There are no re-definitions or emendations of taxa, nor new analysis of type and/or new material. Rather, it is an attempt to provide a practical guide to basic identification and a *summary* of the latest research (in general but not necessarily exclusively post-1985) on stratigraphic and palaeogeographical distribution. However, it seems reasonable to cover in more detail here issues such as LBF classification, morphology, terminology and identification, plus a description of the Cenomanian as a stage in Earth history and the methodology used in our assessments to avoid repetition in intended future articles.

This work is therefore intended to provide a practical guide to the identification of broadly flat to subglobular planispiral LBF in thin-section and therefore an aid to the identification of the same taxa in 3-dimensions. Its focus is determining the stratigraphic range of taxa and their palaeogeographic distribution.

CLASSIFICATION OF THE LBF

Overview

A full description of the development of foraminiferal supra-generic classification is far beyond the scope of this work but a short summary is presented here. Traditionally, classifications based on morphological characteristics have sufficed, culminating in monumental milestone works such as Loeblich & Tappan (1988) which have largely been sufficient for workers on fossils to use (and which publications such as Schroeder & Neuman, 1985 would have used). However, relatively recent developments, particularly with respect to molecular DNA studies in living taxa, have fundamentally rewritten many aspects of higher-level (i.e., above genus level) classification (e.g., Mikhalevich 1995, 2000, 2003, 2004a & b, 2013; Kaminski 2004, 2014; Pawlowski 2000, Pawlowski et al. 2013; Holzmann & Pawlowski 2017). Moreover, the main proponents of the new schemes (Kaminski or Mikhalevich, the former particularly with regard to the agglutinated taxa), although perhaps agreeing on the broad principles, have not yet reached complete universal agreement of the details.

This fundamental re-assessment has resulted in many LBF taxa being re-assigned to different families, superfamilies, suborders, and orders. We have used the classification of Kaminski (2014) for the Cenomanian agglutinated LBF taxa and Mikhalevich (2013) for the non-agglutinated taxa but it should be emphasised this may not be a final position.

At this point a major challenge to both identity and classification is the correct determination of the type of wall possessed by an LBF specimen in routine analysis. Factors including preservation and recrystallisation can greatly influence the appearance of a specimen under the microscope. In some cases, the wall composition and fine structure remains uncertain even for type material. Many genera herein are very similar, almost homeomorphic, and fundamental determination may depend on the type of wall structure observed.

For example, the genera *Moncharmontia* (agglutinated) and *Scandonea* (porcellaneous) are – otherwise – morphologically similar. If the nature of the wall cannot be correctly determined in specimens, then identity is compromised.

In another example, *Neodubrovnikella turonica* (Said & Kenawy) has only very recently been transferred to the Loftusiida (agglutinated) from the Miliolida (porcellaneous) where it was previously known as *Peneroplis turonicus* (Schlagintweit & Yazdi-Moghadam, 2022a).

The alveolar agglutinated genera *Buccicrenata* and *Pseudocyclammina* are morphologically very similar and are referred to herein as "Cenomanian cyclamminids". For a long time, they were members of the Cyclamminidae family (Loeblich & Tappan, 1988). Fundamental reclassifications by Mikhalevich (2004b) and Kaminski (2004) separated the two genera but in different ways. The same two authors published subsequent reclassifications in 2013 and 2104 respectively which resulted in further re-arrangements at the supra-generic level.

A resultant extreme view would be the two genera *Buccicrenata* and *Pseudocyclammina*, formerly part of the same family, and despite their morphological similarities, are now part of two separate *Suborders* of agglutinated foraminifera – the Loftusiina and Orbitolinina respectively.

Table 1 Higher classification of Cenomanian genera discussed in this study. Subclass MILIAMMINANA mainly after Kaminski (2014), Subclass MILIOLANA mainly after Mikhalevich (2013).

Class MILIOLATA; Subclass MILIAMMINANA				
Order	Suborder	Superfamily (1)	Family	Genus included herein
LITUOLIDA Lankester 1885 [Simple, non-perforate agglutinants]	NEZZAZATINA Kaminski 2004	Nezzazatoidea Hamaoui and Saint-Marc 1970	Mayncinidae Loeblich and Tappan 1985	*Biconcava* Hamaoui 1965 *Daxia* Cuvillier and Szakall 1949 *Deuterospira* Hamaoui 1965 *Mayncina* Neumann 1965
			Nezzazatidae Hamaoui and Saint-Marc 1970 (2)	*Biplanata* Hamaoui and Saint-Marc 1970 *Demirina* Ozcan 1994 *Merlingina* Hamaoui 1965
LOFTUSIIDA Kaminski and Mikhalevich 2004 [Bilamellar agglutinated wall, perforate or alveolar]	BIOKOVININA Kaminski 2004	Biokovinoidea Gušić 1977	Biokovinidae Gušić 1977	*Neodubrovnikella* Schlagintweit and Rashidi 2018
			Charentiidae Loeblich and Tappan 1985	*Charentia* Neumann 1965 *Fleuryana* De Castro, Drobne and Gušić 1994 (3) *Moncharmontia* De Castro 1967
	LOFTUSIINA Kaminski and Mikhalevich 2004	Loftusioidea Brady 1884	Cyclamminidae Marie 1941	*Buccicrenata* Loeblich and Tappan 1949 *Hemicyclammina* Maync 1953
			Spirocyclinidae Munier-Chalmas 1887	*Reissella* Hamaoui 1963 *Spirocyclina* Munier-Chalmas 1887
	ORBITOLININA Kaminski 2004	Pfenderinoidea Smout and Sugden 1962	Hauraniidae Septfontaine 1988	*Pseudocyclammina* Yabe and Hanzawa 1926
Subclass MILIOLANA				
MILIOLIDA Delage and Herouard 1896 [Porcellaneous, high magnesium calcite with milioline coiling]	MILIOLINA Delage and Herouard 1896	Quinqueloculinoidea Cushman 1917	Hauerinidae Schwager 1876	*Pseudonummoloculina* Calvez 1988 *Planinummoloculina* Piuz and Vicedo 2020 *Nummoloculinodonta* Puiz and Vicedo 2020
		Cornuspiroidea Schultze 1854	Cornuspiridae Schultze 1854	*Vidalina* Schlumberger 1900
SORITIDA Schultze 1854 [Porcellaneous, non-milioline]		Meandropsinoidea Henson 1948	Meandropsinidae Henson 1948	*Nummofallotia* Barrier and Neumann 1959
		Peneroplidea Schultze 1854	Peneroplidae Schultze 1854	*Peneroplis* De Montfort 1808
		Soritidoidea Ehrenberg 1839	Praerhapydioninidae Hamaoui and Fourcade 1973	*Pseudorhapydionina* De Castro 1971 *Pseudorhipidionina* De Castro 1971 *Praetaberina* Consorti et al. 2015 (4) *Pseudopeneroplis* Consorti et al. 2018 *Rajkanella* Schlagintweit and Rigaud 2015
			Soritidae Ehrenberg 1839	*Scandonea* De Castro 1971 *Perouvianella* Bizon et al. 1975

Notes:
(1) Between 2004 and 2013 standard endings of foraminiferal Superfamily names have undergone a change from –acea to –oidea in order to more easily differentiate zoological (–oidea) from botanical (–acea) nomenclature (Kaminski 2014).
(2) The Family Nezzazatidae Hamaoui and Saint-Marc (1970) is regarded as *Incertae Sedis* by Mikhalevich (2013) which she says belongs in the Subclass MILIOLANA "only partially".
(3) *Fleuryana* not included in Kaminski's classification but assigned to the Charentiidae by Hayward et al. (2020).
(4) See text for *Praetaberina*'s higher classification.

Whether one prefers to follow the supra-generic (i.e., at Family level and above) classifications of Kaminski or Mikhalevich is not an easy decision.

Distinguishing between wall textures/materials is also difficult, such as between calcareous microgranular and finely agglutinated walls, or whether features visible in the test wall such as pseudo-keriotheca/parapores or false keriotheca are present (Schlagintweit & Yazdi-Moghadam 2022b). Additional diagnostic morphological features such as beams, rafters, pillars, septula and others (see below) may be present in both agglutinated and calcareous forms (see Hottinger, 2006 for a full glossary) and may or may not be visible in many specimens.

The fundamental nature of what constitutes a "species" is still debated (see Allmon & Yacobucci, 2016, for a review) but nothing further will be said of that here, save that it is an issue which many palaeontologists often "sidestep". In our work we will be unequivocally dealing with "morphospecies" although Allmon (2016 and references therein) suggests many fossil "morphospecies" are more comparable with modern species-groups or genera than individual modern species.

Alternation of Generations

Workers on foraminifera are aware of dimorphism (sometimes even trimorphism) of species morphology as a result of reproduction that involves alternation of generations by sexual and asexual mechanisms (see Sen Gupta, 1999, Hohenegger, 2011 and BouDagher-Fadel, 2018 for summaries and references therein). The situation with LBF is especially pronounced with specimens termed megalo- (or macro-) spheric and microspheric (also respectively known as "A" and "B" or "Gamont" and "Agamont" forms – a second type of A-form (sometimes called A2 but with similar characteristics to the original A form) may be identified as the third type of a trimorphic arrangement) with respectively larger and smaller embryonic stages and concomitantly respective smaller and larger test sizes.

Megalo- (macro-)spheric "A" Gamont forms (which have smaller test sizes) are *generally* more numerous than micro-spheric "B" Agamont forms (which have larger test sizes). That appears to be reflected in the illustrations of specimens that we have examined but examples of both forms are not necessarily included within our illustrated material herein. Such variations can have an impact on how a fossil specimen might be identified in any sample. For example, it has long been recognised that dimorphism in LBF has caused some degree of taxonomic confusion. In the Palaeogene nummulitids, the megalospheric *Nummulites fichteli* Michelotti and the microspheric *Nummulites intermedius* (d'Archiac) (often co-occurring in the same samples) have long been understood to be the same species (van der Vlerk, 1929, Eames et al., 1962). Likewise, dimorphism is the Jurassic LBF genus *Neokilianina* has recently been recognised (Schlagintweit, 2023). It is possible to capture the full range of views necessary to identify the particular generation of a species where the proloculus is not visible, but that is beyond the scope of this work.

The reader should be always aware that statements herein can refer to either generation unless specifically mentioned, and that descriptions in the literature have tended to apply more to megalo- (macro-)spheric ("A") forms because they are more commonly found in nature (Bou-Dagher-Fadel, 2018).

A GUIDE TO TERMINOLOGY AND IDENTIFICATION

Planispiral LBF

This paper deals with Cenomanian (LBF) morphotypes including forms that are initially planispiral (or nearly so) and those that at some point in their growth have a planispiral (or nearly so) mode of coiling. The planispire can be involute or evolute, and range from flattened, disc-like to almost globular. Uncoiling is also a common feature. Some of these forms do not uncoil, some uncoil slightly, some uncoil fully and have a rectilinear (straight) or "peneropolid" (flaring) or sometimes "flabelliform" uncoiled stage which can be flattened or cylindrical in external view. Internal structures vary widely from none, to an often complex interlink between pillars, septula, beams, joists, rafters and others. For LBF such terminology can be complex, particularly when 3 dimensional objects are viewed in 2 dimensions as in a thin-section.

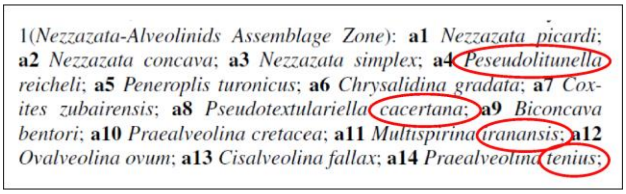
To understand the terminology, the reader is referred to the comprehensive and well-illustrated guide to a glossary of terms used to describe foraminiferal morphology by Hottinger (2006). Some authors (e.g., Vicedo et al., 2013; Consorti et al., 2015, 2018) provide helpful schematic drawings of what certain features in genera or species look like in 3-dimensions, extrapolated from several 2-dimensional views in thin section, which would be almost impossible to concisely describe otherwise (see *P. peruviana* herein for example).

Quality of the literature

A combination of the features described above is required for, at least, a determination of a genus and it would be fair to say that in most specimens revealed by typical sampling, especially when viewed in thin-section, only a few such features may be visible. Even a fundamental higher classification feature such as wall structure (e.g., in agglutinated taxa is the wall “simple” or “alveolar/pseudokeriothecal”?) may not be clear in all specimens (see *H. whitei* and in Simmons & Bidgood, 2022). In some taxa, the original composition of the wall (calcareous or agglutinated) may be uncertain (see *R. ramonensis*). During the course of this study the authors have estimated that more than half of published illustrations of material found in routine studies in the literature are not necessarily wrong in terms of identification (although a significant number are), but they cannot confirm the correct taxonomic identification proposed because features necessary for identification are poorly preserved or absent (see also Schlagintweit & Simmons, 2022). In a significantly large number of cases, occurrences are reported without any kind of confirmatory illustration.

A particular problem is the attempted identification of the taxa included in this study using *only* disaggregated, three dimensional specimens. This approach occurs in studies from all parts of the world but is particularly notable in material from Egypt (e.g., Orabi et al., 2012; Shahin & Elbaz, 2013). Such material cannot be confidently identified without viewing internal features of the test and is hoped that new publications will appear that use thin-sections for identification.

It may also be fair to say that, in some cases, the quality of the literature is not always high, and a subjective judgement may be needed to determine the reliability of a specific data point. On one hand there may always be a certain amount of debate if a specimen is species “A” or species “B” because scientists may have different species concepts in their own minds. On the other hand, many published identifications we have observed are clearly wrong. The reasons (and potential solutions) to this are many and worthy of separate discussion, but when evaluating the literature, it is prudent to consider the quality and nature/degree of peer-review/editing that has been undertaken in producing it. Often this can be revealed by a simple count of the number of spelling mistakes in the published article – especially within taxonomic names – which highlight poorly-chosen reviewers or no true peer-review process at all (Fig. 1).



1(*Nezzazata-Alveolinids Assemblage Zone*): **a1** *Nezzazata picardi*; **a2** *Nezzazata concava*; **a3** *Nezzazata simplex*; **a4** *Peseudolitunella reicheli*; **a5** *Peneroplis turonicus*; **a6** *Chrysalidina gradata*; **a7** *Coxites zubairensis*; **a8** *Pseudotextulariella cacertana*; **a9** *Biconcava bentori*; **a10** *Praealveolina cretacea*; **a11** *Multispirina iranansis*; **a12** *Ovalveolina ovum*; **a13** *Cisalveolina fallax*; **a14** *Praealveolina tenius*;

Fig. 1 Anonymised snapshot of a figure caption from a 2016 paper (by a major publisher) with four taxa spelled incorrectly.

There is a secondary factor which involves a desire among workers to provide a species name for every specimen observed. Such a desire is admirable but often results in the “forcing” of a taxonomic label onto specimens – perhaps poorly preserved or where the section does not cut through the diagnostic features – which cannot be justified. This results in erroneous occurrences in the literature which, in turn, artificially extends the apparent stratigraphic and/or geographic ranges of taxa. One of the authors herein (MS) admits to his guilt here (e.g., some taxa in Simmons & Hart, 1987), identifying taxa based on inadequate material. That said, whilst it is desirable to make many thin-sections to confirm identification (see for example the exemplary work of Vicedo & Piuz, 2017), that may not always be possible.

Identification Issues

Accurate determination of the genus and species of these LBF depend crucially on the ability to see and describe features that may not easily be discerned in many, perhaps the majority, of specimens (see also above). The morphological complexity of the organism’s shell is matched and even exceeded by the descriptive terminology required to classify them. Although constructed several decades ago, Table 1 of Hottinger (1978) remains the foundation of the principles of classification and identification based on the use of structural and ontological features of the LBF shell.

Of critical value at genus and sometimes species level is (a) the nature of the wall and (b) the nature of the aperture. The external appearance of the test wall may hide a wide range of textures and microstructures that may only be discernible in thin-section. Apertures only appear within the plane of the apertural face (and as foramina in the preceding septa) and thus require the plane of the thin-section cut to intersect them exactly, so as to be seen. Several of the established taxa described herein still have little or no knowledge of the exact nature of their aperture which remains an issue for accurate taxonomy and classification at genus level.

Wall structure

Determination that a genus’/species’ wall structure is either calcareous or agglutinated can be difficult (see comments above referring to *Peneroplis turonicus* / *Neodubrovnikella turonica*). The genus *Reissella* appears to be in a position of uncertainty in this respect.

Observing the texture of an agglutinated wall in thin-section can likewise be difficult. In the taxa considered herein, the agglutinated wall (including outer shell and apertural face, and inner septa) can be variously described in terms of being:

- Simple (single-layered) and imperforate
- 2-layered
- Alveolar (and “pseudo-alveolar”)
- Keriothecal (and “pseudo-keriothecal”)

There are obvious difficulties. What is the difference between "alveolar" and "pseudo-alveolar", for example...and are there alveoles or a network of beams and rafters? A superb, very comprehensive, if technical, illustrated glossary of foraminiferal study is provided by Hottinger (2006) (and see also Septfontaine, 1981: fig. 2) but it might be appropriate to consider some of these more general features in a practical way (Fig. 2 herein).

Imperforate – Fig. 2a: lacking pores or parapores. The agglutinated grains are (more-or-less) randomly arranged and cemented to form a close-fitting mosaic. In imperforate walled agglutinated taxa, the grains usually comprise a single (i.e., undivided) layer.

2-Layered – Fig.2b-f: basically, a thin but solid, imperforate, upper (outer) epidermal layer that closes off subepidermal openings such as alveoles and pseudokeriotheca (see below) which are found in the thicker lower (inner) layer.

Alveolar – Fig. 2b, c, e, f): an alveole is a recess of varying depth within a wall, coated by the organic lining of the foraminifer. They occur within the exoskeleton (those parts of the chamber walls exposed to the environment) but end blindly beneath a final, solid epidermal layer (see above). Alveoles are thought to be filled by the foraminiferal protoplasm during life. A "pseudoalveolar" shell is a simple exoskeletal structure consisting of alcoves ("a blind compartment of a chamber lumen delimited by beams and the lateral chamber wall" – Hottinger, 2006 – most likely used as a receptacle for symbionts).

Pseudokeriotheca – Fig. 2d: unlike alveoles, pseudokeriotheca are neither filled with protoplasm during life, nor are they coated with the organic lining. They tend to be more tubular and more distinctly radial than the more sack-like alveoles. They are described as "*fine tubules …which give a fibrous appearance in section*" (Loeblich & Tappan, 1964) and are equivalent to the term "false keriotheca" *sensu* Vachard et al. (2004). Keriotheca is a term Hottinger (2006) reserves for advanced Paleozoic fusulinids. Pseudokeriotheca is reserved for similar (?analogous) structures in Mesozoic and younger agglutinated foraminifera.

Internal wall and chamber modifications

Workers on LBF consider various wall and chamber modifications to be either 'exoskeletal' or 'endoskeletal'. Exactly what constitutes an endo- or exo-skeleton has long been debated (see Hottinger, 2006, for a summary). Hottinger's definitions (Hottinger, 1967, 1978, 2006) distinguish the two, in essence, by stating that endoskeletal structures are those that include "*all structures subdividing the chamber lumen and linked to the patterns of intralocular protoplasmic streaming, in contrast to exoskeletal partitions that are not affected by such patterns*". In simple terms, structures like septula, pillars and chomata (chamber-floor thickening) are endo-skeletal whereas structures like beams, alcoves and alveoles are exoskeletal. However, some variations may apply and features such as tooth*plates* (as distinct from teeth which are endoskeletal) remain unassigned to either.

Modifications, particularly to the inner surfaces of the chambers (the chamber sides and their floors and ceilings – the latter two termed septa), are numerous in LBF and can lead to micro-structures of intricate complexity, which is remarkable for a single-celled organism (Hottinger, 1978, 2006; BouDagher-Fadel, 2018). A single chamber can be subdivided, contain "ridge" or "gridlike" structures on the ceiling, variably thickened layers on the floor, and within can contain sheet-like septula (which can sometimes extend from floor to ceiling) and/or columnar pillars (which always do) with various cross sections. Penetrating the septa are single or numerous openings (foramina) arranged randomly or in a more organised fashion. Some of these are shown schematically in Fig. 2e-j.

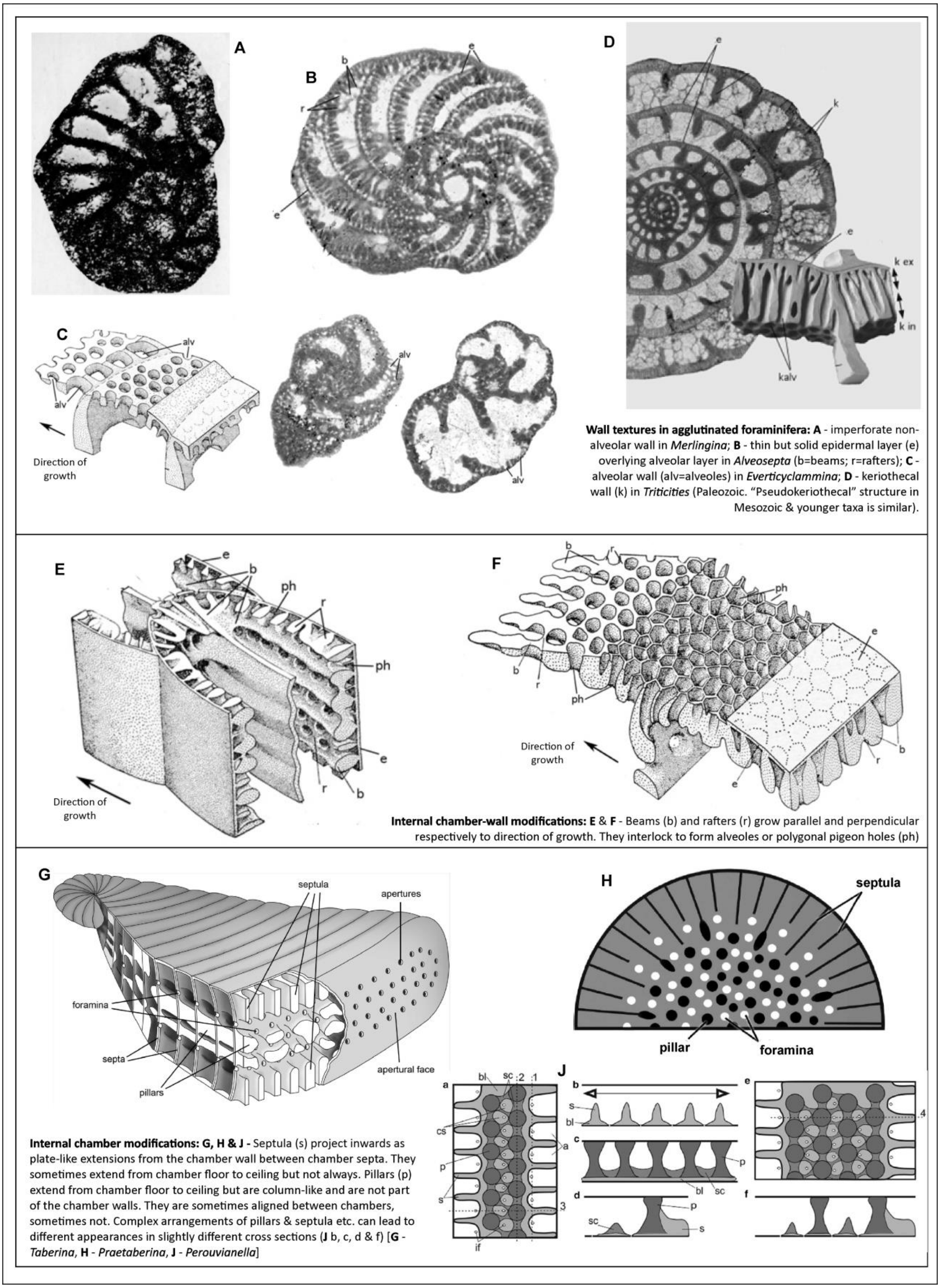
Some or all of these features can only be seen if a thin-section cut is oriented such that the feature is intersected. Slight changes to the position and orientation of a thin-section cut can show a markedly different visual arrangement (Hottinger, 1967), or even remove observable features altogether (see Fig. 2j or BouDagher-Fadel, 2018: fig. 1.7). External apertures and intercameral foramina are often very difficult to observe in thin-section because of this.

Complexities such as these require the observation of good quality material in several different thin-section orientations in order to determine their existence and nature in 3-dimensions. 3-dimensional sketches such as those included in Fig. 2 (i.e., c-j) and other figures herein are extremely useful in this respect and their usage when describing new taxa (or emending existing taxa) should be encouraged.

A summary of key morphological characteristics of the taxa identified herein is shown in the Appendix. Previous authors (e.g., Hottinger, 1967; Neumann, 1967; Septfontaine, 1981; Whittaker et al., 1998 and Rigaud et al., 2014) have also provided identification keys although these have been principally to define and separate genera.

THE CENOMANIAN STAGE

The Cenomanian represents a remarkable time during Earth's history. Climates are typically regarded as relatively warm (Francis & Frakes, 1993; Skelton, 2003; Hart, 2007, 2021; Hong & Lee, 2012; O'Brien et al., 2017; Laugié et al., 2020; Scotese et al., 2021) and sea-levels as relatively high (Haq et al., 1987; McDonough & Cross, 1991; Haq, 2014; Vérard et al., 2015; van der Meer et al., 2017, 2022; Simmons et al., 2020a; Wright et al., 2020). On the other hand, there is growing evidence for significant short-term eustasy (e. g., Haq et al., 1987; Sahagian et al., 1996; Robaszynski et al., 1998; Scott et al., 2018; Hancock 2004; Miller et al., 2004; Simmons et al., 2007; Kominz et al., 2008; van Buchem et al., 2011; Haq, 2014; Ray et al., 2019), possibly linked to



Wall textures in agglutinated foraminifera: A - imperforate non-alveolar wall in *Merlingina*; **B** - thin but solid epidermal layer (e) overlying alveolar layer in *Alveosepta* (b=beams; r=rafters); **C** - alveolar wall (alv=alveoles) in *Everticyclammina*; **D** - keriothecal wall (k) in *Triticities* (Paleozoic. "Pseudokeriothecal" structure in Mesozoic & younger taxa is similar).

Internal chamber-wall modifications: E & **F** - Beams (b) and rafters (r) grow parallel and perpendicular respectively to direction of growth. They interlock to form alveoles or polygonal pigeon holes (ph)

Internal chamber modifications: G, H & J - Septula (s) project inwards as plate-like extensions from the chamber wall between chamber septa. They sometimes extend from chamber floor to ceiling but not always. Pillars (p) extend from chamber floor to ceiling but are column-like and are not part of the chamber walls. They are sometimes aligned between chambers, sometimes not. Complex arrangements of pillars & septula etc. can lead to different appearances in slightly different cross sections (**J** b, c, d & f) [**G** - *Taberina*, **H** - *Praetaberina*, **J** - *Perouvianella*]

Fig. 2 Some morphological descriptions and visualisations of wall and/or chamber components of planispiral or part-planispiral LBF taxa. (**a** after Hamaoui & Saint-Marc, 1970; **b**-**f** after Hottinger, 2006; G: after Vicedo et al., 2013; **h** after Consorti et al., 2015; **j** after Consorti et al., 2018). Other abbreviations shown in image **j** are bl=basal layer; cs=conical spaces; if=intercameral foramina and sc=socculi crest.

ephemeral ice sheets waxing and waning (Miller et al., 2003; Miller et al., 2005; Voigt et al., 2006; Plint & Kreitner, 2007; Koch & Brenner, 2009; Ladant & Donnadieu, 2016; Davies et al., 2020), and/or other eustatic drivers (Wendler & Wendler 2016; Sames et al., 2016; Sames et al., 2020), since the $\delta^{18}O$ record appears stable across certain events (Ando et al., 2009). Orbital forcing of global climate is clearly present in the Cenomanian (Gale et al., 1999; Gale et al., 2002, 2008; Wendler et al., 2010; Wendler et al., 2014; Boulila et al., 2011; Al-Husseini, 2018; Huang, 2018) and is very likely linked to short-term eustasy.

Significant geodynamic developments were taking place during the Cenomanian (Stampfli & Borel, 2002; Giorgioni et al., 2015; Torsvik & Cocks, 2017; Laugié et al., 2021; Scotese, 2021), with the onset of the closure of Neotethys and the opening of the Atlantic. Excursions in the carbon cycle are a notable feature of the mid-Cretaceous (Coccioni & Galeotti, 2003; Jarvis et al., 2006; Cramer & Jarvis, 2020) and include ocean anoxic events (OAEs) 1d and 2 (Jenkyns, 2010; Gertsch et al., 2010; Joo & Sageman, 2014; Gambacorta et al., 2015; Laugié et al., 2021) that lie close to the boundaries of the Cenomanian stage.

Cenomanian sediments also have significant economic potential. For example, petroleum source rocks are developed during times of anoxia, and reservoir rocks were created within the widespread carbonate platforms that typify the stage (Scott et al., 1993; Alsharhan & Scott, 2000; Marlow et al., 2014; Esrafili-Dizaji & Rahimpour-Bonab, 2019; Bromhead et al., 2022).

The Cenomanian represents a period of significant faunal and floral diversity. The relatively warm climate and relatively high long-term eustatic sea-level led to widespread carbonate platform development where many organisms proliferated and diversified (Philip & Airaud-Crumiere, 1991; Höfling & Scott, 2001; Johnson et al., 2001; Steuber et al., 2016; Rineau et al., 2021, Hart, 2021). These included larger benthic foraminifera and rudist bivalves. In the relatively deep waters of the open shelves and basins, ammonites, inoceramid bivalves, planktonic foraminifera, calcareous nannofossils, and dinoflagellates proliferated and diversified. In all settings, several fossil groups displayed rapid evolutionary trends, with several species or genera having short stratigraphic ranges making them useful for biostratigraphy. These evolutionary patterns were linked to short-term climatic, eustatic and oceanographic events (Mitchell & Carr, 1998), not least the OAEs and their precursors (Jarvis et al., 1988; Gertsch et al., 2010).

LBF are a key component of Cenomanian fossil assemblages and can provide useful inputs into the evaluation of many aspects of the Cenomanian world, providing they can be accurately identified and age-calibrated.

Earth's Cenomanian paleogeography is shown in Fig. 3 with regions indicating the locations of most LBF discussed in this study. Scotese et al. (2021) assigned climatic "Paleo-Köppen belts" to these regions as follows:

- Arid – West Atlantic/Caribbean (1), North Africa (5) and southern Iberia (2)
- Tropical – Central-East Mediterranean (3), Arabia (6) and northern Iberia (2)
- Boreotropical – eastern part of the North Tethys Margin (4 - eastwards from Turkey)
- Warm Temperate – western part of the North Tethys Margin (4 - NW Europe) and virtually the rest of the world except extreme polar regions

Note, however, that has shown by Davies et al. (2020), these climatic belts will have shifted markedly during the intra-stage climatic cycles.

The Cenomanian is almost unique, stratigraphically, in that it is one of only a few stages where its boundaries (Albian-Cenomanian – A/C) and (Cenomanian-Turonian – C/T) are located within Oceanic Anoxic Events (i.e., OAE1d and OAE2 respectively). The chronostratigraphic base of the Cenomanian is defined paleontologically by the first appearance datum (FAD) of the planktonic foraminifera *Thalmanninella globotruncanoides* (Sigal) (Kennedy et al., 2004) and the base of the Turonian by the FAD of the ammonite *Watinoceras devonense* Wright & Kennedy (Kennedy et al., 2005). Of the two boundaries, the A/C boundary (and OAE1d) is comparatively less intensively studied than the C/T boundary (OAE2).

Both boundary section GSSPs are, by necessity, located in relatively deep-water settings where deposition is continuous but, unfortunately, LBF are generally absent from these deeper environments.

Ammonites – traditional Mesozoic biozonal markers – across the Albian-Cenomanian boundary are relatively rare in many regions hence the choice to define the boundary on the first appearance of a planktonic foraminifer. However, ammonites soon became more common and widespread, and, at the GSSP section, the first Cenomanian ammonites appear 6 metres above the marker planktonic foraminifera species (Gale et al., 2020).

The warm climate and high sea levels prevalent in the Cenomanian resulted in ammonite faunas showing relatively little endemism. In the early – middle Cenomanian ammonite biozones can be recognised globally except for the Western Interior Basin of North America, however in the late Cenomanian ammonite faunas are almost entirely global in distribution (Wright et al., 2017). Although ammonites are not generally found alongside LBF because of the different habitats occupied by both, LBF occurrences bracketed by datable ammonite occurrences provide useful, calibrated, biostratigraphic data.

In the absence of ammonites, carbon isotope data provides another potentially useful calibration tool. A full review of Cenomanian carbon isotope data is beyond the scope of this work, but the synthesis by Cramer and Jarvis (2020) of work by Jenkyns et al. (1994), Paul et al. (1994), Mitchell et al. (1996), Jarvis et al. (2001, 2006) shows that the Cenomanian (and bounding strata) has a distinctive carbon isotope curve that is useful in correlation and calibration studies.

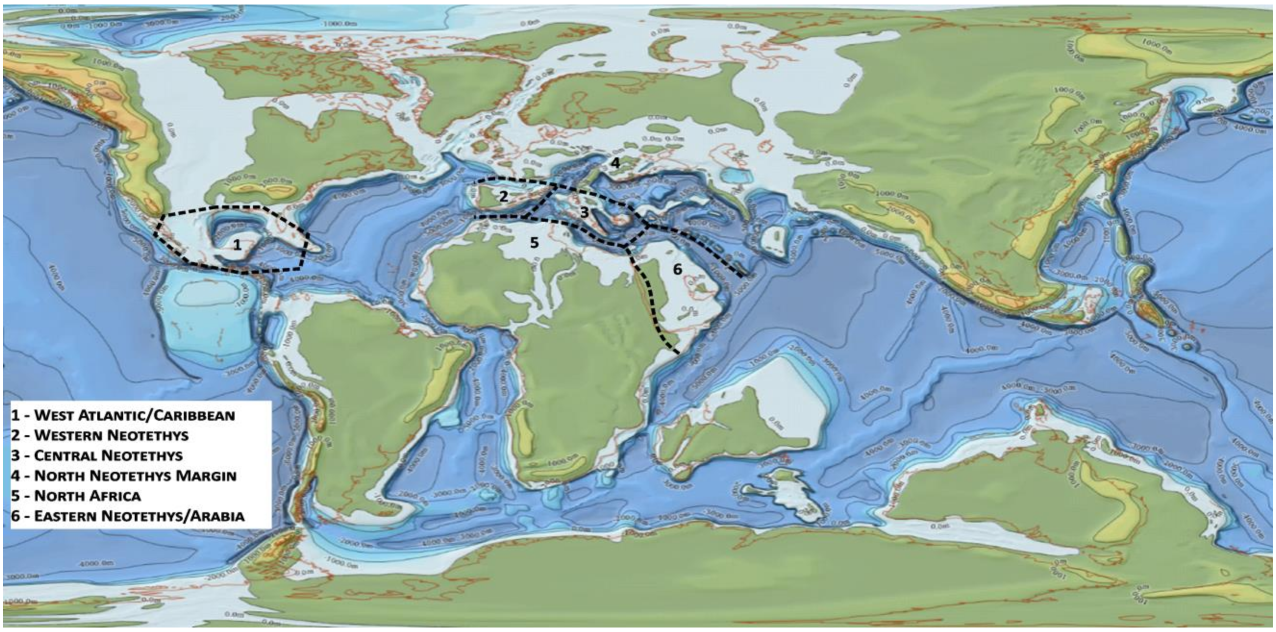


Fig. 3 Cenomanian paleogeography with regions indicating the location of most planispiral LBF in this study. There are a few additional records from, for example, Peru, Afghanistan and Tibet. (Base paleogeographic map courtesy of Halliburton).

Distinctive major carbon isotope excursions occur across the Albian-Cenomanian boundary (OAE1d), the early-middle Cenomanian boundary (termed the Mid Cenomanian Event or "MCE" sensu Paul et al., 1994 and Mitchell et al., 1996) and across the Cenomanian-Turonian boundary (OAE2). In addition, minor excursions in the curve have also been recognised (see Bidgood & Simmons, 2022: fig. 2) which may prove useful correlative signals at local level. Some LBF workers such as Parente et al. (2008) and Frijia et al. (2015) have incorporated carbon isotope data in their work on establishing the upper stratigraphic limits of several LBF taxa. Bidgood & Simmons (2022) reviewed the distribution of Cenomanian planktonic foraminifera bioevents and have calibrated these events to the carbon isotope curve.

The widely accepted duration of the Cenomanian stage is 6.6 Myr based on radiometric dating (Gale et al., 2020 and references therein), although Beil et al. (2018) calculated a 4.8 Myr duration based on recognition of orbital forcing cycles. However, the necessarily continuous deposition of the cored section examined is not convincingly demonstrated by biostratigraphy in the latter case.

The Albian-Cenomanian boundary

The base of the Cenomanian stage is defined by a GSSP at Mont Risou in France (Kennedy et al., 2004). The Albian-Cenomanian boundary occurs within an interval of global anoxia termed OAE1d or the "Breistroffer" event. This is associated with a minor, positive δ^{13}C excursion expressed in 3 or 4 individual peaks with the chronostratigraphic boundary lying between peaks B and C (Cramer & Jarvis, 2020). Unlike most OAEs in the Cretaceous, OAE1d has not been associated with the emplacement of a so-called "Large Igneous Province" (LIP) (cf. OAE2 which is associated with three LIPs) (Ernst et al., 2020). Matsumoto et al. (2022) proposed a mechanism of water-mass stratification triggered by freshwater input caused by the cyclic intensification of monsoonal activity for OAE1d (and for OAE1c lower down in the Albian).

The Albian-Cenomanian boundary is dated as 100.5 Mybp based on an extrapolated measurement of dated tuffs from Hokkaido, Japan (Obradovich et al., 2002; Takashima et al., 2019; Schmitz, 2020) which lie significantly above the first appearance of *T. globotruncanoides*.

Cenomanian substages

The Cenomanian is divided unequally into early, middle and late substages (e.g., Gale et al., 2020). The base of the middle Cenomanian is defined by the first appearance of the ammonite *Cunningtoniceras inerme* (Pervinquière), followed shortly afterwards (~100,000 years) by *Acanthoceras rhotomagense* (Brongniart). The appearance of these two genera is a major biostratigraphic event in Europe, north Africa, India and elsewhere (see Gale et al., 2020 for references). However, a continuous boundary section is missing in many areas because it is coincident with a major sequence boundary.

In the Western Interior Basin (WIB), the base of the middle Cenomanian is marked by the first appearance of the ammonite genus *Conlinoceras* (Gale et al., 2007).

A positive carbon isotope excursion termed the "Mid Cenomanian Event" (MCE) also occurs near the base of the middle Cenomanian. The MCE is calibrated to the *inerme* and lower *rhotomagense* ammonite zones (Jarvis et al., 2006).

The replacement of *Acanthoceras* by *Calycoceras* (the first appearance of C*alycoceras guerangeri* (Spath)) is normally used to define the base of the late Cenomanian (Hancock, 1991; Wright et al., 2017). The *C. guerangeri* zone is approximately coeval with the *Dunveganoceras pondi* Haas zone of the Western Interior Basin, the base of which is used to define the middle/upper substage boundary there (Cobban et al., 2006).

The durations of the respective substages are not evenly spaced, with the early Cenomanian representing almost two-thirds of the duration of the stage (Gale et al., 2020). Substage and zonation durations are in part estimated using cyclostratigraphy, including recognition of the 405-kyr orbital forcing cycle. For example, the duration between the carbon isotope events near the base of the middle Cenomanian ('MCE II') and that within the upper Cenomanian ('OAE2 peak B'), is estimated at approximately 1.9 My. This is supported by radiometric dating of bentonites from near the base of the middle Cenomanian in the WIB as 96.21 ± 0.36 Mybp (Gale et al., 1999; Eldrett et al., 2015; Batenburg et al., 2016) and other intra-Cenomanian radiometric dates (e. g., Cobban et al., 2006; Schmitz, 2020). The base of the upper Cenomanian appears to be slightly older than 95.39 Mybp (+/- 0.37) – a radiometric age from a sample assigned to the *D. pondi* ammonite zone of the WIB (Schmitz, 2020). The boundary is placed at 95.47 Mybp by Gale et al. (2020).

The Cenomanian-Turonian boundary

Whilst the C/T boundary is defined in a (continuous) deep-water GSSP section at Pueblo in Colorado, USA (Kennedy et al., 2005), in many places across Neotethys where shallow-water carbonates dominate, the C/T boundary is omitted by an unconformity or is associated with a OAE2-related drowning event (Arriaga et al., 2016; Bromhead et al., 2022). This makes continuous sections such as those in southern Italy described by Arriaga et al., 2016 (see also Parente et al., 2007, 2008; Frijia et al., 2015) extremely valuable for documenting the stratigraphic distribution of LBF across the stage boundary.

Around the C/T boundary major oceanographic and associated lithological changes across much of the globe resulted in a major perturbation in the carbon cycle, which resulted in a large positive excursion (the largest in the Mesozoic) in the δ^{13}C signal**.** This is known as Oceanic Anoxic Event 2 (OAE2 a.k.a. the "Bonarelli" event). It is also often (but not always, for example at the GSSP section for the base Turonian at Pueblo, Colorado, USA) associated with the deposition of organic-rich dark shales. At this location, the maximum major carbon-isotope excursion associated with OAE2 occurs 0.5 m above the stage boundary, although the boundary lies with a section of overall positive δ^{13}C values that typify OAE2 (Gale et al., 2020).

OAE2 is one of the most intensively studied carbon perturbations on record and the specific cause(s) of this event are complex and numerous and beyond the scope of this work to review. It is most likely that OAE2 was initiated (or at least exacerbated) by Large Igneous Provinces (LIPs) and a period of anoxic (or at least dysaerobic) oxygen levels in the water column was the result (Jones et al., 2023). In the case of OAE2 these LIPs are termed Madagascar (or Kerguelen), the High Arctic, and Caribbean-Colombian (Ernst et al., 2020; Jones et al., 2023). This had a profound impact on much of marine life, particularly in relatively deeper waters where it may be regarded as an intensification and perhaps expansion of the oxygen minimum zone. However, the extent of these dysaerobic/anoxic waters across shallower carbonate platforms and impacting on the life of LBF is not completely understood.

Uncertainty regarding the placement and nature of the C/T boundary in sections which lack ammonite or carbon isotope calibration (i.e., many carbonate platform sections) has led to confusing and/or incorrect placement of range-limits assigned to numerous LBF taxa in the literature. Consequently, it is still not entirely clear as to which taxa, if any, became extinct at the onset of OAE2, or at the chronostratigraphic C/T boundary itself, or at points between the two levels (see for example Parente et al., 2008 and Frijia et al., 2015). A few species clearly continued into middle Turonian and younger strata (Schlagintweit & Yazdi-Moghadam, 2021).

In some regions out-with the Middle East / Neotethys, the effects of OAE2 were small or even absent (for example on the Western Platform of Peru bordering the Pacific Ocean; Navarro-Ramirez et al., 2016, 2017). In Peru, LBF appear to thrive – sometimes becoming rock-forming – at times when in Neotethys most LBF were either becoming extinct or migrating towards more favourable environments (Bizon et al., 1975; Jaillard & Arnaud-Vanneau, 1993; Navarro-Ramirez et al., 2017; Consorti et al., 2018).

The age of the Cenomanian-Turonian boundary is well-constrained as 93.9 ±0.2 Mybp by ^{40}Ar/^{39}Ar ages from bentonites close to the GSSP section in Colorado (Obradovich 1993; Meyers et al., 2012).

Cenomanian LBF Biostratigraphy

Larger benthic foraminifera form a distinctive microfossil component of many Neotethyan Cenomanian shallow-marine carbonate successions (BouDagher-Fadel, 2018), yet despite their established stratigraphic value (e.g., Saint-Marc, 1974a, 1981; Husinec et al., 2000; Calonge et al., 2002), there is no widely accepted Cenomanian biozonation scheme for this group that is applicable across several regions. Arnaud et al. (1981) produced a range chart of Albian-Turonian LBF and subsequently (Arnaud-Vanneau, 1998) noted some bioevents that might have correlative value. The stratigraphic ranges of many important mid-Cretaceous taxa were reviewed in the seminal publication of Schroeder & Neumann (1985) which was almost identical to the ranges of Arnaud et al. (1981), although no biozonation scheme was suggested. However, within the broad Mediterranean region, Cenomanian LBF biozonation schemes have been constructed that, even when comprising informal biostratigraphic units, are helpful in recognising successions of bioevents which form the basis for a pan-Tethyan scheme. These include works by Chiocchini et al. (1994, 2008, 2012); Velić & Vlahović (1994); Velić (2007); Chiocchini (2008a); and Solak et al. (2017). It should be noted that these schemes typically lack independent age calibration or illustration of many of the species mentioned, so that whilst the relative order of inceptions and extinctions that are observed are helpful, their chronostratigraphic calibration is typically based solely on the foraminifera described (Frijia et al., 2015).

By contrast, there has been a recent proliferation of localised biozonation schemes utilising Cenomanian LBF, not least for strata in the Middle East. These are often assemblage zones (following the similar philosophy of building Oppel zones in the Paleogene SBZ scheme of Serra-Kiel et al., 1998), rather than based on specific inceptions and/or extinctions of taxa. Their value has been discussed by Schlagintweit & Simmons (2022), which should be consulted for further details.

It is therefore somewhat paradoxical that on one hand LBF are common and distinctive elements of Cenomanian platform facies, with lineages of both agglutinated and porcelaneous forms undergoing rapid evolution that makes them suitable for biostratigraphy-based correlation, yet on the other hand consensus on key bioevents and their calibration to zonations of other fossil groups and the chronostratigraphic scale is largely absent. Reasons for this include:

(i) Taxonomic uncertainties (i.e., the identify of some taxa remains unclear).

(ii) Misidentifications and records with imprecise or misleading age calibrations has resulted in “smeared” (i.e., overly extended) ranges for some taxa (see tables and discussion in Sari et al., 2009; Consorti et al., 2015; Solak et al., 2020; Schlagintweit & Simmons, 2022).

(iii) Locally, stratigraphic ranges may be truncated because of unsuitable facies and/or non-deposition and erosion at sequence boundaries. This is probably the most difficult problem to overcome (combined with point (v)) when attempting to build a scheme with regional/global applications.

(iv) Some LBF taxa are endemic (Banner et al., 1991; Piuz et al., 2014; Vicedo & Piuz, 2017; Yazdi-Moghadam & Schlagintweit, 2020, 2021, 2022).

(v) LBF do not commonly co-occur, or are reported as co-occurring, with planktonic foraminifera, calcareous nannofossils, dinoflagellates or ammonites. This limits their potential age calibration. In some cases where ammonites or other pelagic fossils are reported alongside LBF (e.g., Saint-Marc, 1974a, 1981), they occur separately in lateral facies equivalents and correlation may be uncertain. A solution is the potential “Rosetta Stone” of carbon isotope stratigraphy (Parente et al., 2008; Frijia et al., 2015) that, in the right circumstances, allows for calibration between platformal and basinal stratigraphy and to the global standard curve that is tied to standard chronostratigraphy.

Given the potential biostratigraphic value of this fossil group, it seems highly desirable to create a zonation scheme based around key bioevents (extinctions and/or inceptions) that can at least be used to assist in recognising the boundaries of the Cenomanian stage, and the substages within it.

As previously noted, simply uncritically collating published information on stratigraphic ranges would result in ‘smeared’, overly long ranges for many taxa (Schlagintweit & Simmons, 2022), with ranges extending throughout the Cenomanian, and in some cases, into the underlying and overlying stages and beyond. Therefore, any synthesis needs to take a critical approach with weighting skewed towards records in which the taxonomic identity can be confirmed as at least likely (e.g., where material is well-preserved and supported by adequate illustration), and in which the independent age calibration seems plausible (e.g., supported by ammonite or other independent fossil occurrences or by non-biostratigraphic methods such as carbon isotope data). Circular reasoning for age-determination must be avoided.

METHODOLOGY AND ‘BEST PRACTICE’

A review paper such as this requires independent assessment of previous LBF research. Taken at face value, a compilation of published age-ranges for individual LBF species would result in excessively long ranges with upper and lower range limits which are too young or too old and consequently of little value for biostratigraphic correlation. The last time this can said to have been undertaken systematically is the major review of Schroeder & Neumann (1985). Since then, a much larger volume of (Cenomanian) LBF data has been published, with much variable quality.

We have attempted to review as much of this work as possible (600+ published references, mostly published after 1985) with a desire to provide some sort of assessment of the quality and therefore the reliability of this work. This involves, in the main, a two-step process:

1. Confirm or otherwise assess the *identification* of the LBF species – normally by their illustration (or lack of it).
2. Confirm or otherwise assess the *age attributed* to that species.

This kind of assessment is significant and necessary at this time, especially with the advent of digital treatment of data in the form of Machine Learning (ML) or other Artificial Intelligence (AI) techniques. The quality of ML/AI output depends significantly on the way algorithms are trained (Simmons et al., 2019). If, for example, all LBF training data (i.e., the previous literature) is treated as equivalent in terms of quality, the output (e.g., stratigraphic upper and lower limits) will be less precise. When a (previously unseen) test data set is then applied for the machine to “interpret”, the resulting age interpretations will be too broad and therefore of less value. ML also has the potential to highlight outliers in data which can potentially aid age refinement.

Verification by illustration

Taxonomic units (e.g., species) are first defined and described with illustrated exemplars of diagnostic features. In the case of most LBF these diagnostic features are only visible internally which usually requires original descriptions supported by oriented thin-section illustrations – ideally axial and/or equatorial views which intersect those same internal taxon-specific features and from several different specimens ("types").

In the case of subsequent records, occurrences of known taxa in studied localities should also be identified with verification by supporting images whenever possible. Often this may not be possible, and it is not guaranteed that thin-sections will be oriented correctly in order establish confident verification based on the visibility of diagnostic features. For example, in the case of *B. peneropliformis*, a total of 65 published references (the majority from the 21st century when the ability to record images is commonplace) in which this species was recorded were examined; of these only 14 references provided supporting imagery and, in the opinion of the present authors, in at least four cases the illustrations were not those of *B. peneropliformis*. Of the remainder, five images were thought to definitely represent the species and five were plausible examples of the species.

Establishing identity by comparison with images of a fossil is, of course, a subjective assessment. We have used the following descriptive terms in the text regarding the accuracy of the images in question in the hope that at least a degree or range of certainty might be established. However, we recognise that there is a "continuum" of possibilities between the four (see also fig. 1 in Schlagintweit & Simmons, 2022):

- Definite: The illustrations (ideally of several different specimens) include correctly oriented specimens which display the diagnostic feature(s) that conforms in all respects to the types. Illustrations of type specimens are, by definition, definite unless stated.
- Plausible: Specimens where some (but not all) diagnostic features are present and secondary features characteristic of the species are present. These specimens can be said to probably represent the species.
- Uncertain: The material illustrated is inadequate to draw firm conclusions as to identity, or there is no illustration. The species name in publication should (ideally) be appended by a question mark, but in practice rarely is.
- Incorrect: No diagnostic or secondary characteristic features are visible, and the specimens are clearly something else.

Studies of LBF in thin-section often require the scientist to visualise what the specimen might look like in three dimensions, based on their observations in two dimensions, and draw conclusions from that. This is a skill not easily learned and is considerably enhanced by experience and exposure to high volumes of comparative material. In references where occurrences are unsupported by illustration it can be difficult to assess how accurate a scientist's species-determination skills may be. Lack of illustration implies that such occurrences can be regarded as no better than "uncertain".

We are keen to point out that unillustrated occurrences reported from references herein are not necessarily always 'incorrect', but that the occurrences are not possible to verify based on current information and in the absence of viewing the original material at first hand.

In the Cenomanian palaeogeographic distribution maps for individual species provided herein, illustrations which are definite or plausible occurrences are shown as a solid circle ●. Uncertain illustrations, and occurrences unverified by any illustration are shown as a circled question mark. Incorrect occurrences are not shown.

Ambiguity and assignment of age

Ambiguity of the age of a fossil specimen, or the age implied to a rock based on the presence of a particular fossil species, is a considerable challenge in stratigraphy (Simmons, 2015). How confident are we to know the precise upper and lower range limits of a single species? Is the species' range the same across its entire geographical spread? If not, can this be quantified? If specimens are few, can we say from what part of the species' total range are the specimens from? Countless books and papers have been written on such matters and these challenges are not new (e.g., see McGowran, 2005, for a treatment of these topics).

In the case of LBF, precise age-calibration is difficult because LBF do not inhabit the same environments as other fossil groups which are more frequently used for age calibration (e.g., planktonic foraminifera, nannofossils, ammonites etc.). Very often, assigned ages to those rock units that contain supposedly age-diagnostic LBF taxa, are the result of circular arguments (e.g., this rock is early Cenomanian because it contains species "X"; How do we know species "X" is early Cenomanian in age? Because it is found in other rocks people have called early Cenomanian based on the presence of species "X").

We also assign age labels to rock units that have inherent ambiguity e.g., "The X Formation is late Albian – early Turonian in age". Does this mean the rocks were deposited continually from late Albian times until early Turonian times – a period of around 13 million years, or do we mean that the true age of the rocks falls somewhere within the interval of late Albian – early Turonian, meaning that the rocks may be just early Cenomanian, or late Cenomanian, or early Turonian in age and were deposited over a much shorter time-span? Or is this a maximum age, but erosion/non-preservation may reduce the age range locally. Anecdotal evidence from the authors' industrial experience suggests biostratigraphers *mean* the latter but non-biostratigraphers *assume* the former.

In the case of many LBF references – some even published this year! – age assignments of both fossils and rock units based on their presence are based upon knowledge that may be decades old and well out-of-date. In the Zagros region of Iran, for example, many recent publications continue to refer to the "biofacies" stratigraphy established by Wynd in 1965 (Schlagintweit & Simmons, 2022). In many cases, ages are assigned unquestionably because a previously published age-assessment was uncritically accepted. In summary, there is often great uncertainty in any age assignment to a particular LBF occurrence.

Stratigraphic ranges of LBF herein

Uncertainties over fossil identification (see above) coupled with sometimes dubious age assignments and age ambiguities mean that assessing the true stratigraphic range of LBF species in the literature is fraught with difficulty. In this work we have attempted to identify and quantify some of these variables to establish what is the "most likely" stratigraphic range of a LBF species. These views are ours alone – many may disagree – and it is likely that they will change with the further gathering of data. The LBF range chart at the end of this article shows our assessment of the following observations based on a combination of confidence in (a) species identity and (b) age assignment.

- Likely Range (shown as a solid line): Based on where species' identification is 'definite' or at least 'plausible' and where age assignment of the record's locality is calibrated correctly.
- Possible Range (shown as a dashed line): Based on 'plausible' identification but uncertain age calibration or better age calibration of the locality but with 'uncertain' species identification.
- Questionable Range (shown as a dotted line): Range that has previously been reported in the literature but is unsubstantiated by either confirmed or plausible species identification or age assignment. Questionable ranges based on occurrences which are clearly unsubstantiated by any meaningful data, or that are extreme outliers, are not included.

Again, it can be seen that there is another "continuum" around and between these categories and it may be that ranges are assigned confidence levels based on additional aspects of the evaluation of the individual reference.

Best Practice

The challenges of establishing the accurate identification of, and the accurate stratigraphic ranges for any fossil species will always be present, perhaps to an even greater degree for the LBF. We recognise that it is not always possible to provide adequate supporting imagery to a fossil identification, nor to undertake fully integrated studies involving simultaneous analysis of different fossil groups and/or independent, non-biostratigraphic stratigraphic analyses such as carbon-isotope stratigraphy, which would help mitigate many of the ambiguities and miscalibrations published in the literature.

However, the conclusions of Schlagintweit & Simmons (2022: p.77) on developing "best practice" in biostratigraphy are worth repeating here to act as a checklist for future LBF work:

- The fossils need to be identified correctly and uncertainty in identification expressed. Not every specimen can be identified precisely.
- Up to date taxonomy needs to be used and introduction of inadequately described or unnecessary new taxa (i.e., synonyms of existing species) should be avoided.
- Biozonation schemes created or employed should, ideally, have genuine value for correlation and be based on the likely stratigraphic ranges of the fossils incorporated.
- Independent age calibration of the rocks in which LBF occur in should be sought and less reliance placed on older interpretations which lacked the benefits of modern age calibration methods.
- Fossil distribution data should be provided alongside unequivocal illustrations of key fossils.

To the final point we would add that to avoid any kind of uncertainty and/or ambiguity, not only should the best diagnostic fossil specimens in a section be illustrated, but that particular specimen or specimens on which stratigraphic boundaries are placed, and ages determined, should also be illustrated (see Bidgood & Simmons, 2022, for examples where such omissions have caused major interpretational controversies).

TREATMENT OF INDIVIDUAL SPECIES

Our treatment includes a representative plate of each taxon using adapted figures from pre-existing published illustrations, comments on the characteristic morphological features and the means to differentiate between the taxon and morphologically similar taxa. This information is summarised and tabulated in a Species Key Chart (Appendix). There then follows an assessment of the stratigraphical and palaeogeographical ranges of each taxon based on occurrences in the literature (generally articles published after the review by Schroeder & Neumann, 1985, but also earlier works which seem to have been overlooked) and subject to our assessment of the reliability of those datum points.

A paleogeographic distribution map for each taxon is provided. These reflect the distribution of each taxon in Cenomanian times only. Several taxa can range above and below the Cenomanian but their paleogeographic distribution outside the Cenomanian is not recorded. A separate distribution map for the location of type specimens (i.e., first descriptions) is shown in Fig. 4.

Finally, a stratigraphic range chart for each taxon is also provided towards the end of this article.

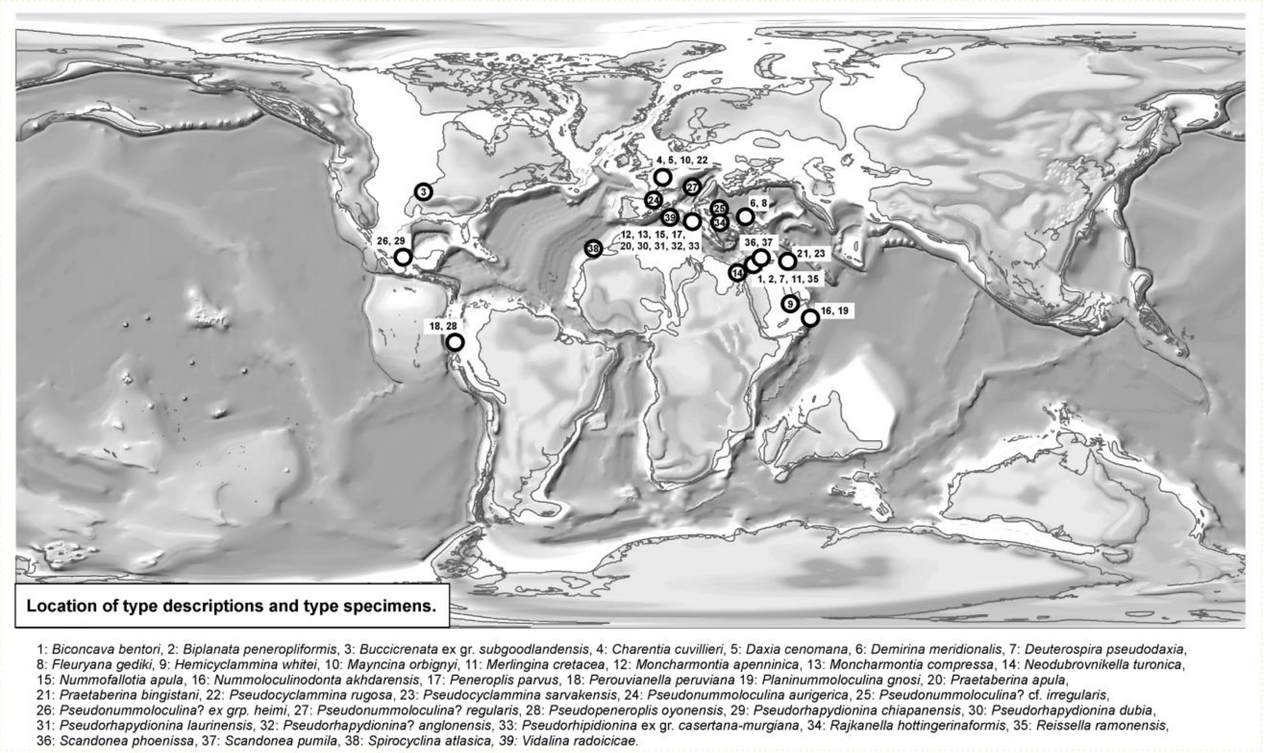


Fig. 4 Distribution map of type descriptions/specimens in this study.

Taxa are listed in broad order of classification, based on Table 1.

Genus ***Biconcava*** Hamaoui, 1965 emended Hamaoui & Saint-Marc, 1970

Type Species: *Biconcava bentori* Hamaoui, 1965 emended Hamaoui & Saint-Marc, 1970

***Biconcava bentori* Hamaoui, 1965 emended Hamaoui & Saint-Marc, 1970**

Reference Illustration & Description

Hamaoui (in Schroeder & Neumann, 1985), Pl. 13, figs. 1-7, p. 34.

The valid source of the original description of the genus *Biconcava* and its type species *B. bentori* has been disputed. They were described and illustrated (in a limited way) as a new genus and species by Hamaoui (1965) in a report for the Israel Geological Survey on the type Hazera Formation (Cenomanian) (see also Arkin et al., 1965; Hamaoui, 1966; Arkin & Hamaoui, 1967; Lipson-Benitah, 2009). However, Hamaoui & Saint-Marc (1970) presented additional description and illustrations (Plates 18-21) and regarded this as the type description (see also Hamaoui in Schroeder & Neumann, 1985). Nonetheless, as noted by Loeblich & Tappan (1988), the 1965 citation by Hamaoui is valid, thus we adopt the type designation as “Hamaoui, 1965 emended Hamaoui & Saint-Marc, 1970” for both genus and species.

The illustrations and description in Hamaoui in Schroeder & Neumann (1985) are adequate for reference purposes and mostly derive from Hamaoui & Saint-Marc (1970) and Saint-Marc (1974a). See the Species Key Chart (Appendix) for diagnostic and other characteristics.

A biumbilicate form with up to 24 chambers in the final whorl, and about three and a half whorls (up to 4) in adult specimens, it is superficially similar to *Biplanata peneropliformis*. *B. bentori* has a more lenticular test (i.e., is less flattened than *B. peneropliformis*), a slower rate of chamber size increase, and possesses a characteristic V-shaped chamber cross-section which *B. peneropliformis* lacks. The internal dental plate in *Biconcava* as mentioned by Hamaoui & Saint-Marc (1970 p. 302) is simply bifurcated but becomes complete and occupies the medial plane of the chamber in *Biplanata*. The plate is very small and is shown and annotated in Hamaoui & Saint-Marc on one figure only (1970, plate 21 figure 1). However, its presence is disputed by Loeblich & Tappan (1988). *Biconcava* can be distinguished from other planispiral taxa such as *Daxia* (which is less evolute and has no internal dental plate) and *Charentia* (which has a pseudokeriothecal test structure and no internal dental plate).

Biconcava is also distinguished from *Daxia* in minor apertural details (an opening in a vertical groove rather than a single opening just above the base of the apertural face) but these are almost impossible to distinguish in thin-section.

A new species described as *Biconcava ribbata* by Shahin & Elbaz (2013) from the late Cenomanian in two sections from Sinai, Egypt appears to conform externally to the generic concept of *Biconcava* but is not supported by internal views or comments about the dental plate (if present). It does not appear to have been recorded subsequently and the “ribbed” appearance is most likely a

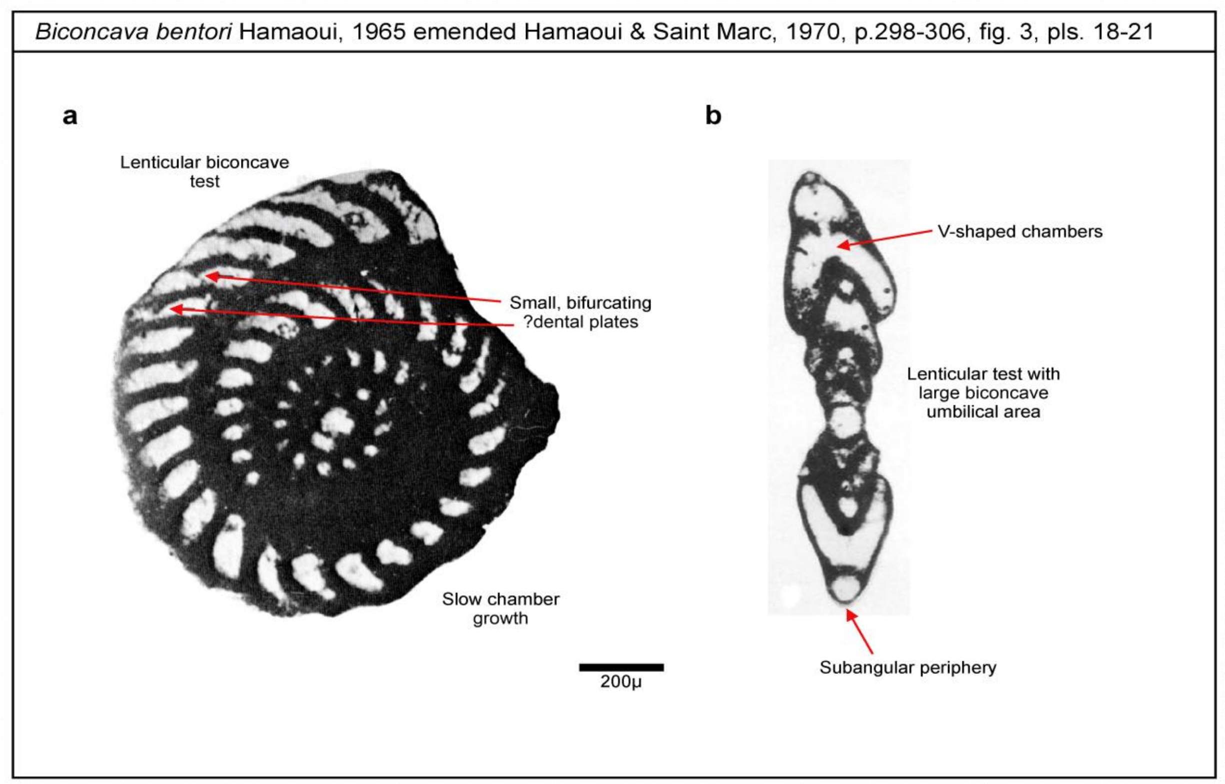


Fig. 5 Representative illustrations of *Biconcava bentori*: **a** Equatorial section, Hamaoui & Saint Marc (1970, pl. 21, fig. 1, Israel); **b** Axial section, Hamaoui in Schroeder & Neumann (1985, pl. 13, fig. 3, Lebanon).

taphonomic effect on *B. bentori* specimens (Dr Lorenzo Consorti, pers. comm., 2023).

Records by Sinanoglu & Erdem, 2016; Sinanoglu et al., 2020 and Sinanoglu, 2021, of occurrences of *B. bentori* (along with other mid Cretaceous taxa) together with demonstrably Maastrichtian taxa in the Garzan Formation of Turkey are intriguing. Some appear superficially similar to *B. bentori*, but the assigned age is clearly anomalous and an approximate 30 My age-range for a single species would seem unusual. Additional illustrations of her specimens kindly provided by Dr. Sinanoglu to the authors suggests that these specimens *may* be of a *Biconcava*, but if so, probably not *B. bentori sensu* Hamaoui & Saint-Marc (1970) and Saint-Marc (1974a). In equatorial section, the type *B. bentori* has between 18-24 chambers in the final whorl (the Turkish specimens have no more than 12) and the chambers of typical *B. bentori* are short and high when viewed from the side compared with the equi-dimensional, almost “square” chambers of the Turkish material. The possibility of mid Cretaceous homeomorphs in the Maastrichtian has been considered (Schlagintweit & Yazdi-Moghadam, 2022a, who recognise the genus *Neodubrovnikella* in the Cenomanian and Maastrichtian with a ‘ghost range’ in between) and this may be an example of that.

The specimens identified as *Biconcava* sp. by Tasli et al. (2006) from the Coniacian-Santonian of the Cehennemdere Formation of southern Turkey (Fig. 7; A & B internal views) would appear superficially at least to conform to the generic concept, but in thin-section the number of chambers in the final whorl is fewer than in the type description and illustration for *B. bentori*.

Stratigraphic Distribution

Early - late Cenomanian.

B. bentori was regarded by Hamaoui (in Schroeder & Neumann, 1985) as ranging from the middle Cenomanian to the Cenomanian-Turonian boundary (see also Arnaud et al., 1981 with tentative extensions into the early Cenomanian and basal Turonian). Plausible illustrated records of *B. bentori* by Bravi et al. (2004) from central Italy, Ghanem et al. (2012) from Syria and Saint-Marc (1981) from Lebanon indicate the presence of this species in early Cenomanian sediments, as old as the base of the stage. This species is commonly recorded in the literature, but most records are not substantiated by illustration. Similarly, few records are supported by independent age verification, which hinders assessment of the true stratigraphic range. Overall, records are almost entirely confined to the Cenomanian although these are skewed towards the middle – late Cenomanian.

Rare, anomalously younger records (e.g., Ghaseminia et al., 2016 – Coniacian to Santonian; Luperto-Sinni, 1976; Luperto-Sinni & Richetti, 1978 – Santonian – Campanian; Šribar & Pleničar, 1990 – late Turonian; Velić, 2007 – early Cenomanian to early Campanian; Solak et al., 2015 – Turonian to Campanian) are not substantiated by plausible illustrations (see also remarks above concerning occurrences reported in the Maastrichtian by Sinanoglu and others).

Weidich & Al-Harithi (1990) illustrate a plausible form from Jordan, noting that the species has middle Albian to Cenomanian range there. This is the most viable evidence that the species ranges older than Cenomanian, but the specimen illustrated is actually from Cenomanian strata. An illustrated record from an interval of "latest Albian to early Cenomanian" age from the Sarvak Formation of the Iranian Zagros (Mohseni & Javanmard, 2020) is not of *B. bentori* (instead a simple unrelated taxon). Thus, illustrated records from Albian strata are lacking.

Those references which are supported by definite (or at least plausible) illustrations mostly indicate a middle – late Cenomanian age (or at least general undifferentiated Cenomanian age). These include:

Morocco: Ettachfini & Andreu (2004) and Ettachfini (2006) illustrate a form attributed to *Moncharmontia* aff. *apenninica* from the late Cenomanian of Morocco, but which seems more compatible with *B. bentori* (see also unillustrated by Piuz & Meister, 2013).

Tunisia: Bismuth et al. (1981) (see also unillustrated by Touir et al., 2017)

Portugal : Berthou (1973)

Italy: Foglia (1992); Tentor et al. (1993); Tentor & Tentor (2007) and Chiocchini et al. (2012) (see also an uncertain illustration by Simone et al., 2012; and unillustrated by Chiocchini, 2008a; Chiocchini et al., 2008; Di Stefano & Ruberti, 2000; Borghi & Pignatti, 2006; Spalluto & Caffau, 2010; Spalluto, 2011; Consorti et al., 2015 and Frijia et al., 2015 - the latter reference is useful as the occurrences it describes are well-calibrated to ammonite zones and carbon isotope data as upper middle – late-but-not-latest Cenomanian)

Croatia: Velić & Vlahović (1994) (see also unillustrated by Husinec et al., 2009 and Korbar et al., 2012)

Serbia and Kosovo: Radoičić (1974a)

Greece: Fleury (1971), Charvet at al. (1976) (see also unillustrated by Fleury, 1980 and Zambetakis-Lekkas, 2006)

Southern Turkey: Tasli et al. (2006); Sari et al. (2009); Solak et al. (2019); Solak (2021) (see also uncertain records by Koç, 2017; Simmons et al., 2020b and Solak et al., 2020)

Egypt/Sinai: Kerdany et al. (1973) as "*Peneroplis turonicus*"; El-Sheikh & Hewaidy (1998) (see also uncertain records by Samuel et al., 2009; Orabi et al., 2012 and Shahin & Elbaz, 2013; and unillustrated by Kuss, 1994; Ismail & Soliman, 1997; Bauer et al., 2001; Bachmann et al., 2003; Ismail et al., 2009; Cherif et al., 1989; Orabi & Hamad, 2018; El Baz & Khalil, 2019; El Baz & Kassem, 2020)

Iranian Zagros: Sartorio & Venturini (1988); Rahimpour-Bonab et al. (2012); Afghah et al. (2014); Ezampanah et al. (2020); Yazdi-Moghadam & Schlagintweit (2020, 2021) and Schlagintweit & Yazdi-Moghadam (2020, 2021) (see also unillustrated by Fourcade et al., 1997; Afghah & Fadaei, 2014; Omidvar et al., 2014a, b; Consorti et al., 2015; Dehghanian & Afghah, 2021; Omidi et al., 2021 and Mohajer, 2022a, 2022b).

Southern Iraq : An illustration of *Pseudorhapydionina laurinensis* by Al-Dulaimy et al., (2022) from the late Cenomanian Mishrif Formation is probably *B. bentori*.

Saudi Arabia: Dr Wyn Hughes (pers. comm., 2022)

Other illustrated references include occurrences which are difficult to verify based on preservation or orientation of the thin-section cut. As such they are classed as "possible" *B. bentori* at best. These include Omaña et al. (2019) from Mexico (see also unillustrated by Hernández-Romano et al., 1997; Aguilera-Franco et al., 2001; Aguilera-Franco, 2003 (but a specimen illustrated as *Moncharmontia apenninica* may be *B. bentori*); Aguilera-Franco & Hernández-Romano, 2004 and Aguilera-Franco & Allison, 2004); Andrade (2018) from Portugal; Božović (2016) from Montenegro; and Ghanem & Kuss (2013) from Syria (see also unillustrated by Mouty et al., 2003) from Syria. Most assigned ages are middle – late Cenomanian with occasional early Cenomanian.

Illustrated references which are not, in fact, of *B. bentori* include Decrouez (1978) from Greece (nothing compatible in photomicrograph); Velić & Sokač (1979) from the Dinarides (simple unrelated indeterminate form); Ghaseminia et al. (2016) (simple unrelated indeterminate form), Assadi et al. (2016) [= *Praetaberina bingistani*], Kiarostami et al. (2019) (indeterminate, but not biconcave), Mohajer et al. (2021a) (indeterminate but not biconcave), Asghari et al., (2022) (indeterminate, but not biconcave) and Esfandyari et al. (2023) (indeterminate but incompatible with *B. bentori*: too few chambers) from the Iranian Zagros, and Ezzulddin & Ibrahim (2022) (simple, probably trochospiral foraminifera) from southern Iraq.

References which record *B. bentori*, but which are not substantiated by illustration are numerous – more than double those with definite, plausible and possible illustrations. The occurrences are, however, also predominantly assigned to a middle – late Cenomanian age with occasional early Cenomanian records, as well as some possible early Turonian records although the latter are questionable. Those not yet mentioned above include Diaz Otero et al. (2001) from Cuba; Berthou & Lauverjat (1979), Crosaz-Galletti (1979), Berthou (1984a, 1984b), Calonge et al. (2002, 2003), Cabral et al., (2008), Caus et al. (2009), Vicedo et al. (2011) and Consorti et al. (2016b) from Iberia; Deloffre & Hamaoui (1979) from France; Boix et al. (2009) from the Mediterranean or western Tethys; Schulze (2003) and Schulze et al. (2004) from Jordan; Mohammed (2007), Al-Dulaimy & Al-Sheikhly (2013), Al-Dulaimy et al. (2022) and Al-Salihi & Ibrahim (2023) from southern Iraq; Youssef et al. (2019) from Kuwait; Menegatti (2004) from Dubai; and

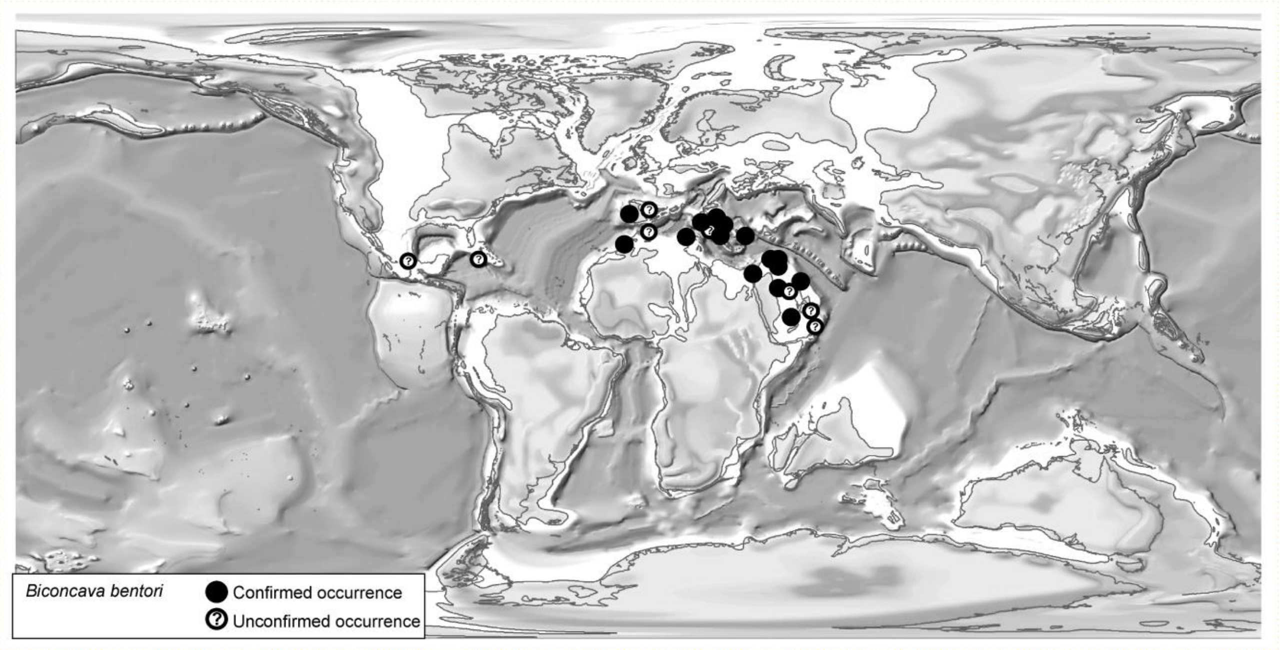


Fig. 6 Cenomanian paleogeographic distribution of *Biconcava bentori*

Scott et al. (2000), Piuz & Meister (2013) and Piuz et al. (2014) from Oman.

Cenomanian Paleogeographic Distribution

Neotethys and ?Caribbean.
The records mentioned above substantiate by illustration definite occurrences in the Zagros-Turkey-North Africa, Eastern and Western Mediterranean region. There are numerous additional records unverified by illustration that could, if proven by new data, further demonstrate the geographic distribution of this species and extend it much more widely. These additional records (west to east) include from Mexico, Cuba, Iberia, Iraq, Kuwait and Oman (see above for references).

Genus ***Daxia*** Cuvillier & Szakall, 1949
Type Species: *Daxia cenomana* Cuvillier & Szakall, 1949
***Daxia cenomana* Cuvillier & Szakall, 1949**

Reference Illustration & Description

Arnaud-Vanneau and Prestat (in Schroeder & Neumann, 1985), Pl. 1, figs. 1-8, p. 15.
The genus *Daxia*, along with the type species, *D. cenomana*, was introduced by Cuvillier & Szakall (1949) based on material from the late Cenomanian of western France. It is a biumbonate to flattened form, planispirally enrolled and evolute, with numerous (~15 in macrospheric forms; ~22 in microspheric forms) sickle or teardrop shaped chambers, wider at the base than at the outer wall. Loeblich & Tappan (1988) confirmed that the aperture of *Daxia* is a single areal opening, just above the base of the apertural face. The suggestion that *Daxia* has a "spiral canal" (as in many rotaloideans including nummulitids) (Laug & Peybernès, 1979) was demonstrated as invalid by Cherchi & Schroeder (1980).
Daxia is similar to *Biconcava*, which is more evolute and, in particular, to *Mayncina* Neumann (type species *Daxia orbignyi* Cuvillier & Szakall, described alongside *D. cenomana*). In axial sections *M. orbignyi* has a more inflated profile, compared to the acute periphery of *D. cenomana*, and in megalospheric forms, a much larger proloculus (up to 190 µm, compared to up to 100 µm in *D. cenomana*). Note the sickle-shaped chambers in equatorial sections of *D. cenomana*, that reduce in height from base to outer wall in comparison to the more regular chamber height in *M. orbignyi* (Dr. Felix Schlagintweit, pers. comm., 2022). See the Species Key Chart (Appendix) for diagnostic and other characteristics.
The key difference of a single aperture in *Daxia* and multiple apertures in *Mayncin*a (Loeblich & Tappan, 1988) can be difficult to observe in thin-section. Many random thin-sections cannot be separated at the generic level. Loeblich & Tappan (1988) pointed out that specimens of *D. cenomana* illustrated by Neumann (1965) are in fact *M. orbignyi* (an error overlooked by Arnaud & Prestat in Schroder & Neumann, 1985).
Other potential confusion taxa include a number of poorly known forms such as *Deuterospira* Hamaoui (type species *Deuterospira pseudodaxia*) reported only from the Cenomanian of Israel and Iraq (see Hamaoui, 1979) which has a low number (typically only 2) of coils, a basal/interio-marginal aperture and a sharp, angular periphery (see herein). Another similar genus, but poorly known, is *Stomatostoecha* Applin, Loeblich & Tappan, 1950 (Type species: *Stomatostoecha plummerae* Applin, Loeblich & Tappan, 1950) described from the Albian of Texas.

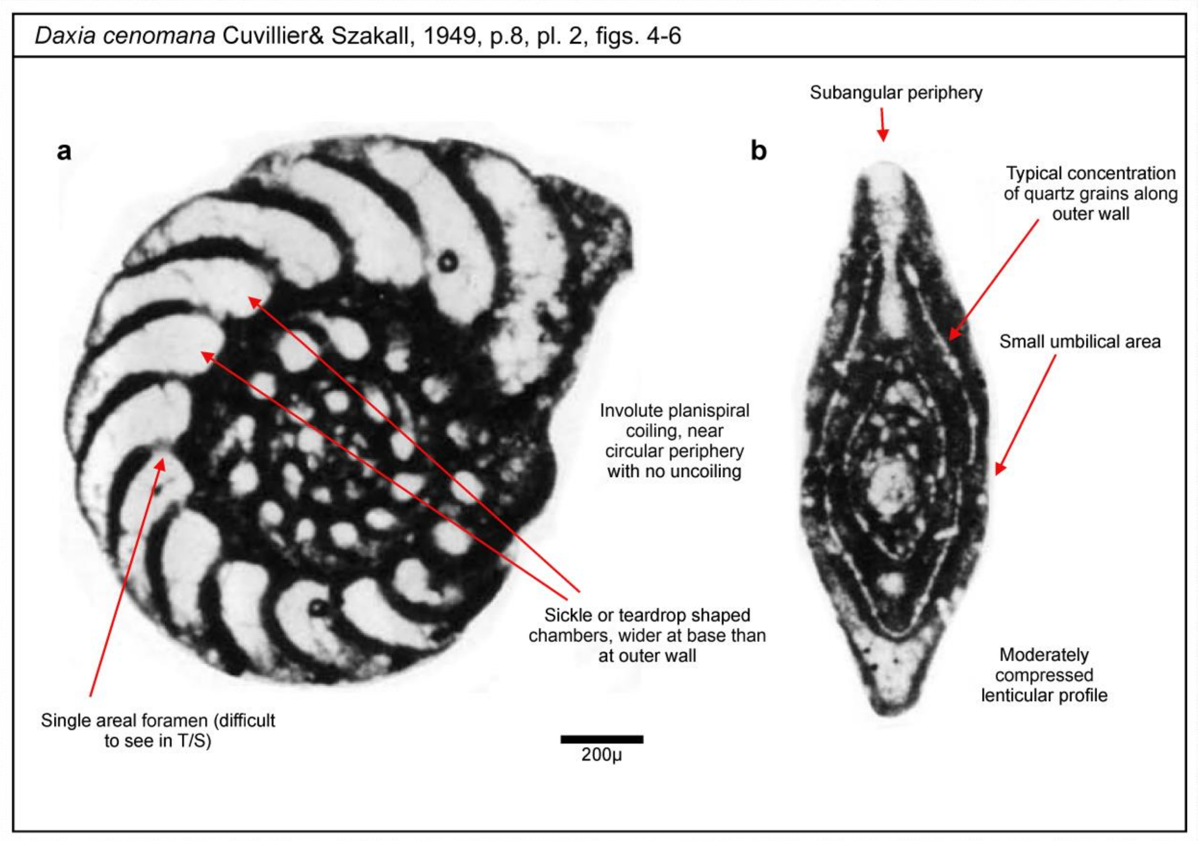


Fig. 7 Representative illustrations of *Daxia cenomana*: **a** Equatorial section, Arnaud-Vanneau & Prestat in Schroeder & Neumann (1985, pl. 1, fig. 2, France); **b** Axial section, Arnaud-Vanneau & Prestat in Schroeder & Neumann (1985, pl. 1, fig.7, France).

It is said to differ from *Daxia* by the presence of an extensive slit-like aperture (Maync, 1972). However, Mikhalevich (2004b) regarded the aperture as a vertical row of rounded openings based on the figures of the holotype in Loeblich & Tappan (1988). It has recently been mentioned from the mid-Cretaceous of Tibet (e.g., Bou-Dagher-Fadel et al., 2017) but without illustration. Finally, *Phenacophragma* Applin, Loeblich & Tappan, 1950 (Type species: *Phenacophragma assurgens* Applin, Loeblich & Tappan, 1950) is similar but with an aperture as a slit at the top of the apertural face. See also *Phenacophragma oezeri* Solak & Tasli described from the Albian of Turkey (Solak & Tasli, 2020). All these potential confusion taxa require thorough taxonomic revision.

Daxia minima Laug & Peybernès is a smaller and older form of *Daxia*, first described from the Aptian of Spain; Laug & Peybernès, 1979) and has relatively thicker septa and more depressed sutures. However, the dimensions for *D. cenomana* given by Schroeder & Neumann (1985) and compared with those given for *D. minima* by Laug & Peybernès (1979) – see below – do show some slight overlap which means that smaller macrospheric specimens of *D. cenomana* might be confused with larger specimens of *D. minima*.

	D. minima	*D. cenomana*
Equat. Diam.	0.37 – 1.10 mm	0.73 – 1.60 mm
Axial Diam.	0.14 – 0.30 mm	0.28 – 0.65 mm
Proloc. Diam.	40 – 50 microns	40 – 100 microns

Arnaud-Vanneau & Prestat (1985) do however state that their measurements are taken from ‘A’ (macrospheric) forms only. ‘B’ form (microspheric) measurements of *D. cenomana* based on earlier data from Neumann (1965, 1967) quoted in Laug & Peybernès (1979) but not quoted in Schroeder & Neumann (1985) are larger: Equatorial diameter = 2.0 – 2.7 mm, Axial diameter = 1.0 mm.

Stratigraphic Distribution

Late Albian – late Cenomanian.

D. cenomana was first described from the late Cenomanian of Landes, France (Cuvillier & Szakall, 1949; Saint-Marc, 1966). More recently, Andrieu et al. (2015) report *D. cenomana* from the middle and late Cenomanian of Aquitaine with good stratigraphic calibration from carbon isotopes but provide no illustration.

It was regarded by Arnaud-Vanneau & Prestat (in Schroeder & Neumann, 1985) as restricted to, but ranging throughout the Cenomanian, but only limited evidence was provided in support. Nonetheless, subsequent more globally extensive records (see below), would suggest that a range throughout the Cenomanian and older into the late Albian is likely.

For example, records from Spain are extensive (see also Arnaud-Vanneau & Prestat (in Schroeder & Neumann, 1985) and include beautifully illustrated material by Hottinger (1967), illustrated middle Cenomanian occurrences by Bilotte (1973, 1985), and records from the early Cenomanian by Calonge et al. (2002, 2003, not illustrated) and from the early-middle Cenomanian by Caus et al. (2009, not illustrated). Cherchi & Schroeder (1998, not illustrated), also report undifferentiated early – middle Cenomanian records from Spain, whilst Gräfe (2005, not illustrated) notes that the species is common in undifferentiated Cenomanian sediments of northern Spain. Hofker (1965) illustrated it as *Haplophragmoides cenomana* from the Aptian - Albian transition of Spain, where it was said to range from Aptian – Cenomanian – this may be because of inclusion of taxa now regarded as *D. minima* in the species concept (see also Arnaud-Vanneau, 1980). Finally, Ramirez del Pozo (1972) records the species from the Cenomanian of Spain as *Haplophragmoides cenomana*, but the illustrations are insufficient to confirm identification.

Dr Felix Schlagintweit (pers. comm., 2022) has indicated that *D. cenomana* can be found in the late Albian of the Iranian Zagros, and possibly Tibet, where it is said to be common in the Langshan Formation (Albian – early Cenomanian) (see also Smith & Juntao, 1988 illustrated as *Daxia* sp. and thought to be late Albian based on associated orbitolinids; and Fossa Mancini, 1928 - unnamed foraminifera pl. XXII, fig. 10). Yang et al. (2015); Bou-Dagher-Fadel et al. (2017); Xu et al. (2019, 2021); and Rao et al. (2020) mention but do not illustrate *Daxia* from Tibet.

Berthou & Lauverjat (1979) and Berthou (1984b) indicated that the species can be found throughout the Albian – middle Cenomanian of western Portugal but provided no illustration (see also Berthou & Schroeder, 1978; Boavida, 2013; Cabral et al., 2014, not illustrated). Andrade (2018) has illustrated the species from the Cenomanian of Portugal (pl. M2, fig. 1) but other illustrations (e.g., pl. M5, fig. 5) are equivocal and may be *M. orbignyi*.

Luger (2018) described and illustrated an equatorial section of "*Daxia* cf. *cenomana*" from the "latest Albian" of Somalia. As noted by Luger (2018), the specimen has a much smaller proloculus than the material described by Arnaud-Vanneau & Prestat (in Schroeder & Neumann, 1985), and the identification is hard to validate from a single equatorial section.

The suggestion by Omidvar et al. (2014a, 2014b) that it may occur in Turonian strata in the Iranian Zagros is neither substantiated by illustration nor associated microfauna. Rare occurrences recorded from the Turonian Buttum Formation in Egypt by Samuel et al. (2009) are also unsubstantiated by illustration and/or are likely misidentified.

Well-illustrated, independently biostratigraphically or chemostratigraphically calibrated records of this species are required.

Cenomanian Paleogeographic Distribution

Possibly Pan-Neotethyan.

Arnaud-Vanneau & Prestat (in Schroeder & Neumann, 1985) only noted limited records from France and Spain. Since then, there are many more published records, which if valid, extend the distribution from the middle – late Cenomanian of Mexico in the west (Omaña et al., 2012, 2016, 2019, illustrated, but specimens may be *M. orbignyi*) to the Cenomanian of Tibet in the east (see above).

The species has been commonly reported from the early – late Cenomanian of Egypt (e.g., Shahin & Kora, 1991; Kora et al., 1994; Shahin, 2007; Ismail et al., 2009; Shahin & Elbaz, 2013, 2014; Deaf & Tahoun, 2018; El Baz & Khalil, 2019; El Baz & Kassem, 2020, but only material illustrated by El-Sheikh & Hewaidy, 1998 from supposedly late Cenomanian strata approaches plausibility based on illustration, although the critical axial section mentioned in the plate caption is missing from the actual plate).

There are many (mostly unillustrated) records from the Iranian Zagros (e.g., Afghah & Fadaei, 2014; Kiarostami et al., 2019; Dehghanian & Afghah, 2021; Omidi et al., 2021) but only the illustration of Mohajer et al. (2021a) approaches plausibility, from supposedly late Cenomanian strata. Illustrations by Afghah et al. (2014) (= *Pseudorhipidionina ex gr. casertana-murgiana*) and Jamalpour et al. (2018) (too few low chambers, non-determinable simple specimen) are not this species. Elsewhere in the Middle East there are possible records from Kuwait (El-Naggar & Al-Rifaiy, 1973, not illustrated).

Other unillustrated records include Parente et al., (2007) who reported it from the late Cenomanian of Italy, co-occurring with *Cisalveolina fraasi* (Gümbel); from the Cenomanian of Albania (Peza & Pirdeni, 1994); Provence (southern France) (Babinot et al., 1988) and Algeria (Alloul, 2019).

A record from Jordan (Weidich & Al-Harithi, 1990) is indeterminate. A record from Armenia (Danelian et al., 2014) is of *Charentia cuvillieri*.

In summary, despite multiple records of this species from many locations, substantive illustrations are lacking. Only Cenomanian records are shown on Figure 8.

Genus ***Deuterospira*** Hamaoui, 1965 emended Hamaoui, 1979

Type Species: *Deuterospira pseudodaxia* Hamaoui, 1965 emended Hamaoui, 1979

***Deuterospira pseudodaxia* Hamaoui, 1965 emended Hamaoui, 1979**

Reference Illustration & Description

Hamaoui (1979), Fig. 2, p. 342.

Only two illustrations of this genus and species are thought to be published (in Hamaoui, 1966, 1979 and in Loeblich & Tappan, 1988).

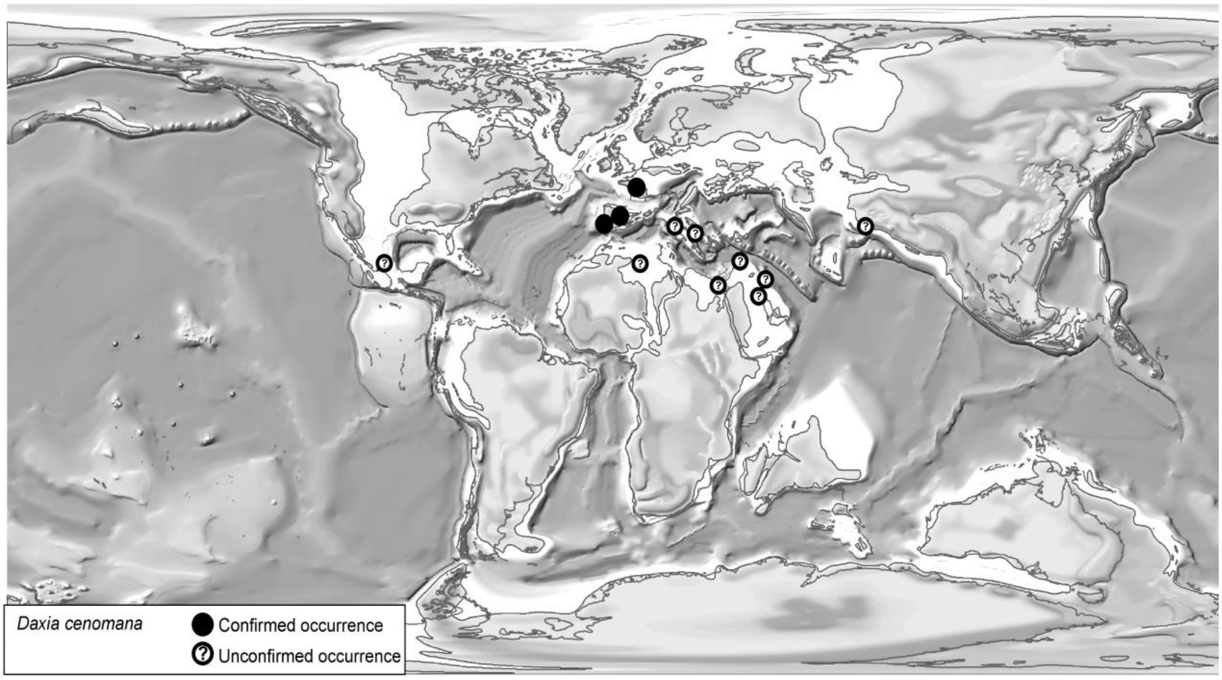


Fig. 8 Cenomanian paleogeographic distribution of *Daxia cenomana*.

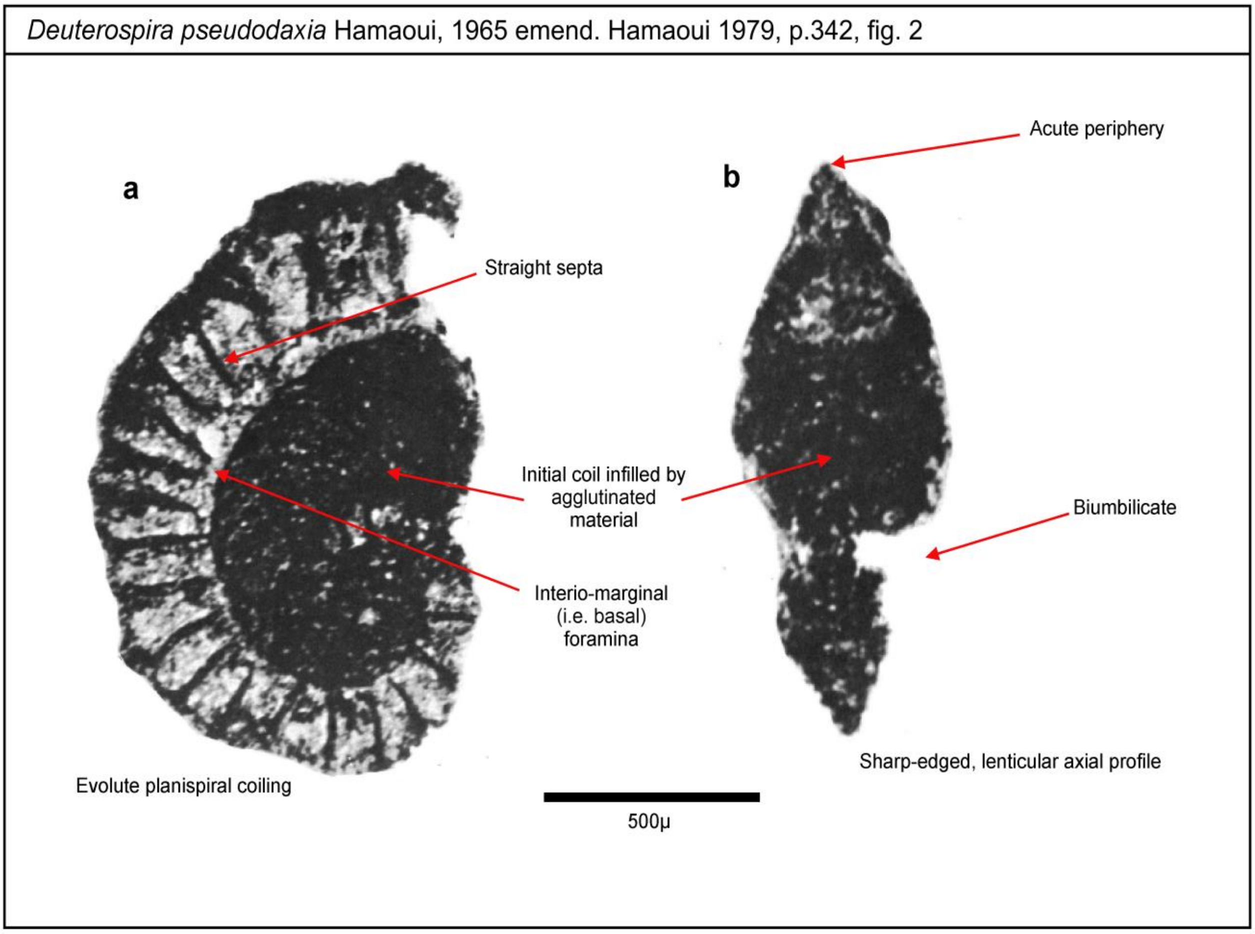


Fig. 9 Representative illustrations of *Deuterospira pseudodaxia*: **a** Equatorial section, Hamaoui (1979, fig. 2a, Israel); **b** Axial section, Hamaoui (1979, fig. 2b, Israel).

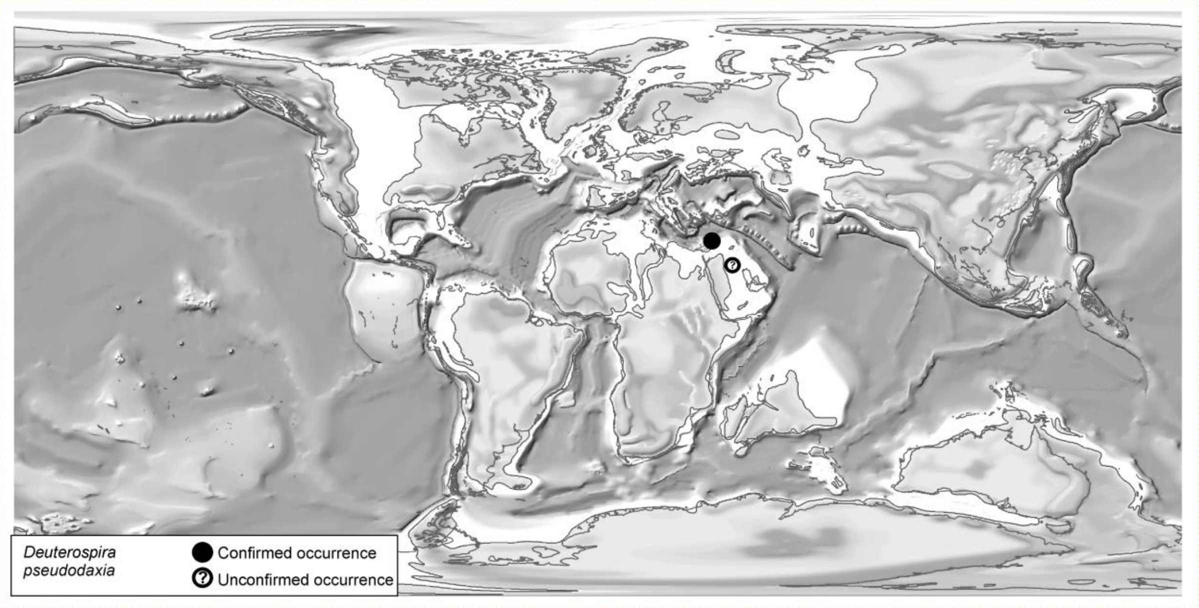


Fig. 10 Cenomanian paleogeographic distribution of *Deuterospira pseudodaxia*

Reported as a new genus and species by Hamaoui (1965) in a Geological Survey of Israel report, it was neither described nor illustrated. It was illustrated by Hamaoui (1966) in another GSI report but not otherwise described. This was corrected in both respects by Hamaoui (1979). Overall, *Deuterospira* is broadly similar to *Daxia cenomana* and *Biconcava bentori*, although it is believed to have only two full coils (from which the name is derived). *Daxia* and *Biconcava* on the other hand, can have up to 4-5 coils. The chamber divisions can apparently only be seen in the second coil, the first coil (in the holotype) is believed to be filled with agglutinated material which obscures any view of chamber partitions such as septa or inward projections into the chamber lumen as in *Demirina* (see below) which could suggest possibly synonymy with *D. meridionalis* (see also Loeblich & Tappan, 1988). The foramina are distinctly basal/interiomarginal in equatorial views (in the second coil at least) but are suggested to become more areal in later chambers (*Daxia*'s are areal throughout) although illustrated evidence is lacking. See the Species Key Chart (Appendix) for diagnostic and other characteristics.

Mayncina is also similar, but that genus is broadly biconvex compared with *Biconcava*, *Daxia* and *Deuterospira* and *Mayncina* also has multiple areal apertures.

D. pseudodaxia is also characterised by the sharpest periphery of the genera and species mentioned. Nonetheless, this genus and species remains very poorly known and more research on topotypic material is required to improve our understanding of its identity.

Stratigraphic Distribution

(Late?) Cenomanian.

Deuterospira pseudodaxia is rarely reported in the literature. Hamaoui (1965, 1966) described it from the Zafit - Avonon Members of the Hazera Formation of Israel, attributing a Cenomanian age ("probably upper part") to the interval.

Hamaoui & Brun (1974) reported it (unillustrated) from the Mishrif Formation of Iraq, also attributing a Cenomanian (lower – upper) age (see also Hamaoui, 1979). Note that according to modern literature (e.g., Bromhead et al., 2022), the Mishrif Formation of southern Iraq is typically late Cenomanian – early Turonian, although usage varies.

Cenomanian Paleogeographic Distribution

Eastern Neotethys.

Limited distribution (see references mentioned above).

Genus ***Mayncina*** Neumann, 1965

Type Species: *Daxia orbignyi* Cuvillier & Szakall, 1949

***Mayncina orbignyi* (Cuvillier & Szakall, 1949)**

Reference Illustration & Description

Arnaud-Vanneau & Prestat (in Schroeder & Neumann, 1985), Pl. 2, figs. 1-9, p. 16.

The genus *Mayncina* was introduced by Neumann (1965) with *Daxia orbignyi* (mistakenly referred to as "*Daxia d'orbignyi*" by Neumann) as the type species. *Mayncina* is similar to *Biconcava* and, in particular, *Daxia*. It is the most involute and broadly biconvex of the three genera and has tiny multiple (areal) apertures while the other two genera have single openings. Other potential confusion taxa include *Stomatostoecha* (Type species: *Stomatostoecha plummerae*) described from the Albian of Texas. It has an aperture variously described as extensive slit-like (Maync, 1972) or a vertical row of rounded openings (Mikhalevich, 2004b) based on the figures of the holotype in Loeblich & Tappan (1988). Finally, *Phenacophragma* (Type species: *Phenacophragma assurgens*) is similar but with an aperture as a slit at the top of the apertural face. All of these potential confusion taxa

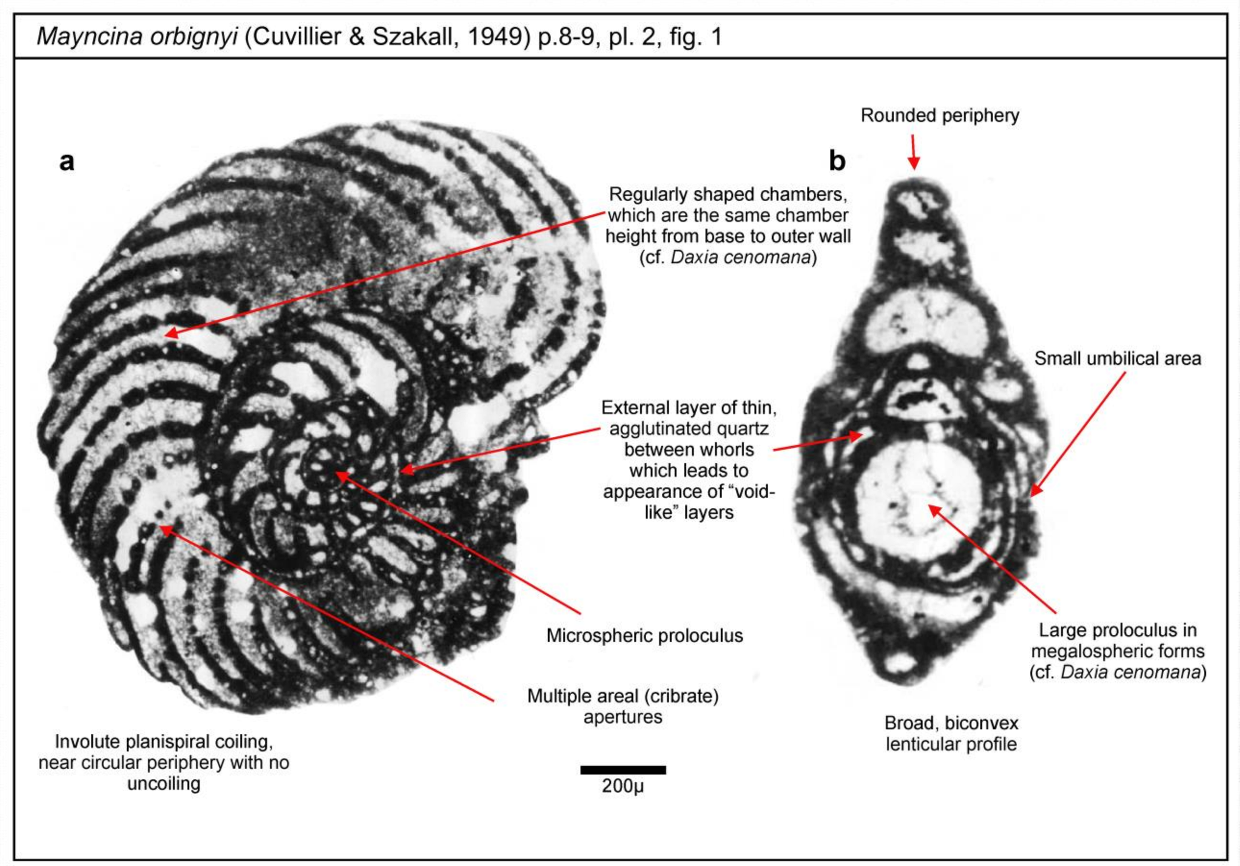


Fig. 11 Representative illustrations of *Mayncina orbignyi*: **a** Equatorial section, Arnaud-Vanneau & Prestat in Schroeder & Neumann (1985, pl. 2, fig. 7, France); **b** Axial section, Arnaud-Vanneau & Prestat in Schroeder & Neumann (1985, pl. 2, fig.8, France).

are difficult to separate in random thin-sections. See the Species Key Chart (Appendix) for diagnostic and other characteristics.

M. orbignyi is superficially very similar to *Daxia cenomana* (see that species discussion for key differences between the two, but note than in addition to the apertural difference, *M. orbignyi* is more inflated and distinctly biumbilicate). Loeblich & Tappan (1988) pointed out that specimens of *D. cenomana* illustrated by Neumann (1965) are in fact *M. orbignyi* (an error overlooked by Arnaud & Prestat in Schroder & Neumann, 1985).

M. orbignyi is the youngest species of *Mayncina*. *Mayncina bulgarica* Laug, Peybernès & Rey is a smaller form with a tendency to uncoil and become peneropliform (see comprehensive description by Maksoud, 2015), and has predominantly been referred to as occurring within the "Neocomian" (= approximately Berriasian – Hauterivian), with possible Albian records – for example, see Husinec et al. (2009) and Solak et al. (2021). Some Jurassic species have also been referred to *Mayncina* in the literature (e.g., *Mayncina termieri* Hottinger) though should properly be referred to *Lituolipora* Gušić & Velić as discussed by Kabal & Tasli (2003) and Fugagnoli & Bassi (2015).

Mayncina hasaensis Basha is a poorly known species introduced from material from the late Cenomanian of Jordan (Basha, 1978). From the limited illustrations it may have some affinity to *Charentia cuvillieri*.

Stratigraphic Distribution

(Late Albian?) middle Cenomanian.

M. orbignyi was first described from the middle Cenomanian of Charente, France (Cuvillier & Szakall, 1949; Neumann, 1965). It was regarded by Arnaud-Vanneau and Prestat (in Schroeder & Neumann, 1985) as restricted to the middle Cenomanian, with tentative extension into the latest early Cenomanian and earliest late Cenomanian, but only limited evidence was provided in support. The only plausible well biostratigraphically calibrated records are those from the middle Cenomanian, with older records being unsubstantiated.

Decrouez (1978) recorded "*Mayncina d'orbignyi*" from the latest Albian – early Cenomanian (and possibly middle Cenomanian) of Greece, but without illustration, whilst Steuber et al. (1993) reported but did not illustrate a "cf." form from the Cenomanian of Greece. Smith et al. (1990) and Orabi & Hamad (2018) also cite a middle Cenomanian age from Oman and Egypt respectively, but without adequate illustration. Both El Baz & Kassem (2020) and Shahin & El Baz (2021) record *M. orbignyi* from the supposed early – middle Cenomanian of the Gulf of Suez, but the illustrations are of disaggregated specimens and cannot have their identity confirmed. Likewise, an early-middle Cenomanian age is cited by Cherif et al. (1989) and by Orabi (1992), both from Sinai but without illustration. Shahin & Elbaz (2013) also cite a general Cenomanian age from Sinai, however their illustration is of an external (SEM) view and inadequate to determine the genus or species. Lastly concerning Egypt, El Baz and Khalil (2019) define a "*Daxia cenomana* – *Mayncina d'orbignyi* Interval Zone" for the early Cenomanian of Sinai but provide no illustrations. A middle Cenomanian specimen from France illustrated by Bilotte (1985) cannot be confirmed as being this species.

De Castro (1991) mentions a "*Mayncina*" biozone for the Turonian carbonate platform in the central Apennines of Italy, but based on the limited information provided, it is difficult to assess this statement. However, it would appear not to refer to *M. orbignyi* or possibly *Mayncina* at all in the sense used herein but rather to *Pseudocyclammina sphaeroidea* Gendrot, which De Castro considered to belong in *Mayncina*.

Cenomanian records from Jordan (Basha, 1978, 1979) are not confirmed by illustration, but an illustrated "cf." form is recorded (as rare) from low in the (undifferentiated) Cenomanian or even "?Upper Albian" interval of Jordan by Weidich & Al-Harithi (1990). From the illustration of a single poorly preserved specimen its identity cannot be confirmed. Peybernès (1984) recorded, but did not illustrate, the species from the late Albian of the Pyrenees. Cherchi & Schroeder (1982) reported, but did not illustrate, a "cf." form from the late Albian of Spain.

The illustrated records of *M. orbignyi* from the Barremian – Early Aptian of Sinai by Abu-Zied (2007) are most likely *Choffatella decipiens* Schlumberger.

Cenomanian Paleogeographic Distribution

Western/southern Neotethyan?

Arnaud-Vanneau & Prestat (in Schroeder & Neumann, 1985) only noted limited records from France and questionably Jordan. Additional reports cited above (whether identification is confirmed or not) indicate at best sporadic occurrences around the western and southern Neotethyan margins. An unusual record is that of Motamed al Shariati et al. (2016) who recorded but did not illustrate the species from the undifferentiated late Albian – early Cenomanian of the Lut Block in eastern central Iran. Specimens attributed to *D. cenomana,* but which may be *M. orbignyi* have been recorded from the middle to late Cenomanian of Mexico (Omaña et al., 2012, 2019). Firm identification requires illustration of further material, not least axial sections. Records ascribed 'cf.' status or generic status only are not included in this geographic summary, nor are records from outside the Cenomanian.

Genus ***Biplanata*** Hamaoui & Saint-Marc, 1970

Type Species: *Biplanata peneropliformis* Hamaoui & Saint-Marc, 1970

***Biplanata peneropliformis* Hamaoui & Saint-Marc, 1970**

Reference Illustration & Description

Hamaoui & Saint-Marc (1970), Pls. 1-11, Fig. 1, p. 262-282.

The description and illustrations of the types in the original publication are excellent and comprehensive. See also Saint-Marc (1974a: plate 5) although some images are duplicated. See the Species Key Chart (Appendix) for diagnostic and other characteristics.

Biplanata possesses an internal plate centrally located within each chamber, which serves to distinguish from similar planispiral forms such as *Daxia*, *Mayncina*, *Charentia*, and *Neodubrovnikella turonica*. Superficially similar to *Biconcava bentori*, *B. peneropliformis* has a more flattened, disc-like test, has faster-growing chambers and lacks the V-shaped chamber cross section of the former. Externally it is a virtually complete homeomorph of *Choffatella* (see Fig 13a herein).

Whittaker et al. (1998), after re-examining Henson's types of *Mangashtia viennoti* (Henson, 1948) and comparing them with the description of *B. peneropliformis* by Hamaoui and Saint-Marc (1970), suggested that Henson's specimens were similar and that *Mangashtia viennoti* Henson was therefore the senior synonym of *B. peneropliformis*. In our view (and that of Dr Felix Schlagintweit, pers. comm., 2023) Henson's material conforms to the concept and (emended) definition of *M. viennoti* by Fourcade et al. (1997; see figs. 5-7) much closer than it does to *B. peneropliformis*. *Mangashtia* may include a small juvenile planispiral growth phase (Henson, 1948, but not observed by Fourcade et al., 1997) but is primarily annular/cyclic in adult growth. The presence of structures in the centre parts of the chambers give the impression of a two-layered mode of growth which in axial and subaxial sections somewhat resembles the presence of the bisecting dental plate in *Biplanata*. *Mangashtia* however has many more 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*. Fourcade et al. (1997) suggested a clear stratigraphic separation of the occurrence of *B. peneropliformis* (Cenomanian) and *M. viennoti* (Turonian) in their studied section in the Iranian Zagros. Nonetheless, it is possible that some records of *M. viennoti* in the literature may be misidentifications that are in fact *B. peneropliformis* (e.g., Omidvar et al., 2014a, b).

Biplanata differs from *Demirina* and *Merlingina* (all three genera are in the Nezzazatidae family) in being flatter throughout and having a fairly uniform axial chamber width throughout the height of the chamber compared with the distinctly wider parts in the middle and upper parts of the chamber height in *Demirina* and *Merlingina* respectively.

Stratigraphic Distribution

Uppermost early?/middle - late (but not latest?) Cenomanian.

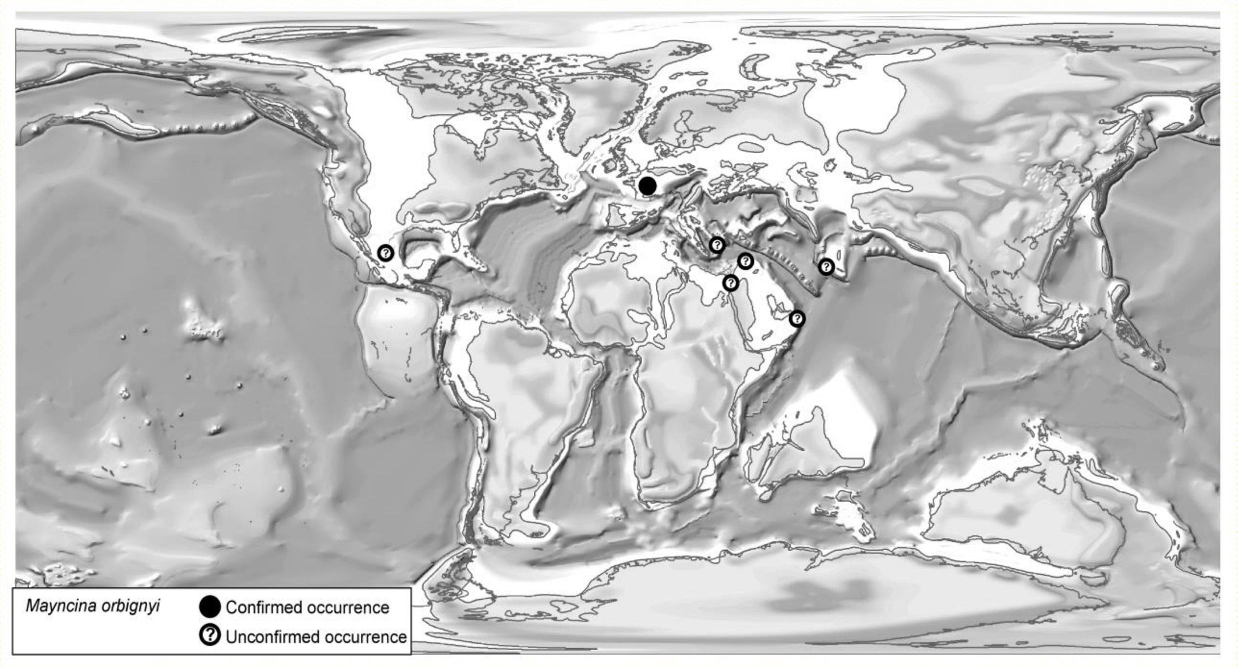


Fig. 12 Cenomanian paleogeographic distribution of *Mayncina orbignyi*.

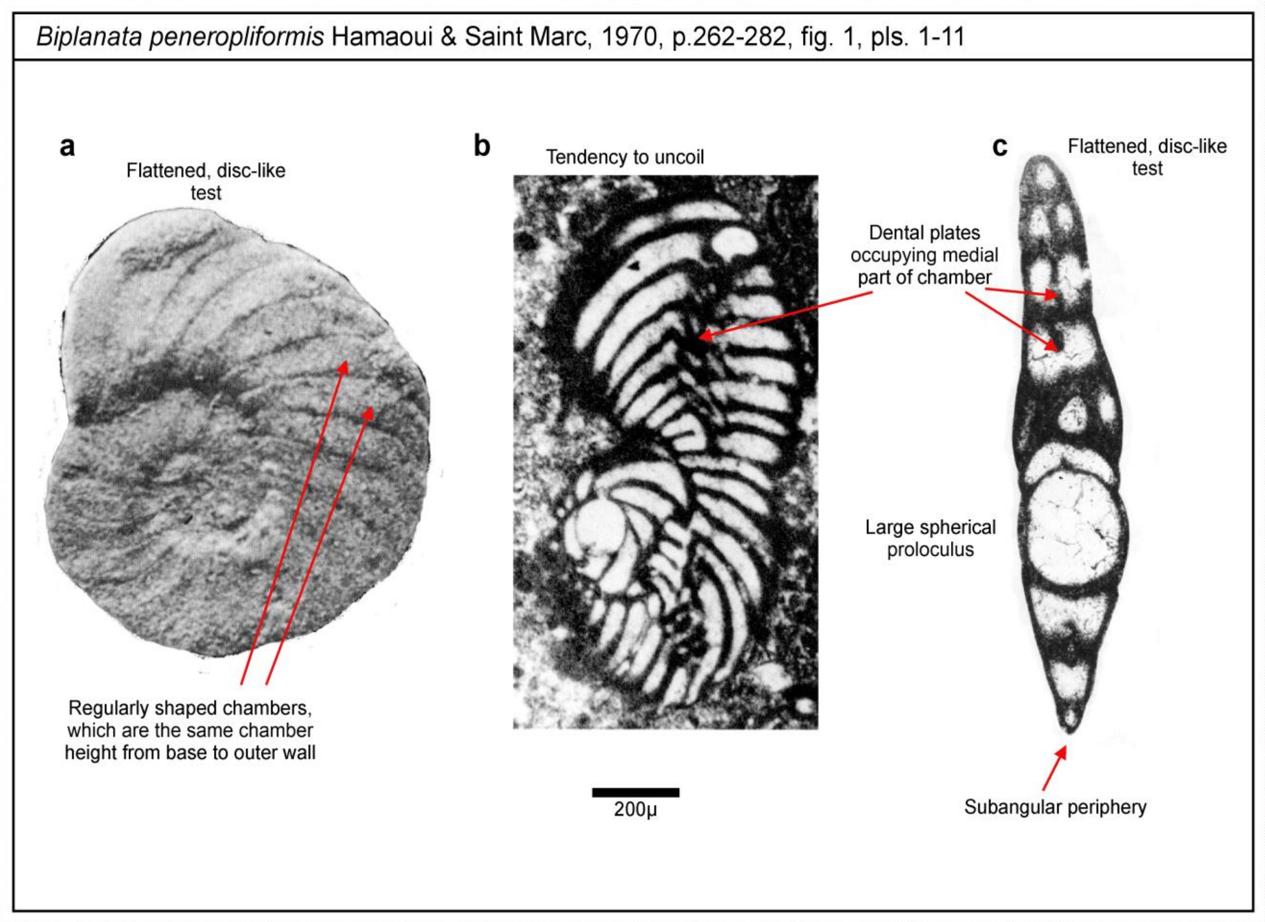


Fig. 13 Representative illustrations of *Biplanata peneropliformis*: **a** External equatorial view, Hamaoui & Saint Marc (1970, pl. 5, fig. 3, Israel, holotype); **b** Oblique equatorial section, Saint Marc (1974, pl. V, fig. 1, Lebanon); **c** Axial section, Hamaoui & Saint Marc (1970, pl. 6, fig.2, Lebanon).

The genus *Biplanata* (as *nomen nudem* – no type species) was first mentioned by Hamaoui (1965), based on material found in the Cenomanian Hazera Formation of Israel. *Biplanata* and *B. peneropliformis* were subsequently formally described from the Cenomanian (undifferentiated) of the Negev, Israel, and the late Cenomanian of Lebanon (Hamaoui & Saint-Marc, 1970). It is worth noting that Arkin & Hamaoui (1967) regarded *Biplanata* as ranging throughout the Cenomanian of Israel, but this view was not held by Hamaoui (in Schroeder & Neumann, 1985) who described *B. peneropliformis* as having a range from the upper part of the early Cenomanian to the Cenomanian-Turonian boundary.

This species is commonly recorded in the literature, but most records are not substantiated by illustration. Similarly, few records are supported by independent age verification, which hinders assessment of stratigraphic range. Overall, records are almost entirely confined to the Cenomanian although skewed towards the middle – late Cenomanian.

Rare younger (e.g., Turonian) records (e.g., Philip et al., 1978; Arnaud et al., 1981) are not substantiated by plausible illustration. Fragmentary specimens from "Senonian" strata from southern Italy (Luperto-Sinni, 1976) described as *B. peneropliformis*, cannot be confirmed as these species, and can be discounted.

Extension of the range of *B. peneropliformis* into (basal) Turonian strata is based on information from Lebanon (e.g., Saint-Marc, 1974a, 1978, 1981), and as with a number of other taxa, this age assignment needs review. The species occurs in beds that from associated ammonite data appear to straddle the Cenomanian – Turonian boundary, but the precise stratigraphic position of *B. peneropliformis* occurrences relative to these ammonite occurrences is uncertain. Given this, and the lack of any other substantiated Turonian records, *B. peneropliformis* is excluded from the Turonian. This agrees with the (unillustrated) record of Parente et al. (2008) who use carbon isotope stratigraphy to suggest *B. peneropliformis* does not extend about the *geslinianum* ammonite zone. See also Schlagintweit & Yazdi-Moghadam (2022a) for discussion of Turonian records from Lebanon. A possible illustrated record from the alleged Santonian of the Zagros (Kiarostami et al., 2019) must be a drafting error as the section contains *Pseudolituonella reicheli* Marie and *Chrysalidina gradata* d'Orbigny amongst other typically Cenomanian taxa.

The oldest records of *B. peneropliformis* are poorly constrained by independent age calibration, but the plausible illustrated records from Serbia (Radoičić, 1974a); southern Turkey (Tasli et al., 2006; Sari et al, 2009; Koç, 2017; Solak et al., 2020; Solak, 2021; and Simmons et al., 2020b), the Iranian Zagros (Sampò, 1969 (as *Nezzazata* sp.); Ezampanah et al., 2020; Mohajer et al., 2021a; Schlagintweit & Yazdi-Moghadam, 2022a; plus numerous unverified records (e.g., Afghah et al., 2014; Mehmandsoti, 2021); central Italy (Chiocchini et al., 2012 – see also Foglia, 1992; Bravi et al., 2006; Borghi & Pignatti, 2006; Parente et al., 2007, 2008; Chiocchini, 2008a and Simone et al., 2012 for unillustrated records); and Albania-Kosovo (Consorti & Schlagintweit, 2021a) are mostly middle – late Cenomanian based on associated microfauna, with only possible extension into the early Cenomanian (the upper part) for some. Other plausible records such as those from Greece (Fleury, 1971), Croatia (Velić & Vlahović, 1994), Syria (Ghanem & Kuss, 2013 – but not figure 14/40 which might be more compatible with *Merlingina cretacea*) and Egypt (Shahin & Elbaz, 2013), are in keeping with this stratigraphic range assessment. Records that show *B. peneropliformis* ranging throughout the Cenomanian (e.g., Velić, 2007 for the Dinarides (see also Husinec et al., 2000, 2009)) are typically unsubstantiated by illustration.

Cenomanian Paleogeographic Distribution

Caribbean – Neotethys.

In addition to the records mentioned above, a key reference that extends the palaeogeographic range of this species is Bomou et al. (2019) who illustrate the species from the late Cenomanian of Mexico (see also no or uncertain illustration by Michaud et al., 1984; Hernández-Romano et al., 1997; Aguilera-Franco et al., 2001; Aguilera-Franco, 2003 and Aguilera-Franco & Allison, 2004).

There are numerous records with either no or questionable illustration that could, if proven by new data, further demonstrate the geographic distribution of this species and extend it much more widely. These records (west to east) include; Morocco (Ettachfini, 2006; Piuz & Meister 2013), Iberia, including Spain and Portugal (Berthou, 1984b; Calonge et al., 2003; Gräfe, 2005; Caus et al., 2009; Vicedo et al., 2011; Consorti et al., 2016b), southern France (Deloffre & Hamaoui 1979); Kosovo (Consorti & Schlagintweit, 2021b); Libya (Dufaure et al., 1984); Slovenia (Jež et al., 2011); Greece (Decrouez 1976, 1978; Tsaila-Monopolis, 1977; Fleury, 1980; Pomoni-Papaaioannou & Zambetakis-Lekkas, 2009); Jordan (Al-Rifaiy et al., 1994; Schulze, 2003 and Schulze et al., 2004), southern Iraq (Bernaus & Masse 2007); and Oman (Smith et al., 1990; Kennedy & Simmons, 1991; Piuz and Meister, 2013).

Genus ***Demirina*** Özcan, 1994

Type Species: *Demirina meridionalis* Özcan, 1994

***Demirina meridionalis* Özcan, 1994**

Reference Illustration & Description

Özcan (1994), Pls. 1-2, Fig. 2, p. 3-4.

The broadly diamond-shaped apertural face with an acute to subangular periphery, and inner partitions (septula) which project inwards from the chamber wall leaving an empty space in the median part of the chamber is characteristic (Kaminski, 2000; Mikhalevich, 2004b). The internal partitions are more numerous and complex than in

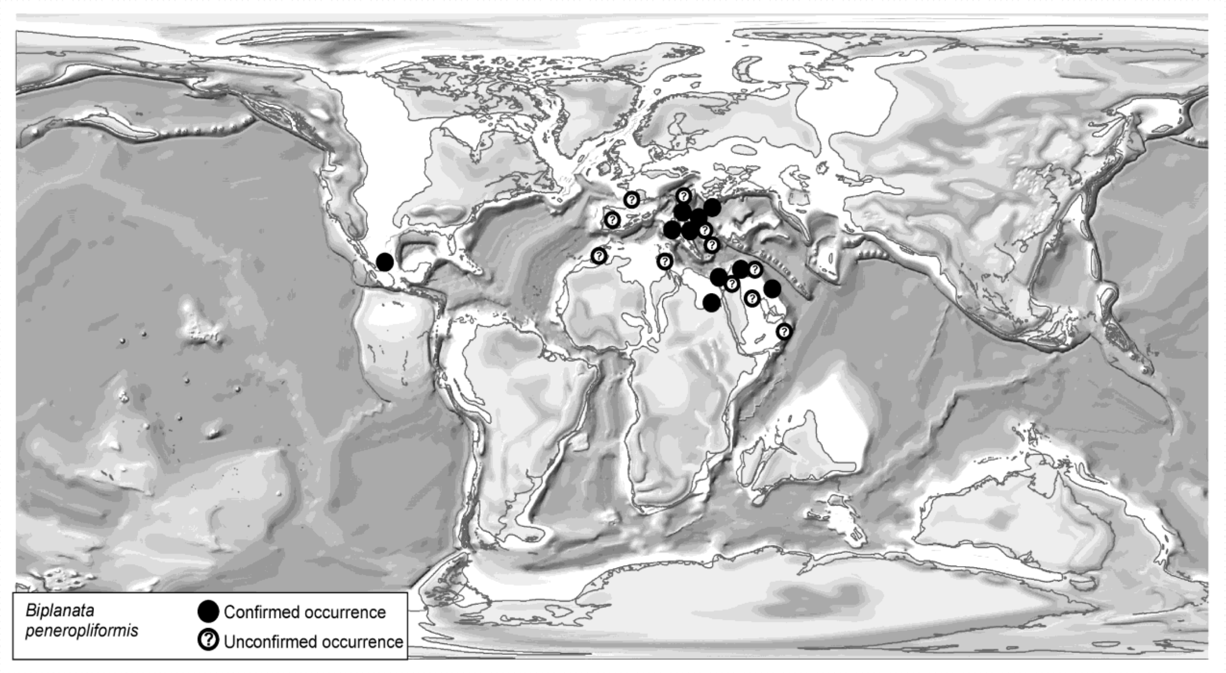


Fig.14 Cenomanian paleogeographic distribution of *Biplanata peneropliformis*.

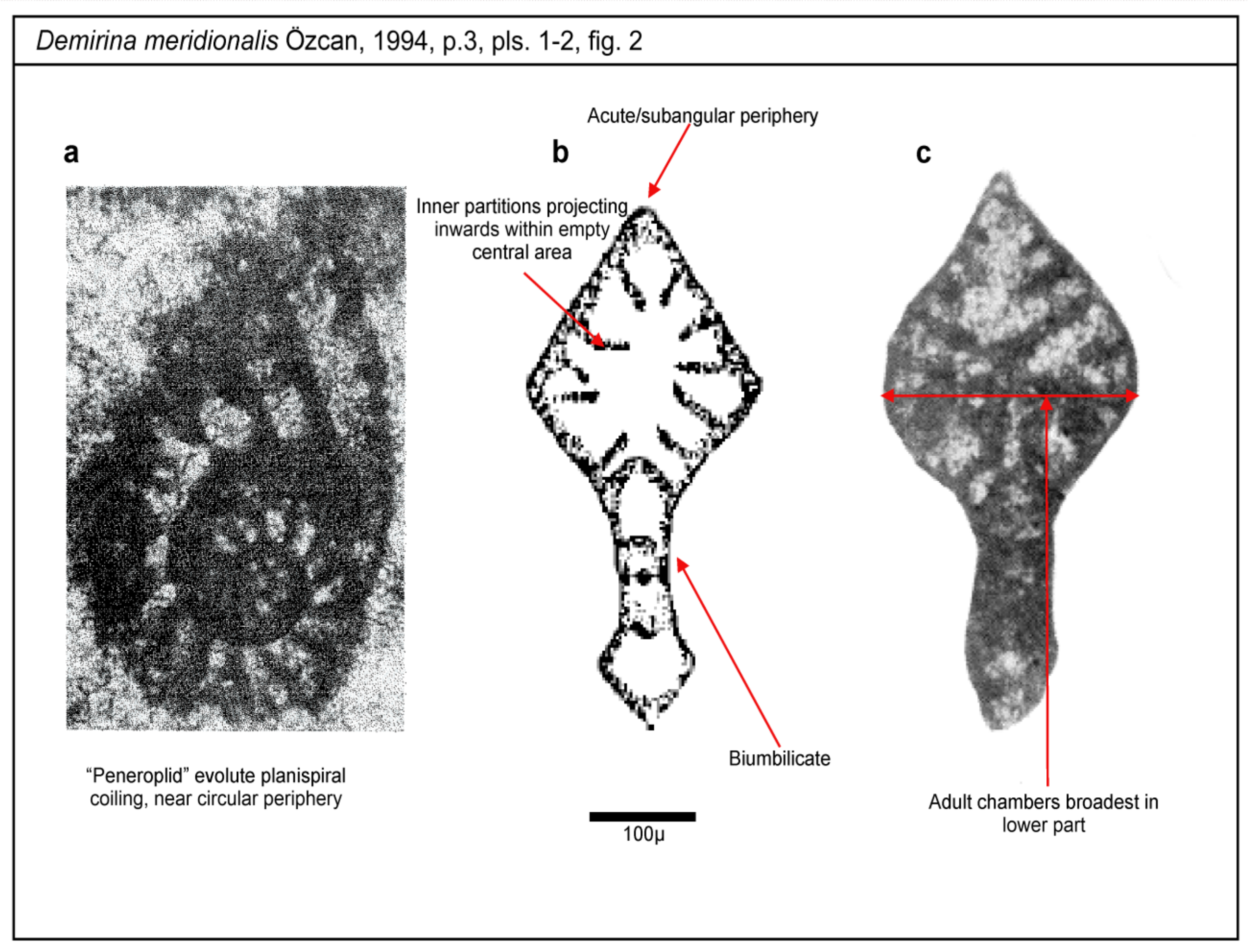


Fig. 15 Representative illustrations of *Demirina meridionalis*: **a** Equatorial section, Özcan (1994, pl. 1, fig. 1, Turkey); **b** Axial section, Özkan in Kaminski (2000, fig. 44 (part), Turkey); **c** Axial section, Özkan (1994, pl. 1, fig. 5, Turkey).

Merlingina and the periphery of the adult chamber is angular/subangular rather than broad and "flat". See the Species Key Chart (Appendix) for diagnostic and other characteristics.

Deuterospira pseudodaxia may be a synonym, but poor illustrations make confirmation difficult.

Stratigraphic Distribution

?Early-middle? Cenomanian.

D. meridionalis was first described from the undifferentiated Cenomanian Karadut Formation of south-east Turkey (Özcan, 1994), where it occurs reworked into synchronous (?) deeper-water deposits. It is recorded from the lower part of the formation with *Praealveolina* grp. *cretacea*, *Orbitolina* sp. and *Rotalipora* sp., suggesting an age no younger than middle Cenomanian. It was subsequently reported from the platformal Derdere Formation of south-east Turkey by Özkan & Altiner (2019).

Cenomanian Paleogeographic Distribution

Eastern Neotethys.

So far reported only from southeast Turkey.

Genus ***Merlingina*** Hamaoui 1965 emended Hamaoui & Saint-Marc, 1970

Type Species: *Merlingina cretacea* Hamaoui 1965 emended Hamaoui & Saint-Marc, 1970

***Merlingina cretacea* Hamaoui 1965 emended Hamaoui & Saint-Marc, 1970**

Reference Illustration & Description

Hamaoui & Saint-Marc (1970), Pls. 22-27, Fig. 4, p. 306-320.

This description and associated illustrations are excellent and comprehensive. See also Saint-Marc (1974a: plate 6) and Hamaoui in Schroeder & Neumann (1985: plate 15).

The introduction of *Merlingina* and its type species *M. cretacea* has a somewhat complex history. Hamaoui (1961) first recognised the taxon as "Gen ? (aff. *Nezzazata* sp.)" from Cenomanian limestones from the Israeli subsurface. The genus and species were first formally described by Hamaoui (1965) with inadequate illustration and limited and inaccurate description. This was acknowledged by Hamaoui & Saint-Marc (1970) who regarded the 1965 description as *nomen nudum* and therefore provided much more comprehensive and accurate diagnoses and descriptions for the genus and species. Nonetheless, Loeblich & Tappan (1988) regarded the 1965 description as "available" (i.e., valid), thus the most suitable way to describe the authorship of the genus and species is as "Hamaoui 1965 emended Hamaoui & Saint-Marc 1970".

Essentially, *Merlingina* is irregularly planispiral throughout; asymmetrical (planoconvex) in the early stage but later becoming more bilaterally symmetrical. In the late stage it tends to uncoil, and the chambers rapidly increase in width so that the apertural face is broad, subcircular, and flattened. The aperture is a U or V-shaped slit (see Hamaoui & Saint-Marc, 1970: fig. 4). Slightly sinuous ribs are prominent in external view. A noticeable characteristic in oblique thin-section views is the combination of widening of later chambers and relatively deep sutures that lead to a (sometimes distinctly pronounced) "saw-tooth" periphery. See the Species Key Chart (Appendix) for diagnostic and other characteristics.

In thin-section (equatorial view) it is similar to *Biplanata peneropliformis* which is regularly planispiral throughout and lacks the increased width of the later chambers in *Merlingina* and therefore the 'saw-tooth' periphery. It differs from *Biconcava bentori* by being asymmetrical in the early stage and plano-convex, not bilaterally biconcave. *Trochospira avnimelechi* is distinctly trochospiral and with a single angular periphery compared with a tendency to form two, subangular peripheries in later chambers of *M. cretacea* which is best visible in axial view (see Fig. 17b).

Demirina and *Merlingina* can appear similar especially in equatorial view where *Demirina* has a circular and relatively smooth periphery and *Merlingina's* periphery attains the least "saw-tooth" appearance. The internal partitions of *Demirina* are also more numerous (and exoskeletal) but may appear similar to the (fewer) toothplates of *Merlingina* and its widest chamber width is across the centre rather than nearer the periphery.

Stratigraphic Distribution

(Early?) middle – late Cenomanian.

Most records of *M. cretacea* are from the middle, late, or undifferentiated middle – late Cenomanian. This follows Saint-Marc (1974a, 1978) who stated the range was middle – late Cenomanian in Lebanon, a range with which Saint-Marc (1981), Arnaud et al. (1981), and Hamaoui in Schroeder & Neumann (1985) concurred but extending the range into the basal Turonian (sometimes questionably). This has led to a certain degree of circular reasoning in subsequent age assignments of the occurrence of the species, in that its presence has been used to argue for an age no older than middle Cenomanian (e.g., Smith et al., 1990; Palci et al., 2008). In fact, it is possible that in the original records of the species from Israel (Hamaoui, 1961, 1965, 1966), it occurs in the early Cenomanian. This was noted by Lipson-Benitah (2009) who gave the taxon an intra-early Cenomanian inception in Israel. The records of Hamaoui (1961, 1965, 1966) do not subdivide the Cenomanian, but long ranges are indicated, and the co-occurrence with such taxa named as "*Trocholina arabica*", "*Orbitolina concava*", "*Praealveolina iberica*", is suggestive of an early Cenomanian age, although the identity of these taxa needs to be confirmed. A further caveat is that the 1961, 1965, and 1966 records by Hamaoui may use a concept of the taxon different from that established by Hamaoui & Saint-Marc (1970).

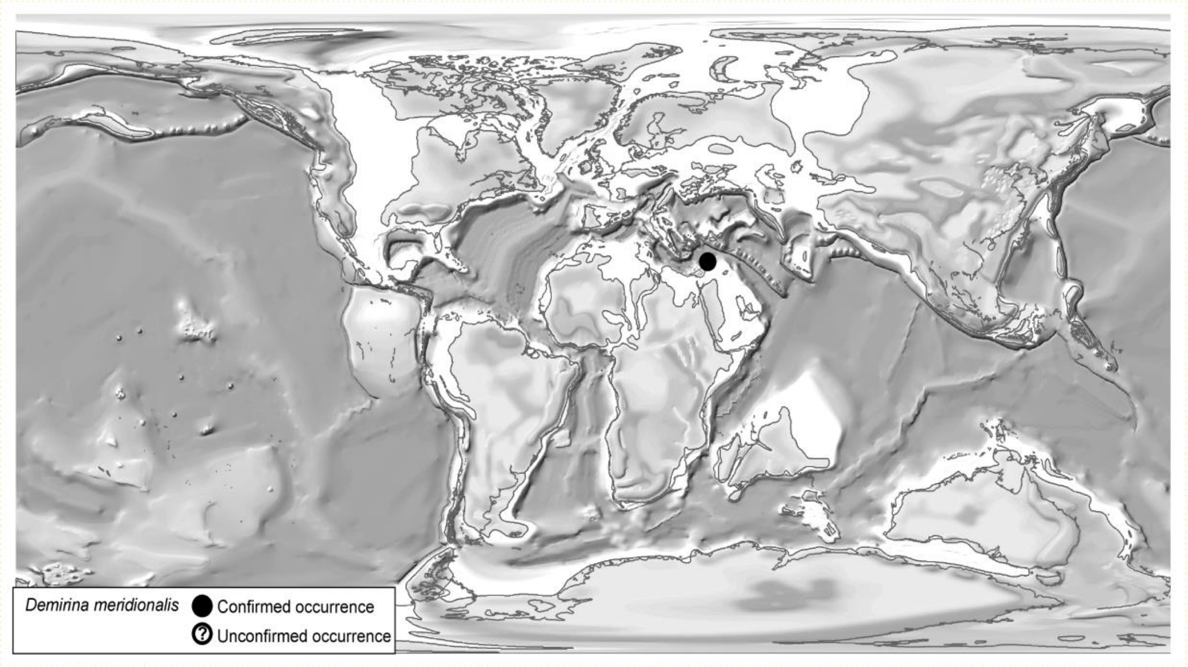


Fig. 16 Cenomanian paleogeographic distribution of *Demirina meridionalis.*

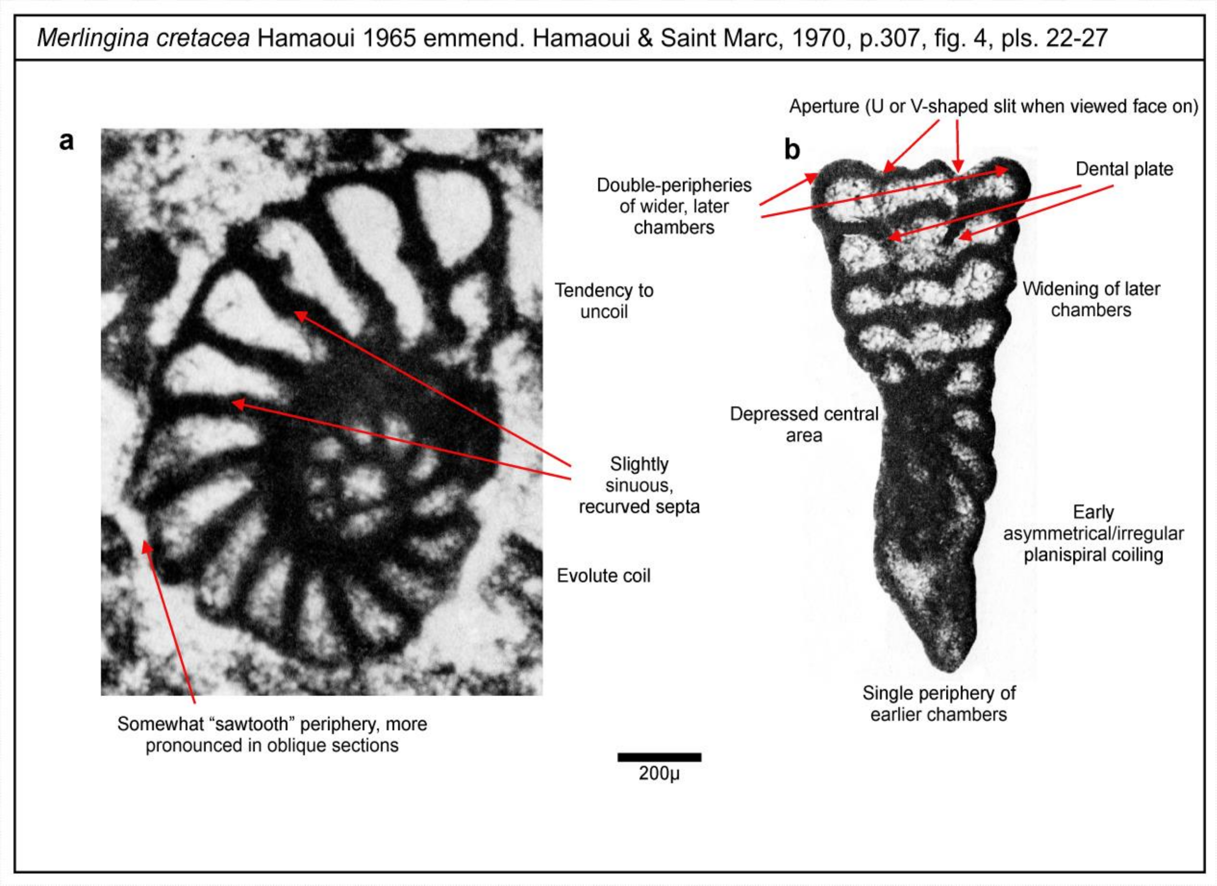


Fig. 17 Representative illustrations of *Merlingina cretacea*: **a** Equatorial section, Saint Marc (1974, pl. VI, fig. 1, Lebanon); **b** Subaxial section, Hamaoui & Saint Marc (1970, pl. 23, fig.3, Lebanon).

It is curious that Hamaoui himself gave no indication of an early Cenomanian age in his 1985 review of this species (Hamaoui in Schroeder & Neumann, 1985), but his statement on the age range of the species contains little supporting data.

Records whose ranges include an attributed early Cenomanian age are infrequent and provide no illustrative material confirming identification. They include Schulze (2003) and Schulze et al. (2004) (Jordan); Ghanem et al. (2012, Syria) and Solak et al. (2020, Turkey; undifferentiated early – middle Cenomanian). Amongst these, of note is that Schulze (2003) and Schulze et al. (2004) who recorded *M. cretacea* from the Naur Formation unit b at one locality (RM2) in Jordan. Using ammonites and calcareous nannofossils they attributed the Naur b to the early Cenomanian *M. mantelli* ammonite zone equivalent. Ghanem et al. (2012) recorded *M. cretacea* in strata containing the planktonic foraminifera *Rotalipora globotruncanoides* and *Rotalipora balernaensis*, which would strongly suggest an early Cenomanian age, but neither have they illustrated any of these forms for confirmation.

Caus et al. (2009) recorded *M. cretacea* from the Santa Fe, Villa de Ves (see also Consorti et al., 2016b) and Moraillas Formations of Spain, which together they assigned an age range of early – late Cenomanian, but only indicated a late Cenomanian age for this species on their accompanying range chart (and with no verification by illustration).

Berthou & Lauverjat (1979) recorded a taxon referred to as *Merlingina* cf. *cretacea* from the latest Albian to earliest Cenomanian from Portugal, but this taxon was unillustrated and undescribed, and its identity cannot be verified.

Shahin & Elbaz (2013, 2014, 2021) illustrate plausible disaggregated specimens of *M. cretacea* from Sinai. These records are said to be early Cenomanian, but the logic of this age assignment is suspect. The presence of *M. cretacea* is one of the reasons for the age assignment, but misreporting information from publications in which the age is actually given as middle to late Cenomanian (e.g., Schroeder & Neumann, 1985).

Plausible illustrations in the relatively recent literature are all middle – late Cenomanian and include Aguilera-Franco (2000) (Mexico); Ghanem & Kuss (2013) (Syria); Rahimpour-Bonab et al. (2012, 2013) and Mohajer et al. (2021a) (Iranian Zagros); Sari et al. (2009) and Solak (2021) (Turkey); Chiocchini et al. (2012) (central Italy). That of Chiocchini et al. (2012) straddles their early – late Cenomanian boundary and is thus broadly equivalent to middle Cenomanian.

Uncertain illustrated occurrences are reported by Smith et al. (1990) (Oman, see also Simmons & Hart (1987); Kennedy & Simmons (1991), and Philip et al. (1995) for unillustrated records); Bomou et al., 2019; Omaña et al. (2012, 2019), and Rosales-Dominguez et al. (1997) (Mexico, see also (e.g.) Michaud et al. (1984) Aguilera-Franco et al. (2001) and Aguilera-Franco (2003) for unillustrated records); Navarro-Ramirez et al. (2017) (Peru, see also Jaillard (1986), Jaillard & Arnaud-Vanneau (1993) and Consorti et al. (2018) for unillustrated records); Hamaoui & Brun (1974) (southern Iraq); Menegatti (2004) (Dubai). Almost all these records are middle – late Cenomanian, albeit with a certain degree of circular reasoning, excluding Navarro-Ramirez et al. (2017) who used carbon and oxygen isotope age proxies (as subsequently followed by Consorti et al. (2018)). The exception to the middle – late Cenomanian range is Michaud et al. (1984) who cite their occurrence of *M. cretacea* within undifferentiated early – middle Cenomanian strata.

Occurrences illustrated as *M. cretacea*, but which are not that species include Mohseni and Javanmard (2020) (= simple biserial foraminifera); Kiarostami et al. (2019) (indeterminate, but incompatible with *M. cretacea*) and Rikhtegarzadeh et al. (2016) (simple biserial to uniserial foraminifera) (all Iranian Zagros – note there are also many unillustrated records from this region e.g., Fourcade et al., 1997). A form illustrated as "*Merlingina* cf. *cretacea*?" from the undifferentiated Upper Cretaceous of Central Iran (Rahiminejad & Hassani, 2016) is not related to true *M. cretacea.* It appears to be a simple trochospiral foraminifera. Fragmentary specimens from "Senonian" strata from southern Italy (Luperto-Sinni, 1976; see also Luperto-Sinni & Ricchetti, 1978) described as *M. cretacea,* cannot be confirmed as this species, and can be discounted, as can an unillustrated record from the Turonian of the Iranian Zagros (Shapourikia et al., 2021).

In previous reviews, extension of the range of *M. cretacea* into (basal) Turonian strata is based on information from Lebanon (e.g., Saint-Marc, 1981), and as with a number of other taxa, this age assignment needs review. The species occurs in beds that from associated ammonite data appear to straddle the Cenomanian – Turonian boundary, but the precise stratigraphic position of *M. cretacea* occurrences relative to these ammonite occurrences is uncertain. Given this, and the lack of any other substantiated Turonian records, *M. cretacea* is excluded from the Turonian.

Cenomanian Paleogeographic Distribution

Neotethys and Caribbean, ?S. America.

In addition to those previously mentioned above, other locations where *M. cretacea* has been recorded (unillustrated) include Algeria (Benyoucef et al., 2012; Slami et al., 2022); Tunisia (Touir et al., 2017); France (Aquitaine) (Deloffre & Hamaoui, 1979); Portugal (Lauverjat, 1976); Croatia (Velić & Vlahović, 1994; Husinec et al., 2000; Velić, 2007; Husinec et al., 2009); Greece (Decrouez, 1978; Fleury, 1980; Pomoni-Papaioannou & Zambetakis-Lekkas, 2009); and Slovenia (Palci et al., 2008).

From the preceding discussion of stratigraphic distribution, it is possible that this species may have originated in the Levant region in the ?early Cenomanian but was very widespread throughout Neotethys by middle – late Cenomanian times.

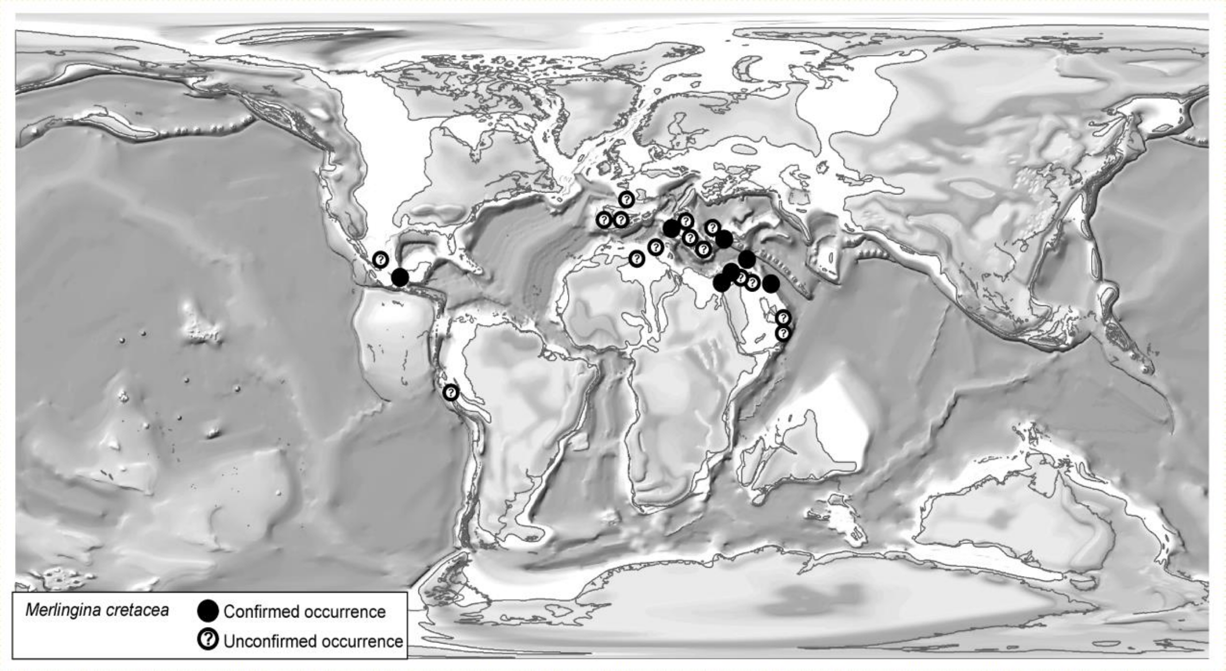


Fig. 18 Cenomanian paleogeographic distribution of *Merlingina cretacea*.

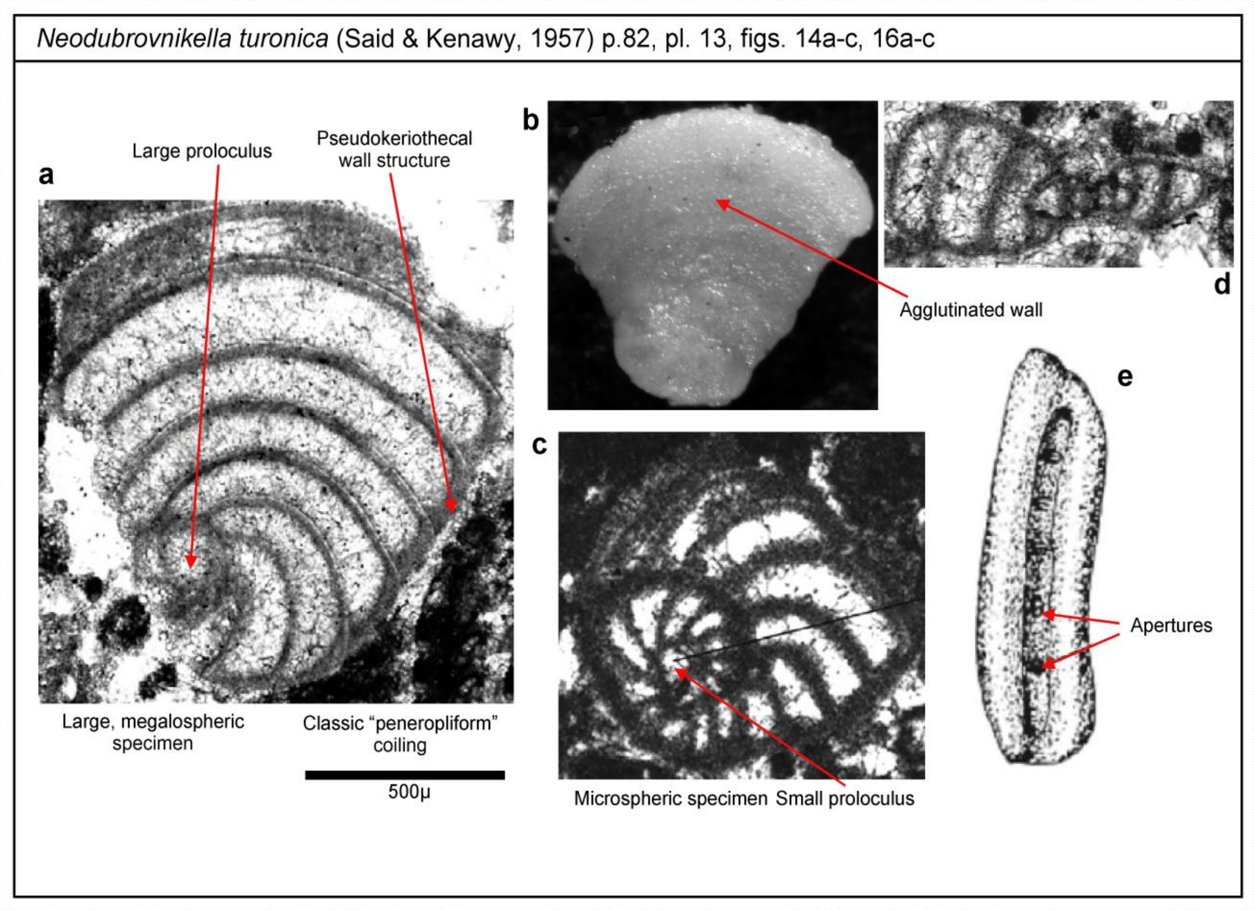


Fig. 19 Representative illustrations of *Neodubrovnikella turonica*: **a** Equatorial section, Schlagintweit & Yazdi-Moghadam (2022, fig. 4(E), Iran); **b** Re-illustration of holotype, Schlagintweit & Yazdi-Moghadam (2022, fig. 4(A), Egypt); **c** Equatorial section, Schlagintweit & Yazdi-Moghadam (2022, 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).

Genus ***Neodubrovnikella*** Schlagintweit & Rashidi, 2018
Type Species: *Neodubrovnikella maastrichtiana* Schlagintweit & Rashidi, 2018
***Neodubrovnikella turonica* (Said & Kenawy, 1957)**

Reference Illustration & Description

Schlagintweit & Yazdi-Moghadam (2022a), Figs. 4 (A-F), 5 & 6, p. 4-8.

The recent review by Schlagintweit & Yazdi-Moghadam (2022a) has clarified the taxonomic status of this species which had for many years been assigned to the porcellaneous genus *Peneroplis* based on its clearly 'peneropliform' shape. However, the true nature of its wall as finely agglutinated and pseudokeriothecal (which is not always discernible) excludes it from the porcellaneous Miliolida and it was transferred to the agglutinated biokovinids within the genus *Neodubrovnikella*. Interestingly, as long ago as 1967 *Peneroplis turonicus* (= *Neodubrovkinella turonica*) was considered as possibly belonging to the agglutinated foraminifera (genus *Stomatostoecha)* (Banner et al., 1967). This notion was largely ignored until the revision of Schlagintweit & Yazdi-Moghadam (2022a). See the Species Key Chart (Appendix) for diagnostic and other characteristics. Dimorphism is distinct in this species (see Fig. 19a & 19c herein).

Peneroplis parvus De Castro is very similar except *N. turonica* has a large proloculus in megalospheric forms, tends to uncoil rapidly with chambers also enlarging rapidly and with septa not 'obviously' perforated. *Peneroplis* is also always planispirally coiled whereas *N. turonica* is frequently not perfectly planispiral (see drawings of holotype in Schlagintweit & Yazdi-Moghadam, 2022a: fig. 4(B, D)). Notwithstanding these differences *N. turonica* can be regarded as an agglutinated isomorphic form of *Peneroplis*.

Schlagintweit & Yazdi-Moghadam (2022a) note the following: "In the literature, *N. turonica* has been confused several times with *Pseudolituonella reicheli*. This Cenomanian species also displays a pseudo-keriothecal wall, but the morphology is different, with a reduced coiled part and continuously widening and uncompressed chambers in the prominent uncoiled part. The septa and the marginal chamber walls are equal in thickness, the foramina larger, cribrate over the apertural face (not in a row) and surrounded by apertural lips that might protrude widely into the chamber lumen".

Stratigraphic Distribution

(Late early?) middle – late Cenomanian.

Originally suggested as a Turonian species and therefore named accordingly, Schlagintweit & Yazdi-Moghadam (2022a) regard *N. turonica* as a Cenomanian-restricted species based on a reassessment of the age of the types from Egypt, their studies of the Sarvak Formation in the Iranian Zagros, together with a review of the literature from numerous other areas (see below) and a biostratigraphic assessment of their associated microfaunas. The vast majority of records are from the middle and late Cenomanian, with extension into the upper part of the early Cenomanian only indicated by data from Greece (Decrouez, 1975; Charvet et al., 1976) and the Iranian Zagros. According to Schlagintweit & Yazdi-Moghadam (2022a) Turonian records can be revaluated as Cenomanian based on updated stratigraphic information and/or reassessment of associated microfauna.

Cenomanian Paleogeographic Distribution

Neotethys.

Schlagintweit & Yazdi-Moghadam (2022a) have recently reviewed the literature on the distribution of *N. turonica* (commonly recorded by others as "*Peneroplis turonicus"* but sometimes recorded as *P.* cf. *turonicus* and mistakenly as *Pseudolituonella reicheli* or *Peneroplis parvus*). This species is confirmed from Italy, Slovenia, Croatia, Kosovo, Serbia, Greece, Lebanon, Syria, Morocco, Egypt, Turkey, Iraq, and Iran.

Genus ***Charentia*** Neumann, 1965
Type Species: *Charentia cuvillieri* Neumann, 1965
***Charentia cuvillieri* Neumann, 1965**

Reference Illustration & Description

Arnaud-Vanneau in Schroeder & Neumann (1985), Pl. 3, p. 17-18. See also Loeblich & Tappan (1985), Pl. 3, p. 6 and Maksoud (2015) Pl. 41, p. 134-138 (with extensive synonymy list, especially of Early Cretaceous occurrences).

The genus *Charentia* was introduced by Neumann (1965) and has a broad planispiral, lenticular test similar to *Mayncina* but often with a late uncoiled portion of up to 4 rectilinear chambers, following 11-13 chambers in the last whorl of up to 4 whorls. Internally the wall structure is pseudokeriothecal (see excellently illustrated material and description by Hottinger (1967) of material from the Cenomanian of Spain) with an imperforate outer layer similar to that seen in the subglobular *Moncharmontia* although *Charentia* is more lenticular and tends to uncoil (and also possesses a different apertural type). Rather thin septa with a build-up at the base of each (= characteristic chomata-like nodes, Loeblich & Tappan, 1985, p. 98) and the aperture varies in shape with ontogeny – a triangular arch progressing to a 3-prong opening with the "vertical" part of the opening becoming longer and ending in a narrow slit along the apertural face. This can be seen in rare external views of Cenomanian material from Egypt (Hassanien & Sigal, 1983) and Somalia (Luger, 2018). *Nautiloculina* Mohler is similar but has a simpler (i.e., non pseudokeriothecal) wall and noticeably thicker septa. See the Species Key Chart (Appendix) for diagnostic and other characteristics.

Loeblich & Tappan (1985) provide a useful review of synonyms of *Charentia* and *C. cuvillieri*.

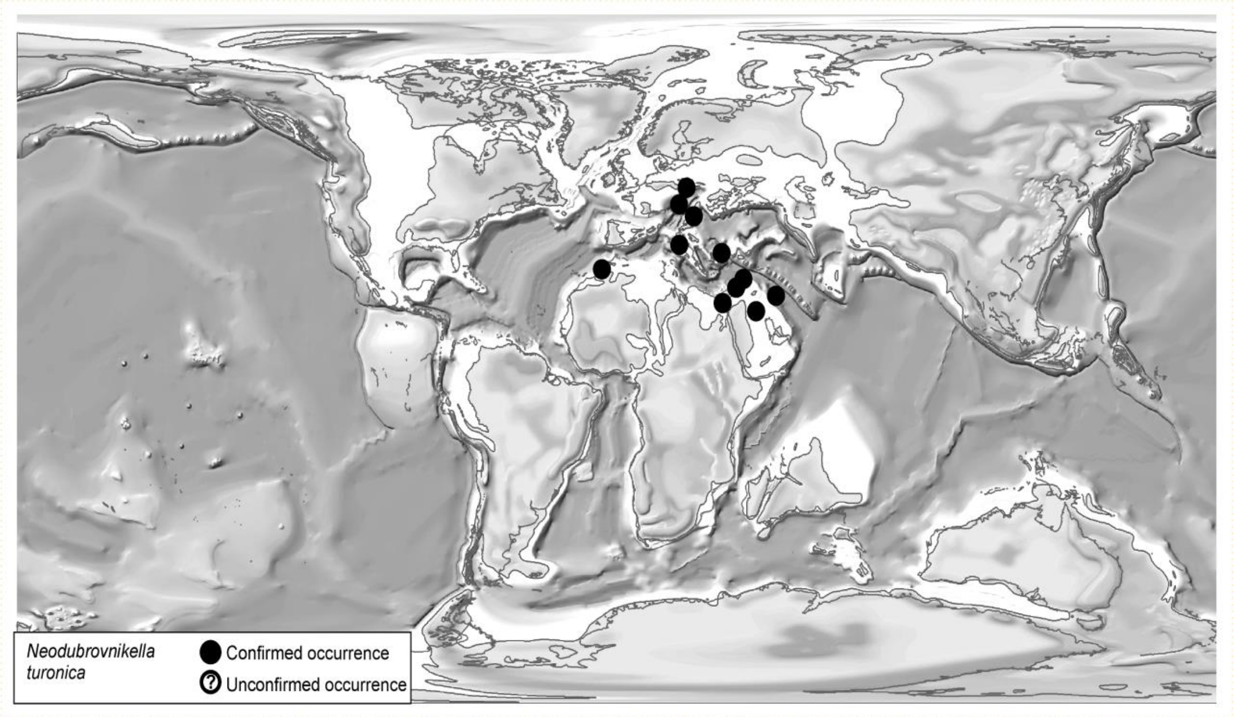


Fig. 20 Cenomanian paleogeographic distribution of *Neodubrovnikella turonica*.

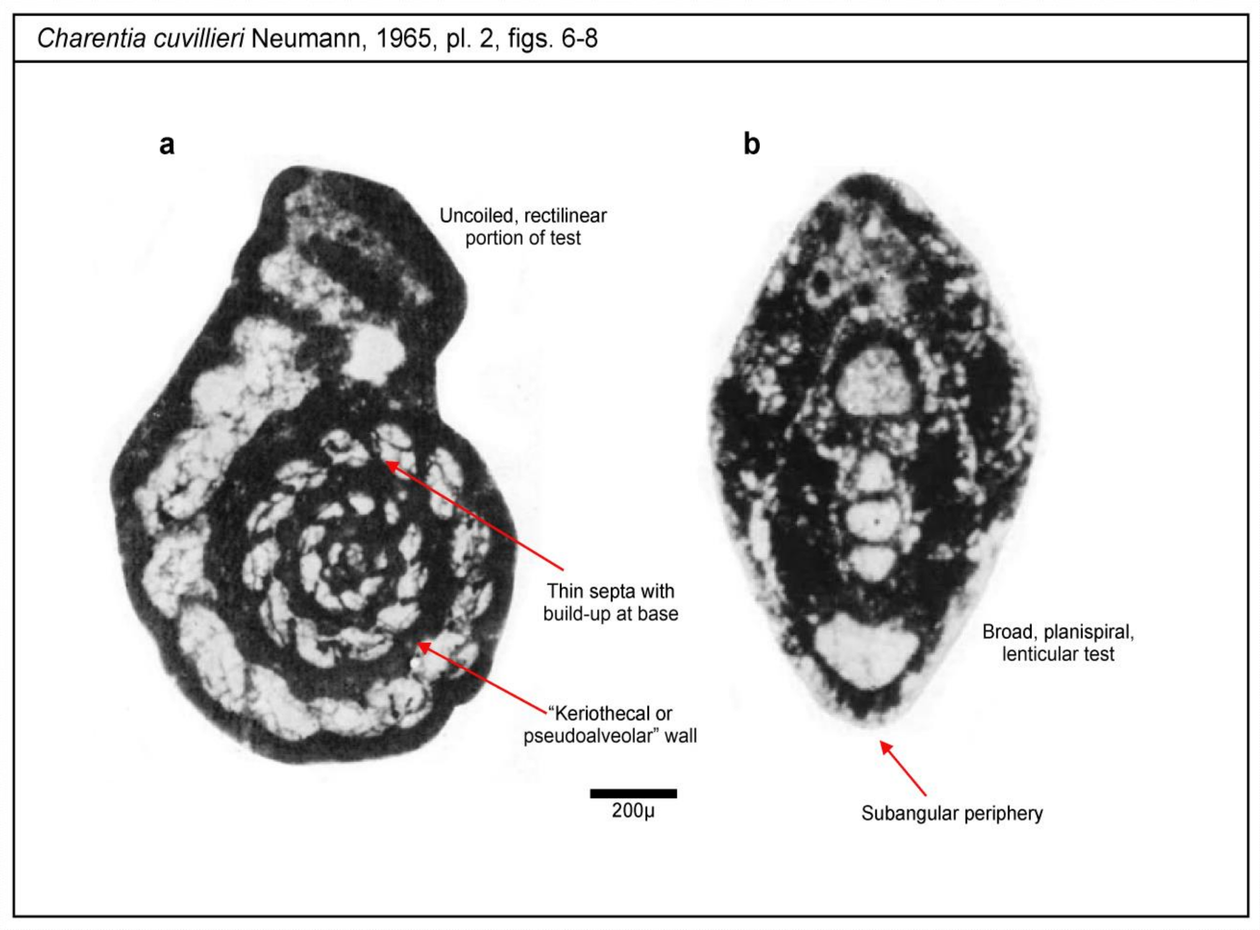


Fig. 21 Representative illustrations of *Charentia cuvillieri*: **a** Equatorial section, Neumann (1965, holotype, pl. 2, fig. 1c, France); **b** Axial section, Schroeder & Neumann (1985, pl. 3, fig. 3, France).

The Late Jurassic genus *Tonasia* Gorbachik is considered as a synonym of *Charentia* (see discussion of the type species *Tonasia evoluta* Gorbachik below), whilst *Hemicyclammina praesigali* Banner (see below) from the Aptian – Albian of Spain is considered a synonym of *C. cuvillieri*. They note that the Barremian – Aptian genus *Melathrokerion* Brönnimann & Conrad is similar to *Charentia* by virtue of its pseudokeriothecal wall and general morphology, but has a thicker wall, a more nautiloid shape, fewer chambers per whorl, and a broadly rounded periphery. *Cribrostomoides paralens* Omara described from the Cenomanian of Egypt (Omara, 1956) is referred to *Charentia* by Loeblich & Tappan (1985). If it proves to be a synonym of *C. cuvillieri* it will have priority (access to type material is being sought at the time of writing).

A superficially similar form to *C. cuvillieri* is *Everticyclammina greigi* (Henson) which is clearly distinguished by its alveolar wall (Banner & Higton, 1990). Additionally, *E. greigi* is less inflated and the chamber sutures are more consistently depressed. *Comaliamma* Loeblich & Tappan is superficially similar to *Charentia* in the discoid early stage and tendency to uncoil but differs in the nature of the aperture and simple rather than canaliculate walls and septa.

Arnaud-Vanneau in Schroeder & Neumann (1985) identifies two morphotypes of *C. cuvillieri* – one large (1.2 – 1.4 mm equatorial diameter) with a thicker wall; the other small (0.780 – 0.830 mm equatorial diameter) with a thinner wall and fewer chambers (9-11) in the last whorl. Material described by Hofker (1965) from the Aptian – Albian of Spain as *Haplophragmoides greigi* (Henson) and later as *Hemicyclammina praesigali* Banner (Banner, 1966) conforms to *C. cuvillieri sensu lato*, suggesting that the smaller morphotype (0.6-0.8 mm cited diameter) might have a pseudokeriothecal wall texture. Small morphotypes of *C. cuvillieri* were described by Gollestaneh (1965) in an unpublished Ph.D. thesis as "*Haplophragmoides persica* n. sp." from the Barremian – Aptian of the Iranian Zagros belt (Schlagintweit, 2015).

The two forms also appear to have different ranges with small forms found from around the Jurassic/Cretaceous boundary (e.g., Altiner, 1991; Schlagintweit & Ebli, 1999; Ivanova & Kolodziej, 2004; Chiocchini et al., 2012; Kobayashi & Wernli, 2014; Bucur et al., 2014, 2020) to the Cenomanian, and the larger forms from the Cenomanian only. However, a full taxonomic review of the many reported occurrences of the species and its possible synonyms from the latest Jurassic to mid-Cretaceous is required to confirm this stratigraphic separation.

Some small specimens have been tentatively recorded from the Late Jurassic – Early Cretaceous as *Charentia evoluta* (Gorbachik) (= *Tonasia evoluta*) (e.g., Bucur et al. (1996) from Italy; Krajewski & Olszewska (2007) from Crimea; Kobayashi & Vuks (2006) from Japan and Pleş et al. (2015) from Romania) although Schlagintweit & Wagreich (2005: p. 117) state that these small morphotypes "can hardly be distinguished from *C. cuvillieri*". Records of *Charentia spp.*, including *C. evoluta* from the mid-Cretaceous of central Iran (Rahiminejad & Hassani, 2015, 2016) require further investigation. Most illustrations are potentially of haplophragminids, small and lacking any form of distinctive wall structure.

Charentia nana Arnaud-Vanneau is a very small species of *Charentia* (equatorial diameter 0.365 – 0.480 mm) (Arnaud-Vanneau, 1980) that is even smaller than the small forms of *C. cuvillieri,* and with only 2.5 – 3 whorls and 7.5 – 8 chambers in the last whorl. A pseudokeriothecal wall structure remains to be demonstrated for this species.

Radoičić (1974a) described a new species from the late Cenomanian of Kosovo called *Charentia kosovica* which she said differed from *C. cuvillieri* by having a more rounded test, being slightly smaller and having fewer (9-10) chambers in the whorl. This corresponds somewhat with Arnaud-Vanneau in Schroeder & Neumann's (1985) description of the smaller morphotype (see above), but the latter's illustrations of the smaller form show a smooth, but clearly more angular periphery in axial view, leading to a lenticular test. Radoičić's specimens have well-rounded peripheries (see also Saint-Marc, 1974a: pl. 1, fig.11) and a much less lenticular profile. Nonetheless, Rey et al. (1977) placed *C. kosovica* in synonymy with *C. cuvillieri*, which if correct, provides evidence for a late Cenomanian age for this species (see below). Arnaud-Vanneau in Schroeder & Neumann (1985) does not mention *C. kosovica* (i.e., she does not synonymise it with any other taxon). Specimens illustrated by Weidich & Al-Harithi (1990) from the Albian of Jordan as *Charentia cf. cuvillieri* and compared to *C. kosovica* do not appear to be *Charentia*. They possess large, broad chambers, separated by short septa, with a marked basal layer. More research is required to assess their identity.

Charentia hasaensis Basha and *Charentia rummanensis* Basha are poorly known species introduced from material from the late Cenomanian of Jordan (Basha, 1978). They appear to have only been mentioned in their type descriptions. From the limited illustrations they may be partly synonymous with *Hemicyclammina whitei* (Henson). Another species from the same publication, *Mayncina hasaensis* Basha might have closer affinity with *C. cuvillieri.* The type material of all these species needs to be re-examined. Likewise, *Charentia granulosa* Kerdany & Eissa, described from the late Cenomanian of Egypt (Kerdany et al., 1973), may include *H. whitei* amongst its types.

Stratigraphic Distribution

Latest Jurassic – late Cenomanian.

C. cuvillieri was originally described from the middle Cenomanian of western France (Neumann, 1965) and was described as ranging from Albian and older to the top of that substage by Schroeder & Neumann (1985). A range chart in Saint-Marc (1981) gave the Neotethyan range of this species to be throughout the Cenomanian, but gave an Albian restricted-range for its occurrence in Lebanon (although the text indicates extension into the earliest Cenomanian). Illustrations in Saint-Marc (1974a) suggest that it is the "small" form of *C. cuvillieri* (equatorial diameter <0.525 mm) that is being referred to for the Lebanese occurrences. As noted by Arnaud-Vanneau (1980) they may be comparable with her species *C. nana*.

Since the publications of Saint-Marc (1981) and Schroeder & Neumann (1985) there have been a great many records of the species published (although relatively few with plausible illustration) and these confirm that the species if treated *sensu lato* pending a full taxonomic study of the genus is long ranging from around the Jurassic/Cretaceous boundary to the top of the Cenomanian. A middle Turonian record (Cherif et al., 1989) from Egypt is not this species. The external-only views are difficult to determine, but the test lacks the broad, lenticular profile of *C. cuvillieri*.

It is possible that *Charentia* can be found in strata younger than Cenomanian. Luperto-Sinni (1976) and Luperto-Sinni & Richetti (1978) illustrated specimens termed "*Navarella*? Sp." from the Santonian and Maastrichtian of southern Italy. These are undoubtedly not *Navarella* Ciry & Rat and were considered as synonymous with specimens termed *Lituola*? Sp. from the Coniacian-Santonian of Austria (Schlagintweit, 1992). Some of the Austrian specimens have hints of a pseudokeriothecal wall. Despite gross morphological similarities with *Charentia*, more material and research are required before drawing any conclusions regarding range extension.

Late Cenomanian occurrence is demonstrated by Ettachfini & Andreu (2004) from Morocco (see also unillustrated by Ettachfini et al., 1989, 2005; Lézin et al., 2012). If *C. kosovica* proves to be a synonym of *C. cuvillieri* (see above), this provides further support for a late Cenomanian age. Other illustrated late Cenomanian records are less dependable. A specimen illustrated from Egypt by El-Sheikh & Hewaidy (1998) cannot be confirmed from the illustration provided which looks close to *Hemicyclammina whitei* (Henson). Nonetheless, the species has been plausibly illustrated from the Cenomanian of Egypt (Hassanien & Sigal, 1983). A late Cenomanian illustration of *Charentia* sp. from southern France by Rineau et al. (2021) is completely unrelated to this genus – it appears to be an indeterminate, but simple trochospiral taxon.

Other relatively biostratigraphically well-constrained records from the Cenomanian include Schlagintweit & Wagreich (2005) from the early Cenomanian of Austria; Simmons et al. (2020b) from the middle Cenomanian of south-east Turkey; and Aguilera-Franco (2000) from Mexico. A single specimen illustrated by Ghanem et al. (2012) from the early Cenomanian of Syria is probably *C. cuvillieri* but cannot be confirmed. Dr. Ian Sharp (pers. comm.) has provided the authors with a plausible illustration of *C. cuvillieri* from the lower Sarvak Formation of the Iranian Zagros and hence early Cenomanian in age (Bromhead et al., 2022) (see also unillustrated from the Zagros by Kiarostami et al. (2019) and Omidvar et al. (2014a, b).

Berthou (1973) recorded and illustrated this species from the early Cenomanian of Portugal, but the illustrations are poor. Rey et al. (1977) illustrated the species from what they termed late Albian strata, although based on the orbitolinids present from the same beds, the age could well be early Cenomanian at least in part (see Berthou & Schroeder, 1978). Later Berthou and Lauverjat (1979) revised the range in Portugal to early Albian to top Cenomanian (unillustrated, see also Rey, 2009), and then Berthou (1984b) extended the range into the early Turonian but provided no further illustrations (see also Andrade (2018) with uncertain illustration).

Cenomanian Paleogeographic Distribution

Neotethys and Caribbean.

A plausible illustrated record from the Cenomanian of the Tajik Basin (Central Asia, Kaya, 2020) represents an interesting palaeogeographic extension to the distribution of this species (see also Kaya et al., 2020). Dufaure et al. (1984) illustrated *C. cuvillieri* from the undifferentiated Cenomanian of Libya, close the border with Chad. It has been illustrated as *Daxia cenomana* from Armenia (Danelian et al., 2014) and from Tunisia (Abdallah et al., 1995) as *Nummofallotia apula* Luperto-Sinni (and as *Charentia* cf. *cuvillieri*) (see also unillustrated records by Bismuth et al. (1981) and Touir et al. (2017).

Additional unconfirmed (because of lack of illustration or uncertain illustration) occurrences in the Cenomanian include from Croatia and the Balkans (Husinec et al., 2000, 2009; Velić & Vlahović, 1994; Velić, 2007 and Radoičić & Schlagintweit, 2007); Greece (Steuber et al, 1993); Egypt (Kerdany et al., 1973; Bachmann et al., 2003; Abu-Zied, 2007; Ismail et al., 2009; Shahin & Elbaz, 2013, 2014; Orabi & Hamad, 2018; El Baz & Khalil, 2019); Levant (Bachmann & Hirsch, 2006); Spain (Cherchi & Schroeder, 1982; Calonge et al., 2002, 2003; Calonge García & López Carrillo, 2003; González-Fernández et al., 2004; Caus et al., 2009; Consorti, 2017; Consorti et al., 2014, 2016b; Gräfe, 2005; and Vicedo et al., 2011); Turkish Taurides (Solak et al., 2020); central Iran (Naraki et al., 2015); Mexico (Aguilera-Franco et al., 2001; Aguilera-Franco, 2003 and Omaña et al., 2019); Algeria (Laouidji & Hafiani, 2021, Slami et al., 2022); southern Iraq (Mohammed, 1996); and Oman (Simmons & Hart, 1987; Rabu, 1993).

Genus ***Fleuryana*** De Castro, Drobne & Gušić, 1994
Type Species: *Fleuryana adriatica* De Castro, Drobne & Gušić, 1994

Fleuryana gediki **Solak et al., 2020**

Reference Illustration & Description

Solak et al. (2020), p. 19, Figs. 14(A-E) & 15.

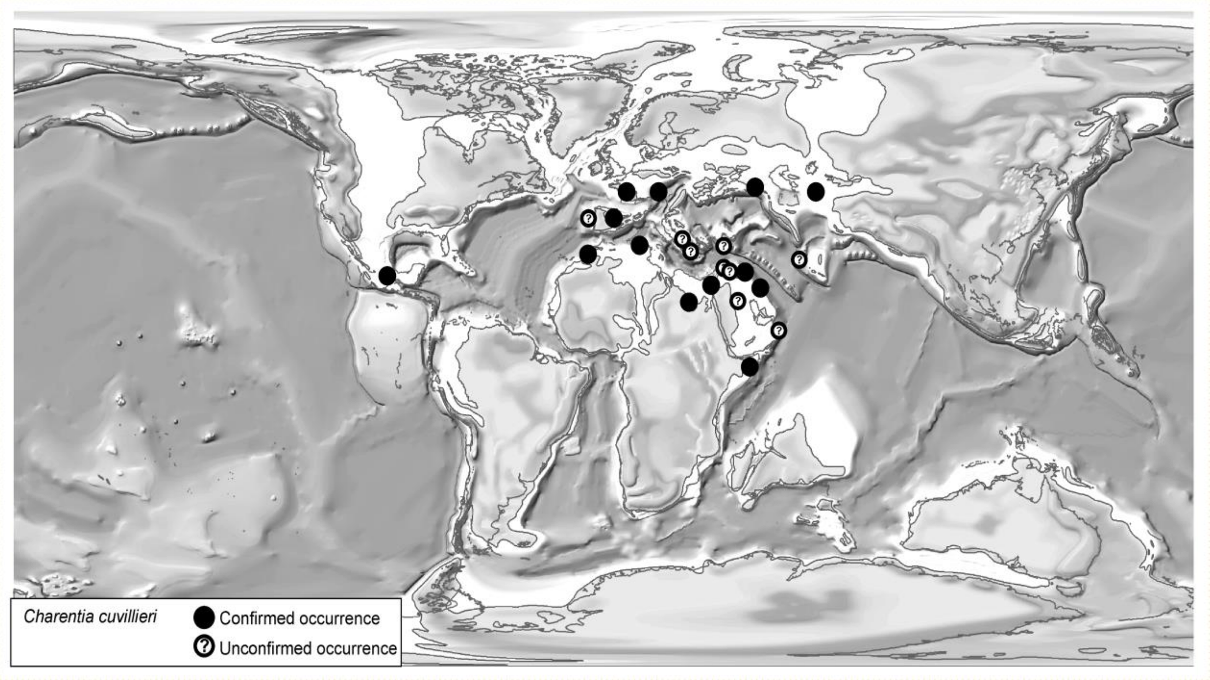


Fig. 22 Cenomanian paleogeographic distribution of *Charentia cuvillieri.*

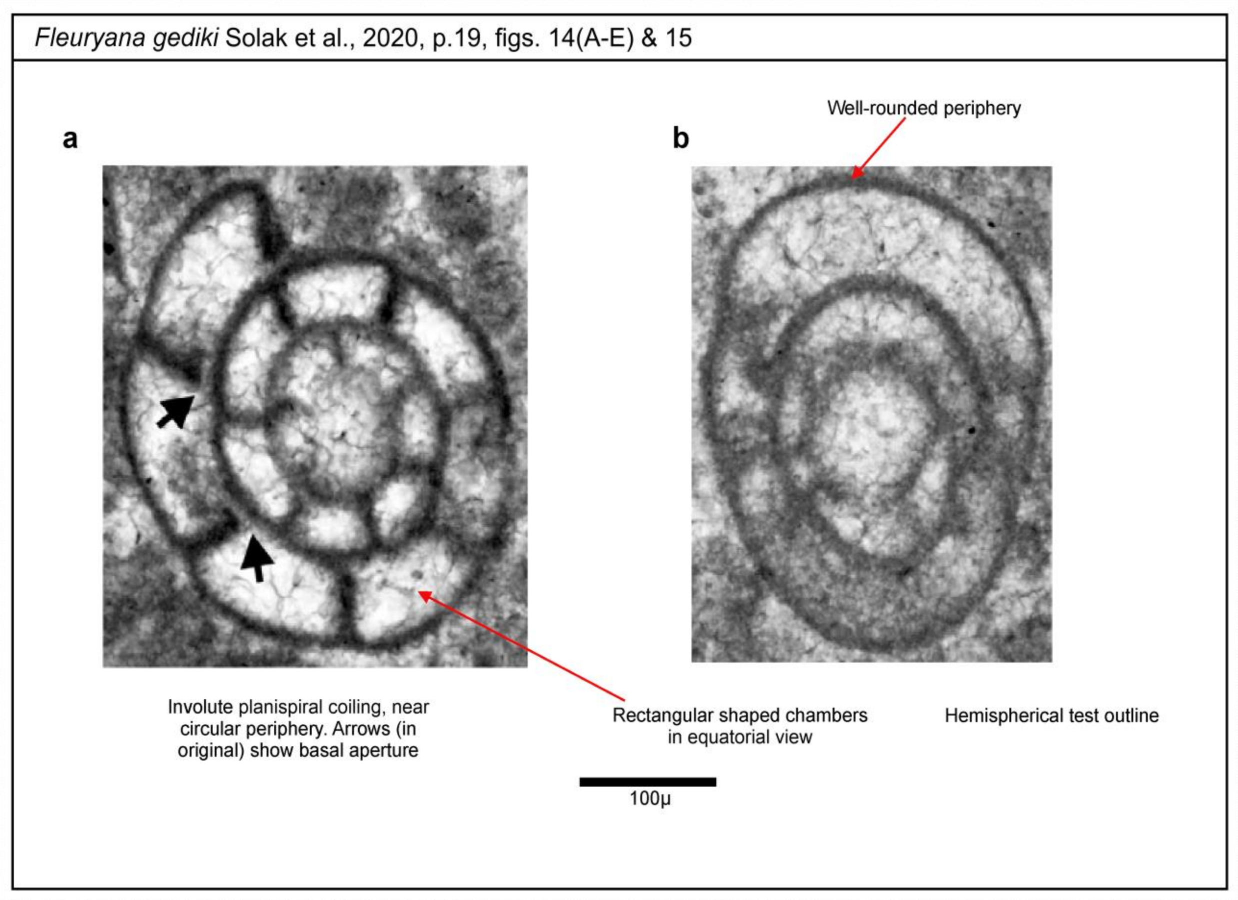


Fig. 23 Representative illustrations of *Fleuryana gediki*: **a** Equatorial section, Solak et al. (2020, fig. 15(R), Turkey); **b** Axial section, Solak et al. (2020, fig. 15(S), Turkey).

This Turonian species (so far only known from its type locality in Turkey – Solak et al., 2020) is included herein because of its close similarity to *Moncharmontia apenninica* (De Castro) which can occur in the Cenomanian (see entry for that species). *F. gediki* is similar to *M. apenninica* in overall shape and structure but differs in having a single, arched slit basal aperture (see Solak et al., 2020, fig. 15G for an axial view), a thinner test wall (8 µm vs 17 µm) and fewer chambers (8, rarely 9 vs 9-10.5). It is also smaller (< 0.40mm) in equatorial diameter than *M. apenninica* (> 0.40mm). In equatorial view its chambers are longer than high compared with *M. apenninica's* which are shorter than high. *Moncharmontia compressa* (De Castro) is somewhat more compressed and lacks the well-rounded periphery. See the Species Key Chart (Appendix) for diagnostic and other characteristics.

F. gediki differs from the type species of *Fleuryana*, *F. adriatica* De Castro, Drobne & Gušić (described originally from the latest Maastrichtian of Croatia), in having a well-rounded, hemiglobular shell (cf. lenticular), fewer chambers and having the aperture in a basal position rather than central as in *F. adriatica*. The chambers in *F. gediki* are also distinctly rectangular in equatorial section. Biometric differences between *F. gediki* and *M. apenninica* & *F. adriatica* are tabulated by Solak et al. (2020; table 2).

The "canaliculate" wall (=pseudokeriothecal) described by Solak et al. (2020) is only highlighted on 3 out of 25 illustrations in their paper and is evidently not easy to determine in the relatively thin walls of *F. gediki* therefore its presence remains equivocal. The definitive presence of such a feature could also call for taxonomic separation of *F. gediki* from the genus *Fleuryana* (see discussion in Schlagintweit & Septfontaine (2023) for the species *Siphopfenderina geyikensis* (Solak)). However, until better material becomes available this taxon can be retained in *Fleuryana*.

Stratigraphic Distribution

Turonian – ?Coniacian.

Reported from "*levels following the extinction of Cenomanian benthic foraminifera… in the Bornova Flysch Zone and Bey Daglari* [of SW Turkey]" (Solak et al., 2020). The type locality is from Turonian strata (*Pseudocyclammina sphaeroidea* Zone sensu Solak et al., 2020) but it is also known from undifferentiated Turonian – Coniacian strata in the region close to the type locality.

Cenomanian Paleogeographic Distribution

Central Neotethys.

So far only recorded from the Taurides of SW Turkey (Solak et al., 2020).

Genus ***Moncharmontia*** De Castro, 1967

Type Species: *Neoendothyra apenninica* De Castro, 1966

***Moncharmontia apenninica* (De Castro, 1966)**

Reference Illustration & Description

[Note: also misspelled as *Montcharmontia* in several publications]

De Castro (1966), Figs. 5-6, Pls. I-V (not pl. III, figs. 4-8), p. 328-333.

The original comprehensive description (De Castro, 1966, 1967) of the genus and two species (*Moncharmontia apenninica* (type species) and *Moncharmontia compressa* De Castro) describes a planispiral (though the final whorl may be slightly irregular compared to the initial planispiral coiling), involute and biumbilicate test with a wall that consists of "one calcareous microgranular layer, apparently perforate" (i.e., pseudokeriothecal) (see also Tešović et al., 2001). The aperture is cribrate with numerous small circular openings in the middle and lower parts of the apertural face – well illustrated in thin-section examples by Chiocchini et al. (2012) and Arriaga et al. (2016). Up to ten chambers can be present in the final whorl, with up to two and half whorls present. In equatorial section, the chambers have a trapezoidal shape, and the septa are straight to slightly convex. On average, the equatorial diameter of shells with two entire whorls is 0.47 mm and the maximum thickness is 0.27 mm (Arriaga et al., 2016). See the Species Key Chart (Appendix) for diagnostic and other characteristics.

The genus *Fleuryana* is very similar but differs in by having slightly fewer chambers in the final whorl (8 cf. 9-10), thinner walls and a single, basal aperture (Solak et al., 2020, see Appendix).

Stratigraphic Distribution

Upper middle Cenomanian – Maastrichtian.

The FAD of *M. apenninica* has long been considered (e.g., Sartorio & Venturini, 1988; Loeblich & Tappan, 1988; Moro & Jelaska, 1994; Koch et al., 1998; Korbar & Husinec, 2003; Velić, 2007; Sari et al., 2009; Chiocchini et al., 2012; Frijia et al., 2015; Arriaga, 2016; Arriaga et al., 2016; Özkan & Altiner, 2019; Solak et al., 2020) to represent the appearance of a new taxon in the Turonian and has been related to faunal renewal after the large-scale extinction event that occurred towards the end of the Cenomanian, linked to OAE2 and calibrated to the *geslinianum* ammonite zone (Parente et al., 2008).

Nonetheless, a plausible specimen of *M. apenninica* was illustrated by Bignot & Poisson (1974) from undoubted Cenomanian strata in the Turkish Taurides. Moreover, plausible illustrated occurrences in Cenomanian strata were recently recorded by Schlagintweit & Yazdi-Moghadam (2021) from the Cenomanian part of the Sarvak Formation of the Iranian Zagros. Co-occurrence with *Chrysalidina gradata*, *Cisalveolina fraasi* and *Simplalveolina simplex* (Reichel) clearly points to a Cenomanian age. Also, Mohajer et al. (2021a) illustrated possible *M. apenninica* from the late Cenomanian part of the Sarvak Formation (and note its occurrence in the Turonian part),

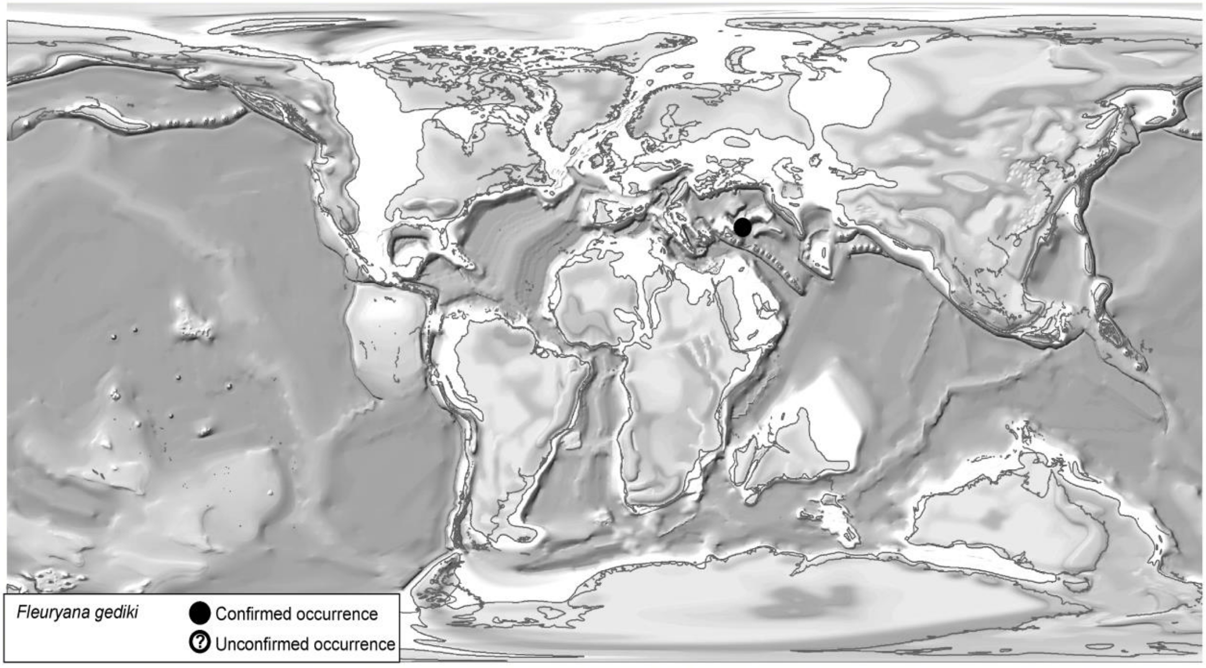


Fig. 24 Cenomanian paleogeographic distribution of *Fleuryana gediki*.

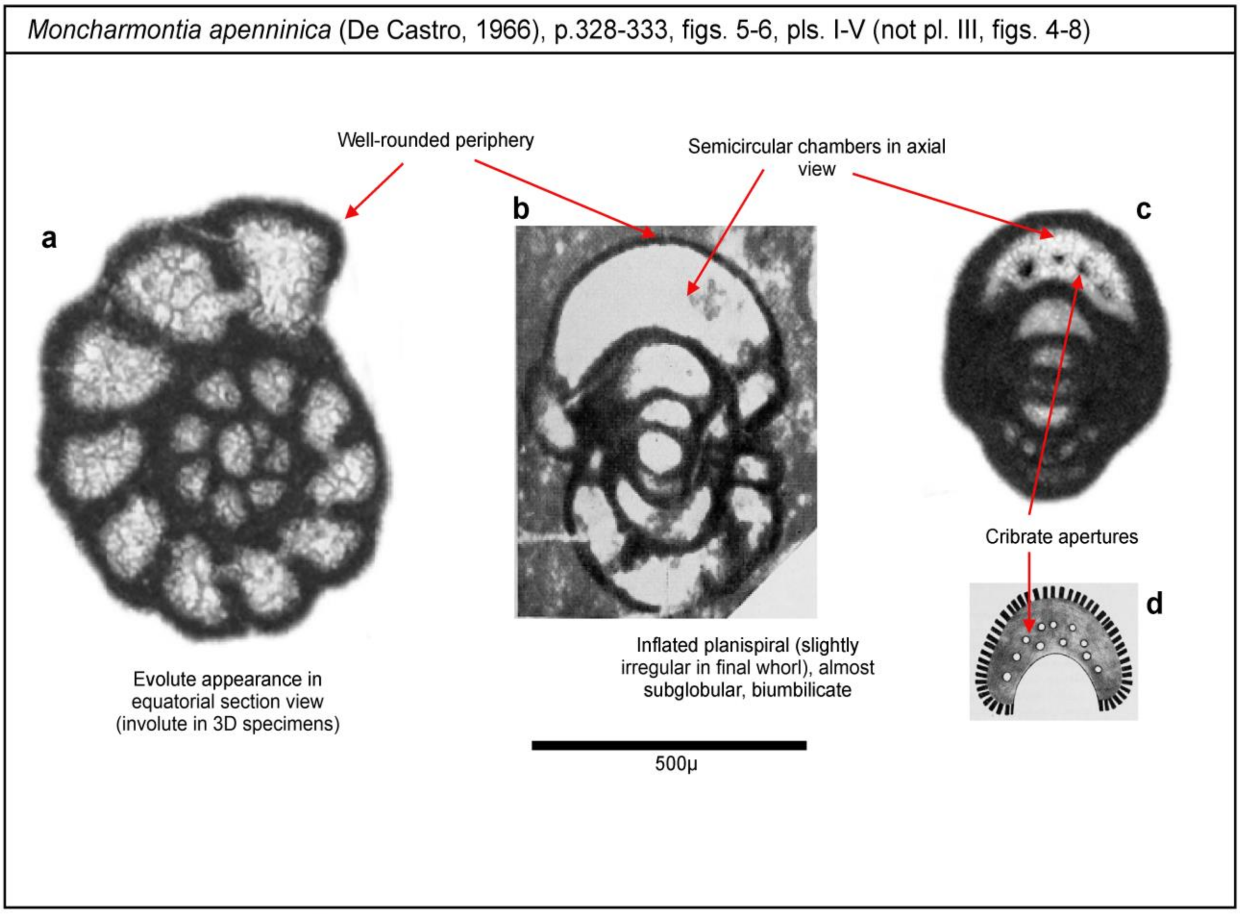


Fig. 25 Representative illustrations of *Moncharmontia apenninica*: **a** Equatorial section, Arriaga et al. (2016, fig. 5(3), Italy); **b** Axial section, De Castro (1966, pl. III, fig. 9, Italy); **c** Axial section, Arriaga et al. (2016, fig. 5(8), Italy); **d** Apertural face, De Castro (1966, fig. 6B).

whilst Rikhtegarzadeh et al. (2017) mention *Moncharmontia* sp. from the Cenomanian part of the Sarvak, but provide no illustration.

Therefore, Schlagintweit & Yazdi-Moghadam (2021) have suggested the FAD of *M. apenninica* occurs "somewhere in the upper part of the middle Cenomanian". They also pointed out Cenomanian occurrences in Mexico (Omaña et al. (2012, 2013) but these are not supported by illustration - see also Aguilera-Franco et al., 2001; Aguilera-Franco & Romano, 2004; Aguilera-Franco & Allison, 2004). There is also an illustrated, but misidentified record (possibly *Biconcava bentori*) (Aguilera-Franco, 2003).

Koç (2017) mention *M. apenninica* in association with a clearly Cenomanian foraminiferal assemblage from the Turkish Taurides. Plausible specimens are illustrated, but these may be from younger stratigraphy (the caption is unclear). Also, from the Taurides, Solak et al. (2020) describes "*Moncharmontia*? sp." from the uppermost Cenomanian (see also Sağaltici & Koç (2021) unillustrated). The specimens are almost certainly this genus, but species identification is not possible. Shanin & Elbaz (2013) record the species from the Cenomanian of Sinai, but the disaggregated specimens illustrated cannot confidently be identified as this species. Another (but unillustrated) record from the Cenomanian comes from the Natih Formation of Oman by Piuz & Meister (2013). Ettachfini & Andreu (2004) and Ettachfini (2006) illustrate a form attributed to *Moncharmontia* aff. *apenninica* from the late Cenomanian of Morocco, but which seems more compatible with *Biconcava bentori*.

Records from strata attributed to the Turonian should be checked for "circular reasoning" – i.e., a Turonian lower age limit is attributed to *M. apenninica* (and the strata it is found in). For example, the illustrations of *M. apenninica* from the upper Derdere Formation of Turkey attributed to the Turonian by Özcan & Altiner (2019) are reasonably plausible. However, these records co-occur with *Cuneolina pavonia* d'Orbigny, *Nezzazata simplex* Omara and *Nezzazatinella picardi* (Henson); all taxa that could be as old as Cenomanian (see Simmons et al., 2020b for further discussion on the age attribution of the Derdere Formation).

Similar arguments can be applied to the records by Rahimpour-Bonab et al. (2012, 2013) and Omidvar et al. (2014a, 2014b) from the Sarvak Formation in the Iranian Zagros where the presence of *M. apenninica* is used to infer a Turonian age. These records may be Turonian, but evidence other than the occurrence of *Moncharmontia* (plausibly illustrated by these authors) should be sought. Recent strontium isotope calibrated ages (Mehrabi et al., 2022a, 2022b) are helpful in this respect and suggest that some *M. apenninica* occurrences in the Iranian Zagros are indeed Turonian. Nonetheless, the statement by Omidvar et al. (2014a, 2014b) that *M. apenninica* is an index fossil for ages no older than Turonian in the Iranian Zagros is incorrect. On the other hand, there is little doubt that the *local* inception of *M. apenninica* (for example in the type area of the Italian Apennines) occurs within the Turonian (e.g., Frijia et al., 2015). It may be that as suggested by Schlagintweit & Yazdi-Moghadam (2021) the species arose elsewhere within the Cenomanian and migrated to the Mediterranean region in the Turonian, occupying palaeoecological niches vacant by the Cenomanian/Turonian boundary extinction event. Lack of comprehensive supporting data is an ever-present challenge to LBF biostratigraphy.

The youngest verifiable record of this species is Maastrichtian (Sinanoğlu et al., 2020; Sinanoğlu, 2021, from Turkey). However, such a long range for a single species seems unusual and there may be further study required. On the other hand, *Moncharmontia* may have been very well adapted to the inner platform niche in which it lived, and as a relatively simple form, persisted through environmental perturbations (see also Consorti & Rashidi, 2018, for a similar example in the genus *Elazigina* Sirel across the Cretaceous-Paleogene boundary).

Cenomanian Paleogeographic Distribution

Eastern Neotethys (and ?Caribbean).

There are scattered records of *M. apenninica* from Cenomanian strata around Neotethys. However, the only proven occurrences are from the Turkish Taurides and the Iranian Zagros. Records from Sinai, Oman and south-east Turkey are unproven or of contentious age.

Records in strata younger than Cenomanian are numerous and widespread around Neotethys.

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

Reference Illustration & Description

[Note: also misspelled as *Montcharmontia* in several publications]

Tasli et al. (2006), Fig. 7(J-K) for illustration.

The original comprehensive description of the genus and the two species (*M. apenninica* and *M. compressa*) by De Castro (1966) only states two differences between the species by referring to *M. compressa* as having heart-shaped chambers in axial view and only one row of apertural openings compared with *M. apenninica*. However, the test is also clearly more laterally compressed than *M. apenninica* and has a more subrounded to subangular periphery.

These and other differences between *M. apenninica* and *M. compressa* are tabulated and illustrated by Tešović et al. (2001) and can be summarised by *M. compressa* being smaller (with an equatorial diameter of <0.34mm), more compressed umbilically and with a smaller proloculus (<0.08mm) compared with *M. apenninica*. Test wall thickness is also less in *M. compressa* (<0.012mm). *M. apenninica* has a well-rounded periphery (some specimens can be almost subglobular in overall shape) compared with the somewhat more subangular periphery

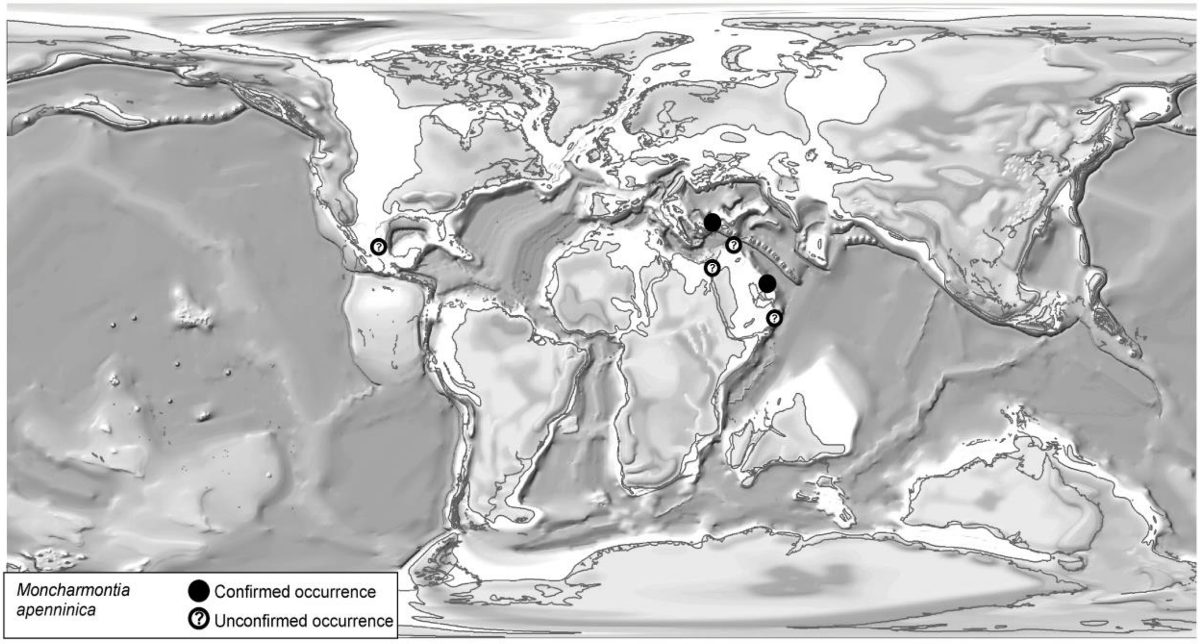


Fig. 26 Cenomanian paleogeographic distribution of *Moncharmontia apenninica*.

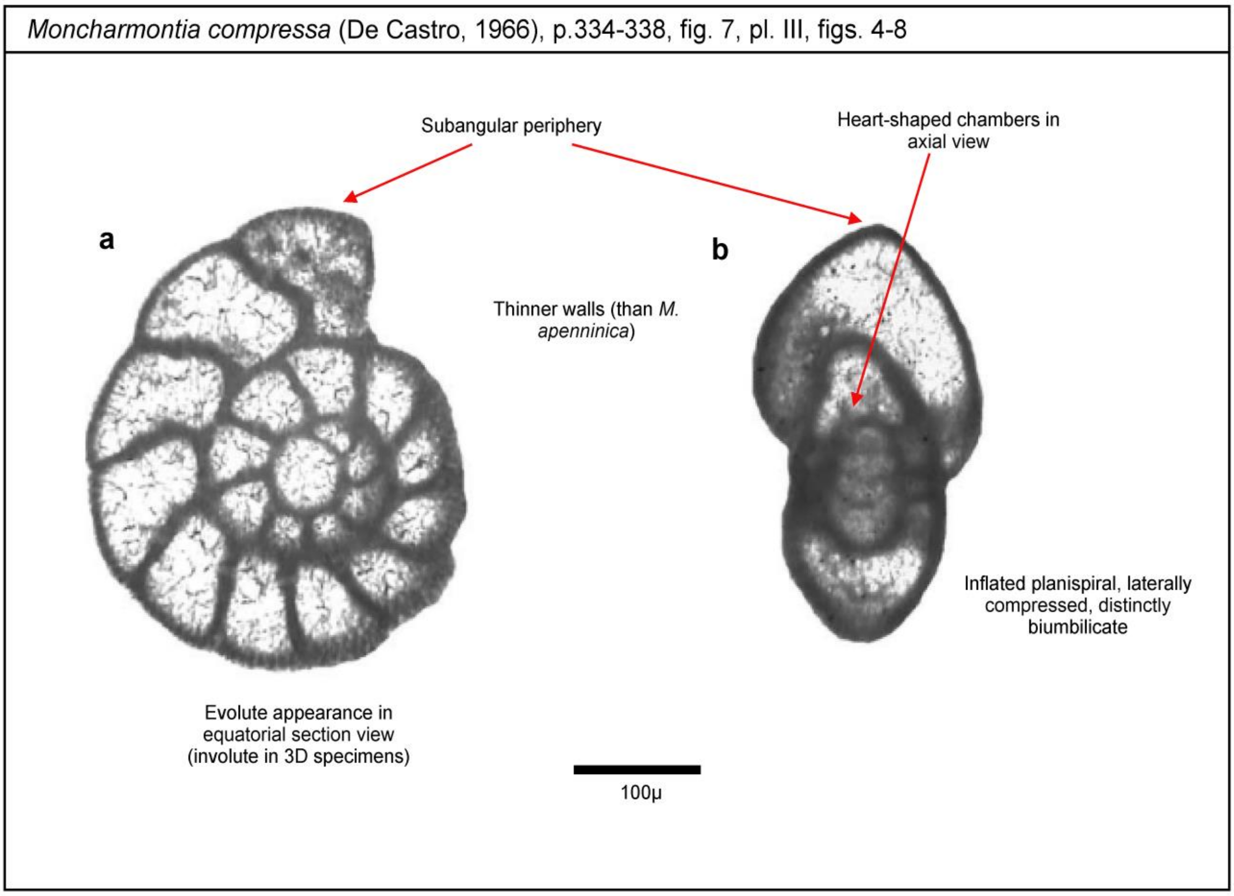


Fig. 27 Representative illustrations of *Moncharmontia compressa*: **a** Equatorial section, Tasli et al. (2006, fig. 7(J), Turkey); **b** Axial section, Tasli et al. (2006, fig. 7(K), Turkey).

(broad lenticular and more obviously biumbilicate) of *M. compressa*. Both species have similar number of chambers in the first (7-8) and second whorls (9-10). See the Species Key Chart (Appendix) for diagnostic and other characteristics.

The records of *Fleuryana adriatica* from the Turonian of SW Turkey by Solak et al. (2020) are virtually indistinguishable from those of *M. compressa* (De Castro). The only taxonomic difference between the two is that *F. adriatica* has a single apertural slit whereas *M. compressa* has a single row of apertural openings. This may be extremely difficult to see in thin section views. *F. adriatica* also ranges to the Maastrichtian and more work needs to be done to establish the degree of separation of these two taxa. Koch et al. (1998) have provided more compelling illustrations of *F. adriatica* from Turonian strata.

Stratigraphic Distribution

Early Cenomanian? – Maastrichtian.

Most plausible and definite illustrated records of *M. compressa* are confined to post-Cenomanian strata, ranging up into the Maastrichtian (Sinanoğlu, 2021, from Turkey). An illustrated form attributed to *M. apenninica* was recorded from the early Cenomanian of Syria (Ghanem et al., 2012) but the illustration has characteristics closer to *M. compressa*. Solak et al. (2017) illustrate a form they describe as "*Moncharmontia*(?) sp." from the mid-late Cenomanian of the Turkish Taurides. From the material illustrated this might be *M. compressa* or *B. bentori.*

Unillustrated records from the Cenomanian include from the Natih Formation of Oman by Piuz & Meister (2013) and Piuz et al. (2014). Berthou & Lauverjat (1979) record a form they term "*Moncharmontia* (?) cf. *apenninica compressa"* from the late Albian of Portugal. However, they provide no illustration.

Cenomanian Paleogeographic Distribution

Probably Eastern Neotethys.

Records of *M. compressa* from Cenomanian strata are all uncertain. The species is more widely and confidently reported from younger stratigraphy.

Cenomanian "cyclamminids"

As throughout much of the Jurassic and Cretaceous, Cenomanian shallow-water carbonate platform sedimentary rocks (including marls) often contain relatively large, planispiral agglutinating foraminifera with alveolar walls. These are included in genera such as *Pseudocyclammina* Yabe & Hanzawa, *Buccicrenata* Loeblich & Tappan, and *Hemicyclammina* Maync, and can informally be termed "cyclamminids", although their higher-level classification continues to be debated (e.g., Mikhalevich 2004a & b; Kaminski, 2014; Albrich et al., 2015 and see above). Despite records of such taxa being known for several decades, there remains uncertainty on the precise identity and taxonomy of some of the genera involved, and a thorough taxonomic revision is required that is outside the scope of this primarily biostratigraphic review.

The genus *Hemicyclammina* has recently been revised by Simmons & Bidgood (2022). That review is summarised herein, with a small amount of additional information that has come to light subsequently. More problematic are *Buccicrenata* and *Pseudocyclammina* and the species assigned to these genera. Further complications are introduced in that it is not always possible to see key features such as the nature of the aperture in random thin-sections, with even the presence of an alveolar wall sometimes being doubtful, especially in coarsely agglutinating specimens. Certainly, there are occurrences of *Pseudocyclammina* and *Buccicrenata* reported in the literature that would be better assigned to the non-alveolar walled genera *Ammobaculites* Cushman or *Lituola* Lamarck. On the other hand, disaggregated, three-dimensional specimens will not show critical internal features.

Genus ***Buccicrenata*** Loeblich & Tappan, 1949

Type Species: *Ammobaculites subgoodlandensis* Vanderpool, 1933

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

Reference Illustration & Description

Loeblich and Tappan (1985) p. 100, pl. 2, figs. 4-10.

Filkorn & Scott (2011) provide a recent review of *Buccicrenata subgoodlandensis* whilst reporting on its occurrence in the Albian of Mexico. The genus *Buccicrenata* was introduced by Loeblich & Tappan (1949) with the type species being *Ammobaculites subgoodlandensis* Vanderpool. The possible alveolar nature of the wall of this species was doubted by Maync (1952, 1955), but mentioned and illustrated by Gohrbandt (1966) for his new species *Buccicrenata libyca*, and eventually proven for *B. subgoodlandensis* by Loeblich & Tappan (1985). However, these authors (see also Loeblich & Tappan, 1988) suggested that the septa were *not* alveolar, an observation that has been contested by Banner & Highton (1990), BouDagher-Fadel (2001) and BouDagher-Fadel et al. (2017). The presence of alveolar septa distinguishes *Buccicrenata* from *Everticyclammina* Redmond. Note that if the septa of *Buccicrenata* are proved to be non-alveolar, it would be the senior synonym of *Everticyclammina,* unless other differences can be identified. Similar to *Pseudocyclammina*, the alveoles in the wall of *Buccicrenata* are broad, can bifurcate, and are widely spaced compared to, for example, *Choffatella* Schlumberger. See the Species Key Chart (Appendix) for diagnostic and other characteristics.

If both the wall and septa are alveolar as seems likely, then the key difference between *Buccicrenata* and *Pseudocyclammina* is the nature of the aperture, which is cribrate in *Pseudocyclammina*, but a single sinuous slit with projections in *Buccicrenata* (Loeblich & Tappan,

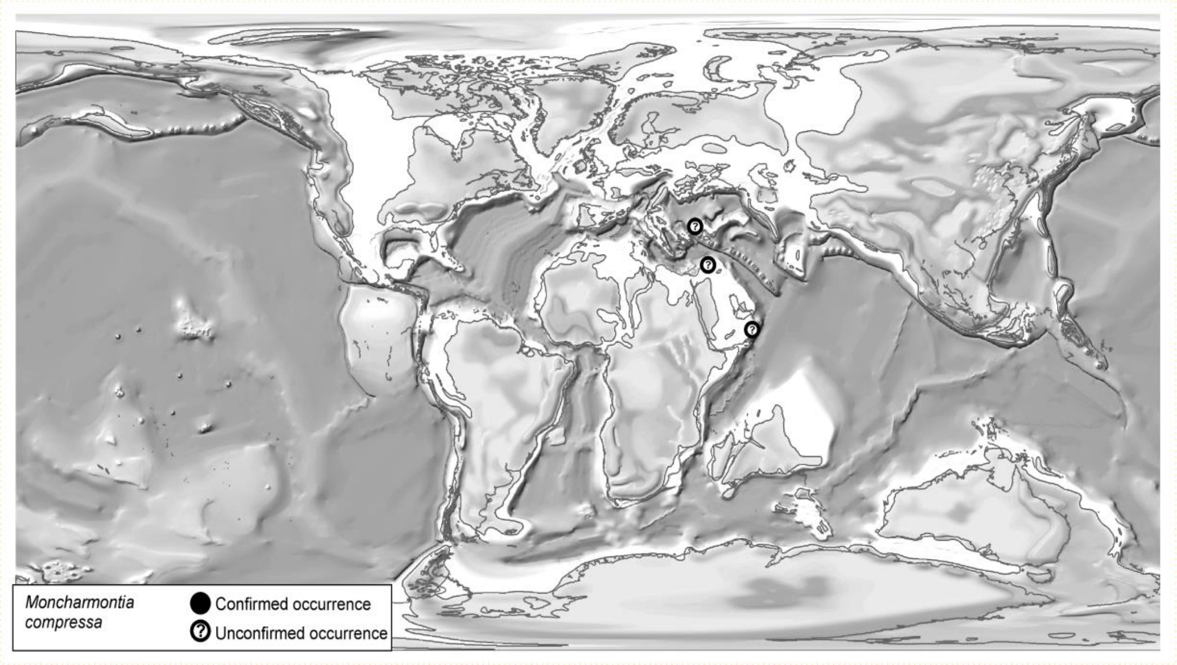


Fig. 28 Cenomanian paleogeographic distribution of *Moncharmontia compressa*.

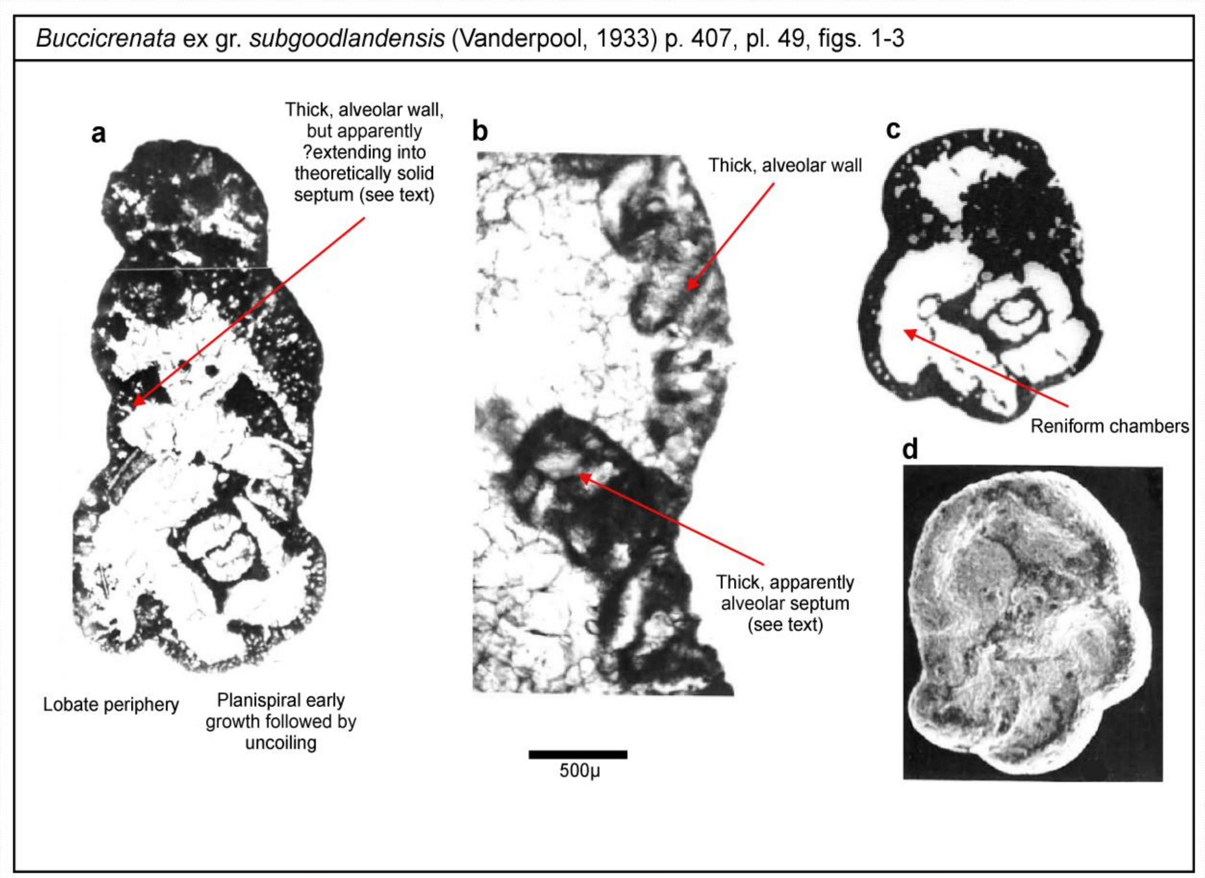


Fig. 29 Representative illustrations of *Buccicrenata* ex gr. *subgoodlandensis*: **a** Uncoiled equatorial section, Loeblich & Tappan (1985, pl. 2, fig. 7, Texas); **b** Close up of section through wall and septum, Loeblich & Tappan (1985, pl. 2, fig. 10, Texas); **c** Equatorial section, Loeblich & Tappan (1985, pl. 2, fig. 5, Texas); **d** External view, Loeblich & Tappan (1985, pl. 2, fig. 9, Texas).

1949). However, this feature is not always clear in thin-sections and BouDagher-Fadel (2001) noted that the sinuous nature of the slit aperture of *Buccicrenata* means that oblique cuts in thin-section can give the impression of multiple apertures being present. This illustrates a general challenge to LBF biostratigraphy in that access to good-quality material in thin section is desirable, but not always possible. Arnaud-Vanneau (1980) suggested that for *Everticyclammina hedbergi* (Maync) (= *Buccicrenata hedbergi*) the aperture varies with generation: a terminal slit in microspheric forms, and occasionally multiple in macrospheric forms. Her illustrations (hand drawn, external views of disaggregated specimens; fig. 178 on page 491) do not confirm this unequivocally but examination of more/better material may help with clarification. However, this somewhat controversial opinion has not been followed-up by subsequent workers. A practical distinction between *Buccicrenata* and *Pseudocyclammina* is the distinctive reniform shape of the chambers in *Buccicrenata* caused by the septa being continuous, smooth outgrowths of the chamber wall. All mid-Cretaceous species of *Buccicrenata* show a distinctive lobate, almost notched profile in equatorial view and can (as can *Pseudocyclammina*) have an uncoiled, rectilinear terminal stage. In *Buccicrenata*, the chambers are rapidly enlarging, whilst in *Pseudocyclammina* the chambers enlarge more slowly.

Three species of *Buccicrenata* have been described from the mid-Cretaceous (see BouDagher-Fadel, 2001 for discussion of older species). These are *B. hedbergi*, *B. subgoodlandensis*, and *B. libyca*. *B. hedbergi* was first described as *Pseudocyclammina hedbergi* by Maync (1953a) from the Aptian-Albian of Venezuela; *B. subgoodlandensis* was first described from Albian strata in Oklahoma, USA (Vanderpool, 1933) with topotypes illustrated and described by Loeblich & Tappan (1949, 1985) (note that in the 1949 publication it is arguable that alongside juvenile forms, more than one adult species is shown given the variations in chamber morphology); and *B. libyca* was first described from Cenomanian strata in Libya (Gohrbandt, 1966). All three species are remarkably similar (Table 2) in dimensions, shape, number of chambers, tendency to uncoil, and nature of the alveolar wall, such that pending detailed taxonomic studies, these species can be considered under the single name "*Buccicrenata* ex. gr. *subgoodlandensis*" when identifying random thin-section material. Indeed, Banner & Highton (1990) suggested that *B. libyca* was a junior synonym of *B. hedbergi*. BouDagher-Fadel (2001) maintained three separate species but noted there were great similarities between them. Of the three species that fall within this grouping, it is *B. hedbergi* that is the most widely reported. Although the nature of the aperture of this species was not reported in its type description (Maync, 1953a), the illustrations presented suggest that it is a single slit and that it should be regarded as a species of *Buccicrenata* as noted by Loeblich & Tappan (1985). There are also records of *Everticyclammina virguliana* (Koechlin) that are in fact *B.* ex. gr. *subgoodlandensis* (e.g., Gušić, 1975).

Stratigraphic Distribution

Early Cretaceous – latest (?) Cenomanian.

The inclusion of *B. hedbergi* forms within the taxonomic grouping here places its inception within the Early Cretaceous (e.g., Simmons & Hart, 1987 – see also for an illustration of *B.* ex. gr. *subgoodlandensis* from the late Albian of the Oman Mountains, and possibly from the Cenomanian as "*Buccicrenata*? *rugosa*"). For the purpose of this Cenomanian stratigraphic review, there are relatively few records under any plausible name, and even fewer with biostratigraphic calibration, meaning that its range within the Cenomanian is difficult to determine. Note that there are records of *P. rugosa* that are in fact *B.* ex. gr. *subgoodlandensis*, as noted herein.

Confirmed illustrated Cenomanian records of *B.* ex. gr. *subgoodlandensis* include the type description of *B. libyca* from Libya (association with *Praealveolina tenuis* Reichel suggests a middle – late Cenomanian age (Calonge et al., 2002); *Pseudocyclammina* cf. *hedbergi* from Libya (Banner, 1966, 1970); *Pseudocyclammina* aff. *hedbergi* from Abu Dhabi (Banner, 1966, 1970); *P. hedbergi* from Jordan (Weidich & Al Harithi, 1990, see also Basha, 1978 for an unillustrated record of *B. subgoodlandensis*); *Buccicrenata* aff. *hedbergi* and possibly *P. rugosa* from Portugal (Andrade, 2018); and *B. hedbergi* from the middle Cenomanian (and older) sediments of north Somalia (Luger, 2018). Also recorded and illustrated as *Pseudocyclammina* cf. *rugosa* from the Cenomanian of the Iranian Zagros (Kalantari, 1976) and Israel (Hamaoui, 1965; Arkin & Hamaoui, 1967); illustrated as *Pseudocyclammina* sp. from south-eastern Turkey (Özkan & Altiner, 2019); and as *P. rugosa* from Serbia (Radoičić, 1974a).

An illustrated record from the Coniacian of Egypt (Ismail & Soliman, 1997) cannot be confirmed as being of this species as the external view is non-diagnostic.

Cenomanian Paleogeographic Distribution

Neotethys.

In addition to the confirmed illustrated records noted above, *B. subgoodlandensis* is said to be abundant in the early Cenomanian of Sinai (Ayyad et al., 1997) but the illustrations are of disaggregated specimens only which precludes confident identification. Reports of *B. libyca* from Sinai and the Gulf of Suez are either not illustrated (El Baz & Khalil, 2019) or illustrated by disaggregated specimens (Shahin & El Baz, 2013, 2021) that are indeterminate. Illustrations of *Pseudocyclammina lituus* Yokoyama and *Pseudocyclammina massiliensis* Maync from the same Cenomanian strata are likely to be misidentifications (they are not typical Cenomanian taxa) and in any case cannot be confirmed from the disaggregated specimens presented. Records of *B. subgoodlandensis* from the Cenomanian without illustration include from Spain (Ramirez del Pozo, 1972). *B. hedbergi* is reported but not illustrated from the early Cenomanian of Jordan

Table 2 Comparative measurements for mid-Cretaceous species of *Buccicrenata* based on type or topotype descriptions and illustrations. Also compare with measurements for *Pseudocyclammina rugosa* (d'Orbigny). Note that measurements are from a very limited number of specimens, and a lack of clarity on microspheric vs macrospheric specimens.

Feature	*B. libyca* Gohrbandt 1966	*B. subgoodlandensis* (Vanderpool, 1933) – data from Loeblich & Tappan (1949, 1985)	*B. hedbergi* (Maync, 1953a) – data also from Maync (1959a)
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

(Schulze et al., 2004) and the Cenomanian of Kuwait (Youssef et al., 2019).

Genus ***Pseudocyclammina*** Yabe & Hanzawa, 1926
Type Species: *Cyclammina lituus* Yokoyama, 1890
***Pseudocyclammina rugosa* (d'Orbigny, 1850)**

Reference Illustration & Description

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

Pseudocyclammina is a well-established genus, occurring throughout the Jurassic and Cretaceous, and well known from its type species, *P. lituus*, which can be common in suitable Late Jurassic and Early Cretaceous facies from a number of locations across Tethys (e.g., Maync, 1959a; Banner, 1970; Kobayashi & Vuks, 2006). The test of *Pseudocyclammina* is typically a subspherical planispire, with relatively thick alveolar walls and septa. There is often an uncoiled stage. The aperture is cribrate (which distinguishes it from *Buccicrenata*). *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.

The typical Cenomanian representative of the genus is *P. rugosa*, that despite illustration by Maync (1952, 1959a) remains poorly known. *Lituola rugosa* was introduced by d'Orbigny (1850) with a very short entry in a list of Cenomanian foraminifera, and there is no illustration. Maync (1952, 1959a) illustrated topotype specimens from the Cenomanian of Charente, France (see also Bou-Dagher-Fadel et al., 2017) and discussed elements of the taxonomy (including his justification for placing the species in *Pseudocyclammina*) and differences with similar taxa.

P. rugosa appears to be relatively large (0.8 – 4.3 mm in external diameter of the coiled whorl according to Maync (1959a) although illustrations in Maync (1952, 1959a) 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 – 1.9, typically 1.4) and 5-7 chambers in the last whorl serve to distinguish it from other species of *Pseudocyclammina* 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*. See the Species Key Chart (Appendix) for diagnostic and other characteristics.

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 (e.g., possibly Esfandyari et al., 2023). This form has new been described as a new species – *Pseudocyclammina sarvakensis* – by Schlagintweit & Yazdi-Moghadam (2023) (see below).

Stratigraphic Distribution

Albian – latest (?) Cenomanian.

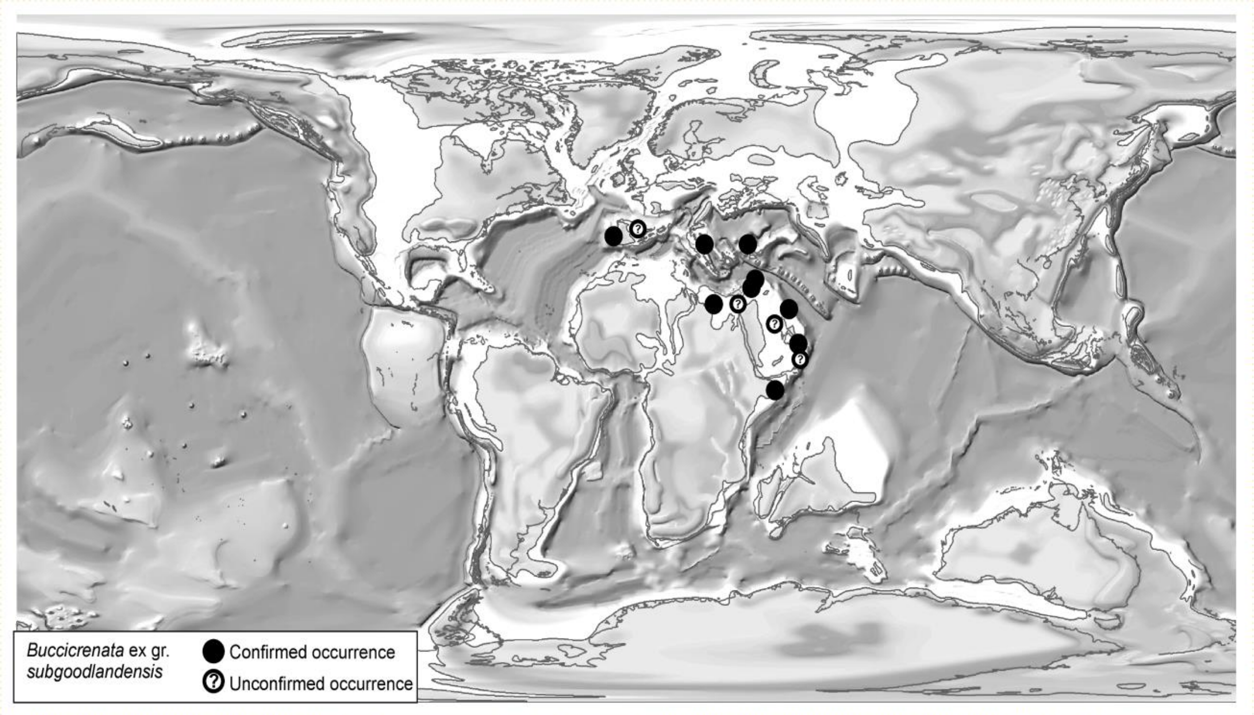


Fig. 30 Cenomanian paleogeographic distribution of *Buccicrenata* ex gr. *subgoodlandensis*.

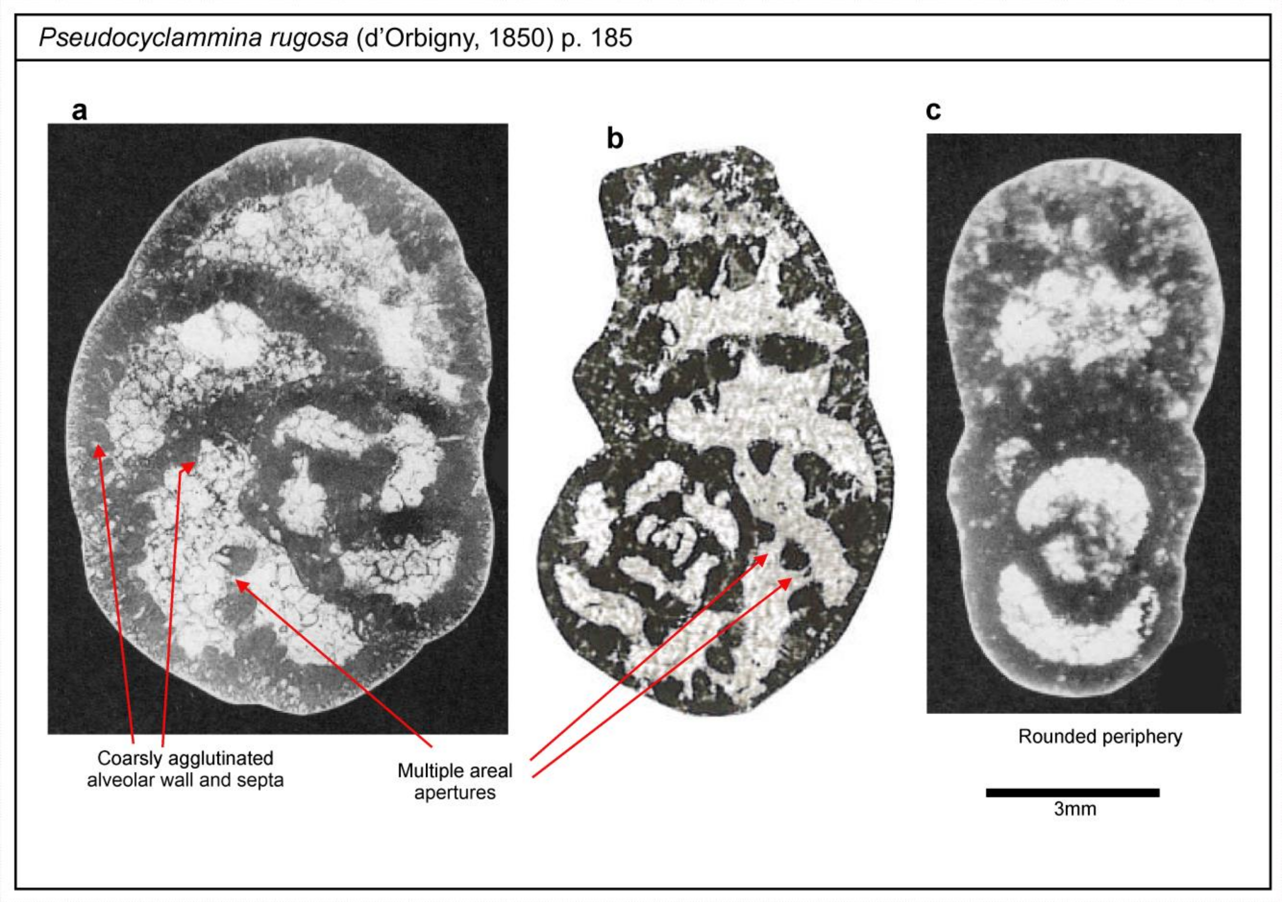


Fig. 31 Representative illustrations of *Pseudocyclammina rugosa*: a Equatorial section, Maync (1952, pl. 12, fig. 9, France); **b** Equatorial section of uncoiled specimen, Maync (1959b, pl. 1, fig. 14, France); **c** Axial section, Maync (1952, pl. 12, fig. 8, France).

Neumann et al. (1974) indicated that at its type locality, the species has a middle – late Cenomanian range. Rey et al. (1977) and Saint-Marc (1981) 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. Its stratigraphic range may be confused by misidentification of, for example, *Buccicrenata* ex gr. *subgoodlandensis*.

Regarding its distribution within the Cenomanian, Bilotte (1973, 1985) illustrated plausible specimens from the Pyrenees and indicated that the species ranges throughout the Albian and Cenomanian in that region. Simmons et al. (2020b) illustrated a probable specimen of *P. rugosa* from the middle Cenomanian of south-east Turkey. However, a single axial specimen precludes confident identification.

The Cenomanian record of Kalantari (1976) is of *B.* ex. gr. *subgoodlandensis*, likewise the Albian record from the Zagros of Sampò (1969). Illustrated records from the late Cenomanian of Mexico (Aguilera-Franco, 2003; Omaña et al., 2013) are most likely of *Ammobaculites* sp. (see also unillustrated record by Aguilera-Franco et al., 2001). Some illustrated records from the Cenomanian of Portugal (Berthou, 1973; Boavida, 2013; Andrade, 2018), appear to be more compatible with *B.* ex. gr. *subgoodlandensi*s or cannot be confirmed as *P. rugosa*. Illustrated records from the Late Cenomanian of Morocco (Ettachfini, 1993, 2006; Ettachfini & Andreu, 2004) appear to be of *Ammobaculites*/*Lituola* sp., *B.* ex. gr. *subgoodlandensis*, or are indeterminate.

A form named as *Pseudocyclammina* cf. *rugosa* from the Cenomanian of Tunisia (Bismuth et al., 1967) is small and its identity unclear (see also Bismuth et al., 1981 for an unillustrated record). Likewise, the records of relatively small "*P. rugosa"* from the Cenomanian of Armenia (Danelian et al., 2014).

Illustrated records from the Aptian or older (e.g., Kalantari, 1976; Afghah & Haghighi, 2014 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., 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.

Cenomanian Paleogeographic 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. It has been described without illustration from the Albian – top Cenomanian of Lebanon (Saint-Marc, 1970, 1974a, 1980, 1981); the early Cenomanian of the Dinarides (Velić, 2007); the middle and late Cenomanian of Tunisia (Abdallah et al., 1995; Touir et al., 2017); the middle – late Cenomanian of southern Iraq (Al-Dulaimy et al., 2022); the Sarvak Formation of the Iranian Zagros (Omidvar et al., 2014a, b; Assadi et al., 2016; Navidtalab et al., 2020; Ashgari et al., 2022); Provence (Babinot et al., 1988); early Albian – top Cenomanian of Portugal (Rey et al., 1977; Berthou & Schroeder, 1978; Berthou & Lauverjat, 1979; Crosaz-Galletti, 1979; Rey, 1979); Aquitaine (Deloffre & Hamaoui, 1979); Syria (Mouty et al., 2003); and Kuwait (El-Naggar & Al-Rifaiy, 1973). An illustration from the Cenomanian of Greece is unclear (Decrouez, 1978). A specimen illustrated as "*Buccicrenata*? *rugosa*" from the early Cenomanian of the Oman Mountains (Simmons & Hart, 1987) is not clearly this species (it may be *Buccicrenata* ex. grp. *subgoodlandensis*), whilst unillustrated *P. rugosa* has been mentioned from the late Cenomanian of the Oman Mountains (Rabu, 1993).

Pseudocyclammina sarvakensis **Schlagintweit & Yazdi-Moghadam, 2023**

Reference Illustration & Description

Schlagintweit & Yazdi-Moghadam (2023), Fig. 4a-g, p. 7.

A very recently described new species from the Sarvak Formation of the Iranian Zagros, *P. sarvakensis* is distinguished from all previously described *Pseudocyclammina* species by the relatively larger number of chambers (14-16) in the final whorl. It has been sometimes conflated with *P. rugosa* in the Cenomanian literature (the only other Cenomanian pseudocyclamminid), but Schlagintweit & Yazdi-Moghadam's (2023) illustrated, and newly-described material provides clear reason for separation. It is also smaller than *P. rugosa* (max diameter 1.35mm cf. 3.1-3.8mm) and no specimen of *P. sarvakensis* has so far been observed to uncoil. See the Species Key Chart (Appendix) for diagnostic and other characteristics.

These authors consider occurrences recorded elsewhere in the Iranian Zagros by Sampò (1969) (as *Cyclammina* sp.), and by Omidi et al. (2018) and Esfandyari et al. (2023) (as *P. rugosa*) to be *P. sarvakensis*.

Stratigraphic Distribution

Middle - late Cenomanian.

Schlagintweit & Yazdi-Moghadam (2023) recorded *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* see above) come from the mid – upper parts of their Cenomanian interval. Esfandyari et al. (2023) recorded *P. rugose* (sic) (= *P. sarvakensis* see above) from the Sarvak Formation but with no age indication given.

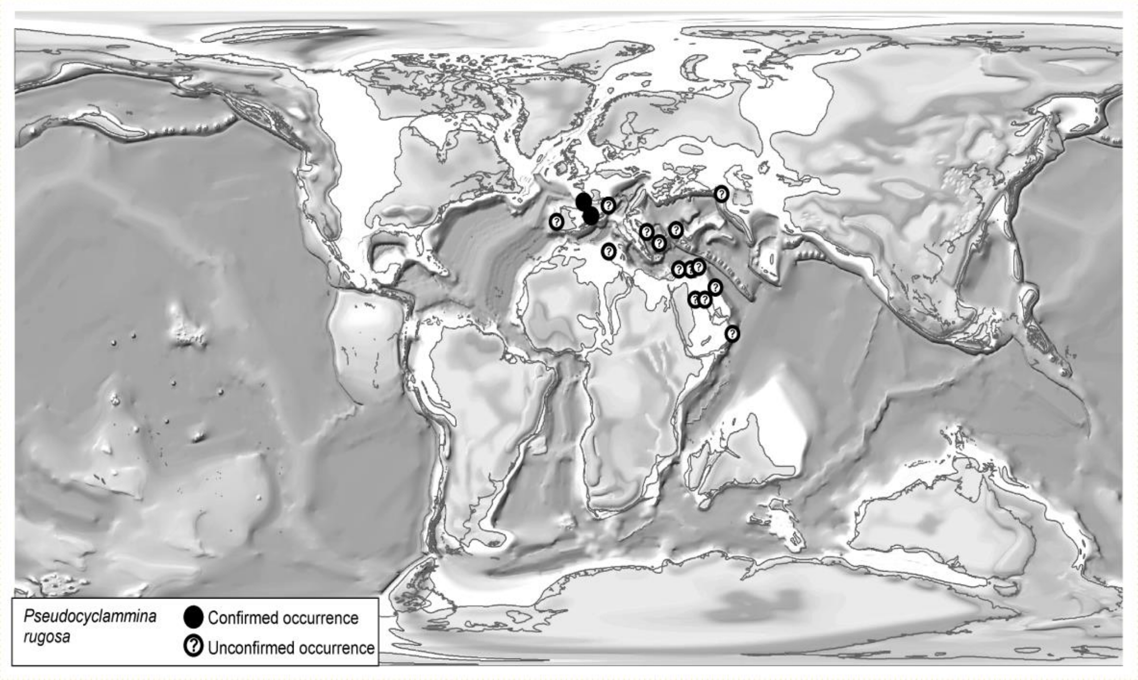


Fig. 32 Cenomanian paleogeographic distribution of *Pseudocyclammina rugosa*.

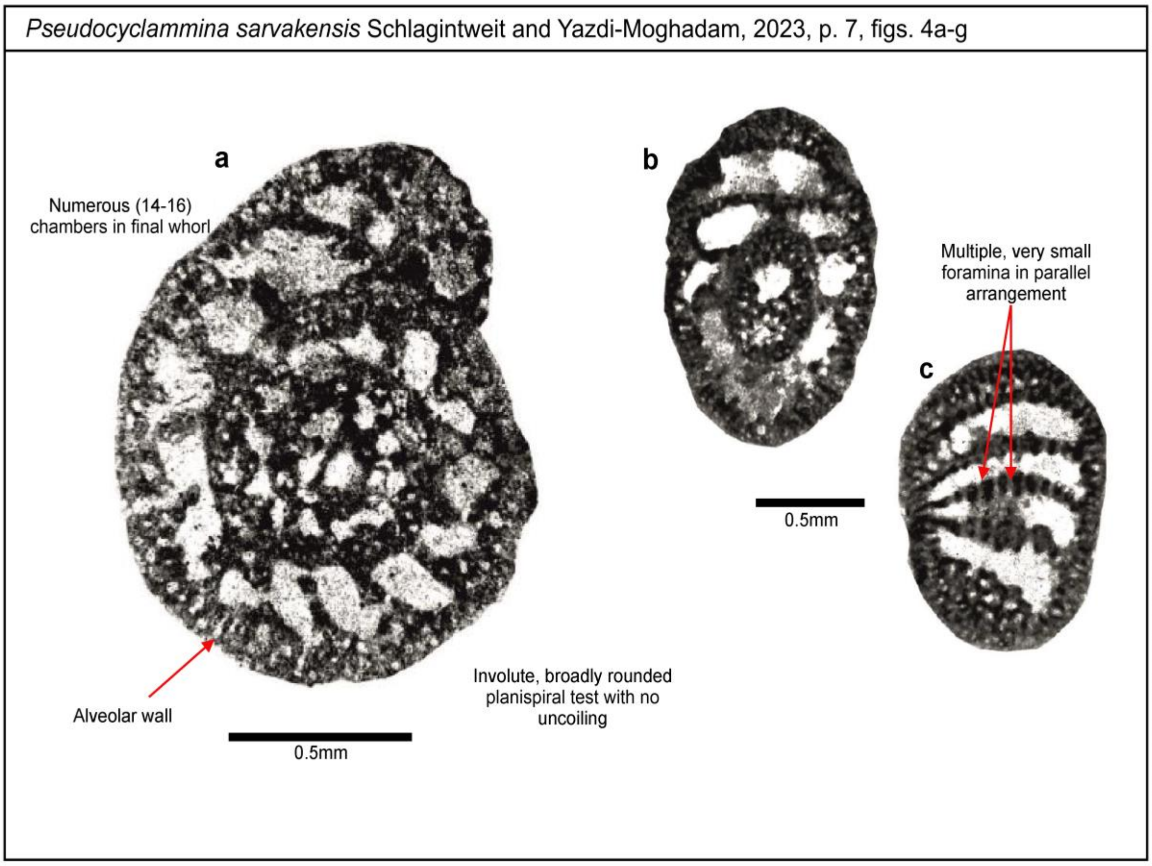


Fig. 33 Representative illustrations of *Pseudocyclammina sarvakensis*: **a** Equatorial section, Schlagintweit & Yazdi-Moghadam (2023, fig. 4b, Iran, holotype); **b** Subaxial section, Ibid. (2023, fig. 4d, Iran); **c** Oblique tangential section, Ibid. (2023, fig. 4f, Iran). Not scale bar change for figs. b & c.

Cenomanian Paleogeographic Distribution

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

Genus ***Hemicyclammina*** Maync 1953b
Type species *Cyclammina whitei* Henson 1948 (= *Hemicyclammina sigali* Maync 1953b)
***Hemicyclammina whitei* (Henson, 1948)**

Reference Illustration & Description

Simmons & Bidgood (2022) p. 27-30, figs. 1-4.
The status of *H. whitei* with respect to its senior synonymy with *H. sigali* Maync and a number of other taxa have been discussed by Simmons & Bidgood (2022). They noted that when Maync (1953b) introduced the genus *Hemicyclammina*, he was seemingly unaware of the publication of Henson (1948) that introduced "*Cyclammina whitei*". Examination of type and associated material indicates that this species is identical to *H. sigali* and thus should be regarded as the type species of the genus. See the Species Key Chart (Appendix) for diagnostic and other characteristics.
The alveolar nature of the wall but with solid, pointed septa which do not reach the previous whorl in equatorial section is characteristic. The solid ("semi-" or "hemi-") septa serve to distinguish the genus from *Buccicrenata* with 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*. *Everticyclammina* Redmond (Late Jurassic – Early Cretaceous) is very similar in almost every respect, but its aperture is areal rather than extending upwards from the base as in *Hemicyclammina* and which is also rather large, resulting in shorter septa. The poorly known genus *Alveocyclammina* Hillebrandt from the lower Albian of Peru (Hillebrandt, 1971) is also similar possessing an alveolar wall, but its septa are also alveolar and appear to be very short.
The following poorly known taxa are considered by Simmons & Bidgood (2022) to be probable synonyms of *H. whitei*: *Hemicyclammina evoluta* Hamaoui, *Ismailia neumannae* El-Dakkak, and *Sinainella aegyptiaca* El-Dakkak. *I. neumannae* continues to be a name used in the Egyptian literature for specimens that might be *H. whitei*, although with external views that are not diagnostic (e.g., Shahin & El Baz, 2021). A specimen illustrated from the late Cenomanian of Egypt as *Charentia cuvillieri* Neumann by El-Sheikh and Hewaidy (1998) looks close to *H. whitei*.
Charentia hasaensis Basha, *Charentia rummanensis* Basha and *Lituola hasaensis* Basha are poorly known species introduced from material from the late Cenomanian of Jordan (Basha, 1978). From the limited illustrations they may be partly synonymous with *H. whitei*. The type material needs to be re-examined. The same author reports but does not illustrate *C. cuvillieri* from the same rocks as his new species and he also reports the occurrence of *H. sigali* and *H. whitei*, but without illustration. Likewise, *Charentia granulosa* Kerdany & Eissa, described from the late Cenomanian of Egypt (Kerdany et al., 1973), may include *H. whitei* amongst its types.
Dimitrova (1995) described "*Pseudonummoloculina* sp." from the Cenomanian of Bulgaria and compared it to *P. aurigerica*. However, her illustration appears to have closer affinity to *H. whitei*.

Stratigraphic Distribution

Early Albian – intra-Late Cenomanian.
Simmons & Bidgood (2022) have reviewed the stratigraphic distribution of *H. whitei* and its common synonym *H. sigali*. *H. whitei* was first described (Henson, 1948) from the Dukhan-3 well in Qatar at a depth of 3542-3543'. Although said to be "probably early Cenomanian", this depth equates to the Mauddud/Nahr Umr Formation boundary and is of latest Albian age (Bromhead et al., 2022). Henson (1948) also recorded the species from the Nahr Umr Formation at Rumaila-1 in Iraq, suggestive of an Albian age (Aqrawi et al., 2010). The type material of *H. sigali* is from the middle Cenomanian of Algeria (Maync, 1953b).
Records commonly show a general composited Albian-Cenomanian age range. See, for example: Ansary et al. (1962); Wynd (1965); Sampò (1969); Kalantari (1992); Shirazi (2009); Shirazi et al. (2011); Omidvar et al. (2014a, b) from the Iranian Zagros; Saint-Marc (1970, 1974a, 1981) from Lebanon; Simmons & Hart (1987), Forbes et al. (2010) from Oman; and general summaries by Saint-Marc (1977); Sartorio & Venturini (1988), and Schroeder et al. (2010). Statements that the species does not range above the Albian (e.g., Afghah & Dookh, 2014) should be discounted at both a local and inter-regional level.
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 planktonic foraminifera *Helvetoglobotruncana praehelvetica* (Trujillo) and *Whiteinella* spp. These records confer an upper range age limit of intra-late Cenomanian.
Pre-Albian records of the species are believed to be of a potentially ancestral form ("*Hemicyclammina*? sp.") and include those of Hosseini et al. (2016) who illustrate material under the name *H. sigali* from the Barremian Gadvan Formation of the Iranian Zagros. However, the specimens are very small (0.2 – 0.3 mm in diameter), and the presence of an alveolar wall is not demonstrated.

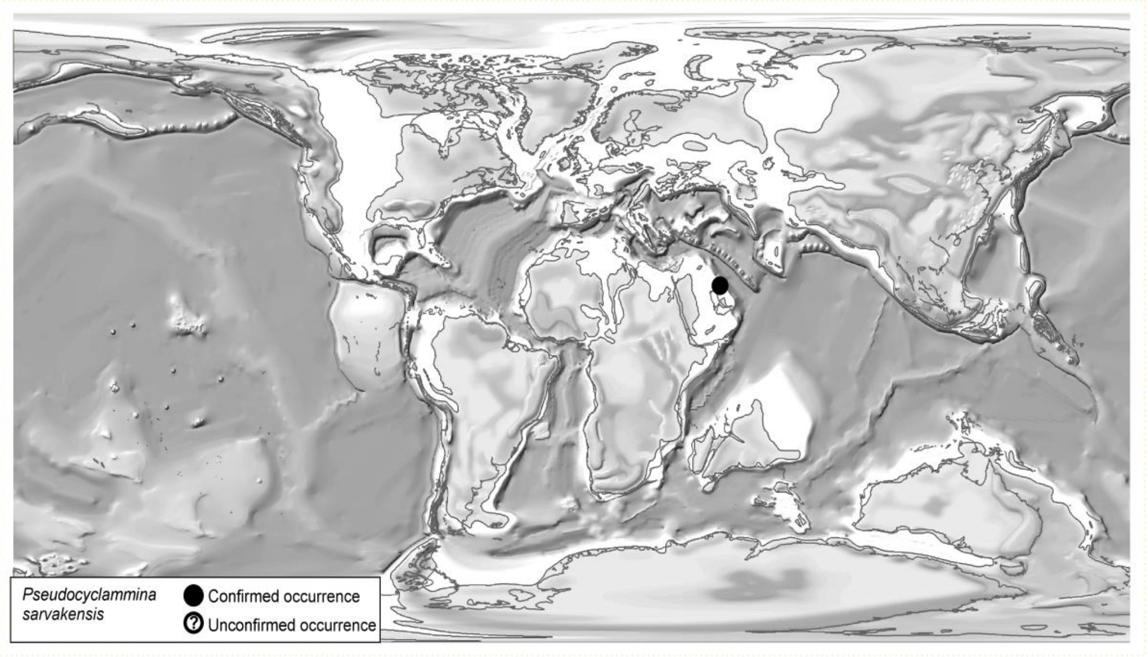


Fig. 34 Cenomanian paleogeographic distribution of *Pseudocyclammina sarvakensis.*

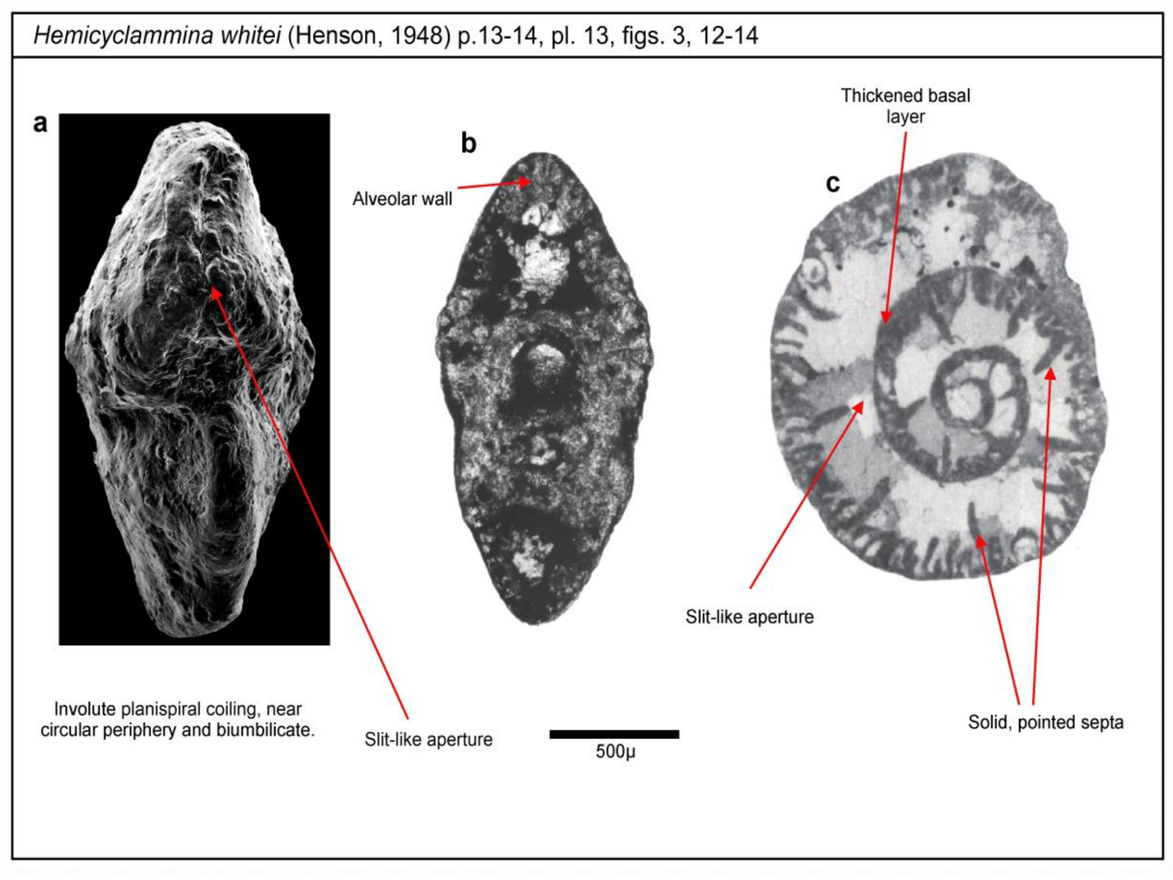


Fig. 35 Representative illustrations of *Hemicyclammina whitei*: **a** Axial view, Whittaker et al. (1998, pl. 12, fig. 1a, Qatar - see also Simmons & Bidgood, 2022, fig. 1a); **b** Axial section, Whittaker et al. (1998, pl. 59, fig. 8, U.A.E. - see also Simmons & Bidgood, 2022, fig. 3c); **c** Equatorial section, Simmons & Bidgood (2022, fig. 3a, Abu Dhabi).

A similar, slight larger (0.3 mm diameter) specimen has been illustrated by Özkan and Altiner (2019) from the early Aptian of south-east Turkey as "*Hemicyclammina*? sp.".

Cenomanian Paleogeographic Distribution

Broadly across Neotethys, the Atlantic and the Caribbean. *H. whitei* has a broad palaeogeographic distribution across Neotethys and seemed to thrive in marly sediments deposited on middle – outer shelves. Confirmed records in addition to those previously mentioned above include from Brazil (Berthou & Bengtson, 1988); Mexico (Omaña et al., 2019); Morocco (Andreu et al., 1996); Turkey (Bignot & Poisson, 1974); Jordan (Weidich & Al-Harithi, 1990); Saudi Arabia (Dr. Wyn Hughes, pers. comm., 2022); Abu Dhabi (Banner, 1970), and Somalia (Luger, 2018). Unillustrated records are known from numerous intermediate locations (Pyrenees – Peybernès, 1984; Tunisia – Robaszynski et al., 2010; Libya – Megerisi & Mamgain, 1980; Italy – Simone et al., 2012; Croatia – Husinec et al., 2000; Serbia – Radoičić and Schlagintweit, 2007; Kuwait – Youssef et al., 2019), and possibly Tibet (BouDagher-Fadel et al., 2017).

Genus ***Reissella*** Hamaoui, 1963
Type Species: *Reissella ramonensis* Hamaoui, 1963
***Reissella ramonensis* Hamaoui, 1963**

Reference Illustration & Description

Hamaoui (1963), p. 62-64, pl. 1 (1-13), fig. 1.
This is a small but internally complex species with a taxonomically uncertain status. It is planispiral becoming flaring (to "peneropliform"), with chambers incompletely divided internally by (1) primary and (2) secondary "vertical subepidermal partitions" and (3) "horizontal partitions" (respectively (1) "beams", (2) "intercalary beams" and (3) "rafters" *sensu* Loeblich & Tappan 1985 and Hottinger 2006) which continue between septa. These form an internal mesh described by Hamaoui, 1963, as a "regular, pigeon-hole (honey-comb) pattern", apparently following the terminology used by Henson (1948).

The main aperture in *Reissella* is basal in the apertural face in earlier chambers and progresses to the middle of the face in later chambers where it is projected on a short neck. It is surrounded by numerous, smaller, supplementary apertures. See the Species Key Chart (Appendix) for diagnostic and other characteristics.

A "subepidermal pigeon-hole" pattern is now referred to as a "polygonal subepidermal network" and is a feature not observed in living foraminifera (Hottinger 2006). Hottinger goes on to state that…

"*The extremely thin, often transparent epiderm in agglutinated foraminifera suggests, that the polygonal network is a device to keep symbionts exposed to light and in the immediate vicinity of the location where gas exchange through the shell should be enhanced by particular, porous textures.*"

This may be the case for larger agglutinated foraminifera such as the orbitolinids. However, the small overall size of this species (<1mm) suggests that these are perhaps not cells for photosymbionts in which case their exact function is unknown. The primary partitions do not reach the middle of the chamber and the secondary and horizontal partitions are even more limited to the marginal area.

Although regarded as agglutinated and classified accordingly (Loeblich & Tappan 1988, Mikhalevich 2004b; Kaminski, 2004, 2014) there remains questions about the exact nature of the wall of *Reissella* and that it may have "possibly" originally been porcelaneous (Hamaoui, 1963). This would place *Reissella* in the Soritids (i.e., "probably the Peneroplidae" according to Hamaoui 1963). However, Hamaoui (1963) also states that the main areal aperture surrounded by supplementary apertures, and the presence of secondary radial subepidermal horizontal partitions (which are parallel to the septa) would be considered unusual features for a Peneropolid and was more typically "lituolid" following the concept of the latter by Smout (1963). Nevertheless, examination of the type illustrations in Hamaoui (1963) cannot remove a suspicion that *Reissella* is a soritid although its general similarity with the soritid *Pseudorhipidionina casertana* (see below) is perhaps superficial. The higher taxonomic classification of this taxon (Family level and above) remains an enigma.

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*. However, *P. casertana* and *R. ramonensis* are also remarked upon regarding their similarities in stratigraphic and ecological distribution (De Castro, 1981).

In the original description (Hamaoui 1963) no thin-section examples are shown with only light-microscope photographs and schematic drawings provided. The form illustrated in thin-section as *R. ramonensis* by Hamaoui & Saint-Marc (1970: pl. 40, fig. 8) from the late Cenomanian of Lebanon strangely does not appear to conform to the concept of the original description and lacks the "peneropolid-like" appearance. It appears to tend towards the concept of *P. casertana*. In other illustrations by Hamaoui (1966), De Castro (1981) notes that one illustration (pl. 3, fig. 6) looks very similar to *P. casertana*.

In summary, considering morphological, stratigraphic and ecological similarities, the taxonomic relationship between *Reissella ramonensis* Hamaoui (1963) and *Pseudorhipidionina casertana* (De Castro 1965) may be synonymous in which case the former name would take priority. However, there are subtle differences although such differences may not be easy to determine except in good

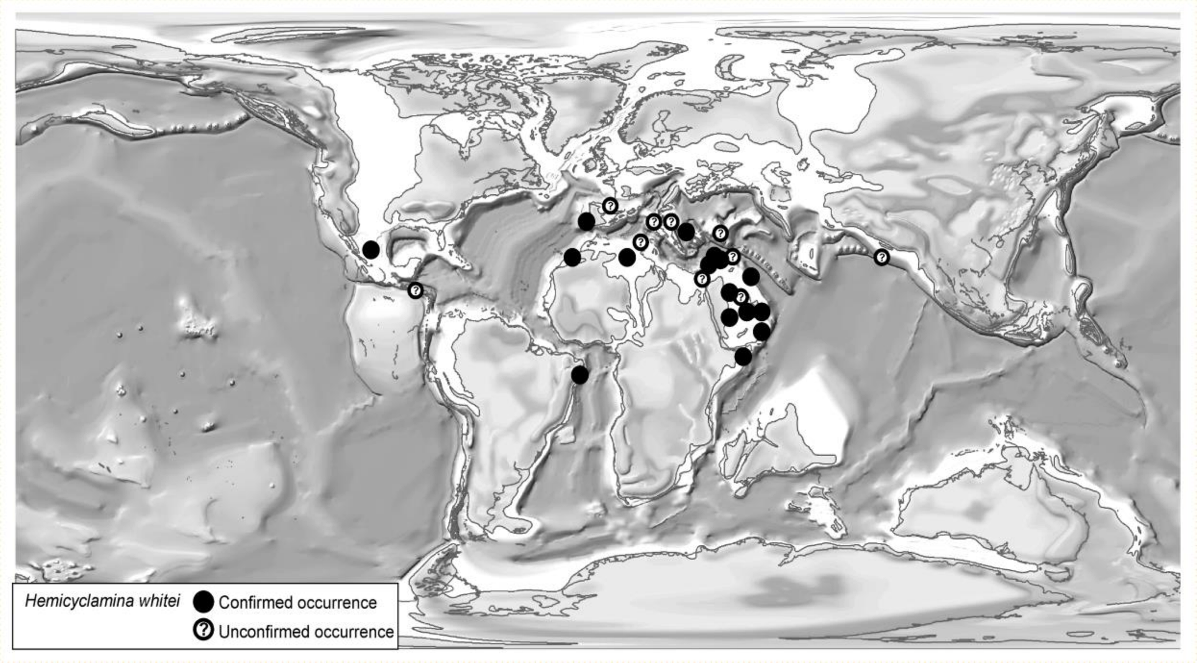


Fig. 36 Cenomanian paleogeographic distribution of *Hemicyclammina whitei*.

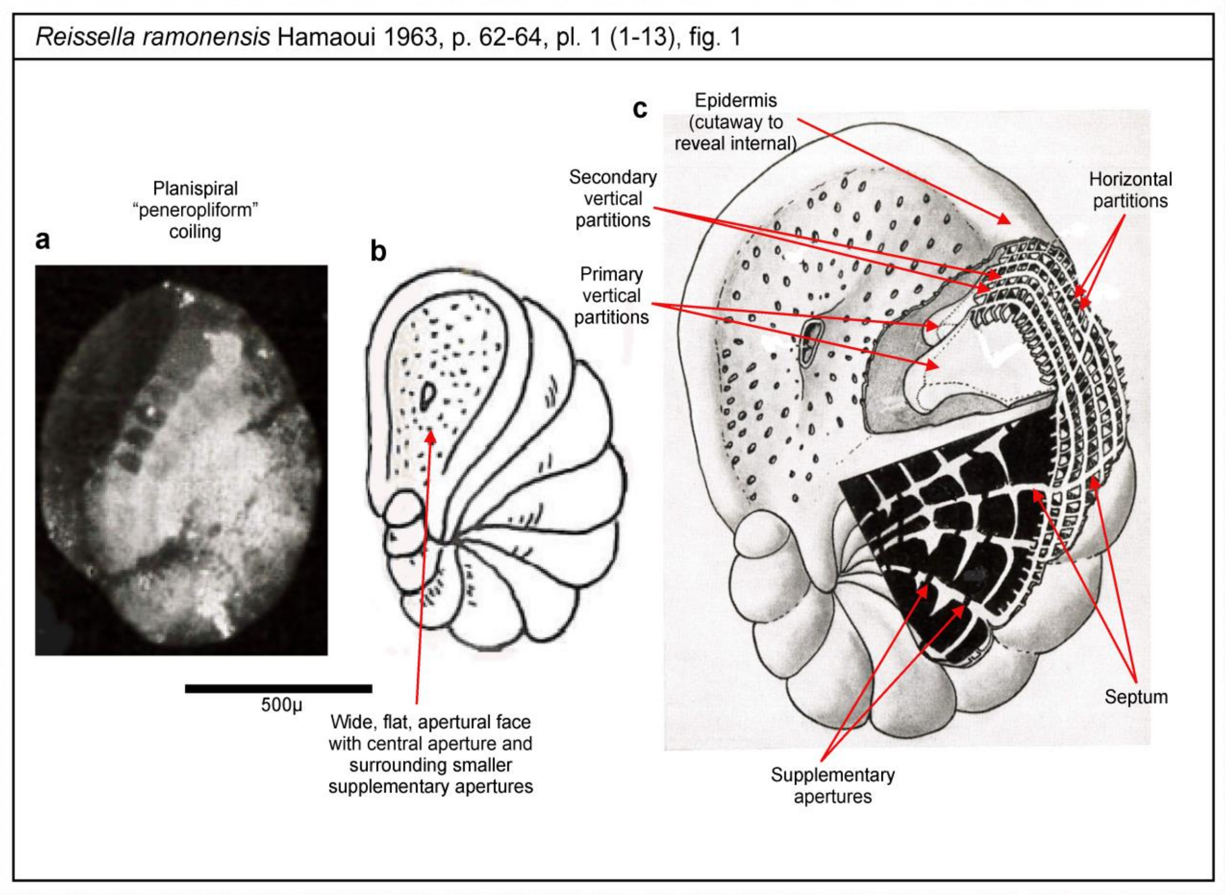


Fig. 37 Representative illustrations of *Reissella ramonensis*: **a** Exterior view, (Hamaoui 1963, pl. 1, fig. 3, holotype, Israel); **b** Exterior view (schematic), (Hamaoui 1963, pl. 1, fig. 11, Israel); **c** Enlarged cutaway exterior view showing internal features (Hamaoui 1963, text fig. 1, Israel).

quality thin-section examples. The two taxa may be micro- and macro-spheric forms of the same species. On the other hand, the differences in wall composition (if confirmed and maintained) indicates clear taxonomic separation with *R. ramonensis* being the agglutinated isomorph of *P. casertana* (the position tentatively adopted here).

Stratigraphic Distribution

Late Cenomanian.

Hamaoui's original description from Israel (Hamaoui 1963) indicates his specimens were recorded from unnamed clays of the Judea Limestone Group, dated as late Cenomanian based on associated microfaunas. Arkin and Hamaoui (1967) confirmed an approximate late Cenomanian age.

It was subsequently reported (though poorly illustrated) by Hamaoui (1965) from the Hazera Formation of Israel. Lipson-Benitah (2009) reported this as "in association with" the planktonic foraminifera *Helvetoglobotruncana helvetica* (Bolli) which – she stated – therefore conferred a middle Turonian youngest age for *R. ramonensis*. However, the only occurrences of *R. ramonensis positively* identified by Hamaoui were recorded below the lowest occurrence of *H. helvetica*. It is also possible that Hamaoui (1965) was using an outdated concept of *H. helvetica* and may have in fact recorded *H. praehelvetica* which ranges down into the late Cenomanian.

"*Reissella* sp" was described from the Albian of Turkey by Solak et al. (2021). This might be ancestral to *R. ramonensis* or the *Pseudorhipidionina* group.

Cenomanian Paleogeographic Distribution

Central Neotethys.

Limited distribution, confirmed by illustration from Israel and unconfirmed from undifferentiated Cenomanian – Turonian strata of Crete by Leppig (1976).

Genus ***Spirocyclina*** Munier-Chalmas, 1887

Type Species: *Spirocyclina choffati* Munier-Chalmas, 1887

***Spirocyclina atlasica* Saint-Marc & Rahhali, 1982**

Reference Illustration & Description

Saint-Marc & Rahhali (1982), p. 134-136, pls. 1-2.

The genus *Spirocyclina* has a rather scattered stratigraphic distribution from the Late Jurassic (Kimmeridgian) to the Late Cretaceous (Santonian) (see Maync, 1959b, for a review up to that date and an emended redescription of the type species and the genus). However, it had not been recorded from the Cenomanian (and the mid-Cretaceous as a whole) until Saint-Marc & Rahhali (1982) described a new species, *S. atlasica*, from the Late Cenomanian of the Moroccan Atlas.

It is assigned to the Spirocyclinidae (Loeblich & Tappan, 1988; Kaminski, 2014) together with *Reissella* and others. Saint-Marc & Rahhali's figures (1982) show a form about 1.4mm across which is a symmetrically flattened planispiral, but which uncoils in a distinctly, almost dramatically, peneropliform style. The generic characteristic of a double row of pores in the apertural face (which can increase to three rows in the later/final stage) is visible in suitably oriented thin-section. See the Species Key Chart (Appendix) for diagnostic and other characteristics.

Saint-Marc & Rahhali (1982) remark on the similarity between *Spirocyclina* and the Late Cretaceous genus *Sornayina* Marie. The latter genus forms a slightly more asymmetrical planispiral, has a lesser tendency to uncoil, and has a more randomly scattered cribrate aperture and a much more acute periphery.

Reissella ramonensis differs in not being as flattened as *S. atlasica*. It also has a single main aperture with smaller secondary pores scattered across the apertural face, rather than two rows of openings.

Stratigraphic Distribution

Late Cenomanian.

Saint-Marc & Rahhali (1982) recorded *S. atlasica* from the late Cenomanian of Morocco. Further illustrated late Cenomanian Moroccan records are provided by Ettachfini (1993, 2006); Charrière et al. (1998), and Ettachfini et al. (2005), along with unillustrated records (e.g., Ciszak et al., 1999).

The record of *Spirocyclina* sp. from the late Cenomanian of SE France by Rineau et al. (2021) appears to be better referred to *Pseudorhapydionina dubia*.

Cenomanian Paleogeographic Distribution

North Africa.

In addition to the records from various parts of Morocco discussed above, the species is plausibly illustrated from Libya (Dufaure et al., 1984) where its presence is used to infer a late Cenomanian age for the strata it occurs in.

Cenomanian 'nummoloculinids'

Of all the taxa discussed in this review, the 'nummolculinids' exemplify the issues to be overcome in establishing an understanding of stratigraphic and palaeogeographic distribution of taxa. The identity of species is uncertain or disputed, names have been used as "buckets", no matter if material is sufficent for identification, or, more often, if it is not. This was recognised by Radoičić (1978), and more recently by Schlagintweit (2008) and Piuz & Vicedo (2020). Of the 150 or so papers that we know of that mention Cenomanian 'nummoloculinids', the majority lack illustration to confirm identification, notwithstanding the difficulties in doing so. The inevitable end-result is a smearing of ranges. Furthermore, single random sections of nummoloulinds may be confused with other taxa that show some broad similarities in coiling mode (and vice versa).

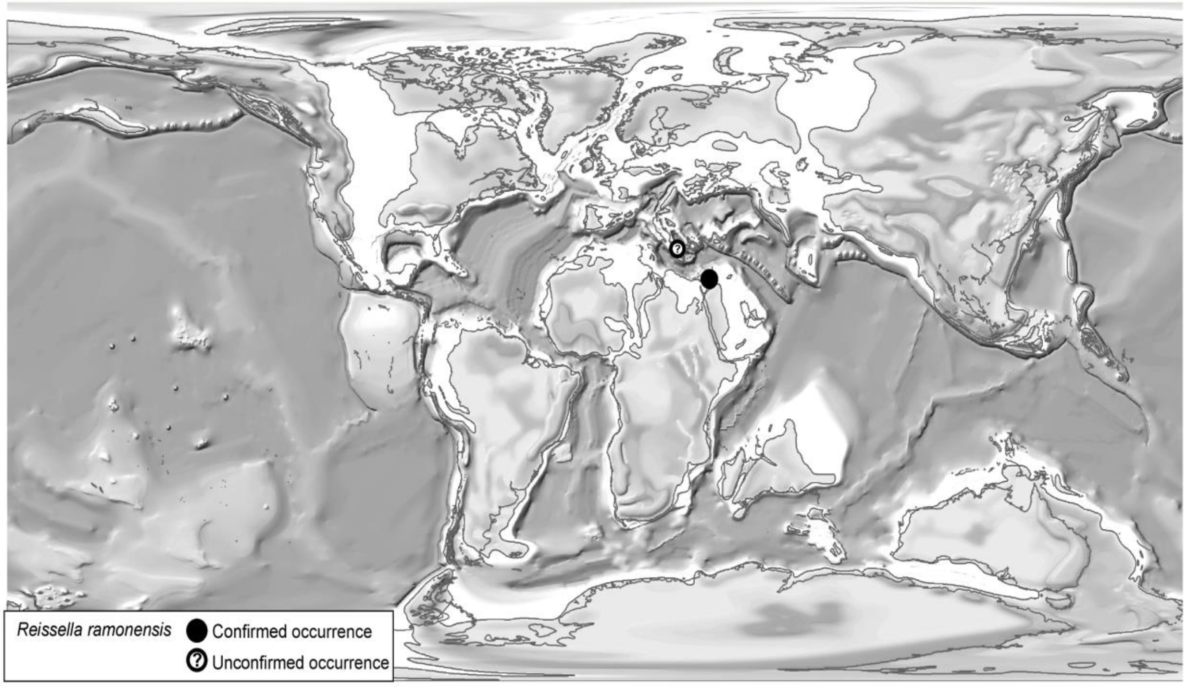


Fig. 38 Cenomanian paleogeographic distribution of *Reissella ramonensis.*

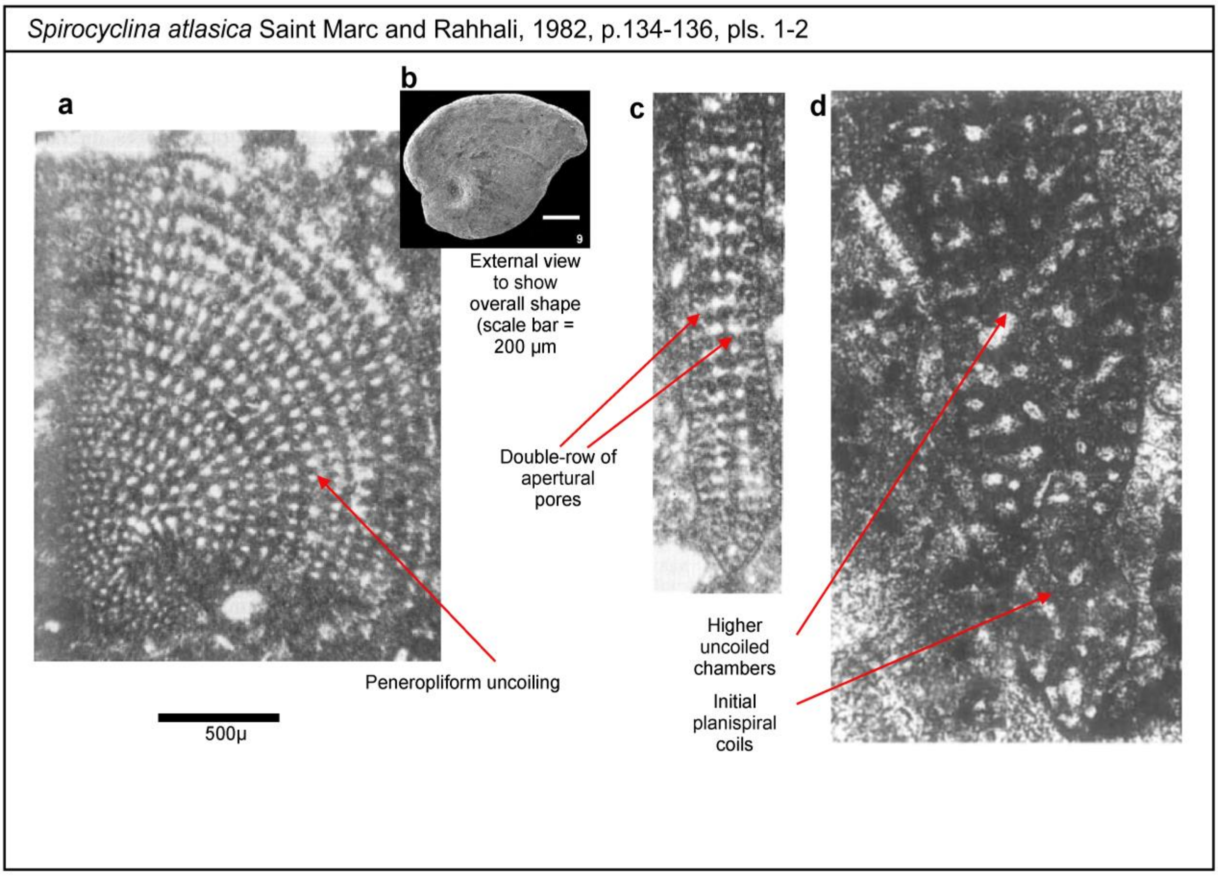


Fig. 39 Representative illustrations of *Spirocyclina atlasica*: a Equatorial section, Saint Marc and Rahhali (1982, pl. 2, fig. 1, Morocco); **b** External View, Etachfini (2006, pl. 13, fig. 9, Morocco); **c** Subaxial section, Saint Marc and Rahhali (1982, pl. 2, fig. 8, Morocco); **d** Axial section, Charriere et al. (1998, fig. 7(1), Morocco).

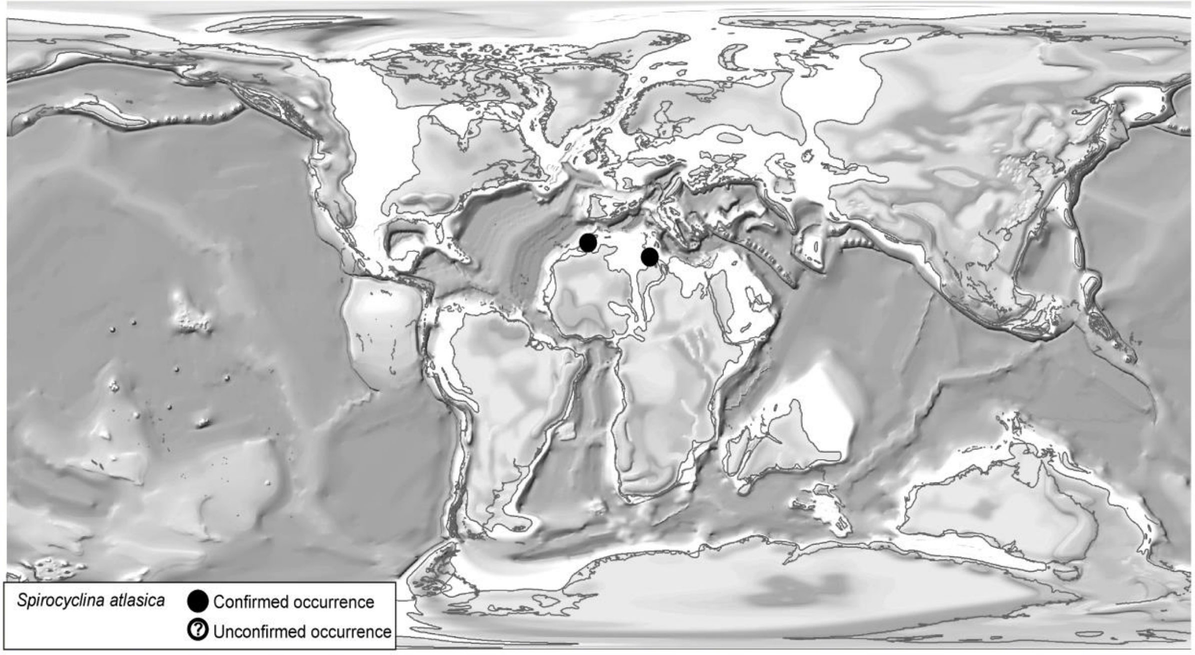


Fig. 40 Cenomanian paleogeographic distribution of *Spirocyclina atlasica.*

These include genera such as *Vidalina* Schlumberger, *Spiroloculina* d'Orbigny, *Idalina* Schlumberger & Munier-Chalmas, alveolinids such as *Ovalveolina* Reichel and *Cisalveolina* Reichel, and also inlcudes the Lower Cretaceous *Derventina* Neagu (see for example Arnaud-Vanneau 1980, pl. 86 and Schlagintweit, 1991).

The Cretaceous (Albian - Cenomanian) 'nummoloculinids' are a group of broadly similar miliolids whose taxonomy, with some exceptions, remains unstabilised but which have frequently been associated with the Neogene genus *Nummoloculina* in the literature. Six "taxa" in three, possibly more, genera are included here. The authors feel that treating them together is a useful way of discussing their similarities/differences and their stratigraphic and paleogeographic distribution, although a full taxonomic review is necessary.

As noted above, the literature for this group is fairly extensive but suffers from a lack of suitably oriented specimens by which critical diagnostic features are visible. It is not uncommon to see views of tens of specimens with only a few showing some diagnostic features and very few (if any) showing all diagnostic features together.

The more-or-less common feature of the group is that they are miliolids (unlike all other taxa in this work) and are planispirally (or nearly so) coiled in the adult stage, hence their inclusion in this work. However, their early stages (after the proloculus) can be variously planispiral, streptospiral or milioline (up to quinqueloculine). The size of the early post-prolocular stage and the point of its transition to the planispiral or near-planispiral, adult stage can vary, especially between micro- and macrospheric generations. They can vary in external shape from a broad, rounded disc to almost spherical in overall form, and their apertures can also vary as can some internal features. This makes separation of species often extremely difficult.

Much of the introductory remarks on these taxa are taken from Schlagintweit (2008) and Piuz & Vicedo (2020), who have described aspects of the taxonomic history of this 'group'. The genus *Nummoloculina* was first described by Steinmann (1881) for material from the Miocene of Austria. Several species attributed to the genus *Nummoloculina* (or *Nummoloculina*-like genera) recorded from the Albian (or older) to the Maastrichtian exist in the literature, and are widely recorded from Mexico to Oman. However, *Nummoloculina* as most recently defined (see Loeblich & Tappan, 1988) is demonstrably a Neogene genus. The genus or 'group' was not discussed by Schroeder & Neumann (1985) in their extensive treatment of Cretaceous LBF.

The genus *Pseudonummoloculina* was established by Calvez from the Albian of France (Calvez, 1988) for taxa formerly assigned to *Nummoloculina* but with a notched aperture and a quinqueloculine early stage. He designated the type species of this genus as *P. aurigerica*. As a consequence, some other Cretaceous '*Nummoloculinas*' were thenceforth also regarded as *Pseudonummoloculina* by, for example, De Castro (1987) and Hottinger et al. (1989) (e.g., regarding "*Nummoloculina heimi").* This would, of course, require these taxa to possess notched apertures. The visibility of the notched aperture in thin section depends entirely on a fortuitous thin section orientation and cut and the vast majority of illustrated specimes do not feature this crucial diagnostic character. When first describing *N. heimi* for example, Bonet (1956) stated "*Apertural characters not observed despite its abundance*." The debate on whether the taxon referred to as *heimi* possesses a notched (or sometimes referred to as 'crenulated') aperture still continues (e.g., Piuz & Vicedo, 2020, and see below).

In general, it seems that most Cretaceous 'nummoloculinids' do not appear to posses notched apertures with the exceptions of *P. aurigerica* (type species of *Pseudonummoloculina*) (also see the Maastrichtian *P. kalantari* Schlagintweit & Rashidi, 2016) and the new species of Piuz & Vicedo (2020) *P. gnosi* (type species of *Planinummoloculina* – see below) – placed in a separate genus because it is basically planispiral throughout, lacking a post-prolocular milioline or streptospiral stage. Some taxa below are therefore questionably assigned to *Pseudonummoloculina* for practical purposes here only, and we recognise that a new genus (or even new genera) could be created for these taxa.

Piuz & Vicedo (2020) identified and described two new 'nummoloculinid' genera and species (*Planinummoloculina gnosi* and *Nummoloculinodonta akhdarensis*) from two separate levels within the Cenomanian Natih Formation of Oman. They state "*Both populations are architecturally different from any other species of 'nummoloculinas' described so far…"* but include some records of 'nummoloculinid' taxa in possible synonymy.

Other putative 'nummoloculind' taxa recorded from Cenomanian or proximate strata include the aforementioned *P. aurigerica* from the Albian of France and a form from the Albian-Cenomanian of southern North America (and also found elsewhere) – *P?* ex. grp. *heimi* (Bonet) – see also Conkin & Conkin (1958) and Piuz & Vicedo (2020) for a discussion of *P?* ex. grp. *heimi*. A taxon known as *N. regularis* Philippson is also discussed and also questionably reassigned to *Pseudonummoloculina*.

Another taxon is *Nummoloculina irregularis* first described from the Santonian of Serbia (Decrouez & Radoičić, 1977). Some authors have identified and illustrated forms assigned as *N.* cf. *irregularis* to sediments of Turonian – Santonian age (e.g. Chiocchini et al., 2012). Some 'nummoloculinid' specimens which appear to continue across the Cenomanian-Turonian boundary (e.g. those of Solak et al., 2020 identified as *Pseudonummoloculina* sp.) have been compared to these *N.* cf. *irregularis* forms and therefore justifies including in the discussion herein.

The six taxa included here in this 'group' are therefore:

- *Pseudonummoloculina aurigerica* Calvez
- *Pseudonummoloculina?* ex. grp. *heimi* (Bonet emmend. Conkin & Conkin)
- *Pseudonummoloculina? regularis* (Philippson) *sensu* Chiocchini et al. (2012):
- *Pseudonummoloculina?* cf. *irregularis* (Decrouez & Radoičić, 1977) *sensu* Chiocchini et al. (2012)
- *Planinummoloculina gnosi* Piuz & Vicendo
- *Nummoloculinodonta akhdarensis* Piuz & Vicedo

Nevertheless, the group is in need of a thorough monographic review and re-examination of type material to better formalise species definitions and hence stratigraphic and paleogeographic ranges.

Genus ***Pseudonummoloculina*** Calvez, 1988
Type Species: *Pseudonummoloculina aurigerica* Calvez, 1988

Pseudonummoloculina aurigerica **Calvez, 1988**

Reference Illustration & Description

Calvez (1988), pl. 1, text figs. 2-3, p. 393-395.

P. aurigerica is the type species of the genus *Pseudonummoculina* which is partly defined by the presence of 'notches/crenulations' formed by longitudinal ribs in the roof of the chambers which lead to an aperture bordered by what looks broadly similar to a bicycle cog wheel. *P. aurigerica* is slightly smaller, broader, has fewer (adult) planispiral whorls and fewer chambers per whorl than *P? heimi*.

No other illustrated material of this species appears to show the apertural notches/crenulations diagnostic of the genus and identification is usually based on biometric similarities (if explained at all). See the Species Key Chart (Appendix) for diagnostic and other characteristics.

Piuz & Vicedo (2020) remark on the similarity between this species and their new species *Nummoloculinodonta akhdarensis* from the middle Cenomanian of Oman (see remarks under that species below). It is also similar to their new species *Planinummoloculina gnosi* which also possesses a notched/crenulated aperture, but that species is planispiral virtually throughout.

Stratigraphic Distribution

(?Hauterivian) latest Barremian – late Albian (?middle Cenomanian).

P. aurigerica was first described from the late early – middle Albian of the Pyrenees (Calvez, 1988). Since then, its stratigraphic range has been extended. Velić (2007) describes – without illustration – *P. aurigerica* ranging down to the latest Barremian from the Dinarides of the Balkan countries, although he also states that *"…species of* Pseudonummoloculina *similar to* P. aurigerica" are also found in the latest Hauterivian (Velić, 2007: p. 14). Solak et al. (2021) provides a composite range chart from several sources which shows FADs of *P. aurigerica* in the latest Barremian (Velić, 2007), uppermost early Aptian (Husinec et al., 2009 and Tešović et al., 2011 – see also Cociuba, 2000), basal Albian (Calvez, 1988; Hottinger et al., 1989 and Mancinelli & Chiocchini, 2006) and intra-Early Albian (Chiocchini et al., 2012 and Arnaud-Vanneau & Premoli-Silva, 1995 – see also Cruz-Abad et al., 2017). Solak et al. (2021) provided illustrations of *P. aurigerica* from Albian platform limestones of Turkey. The illustrations are plausible, but those authors admitted that none show the notched aperture characteristic of the genus.

In addition, Ghanem & Kuss (2013) reported and illustrated this species (though again with no notched aperture visible) from the early Aptian to the lower late Albian of Syria.

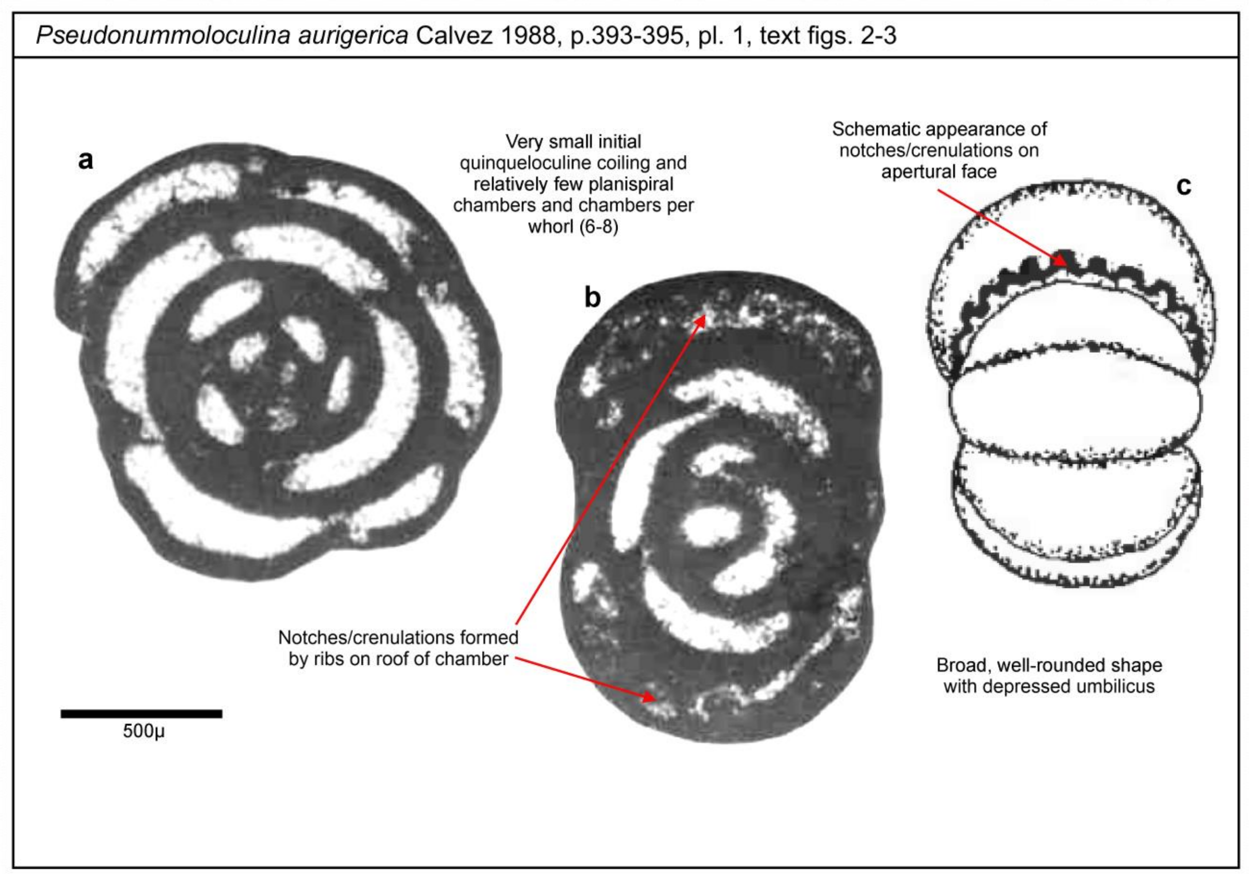


Fig. 41 Representative illustrations of *Pseudonummoloculina aurigerica*: **a** Equatorial section, Calvez (1988, pl. 1, fig. 1, Pyrenees); **b** Axial section (holotype), Calvez (1988, pl. 1, fig. 5, Pyrenees); **c** Axial external view (schematic), Calvez (1988, text fig. 3C).

An uncertain specimen has been illustrated from the lowermost Sarvak Formation (late Albian) of the Iranian Zagros (Mohseni & Javanmard, 2020).

Chiocchini et al. (2008, 2012) shows an LAD for this species in the lowermost late Cenomanian, although unillustrated. Chiocchini et al. (2008, 2012) do not recognise a middle Cenomanian substage and so this LAD may be considered to occur within the chronostratigraphic middle Cenomanian. Almost all other records appear to restrict the LAD of *P. aurigerica* to the Albian (see Solak et al., 2021: p. 690) although they (Solak et al., 2021) list an exception in Velić (2007) from the Dinarides and Bou-Dagher-Fadel et al. (2017) from Tibet. However, the present authors could find no record of this species in that latter publication. In Velić (2007), although the species is mentioned in the text from Barremian to Albian it is for some reason not included on any of Velić's appropriate range charts for that stratigraphic interval or younger. However in the text of that article it is stated that it "…continued into the Late Cretaceous [i.e. Cenomanian] (Gušić & Jelaska, 1990; Velić & Vlahović, 1994)". However, *P. aurigerica* is not mentioned in the latter reference. Dimitrova (1995) described "*Pseudonummoloculina* sp." from the early Cenomanian of Bulgaria and compared it to *P. aurigerica*. However, her illustration appears to have closer afinity to *Hemicyclammina whitei* Henson, although an illustration of "*Ammodiscus cretaceous* (Reuss)" from the same aged strata could be a *Pseudonummoloculina*. Schlagintweit (1991) recorded forms without apertural notches but assigned to this species from the German Northern Calcareous Alps. He considers these specimens – and perhaps many other Early Cretaceous references to *P. aurigerica* – as probably attributable to *Derventina filipescui* Neagu (Dr Felix Schlagintweit *pers. comm*., 2023). In summary, the Cenomanian occurrence of *P. aurigerica* is poorly established.

Cenomanian Paleogeographic Distribution

Probably Central Neotethys.

Albian records are widespread (including MIT Guyot in the Pacific (Arnaud-Vanneau & Premoli Silva, 1995; note this form corresponds to the specimens from the upper Aptian of Germany-Austria, Schlagintweit, 1991, pl. 15, figs. 26-29), but uncertain Cenomanian records (see discussion above) are limited to Italy (Chiocchini et al., 2008, 2012) and the Dinarides (Velić, 2007). In both cases, illustrations are lacking.

Pseudonummoloculina? ex. grp. *heimi* (Bonet 1956, emmend. Conkin & Conkin, 1958)

Reference Illustration & Description

Conkin & Conkin (1958), pl. 1, text figs. 1-25, p. 152-156.

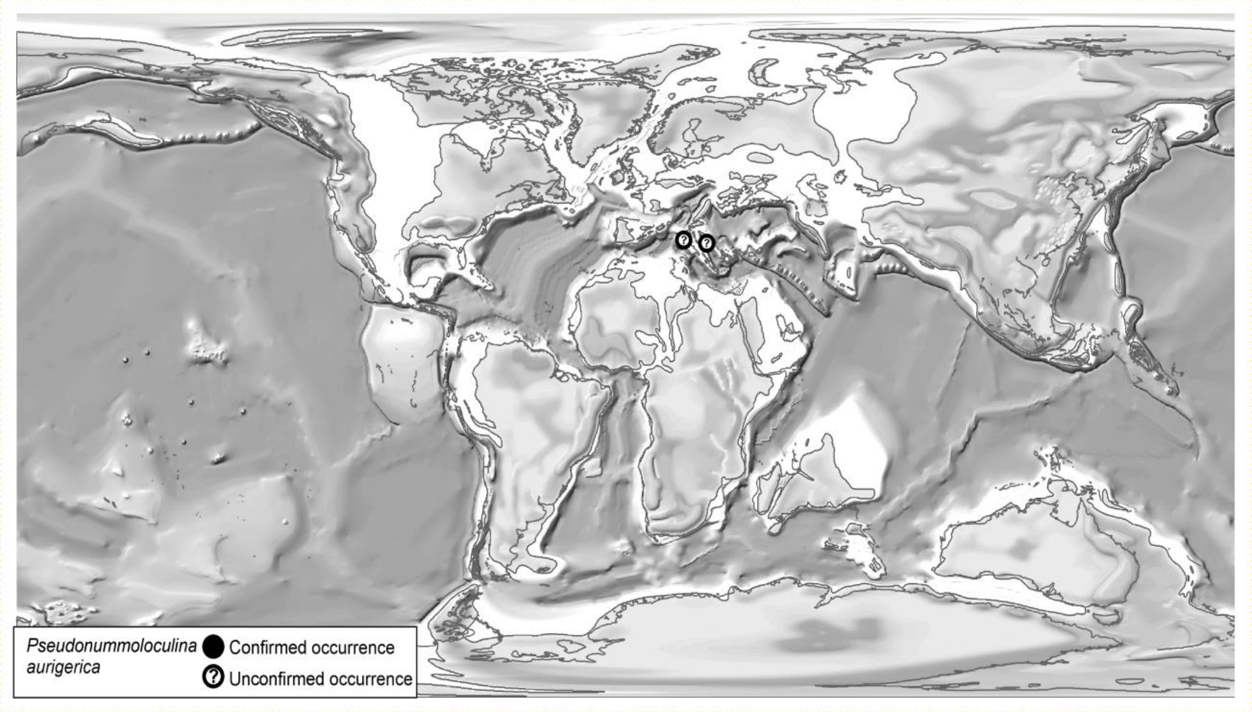


Fig. 42 Cenomanian paleogeographic distribution of *Pseudonummoloculina aurigerica*

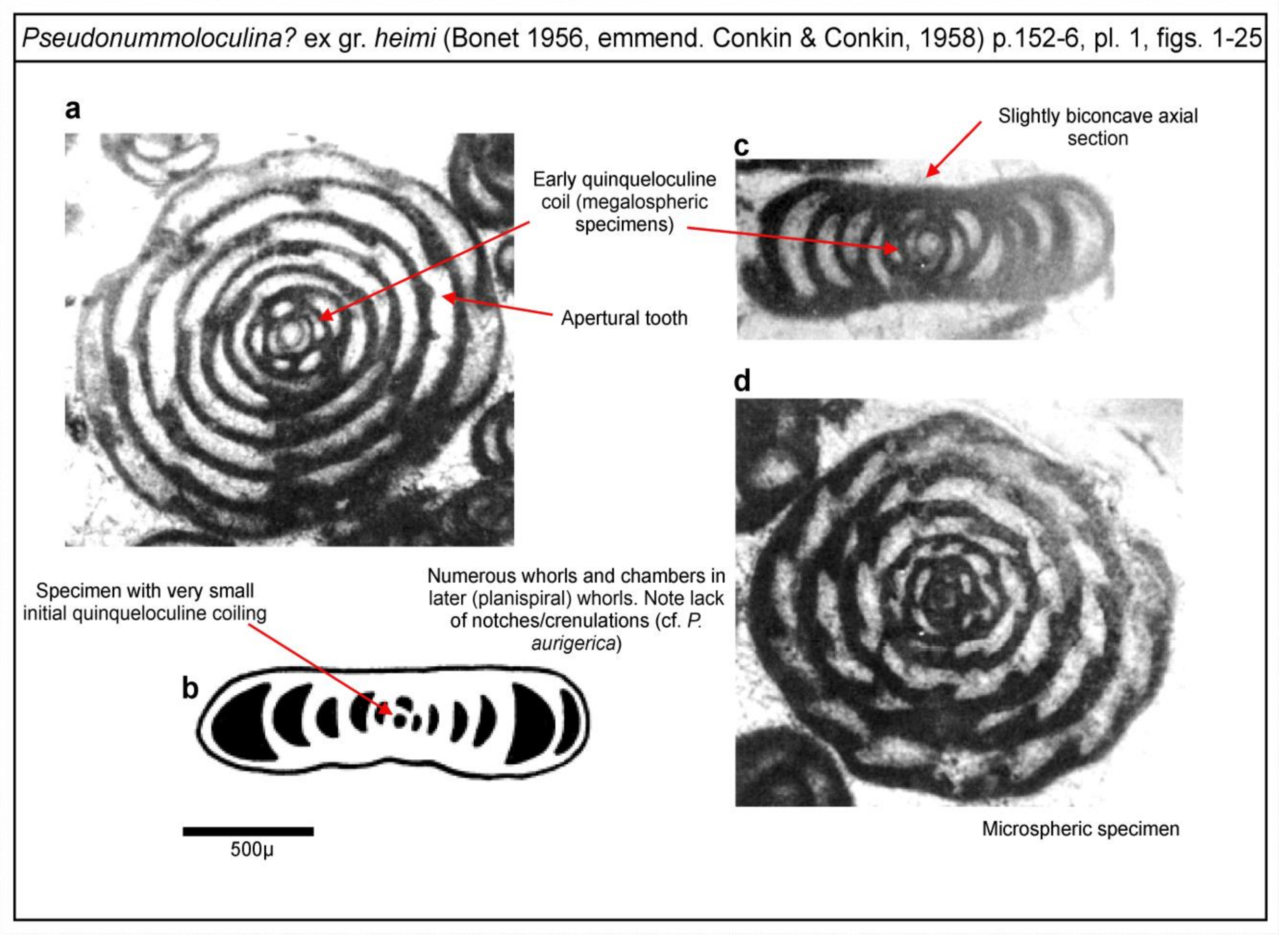


Fig. 43 Representative illustrations of *Pseudonummoloculina* ex gr. *heimi*: **a** Equatorial section, Conkin & Conkin (1958, pl. 1, fig. 1, Mexico); **b** Axial section (schematic), Conkin & Conkin (1958, text fig. 13, Texas); **c** Axial section, Conkin & Conkin (1958, pl. 1, fig. 6, Mexico); **d** Equatorial section (schematic), Conkin & Conkin (1958, pl. 1, fig. 3, Mexico).

In addition to the correct generic classification of nummoloculinids in general, a separate issue relates to the status of the species *heimi*. *Nummoloculina heimi* was first described from the Albian-Cenomanian of Mexico by Bonet (1956). Bonet's descriptions and illustrations were – according to Conkin & Conkin (1958) – unsatisfactory, and they emended the definition based on their own material which was also from Mexico and from the southern United States of America. Some of this material came from the same lithostratigraphic unit in Mexico as Bonet's, but not from the same (type) locality.

Conkin & Conkin (1958) recognised two macrospheric morphotypes, essentially: (i) with a quinqueloculine nepionic stage followed by a planispiral coil and (ii) planispirally coiled throughout.

Subsequent studies by Hottinger et al. (1989) from Mexico resulted in them attributing forms to *heimi* ("as revised by Conkin & Conkin, 1958") characterised by an early *streptospiral* (not quinqueloculine) stage followed by whorls which gradually stabilised their coiling axis without becoming completely stable; part of their so-called "stem miliolids" (Hottinger et al., 1989; p. 103).

A separate but related issue also arises over the nature of the aperture. The presence of folds or notches/crenulations in the aperture is fundamental (among other things) for a generic assignment to *Pseudonummoloculina*. Neither Bonet (1956) nor Conkin & Conkin (1958) observed such features in their North American material. Hottinger et al. (1989) only observed a row of notches in one illustrated specimen [see Fig. 44 (right) herein] of a near-completely planispiral form but not observed at all in specimens with initial streptospiral coiling. Piuz and Vicedo (2020) tentatively suggested assigning this specimen to their new nummoloculinid species – *Nummoloculinodonta akhdarensis* thus removing any suggestion of notched/crenulated apertures as a characteristic of *heimi* forms. However, Solak et al. (2021) contradict this by stating "*…the widespread Cretaceous species* Nummoloculina heimi *Bonet, 1956, with a clear notched aperture (De Castro, 1987; Hottinger et al., 1989) was transferred to* Pseudonummoloculina". It should be noted that Solak et al. (2021) did not themselves observe the notched aperture in their own material either. De Castro's material from the Cenomanian of Apennine Italy shows one specimen (out of 4 examples) which shows an aperture with "wavy margins". Hottinger et al. (1989)'s material from the Cenomanian of Mexico shows a single specimen (out of several tens of examples) with "notches in distal apertural margin". This particular specimen (a subaxial section, bottom right corner of pl. 22, fig. 6 – see Figure 44 b) is very similar to Fig. 48b herein for *P*? cf. *irregularis*.

Piuz & Vicedo (2020) discussed the implications of these observations (and others) and concluded that "…the different morphotypes mentioned above as *P. heimi* [are] likely separate taxa". However, both they and we agree that many forms displaying this variety of morphological characteristics have been attributed to *heimi* in the literature and that a comprehensive revision is required. The solution would require the adequate stratigraphic separation of similar morphotypes to determine if relationships were evolutionary or of intra-specific variability.

We agree in part with Piuz & Vicedo's (2020) proposal to restrict *heimi sensu stricto* to the morphotypes described by Bonet (1956) and Conkin & Conkin (1958) – essentially the North American specimens – although recognising that these themselves may comprise several separate taxa. Their characteristics are:

- compressed axially and lacks umbilical axial thickening
- small quinqueloculine nepionic stage (max 4 whorls/8 chambers)
- numerous planispiral whorls (up to 7)
- numerous chambers per whorl (6 up to 16)
- aperture with "stocky tooth" but no notch/ridge/crenulations

Our observations suggest that, in the majority and possibly all cases, forms attributed to *heimi* in Europe/Africa/Middle East do not appear to conform wholly to these criteria and that further taxonomic revision is required to determine if they are – as we suspect - additional, separate taxa. Some may be attributable with further research to *Nummoloculinodonta akhdarensis*, others to *P*.? *regularis sensu* Chiocchini et al., or a completely new species. Such work is beyond the scope of this article, and we have therefore, reluctantly, placed *heimi* in open nomenclature ("ex gr.") and assigned it to an unsatisfactory genus, as a problem to be solved in the future.

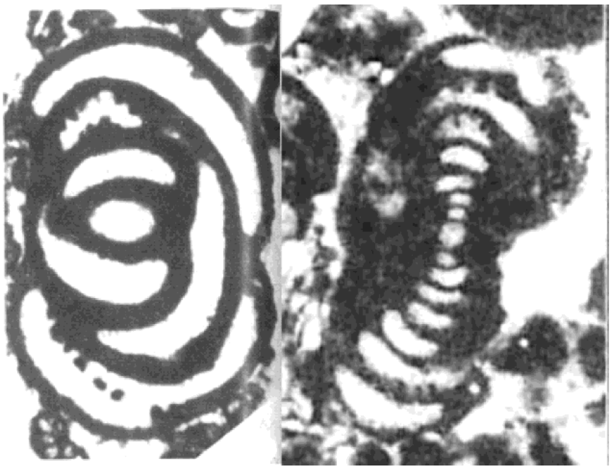


Fig. 44 *Pseudonummoloculina heimi* (Bonet) left – after De Castro (1987: fig. 3-2) and right –after Hottinger et al. (1989: pl. 22, fig. 6-part). Both specimens purported to show notched apertures. Neither specimen can, however, be attributed to *heimi* based on the criteria established by Piuz & Vicedo (2020, see text). Those authors place both specimens in tentative synonymy with their new species *Nummoloculinodonta akhdarensis*.

P.? heimi is more axially compressed than *P. aurigerica*, has more numerous planispiral whorls and chambers per whorl and does not appear to have notches or crenulations.

Despite having fewer chambers in each post-embryonic whorl (3-5 cf. 6-16) *P.? regularis sensu* Chiocchini et al. can also appear similar in some random section orientations with a similar number of post embryonic planispiral coils (up to 7), although unlike *P.?* ex. grp. *heimi*, *P.? regularis* sensu Chiocchini et al. is planispiral virtually throughout its growth.

Stratigraphic Distribution

(late Aptian?) Albian – Cenomanian (?Turonian and younger).

Notwithstanding the comments made above, an evaluation of published records suggests *P.?* ex grp. *heimi* is widely distributed with the majority from Albian-Cenomanian strata. Many records are accompanied by illustration but some of these illustrations do not necessarily confirm identity. In addition, the generic assignment (*Pseudonummoloculina* or *Nummoloculina*) varies between authors. The upper age limit of this species is difficult to pinpoint although an extension into the Turonian appears possible. Records above this level need further evaluation (e.g., Tsaila-Monopolis, 1977).

Pseudonummoloculina? heimi was first described from the Albian – Cenomanian El Abra formation of Mexico (Bonet, 1956). Conkin & Conkin's (1958) material was from Mexico (El Abra Formation), and Texas (Devil's River, Edwards and Glen Rose Formations) and Florida (Fredericksburg Formation) of the USA (see also Applin & Applin, 1965).

Other confirmed illustrated records of this species from Mexico include Rosales-Dominguez (1989); Rosales-Dominguez et al. (1997) and Omaña et al. (2013, 2019) respectively from the Albian – early Cenomanian Sierra Madre Formation and the Albian – Cenomanian El Abra Formation. Scott & Gonzalez-Leon (1991) recorded the species from the middle Albian Espinazo del Diablo and Nogal formations of the Lampazos region. Unillustrated records include Ontiveros-Tarango (1973; Cenomanian); Hernández-Romano et al. (1997; late Cenomanian); Cros et al. (1998; Cenomanian); Aguilera-Franco et al. (2001) and Aguilera-Franco (2003) (from the middle – late Cenomanian); and Aguilera-Franco & Allison (2004; undated) from the Morelos Formation. However, the illustration in Aguilera-Franco (2000) is not identifiable at species level but appears incompatible with *P.?* ex. grp. *heimi* as described herein. Lucas et al. (2015) provided an illustrated record from New Mexico.

Ashworth (1974); Caceres Flores (2016) and Radmacher et al. (2021) have plausible illustrated records from the Albian – Cenomanian Coban Formation of Guatemala (see also Fourcade et al., 1999, unillustrated, but Albian). However, the record by Moeschler (2009) is probably not this species (it may be *Spiroloculina* sp.). Ayala-Castañares & Furrazola-Bermúdez (1962) provide excellent illustrations of this species from the Albian – Cenomanian of Cuba, whilst Diaz Otero et al. (2001) records but does not illustrate this species. Rogers et al. (2007) report the species from the Albian of Honduras.

In Western Europe records from Portugal by Berthou (1973) and Andrade (2018) are illustrated but the illustration cannot be confirmed as *P.?* ex. grp. *heimi*. Records by Berthou & Lauverjat (1979) and Crosaz-Galletti (1979) are unillustrated. Most assign a middle – late Cenomanian age.

Records from Italy are numerous (De Castro (1965; 1987 – see comments above regarding synonymy with *N. akhdarensis*); Borghi & Pignatti (2006); Consorti et al. (2015); Crescenti (1969); Di Stefano & Ruberti (2000); Spalluto & Caffau (2010) and Spalluto (2011)) but only the record of Spalluto & Caffau (2010) is confirmed by illustration. Ages assigned are from early – late Cenomanian, but Crescenti (1969) indicates this species ranges up to the "Senonian" (see also Tsaila-Monopolis, 1977 from Greece). Parente et al. (2010) provide an unillustrated record of "*Nummoloculina* cf. *heimi*" from the late Turonian. Chiocchini and Mancinelli (1977) mention the species as having biozonal value for the Turonian of the Apennines, but perhaps like other records, this may be because of loose use of the species concept of *heimi*. In subsequent papers (e.g., Chiocchini et al., 2008), the zonal index is called "*Nummoloculina* cf. *irregularis*". This may explain the illustrated Turonian record of "*Nummoloculina* cf. *heimi*" by Foglia (1992).

Records from Slovenia and the Balkans (mainly Croatia) are also numerous (e.g., Radoičić, 1965, illustrated from Cenomanian strata). Koch et al. (1998) from Slovenia illustrates a form which is possibly *P.?* ex. grp. *heimi* from the Cenomanian – Turonian and Jez et al. (2011) records unillustrated material from the late Cenomanian. Croatian records are more numerous with illustrated records: Husinec & Sokač (2006) (illustrated as "*Pseudonummoloculina* sp." but mentioned as *Pseudonummoloculina heimi* in the text and range charts - Albian), Tešović et al. (2011) from the early – late Albian, and Velić & Sokač (1979) undated. The illustrated records of Ritossa (2018), also undated, and Brčić et al. (2021) (late Cenomanian) cannot be verified as this species. Additional records unconfirmed by illustration include Brčić et al. (2017); Husinec et al. (2000, 2009); Tišljar et al. (1998); Velić (2007); Korbar & Husinec (2003), and Velić & Vlahović (1994). Assigned ages range from the early Albian to the early Campanian (e.g., Velić, 2007). A record from the late Turonian – Coniacian of Croatia (Gušić et al., 1988) is a nummoloculinid, but difficult to assign to a species. A single record from Montenegro (Božović, 2016) is unillustrated and has no assigned age.

Most records from Greece (e.g., Fleury, 1971; Decrouez, 1976, 1978; early – late Cenomanian) are unillustrated, but that of Charvet et al. (1976) is, but might be *P.*? *regularis* sensu Chiocchini et al. or *Nummoloculinodonta akhdarensis*. Tsaila-Monopolis (1977) illustrated the species from the "Cenomanian - Turonian" and "Senonian" of Greece. Some illustrations are more compatible with *P.*? *regularis sensu* Chiocchini et al. (2012). Another record from Greece (Zambetakis-Lekkas, 2006) is unillustrated and is said to range from the late Cenomanian to the Maastrichtian, although that seems unlikely. Zambetakis-Lekkas et al. (2006) also records the species (unillustrated) from Crete and assigns the same age range.

North Africa records include from Tunisia (Bismuth et al., 1967; Saïdi et al., 1995 and Touir et al., 2017). Only the former record is confirmed by illustration and may include *P.*? *regularis sensu* Chiocchini et al. (2012) but all authors assign a Cenomanian age. By contrast, Lüning et al. (2000) report the species from the Kufra Basin of Libya and assign a Campanian? – Maastrichtian age, although they provide no illustration but note that "*the present specimen is similar to those described in Hottinger et al. (1989, pl. 22, fig. 6) and by Calvez (1988); the only difference is the smaller size compared to the material described by Calvez. The specimen figured by De Castro (1987, fig. 3) also shows all features of the present material.*" In this respect it is worth noting that Calvez (1988) did not illustrate *P.? heimi*, but *P. aurigerica*.

Numerous illustrated records occur from Turkey of which those of Sari et al. (2009) and Solak et al. (2020, 2021) are confirmed by illustration. The records of Ozkan & Altiner (2019), Solak (2021) and Solak et al. (2017, 2019) are also illustrated but the specimens are only *possibly* of this species. Most records are assigned a middle – late Cenomanian age although Solak et al. (2021) indicates an age as old as late Albian and Sari et al. (2009) an age as young as Coniacian. The record of Ozkan & Altiner (2019) is thought to be from the early Cenomanian. Sinanoglu (2021) provides an unillustrated record.

In the eastern Mediterranean area *P.?* ex. grp. *heimi* has been reported from Syria, Lebanon, and Israel, although confirmed by illustration only from the first two (i.e., Ghanem & Kuss, 2013, and Saint-Marc, 1974a, 1981). Note the illustrated records of Ghanem et al. (2012) are insufficient to confirm their identity. Unconfirmed Israeli records are from Hamaoui (1965, 1966). All of these records are from throughout the Cenomanian, with Turonian records (e.g., Saint-Marc, 1970) being revisable as late Cenomanian (e.g., Saint-Marc, 1978). Mouty et al. (2003) have reported the species from the late Cenomanian of Syria.

Records from the Sarvak Formation of Iran and the Mishrif Formation in Iraq are numerous, especially from the former, but the quality of confirmatory illustrations is variable. Records with good or plausible illustration in the sense of *P.*? ex. grp. *heimi* include Esfandyari et al. (2023), Rahimpour-Bonab et al. (2013) and Mohajer et al., (2021b). Records with questionable or no illustration include Assadi et al. (2016) (probably *P.*? *regularis sensu* Chiocchini et al.); Daneshian et al. (2016); Kiarostami et al. (2019); Saeedi Razavi et al. (2019, 2021); Mohajer et al. (2022b); Omidvar (2014a); Rikhtegarzadeh et al. (2016, 2017) and Al-Salihi & Ibrahim (2023). Even though considered of biozonal value by the authors, the illustrations of *P.?* ex. grp. *heimi* (as *Nummoloculina heimi)* by Afghah et al. (2014) and Afghah & Fadaei (2014) cannot be confirmed as being of this species. The illustration by Afghah & Dookh (2014) is of an alveolinid. These records are predominantly assigned a Cenomanian age, although Rahimpour-Bonab et al. (2013) provide a combined total range of late Albian – Turonian. An illustrated record by Gollesstaneh (1965) from the "late Aptian – early Albian" of the Iranian Zagros, represents one of the oldest records of this species *sensu lato*.

Records from Iraq are fewer and include illustrated forms by Al-Dulaimy & Al-Sheikhly (2013) which are possibly *P.?* ex. grp. *heimi*. Illustrations by Al-Dulaimy et al. (2022) from the late Cenomanian Mishrif Formation may well be alveolinids.

Additional unillustrated records occur from the Natih Formation of Oman (Kennedy & Simmons, 1991; Simmons & Hart, 1987) and are assigned a middle – late Cenomanian age.

Cenomanian Paleogeographic Distribution

Pan-Neotethyan, America and the Caribbean.

See references above. As a note, pre-Cenomanian records can be extended further since Arnaud-Vanneau & Premoli-Silva (1995) note that their "*Nummoloculina* sp." recorded from the late Albian (?) of MIT Guyot in the Pacific is very similar to *P.?* ex. grp. *heimi*.

Pseudonummoloculina? regularis **(Philippson, 1887) *sensu* Chiocchini et al. 2012**

Reference Illustration & Description

Chiocchini et al. (2012), pl. 83, figs. 2-8.

Nummoloculina regularis Philppson, a species first described from Late Cretaceous marls in the region of Lake Wolfgang, Austria (Philippson, 1887), is often referred to from Cenomanian strata in the literature (as *Nummoloculina* or *Pseudonummoloculina*), but Schlagintweit (2008) has discussed the identification, taxonomy and distribution of Philippson's specimens and restricts its occurrence (in Austria at least) to no older than the late Turonian. Schlagintweit (2008) believes the specimens described and illustrated by Phillippson (1887) are better attributable to *Vidalina hispanica* Schlumberger, and, as first pointed out by Radoičić (1978), are not the same as those specimens variously assigned to *regularis* in the Cenomanian of other localities around Neotethys in having no true septa (in any case it is believed Phillippson's types are lost so confirmation is impossible – Dr Lorenzo Consorti, pers. comm., 2023). If (hypothetically) correct (see Piuz & Vicedo, 2020 for discussion), the new combination – *Vidalina regularis* (Schlumberger) would become the type species of the genus *Vidalina*. However, Schlagintweit (2008) does not speculate on what this means for Cenomanian specimens attributed to the species *regularis* (nor do Piuz & Vicedo, 2020).

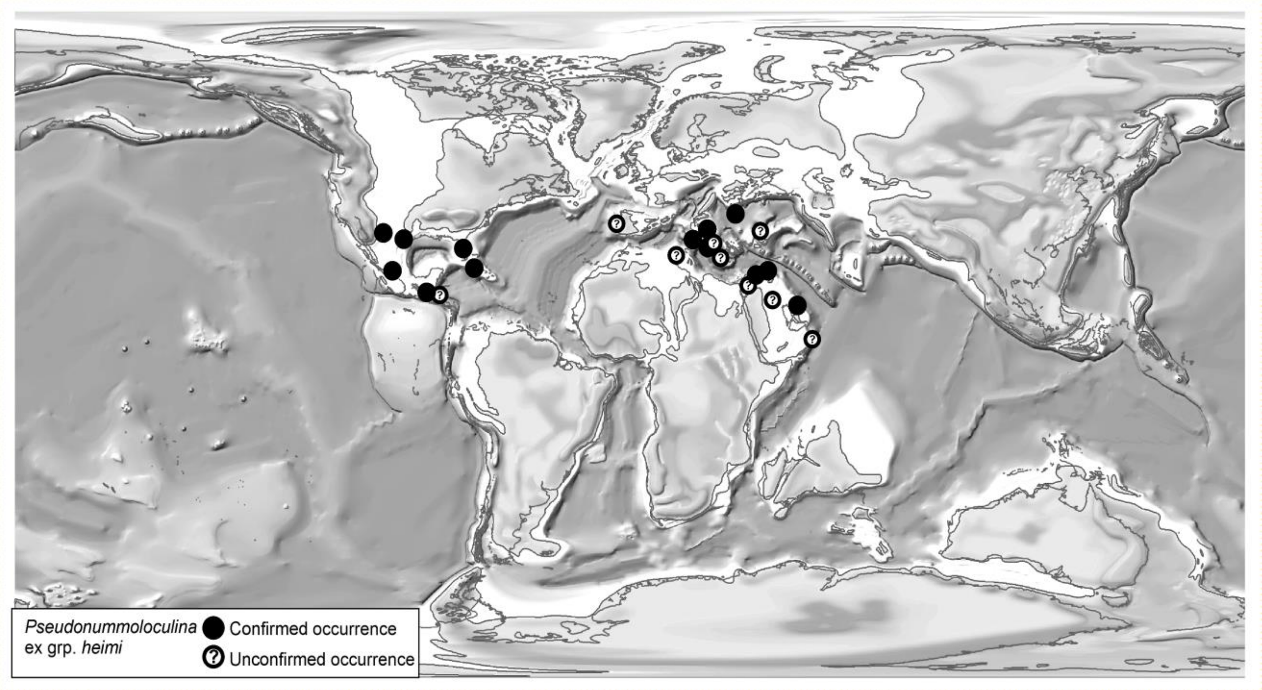


Fig. 45 Cenomanian paleogeographic distribution of *Pseudonummoloculina* ex gr. *heimi*

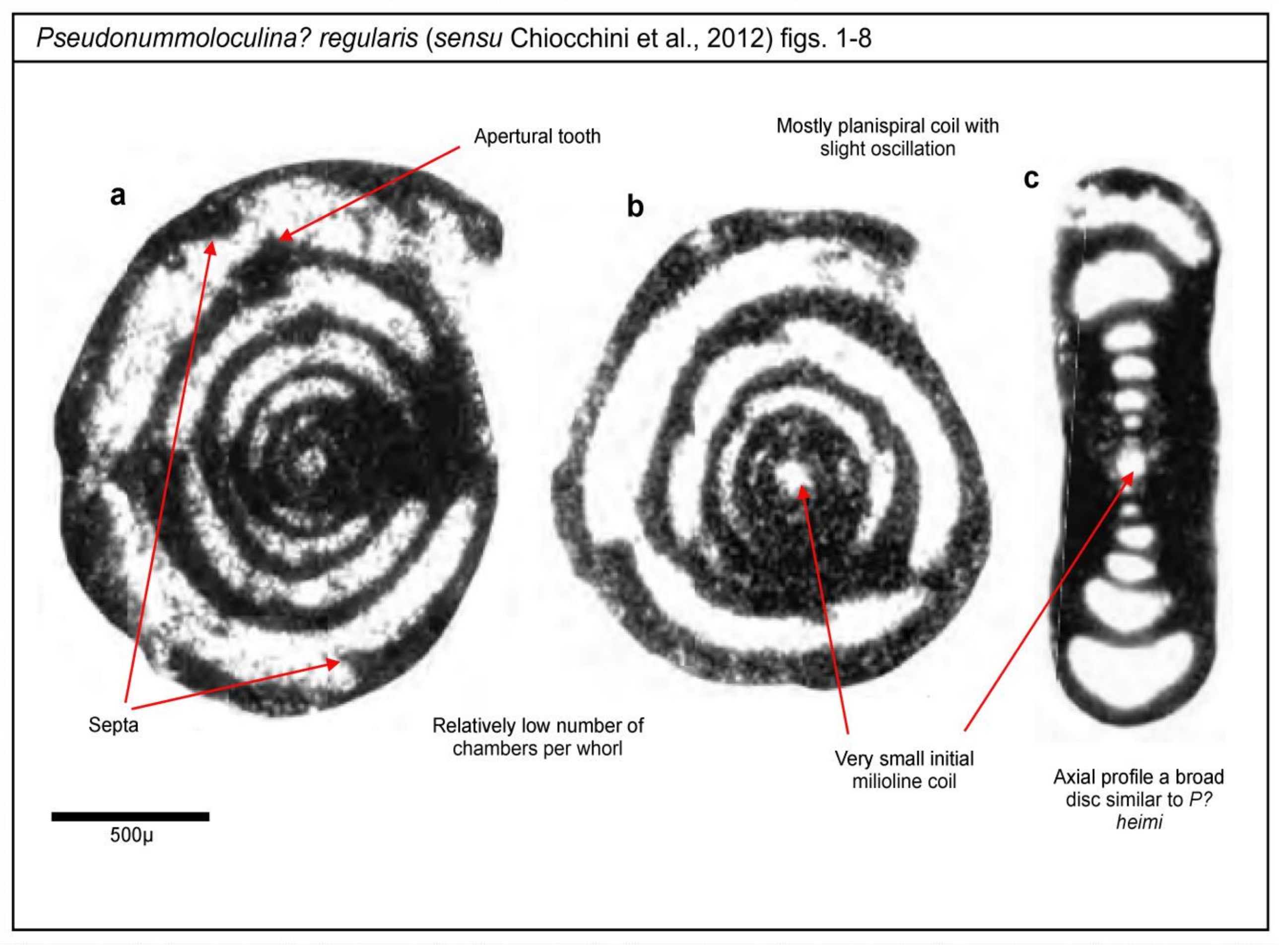


Fig. 46 Representative illustrations of *Pseudonummoloculina? regularis*: a - Equatorial section, Chiocchini et al. (2012, pl. 83, fig. 2, Italy; b - Equatorial section, Chiocchini et al. (2012, pl. 83, fig. 3, Italy); c - Axial section, Chiocchini et al. (2012, pl. 83, fig. 4, Italy).

See the Species Key Chart (Appendix) for diagnostic and other characteristics.

The best illustrations of what we refer to as *regularis* which are demonstrably Cenomanian are from Chiocchini et al. (2012) figured herein. Assigned by them to *Nummoloculina*, they are, for the present, here questionably (and pending review) assigned to *Pseudonummoloculina* in the same way as *P? heimi*, as *Nummoloculina* is not a Cretaceous genus. Thus herein we discuss *Pseudonummoluculina? regularis sensu* Chiocchini et al. (2012). These are comparable with *Nummoloculina* sp. (aff. *regularis*) as described and illustrated by Radoičić (1978).

As its name suggests, *P.? regularis* begins coiling planispirally in a single plane from very early on in the post-embryonic stage. In axial views a post-prolocular milioline stage is either very small or absent. In this respect it is also similar (in axial view) to *Vidalina radoicicae*.

P? regularis has a similar equatorial profile to *P? heimi* but with many fewer chambers per (later) whorl (3-5 cf. 6-16), as well as more regular planispiral coiling. *P. gnosi* has a more biconvex axial profile with more umbilical thickening and devlops ribs/notching, although *P. gnosi* and *P? regularis* appear to share a lack of a distinctly milioline early stage.

P. aurigerica is more inflated and biconvex in axial profile compared with *P? regularis* and with a more lobate periphery. It also posesses apertural notches/crenulations (caused by ribs in the chamber roof).

Stratigraphic Distribution

Early Cenomanian - late Cenomanian (?early Turonian).

The material of Chiocchini et al. (2012) is from the early Cenomanian in the concept of those authors, which may include part of the middle Cenomanian of the current international standard. Elsewhere in western Europe, the following records may refer to *P*.? *regularis sensu* Chiocchini et al.: Cenomanian of Portugal (Berthou, 1978; Berthou and Lauverjat, 1979; Crosaz-Galletti, 1979; Andrade, 2018), Spain (Cherchi & Scroeder, 1998) and Italy (Chiocchini, 2008a). With the exception of Andrade (2018), these records are unillustrated. Bilotte (1984) illustrated *N. regularis* from the Pyrenenes, but the specimens are large (up to 2.1 mm) and broad in axial profile, making comparison to *P*.? *regularis sensu* Chiocchini et al. uncertain.

Records from eastern Europe, Greece and the Balkans area are numerous (mostly middle – late Cenomanian) but are all unillustrated apart from Radoičić (1974a & b, 1978) (as "*Nummoloculin*a cf. *regularis*" and *Nummolulina* sp. (aff. *regularis*)") from the late Cenomanian – ?early Turonian of Serbia, Schlagintweit & Rigaud (2015) from the upper middle – late Cenomanian of Kosovo and Tsaila-Monopolis (1977) from the "Cenomanian – Turonian" of Greece. The unillustrated records are from Albania (Consorti & Schlagintweit, 2021a); Croatia (Husinec et al., 2000, 2009; Tišljar et al., 1998; Velić & Vlahović, 1994; Velić, 2007); Greece/Crete (Decrouez, 1976, 1978; Fleury, 1980; Zambetakis-Lekkas, 2006; Zambetakis-Lekkas et al., 2006; Pomoni-Papaioannou & Zambetakis-Lekkas, 2009) and Slovenia (Šribar & Pleničar, 1990; Jez et al., 2011). An illustration by Fleury (1971) from Greece is most likely *Vidalina radoicicae*.

Records from North Africa are comparatively rare but with an uncertain illustration from the late Cenomanian of Morocco (Ettachfini, 1993) and an unillustrated record from the late Cenomanian of Tunisia (Touir et al., 2017).

Solak et al. (2020) provides illustrated records from throughout the Cenomanian of the Turkish Taurides. Sari et al. (2009) also provides an illustration from a section assigned to the middle Cenomanian – Turonian, but this specimen, though regularly planispiral, appears axially too broad to be definitely assigned to this species and is most likely a different taxon. Other records from Turkey include Solak et al. (2015) and Koç (2017) but are unillustrated. They are assigned age ranges of Cenomanian – Conician and Cenomanian – ?early Turonian respectively.

In the eastern Mediterannean area illustrated records are found from Lebanon (Saint-Marc, 1974a, 1981) and Syria (Ghanem et al., 2012 (uncertain); Ghanem & Kuss, 2013). As noted by Radoičić (1978), the dimensions mentioned by Saint-Marc (1974a) are small for the Cenomanian form of *P*.? *regularis*, but the illustrations in both his 1974 and 1981 paper indicate a larger size which is compatable. Saint-Marc (1978, 1981) regarded the species as having a late middle – late Cenomanian range. Records from the Naur (b-d) Formation in Jordan (Schulze, 2003; Schulze et al., 2004) are unillustrated.

Records from the Sarvak Formation of the Iranian Zagros are relatively numerous with several confirmed by illustration. These are Afghah et al. (2014); Dehghanian & Afghah (2021); Esfandyari et al. (2023); Kiarostami et al. (2019); Mohajer et al. (2021b); Parnian et al. (2019); Saeedi Razavi et al. (2019) and Saeedi Razavi et al. (2021). An illustration by Afghah & Fadaei (2014) (note transposition of plate captions) is uncertain, whilst "*Nummoloculina* sp." as illustrated by Sampò (1969) may, questionably, be this species, as might the illustration of "*Nummoloculina* sp." by Ahmadi et al. (2008). However, illustrations by Rahimpour-Bonab et al. (2013) [= *Pseudonummoluculina*? cf. *irregularis* sensu Chiocchini et al., 2012], Omidvar et al. (2014a) [= *Pseudonummoluculina*? cf. *irregularis* sensu Chiocchini et al., 2012], and Rikhtegarzadeh et al. (2016) [indeterminate nummoloculinid] are probably not this species, whilst the illustration by Afghah & Dookh (2014) is of an alveolinid. Assigned ages are Cenomanian. Unillustrated records by Fourcade et al. (1997) and Shapourikia et al. (2021) are middle - late Cenomanian.

An unillustrated record from the Cenomanian Natih Formation of Oman is also noted by Rabu (1993).

In the Caribbean area *P*.? *regularis sensu* Chiocchini et al. has been recorded from the late middle – late Cenomanian of Mexico with illustration by Aguilera-Franco (2000) and Aguilera-Franco et al. (2001) (see also

Aguilera-Franco, 2003; Aguilera-Franco & Allison, 2004 and Michaud et al., 1984 but without any illustration). It has been questionably illustrated from Guatemala by Moeschler (2009).

Cenomanian Paleogeographic Distribution

Neotethys and Caribbean.
See above references.

Pseudonummoloculina? cf. *irregularis* (Decrouez & Radoičić, 1977) *sensu* Chiocchini et al. 2012

Reference Illustration & Description

Chiocchini et al. (2012), pl. 120, figs. 2-7.
N. irregularis was first described by Decrouez & Radoičić (1977) from Santonian - ?Campanian rocks of Serbia. It is not, apparently, connected to the Recent form *Biloculina irregularis* d'Orbigny as apparently indicated in the World Foraminifera Database (Hayward et al., 2020). There are, however, numerous records from the Quaternary of *Nummoloculina irregularis* (d'Orbigny). If d'Orbigny's species is, in fact, a *Nummoloculina,* then the validity of Decrouez and Radoičić's taxon would be questionable. See the Species Key Chart (Appendix) for diagnostic and other characteristics.
Chiocchini et al. (2012) recorded forms they assigned to *Nummoloculina* cf. *irregularis* from the Turonian (with a range up to the Santonian) but it is not clear why they chose the 'cf.' modifier as the illustrations look to be comparable with those of Decrouez and Radoičić (1977). The somewhat more 'angular' appearance of the periphery in equatorial view seems characteristic.
Solak et al. (2020) recorded forms they attributed to *Pseudonummoloculina* sp. from sediments just above the Cenomanian-Turonian boundary in Turkey. They stated that this taxon was "similar to *Nummoloculina* cf. *irregularis* of Chiocchini et al. (2012)". Their illustration of *Pseudonummoloculina* sp. is included within Figure 48 herein.
The illustrations of Chiocchini et al.'s (2012) and Solak et al.'s (2020) forms appear comparable and show a 'nummoloculinid' with a relatively large initial milioline coil and later coils which appear streptospiral and which may not achieve planispiral status until a very late growth stage.
For the practical reasons discussed above we have questionably assigned this taxon to *Pseudonummoloculina*. However, Schlagintweit & Rashidi (2016) note that *N. irregularis sensu stricto* is not atributable to *Pseudonummoloculina* and it is likely that a new genus will be needed to incorporate this species and others mentioned herein. Included in this revision could be *Fischerina*? *carinata* Peybernes, a distinctive simple biumblicate planispiral taxon described by Peybernes (1984) from the late Albian of Spain (Dr. Felix Schlagintweit, pers. comm., 2023). It is clear that much work needs to be undertaken to establish the taxonomy of the "nummoloculinids" *sensu lato*.

Stratigraphic Distribution

Cenomanian?/Turonian – earliest Santonian.
Chiocchini et al. (2012) record this taxon from the intra-early Turonian to the lower early Santonian of Italy (their illustrated specimens are from the Turonian). Solak et al. (2020) do not show the occurrence of this species on any range chart or section distribution chart, but their illustrated specimen (reproduced here) is attributed to their sample 206 which lies less than 1m above where they have placed the Cenomanian-Turonian boundary.
Records of "*Nummoloculina regularis*" from the Turonian uppermost Sarvak Formation of the Iranian Zagros (Rahimpour-Bonab et al., 2013; Omidvar et al., 2014a) may well be *P*? cf. *irregularis sensu* Chioccini et al. 2012, and provide support for the Turonian age assignment of these strata.
However, the specimen illustrated by Hottinger et al. (1989) as *P. heimi* (pl. 22, fig. 6, bottom right) from the Cenomanian of Mexico (see Fig. 44 (right) herein) is somewhat more similar to the illustration of *P*? cf. *irregularis sensu* Chiocchini et al. 2012 herein (Fig. 48b) and, if confirmed, suggests an older FAD for this taxon. This is a different viewpoint to Piuz & Vicedo (2020) who place the same Mexico specimen in tentative synonymy with their species *Nummoloculinodonta akhdarensis* from Oman (see below). This is an example of the difficulties in separating 'nummoloculinid' species in random thin section.

Cenomanian Paleogeographic Distribution

Central America?
Whilst this taxa is known from the Mediterranean in post-Cenomanian stratigraphy, the only possible Cenomanian record is from Mexico (see above).

Planinummoloculina gnosi Piuz & Vicendo, 2020

Reference Illustration & Description

Piuz & Vicedo (2020), fig. 3(A-U), p. 11-13.
P. gnosi is characterised by planispiral (occasionally slightly oscillating) coiling throughout, rather than having a distinctly milioline nepionic stage cf. *Pseudonummoloculina? heimi* and *P. aurigerica*. Apertural notches/crenulations similar to those seen in *P. aurigerica* are visible from the 5th whorl onwards.
Piuz & Vicedo (2020) describe an adult test of 10-11 whorls with 3-4 chambers per whorl, but do not illustrate an equatorial view of their specimens. The test of *P. gnosi* is also reported as being larger (up to 3mm diameter) than both *P. aurigerica* and *P? heimi*. Axial/subaxial views show that *P. gnosi* has an axial profile broader to those of *P? heimi* and *P? regularis*, or tending towards

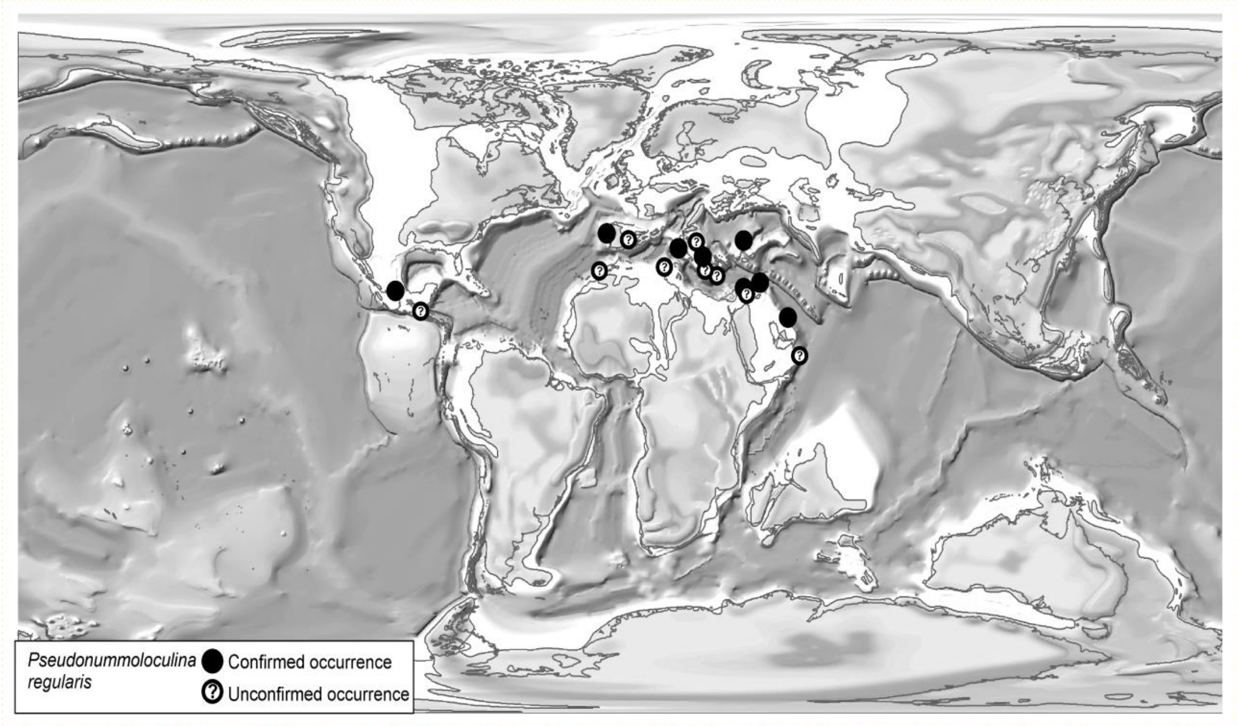


Fig. 47 Cenomanian paleogeographic distribution of *Pseudonummoloculina? regularis.*

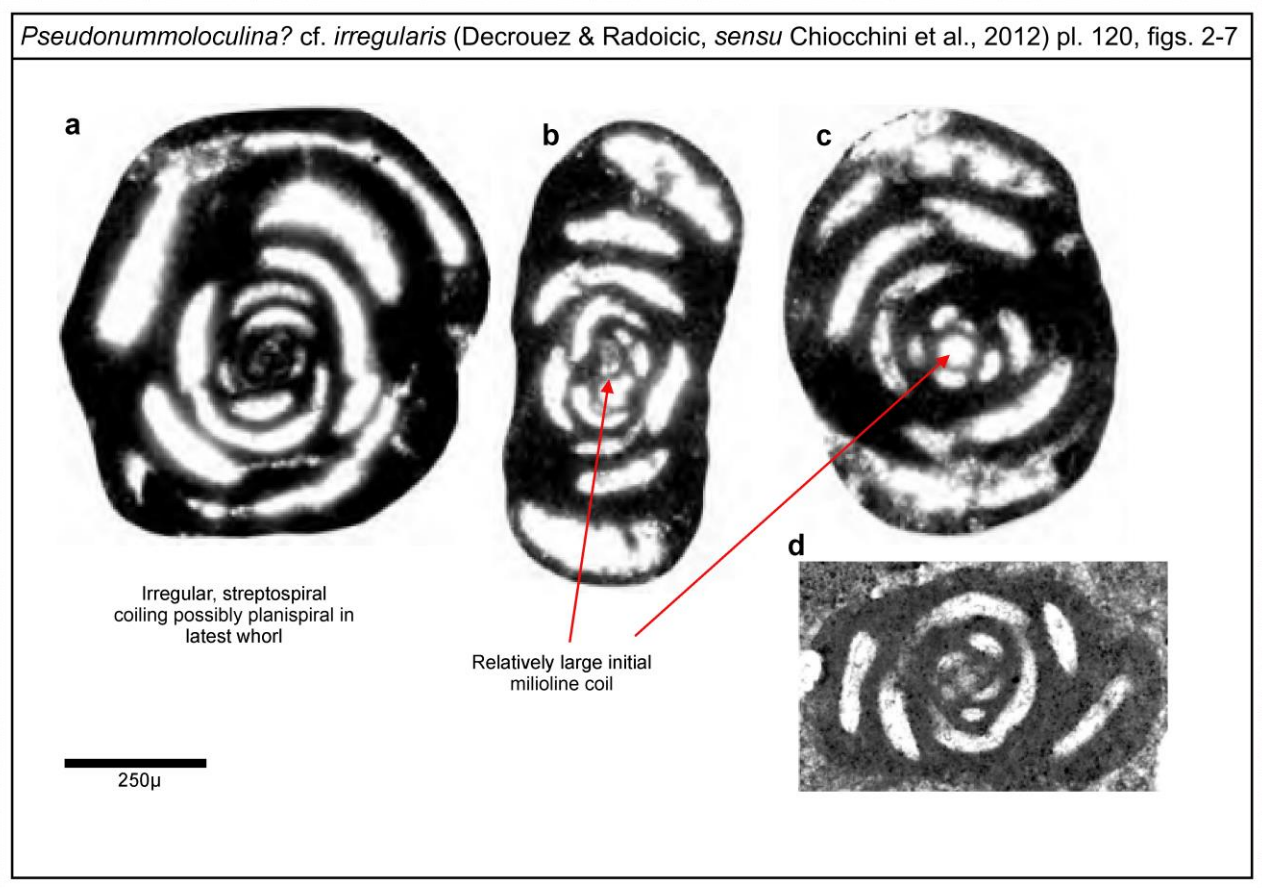


Fig. 48 Representative illustrations of *Pseudonummoloculina?* cf. *irregularis*: a Subequatorial section, Chiocchini et al. (2012, pl. 1, fig. 3, Italy); **b** Subaxial section, Chiocchini et al. (2012, pl. 120,fig. 2, Italy); **c** Subequatorial section, Chiocchini et al. (2012, pl. 120, fig. 4, Italy); **d** *Pseudonummoloculina* sp. sensu Solak et al. (2020, fig. 14V, Turkey).

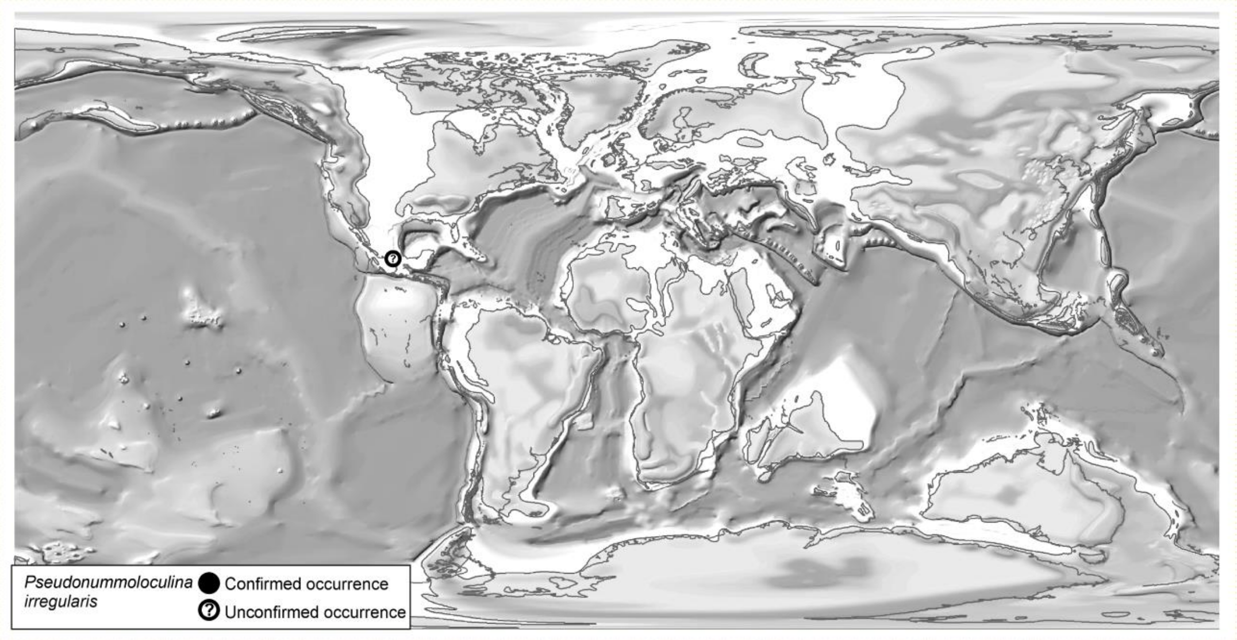


Fig. 49 Cenomanian paleogeographic distribution of *Pseudonummoloculina?* cf. *irregularis*

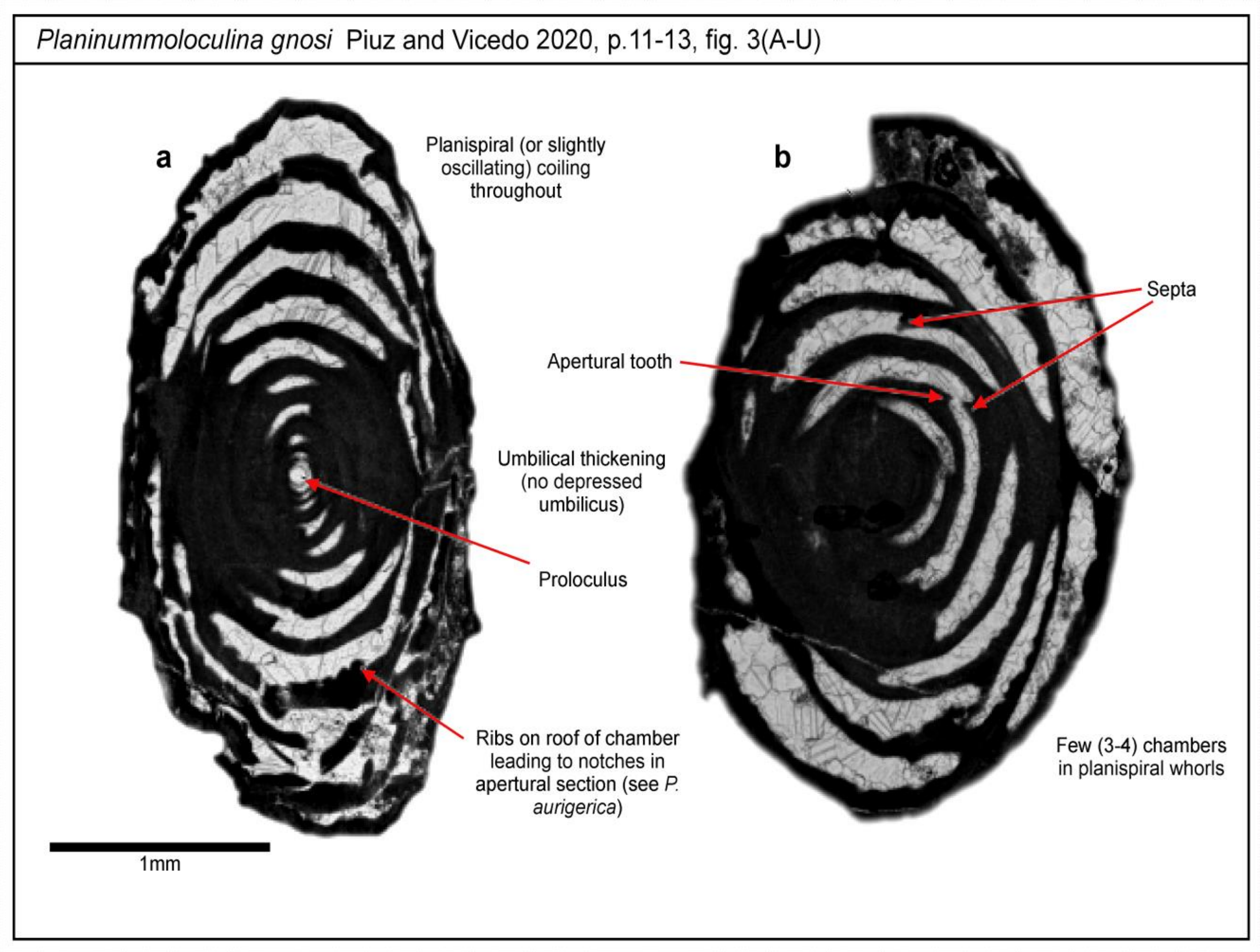


Fig. 50 Representative illustrations of *Planinummoloculina gnosi*: **a** Axial section, Piuz and Vicedo (2020, fig. 3N, Oman); **b** Tangential section, Piuz and Vicedo (2020, fig. 3R, Oman).

that of *P. aurigerica* but does not appear to be biconcave (cf. *P? heimi*) or have a depressed umbilicus (cf. *P. aurigerica*). See the Species Key Chart (Appendix) for diagnostic and other characteristics.

Stratigraphic Distribution

Close to middle/late Cenomanian boundary.
So far only confidently described from the Cenomanian (unit B of the Natih Formation) of the Oman Mountains. Regarded as middle Cenomanian by Piuz & Vicedo (2020), this unit most likely contains the middle/late Cenomanian boundary (Bromhead et al., 2022). Piuz & Vicedo (2020) regard specimens identified as *Nummoloculina regularis* by Afghah et al. (2014) from the Sarvak Formation of the Iranian Zagros as possibly attributable to this species. This occurrence, if valid, might be middle Cenomanian in age but requires a complete re-evaluation of the associated microfauna (Schlagintweit & Simmons, 2022). Dr Felix Schlagintweit (pers.comm., 2023) believes he has specimens of this species from the Sarvak Formation.

Cenomanian Paleogeographic Distribution

Arabian Plate.
So far described only from the Cenomanian of the Oman Mountains and the Iranian Zagros (Piuz & Vicedo, 2020 and Dr Felix Schlagintweit *pers. comm*., 2023).

Nummoloculinodonta akhdarensis **Piuz & Vicedo, 2020**

Reference Illustration & Description

Piuz & Vicedo (2020), fig. 4(A-I) & fig. 5(A-AB), p. 13-14.
Originally described and recorded from the Cenomanian Natih Formation of the Oman Mountains. Piuz & Vicedo (2020) remark that the complex apertural features of this genus are still poorly understood (although a tooth seems to be present) and are seldom visible in random this sections. *N. akhdarensis* appears to be characterised by a well-developed milioline (mostly quinqueloculine) nepionic stage of up to 6 whorls followed by an adult planispiral stage which coils in another plane. This adult stage can show up to 4 whorls with a maximum of 4 chambers per whorl. Apertural notches/ribs are seen in the later (gerontic) stage and pillars or pillar-like structures can also be seen. The overall shape is probably the most broadly rounded biconvex or globular of all the Albian-Turonian 'nummoloculinids' though can approach an axial profile similar to that of *Pseudonummoloculina aurigerica*. See the Species Key Chart (Appendix) for diagnostic and other characteristics.
This new genus differs from *Pseudonummoloculina* in the posession of an apertural tooth and a general absence (except in gerontic forms) of apertural crenulations. However, Piuz & Vicedo (2020) also admit that the genus may correspond partially to the (invalid) genus *Nummoloculina* emend. Conkin & Conkin (1958) and that more work on the nature of the aperture is required.
N. akhdarensis differs from *P. aurigerica* in being somewhat more globular, by posessing an aperture with a complex tooth, fewer chambers (maximum 4 cf. 6-8) and posessing notches only within the last (gerontic) stage of development.

Stratigraphic Distribution

(Barremian) early - ?middle Cenomanian (Santonian).
The type material is from unit E of the Natih Formation of the Oman Mountains (Piuz & Vicedo, 2020). This is most likely early Cenomanian in age (Bromhead et al., 2022), although extension into the middle Cenomanian cannot be completely excluded. However, Piuz & Vicedo (2020) include the following published occurrences in possible/probable synonymy with *N. akhdarensis*. These attributions are tentative as not all diagnostic details are visible:
Nummoloculina sp. in Arnaud-Vanneau (1980), France, which is recorded as Barremian in age.
Nummoloculina sp. in Arnaud-Vanneau & Darsac (1984), France, recorded as Barremian – Aptian in age.
Pseudonummoloculina n. sp. indet. in Hottinger et al. (1989), Mexico, recorded as late Santonian in age.
Pseudonummoloculina sp. cf. *N. heimi* in De Castro (1987), Italy, recorded as Cenomanian in age.
Pseudonummoloculina sp. in Radoičić (1994), the Balkans, recorded as late Cenomanian in age.
Pseudonummoloculina heimi in Hottinger et al. (1989), Mexico, recorded as Cenomanian in age.
If confirmed, these would greatly extend the range of the species. However herein, only the confirmed range is shown.

Cenomanian Paleogeographic Distribution

(Caribbean/Neotethys?) Arabian Plate.
Confirmed Cenomanian occurrences are restricted to the type description from the Oman Mountains (Piuz & Vicedo, 2020) but possible occurrences are recorded from Mexico, Italy, and the Balkans (see references above). Revisions to *P*.? ex. grp. *heimi* (see above) may extend the distribution further.

Genus ***Vidalina*** Schlumberger, 1900
Type species: *Vidalina hispanica* Schlumberger, 1900
Vidalina radoicicae **Cherchi & Schroeder, 1986**

Reference Illustration & Description

Cherchi & Schroeder (1986), pl. 1. figs. 1-3, 5, p. 185-188.
Vidalina is a relatively simple genus consisting of a subspherical proloculus followed by an unsegmented post embryonic tubular chamber arranged in a planispiral coil.

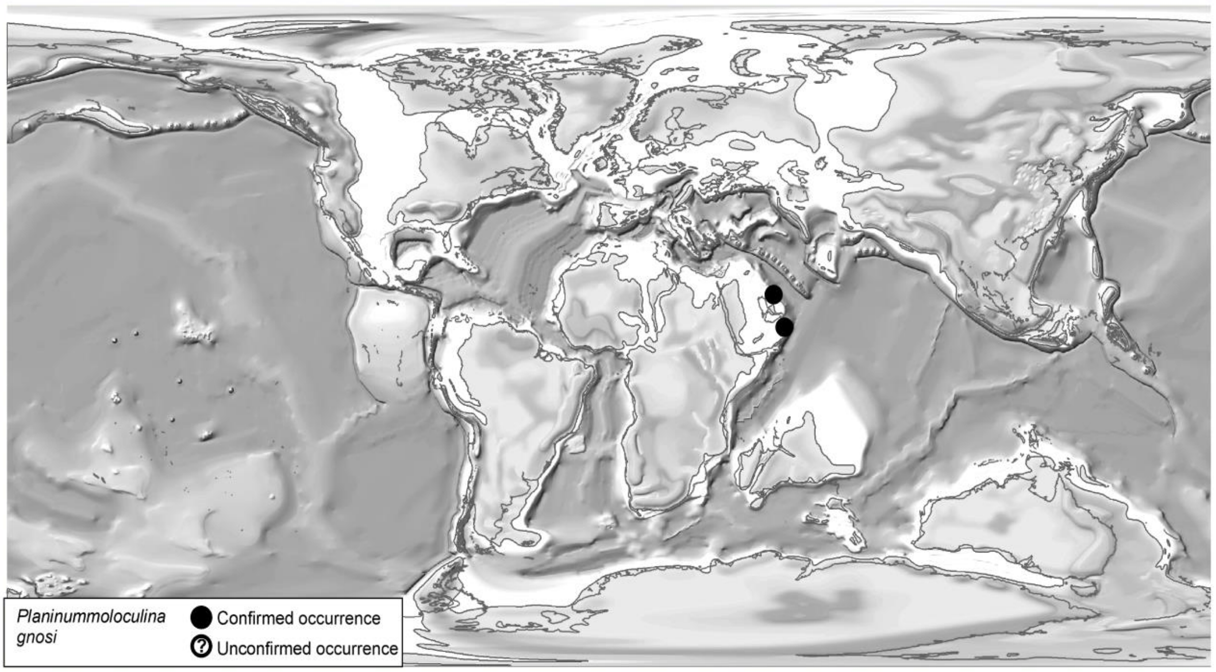


Fig. 51 Cenomanian paleogeographic distribution of *Planinummoloculina gnosi.*

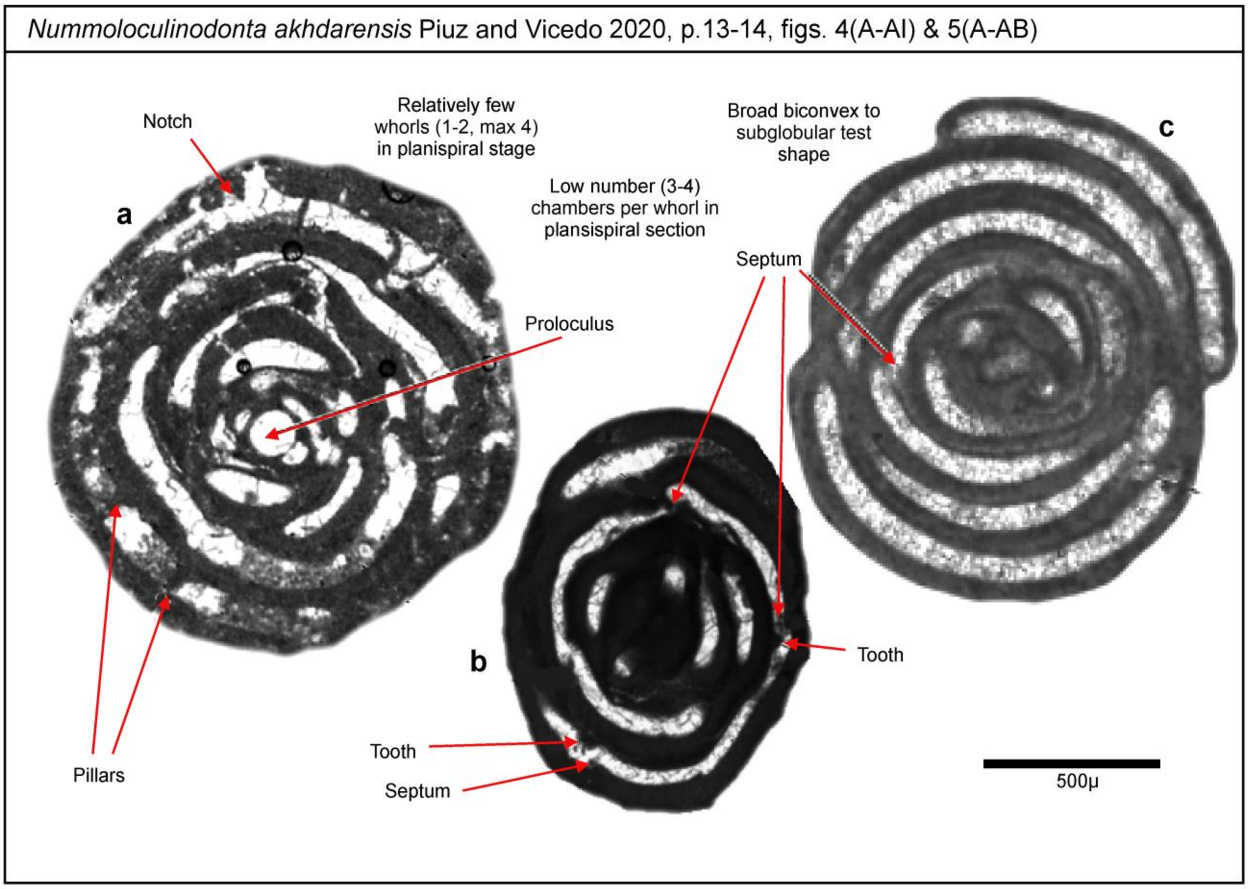


Fig. 52 Representative illustrations of *Nummoloculinodonta akhdarensis*: **a** Tangential section (near equatorial), Piuz and Vicedo (2020, fig. 4Z, Oman); **b** Tangential section, Piuz and Vicedo (2020, fig. 5F, Oman); **c** Tangential section (near axial), Piuz and Vicedo (2020, fig. 4AG, Oman).

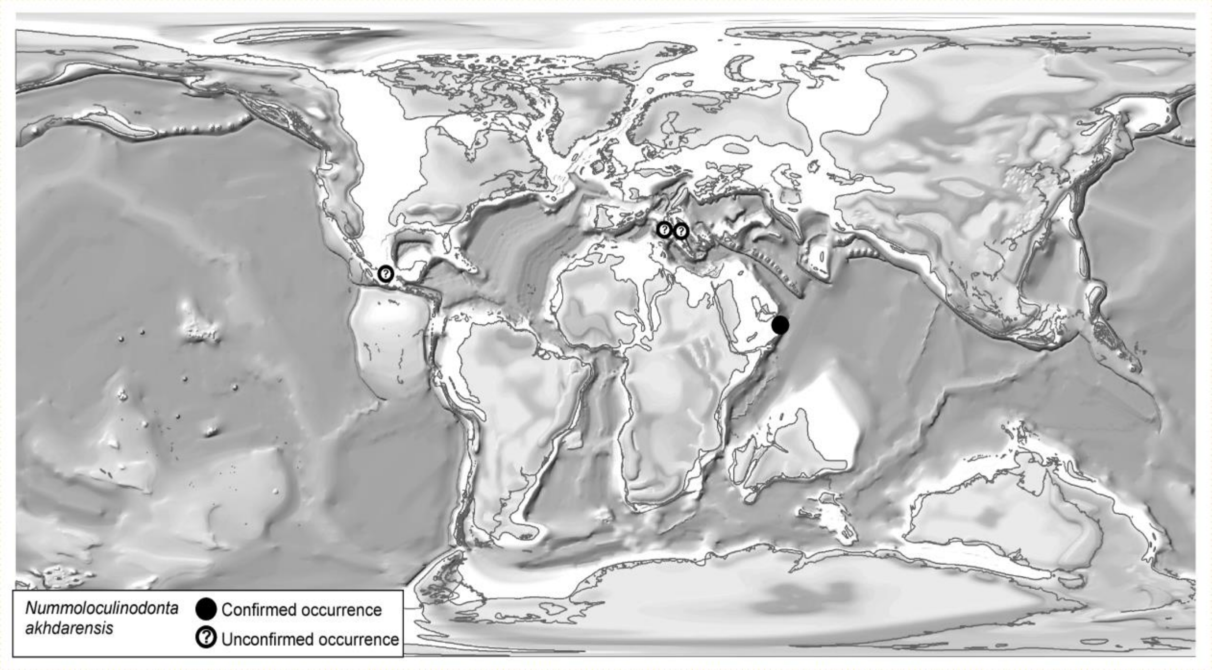


Fig. 53 Cenomanian paleogeographic distribution of *Nummoloculinodonta akhdarensis*.

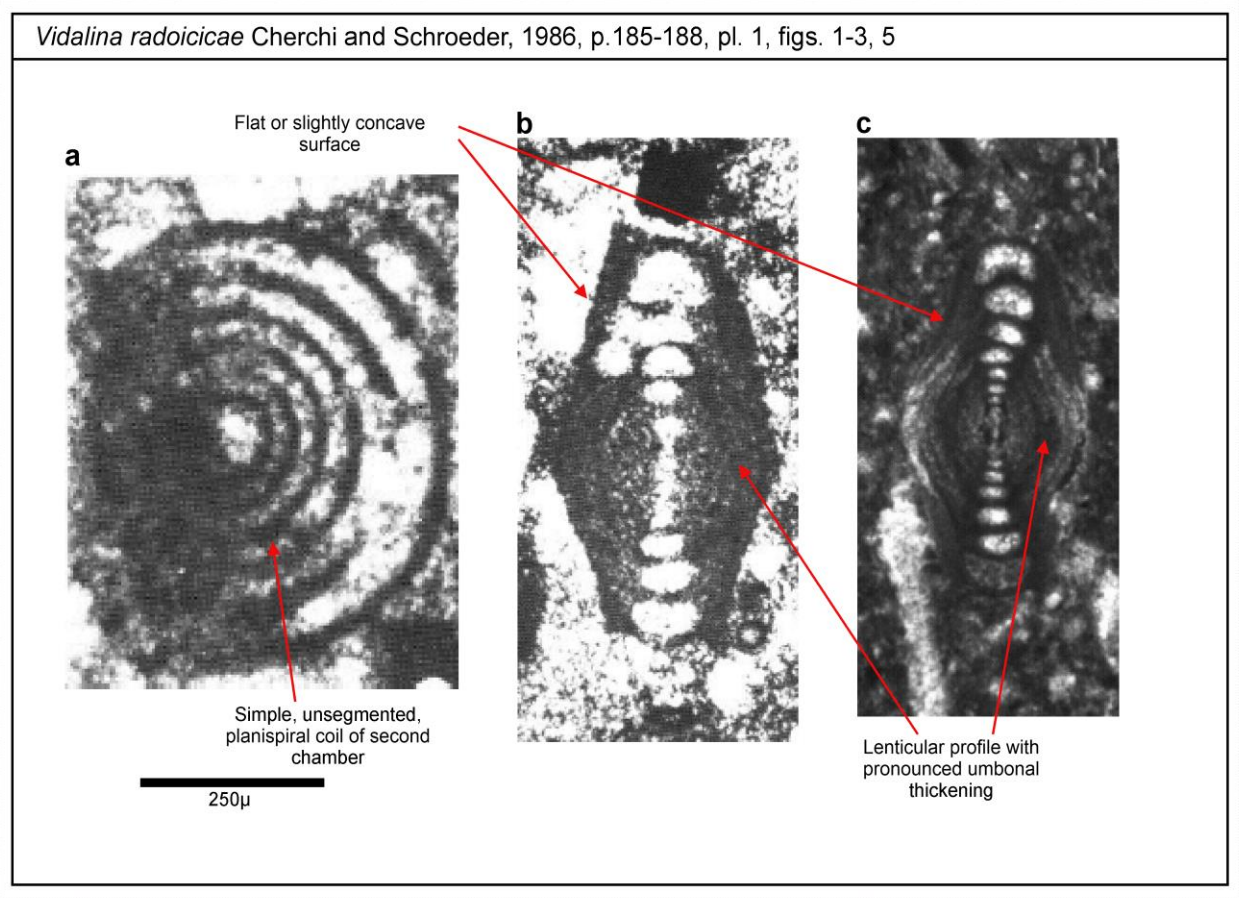


Fig. 54 Representative illustrations of *Vidalina radoicicae*: **a** Equatorial section, Cherchi and Schroder (1986, pl. 1, fig. 5, Sardinia); **b** Axial section, Cherchi and Schroeder (1986, pl. 1, fig. 2, Sardinia); **c** Axial section, Frijia et al. (2015, fig. 7M, Italy).

The wall is porcelaneous, and the aperture is a simple opening at the end of the tube. Additional lamellae are laid down with each coil, so the central part of the coil is continually thickened. *V. radoicicae* – first formally described from the late Cenomanian of the Anglona region, NW Sardinia by Cherchi & Schroeder (1986) – has a more-or-less lenticular axial cross-section with 6-7 adult coils. Of the other known species, *Vidalina hispanica* Schlumberger (see Decrouez et al., 1978; Farinacci, 1991; Schlagintweit, 1992), has more coils (12-14), is larger (maximum equatorial dimension 1.0-1.5mm compared with 0.25-0.43 mm) and is more disc-like with a thick central boss rather than being lenticular, whilst *V. discoidea* Schlagintweit is very disc-like with only limited umbilical thickening (Schlagintweit, 1992). *V. carpathica* Neagu & Popescu is not thought to range above the Barremian (Neagu & Popescu, 1966). See the Species Key Chart (Appendix) for diagnostic and other characteristics.

V. radoicicae is thought to be restricted to the Cenomanian whereas *V. hispanica* was first described from the Santonian, although Schlagintweit (2008) suggests *V. hispanica* could have been identified (as the type material of *Nummoloculina regularis* Philippson – a view disputed by Piuz & Vicedo (2020)) from as old as the Late Turonian in Austria. Cherchi & Schroeder (1986) consider that *V. hispanica* is possibly a descendant of *V. radoicicae*.

V. radoicicae can potentially be confused with nummoloculinids in equatorial views if the post-embryonic chamber appears segmented. "*Short indentations of the wall from the upper side into the tube lumen*" were observed by Schlagintweit (2008) in specimens he regards as *V. hispanica* (see above), giving a false appearance of chambering. Axial views are potentially confusable with taxa such as *Charentia cuvillieri* (see Korbar et al., 2012). Ideally, both axial and equatorial views are required to confirm illustration but are seldom provided in the literature.

Some authors (Chiocchini et al., 2012 from the Italian Apennines (as "?*V. radoicicae*", late Cenomanian); Jez et al., 2011, from Slovenia (as "*Vidalina* cf. *radoicicae*", late Cenomanian); Tentor & Tentor 2007, from northeast Italy (late Cenomanian); Solak et al., 2020, from the Turkish Taurides (middle – late Cenomanian) have illustrated axial views of forms identified as *Vidalina* but which do not show the characteristic lenticular axial profile of *V. radoicicae* and whose specimens appear rather more parallel-sided and are confusable with *Pseudonummoloculina*? *regularis* herein. These are treated as unconfirmed and may represent as yet undescribed taxa. On the other hand, specimens of *Vidalina* appear to be easily transported and often appear to be abraded or coated in micrite, making the true external shape difficult to determine.

Ghanem & Kuss (2013) illustrate "*Vidalina* cf. *radoicicae*" from the late Aptian of northwest Syria, but these specimens are clearly very distinct from true *V. radoicicae* and represent a different taxon. This is also true for their late Albian "*Vidalina* sp.". The equatorial view of a specimen attributed to *V. radoicicae* by Ghanem & Kuss (2013) has some hints of chamber segmentation and is also therefore regarded as unconfirmed – note that these authors regard this species as being of biozonal value and useful for distinguishing the late Cenomanian (see below).

Stratigraphic Distribution

(Late early?) middle – late Cenomanian.

V. radoicicae was first recorded from the late Cenomanian (associated with *Cisalveolina fraasi*) of western Serbia as "*Vidalina* sp. 1 (nov. sp.?)" by Radoičić (1972). Subsequently it was formally described from the late Cenomanian of Sardinia (Cherchi & Schroeder, 1986), and has been regarded as a marker for this substage by some (e.g., Velić & Vlahović, 1994; Velić, 2007; Rahimpour-Bonab et al., 2012; Ghanem & Kuss, 2013), but a literature review suggests a longer range into at least the middle Cenomanian.

All confirmed illustrated material are assigned a late Cenomanian or middle – late Cenomanian age. From Italy, these include Barattolo (1984) (as *Vidalina* sp.); Foglia (1992) (late middle – early late Cenomanian); Benedetti et al. (2000) (early late Cenomanian); Simone et al. (2012) (middle Cenomanian) and Frijia et al. (2015) (late Cenomanian); from Greece Fleury (1971) (as *Nummoloculina regularis*); Decrouez et al. (1978) (as *V. hispanica*); from Croatia Velić & Vlahović (1994) and Velić (2007); from the Turkish Taurides Tasli et al. (2006) (middle – late Cenomanian), Sari et al. (2009) (middle – late Cenomanian), Solak (2021) (as "*Vidalina* sp.") (middle – late Cenomanian) (the illustration by Solak et al., 2017 is more uncertain); and from the Iranian Zagros Rahimpour-Bonab et al. (2012) (late Cenomanian) and Mohajer et al. (2021a) (late Cenomanian). An illustration by Schlagintweit & Rigaud (2015) from the late middle – early Cenomanian of Kosovo is uncertain. An illustration of "*Vidalina* sp." by Hamaoui (1962) from the late (?) Cenomanian of Israel may be *V. radoicicae*.

Records unconfirmed by illustration are assigned to ages confined within the Cenomanian, mostly middle – late Cenomanian. From Spain these include Calonge et al. (2002, 2003); from the Italian Apennines Bravi et al. (2006); Chiocchini (2008a, 2008b); Chiocchini et al. (2008); Mancinelli & Chiocchini (2006); Parente et al. (2007, 2008) – who places the LAD of *V. radoicicae* within the *geslinianum* ammonite zone, Frijia & Parente (2008); Spalluto (2011) and Spalluto & Caffau (2010); from the Balkans Brčić et al. (2017) (the specimen illustrated by Brčić (2015) is probably *Charentia cuvillieri*, but that by Brčić et al. (2021) (late Cenomanian) may be valid), Božović (2016), Husinec et al. (2000), Del Viscio et al. (2022); and from the Iranian Zagros Mohajer et al. (2022a, 2022b), Omidvar et al. (2014b) and Rahimpour-Bonab et al. (2013). An unillustrated record by Cruz-

Abad (2018) is from the early Cenomanian of the Italian Apennines, as is a somewhat uncertain illustrated record by Bravi et al. (2004), and if valid they would be the oldest records known. "*Vidalina* sp." from the supposed early Cenomanian of southeast Turkey (Ozkan & Altiner, 2019) (but possibly middle Cenomanian (see Simmons et al., 2020b)) is a distinctly separate taxon.

Cenomanian Paleogeographic Distribution

Neotethys.
Not particularly widely reported except for the area around Italy and the Balkans but confirmed as far east as the Iranian Zagros.

Genus ***Nummofallotia*** Barrier & Neumann, 1959
Type Species: *Nonionina cretacea* Schlumberger, 1900
***Nummofallotia*? *apula* Luperto-Sinni, 1968**

Reference Illustration & Description

Luperto-Sinni in Schroeder & Neumann (1985), pl. 48, p. 100-101 (but see below for issues regarding stated magnifications). The species is also well illustrated by Saint-Marc (1970, pl. 2, figs. 10-15; 1974a, pl. XIII, figs. 13-19).

Nummofallotia was introduced by Barrier & Neumann (1959) with the Late Cretaceous (Coniacian - Maastrichtian) taxon *Nonionina cretacea* Schlumberger as type species. The test is lenticular, planispirally enrolled, periphery rounded to subangular, with a globular proloculus followed by whorls of regularly enlarging chambers. Adults are involute with septa that are slightly oblique and slope backwards at the periphery. An umbo (also sometimes called umbilical "plug" or "button") of radial fibrous calcite is a distinctive feature in most specimens (Hottinger & Caus, 2009).

Luperto-Sinni (1968) introduced a new species, *Nummofallotia apula*, with type material from the "Senonian" of southern Italy, which is smaller and with fewer whorls than *N. cretacea*. Originally described as possessing a single-layered wall, Bilotte & Decrouez (1979) subsequently stated that the test wall of *N. apula* is, in its entirety, made up of two layers: an inner layer dark microgranular, and a clear outer layer hyaline-radiated, thicker in the axial zone (see for example illustrations by Saint-Marc, 1970, 1974a), leading them to introduce a new genus, *Murgeina*, with *N. apula* as the type species. Although accepted by, for example, Loeblich & Tappan (1988), the necessity to introduce this genus was subsequently questioned by Luperto-Sinni in Schroeder & Neumann (1985) who noted that the two layered wall structure is a variable, inconsistent feature, and that otherwise *N. apula* conforms perfectly to the nature of *Nummofallotia*. That said, in 1998, she introduced a further new species of *Nummofallotia*, *Nummofallotia cenomana*, which alongside its supposedly very small size (see below), a distinguishing feature was said to be a consistent two layered wall structure. Therefore, there is some debate if *Murgeina* is a valid genus. A detailed taxonomic revision of all species of *Nummofallotia/Murgeina* is required using pristine material. This is outside the scope of this primarily stratigraphic/biogeographic review and therefore we tentatively retain *N. apula* within *Nummofallotia* as "*N.*? *apula*".

N.? apula is a small biumbonate form, with maximum dimensions (diameter) of around 0.3 – 0.5 mm (holotype 0.32 mm), a thickness of around 0.15 – 0.25 mm (holotype 0.18mm) a large, 0.06-0.08 mm (holotype 0.06 mm), globular proloculus in macrospheric forms, followed by 3 whorls with 16-20 quadrangular chambers in the last whorl. It is distinctively smaller than *N. cretacea*, that has typical diameters of around 0.6 – 0.8 mm (although possibly as small as 0.36 mm (Bilotte & Decrouez, 1979) and note that if the illustrations of Barrier & Neumann (1959) are correctly scaled, then specimens can be 2.0 – 3.0 mm in diameter, although this must be judged unlikely), thickness of 0.4 – 0.5 mm, 5 - 8 whorls, with more than 20 chambers in the last whorl (e.g., Luperto-Sinni, 1968). Although the same specimens of *N.? apula* are illustrated by Luperto-Sinni (1968) and Luperto-Sinni in Schroeder & Neumann (1985), including the types, there are small differences in size based on the magnifications provided.

N. cenomana was described as a distinctively small (stated diameter dimensions: 0.09 – 0.1 mm) species (Luperto-Sinni, 1998), known from the Cenomanian of southern Italy. If the figures provided by Luperto-Sinni (1998) are taken on face value, using the magnifications as given, the diameters are larger (c. 0.23 mm), but still distinctly small compared to *N.? apula*. Luperto-Sinni (1998) implied that *N. cenomana* was the Cenomanian form of *Nummofallotia*, whilst *N.? apula* was the "Senonian" form. However, she did not discuss further the various Cenomanian records of *N.? apula* (see below), which conform to the type description of this species. Thus, the notion that *N.? apula* does not occur in the Cenomanian is rejected. Other than its type description, the only other mentions of *N. cenomana* in the literature are from the Iranian Zagros (e.g., Schlagintweit & Yazdi-Moghadam, 2020, as "*N.*? *cenomana"*), where the specimens would be better assigned to *N.? apula*, based on size and morphology. The types of *N. cenomana* need to be examined and re-illustrated as part of a taxonomic re-evaluation of *Nummofallotia/Murgeina*, and this taxon is not considered further herein. (As this paper was going to press, Schlagintweit et al. (2023) published a review of this species (as *Murgeina apula*) with illustration from the Cenomanian Sarvak Formation of the Iranian Zagros.)

Nummofallotia kastomonica Özgen Erdem is an upper Maastrichtian species described from northern Turkey (Özgen Erdem, 2001). It differs from *N. apula* by virtue of its large size (stated diameter 0.43 – 1.02 mm; a possible expression of Cope's Rule?), tighter coiling, greater number of whorls and chambers, straight septa, and smaller umbo.

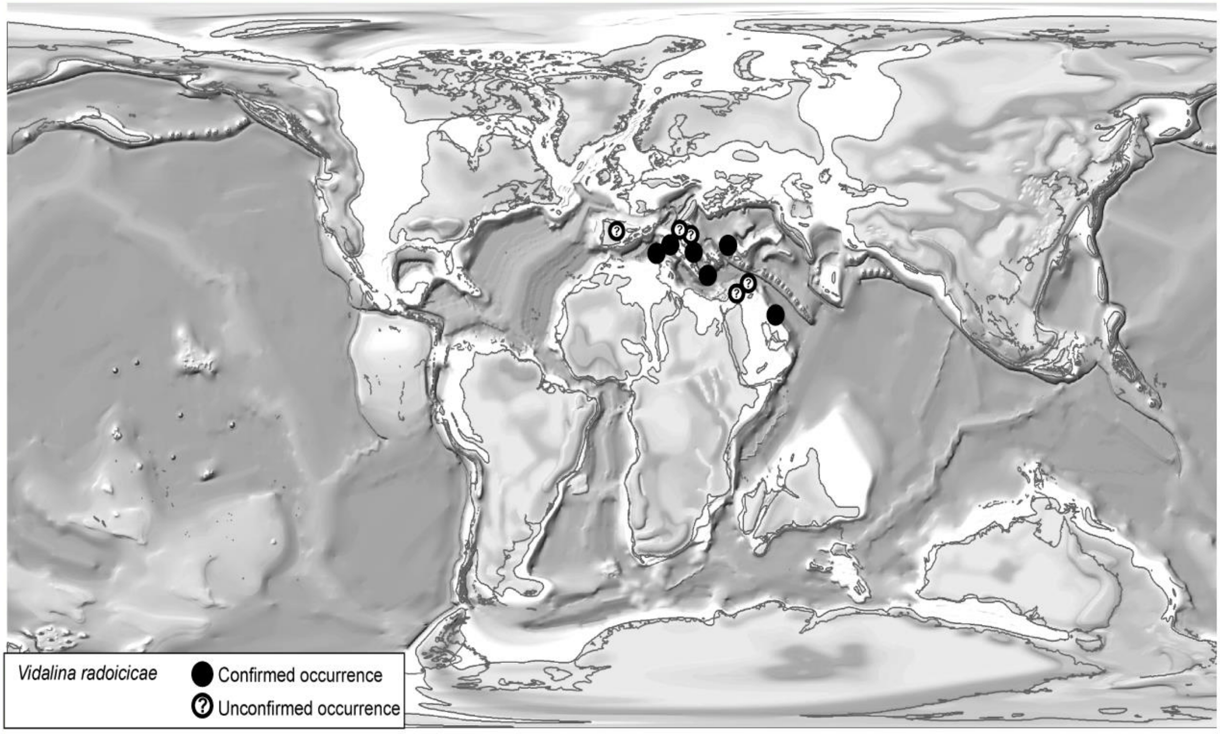


Fig. 55 Cenomanian paleogeographic distribution of *Vidalina radoicicae.*

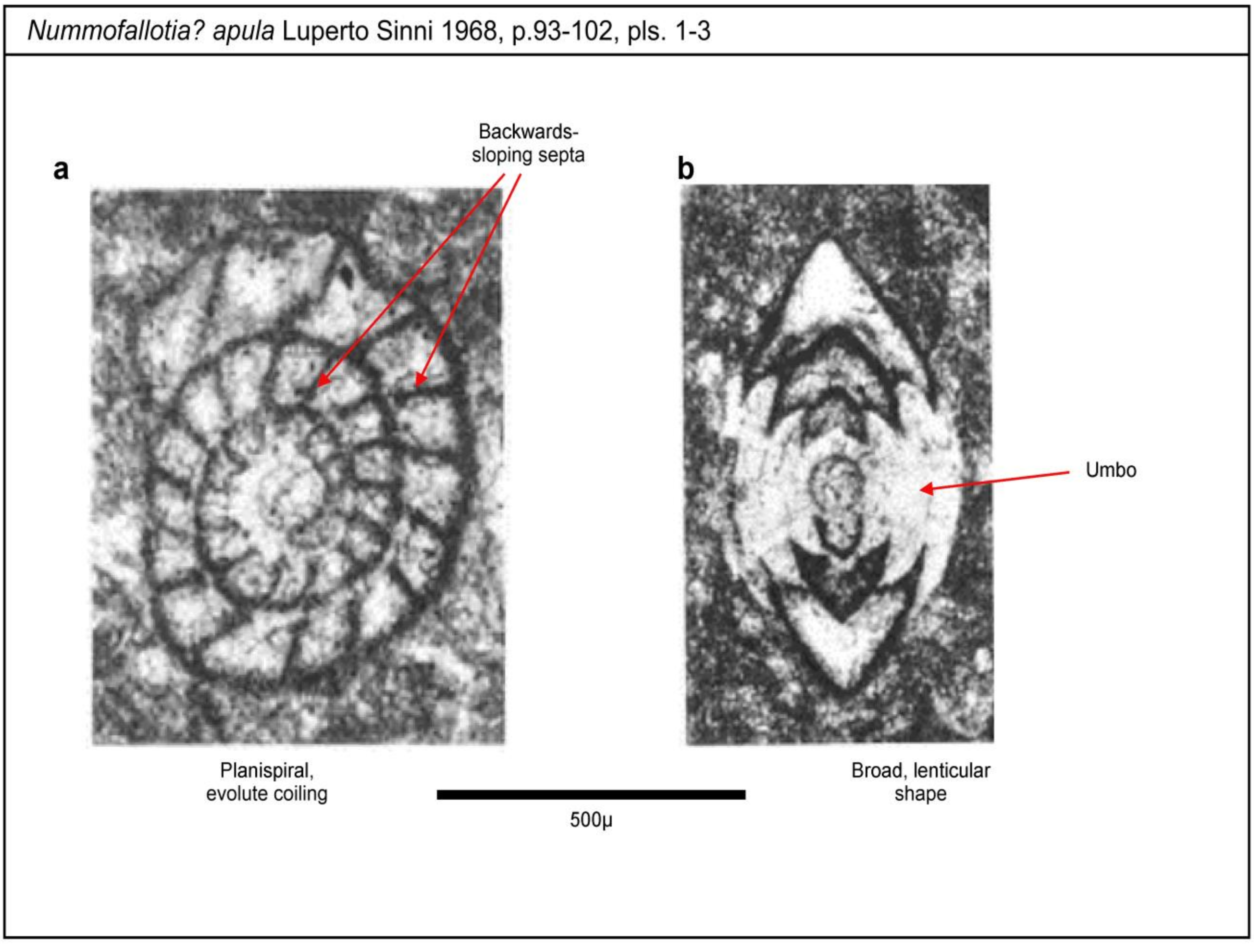


Fig. 56 Representative illustrations of *Nummofallotia? apula*: **a** Equatorial section, Saint-Marc (1974, pl. XIII, fig. 16, Lebanon); **b** Axial section, Saint-Marc (1970, pl. 2, fig. 12, Lebanon).

Stratigraphic Distribution

Middle Cenomanian – ?Maastrichtian.

N.? apula was originally described from the "upper Senonian" (possibly Maastrichtian but probably no younger than middle Campanian) of southern Italy (Luperto-Sinni, 1968). It appears to have an unusually long stratigraphic range almost throughout the Late Cretaceous (e.g., Luperto-Sinni & Ricchetti, 1978; Perugini, 2006; Velić, 2007; Sari et al., 2009), but its FAD lies within the Cenomanian.

Unillustrated records of *N.? apula* from the Barremian of the Iranian Zagros (Abyat et al., 2016) must be discounted, as probably should the comment by Keshavarzi et al. (2021) that the oldest occurrence of *N.? apula* marks the base of the Sarvak Formation in the Iranian Zagros which would place it close to the Albian/Cenomanian boundary (Bromhead et al., 2022). No illustration is provided. A Lower Cenomanian record by Radoičić et al. (2010) can be reassessed as middle Cenomanian based on associated fauna. Finally, a record of *N.? apula* from the Yamama Formation of southern Iraq (Al-Hassani & Al-Dulaimi, 2021) which is Berriasian – Valanginian in age (although the authors describe the material as "early Aptian") illustrates a fragmentary specimen of *Lenticulina* sp. or *Epistomina* sp. Although many records are from the late Cenomanian, Bachmann et al. (2003 - unillustrated) using graphic correlation between sections in Egypt positioned the FAD at or close to the early-middle Cenomanian boundary (following Saint-Marc, 1978; Luperto-Sinni in Schroeder & Neumann, 1985). Chiocchini (2008a - unillustrated) showed a short range for the species in the lowest part of the "late" Cenomanian (Chiocchini used only early and late subdivisions of the Cenomanian which would suggest this range FAD is approximately within the chronostratigraphic middle Cenomanian). Ghanem & Kuss (2013) showed the range of this species (although they illustrated it as cf.) extending into the (upper) middle Cenomanian of Syria, calibrated by planktonic foraminifera. A similar FAD was placed by Schlagintweit (1992) from Austria, and Simone et al. (2012) from Italy, although without independent calibration. Bravi et al. (2004) plausibly illustrate this species from the middle Cenomanian of Central Italy.

Cenomanian Paleogeographic Distribution

Caribbean/North Africa? - Neotethys.

References in Luperto-Sinni in Schroeder & Neumann (1985) indicate Cenomanian records from Lebanon (Hamaoui & Saint-Marc 1970; Saint-Marc 1970, 1974a, 1981), Greece (Decrouez, 1975, 1977; Charvet et al., 1976; see also Fleury, 1971), and Serbia (Radoičić 1974a). In addition, records confirmed by definite or plausible illustration include Italy (Benedetti et al., 2000), south-east Turkey (Özcan & Altiner 2019); and the Iranian Zagros (Sartorio & Venturini, 1988; Jamalpour et al. 2018, Kiarostami et al. 2019, Mohajer et al. 2021a, 2022a, b; an illustration by Mohseni & Javanmard, 2020 is uncertain). Illustrations from Tunisia (Bismuth et al. 1981) and Syria (Ghanem & Kuss 2013 – as cf.), may be more compatible with *N. cenomana* based on their small size (diameter 0.2 – 0.3 mm). Another record from Tunisia (Abdallah et al., 1995) is more likely *Charentia cuvillieri* Neumann.

Cenomanian records from other locations but unconfirmed by illustration include Cuba (Diaz Otero, 1985); Mexico (Michaud et al., 1984; Hernández-Romano et al., 1997; Aguilera-Franco, 2000; Aguilera-Franco & Allison, 2004); Morocco (El-Kadiri et al., 2003, Piuz & Meister, 2013); Egypt (Bachmann et al., 2003; an illustration by Orabi, 1992 is uncertain); Iraq (Hamaoui & Brun, 1974; Bernaus & Masse, 2007; Mahdi et al., 2013), Jordan (Schulze 2003, Schulze et al., 2004) and the Oman Mountains (Rabu 1993; Al-Balushi & Macquaker, 2011; Piuz & Meister, 2013).

Localities from strata younger than Cenomanian are not included herein.

Genus ***Peneroplis*** De Monfort, 1808

Type Species: *Peneroplis planatus* (Fichtel & Moll, 1798) (type by original designation)

Peneroplis parvus **De Castro 1965**

Reference Illustration & Description

De Castro in Schroeder & Neumann (1985), Pl. 39, p. 86-88.

Originally described as *Peneroplis planatus* (Fichtel & Moll) n. ssp. *parvus*, the type and subsequent descriptions of the species by De Castro (1965, 1985) are comprehensive and allow for confident identification (see also Calonge-Garcia, 1996; p. 38, pl. 2, figs. 8-13). A peneropolid with a porcelaneous, imperforate wall and multiple cribrate apertures. 5-6 chambers in the first whorl, 7-11 in the last (second) whorl. May become flabelliform. The species is very similar to the extant *Peneroplis planatus* (Fitchell & Moll), but with a smaller size (equatorial diameter c. 0.82mm), plus more adult chambers per mm (11.5-17.5). See the Species Key Chart (Appendix) for diagnostic and other characteristics.

P. parvus is amongst the oldest known representatives of *Peneroplis*, a genus often regarded as restricted to the Cenozoic and Recent (Loeblich & Tappan, 1988; Bou-Dagher-Fadel, 2008). Chiocchini (2008a) introduced *Peneroplis cairoensis* from the initial part of their late Cenomanian (=intra-middle Cenomanian) of central Italy. This species is slightly larger than *P. parvus* (c. 1.2 mm diameter), has a greater number of chambers in the uncoiled stage and a larger diameter of apertural pores. It has not been recorded from outside its type area and is not considered further. *Peneroplis aragonensis* is a species introduced from the late Albian of the Spanish Pyrenees by Peybernès (1984) as *Broeckinella? aragonensis* and subsequently transferred to *Peneroplis* by Schlagintweit & Rashidi (2020). This species is much larger than

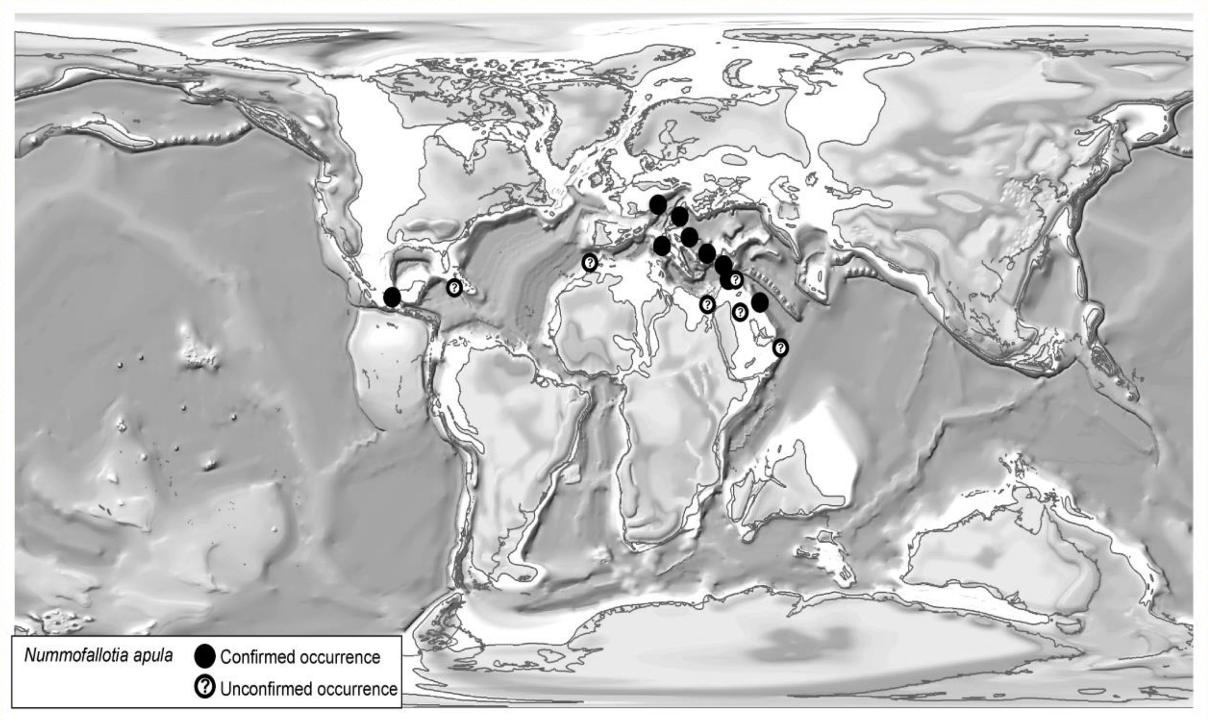


Fig. 57 Cenomanian paleogeographic distribution of *Nummofallotia? apula*.

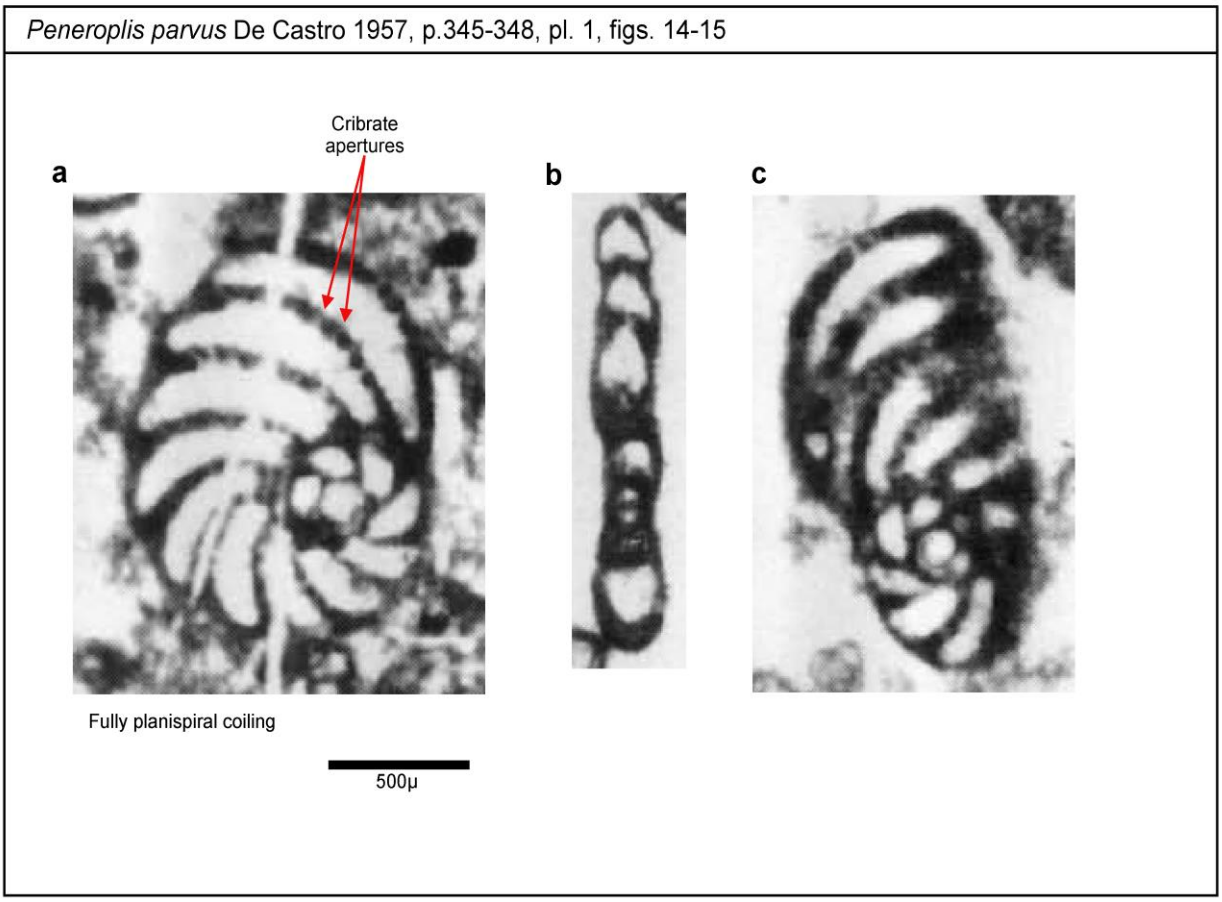


Fig. 58 Representative illustrations of *Peneroplis parvus*: **a** Equatorial section, De Castro in Schroeder & Neumann (1985, pl. 39, fig. 1, Italy); **b** Axial section, De Castro in Schroeder & Neumann (1985, pl. 39, fig. 13, Italy); **c** Oblique axial section, De Castro in Schroeder & Neumann (1985, pl. 39, fig. 5, Italy).

P. parvus (diameter c. 4.5mm) with a tendency to become sub-annular in macrospheric forms. It too has not been recorded outside its type area and is not considered further. Saint-Marc (1974a) illustrated a "*Peneroplis* sp." from the late Albian of Lebanon. This is a rapidly uncoiling form, broader and more rounded than *P. parvus* in axial section, and slightly larger. Consorti (in Consorti et al., 2018) introduced a new genus and species, *Pseudopeneroplis oyonensis*, from the upper Cenomanian of Peru. In contrast to *Peneroplis* this taxon develops subdivisions in the marginal area of the chamber lumen but is otherwise similar.

A potential confusion species is *Neodubrovkinella turonica* Said & Kenawy. Originally described as a species of *Peneroplis* ("*Peneroplis turonicus*") from Egypt (Said & Kenawy, 1957), this taxon has been shown by Schlagintweit & Yazdi-Moghadam (2022a) to be a biokovinid (and Cenomanian, not Turonian). In well-preserved material the finely agglutinating wall with a pseudo-keriothecal structure is visible, excluding it from the Miliolida. In specimens where the wall structure is not clear, a large proloculus in megalospheric forms, a tendency to rapidly uncoil with chambers enlarging rapidly, are sufficient to distinguish *N. turonica* from *P. parvus,* as is occasional streptospiral coiling in early chambers. It is worth noting that in many thin-sections, and even illustrations of three-dimensional specimens, the porecellanous nature of the wall of *P. parvus* can be difficult to determine.

Stratigraphic Distribution

Late Albian/early Cenomanian – late Cenomanian.

The stratigraphic range of *P. parvus* has been the subject of a range of opinions in the literature. In his original description, De Castro (1965) thought the type material (from central Italy) to be probably middle Cenomanian in age, a view maintained by him in 1985 (De Castro in Schroeder & Neumann, 1985), although he considered the overall range to be latest Albian to intra-middle Cenomanian based on his assessment of known occurrences to that time. However, in 1991 he considered that in the broad type area an upper Albian – lower Cenomanian biozone could be introduced based on the total range of the species. Similarly, Chiocchini et al. (2012) illustrated the species and limited its range to the around the Albian – Cenomanian boundary. By contrast Calonge-Garcia (1996) and Bilotte (1998) restricted the species to the lower Cenomanian, and Velić (2007) to the upper Cenomanian.

Determining the range of this species is hampered by a lack of unequivocal illustrations in the literature coupled with a lack of independent age calibration. De Lapparent et al. (1974) provided an unillustrated record of *P. parvus* from Afghanistan and also points out the difficulties in establishing the difference between the Cenomanian and Turonian in sections devoid of ammonites. Upper Cenomanian records can be supported by the illustrated record from Croatia of Velić & Vlahović (1994), the illustrated occurrence from undifferentiated middle – upper Cenomanian of central Mexico by Omaña et al. (2013, 2014, 2019), and the illustrated record of Shahin & El Baz (2010, 2013) from Sinai. An additional illustrated record from southeast Mexico is that of Rosales-Dominguez et al. (1997) but their assessment that it is "post Cenomanian" in age is based partly on circular reasoning and is incorrect. The unusual Turonian record of Orabi & Khalil (2001) from Sinai is not substantiated by illustration.

Other than Chiocchini et al., (2012), late Albian and early Cenomanian records of the species lack substantiation by illustration but include Scott (2002) from Mexico; Calonge et al., (2002); Caus et al. (2009); Vicedo et al., (2011) and Consorti et al., (2016b) from Spain; Bachmann et al. (2003) from Sinai; and Ilavsky & Salaj (1969) from Tunisia. Although not illustrated, the middle Cenomanian record from Lebanon of Saint-Marc (1981) is important as the co-occurrence with the ammonite *Calycoceras gentoni* (Brongniart) supports a middle Cenomanian age calibration.

Cenomanian Paleogeographic Distribution

Caribbean – Neotethys (and ?Afghanistan).

In addition to the records above, the species as been recorded from other parts of southern Italy (Luperto-Sinni & Borgomano, 1989 (late Cenomanian); Borghi & Pignatti, 2006 (late Cenomanian); Di Stefano & Ruberti, 2000, all without illustration) and the Iranian Zagros (Jamalpour et al., 2018 (illustrated), (but not Omidi et al., 2018; Mohajer et al., 2021a, 2022a, b).

The records from Greece (Fleury, 1980 (also 1971, unillustrated) = possible *Pseudorhapydionina sp.*) and Syria (Ghanem & Kuss, 2013 = possible peneropolid, but not *P. parvus*) have illustrations which are not compatible with this species, whilst those from southern Turkey (Tasli et al., 2006; Sari et al., 2009) and southern Iraq (Al-Salihi & Ibrahim, 2023) are tentative or unconfirmed by illustration.

Genus ***Pseudorhapydionina*** De Castro, 1972

Type Species: *Rhapydionina laurinensis* De Castro, 1965

***Pseudorhapydionina anglonensis* Cherchi & Schroeder, 1986**

Reference Illustration & Description

Cherchi & Schroeder (1986), Pl. 1 (figs. 4, 6, 8-11), p. 188. First proposed in a 1985 field guide and declared *nomen nudum* by the authors in their 1986 publication.

P. anglonensis is atypical for the genus and may not even be correctly assigned to it (as indicated by Cherchi and Schroeder by a "?" in their original description) in that there is no uncoiled portion. Cherchi & Schroeder (1986) were unable to confirm the presence of a cribrate aperture except in the last few chambers and therefore questioned the generic assignment, but Consorti et al. (2016b) using material from Spain confirmed it from early chambers

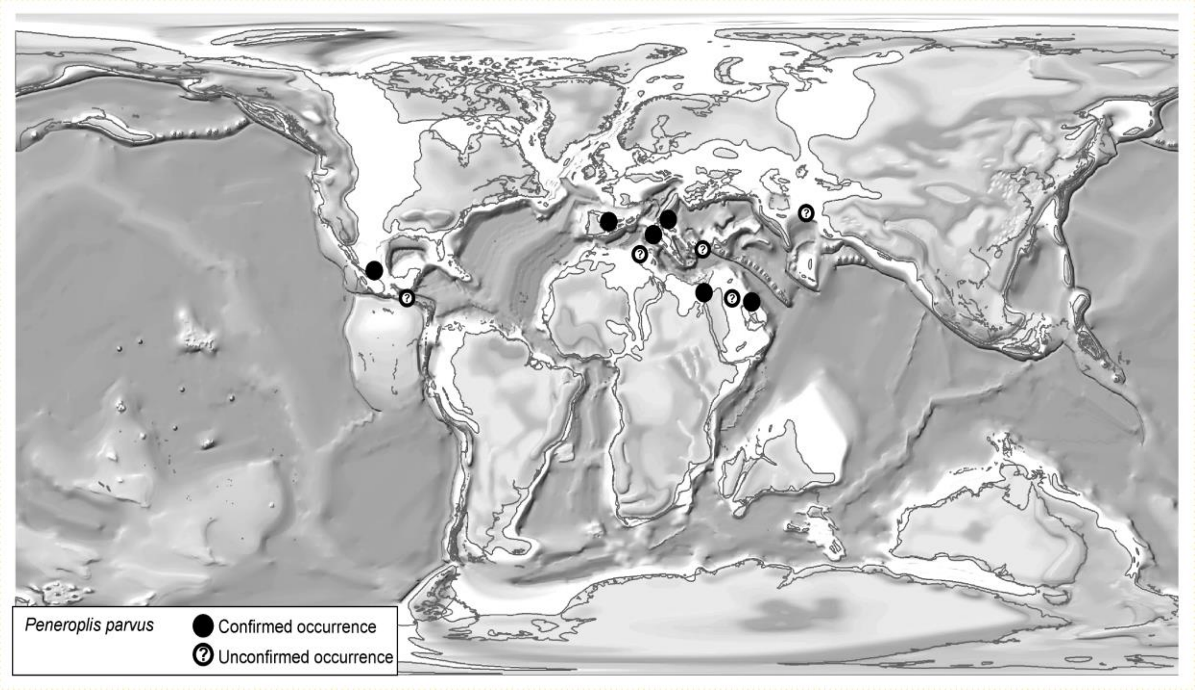


Fig. 59 Cenomanian paleogeographic distribution of *Peneroplis parvus.*

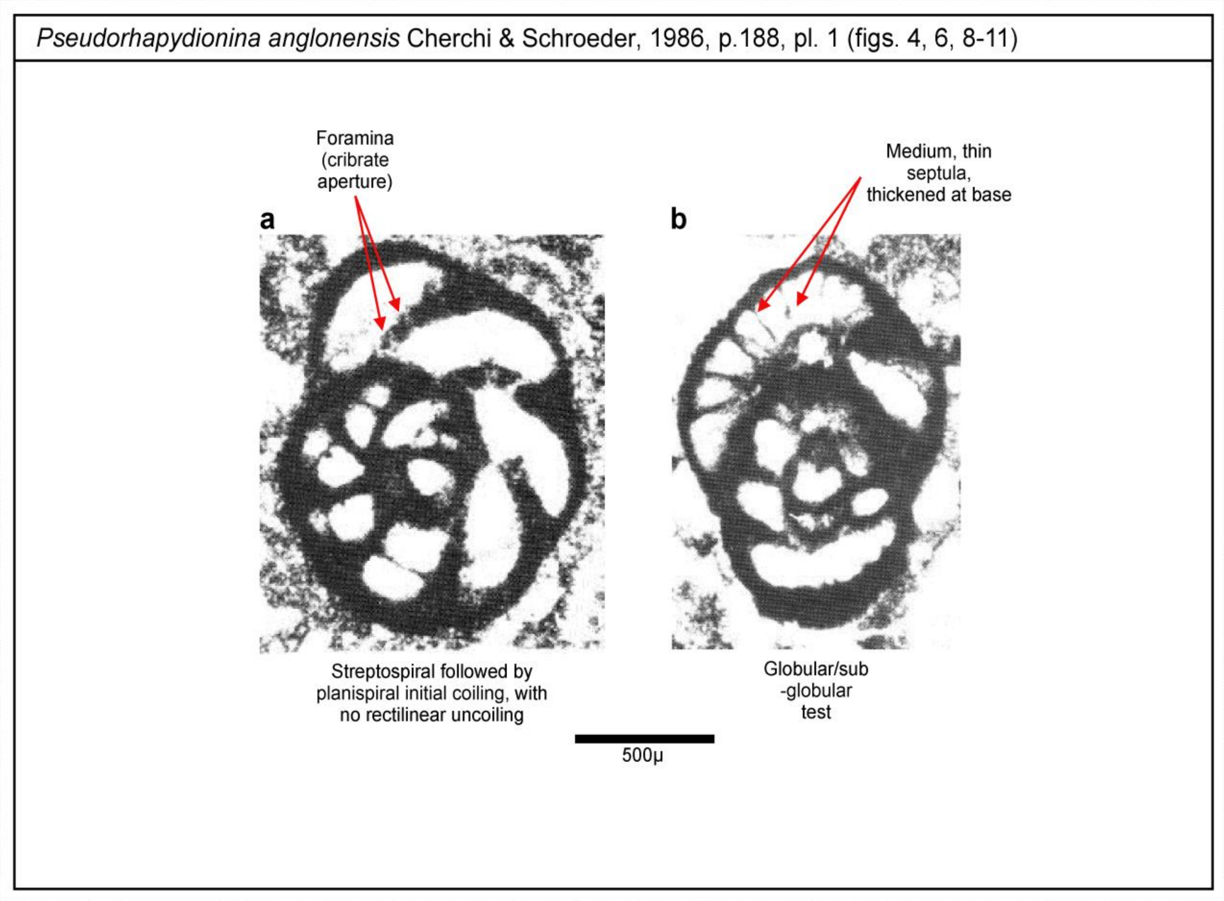


Fig. 60 Representative illustrations of *Pseudorhapydionina anglonensis*: **a** Equatorial section, Cherchi & Schroeder (1986, pl. 1, fig. 11, Sardinia); **b** Axial section, Cherchi & Schroeder (1986, pl. 1, fig. 4, Sardinia).

and thus the generic assignment. However, the total observed material is relatively limited in scope and abundance and uncoiled examples may be recorded in the future. Typical characteristics of the genus are discussed under *P. laurinensis* (De Castro) herein.

Solak et al. (2017) illustrated *P. anglonensis* from southern Turkey together with *P. dubia*. Their illustration of *P. anglonensis* (see Solak et al., 2017: fig. 8V) is very similar to the coiled stage of one of their *P. dubia* specimens (see Solak et al., 2017: fig. 8R). This leads to the suspicion that the former species is simply a juvenile (uncoiled) form of the latter (see also comparative illustrations herein) with which it often co-occurs, and this name should appear in synonymy with *P. dubia*. Further studies are needed to test this view.

P. anglonensis (as currently defined) differs from all other *Pseudorhapydionina* species in apparently lacking an uncoiled, seriate stage. It has 10-12 total coiled chambers and septula which are thin and medium, thickened peripherally. See the Species Key Chart (Appendix) for diagnostic and other characteristics.

It is broadly similar to *Scandonea* spp. and *Moncharmontia* spp., but these do not have internal septula and, in the case of the latter, has more chambers. Note that some specimens described as *P. dubia* by De Castro in Schroeder & Neumann (1985) are considered as *P. anglonensis* by Cherchi & Schroeder (1986) and Mancinelli & Chiocchini (2006).

Fissumella motolae Cruz-Abad et al., a genus and species introduced from the early Albian of Italy (Cruz-Abad et al., 2017), resembles *P. anglonensis* with the presence of a few incomplete radial septula. However, these two genera differ in the nature of the aperture, which is cribrate in *Pseudorhapydionina*, but single and fissure-shaped in *Fissumella*.

Stratigraphic Distribution

Middle? – Intra-late Cenomanian.

Rarely recorded in the literature. Cherchi & Schroeder (1986) in their original description from Sardinia described the occurrence of *P. anglonensis* as late Cenomanian, a view upheld by Consorti et al. (2016b). Illustrations of *P. dubia* from the late Cenomanian of the Pyrenees by Bilotte (1984) may be *P. anglonensis*. However, in the Italian literature, where the species is often well illustrated (e.g., Mancinelli & Chiocchini, 2006; Chiocchini, 2008a, 2008b; Chiocchini et al., 2008, 2012), its occurrence is the lower part of the upper Cenomanian, where only a bipartite subdivision of the Cenomanian is used. This might equate to the middle Cenomanian or very low in the late Cenomanian of other authors.

Cenomanian Paleogeographic Distribution

Central Neotethys.

Recorded and plausibly illustrated only from Spain, Sardinia, Italy and the Turkish Taurides (see references mentioned above).

***Pseudorhapydionina dubia* (De Castro, 1965)**

Reference Illustration & Description

De Castro in Schroeder & Neumann (1985), pls. 40-42, p. 88-91.

The treatment of the genus and species by De Castro in Schroeder & Neumann (1985) is comprehensive and allows for confident identification. See also more comments on the genus under *P. laurinensis*, the type species. However, Cherchi & Schroeder (1986) regard some of De Castro's 1985 illustrations of *P. dubia* (pl. 42, figs. 6 & 15) as *P. anglonensis*.

Consorti et al. (2016b) provide useful illustration of *P. dubia* from the late Cenomanian of Spain (see also Calonge-Garcia, 1996; p. 34, pl. 2, figs. 4-7) together with a succinct description: "*Porcelaneous shell with subglobular to cylindrical morphology. The chambers in the early stage of growth are arranged in one and a half to two whorls. The specimens of the Iberian Ranges show four chambers in the first whorl and six or seven in the second one. The uncoiled adult stage consists generally of five cylindrical chambers. The globular early stage reaches a maximum diameter of 0.35 mm with an average of 0.29 mm. The seriate adult stage has an average length of 0.6 mm, and the height of the chambers is approximately 0.06 mm. The scarce centred sections show a proloculus of about 40 μm in diameter. The apertural face is convex and the aperture cribrate. The intercameral foramina are regularly disposed, forming a circular pattern with three concentric stipple rings in the septa. The chamber lumen is partially divided by radial septula, which number approximately 5-6 per quadrant in the seriate adult stage of growth. Septula are short and their thickness is less than 10 μm*." See the Species Key Chart (Appendix) for diagnostic and other characteristics.

When visible, the very early coiling may be streptospiral which may place this species as a miliolid rather than a soritid (De Castro in Schroeder & Neumann 1985).

P. dubia is very similar to the Central America endemic homeomorph *P. chiapanensis* but has fewer total coiled chambers (7-11 cf. 12-13); slightly fewer chambers in the seriate stage (3-7 cf. 4-9); septula which are thin and short (cf. thick and medium length); and more septula per quadrant in the seriate stage (7-9 cf. 5). Nonetheless, *P. dubia* occurs in the middle – late Cenomanian of Mexico as confirmed by illustration (Aguilera-Franco, 2000; Aguilera-Franco et al., 2001).

It differs from *P. laurinensis* in having generally parallel sides (= cylindrical) in the seriate stage rather than flaring and non-depressed sutures. The more extensive presence of long radial septula in *P. laurinensis* is a key difference.

P. dubia differs from *P. anglonensis* in possessing an uncoiled (seriate) stage, but also a smaller coiled stage

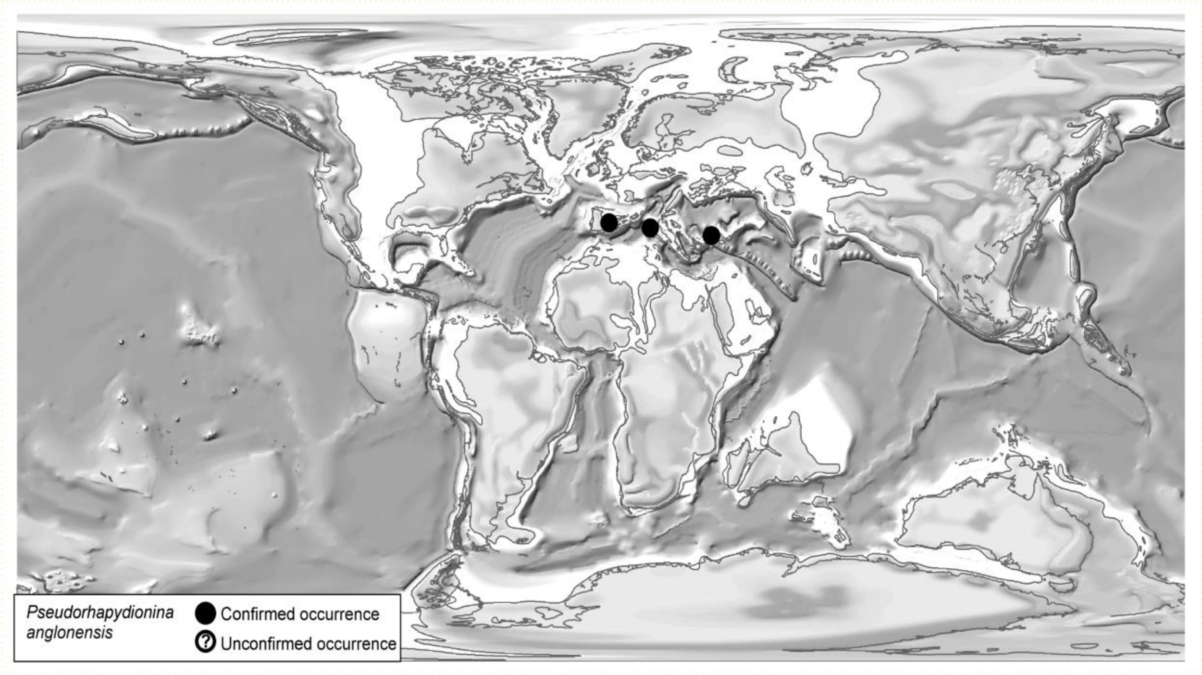


Fig. 61 Cenomanian paleogeographic distribution of *Pseudorhapydionina anglonensis*.

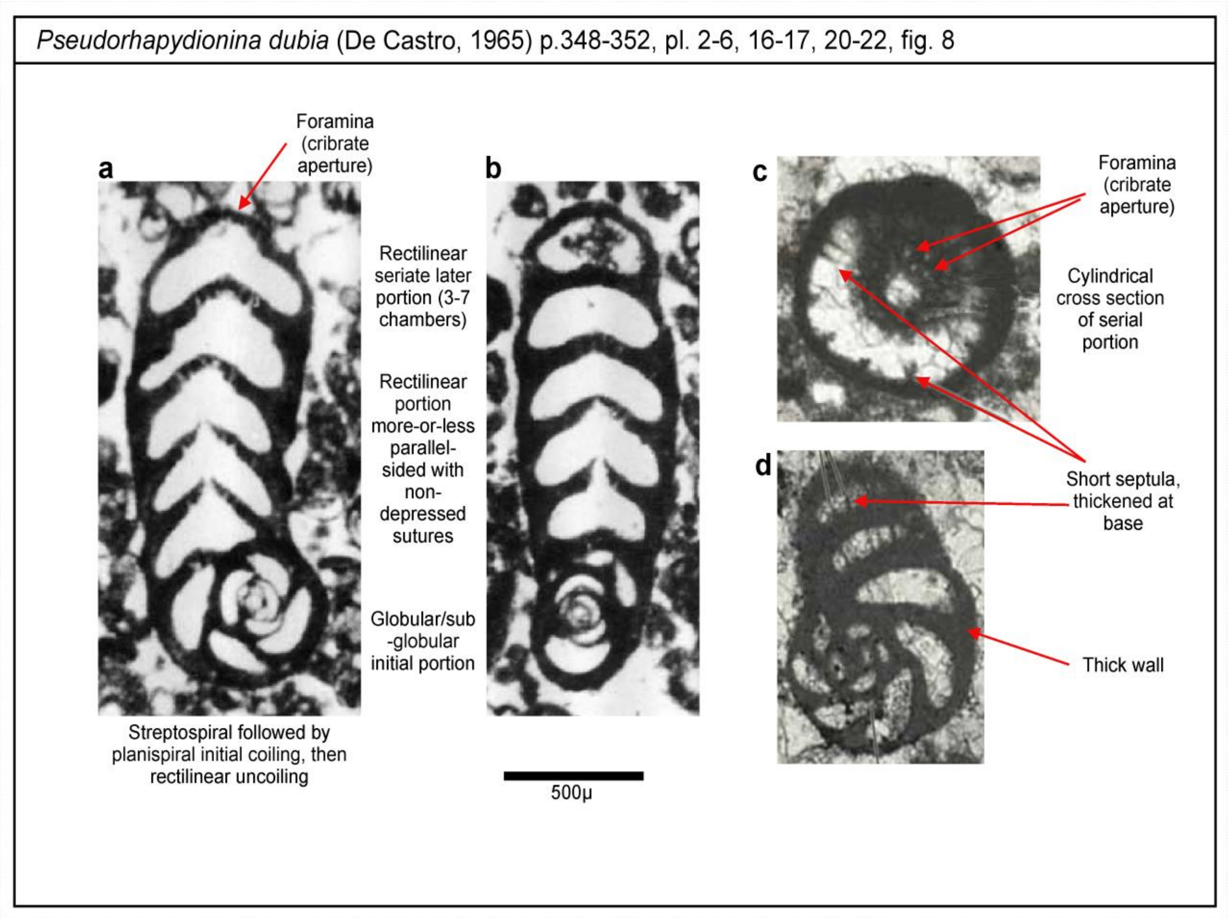


Fig. 62 Representative illustrations of *Pseudorhapydionina dubia*: **a** Equatorial section, De Castro in Schroeder & Neumann (1985, pl. 40, fig. 1, Italy); **b** Axial section, De Castro in Schroeder & Neumann (1985, pl. 40, fig. 10, Italy); **c** Transverse section (uncoiled), Consorti et al. (2016b, fig. 5d, Spain); **d** Equatorial section showing septula, Consorti et al. (2016b, fig. 5e, Spain).

and less well-developed septula. The two taxa are very similar and can be confused when a seriate stage is absent. Illustrations of *P. dubia* from the late Cenomanian of the Pyrenees by Bilotte (1984) may be *P. anglonensis*.

Scandonea phoenissa Saint-Marc and *Charentia cuvillieri* Neumann are also similar to *P. dubia* in that they have a short uncoiled rectilinear portion, but which is non-cylindrical, and with a somewhat more compressed or lenticular initial stage and no internal septula.

Some (pl. 8, figs. 15-18) but not all of the forms illustrated by Hamaoui (1961) as "*Taberina* sp. (sp. nov?)" from the Cenomanian of Israel may be synonymous with *P. dubia*. However, more research is required.

Stratigraphic Distribution

(Early Cenomanian) middle – late Cenomanian.

Arnaud et al. (1981) and Schroder & Neumann (1985) summarise the range of *P. dubia* as having an inception within the early Cenomanian, then ranging through the middle and late Cenomanian, into the early Turonian. A review of all the many records of *P. dubia* to date suggests that most specimens confirmed by illustration occur within the middle to late Cenomanian (although local ranges may be shorter). Indeed, the species was introduced from sediments of this age from southern Italy (De Castro, 1965) classically attributable to the middle and late Cenomanian (see also De Castro in Schroeder & Neumann, 1985; Chiocchini et al., 2012). None of those records where a Turonian extension is suggested is supported by plausible or definite identification (Saint-Marc, 1974a, 1978, 1981), and/or where identification is better (e.g., Fleury, 1980), the Turonian age itself is questioned (De Castro in Schroeder & Neumann 1985). An illustrated "Senonian" record by Tsaila-Monopolis (1977) from Greece is poorly preserved and needs further research into its chronostratigraphic calibration.

Calonge-Garcia (1996) regards the species as ranging from the middle Cenomanian to the top of the Cenomanian based on material from Spain.

P. dubia has been plausibly illustrated from the latest Cenomanian of Morocco (Charrière et al. 1998; Ettachfini, 2006) (see also Ettachfini et al., 2005 unillustrated). Parente et al. (2007, 2008) calibrated the LAD of *P. dubia* in Italy to within the *N. juddi* ammonite zone although the specimens were not illustrated. Using carbon isotope stratigraphy, Frijia et al. (2015) placed the extinction of *P. dubia* just below the Cenomanian/Turonian boundary in Italy.

Records of *P. dubia* in the early Cenomanian are generally rare (e.g., Decrouez, 1978; Berthou and Lauverjat, 1979; Michaud et al., 1984; Golubic et al., 2006; Ghanem et al., 2012). Berthou (1973) is a key reference, but only illustrates specimens from the middle and late Cenomanian in Portugal, although expands the range into the early Cenomanian. Ghanem & Kuss (2013) provide reasonable evidence that the species ranges throughout the Cenomanian in northwest Syria. Mohammed (2005), who illustrated *P. dubia* from southern Iraq, thought it might range throughout the Cenomanian there, but the age calibration evidence for that is less clear.

Simone et al. (2012) reported a single *P. dubia* specimen from supposed latest Albian strata in Italy (in addition to more common occurrences recorded from middle and late Cenomanian strata). They remark that this occurrence is atypical (see also Decrouez & Moullade, 1974) but the age is supposedly supported by orbitolinid faunas from a few metres above the sample (which include *Neoiraqia insolita* (Decrouez & Moullade), *Paracoskinolina tunesiana* Peybernes (= *Carseyella tunesiana*) and *Valdanchella dercourti* Decrouez & Moullade). This assemblage is a confusing mix of mid-Cretaceous and Early Cretaceous taxa. *Carseyella tunesiana* (late Aptian – early Albian, Solak, 2021) is probably misidentified, and the other taxa could be as young as middle Cenomanian (Schroeder & Neumann, 1985). Furthermore, the identification of this particular specimen of *P. dubia* by Simone et al. (2012) is not confirmed by illustration, thus extending the range of the species into the late Albian appears unjustified.

In Mexico, Aguilera-Franco (2000, 2003); Aguilera-Franco et al. (2001), Aguilera-Franco & Allison (2004) and Aguilera-Franco & Romano (2004) defined a Total Range Zone for this species that encompasses the upper middle and lower upper Cenomanian (see also Michaud et al., 1984; Hernández-Romano et al., 1997; Bomou et al., 2019 – in the last-named paper *P. dubia* is illustrated, but it may well be *P. chiapanensis*). But somewhat confusingly, and without explanation, in some figures and text they extend the range of this zone into the early Cenomanian. An upper middle to lower Cenomanian Total Range Zone broadly corresponds to the similarly aged "*P. dubia* and *P. laurinensis* zone" in central Italy (Chiocchini et al., 1979, 2008, 2012). In Egypt a zone of this name is restricted to the intra-late Cenomanian (Shahin & Elbaz, 2013, 2014), a clear case of facies control on ranges and hence calibration of the zonation. Tasli et al. (2006) defined a "*Pseudorhapydionina dubia* and *Biconcava bentori* Cenozone" encompassing the entire middle and late Cenomanian, equivalent to the "*Pseudolituonella reicheli* - *Pseudorhapydionina dubia* Concurrent Range Zone" of Sari et al. (2009) (see also Solak et al., 2020, who also reviews past interpretations of age range). Velić (2007) considered *P. dubia* to range from middle – late Cenomanian in the Dinarides.

Cenomanian Paleogeographic Distribution

Caribbean - Neotethys.

Widely reported, *P. dubia* is the most widespread species of the genus, although records are not always confirmed by illustration.

Confirmed illustrated records are from: Mexico (Aguilera-Franco, 2000; Aguilera-Franco et al., 2001); Portugal (Berthou, 1973; Michaud et al., 1984) (also no or uncertain illustration by Berthou & Lauverjat 1979;

Berthou, 1984b; Andrade, 2018); Spain (Calonge-Garcia, 1996; Consorti et al., 2016b); Morocco (Charrière et al. 1998; Ettachfini, 2006) (also no or uncertain illustration by Ettachfini et al., 2005); Algeria (Vila, 1974) (the illustrations by Salhi et al. (2020) are indeterminate, but clearly not this species); Egypt (Shahin & Elbaz 2013, 2014); (the illustrations by Orabi (1992) from Sinai are indeterminate but clearly not this species); Albania (Consorti & Schlagintweit 2021b) (also no or uncertain illustration by Heba, 2008); Italy (De Castro, 1965; Chiocchini & Mancinelli, 1977; De Castro in Schroeder & Neumann 1985; Sartorio & Venturini, 1988; Spalluto & Caffau, 2010; Chiocchini et al., 2012; Simone et al., 2012) (also no or uncertain illustration by Foglia, 1992; Borghi & Pignatti, 2006; Randazzo et al. 2020); Sardinia (Cherchi & Schroeder, 1976); Serbia (Radoičić, 1972, 1974a, b) (also no or uncertain illustration by Golubic et al., 2006); Croatia (Velić, 1973; Velić & Vlahović, 1994, Brčić et al., 2017, 2021) (also no or uncertain illustration by Veseli, 1994; Husinec et al., 2000, 2009; Korbar et al., 2001, 2012; Velić, 2007); Kosovo (Schlagintweit & Rigaud, 2015); Greece (Fleury, 1980) (also no or uncertain illustration by Fleury 1971; Decrouez & Moullade, 1974; Charvet et al., 1976; Decrouez, 1978; Zambetakis-Lekkas, 2006; Pomoni-Papaioannou & Zambetakis-Lekkas, 2009); Turkish Taurides (Tasli et al., 2006; Sari et al., 2009; Koç, 2017; Robertson et al., 2020; Solak, 2021; Solak et al., 2017, 2019, 2020) (also no or uncertain illustration by Bignot & Poisson, 1974; Sağaltici & Koç, 2021); Jordan (Schulze et al., 2005) (also no or uncertain illustration by Kuss, 1994); Syria (Ghanem and Kuss, 2013) (also no or uncertain illustration by Saint-Marc, 1977; Ghanem et al., 2012); Southern Iraq (Mohammed, 2005) (also no and uncertain illustration by Hamaoui & Brun, 1974; Mohammed, 2007, Al-Salihi & Ibrahim, 2023).

Location records with no or questionable illustrations include: Mexico (Hernández-Romano et al., 1997; Aguilera-Franco, 2003; Aguilera-Franco & Allison, 2004; Aguilera-Franco & Romano, 2004; Bomou et al., 2019); SE France (Rineau et al., 2021); Tunisia (Bismuth et al., 1967; Saïdi et al., 1995; Touir et al. 2017); Slovenia (Šribar & Pleničar, 1990); Montenegro (Božović, 2016); Israel (Hamaoui, 1961); Lebanon (Saint-Marc, 1970, 1974a, 1978, 1981); Iranian Zagros (Mohajer et al., 2021a; Rahimpour-Bonab et al., 2013; Omidvar et al., 2014a, b; Consorti et al., 2015; Rikhtegarzadeh et al., 2016, 2017; Saeedi Razavi et al., 2019, 2021; Dehghanian & Afghah, 2021; Asghari et al., 2022). The illustration by Schlagintweit & Yazdi-Moghadam (2022a) is possible, but it also might be *P. anglonensis* (illustrating the difficulty of separating these taxa), or indeed something else. The illustrations from the Iranian Zagros by Kiarostami et al. (2012) Esfandyari et al. (2023), and Mohajer et al. (2022a) are all indeterminate but cannot be reconciled with this species.

Pseudorhapydionina chiapanensis **Michaud et al., 1984**

Reference Illustration & Description

Michaud et al. (1984), Pls. 1 & 2 (not 11-14), p. 35-37.

Pseudorhapydionina chiapanensis is similar in respects to both *P. dubia* and *P. laurinensis*. Michaud et al. (1984) outlines the main differences as *P. chiapanensis* having a thicker wall and less depressed sutures compared with *P. laurinensis* and a more parallel-sided seriate portion compared with *P. laurinensis* which is more flaring. It has somewhat more chambers in the seriate portion than *P. dubia*. Consorti et al. (2016b) notes it has fewer internal septula in the seriate portion than *P. dubia* and *P. laurinensis*, and which are thick, medium length and thickened at the base. See the Species Key Chart (Appendix) for diagnostic and other characteristics.

Stratigraphic Distribution

Early – late (but not latest) Cenomanian.

Originally described from the early – middle Cenomanian of southern Mexico by Michaud et al. (1984) who associated the new species with *Rotalipora apenninica* (Renz) (= *Thalmanninella appenninica*) (late Albian – lower late Cenomanian; Bidgood & Simmons, 2022). However, *T. apenninica* is not illustrated, so there is something of a question mark over the oldest age of *P. chiapanensis*. Aguilera-Franco (2000, 2003) associated *P. chiapanensis* with *P. dubia* which she stated was a middle – late Cenomanian species. Aguilera-Franco & Allison (2004) placed the extinction of *P. dubia* within the late Cenomanian.

Cenomanian Paleogeographic Distribution

Central America/Caribbean.

This species was originally described and illustrated from the Chiapas region in the far south of Mexico (Michaud et al. 1984) and has subsequently only been reported from that region (i.e., the Maya Block), including Guatemala. Records include from the Guerrero-Morelos Platform (Aguilera-Franco et al., 2001; Aguilera-Franco, 2000, 2003 (illustrated); Aguilera-Franco & Romano, 2004; Aguilera-Franco & Allison, 2004; Bomou et al., 2019). Other records from southern Mexico include Michaud & Fourcade (1989), Rosales-Dominguez et al. (1997, 1998 illustrated); Cros et al. (1998) and Martens & Sierra-Rojas (2021). Records from Guatemala include Michaud et al. (1992); Fourcade et al. (1999); Moeschler (2009, illustrated); Caceres Flores (2016, illustrated) and Radmacher et al. (2021, illustrated). It was not reported by Omaña et al. (2012, 2019) from central Mexico which suggests a very restricted area of distribution.

Pseudorhapydionina laurinensis (De Castro, 1965)

Reference Illustration & Description

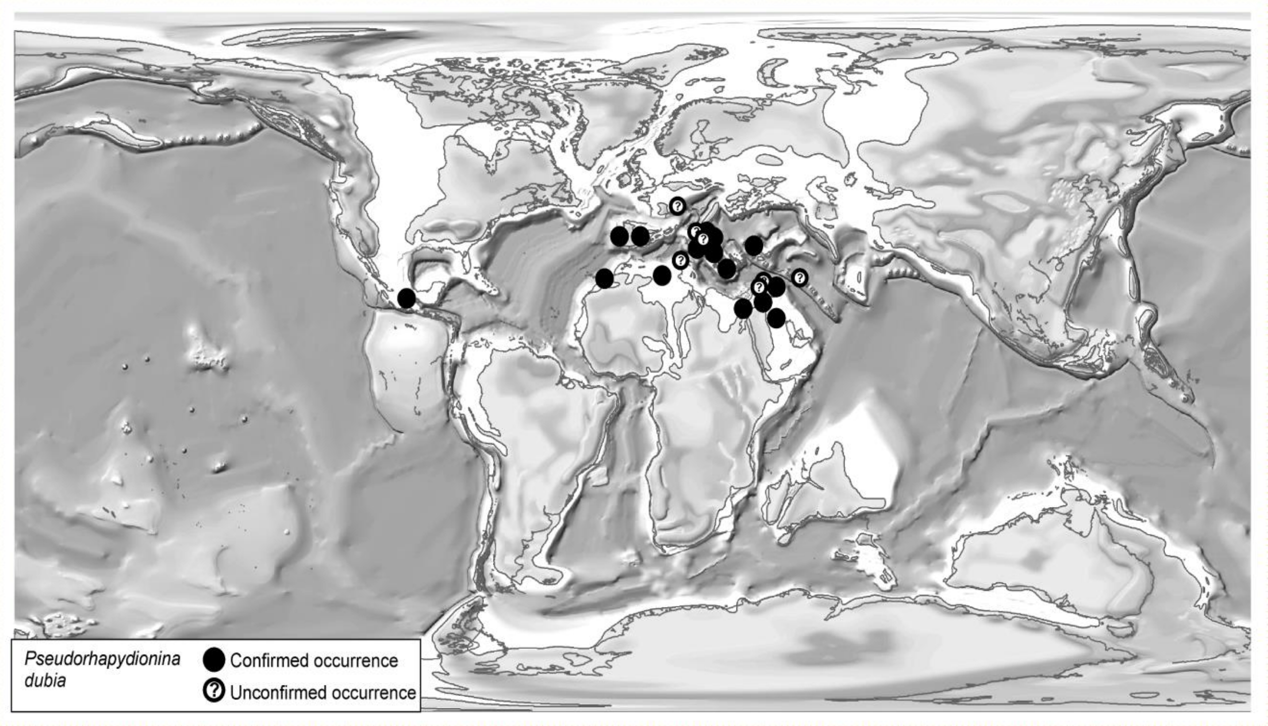


Fig. 63 Cenomanian paleogeographic distribution of *Pseudorhapydionina dubia*.

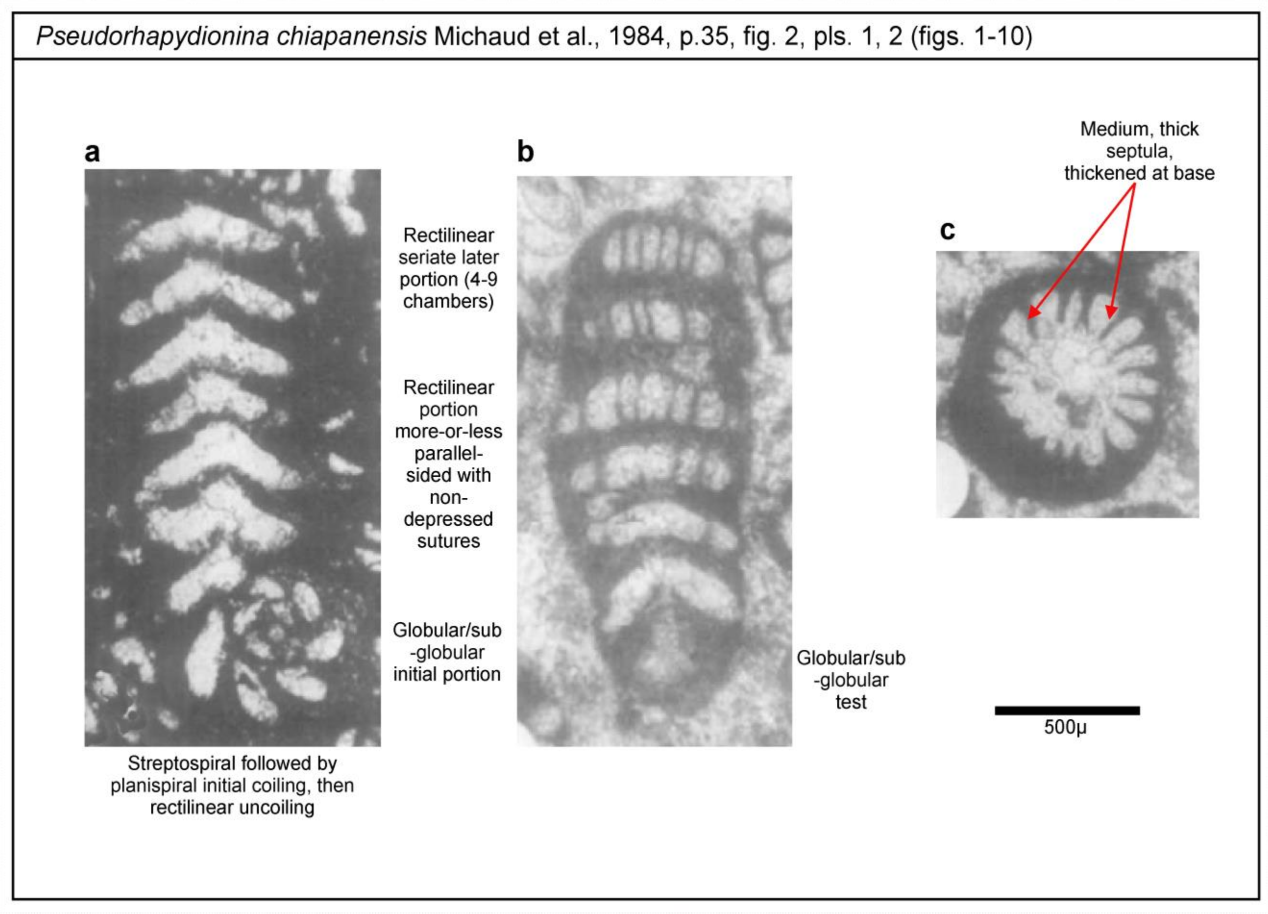


Fig. 64 Representative illustrations of *Pseudorhapydionina chiapanensis*: **a** Equatorial section, Michaud et al. (1984, pl. 1, fig. 10, Mexico); **b** Axial section, Michaud et al. (1984, pl. 1, fig. 6, Mexico); **c** Transverse section (uncoiled), Michaud et al. (1985, pl. 2, fig. 1, Mexico).

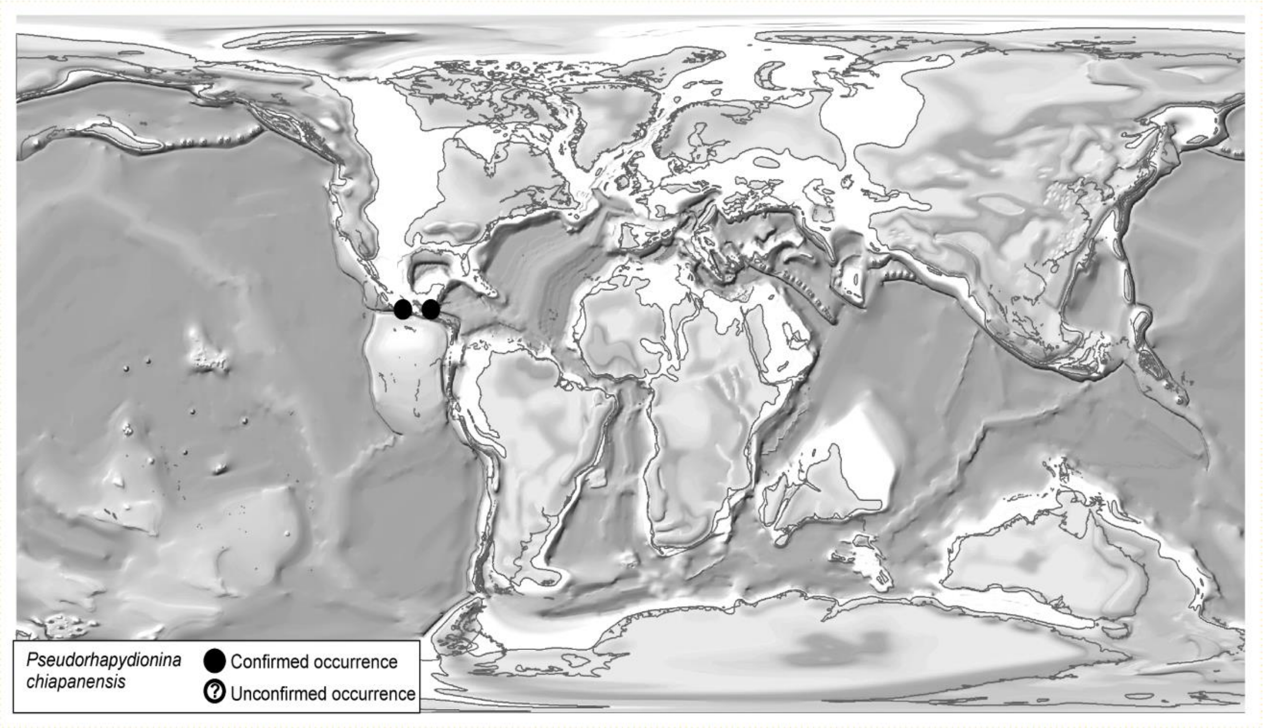


Fig. 65 Cenomanian paleogeographic distribution of *Pseudorhapydionina chiapanensis*.

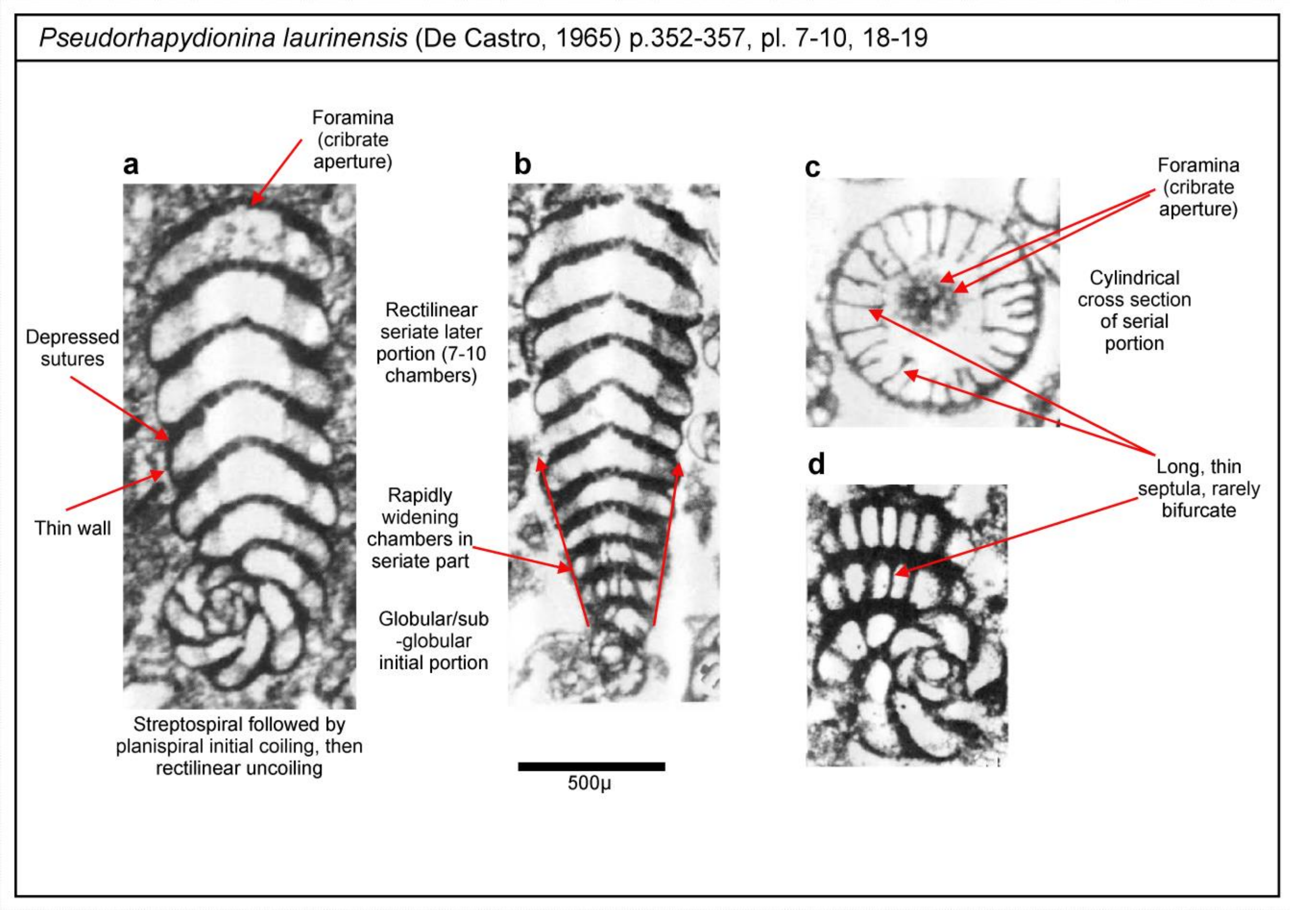


Fig. 66 Representative illustrations of *Pseudorhapydionina laurinensis*: **a** Equatorial section, De Castro in Schroeder & Neumann (1985, pl. 43, fig. 1, holotype, Italy); **b** Axial section, De Castro in Schroeder & Neumann (1985, pl. 43, fig. 4, Italy); **c** Transverse section (uncoiled), De Castro in Schroeder & Neumann (1985, pl. 43, fig. 6, Italy); **d** Equatorial section showing septula, Ibid. (1985, pl. 43, fig. 18, Italy).

De Castro in Schroeder & Neumann (1985), Pl. 43, p. 91-95. Good illustrations of this species are provided by Chiocchini et al. (2012) (see also Sartorio & Venturini, 1988).

The genus *Pseudorhapydionina* was introduced by De Castro (1972), with *Rhapydionina laurinensis* as described by De Castro (1965) from the early late Cenomanian of southern Italy as the type species. In contrast to *Rhapydionina* Stache – an alveolinid with a thick, perforated basal layer – *Pseudorhapydionina* – a soritid without a thick perforated basal layer – has a somewhat simpler, less complex endoskeleton where pillars and blades do not fuse to form marginal chambers and a pre-septal void, which is characteristic of the former. Beams are irregularly alternating between well developed and less well developed and are numerous (De Castro in Schroeder & Neumann, 1985). De Castro (1972) also introduced the closely related genus *Pseudorhipidionina. Pseudorhapydionina* is essentially globular to (uncoiled) subcylindrical whereas *Pseudorhipidionina* is flatter and (uncoiled) flabelliform. Loeblich & Tappan (1988) describe a cribrate aperture in both genera, although pores are "scattered" in *Pseudorhapydionina* and present as "a row of pores" in *Pseudorhipidionina*. *Demirina* also has internal septula, although fewer, and with a more 'peneroplid' overall shape and *Praetaberina* possesses pillars which *Pseudorhapydionina* lacks (Consorti et al., 2015).

The treatment of the genus and of *P. laurinensis* by De Castro in Schroeder & Neumann (1985) is comprehensive and allows for confident identification. See also the description and illustrations from Sapin in Calonge-Garcia (1996). Consorti et al. (2016b) tabulates differences between the various species of *Pseudorhapydionina*, although comparative stratigraphic ranges are not discussed. They provide a useful succinct description of *P. laurinensis*: "*porcelaneous, subgloblar-to-cylindrical shell. The subglobular early stage, with a size of about 0.33 mm of diameter, consists of two whorls of planispiral chambers. The first whorl hosts six chambers, while the second one has ten. The diameter of the proloculus is approximately 30 μm. The height of the cylindrical chambers is approximately 0.05 mm. The chamber lumen is partially divided by long radial septula, which number approximately 5-6 per quadrant in the seriate stage of growth [though illustrations show more]. Septula thickness is around 15 μm.*" See the Species Key Chart (Appendix) for diagnostic and other characteristics.

P. laurinensis differs from all other *Pseudorhapydionina* species in having a somewhat flared uncoiled, seriate portion (especially in the early part) whereas other uncoiled species (*P. chiapanensis* and *P. dubia*) have more-or-less parallel-sided seriate portions. *P. laurinensis* also has more depressed sutures on the seriate part compared to the other species. *P. anglonensis* has no uncoiled portion but this is subject to further investigation.

The four species of *Pseudorhapydionina* recorded herein (*P. chiapanensis* Michaud et al., *P. dubia* (De Castro), *P. laurinensis* (De Castro) and *P. anglonensis* Cherchi & Schroeder), all have a stratigraphic record limited to within the Cenomanian. A Santonian species from the Pyrenees, *P. bilottei* Consorti et al. (2016b), is not discussed in detail here, although it was based on specimens assigned to *P. laurinensis* by Bilotte in 1984. Compared to *P. laurinensis*, it has a greater maximum diameter of the early planispiral stage and number of chambers per whorl. The radial septula of *P. laurinensis* are longer but thinner than in *P. bilottei*; moreover, the width/height ratio of the seriate chambers is higher in *P. laurinensis* than in *P. bilottei* (see Consorti et al., 2016b).

P. laurinensis was introduced in 1965 by De Castro, but forms that are this species had been known for some time under different names. These include "*Ouladnailla*" *nom. nud.* by Emberger (1955) from the Cenomanian of Algeria and "*Taberina* sp. (sp. nov?)" of Hamaoui (1961) illustrated from the Cenomanian of Israel.

Stratigraphic Distribution

Middle – late (but not latest) Cenomanian.

As a genus, *Pseudorhapydionina* seems to have evolved in the early (?earliest) Cenomanian by a species referred to as *P.* aff. *laurinensis* in Iberian sediments of the Chera Formation (Consorti et al. 2016a; see also De Castro in Schroeder & Neumann, 1985, who mentions *P. laurinensis* from the early Cenomanian of Italy, although without illustration).

De Castro (1965) and De Castro in Schroeder & Neumann (1985) indicated that the type material of *P. laurinensis* is from the early part of the late Cenomanian. The notion that the species is restricted to this age interval has been followed by a number of authors, potentially sometimes with circular reasoning for the age assignment. Saint-Marc (1974a, 1978, 1981, illustrated) constructed a *P. laurinensis* Total Range Zone for the "lower part of the upper Cenomanian" of Lebanon, with age constrained from other fauna. Fleury (1971) illustrated *P. laurinensis* from rocks attributed with a late Cenomanian age from Greece, although the presence of the species was cited as one of the arguments for the age assignment. On the other hand, Decrouez (1978) recorded (with uncertain illustration) *P. laurinensis* together with *Conicorbitolina conica* (d'Archiac) in Greece. The latter species ranges no higher than middle Cenomanian (Schroeder & Neumann, 1985). Calonge-Garcia (1996) follows De Castro (1985) in restricting the species to the middle and (lower) late Cenomanian of Spain.

Velić (2007, unillustrated) confined the total range of *P. laurinensis* to his *Vidalina radoicicae-Chrysalidina gradata* Concurrent Range Zone, to which he assigned a late Cenomanian age, in the Dinarides of the Adriatic coast. In sections from Morocco where there is good ammonite-based age calibration, *P. laurinensis* occurs (illustrated) within the late but not latest Cenomanian (Charrière et al., 1998) (see also Ettachfini & Andreu (2004); Ettachfini et al. (1989, 2005) and Ettachfini (2006) for unillustrated or uncertain records). Consorti et al. (2016b) record and illustrate a *sensu stricto* form from the late Cenomanian of the Iberian Ranges of Spain (see below for discussion of another form described as "*P*. aff. *laurinensis*").

Chiocchini & Mancinelli (1977), Chiocchini (2008a, b) and Chiocchini et al. (2008, 2012) use the total range of *P. laurinensis* in Central Italy to define a "*P. dubia* and *P. laurinensis* biozone" which encompasses much of what they term "late Cenomanian", but not the latest. Note however, that they do not use the term middle Cenomanian, so the meaning of their "late Cenomanian" most likely incorporates some middle Cenomanian of the current international standard.

Similar occurrences may have led Arnaud et al. (1981) to consider the range of *P. laurinensis* as middle – possibly upper Cenomanian in the Mediterranean region, a view upheld in the range chart of Schroeder & Neumann (1985), although as discussed above, its presence in the lower part of the late Cenomanian appears certain. Orabi et al. (2012) (with plausible illustration) constructed a *P. laurinensis* zone of middle Cenomanian age in Egypt with the FAD of *P. laurinensis* as the base zonal marker although it is shown ranging to the top of the overlying biozone which is assigned a (lower) late Cenomanian age (see also Shahin & Elbaz 2013, 2014).

The form referred to as *P*. aff. *laurinensis* by Consorti et al. (2016b) deserves further discussion. Consorti et al. (2016b) illustrated this form but gave no other diagnostic means of separating it from *P. laurinensis s.s.* other than that it was "smaller". There is a suggestion in the single illustration that the aff form may have fewer septula than the *s.s.* form. The aff form is also uncoiled which suggests it is not a juvenile. Comparison between the figures in Consorti et al. (2016b: aff form Figure 4a, *s.s.* form Figure 4b – both are equatorial sections) shows the aff form is about 75% the size of the *s.s.* form with both illustrations shown as being smaller than the scale bar of 0.5mm length. *P*. aff. *laurinensis* was recorded from the Chera Formation, near Castellon in Spain which is shown as being latest Albian to earliest Cenomanian in age.

Another possible record of the genus stated to be early Cenomanian are specimens designated as *P*. cf. *laurinensis* by Luger (2018) from Somalia. However, Luger's illustrations are more equivocal, and the specimens are not oriented favourably although the uncoiled (seriate) part does at least seem cylindrical. This makes size measurement of the specimens difficult, but the maximum dimension appears to be around 1.8mm – much larger than Consorti et al.'s (2016b) *P*. aff. *laurinensis*. Luger's specimens occur with *Praealveolina iberica* Reichel which can range into the middle Cenomanian, so an early Cenomanian age is not definite.

In our view the specimens from Spain designated *P*. aff. *laurinensis* (Consorti et al., 2016b) may – until more material is examined – be regarded as "primitive" examples of *P. laurinensis* but may be a separate taxon. The specimens of Luger (2018) from Somalia are more equivocal but with better age calibration may be included within *P. laurinensis* or *P. dubia*. There is insufficient material to consider a separate taxon.

In summary the overall consistent range of *P. laurinensis* appears to be from the middle to the late but not latest Cenomanian, but the range locally – especially the position of the FAD – appears to be strongly facies-restricted. Specimens "comparable with" or which have "affinity" with *P. laurinensis* have been recorded from the early Cenomanian (in more peripheral localities – see below) but their exact taxonomic relationship with *P. laurinensis s.s.* needs further examples and study. A Maastrichtian record (Bilotte, 1978) is known to be erroneous (Bilotte, 1984).

Cenomanian Paleogeographic Distribution

Neotethys.

In addition to the references cited above, *P. laurinensis* is recorded with confirmed or plausible illustration from the late Cenomanian of Albania/Kosovo (Consorti & Schlagintweit, 2021a); the Dinarides (Radoičić, 1972, 1974a; Velić & Vlahović, 1994); and the Turkish Taurides (Bignot & Poisson, 1974; Sari et al., 2009; Solak et al., 2020). Unillustrated records or records with questionable illustrations are from Serbia (Radoičić & Schlagintweit, 2007); Albania (Heba, 2008); Tunisia (Philip et al., 1988; Saïdi et al., 1995; Touir et al., 2017); Syria (Mouty et al., 2003; Ghanem et al., 2012); Israel (Hamaoui, 1966); Dubai (Menegatti, 2004) and Oman (Smith et al., 1990; Piuz & Meister, 2013).

It seems likely that *P. laurinensis* does not occur in Mexico, being replaced by the similar, but endemic form, *P. chiapanensis* (Aguilera-Franco, 2003). Unillustrated records of *P. laurinensis* from Mexico (Hernández-Romano et al., 1997; Aguilera-Franco et al., 2001) may therefore be of *P. chiapanensis*.

The forms above designated as "cf" from Somalia are included as unconfirmed occurrences here.

A questionable illustration from Algeria (Alloul, 2019) is indeterminate – but see Hamaoui & Fourcade (1973) for confirmed records from there. They also illustrate specimens from Israel. *P. laurinensis* is regarded as important for biozonation in the Mishrif Formation of southern Iraq (Al-Dulaimy et al., 2022), but the illustration is not this species or even genus (probably = *Biconcava bentori*), however, illustrations by Mohammed (2005) from the same rock unit seem plausible (see also Al-Salihi & Ibrahim, 2023 for an unillustrated record). Interestingly, there is no reliable record of the species from the Iranian Zagros.

Genus ***Pseudorhipidionina*** De Castro, 1972

Type Species: *Rhipidionina casertana* De Castro, 1965

***Pseudorhipidionina* ex gr. *casertana-murgiana sensu* De Castro, 1965, 2006**

Reference Illustration & Description

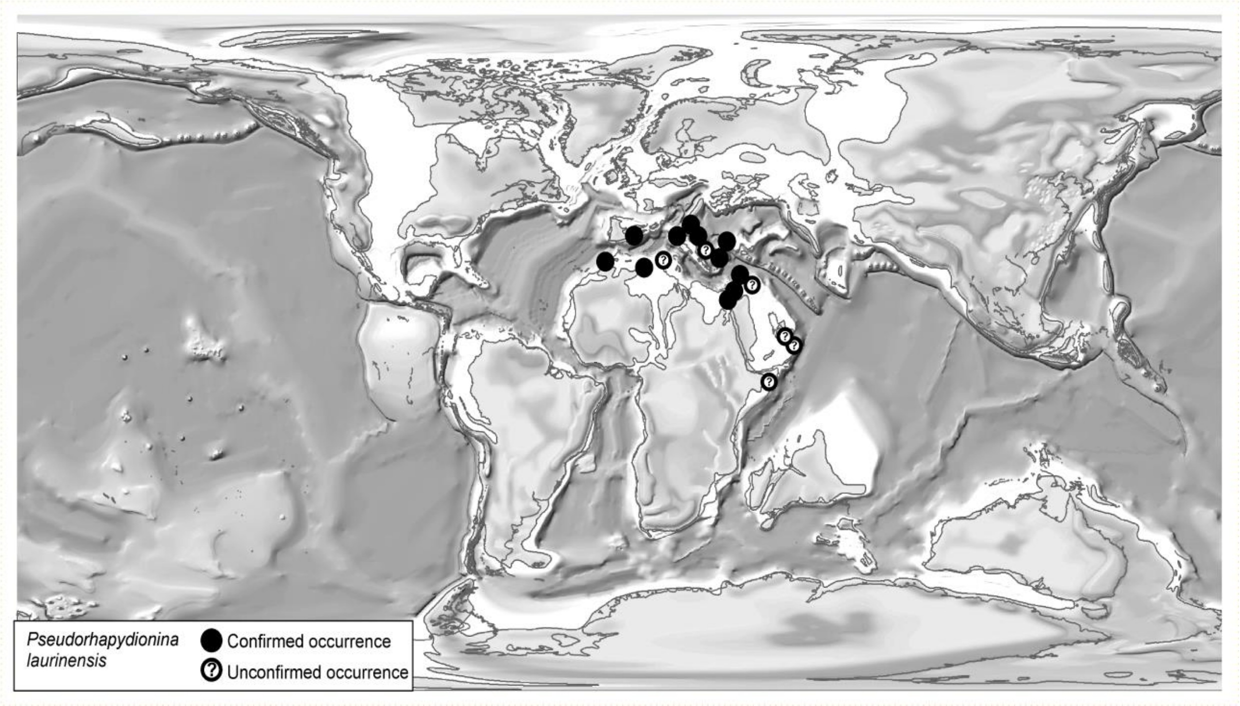


Fig. 67 Cenomanian paleogeographic distribution of *Pseudorhapydionina laurinensis*.

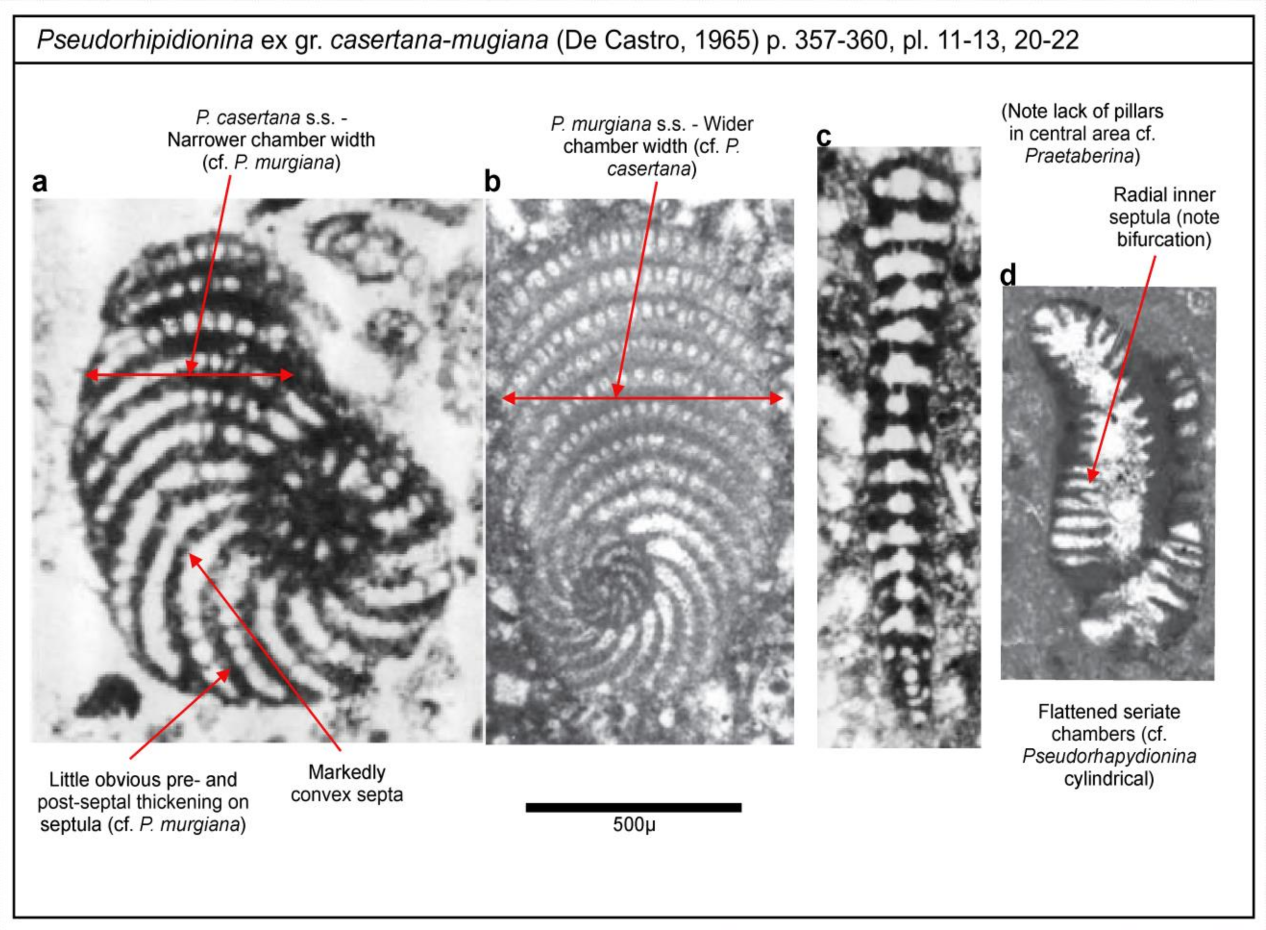


Fig. 68 Representative illustrations of *Pseudorhipidionina* ex gr. *casertana-murgiana*: **a** Equatorial section *P. casertana* s.s, De Castro in Schroeder & Neumann (1985, pl. 44, fig. 10, Italy); **b** Equatorial section *P. murgiana* s.s., De Castro (2006, pl. 1, fig. 1, neotype, Italy); **c** Axial section, De Castro in Schroeder & Neumann (1985, pl. 44, fig. 1, Italy); **d** Transverse section (uncoiled), Consorti et al. (2016b, fig. 4d, Spain).

De Castro in Schroeder & Neumann (1985), Pls. 44-45, p. 95-97; see also De Castro (2006), Pls.2-4 and Consorti et al. (2016b), Figs 4d-4e, 4h, 5a-5j, p. 276.

*Pseudorhipidionina murgiana (*Crescenti, 1964, emend. De Castro, 2006) and *Pseudorhipidionina casertana* (De Castro, 1965) were both first described from southern Italy around the same time. *P. murgiana* was described from eastern southern Italy, whilst *P. casertana* was described from its western-central part. The history of their description, taxonomic assignment, and occurrence is documented by De Castro (2006), who illustrated topotypes of P. *murgiana* alongside illustrations of *P. casertana*. The original illustrations of *P. murgiana* (Crescenti, 1964) are rather poor and had led to the species being somewhat overlooked in the literature, whilst there are quite numerous records of *P. casertana*. Nonetheless the taxa are extremely similar (De Castro, 2006; Consorti et al., 2016b) although no firm conclusion on their possible synonymy has been made.

Herein we use the formulation *Pseudorhipidionina* ex gr. *casertana-murgiana*. In 1981 De Castro stated "Mi sembra probabile che *Pseudorhipidionina casertana*, possa essere un sinonimo non valido di *Praerhapydionina murgiana*" [It seems probable to me that *Pseudorhipidionina casertana* could be an invalid synonym of *Praerhapydionina murgiana*]. Subsequently, De Castro (2006) – although providing a series of quantitative differences between the two taxa – appeared somewhat equivocal when committing firmly to their separation. *P. casertana* is indeed very similar to *P. murgiana*, having a slightly larger proloculus while other features such as test-size, length and breadth of the chambers, and pre-/post-septum-thickness are slightly larger in *P. murgiana* than in *P. casertana* (De Castro, 2006). They are also, more or less, contemporary in stratigraphic range.

De Castro's main criterion for separation relies on their reported geographically separate occurrences in Italy (on the Apula Platform for *P. murgiana*, and the Abruzzese-Campana Platform for *P. casertana*) as justification. On the other hand, both "species" may be present in the Middle East (see below).

Calonge-Garcia (1996) was also somewhat equivocal on the relationship between the two taxa, stating the difference between the two was that *P. murgiana* possessed a single opening, but admitted the lack of published material on that species could not rule out synonymy with *P. casertana*.

More recently, Consorti et al. (2016b) studied the taxa and could not propose a solution although recommended further study. However, they suggested *P. casertana* and *P. murgiana* are synonymous. They first mention the presence of bifurcated septula in *P. casertana*, especially in the uncoiled portion, a feature not noted in De Castro's description (in Schroeder & Neumann 1985). As an example of the difficulty in separating the taxa, Chiocchini et al. (2012) illustrated *P. murgiana* from the very latest Cenomanian of central Italy. However, their illustrations lack the supposedly characteristic broader uncoiled chambers as compared with *P. casertana*.

The description of *P. casertana* by Consorti et al. (2016b) is succinct and useful: "*Porcelaneous flabelliform shell with an acute periphery. The early planispiral-involute stage of growth consists of elongated chambers arranged in one and a half to two whorls, reaching a diameter of 0.55 mm, approximately. The seriate stage is composed, at least, of 10 wide and short chambers averaging 0.04 mm in height. The septa are markedly convex and cribbed by numerous intercameral foramina. The external part of the chamber lumen is partially divided by radial septula. The septula, which has a thickness of around 15-18 μm, may bifurcate at their inner end. They occupy one-third of the chamber lumen*". See the Species Key Chart (Appendix) for diagnostic and other characteristics.

Like *Pseudorhapydionina*, species of *Pseudorhipidionina* have also undergone a rather convoluted journey through various generic assignments, due seemingly in this case to a lack of adequate type material and new (or amended) diagnostic features being observed subsequently in better preserved/new specimens. There were, essentially two species of Cenomanian *Pseudorhipidionina*: *P. casertana* (De Castro) and *P. murgiana* (Crescenti), the former originally assigned to *Rhipidionina* Stache, the latter originally to *Praerhapydionina* Van Wessem. For example, *Praerhapydionina murgiana* was originally believed to have had a single aperture (diagnostic of that genus) but later specimens were observed with multiple apertures (diagnostic of *Pseudorhipidionina*). The reader is referred to the discussions in De Castro (in Schroeder & Neumann, 1985) and De Castro (2006) for an historical overview.

In gross terms, *Pseudorhipidionina* has a more flattened, almost "peneropolid"-like uncoiled portion compared to *Pseudorhapydionina* whose uncoiled portion is subcylindrical to cylindrical.

Pseudorhipidionina ex gr. *casertana-murgiana* is also very similar to the ?agglutinated taxon *Reissella ramonensis* Hamaoui which has a more complex endoskeleton, and which includes beams and joists/rafters rather than just beams (De Castro, 1981; De Castro in Schroeder & Neumann 1985; Mikhalevich 2004a & b). See also Hottinger 2006: fig. 19 and Fig. 2 herein for diagrammatic explanation of these morphological features.

Borghi and Pignatti (2006) remarked on the similarity between *P.* ex gr. *casertana-murgiana* and *Praetaberina bingistani* (Henson) in random thin-sections, although they note that *Praetaberina* is more "complex" and has a cylindrical uncoiled portion where such features can be observed. *Praetaberina* also possesses pillars which *Pseudorhipidionina* (and *Pseudorhapydionina*) lack (Consorti et al., 2015).

It is the presence of pillars in *Pseudorhipidionina tubaensis* Mohammed (described from the Mishrif Formation of the Tuba-1 well in southern Iraq; Mohammed, 2007), as illustrated, that precludes it from assignment to *Pseudorhipidionina*. In fact, the published illustrations by

Mohammed (2007) comprise two different species; *Praetaberina bingistani* and *Cycledomia iranica* and *P. tubaensis* is therefore a junior synonym of both (Consorti & Schlagintweit, 2021b).

In summary, unless material is well preserved and is oriented in ways in which critical taxonomic features are visible, *Pseudorhipidionina*, *Praetaberina* and *Reissella* may appear very similar in tangential-longitudinally oriented sections.

Stratigraphic Distribution

Upper middle? – late Cenomanian.

The majority of illustrated records in the literature attribute a late Cenomanian age range to both *P. murgiana* and *P. casertana* (herein *Pseudorhipidionina* ex gr. *casertana-murgiana*). There is some debate as to whether *Pseudorhipidionina casertana* ranges as far as the actual Cenomanian-Turonian boundary, above the boundary, or if it becomes extinct just below the boundary.

De Castro in Schroeder & Neumann (1985) estimated the age of *P. casertana* to be late Cenomanian (?upper part) based on association with the extinction of *Pseudorhapydionina laurinensis* and the "acrozone" of *Cisalveolina fraasi*. He also suggested that previous records which alluded to an early Turonian age (e.g., Saint-Marc, 1974a, 1978, 1981; Arnaud et al., 1981) should be treated with caution because of the uncertainty of the position of that boundary in those sections mentioned. Calonge-Garcia (1996) also follows this position. Nonetheless the range chart in Schroeder & Neumann (1985) shows a range from the late middle Cenomanian into the earliest Turonian. Subsequently, De Castro (2006) remarked that "*P. murgiana* and *P. casertana* have the same age (late Cenomanian) and both are associated with … *Cisalveolina fraasi* and *Coxites zubairensis*." As noted elsewhere herein, the supposed Turonian records from Lebanon (Saint-Marc, 1974a, 1978, 1981) are from beds that, based on associated ammonite data, appear to straddle the Cenomanian – Turonian boundary, but the precise stratigraphic position of *P. casertana* occurrences relative to these ammonite occurrences is uncertain. Given this, and the lack of any other substantiated Turonian records, *Pseudorhipidionina* ex gr. *casertana-murgiana* is excluded from the Turonian.

Solak et al. (2020) defined the *Pseudorhipidionina casertana* Assemblage Zone in studies from Turkey based on the FAD of *P. casertana* and other taxa including *Pseudorhapydionina dubia*, *P. laurinensis* and *Vidalina radoicicae*. They imply that *P. casertana* is restricted to this zone to which they assign a late-but-not-latest Cenomanian age. Velić (2007) considered the species (both *P. murgiana* and *P. casertana*) important late Cenomanian markers in the Dinarides. Berthou & Lauverjat (1979) and Berthou (1984a, b) restrict the species to the lower half of the late Cenomanian in Portugal (see illustration in Berthou, 1973). Charrière et al. (1998) places the LAD of *P. casertana* in Morocco below those beds containing the ammonite *Vascoceras cauvini* (Chudeau) which, they state, is also below the base of the *W. archaeocretacea* planktonic foraminiferal zone. Ettachfini (2006 - illustrated) also from Morocco, places the LAD no younger than the *juddi* ammonite zone (see also Ettachfini et al., 2005; Piuz & Meister, 2013, unillustrated).

Parente et al. (2007, 2008) used integrated ammonite and Carbon-isotope data to suggest the LAD of *P. casertana* occurs around the middle part of the *geslinianum* ammonite zone. Simone et al. (2012) and Frijia et al. (2015) essentially agree, with the latter placing the LAD slightly higher near the top of the *geslinianum* zone.

Frijia et al. (2015: fig. 15) place the FAD of *P. casertana* at the base of the *jukesbrownei* ammonite zone (upper middle Cenomanian). See also Arnaud et al. (1981) who also positions the FAD at the base of the *jukesbrownei* zone, although the basis for this is unclear.

Ghanem & Kuss (2013) illustrate the species from the late Cenomanian of Syria. Their range chart restricts the species to the late Cenomanian, but in the text they mention middle Cenomanian occurrences. On the other hand, Mouty et al. (2003) attribute an early Turonian extension to the range in Syria citing Turonian ammonites (*Thomasites rollandi* (Thomas & Peron), *Choffaticeras* (*Leoniceras*) sp., *Hemitissotia morreni* (Qoquand) and *Coilopoceras* sp.) although no fossils are illustrated. As with other "Turonian" records (see above), this is discounted.

Radoičić et al. (2010) mention *P. casertana* from lower Cenomanian limestones in Serbia, but there is no illustration and based on associated fauna could easily be younger within the Cenomanian. However, Radoičić (1974a) did illustrate the species from the same region.

Cenomanian Paleogeographic Distribution

Neotethys.

References in De Castro in Schroeder & Neumann (1985) and De Castro (2006) indicate plausible records from eastern Algeria, Tunisia, Greece, Italy, Sardinia, Lebanon, Iberia, and the Balkans and Dinarides. In addition to these and records mentioned above, occurrences confirmed by definite or plausible illustration as mentioned above include Portugal (Andrade, 2018) and from the late Cenomanian of Egypt (Nagm, 2009 – although as cf.). *P.* ex gr. *casertana-murgiana* is known to occur in the upper Wasia Group of subsurface Saudi Arabia (Dr. Wyn Hughes, pers. comm., 2022) and has been illustrated from the Iberian Ranges, Spain by Consorti et al. (2016b). Al-Rifaiy and Cherif (1987) illustrate this species as *Taberina* sp. from the Cenomanian Shueib Formation of Jordan (see also Schulze et al. 2004, unillustrated)

P. ex gr. *casertana-murgiana* has been reported and illustrated from the upper Sarvak Formation from the Iranian Zagros. Afghah & Fadaei (2014) provide good illustrations, although there are errors in the labelling of the plates. Plate 8d "*Nezzazata simplex* Omara" is this species, as is plate 9f labelled as "*Neorbitolinopsis conulus*

Douville”. Plate 8e labelled as “*Pseudorhipidionina casertana*” is an orbitolinid. There are other illustrations in this paper that may be this species or *P. bingistani*. A record of “*Pseudotextulariella cacertana*” by Assadi et al. (2016) is more likely *P. bingistani,* whilst a record of *Daxia cenomana* by Afghah et al. (2014) is most likely *P.* ex gr. *casertana-murgiana*. Esfandyari et al. (2023) provide more recent plausible illustrations. There are also unillustrated records from the Iranian Zagros: Rahimpour-Bonab et al. (2013) (as well as being mentioned, an illustration of “*Pseudorhipidionina bingistani”* may be *P. casertana*); Jamalpour et al. (2017); Rikhtegarzadeh et al. (2017); Omidi et al. (2021); Mohajer et al. (2022a, 2022b); and Ashgari et al. (2022); but also see Kiarostami et al. (2019) and Dehghanian & Afghah (2021) for illustrated records but where identification is at best uncertain. Mohammed (2005 as “*Pseudorhapydionina casertana”* and 2007) recorded and illustrated *P. casertana* from southern Iraq (alongside the invalidated *P. tubaensis* – see above) but Consorti & Schlagintweit (2021b) thought (though more equivocally) the illustration was more likely to be *P. murgiana*. Al Dulaimi et al. (2013) illustrate *P. casertana* from the Mishrif Formation (undifferentiated late Cenomanian – early Turonian) of the well Nasiriyah-2 from southern Iraq. However, another specimen referred to “*Pseudotextulariella casertana”* from West Qurna-215 is actually *P. bingistani*. An unillustrated record from southern Iraq is that of Al-Salihi & Ibrahim (2023).

Unconfirmed (by lack of illustration or uncertain illustration) occurrences are also recorded from Egypt (Orabi, 1992; Orabi et al., 2012; Shahin & Elbaz, 2013; Orabi & Hamad, 2018); and offshore Dubai (Menegatti, 2004). Dufaure et al. (1984) reported – unillustrated – “*Pseudorhipidionina* (ex *casertana*) *murgiana*” from the middle – late Cenomanian of southeast Libya.

Genus ***Praetaberina*** Consorti et al., 2015

Type Species: *Taberina bingistani* Henson, 1948

***Praetaberina bingistani* (Henson, 1948)**

Reference Illustration & Description

Consorti et al. (2015), Figs. 5-7, p. 382.

The taxonomic status, history, description, and illustration of *Praetaberina* Consorti et al. and its two species – *P. bingistani* (Henson) and *P. apula* (Consorti et al.) is comprehensively reviewed by Consorti et al. (2015). These authors re-examined material from Iran including the type material of *Taberina bingistani* illustrated by Henson (1948) from Kuh-i-Bingistani in the Iranian Zagros, as well as new material from Italy.

Essentially, *Praetaberina* is very similar to *Pseudorhapydionina* (*bingistani* was assigned to *Pseudorhapydionina* by Whittaker et al., 1998) but possesses pillars between consecutive septa in the central part of the chamber. *Pseudorhipidionina* is also very similar (Borghi & Pignatti, 2006) but also lacks pillars and also tends to have a more compressed uncoiled portion whereas *Praetaberina* tends to be more cylindrical. Species of *Pseudorhipidionina* are often confused with *Praetaberina* (and vice versa) in the literature – see comments on that genus). *P. bingistani* has a more complex internal structure than its original assigned genus – *Taberina* – which is now restricted to the Paleogene (see Vicedo et al., 2013 for a comprehensive review of this genus).

Another similar genus is the Paleogene *Neotaberina* Hottinger, 2007, which has apertures that extend almost to the periphery of the chamber and the pillared zone overlaps with the distal ends of the septula. The initial subglobular, planispiral stage is poorly developed in *Neotaberina*.

P. bingistani has numerous chambers in the coiled portion – over 50 within two and a half to three whorls before uncoiling sub-cylindrically to between 10-15 chambers and which stage can be up to 2.1mm in length. Septula alternate relatively short-long but only extend inwards about a quarter of the diameter of the chamber. The pillars in the central part are inverted cone-shaped (Consorti et al., 2015). See the Species Key Chart (Appendix) for diagnostic and other characteristics.

P. apula is smaller overall and has a maximum of only two initially coiled whorls. The septula are fewer, but they extend further inwards within the chamber than *P. bingistani*, thus reducing the central chamber space available for the foramina and pillars.

Pseudorhipidionina tubaensis, a new species described from the Mishrif Formation of the Tuba-1 well in southern Iraq (Mohammed, 2007), was found to contain pillars by Consorti & Schlagintweit (2021b) thus precluding it from *Pseudorhipidionina*. Those authors consider it as a partial junior synonym of *P. bingistani*.

Stratigraphic Distribution

Middle – late (but not latest) Cenomanian.

The various published ages attributed to *P. bingistani* are fully reviewed by Consorti et al. (2015) and, essentially, restrict its range to the late (but not latest) Cenomanian (but without excluding a middle Cenomanian age). However, they indicate that the FAD of *P. bingistani* is associated with the MCE I and II Carbon-isotope peaks of Jarvis et al. (2006) as observed in sections from the Iranian Zagros. They suggest therefore that the FAD of *P. bingistani* as “very early late Cenomanian”. Our studies elsewhere (Bidgood & Simmons 2022) calibrate both these peaks to within the middle Cenomanian based on Jarvis et al. (2006) and Joo & Sageman (2014). See also data presented in poster form by Vicedo et al. (2013) that suggests a middle Cenomanian age for carbon isotope calibrated occurrences from Iran.

Smith et al. (1990) and Kennedy & Simmons (1991) recorded *P. bingistani* (unillustrated) from strata from Oman (Natih C – Natih E) around the early/middle Cenomanian boundary (age based on carbon isotope data and ammonites – see Bromhead et al., 2022).

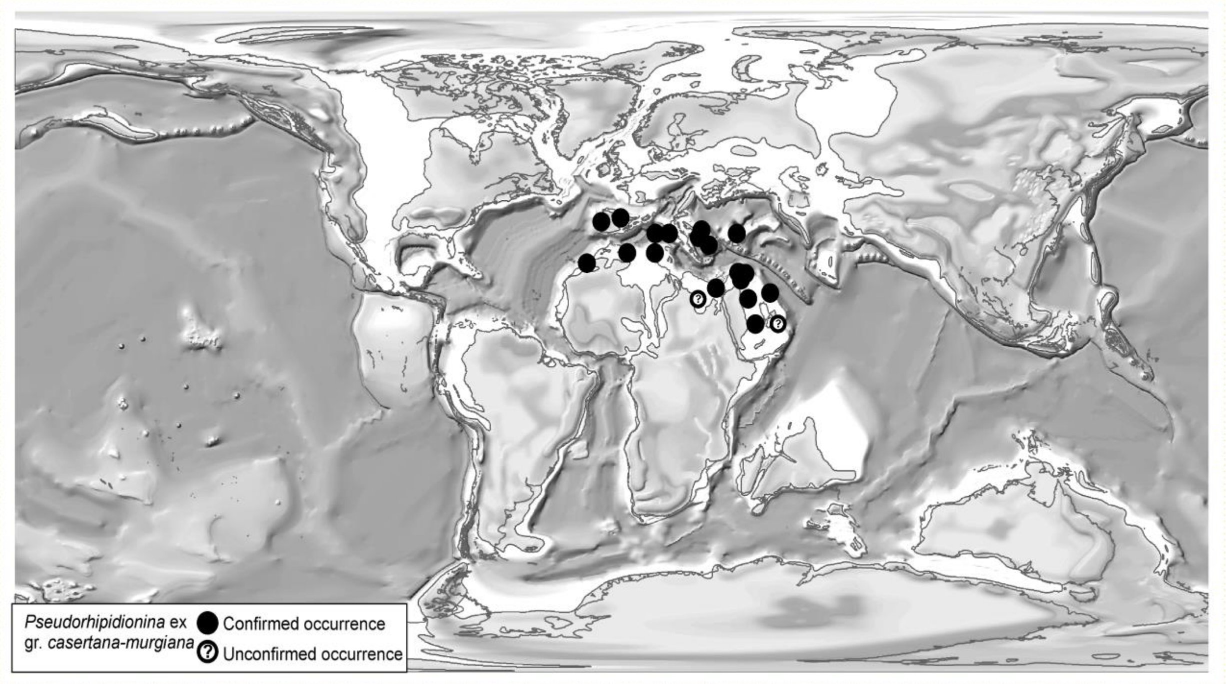


Fig. 69 Cenomanian paleogeographic distribution of *Pseudorhipidionina* ex gr. *casertana-murgiana.*

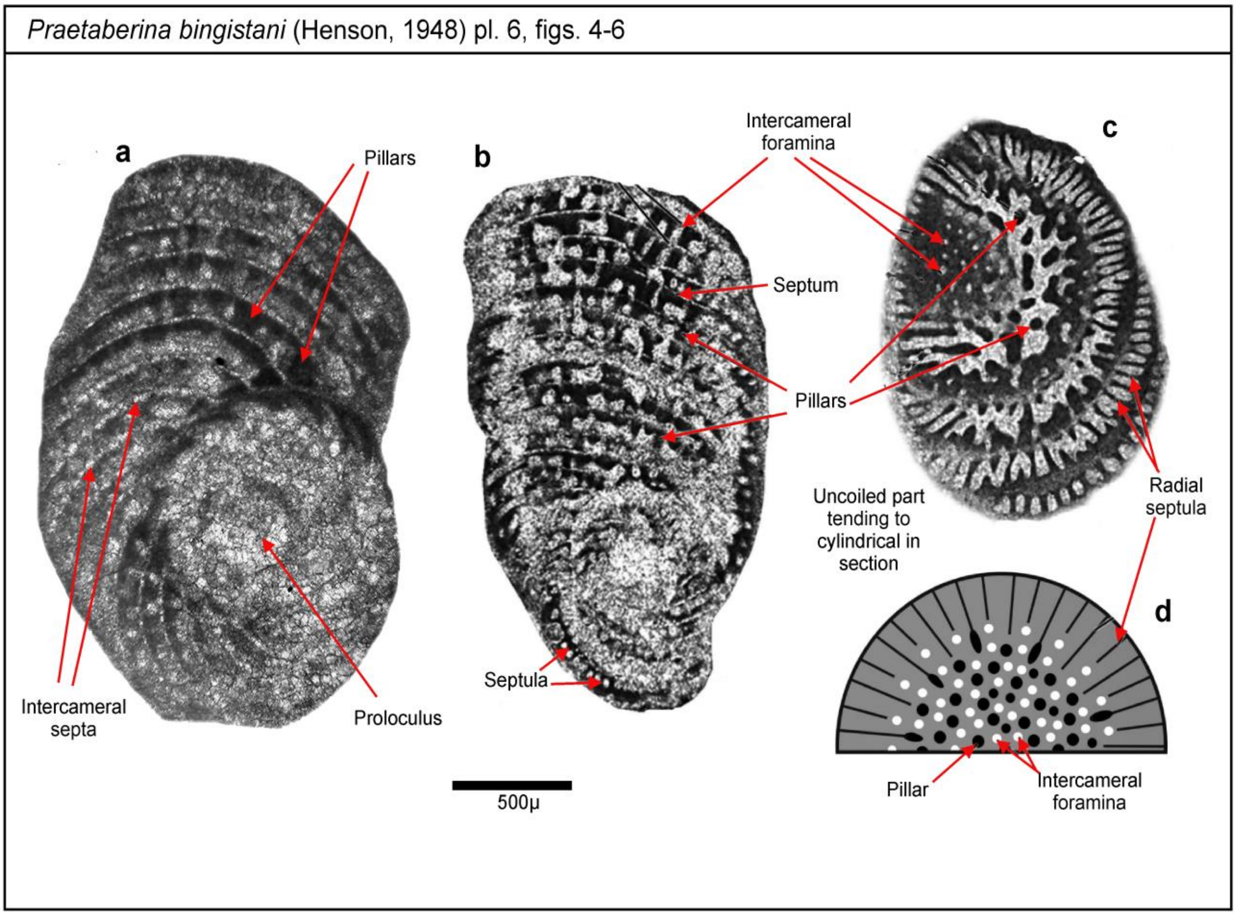


Fig. 70 Representative illustrations of *Praetaberina bingistani*: **a** Subequatorial section, Henson type refigured by Consorti et al. (2015, fig. 5(1), Iran); **b** Oblique section, Consorti et al. (2015, fig. 6(4), Iran); **c** Oblique section, Consorti et al. (2015, fig. 5(7), Iran); **d** Schematic half-chamber section across uncoiled portion, Consorti et al. (2015, fig. 4).

Saint-Marc (1974a, 1981) records it as old as late early Cenomanian in Lebanon (although the illustrated material is late Cenomanian). The less well calibrated records from Israel of Hamaoui (1966) and Arkin & Hamaoui (1967) are also suggestive of middle – late Cenomanian range.

Consorti et al. (2015 *fide* Frijia et al., 2015) position the LAD of *P. bingistani* to the "middle part of the upper Cenomanian".

A statement by Razin et al. (2010) that the presence of *P. bingistani* can be used to define a Turonian age in the Iranian Zagros is erroneous and not substantiated by the cited views of Wynd (1965). Wynd (1965) considered *P. bingistani* as an element of his *Nezzazata* - alveolinid assemblage zone (zone 25), to which he ascribed a Cenomanian - ?Turonian age. More modern views (e.g., Omidvar et al., 2014a, b; Kazemzadeh & Lotfpoor, 2016) tend to restrict this zone to the Cenomanian.

Records published after Consorti et al. (2015) or not noted by them include Mahdi & Aqrawi (2014, unillustrated); Awadeesian et al. (2018, illustrated) and Al-Dulaimy et al. (2022 – unillustrated as "*Tabarian bingstani*") from the late Cenomanian part of the Mishrif Formation of southern Iraq. Al Dulaimi et al. (2013) illustrate *P. bingistani* as "*Pseudotextulariella casertana"* (pl. 10, fig. 8) from the Mishrif Formation (undifferentiated late Cenomanian – early Turonian) of the well West Qurna-215 from southern Iraq. However, another specimen (pl. 9, fig. 6) actually referred to *P. bingistani* is indeterminate. The species is illustrated from southern Iraq by Al-Salihi & Ibrahim (2023).

From the Iranian Zagros, illustrations by Kalantari (1976) are indeterminate, whilst Assadi et al. (2016: fig. 6 a8) illustrate "*Pseudotextulariella cacertana*" which is probably *P. bingistani,* as is the specimen (fig. 6 a9) illustrated as "*Biconcava bentori*". Additional records from the late Cenomanian of the Iranian Zagros include Rahimpour-Bonab et al. (2013, uncertain illustration); Omidvar et al. (2014b, uncertain illustration); Kazemzadeh & Lotfpoor (2016, illustrated); Jamalpour et al. (2017, illustrated); Navidtalab et al. (2020, unillustrated); Ezampanah et al. (2022, illustrated); Kiarostami et al. (2019, illustrated though assigned to *Pseudorhipidionina*) and Schlagintweit & Yazdi-Moghadam (2021, illustrated). However, several recent records from the Iranian Zagros are less reliable; including Haftlang et al. (2020) which attributes a middle Cenomanian age to the "*Taberina bingistani* taxon range zone" based on associations with "other early to mid-Cenomanian taxa" (*Cuneolina parva* Henson and *Praealveolina tenuis* Reichel, but the latter is unlikely to be early Cenomanian). Moreover, Haftlang et al.'s. illustration of *P. bingistani* is inconclusive and they do not refer to Consorti et al. (2015) at all. On the other hand, Mohajer et al. (2021a, 2022a) attribute their "*Cisalveolina lehneri – Praetaberina bingistani* assemblage zone" to the late Cenomanian based on Consorti et al. (2015) and more recent literature and a somewhat better illustration. Finally, without illustration, and substantive explanation, Mohajer et al. (2021b, 2022c) refer to both middle and late Cenomanian records of *P. bingistani* (a *"Chrysalidina gradata—Praetaberina bingistani* Interval Zone (Middle Cenomanian)", and a "*Cisalveolina fraasi* (*fallax*) & *Cisalveolina lehneri—Praetaberina bingistani* Assemblage Zone (Late Cenomanian)", although it seems that the consensus view of these authors is that *P. bingistani* indicates a late Cenomanian age in the Iranian Zagros.

In summary, *P. bingistani* seems to range from the middle to late (but not latest) Cenomanian but the majority of plausible substantiated records are from the late Cenomanian.

Cenomanian Paleogeographic Distribution

Eastern Neotethys (Arabian Plate).

Consorti et al. (2015) note that *P. bingistani* has been confidently recorded from localities in the Iranian Zagros, Iraq (see also Hamaoui & Brun, 1974; Whittaker et al. 1998); Oman; Syria (see also illustrated by Ghanem & Kuss, 2013); Lebanon and Israel and "probably" from Egypt and Somalia (see their paper for sources). In addition to references above there is also an unconfirmed record from Abu Dhabi (Le Blanc, 2015).

In Europe the species has been reported from Greece (Fleury, 1980) and from Italy (Borghi & Pignatti, 2006). However, the specimens recorded in both these countries are considered by Consorti et al. (2015) to be referable to their new species, *P. apula* (see below).

P. bingistani therefore seems to be restricted to localities on or around the Arabian Plate.

***Praetaberina apula* Consorti et al., 2015**

Reference Illustration & Description

Consorti et al. (2015), Fig. 8, p. 382-384.

This is a relatively new species defined by Consorti et al. (2015) based on new samples from the Bari Formation of Italy and re-examination of specimens previously attributed to *Taberina bingistani* by Fleury (1980) in Greece and by Borghi & Pignatti (2006) in Italy.

Specimens of *P. bingistani* are larger overall and have up to three and a half initially coiled whorls compared with a maximum of only two initially coiled whorls in *P. apula*. The septula are fewer, but they extend further inwards within the chamber than *P. bingistani*, thus reducing the central chamber space available for the apertures and pillars. See the Species Key Chart (Appendix) for diagnostic and other characteristics.

Stratigraphic Distribution

Late Cenomanian
See Consorti et al. (2015).

Cenomanian Paleogeographic Distribution

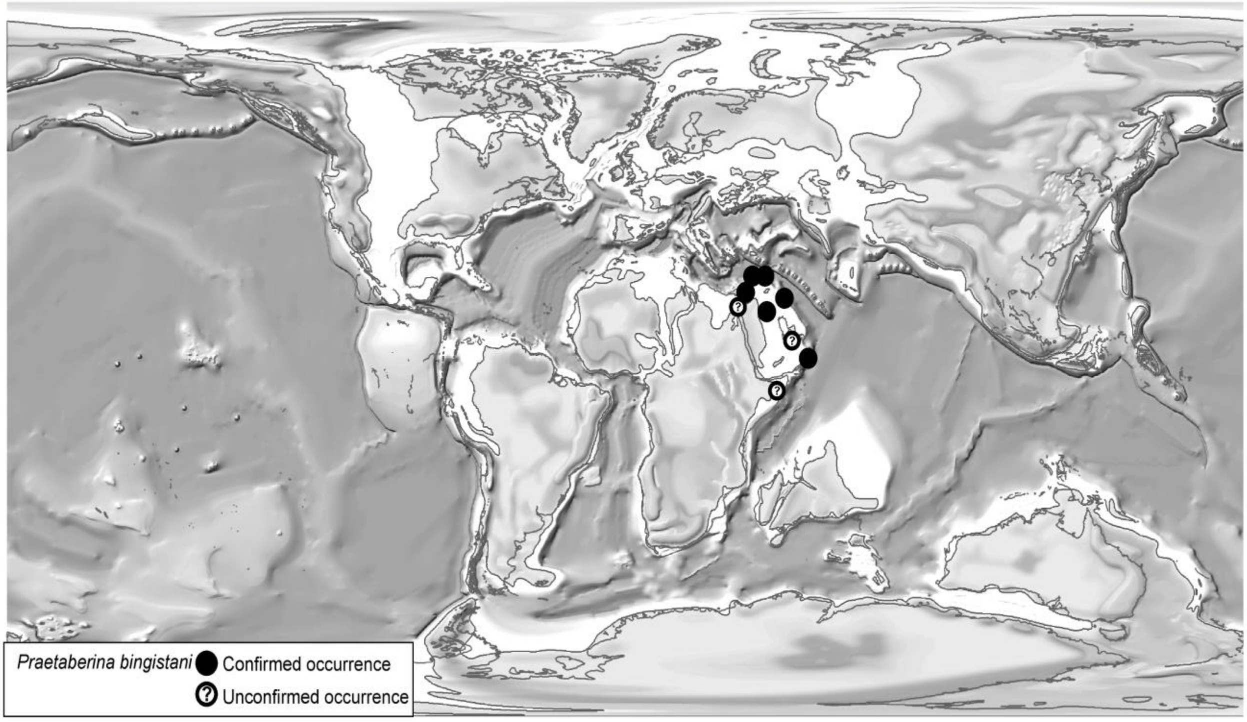


Fig. 71 Cenomanian paleogeographic distribution of *Praetaberina bingistani*.

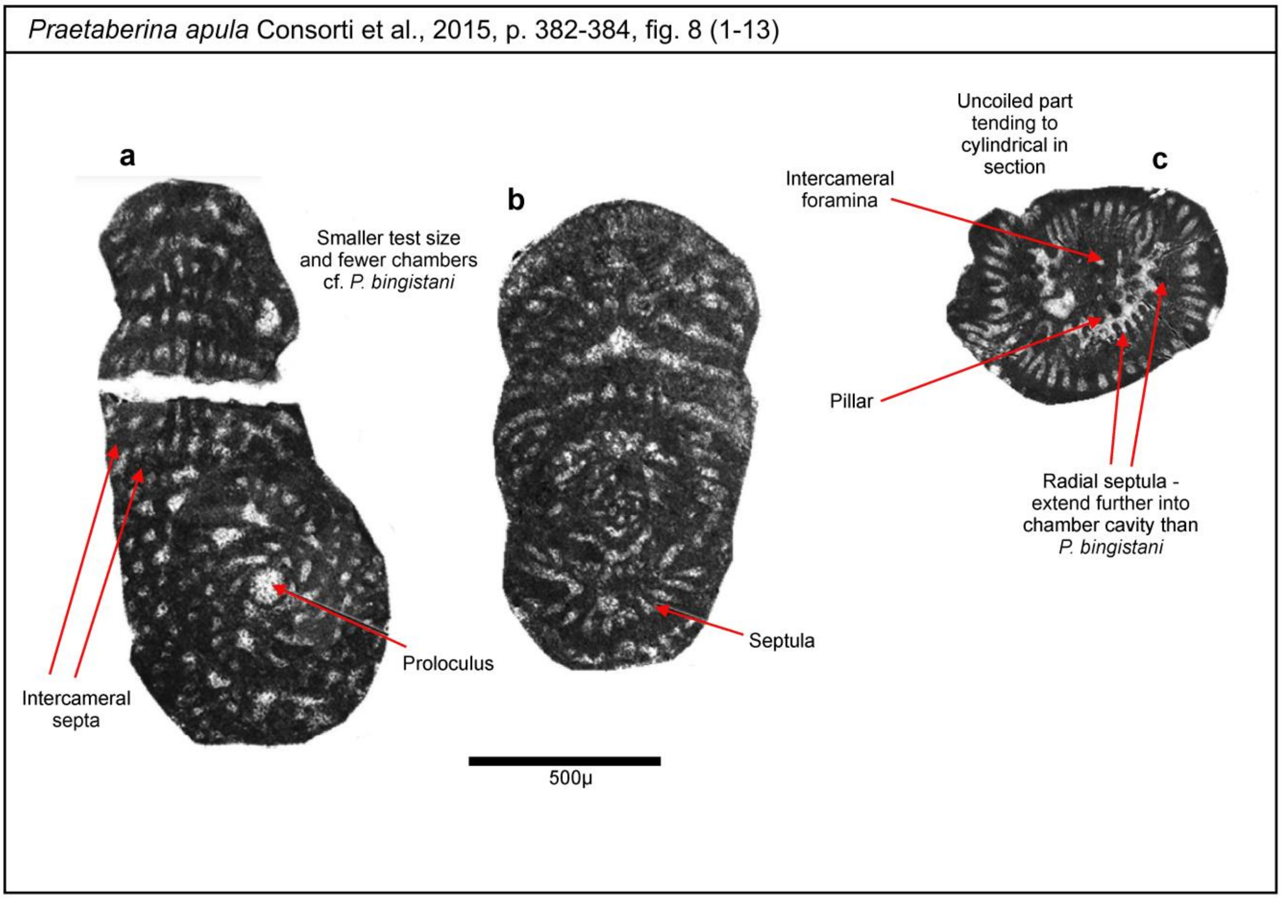


Fig. 72 Representative illustrations of *Praetaberina apula*: **a** Subequatorial section, Consorti et al. (2015, fig. 8(4), Italy); **b** Oblique section, Consorti et al. (2015, fig. 8(11), Italy); **c** Oblique section, Consorti et al. (2015, fig. 8(2), Italy).

Central Neotethys.
Reported only from Greece (Fleury, 1980) and Italy (Borghi & Pignatti, 2006) as *P. bingistani* but now referable to *P. apula* (following Consorti et al. 2015). The two species of *Praetaberina* discussed here would therefore appear to have mutually exclusive distribution patterns.
Mohajer et al. (2022b) reports the occurrence of *P. apula* from the Izeh Zone of the Iranian Zagros, but only as originally reported by Khosrow Tehrani & Fonooni (1994) i.e., before the species was first described. It is not known by what means Mohajer et al. (2022b) concluded that this occurrence is, in fact, *P. apula*. This record is not included on the distribution map.

Genus ***Pseudopeneroplis*** Consorti et al., 2018
Type Species: *Pseudopeneroplis oyonensis* Consorti et al., 2018
Pseudopeneroplis oyonensis **Consorti et al., 2018**

Reference Illustration & Description

Consorti et al. (2018), Figs. 5-6, p. 6-10.
Pseudopeneroplis oyonensis is an apparently endemic species at present only known from the coastline of the Eastern Pacific, specifically Peru. Consorti et al. (2018) assigned the genus to the Praerhapydioninidae.
Pseudopeneroplis has the same chamber/coiling arrangement as *Peneroplis* Montfort, but develops short, thick subdivisions (septula) in the chamber margins. *Pseudopeneroplis* has a single row of rounded openings in the middle of the apertural face (and which are aligned between chambers) whereas *Pseudorhipidionina* has two rows of apertures and longer septula which sometimes bifurcate. Both genera lack pillars. See the Species Key Chart (Appendix) for diagnostic and other characteristics.
Pseudorhapydionina and *Praetaberina* have more cylindrical uncoiled portions, and with septula arranged more radially rather than linearly in *Pseudopeneroplis*. *Praetaberina* also possesses central pillars which *Pseudopeneroplis* does not. In equatorial sections *Pseudopeneroplis* also resembles *Scandonea* (especially *S.? phoenissa* when uncoiled) but the latter genus lacks septula.
Consorti et al. (2018) mention that, despite whether a specimen is megalospheric or microspheric, the dimensions of the overall shell are unaffected (up to 0.52mm equatorial diameter and maximum length of uncoiled specimen c. 1.00mm).

Stratigraphic Distribution

Late Cenomanian.
The type locality is the Jumasha 4 unit, Uchucchacua section, Peru, dated as late Cenomanian using Carbon-isotope stratigraphy (Navarro-Ramirez et al., 2017).

Cenomanian Paleogeographic Distribution

Eastern Pacific.
Recorded from Peru only (on the Western Platform of South America).

Genus ***Rajkanella*** Schlagintweit & Rigaud, 2015
Type Species: *Rajkanella hottingerinaformis* Schlagintweit & Rigaud, 2015
Rajkanella hottingerinaformis **Schlagintweit & Rigaud, 2015**

Reference Illustration & Description

Schlagintweit & Rigaud (2015), Figs. 3 & 4, p. 195-198.
Schlagintweit & Rigaud (2015) described this form from the middle-upper Cenomanian of Kosovo and remarked upon its similarity with the Paleocene genus *Hottingerina* Drobne, 1975, from which it differs mainly by retaining a rounded aperture throughout growth, by possessing striate ornamentation and by not uncoiling. See the Species Key Chart (Appendix) for diagnostic and other characteristics.
Although the presence of numerous, interiorly-peripheral, short, beams convey a superficial similarity, it differs from contemporary genera such as *Pseudorhapydionina* and *Pseudorhipidionina* by having a coiled, lenticular test, a less complex aperture and lacks the tendency to uncoil. *Fissumella*, an early Albian genus introduced by Cruz-Abad et al. (2017) is morphologically close to *Rajkanella*, but in the latter genus the aperture is rounded whereas in *Fissumella* it is an elongate fissure.
Schlagintweit & Rigaud (2015) did not come to any conclusions regarding dimorphism in *Rajkanella*, but which was noted in *Hottingerina* species (Drobne, 1975).

Stratigraphic Distribution

Middle – late Cenomanian.
Although compared with Paleocene forms, Schlagintweit & Rigaud (2015) recorded this species alongside middle-late Cenomanian taxa such as *Pseudorhapydionina dubia*, *Vidalina radoicicae*, *Pastrikella balkanica* (Cherchi, Radoičić & Schroeder), *Pseudonummoloculina regularis*, *Chrysalidina* cf. *gradata* and *Nezzazata* cf. *simplex* from their material in Kosovo. Consorti & Schlagintweit (2021a) using additional Kosovan-Albanian material and the co-occurrence of other age-diagnostic taxa, confirm a late Cenomanian age.
It was also found in the middle and upper parts of the Sarvak Formation (=middle-late Cenomanian), Iranian Zagros, by Yazdi-Moghadam & Schlagintweit (2020, 2021) and Schlagintweit & Yazdi-Moghadam (2020, 2021, 2022a).

Cenomanian Paleogeographic Distribution

(Central – Eastern) Neotethys.
Not widely recorded except from those references mentioned above (i.e., confirmed by illustration in Kosovo-Albania and the Iranian Zagros).

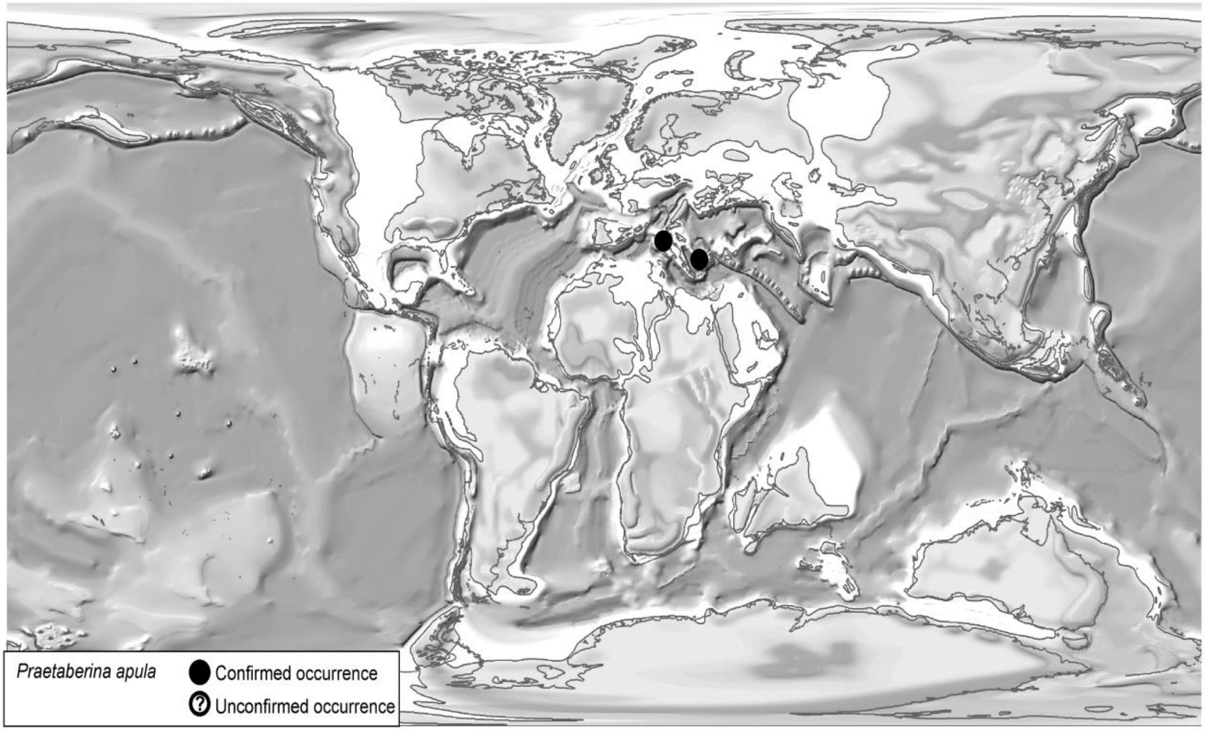


Fig. 73 Cenomanian paleogeographic distribution of *Praetaberina apula*.

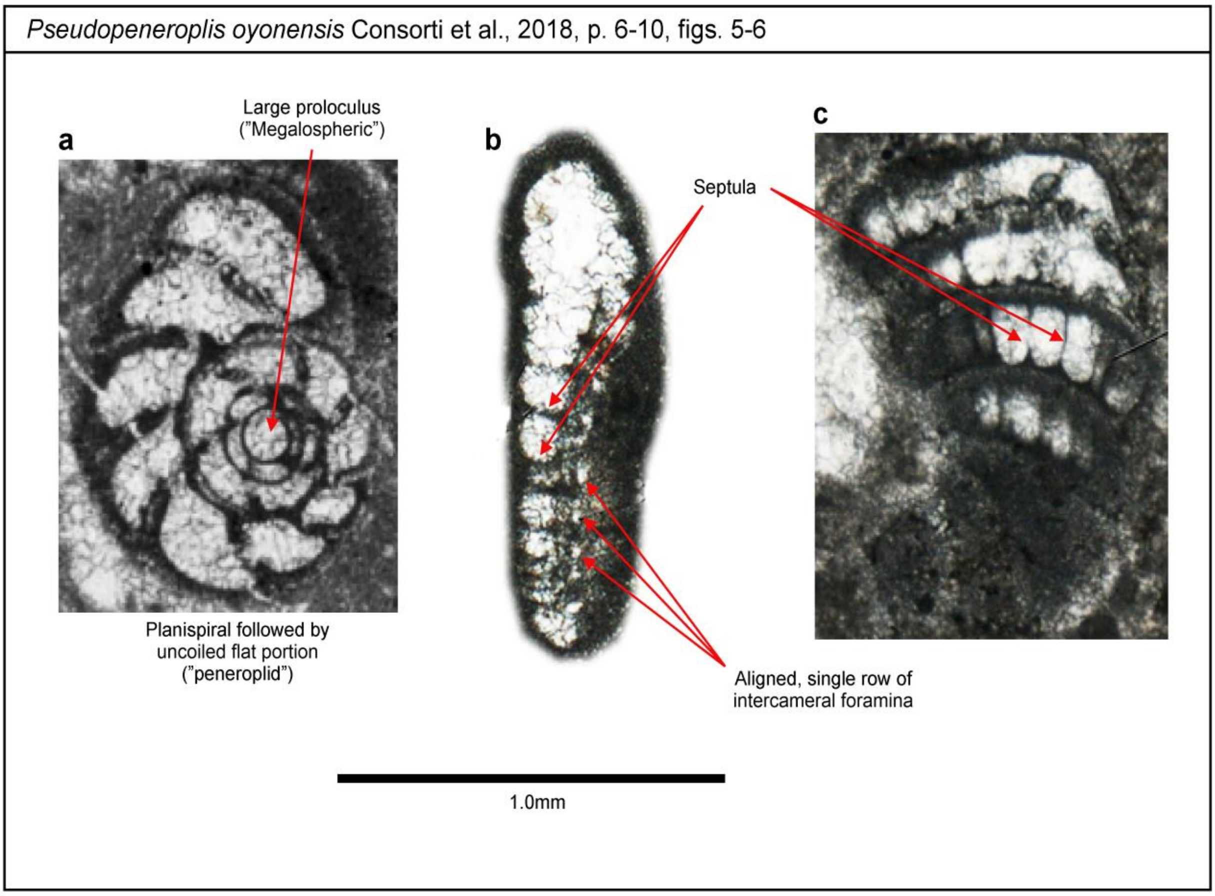


Fig. 74 Representative illustrations of *Pseudopeneroplis oyonensis*: **a** Equatorial section, Consorti et al. (2018, fig. 5a, holotype, Peru); **b** Subaxial section, Consorti et al. (2018, fig. 6d, Peru); **c** Tangential section, Consorti et al. (2018, fig, 5f, Peru).

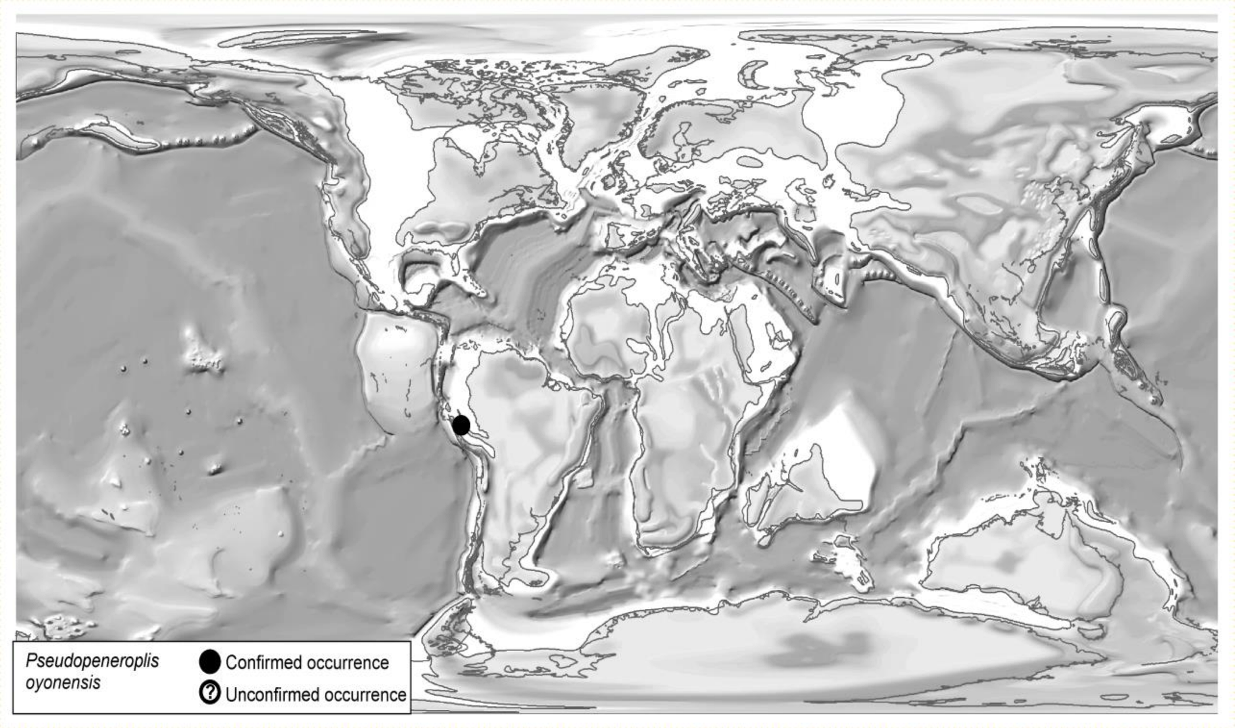


Fig. 75 Cenomanian paleogeographic distribution of *Pseudopeneroplis oyonensis.*

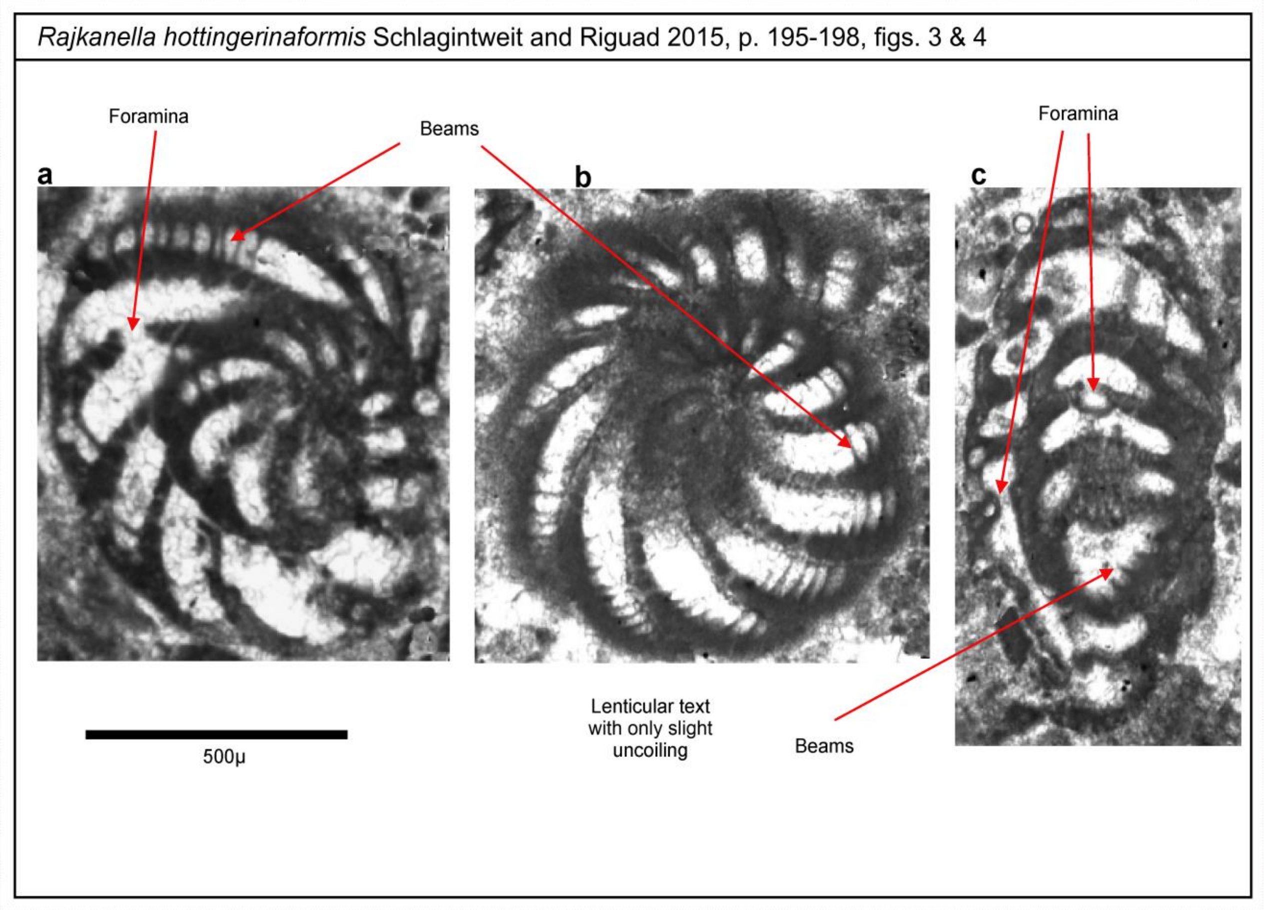


Fig. 76 Representative illustrations of *Rajkanella hottingerinaformis*: **a** Slightly Oblique Equatorial section, Schlagintweit & Rigaud (2015, fig. 3O, Kosovo); **b** Oblique section, Schlagintweit & Rigaud (2015, fig. 3D, Kosovo); **c** Axial section Schlagintweit & Rigaud (2015, fig. 3G, holotype, Kosovo).

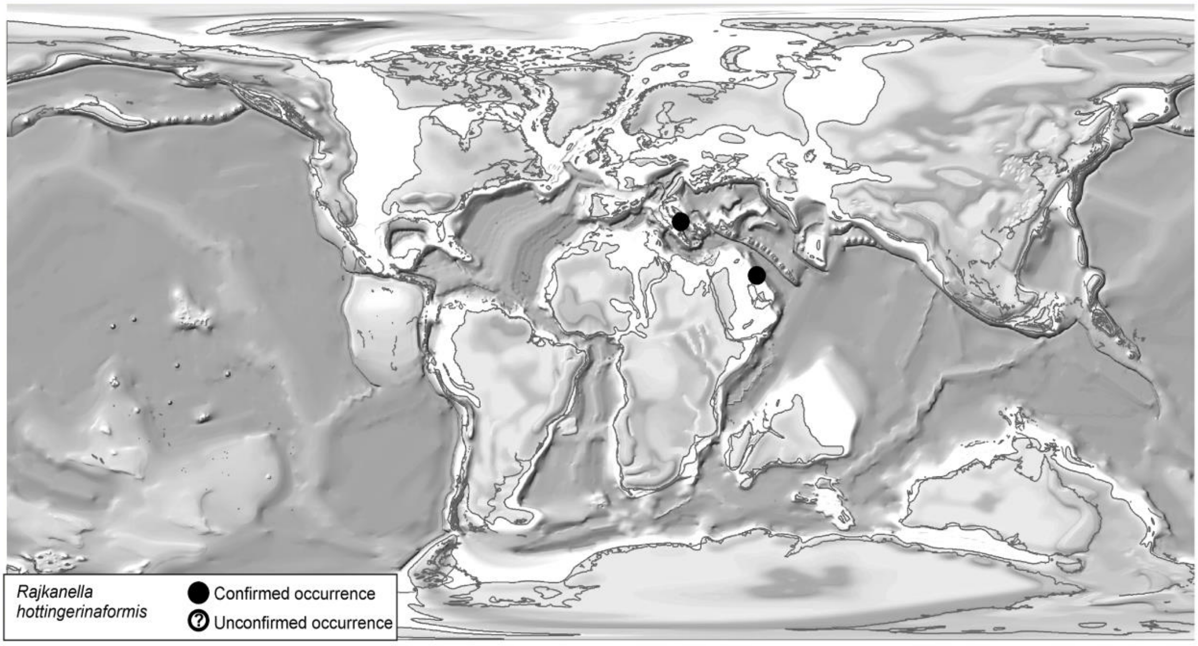


Fig. 77 Cenomanian paleogeographic distribution of *Rajkanella hottingerinaformis*.

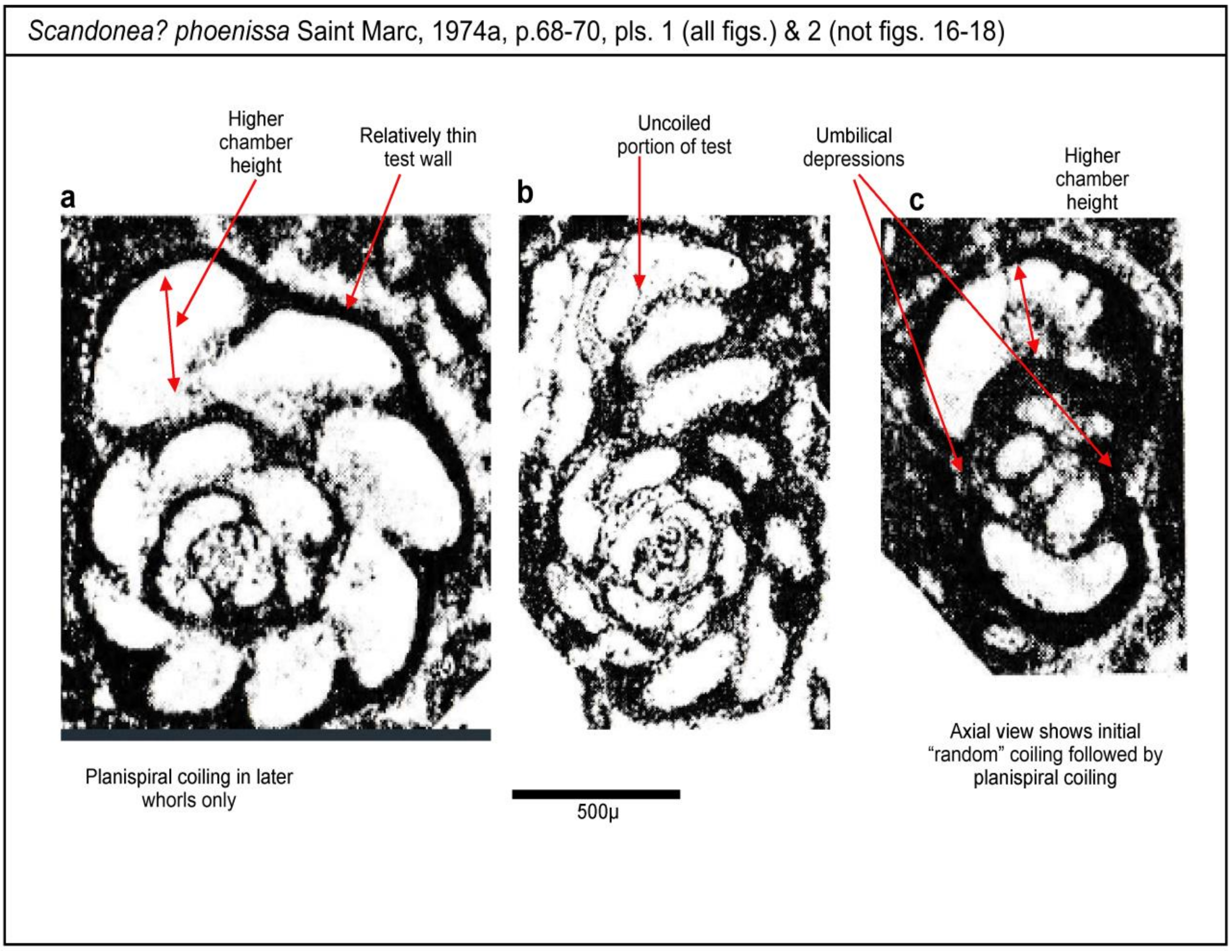


Fig. 78 Representative illustrations of *Scandonea? phoenissa*: **a** Equatorial section, Saint Marc (1974a, pl. 1, fig. 11, Lebanon); **b** Equatorial section, Saint Marc (1974a, pl. 1, fig. 3, Lebanon); **c** Axial section, Saint Marc (1974a, pl. 1, fig. 9, Lebanon).

Genus ***Scandonea*** De Castro, 1971
Type Species: *Scandonea samnitica* De Castro, 1971

***Scandonea*? *phoenissa* Saint-Marc, 1974**

Reference Illustration & Description

Saint-Marc (1974b), Pl. 1 & 2 (not 16-18), p. 68-70.

The type description of the species by Saint-Marc (1974b, from the middle Cenomanian of Lebanon) is comprehensive and allows for confident identification.

De Castro (1971) introduced the genus *Scandonea*, with the type species as the Late Cretaceous (Turonian and younger) species *S. samnitica*. Based on the type species, *Scandonea* is a distinctive porcellaneous walled form, with initial coiling being milioliform/streptospiral, then planispiral involute. The type species has basal thickening to each chamber wall (for a recent review see Arriaga et al., 2016).

Saint-Marc (1974b) erected *S.*? *phoenissa* on the basis of differences from *S. samnitica:* smaller dimensions; a reduced number of whorls in the coiled planispiral stage; the lack of basal thickening inside the chambers, and the lack of a tooth in the aperture. These differences are sufficient to make the assignment to the genus questionable, and this rarely described species requires a full taxonomic review that is outside the scope of this primarily biostratigraphic study. See the Species Key Chart (Appendix) for diagnostic and other characteristics.

S? phoenissa is a poorly known species and the possibility exists that the type material is synonymous with species of *Pseudorhapydionina* (as partial, incomplete specimens) – compare, for example, with the illustrations of *P. dubia* herein. More work is required to confirm this suspicion (Dr. Lorenzo Consorti, pers. comm., 2023), so, for the moment, *S? phoenissa* is retained as a separate species.

S.? *phoenissa* is similar to *S.*? *pumila* Saint-Marc (see remarks under that species for distinguishing features).

Similar taxa include *Moncharmontia apenninica* and *Charentia cuvillieri*, but which are both planispiral throughout and agglutinated. The latter also tends to uncoil like some specimens of *S.*? *phoenissa*. In addition to the above differences, *Moncharmontia compressa* has a subangular periphery not observed in *S.*? *phoenissa* (or *S.*? *pumila* – see below).

Stratigraphic Distribution

(Latest Albian?) early - middle Cenomanian (earliest late Cenomanian?).

Not a widely recorded species, Saint-Marc (1974b) originally described this species from Lebanon from sediments containing *Sellialveolina viallii* (Colalongo) and *Ovalveolina maccagnoae* De Castro which were assigned a middle Cenomanian age. However, the associated taxa mentioned occur in early Cenomanian sediments, and possibly latest Albian (Schroeder & Neumann, 1985). However, its occurrence is at the top of Saint-Marc's *P. viallii* biozone, suggesting mostly likely a middle Cenomanian age. Subsequent plausible records are few. Solak et al. (2020) recorded and illustrated this species from the early – middle Cenomanian *Sellialveolina* gr. *viallii* zone in the western Taurides of Turkey, with a reported occurrence in the basal part of the late Cenomanian *Pseudorhipidionina casertana* zone.

Velić & Sokač (1979) illustrated plausible specimens from the supposed latest Albian of Croatia in association with a number of species of orbitolinids (e.g., "*Valdanchella*" *dercourti*). These orbitolinids are not well illustrated and in any case might well be Cenomanian (see synonymy lists and range charts in Schroeder & Neumann, 1985). Subsequently, Husinec et al. (2000) recorded this species (unillustrated) from the lowest part of the *Orbitolina* (*Conicorbitolina*) *conica* abundance zone of Croatia, attributing this zone to the early – middle Cenomanian. However, Husinec et al. (2009) later indicated the range of this species in Croatia as latest Albian only. Meanwhile, Velić (2007) recorded this species (unillustrated) from the late Albian of Croatia, noting in the text (not the range chart), that the species range extends into the Late Cretaceous (i.e., Cenomanian). In summary, there are question marks regarding the late Albian age attribution of records in Croatia, stemming from uncertainty in the associated orbitolinid identifications and their perceived biostratigraphic calibration. The late Albian records could well be proved to be early Cenomanian, pending further research.

Forms recorded and illustrated as *Scandonea* aff. *phoenissa* by Tešović et al. (2011) and, separately, by Ritossa (2018) also from Croatia are from strata dated variously between the Albian and Aptian. The illustrations in both sources are insufficient to assign a definite species (or genus) to the specimens and do not therefore affect the range attributed herein.

Cenomanian Paleogeographic Distribution

Central Neotethys.

Not widely recorded except from those references mentioned above (i.e., confirmed by illustration in Lebanon, Turkey, and Croatia). Records from Croatia appear to be common.

***Scandonea*? *pumila* Saint-Marc, 1974b**

Reference Illustration & Description

Saint-Marc (1974b), Pl. 2 (16-18), p. 70-71.

The type and subsequent description of the species by Saint-Marc (1974b, from the upper Cenomanian of Lebanon) is comprehensive and allows for confident identification.

S.? *pumila* differs from *S.*? *phoenissa* by its more globular shape and the absence of an umbilical depression; the greater thickness of the test wall; the absence of an unrolled stage (this character is not decisive however due to

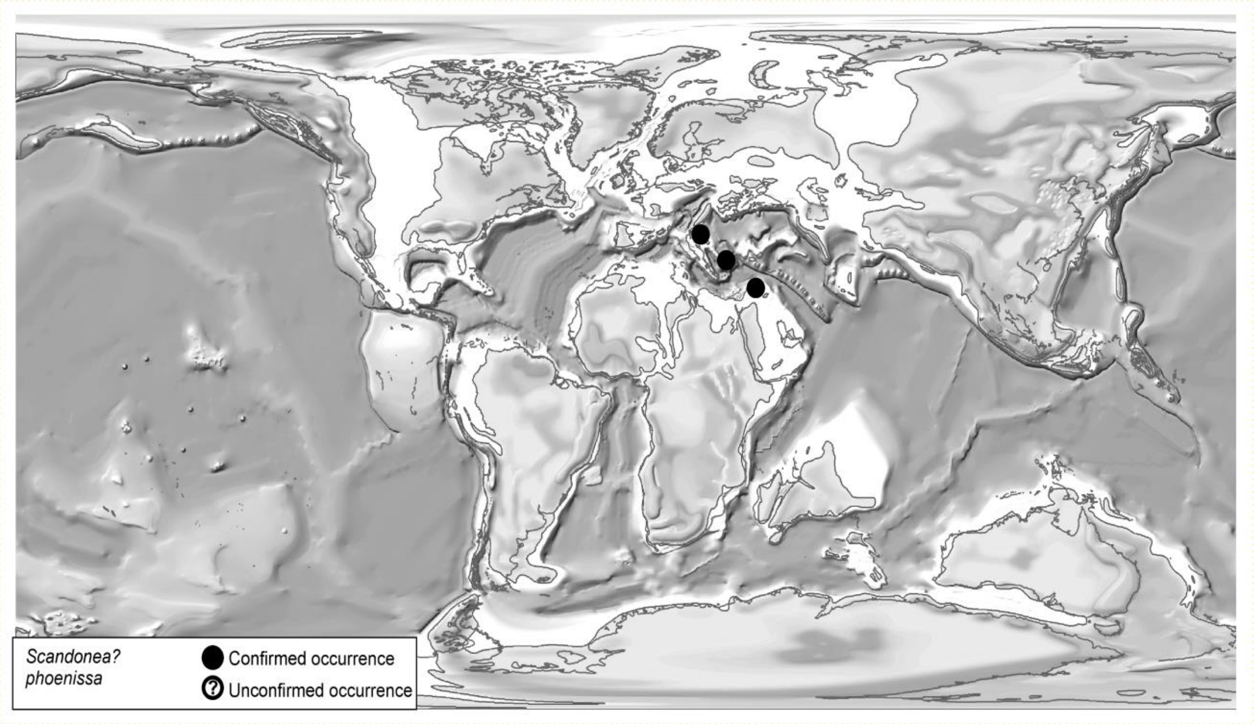


Fig. 79 Cenomanian paleogeographic distribution of *Scandonea? phoenissa.*

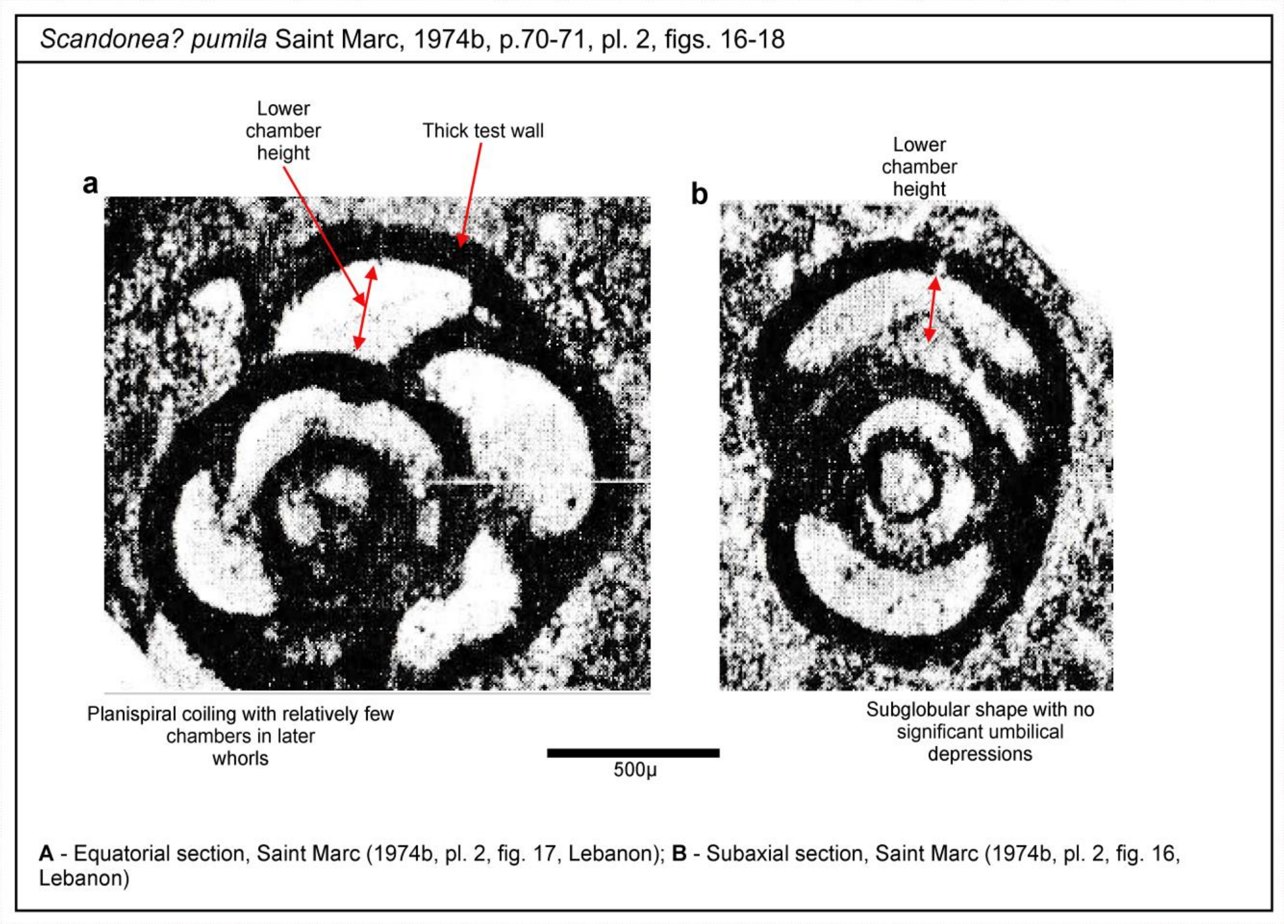


Fig. 80 Representative illustrations of *Scandonea? pumila*: **a** Equatorial section, Saint Marc (1974b, pl. 2, fig. 17, Lebanon); **b** Subaxial section, Saint Marc (1974b, pl. 2, fig. 16, Lebanon).

the insufficient number of sections studied and illustrated by Saint-Marc, 1974b); the reduced number of chambers in the planispiral stage; the reduced chamber height in the planispiral stage. See the Species Key Chart (Appendix) for diagnostic and other characteristics.

S.? *pumila* has a test shape similar to the globular/subglobular test of the agglutinated species *Fleuryana gediki*, but has a much thicker wall, fewer chambers, and less rectangular-shaped chambers (in equatorial view) than *F. gediki*.

S.? *pumila* also bears a resemblance to microspheric forms of *S. samnitica* but is smaller; has no basal layer, and no tooth at the base of the aperture. As for *S.*? *phoenissa*, these differences are sufficient to make the assignment to the genus questionable, and this rarely described species requires a full taxonomic review that is outside the scope of this primarily biostratigraphic study.

S.? pumila is a poorly known species and the possibility exists that the type material is synonymous with species of *Pseudorhapydionina* (as partial, incomplete specimens) – compare, for example, with the illustrations of *P. dubia* herein. More work is required to confirm this suspicion (Dr. Lorenzo Consorti, pers. comm., 2023), so, for the moment, *S.? pumila* is retained as a separate species.

Stratigraphic Distribution

(Latest Albian?) middle - late Cenomanian.

Not a widely recorded species, Saint-Marc (1974b) originally described this species from Lebanon, in association with *Pseudorhapydionina laurinensis*, *Chrysalidina gradata*, *Praetaberina bingistani*, *Biplanata peneropliformis*, , *Biconcava bentori* and a number of other Cenomanian LBF. Although assigned a late Cenomanian age by Saint-Marc (1974b), a late middle Cenomanian age cannot be discounted for this assemblage based on our review herein.

Charrière et al. (1998) recorded and illustrated plausible specimens from several localities dated as late Cenomanian (age calibrated by ammonite occurrences) in the Atlas of Morocco. Ciszak et al. (1999) and Ettachfini (2006) also provides records (but unillustrated) from the late Cenomanian of Morocco.

Velić & Vlahović (1994) recorded and illustrated rare occurrences from a single sample in the lowermost CEN-4 zone of the middle Cenomanian (approximately at the mid point of the middle Cenomanian interval). Velić (2007) recorded it (unillustrated) from the latest Albian – middle Cenomanian of Croatia. Likewise, Husinec et al. (2009) recorded (unillustrated) a bimodal range for this species in the latest Albian and separately in the lower middle Cenomanian of Croatia.

Solak et al. (2021) record a “cf” form from the Albian of central Turkey, however, their illustrations do not quite conform to the Saint-Marc types and no axial views are shown.

Cenomanian Paleogeographic Distribution

Neotethys.

Not widely recorded except from those references mentioned above (i.e., confirmed by illustration in Lebanon, Morocco, and Croatia).

Genus ***Perouvianella*** Bizon et al., 1975

Type Species: *Orbiculina peruviana* Steinmann, 1929

Perouvianella peruviana **(Steinmann, 1929)**

Reference Illustration & Description

Consorti et al. (2018), Figs. 2-4, p. 5-6.

The illustrations in Jaillard & Arnaud-Vanneau (1993) are also useful. *Perouvianella peruviana* is a highly endemic species seemingly confined to the coastline of the Eastern Pacific, specifically central Peru. It is internally complex with 2-4 sets of pillars (sometimes interlocking) in the chambers. The diagnosis of the genus was recently emended by Consorti et al. (2018) and the species was also comprehensively redescribed and illustrated to which the reader is referred to for details.

P. peruviana is a large species, 2-7 mm in diameter. Its mode of coiling (planispiral at first then uncoiling into a flat, flabelliform shape) and complex internal chamber structures are superficially similar to *Pseudorhipidionina* and *Praetaberina* in certain thin section views, but it is not closely related. It has 2-4 whorls disposed in a planispiral involute arrangement with 8-10 chambers in the first whorl and 13-15 in the second whorl. The megalospheric proloculus can be large: 0.2 – 0.33 mm. See the Species Key Chart (Appendix) for diagnostic and other characteristics.

The porcellaneous wall, presence of several rows of both radial and intercameral pillars, as well as alternating septula (although the latter may be hard to confirm, see for example Fig. 82A herein), caused Consorti et al. (2018) to provisionally assign it to the family Soritidae.

The species was introduced by Steinmann (1929) as *Orbiculina peruviana* with illustration and limited description, then subsequently made type species of the new subgenus *Perouvianella* (genus *Archaias* Montfort) by Bizon et al. (1975). *Perouvianella* was subsequently raised to generic status (e.g., Loeblich & Tappan, 1988).

Stratigraphic Distribution

Late Cenomanian – early Turonian.

The stratigraphic distribution of *P. peruviana* is noteworthy because (a) it represents a data point significantly outside the Caribbean-Atlantic-Neotethyan realm to where the vast majority of species in this study are confined and (b) it was seemingly unaffected by events around the Cenomanian-Turonian boundary that led to the general extinction of the vast majority of LBF elsewhere (Consorti et al., 2018; Consorti & Schlagintweit, 2021a; Schlagintweit & Yazdi-Moghadam, 2021). Jaillard & Arnaud-Vanneau (1993) attribute this to less drastic anoxic conditions on the more open Western Platform

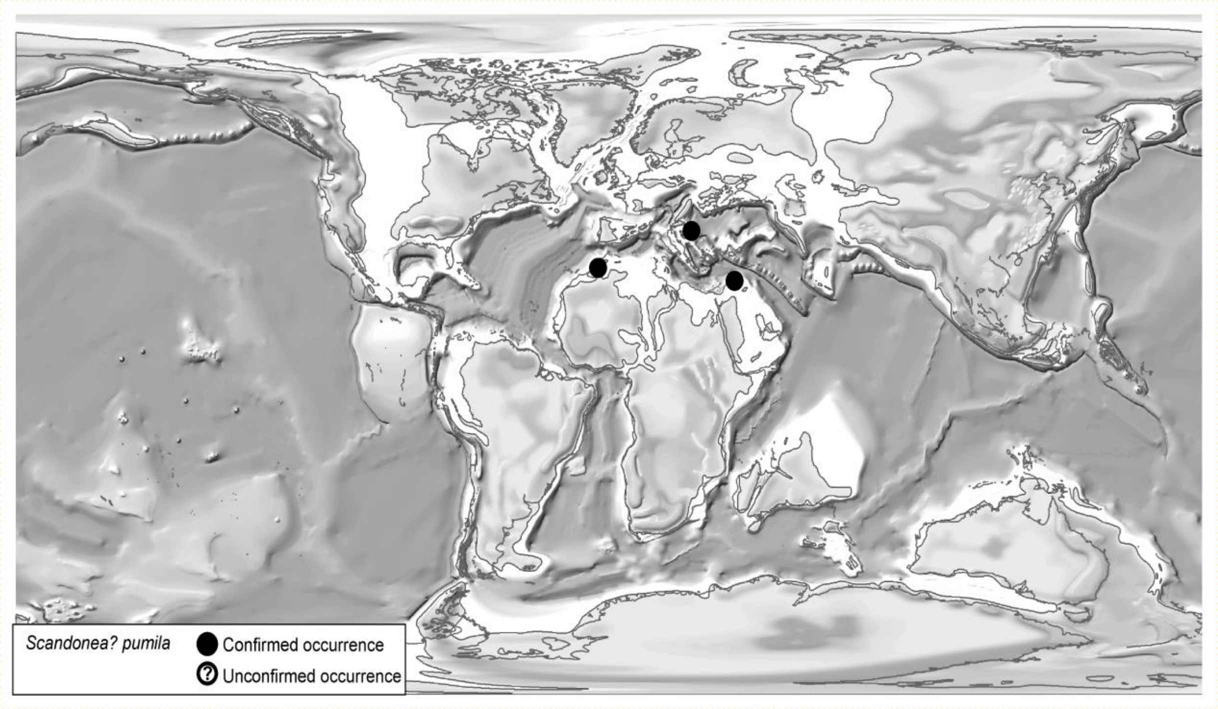


Fig. 81 Cenomanian paleogeographic distribution of *Scandonea? pumila*.

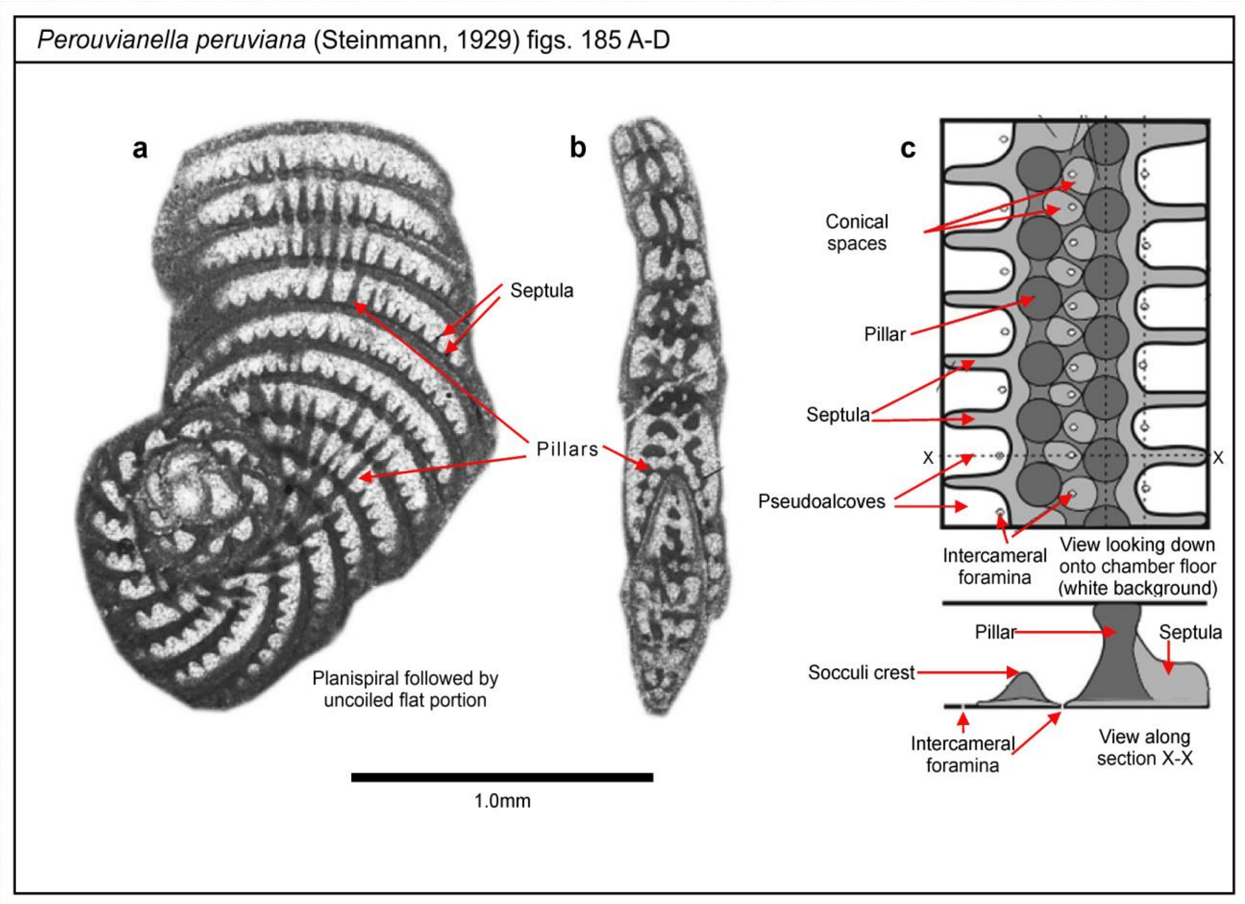


Fig. 82 Representative illustrations of *Perouvianella peruviana*: **a** Equatorial section, Consorti et al. (2018, fig. 4b, Peru); **b** Sub-axial section, Consorti et al. (2018, fig. 4j, Peru); **c** Schematic chamber section with 2 rows of pillars, Consorti et al. (2018, figs. 2a, 2d).

of Peru compared with those around the Tethys-Atlantic-Caribbean margins.

In Peru, *P. peruviana* is often present in near rock-forming abundances throughout sediments associated with (and slightly above and below) OAE2 (Navarro-Ramirez et al., 2017; Consorti et al., 2018). Consorti et al. (2018) consider this to have been related to "*local mesotrophic conditions and salinity changes of shallow-shelf water masses that were severely restricted and separated from oceanic blue water aquafacies*". Clearly, *P. peruviana* thrived in the localised environmental conditions (oxic, but with significant environmental perturbations) that existed in the Peru region in the late Cenomanian and early Turonian (Navarro-Ramirez et al., 2016, 2017).

Using carbon isotope chronostratigraphic calibration and ammonite occurrences, Navarro-Ramirez et al. (2016, 2017) showed that *P. peruviana* ranges from as old as the regional *Neolobites vibrayeanus* ammonite zone to as young as the *nodosoides* Tethyan ammonite zone (upper early Turonian). *Neolobites vibrayeanus* (d'Orbigny) is said to have its main occurrence in the *guerangeri* Tethyan ammonite zone (lower late Cenomanian), at least in the Middle East (Wiese & Schulze, 2005; Meister & Piuz, 2015).

Jaillard & Arnaud-Vanneau (1993) slightly extend the range downwards into the latest middle Cenomanian, and upwards into the earliest middle Turonian, but these are shown as uncertain occurrences. Furthermore, the precise age interpretations of these authors are challenged by the new chronostratigraphic calibration presented by Navarro-Ramirez et al. (2016, 2017).

The species was originally considered to be a Santonian marker (e.g., Bizon et al., 1975; Loeblich & Tappan, 1988), but its correct age calibration was demonstrated by Jaillard & Arnaud-Vanneau (1993). Nonetheless, there are relatively recent literature statements that mistakenly continue to mention it as a Santonian species (e.g., Caus et al., 2013; BouDagher-Fadel et al., 2017).

Cenomanian Paleogeographic Distribution

Eastern Pacific.

Recorded from Peru only - see references in previous discussion.

DISCUSSION

Identity

It is evident that despite the quantity of new literature published in the last 3-4 decades, the quality of literature with respect to identifying the "planispiral" LBF, and assigning credible ages to stratigraphic distribution, is variable in quality, ranging from very good to very poor. Of course, so much depends on the quality of the studied material and the orientation of the thin-section necessary to examine the specimen, which is often outwith the control of the palaeontologist. We have attempted to review the difficulties in identification and, we hope, have provided tools such as the Species Key chart (Appendix) and annotated illustrations to assist workers.

Notwithstanding, there are several "confusion" groups which can easily lead to incorrect identification of planispiral LBF, particularly where not well preserved or oriented. This also applies to other LBF groups not discussed here (e.g., alveolinids). Even when material is good, some taxa remain difficult to separate with multiple sections and multiple orientations.

There is an overall lack of confirmatory illustration in many publications and accepting an (unillustrated) identification as correct at face value can be risky. Similarly, a stated age assignment to the range of a taxon in a well or outcrop section can also be prone to error without confirmation from another biostratigraphic or non-biostratigraphic source.

These sources of error may even be compounded by a tendency for workers to "force" a taxonomic (i.e., species) label onto a specimen which cannot be justified (Schlagintweit & Simmons, 2022). Where differences between species can only be measured by seemingly trivial details like the number of septula per chamber quadrant, or the degree at which the septula extend into the chamber lumen, correct taxonomic assignment may not be possible if such characters are not observed. Workers should accept that only identification to a higher taxonomic level (e.g., genus or family) may be possible if material is poor.

Biostratigraphy and paleobiogeography

Another factor to consider is the nature and habitat of LBF which makes them vulnerable to environmental (i.e., facies) change and therefore their biostratigraphic ranges at a single locality can potentially be very sporadic (see also below). By applying a more critical set of criteria to establish identity, we believe we have at least identified a "core biostratigraphic range" for Cenomanian planispiral LBF taxa and can apply a degree of confidence to their paleogeographic distribution patterns. This is important as in the future, studies of, for example, dispersal routes – especially in the context of current Cenomanian palaeocurrent models (Fig. 84) may throw some additional light on the distributional envelope (i.e., in space and time) of a taxon.

In general, we have concluded that many Cenomanian planispiral LBF are relatively long-ranging, possibly because their relatively simple structure lends itself to evolutionary conservatism in a way that more complex Cenomanian LBF (e.g., the alveolinids, orbitolinids etc.) tend to have very short ranges. However, some planispiral LBF taxa appear to have shorter stratigraphic ranges provided they are identified correctly. Diversity clearly increases towards the upper middle and late Cenomanian and enhances the Cenomanian's reputation as the geological time period (together with the Holocene) with the maximum number of reported (agglutinated foraminiferal) taxa (Kaminski et al., 2010).

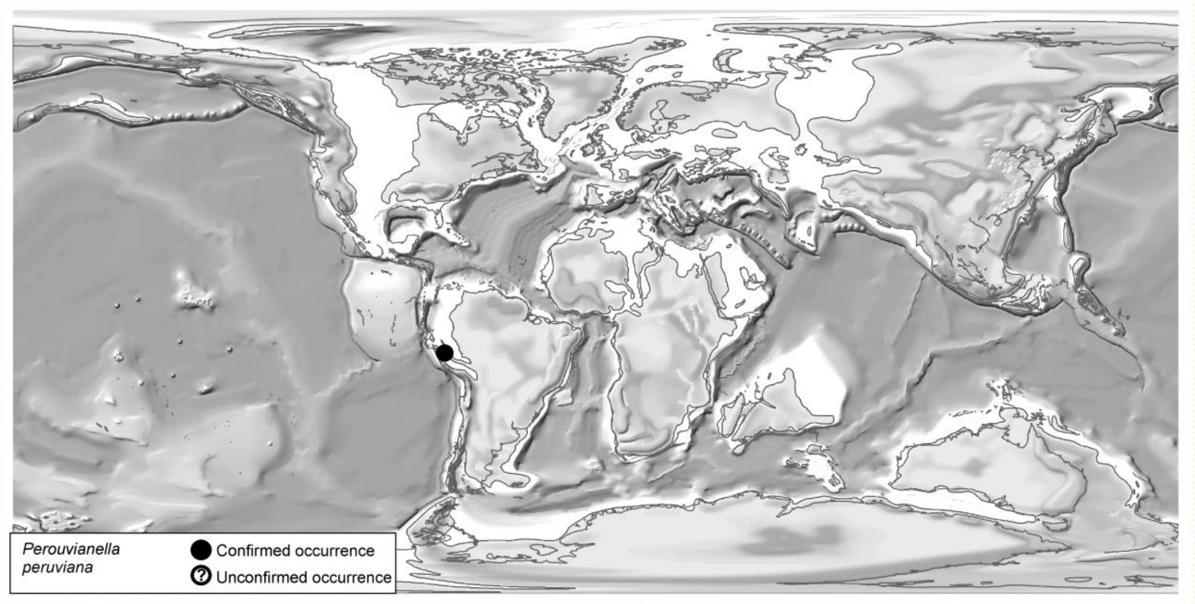


Fig. 83 Cenomanian paleogeographic distribution of *Perouvianella peruviana*.

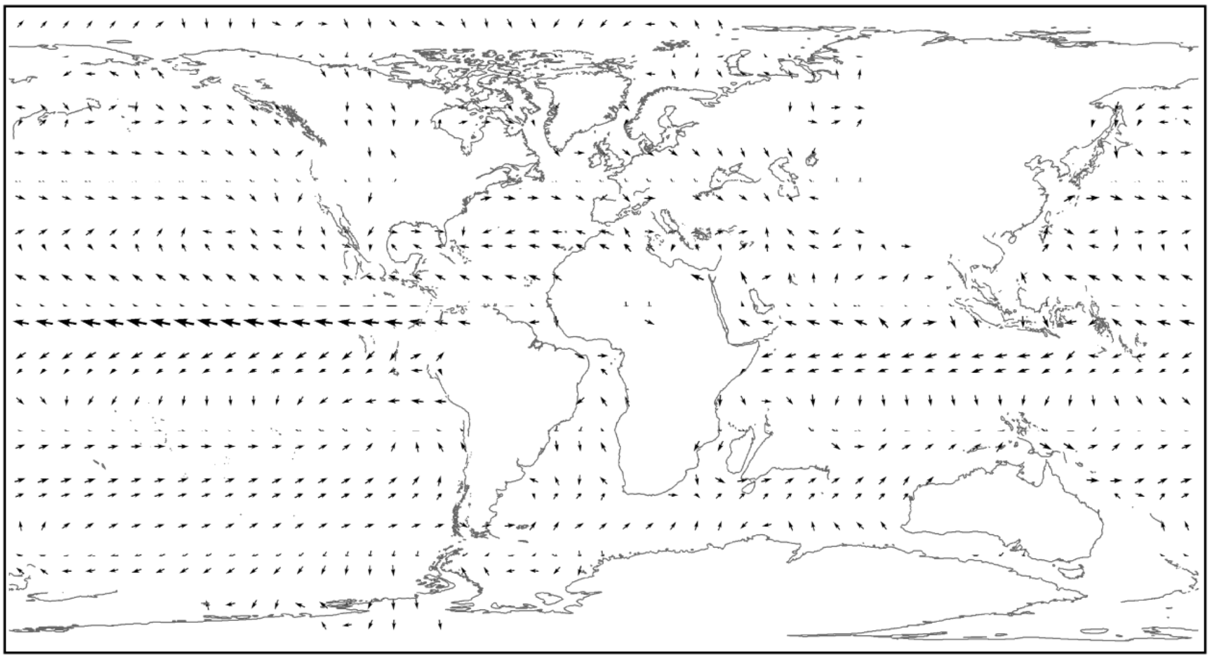


Fig. 84 Late Cenomanian palaeocurrent map (courtesy of Halliburton). Integrating this information with LBF distribution patterns in time and space could provide useful understanding of species dispersal. Note the dominant east-west currents in the equatorial region. This is suggestive of Cenomanian LBF taxa arising in the Middle East and dispersing westwards (see for example comments on *Moncharmontia apenninica* and Schlagintweit & Yazdi-Moghadam (2021)).

Improvements

A feature often observed during our evaluation of the literature is how commonly we have seen workers referring to outdated references in respect of (a) taxonomic understanding and (b) age assignments, often referring only to previous work carried out in the period between the 1940s and 1980s. The availability of up-to-date references is no longer a difficult, insurmountable issue but whilst illustrations of specimens in older works are still valid and useful, the interpretations surrounding those occurrences may be outdated.

Authors should be encouraged to provide confirmatory illustrations of identified specimens wherever possible. This is not standard practice, particularly in comparison to other fossil groups such as planktonic foraminifera or nannofossils, where comparative illustrations are abundant and, in most cases, the taxonomy and identity is well understood. However, as the taxonomy of LBF improves, diagnostic characters – the criteria for species separation – appear to become more finely subdivided and perhaps only resolvable in excellent quality material.

Workers on other microfossil groups have improved their collective knowledge by collating data such as images and age-ranges onto bespoke websites with open access and the ability of users to contribute to and even disagree with interpretations therein. Sites such as “Mikrotax”

(Huber et al., 2017) (for planktonic foraminifera and nannoplankton) and "Dinoflaj3" (Williams et al., 2017) (for dinocysts) and others, have become key locations for obtaining the latest information and guides to identification of taxa and their biostratigraphy. Databases such as the World Register of Marine Species (WORMS) (Hayward et al., 2020) are useful research tools for the status of foraminiferal taxonomy. Such a device would surely be easy to produce for LBF and it seems odd that there isn't one – to our knowledge – currently in development.

Moreover, our review suggests that of the 39 taxa reviewed, more than two-thirds require thorough taxonomic revision through re-evaluation of types, study of topotype material, and study of other pristine material. Such studies can seem to be out of fashion and require a specialist set of skills to execute well, but they are fundamental to the correct establishment of identity and stratigraphic and palaeogeographic range. Good examples of this type of research for the Cenomanian LBF include Consorti et al. (2015), Vicedo & Piuz (2017) and Schlagintweit & Yazdi-Moghadam (2022a). We hope that this review will encourage more of these studies in the future.

Biostratigraphic Ranges

Evaluating the total biostratigraphic range of a species is an incompletable task for numerous reasons, not least how to deal with the discovery of new occurrences outside the currently accepted range limits.

Many well-studied fossil groups over hundreds or even thousands of locations, particularly those with a planktonic or nektonic lifestyle, are nearly ideal for biostratigraphic purposes because they have almost simultaneous (at least within geological time scale resolutions) global inceptions and extinctions and a rapid, widespread, area of distribution independent of facies control (McGowran, 2005). Neither of these characteristics, however, apply to LBF which are seldom found in rocks which also contain biostratigraphically-ideal fossils such as ammonites or planktonic foraminifera. There is little opportunity therefore to cross-calibrate between LBF and other, more age-diagnostic, fossil groups.

A possible solution is the use of Carbon-isotope stratigraphy (see Cramer & Jarvis, 2020 for a recent review). Whilst this technique offers non-unique solutions to age calibration, the pattern of positive and negative excursions in the $\delta^{13}C$ curve provide a potential "Rosetta Stone" to calibration between carbonate platform sections (that contain LBF) and basin stratigraphy (in which key chronostratigraphic fossil proxies occur). The technique is already showing encouraging signs as a means to generate valuable constraint on understanding the stratigraphic ranges of LBF (Parente et al., 2007, 2008; Frijia et al., 2015; Wohlwend et al., 2016; Bromhead et al., 2022; Mehrabi et al., 2022a, b).

Fig. 85 shows that, even with numerous sections studied (many of which have frequent gaps in succession), organisms subject to (a) facies control and (b) relatively slow dispersal times, like LBF, can have a sporadic distribution in time and space which makes evaluating an absolute global biostratigraphic range difficult. While several taxa studied here have a relatively widespread distribution throughout Neotethys and adjacent areas, many do not. Or the widespread distribution is very sporadic due to local facies control.

Many of the species herein have only been recorded from a relatively limited number of localities. Those with a broader area of occurrence have uncertainties about the correctness of their identification. Recording a new occurrence outside of currently-known biostratigraphic limits is predicated – amongst other factors – on (a) the correct taxonomic identification and (b) the correct age-calibration at that locality (e.g., section 1 on Fig. 85). Our review has demonstrated that, often, many occurrences (in the literature) are in error on one or both criteria.

We have attempted to evaluate our datapoints in terms of (a) identity and (b) age-calibration by the methodology discussed extensively above, which has resulted in the range chart shown in Fig. 86. In most cases we can resolve an LBF range top or base to a substage boundary or approximately within a substage. Calibrating an LBF range top or base to smaller time units such as ammonite zones, planktonic foraminifera zones or carbon-isotope events has proven difficult due to reasons discussed above but has been possible in some cases.

A positive outcome of this work is that a number of the Cenomanian "planispiral" LBF reviewed herein have the potential to help provide biostratigraphic calibration at the substage level, especially when combined with other LBF taxa such as alveolinids and orbitolinids that are known (Schroeder & Neumann, 1985; Calonge et al., 2002) to have a series of useful inception and extinction events. For example, the following LBF bioevents are a potential useful basis for Cenomanian biozonation:

Cenomanian LBF Events 1 - (approximates to base early Cenomanian) FAD *Praealveolina* (i.e., *Praealveolina iberica*). The FAD of *Orbitolina concava* (Lamarck) and probable FAD of *Conicorbitolina conica* are ancillary events.

The inception of the distinctive genus *Praealveolina* forms a useful bioevent and serves to distinguish Cenomanian strata from Albian strata. Older alveolinids occur (e.g., *Ovalveolina*), but the oldest species of *Praealveolina* (*P. iberica*) arises in the early Cenomanian at or near its base (Schroeder & Neumann, 1985; Calonge et al., 2002; Caus et al., 2009). There is some uncertainty as to if the FAD of *Praealveolina* coincides with the stage boundary (e.g., Vicedo et al., 2011), but the genus is excluded from Albian strata.

The FAD of *O. concava* is widely accepted as being associated with base of the Cenomanian (Schroeder & Neumann, 1985; Tröger & Kennedy, 1996; Velić, 2007; Schlagintweit et al., 2015), although care is needed to separate this species from similar forms that can occur in the late Albian (e.g., *Orbitolina seifini* Henson,

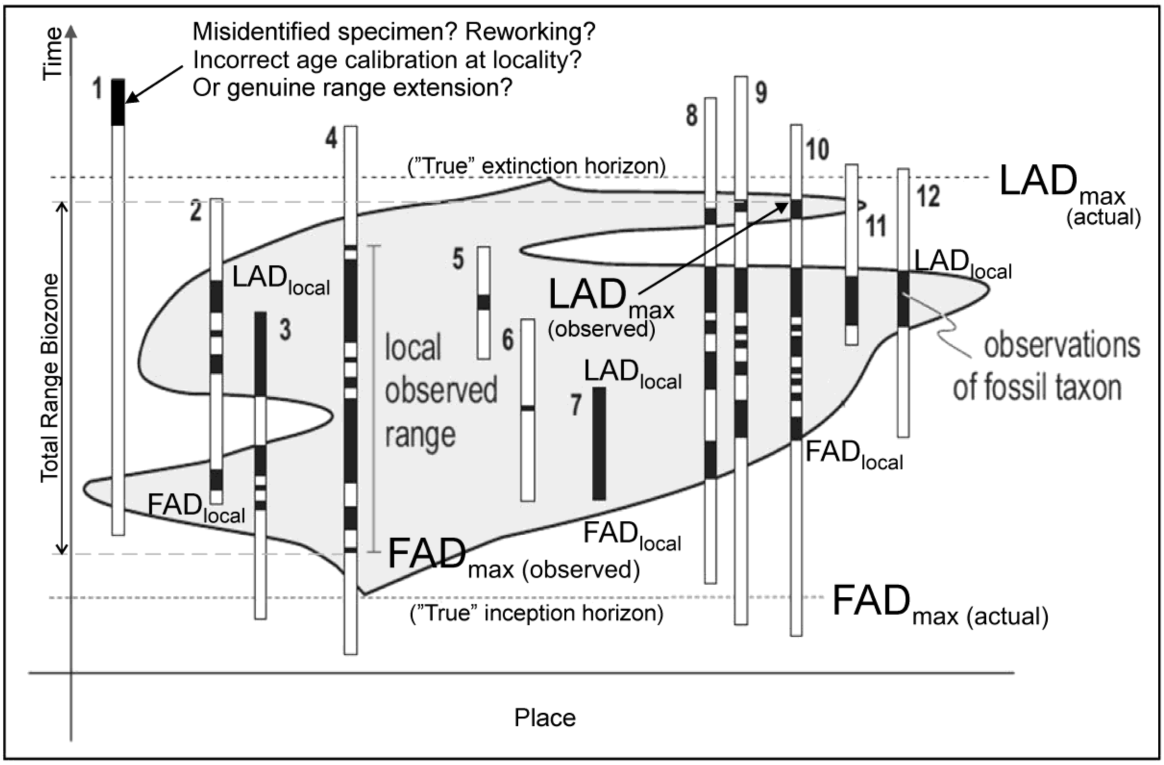


Fig. 85 Problems faced when attempting to evaluate the full biostratigraphic range of a benthic fossil species (based on Pearson, 1998 and Sadler, 2010 with modifications).

Orbitolina hensoni Simmons, Jones & Whittaker). Late Albian records of *O. concava* (e.g., Grafe, 2005; Caus et al., 2009) can most likely be discounted. The FAD of *C. conica* is often assumed to be coincident with the base of the Cenomanian (e.g., Velić, 2007), although Schroeder & Neumann (1985) did not exclude the possibility that the species might occur in the latest Albian (see also Lopez-Horgue et al., 2009).

Our research herein would suggest that the LAD of *Pseudonummoloculina aurigerica* most likely lies at this event, as does the FAD of *Pseudonummoloculina? regularis*.

Cenomanian LBF Events 2 - (approximates to base middle Cenomanian) FAD *Cisalveolina* (i.e., *Cisalveolina lehneri* Reichel). The FAD of *Praealveolina cretacea* (d'Archiac), FAD *Ovalveolina ovum* Reichel and possible LAD of *O. concava* are ancillary events.

The oldest species of *Cisalveolina* (*C. lehneri*) arises in the middle Cenomanian (e.g., Schroeder & Neumann 1985), although there are suggestions that its inception could be latest early Cenomanian (Velić, 2007; Chiocchini, 2008). Complex large *Praealveolina* (e.g., *Praealveolina cretacea* (d'Archiac) and *Praealveolina tenuis)* are typically no older than middle Cenomanian (Bilotte et al., 1978; Schroeder & Neumann 1985; Calonge et al., 2002), which is probably true for similar (near-homeomorphic) forms that are endemic to the Middle East (e.g., *Praealveolina arabica* Vicedo & Piuz, *Decastroia oblonga* Vicedo & Piuz) (Vicedo & Piuz, 2017; Simmons et al., 2020b). There seems to be agreement from reliable records that *O. ovum* is no older than middle Cenomanian (Schroeder & Neumann, 1985; Boix et al., 2009). This event also relates to a marked increase in the diversity of "planispiral" LBF (see Figure 86). Taxa such *Nummofallotia*? *apula* have their FAD at this event, and many others, although potentially ranging older, are more confidently known from the middle Cenomanian than the early Cenomanian. This includes well known taxa such as *Pseudorhapydionina laurinensis*, *Merlingina cretacea* and *Biplanata peneropliformis*.

Cenomanian LBF Events 3 - (approximates to base late Cenomanian) defined by FAD *Cisalveolina fraasi* (Gümbel). FAD *Multisprina iranensis* Henson and LAD *C. conica* are ancillary events.

C. fraasi appears to be the evolutionary successor of *C. lehneri* (their ranges do not overlap according to Schroeder & Neumann, 1985), with an inception in the late Cenomanian. This is seldom disputed in the literature, although Spalluto & Caffau (2010) and Spalluto (2011) mention possible middle Cenomanian occurrences. *M. iranensis* is a distinctive alveolinid that seems restricted to the Middle East. There is limited data on its stratigraphic range, but it appears to have an inception in the late Cenomanian (Consorti et al., 2015). The extinction of orbitolinids appears to be a useful proxy for the base of the late Cenomanian, with the youngest species being *C. conica* (Schroeder & Neumann, 1985, Velić, 2007).

Amongst the planispiral LBF, the FADs of *Moncharmontia apenninica*, *Praetaberina bingistani* and *Pseudorhipidionina* ex. grp. *casertana-murgiana* lie close to this event, if not exactly coinciding with it, as does the LAD of *Mayncina orbignyi*.

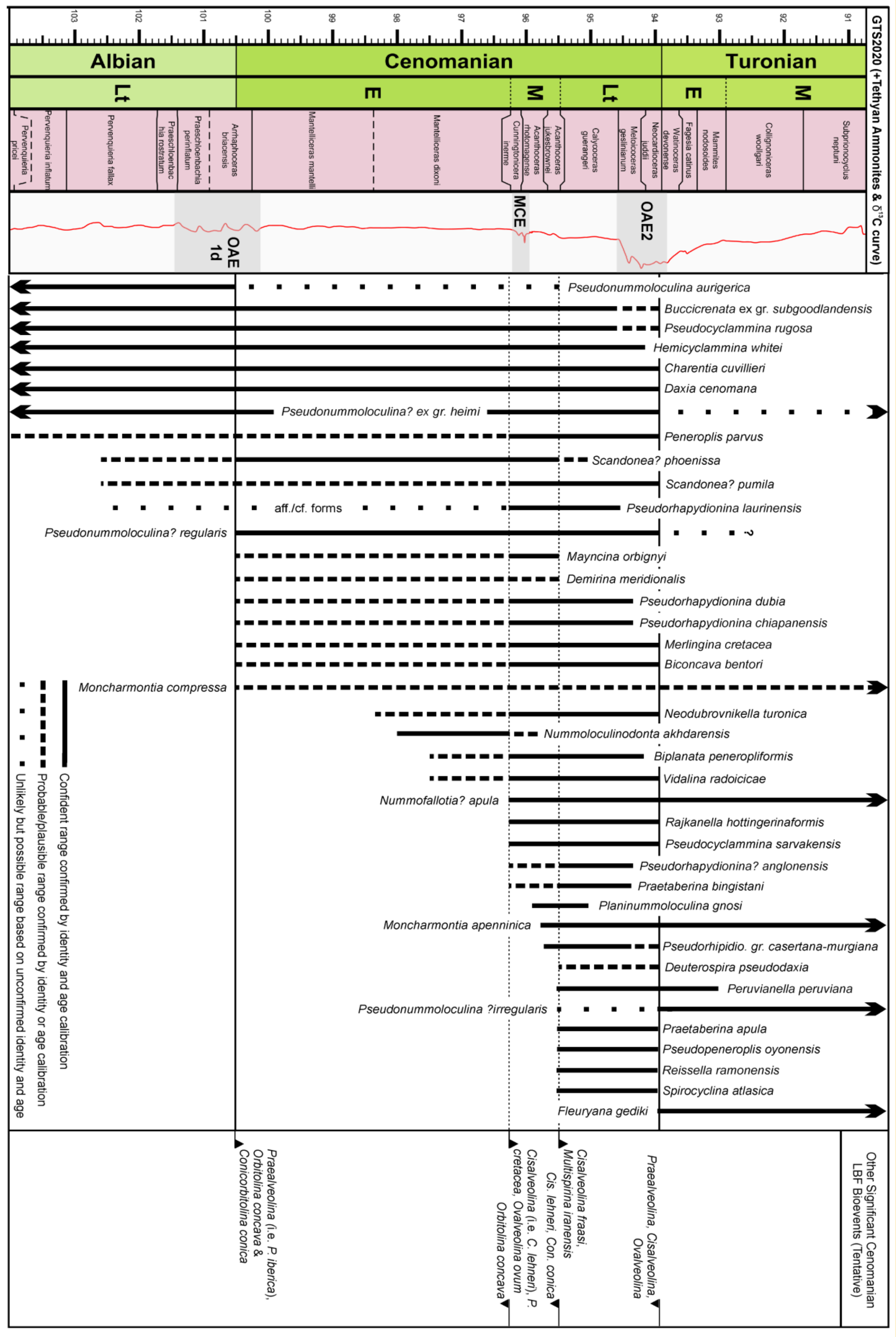


Fig. 86 Biostratigraphic range chart for planispiral LBF in this study. Chronostratigraphy, timescale and ammonite biostratigraphy based on Gale et al., 2020; Carbon isotope curve based on Cramer & Jarvis, 2020. Additional foraminiferal data based on Schroeder & Neumann (1985), Calonge et al. (2002) and sources mentioned in the text.

Cenomanian LBF Events 4 - (approximates to near base Turonian) defined by LAD of multiple LBF lineages including *Praealveolina, Cisalveolina,* and *Ovalveolina*

A major extinction event in larger benthic foraminifera occurs at, or more likely, just below the Cenomanian/Turonian boundary, associated with the onset of Ocean Anoxic Event 2 (Floquet et al., 1987; Philip & Airaud-Crumiere, 1991; Aguilera-Franco, 2003; Parente et al., 2007, 2008; Frijia et al., 2015; Solak et al., 2020). This would place the extinction event near the top of the *geslinianum* ammonite zone and around the top of the *cushmani* planktonic foraminifera zone. Palaeoceanographic changes caused the demise of many carbonate platforms along with their associated larger benthic foraminifera faunas at this time. Large and complex alveolinid genera such *Praealveolina, Cisalveolina* and *Ovalveolina* became extinct, along with complex textularids such as *Chrysalidina gradata.* Many species of Cenomanian "planispiral" LBF become extinct at or near this event (i.e., not extending into the Turonian) (Figure 86) and include well-known taxa such as *Hemicyclammina whitei, Charentia cuvillieri, Daxia cenomana, Merlingina cretacea, Biconcava bentori, Neodubrovkinella turonica, Biplanata peneropliformis, Vidalina radoicicae, Praetaberina bingistani,* and *Pseudorhipidionina* ex. grp. *casertana-murgiana.*

CONCLUSIONS

LBF are potentially valuable biostratigraphic and paleogeographic indicators, not only in Cenomanian strata, but from Paleozoic to Recent strata, as long as critical assessment of both identity and age calibration are applied to their occurrences.

We have reviewed the available literature from (mostly) post-1985 and have critically applied both identity and age criteria for a Cenomanian LBF subgroup with a planispiral aspect to their morphology. Thirty-nine separate planispiral LBF taxa (including three with "ex gr." status) have been identified. This encompasses the evaluation of around 600+ reference items, although the majority of these have shortcomings in respect of establishing correct identity or age calibration.

We have constructed a biostratigraphic range chart and paleogeographic distribution maps 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). This shows potential biostratigraphic resolution down to at least substage level although other morphogroups of LBF will need to be evaluated in a similar way before a fully-formed LBF biozonation scheme for the Cenomanian can be constructed.

Many planispiral LBF taxa still require further study (and access to new/additional material) to improve our taxonomic understanding, and the evolutionary relationships between them.

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Michael McKimm of the Geological Society of London Library helped find a great deal of literature, some of it remarkably obscure. Oksana Zarinsky kindly helped provide literature from the Geological Survey of Israel.

We have tried to be comprehensive in our assessment of the literature but offer our apologies to authors of any papers that "slipped through the net".

Halliburton is thanked for permission to use the Cenomanian palaeogeography images that form part of the Neftex product suite.

Whilst this paper was being finalised, three esteemed LBF micropalaeontologists sadly passed away – Rajka Radoičić, Ercan Özcan and Piero De Castro. This publication is dedicated to their memory.

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FAMILY	MAYNCINIDAE				NEZZAZATIDAE			BIOKOVINIDAE
Species	***Biconcava bentori***	***Daxia cenomana***	***Deuterospira pseudodaxia***	***Mayncina orbignyi***	***Biplanata peneropliformis***	***Demirina meridionalis***	***Merlingina cretacea***	***Neodubrovnikella turonica***
Wall	Simple, agglutinated, imperforate, non-alveolar							Finely agglutinated, perforate, single layer with pseudokeriotheca
Basic shape	Planispiral, moderately lenticular, evolute, biumbilicate	Planispiral, lenticular, involute-evolute, biumbilicate	Planispiral, lenticular, evolute, biumbilicate	Planispiral, inflated, lenticular, involute	Planispiral, flattened, semi-involute, flaring and chamber-widening when uncoiled, biumbilicate	Planispiral, evolute, somewhat flaring and chamber-widening when uncoilded, biumbilicate	Almost but irregularly planispiral, semi-evolute, flaring and chamber-widening when uncoiled, biumbilicate	Irregular flattened planispiral at first, semi-evolute, flaring and chamber-lengthening when uncoiled, biumbilicate
Uncoil?	No	No	No	No	Yes peneropliform	Yes slightly, peneropliform	Yes slightly, peneropliform	Yes, peneropliform
Number of whorls	up to 4	up to 5	2	up to 4	2-3 before uncoiling	c. 3-4	c. 2	1-2 before uncoiling
Number of chambers	18-24 (final coil)	c. 15 (macrosph.); c.22 (microsph.)	c.20 (final coil)	c. 17 (final coil)	c. 22 (final coil) c. 9 uncoiled	c. 13-14 (final coil)	c. 16-17 (final coil)	c. 12 (final coil) c.4-6 (uncoiled)
Chamber shape	Short, oblong (eq.); V-shape (ax.)	Tear-drop (eq.); V-shape (ax.)	Oblong (eq.); heart-shape (ax.)	Long & low (eq.); bean-shape (ax.)	Broad, oblong (eq.); bean-shape (ax.)	Oblong (eq.); almost diamond-shape (ax.)	Oblong, sl wider at periphery (eq.); becoming broader	Oblong, becoming broader and curved when uncoiled
Nature of septa	Rel. thick, recurved	Rel. thick, recurved	Rel. thin, mostly straight	Rel. thin, strongly recurved	Rel. thin, slightly recurved	Straight, slightly backwards-pointing	Slightly sinuous, recurved, rel. deep sutures externally	Straight when coiled, curved when uncoiled
Chamber subdivisions	?Small dental plate	None	None	None	Dental plate in median part of chamber	c. 10 inward-pointing partitions	2 dental plates extending inwards from aperture	None
Aperture	Early: interio-marginal arch with extension up the apertural face; Later: areal in a median groove	Small, single, areal opening just above base of apertural face	Basal, interio-marginal, ?becoming more areal later	Cribrate, multiple, areal, with pores scattered up the apertural face	Row of openings along apertural face	Early: interio-marginal; Later: ?areal, then cribrate	U- or V-shape slit in apertural face	Cribrate over the apertural face, probably not in a row (but see text)
Periphery (axial, equatorial)	Subangular, circular	Subangular, circular	Sharp, angular, oval	Rounded, circular	Angular, drop-shaped	Angular-subangular, drop-shaped	Subangular with double-periphery in later chambers, oval and "saw tooth"	Rounded, "peneroplid" shape
Dimensions (mm) **Ma = Macrospheric** **Mi = Microspheric** **Eq = Equatorial** **Ax = Axial**	Eq.: ~1.0 Ax.: ~0.1	Pro.: <0.1 Ma-Eq.: 0.73-1.60 Ma-Ax.: 0.28-0.65 Mi-Eq.: 2.0-2.7 Mi-Ax.: 1.0	Eq.: ~1.0 Ax.: ~0.25	Eq.: ~1.5 Ax: ~0.5	Eq.: ~1.0-1.5 Ax.: ~0.2	Pro: 0.025 Eq.: 0.30-0.56 Ax.: 0.045-0.09	Eq.: ~1.2 Ax.: ~0.2	Length: 0.25-1.5 Width (last chamber): 0.22-0.70
Wall thickness	Relatively thin	Relatively thick	Relatively thin	Thin	Thin	Relatively thin	Relatively thick	Relatively thin
Other	Slow rate of chamber growth	Spiral canal (described by Laug & Peybernes, 1979) is NOT present. Smaller specimens confusable with *D. minima*	First whorl appears infilled by agglutinated material	Relatively large proloculus	Relatively rapid rate of chamber growth; chamber width relatively constant	Chamber width broadest (in axial view) in lower part of chamber	Apertural face broad & flattened	Agglutinated homeomorph of *Peneroplis.* Chamber height increases in coiled part, remains constant in uncoiled part

FAMILY	CHARENTIIDAE				CYCLAMMINIIDAE		SPIROCYCLINIDAE		HAURANIIDAE	
Species	***Charentia cuvillieri***	***Fleuryana gediki***	***Moncharmontia apenninica***	***Moncharmontia compressa***	***Buccicrenata* ex gr. *subgoodlandensis***	***Hemicyclammina whitei***	***Reissella ramonensis***	***Spirocyclina atlasica***	***Pseudocyclammina rugosa***	***Pseudocyclammina sarvakensis***
Wall	Agglutinated 2-layered, solid outer layer with "pseudoalveolar/keriothecal" inner layer				Agglutinated 2-layered, solid outer layer with alveolar inner layer		Finely agglutinated 2-layered, solid outer layer with epidermal layer with complex internal layer of horizontal and vertical partitions		Coarsley agglutinated 2-layered, solid outer layer with alveolar inner layer	
Basic shape	Broad, lenticular planispiral, involute, followed by uncoiled part	Broad, subglobular planispiral, involute	Broadly subglobular, planispiral, involute	Broadly compressed, lenticular, planispiral, mainly involute, biumbilicate	Initially broadly planispiral but (sometimes) quickly uncoiling in rectilinear fashion	Planispiral, lenticular, involute to evolute	Planispiral, involute, rapid chamber enlargement ("Nonion"-like)	Flattened planispiral, distinctly even dramatically peneropliform	Initially planispiral but (sometimes) uncoiling in rectilinear fashion	Planispral, broadly rounded
Uncoil?	Yes, rectilinear	No	No	No	Yes, rectilinear	Only rarely, rectilinear	No but almost peneropliform	Yes, distinctly peneropliform	Occasionally, rectilinear	No
Number of whorls	3-4 before uncoiling	2-3	2-3	2-3	1-2 before uncoiling	2-3	c. 2	c.2 before uncoiling	2-3	2.5-3.5
Number of chambers	c. 13 (final coil) c. 3-4 (uncoiled)	8- (rarely) 9 (final coil)	c. 9-11 (final coil)	c. 9-11 (final coil)	c. 5 (final coil) c. 2-4 (uncoiled)	c. 11 (final coil)	c. 10 (final coil)	c. 25 (final coil)	c. 5-7 (final coil) c. 2-3 (uncoiled)	14-16 (final coil)
Chamber shape	Broadly equidimensional (eq.); U-shape (ax.)	Oblong longer > height (eq.); U-shape (ax.)	Broadly equidemensional (eq.); U-shape to semicircular (ax.)	Slightly higher than long (eq.); heart-shape (ax.)	Reniform shape (eq.)	Broadly equidimensional (eq.); somewhat triangular (ax.)	Wider >> long (eq.); elongate tear-drop (ax.)	Broad, arcuate/crescentic	Teardrop to reniform shape (eq.); broadly U-shape (ax.)	Broadly rounded, equidimensional (eq.); broadly U-shape (ax.)
Nature of septa	Mainly straight, built-up at base, recurved, straight when uncoiled	Straight, perpendicular	Straight, slightly backwards pointing	Straight - slightly sinuous, slightly recurved	Solid but possibly alveolar. Continuous, smooth outgrowths of chamber wall	Solid, pointed, perpendicular to outer wall, do not reach inner wall	Solid, somewhat recurved, not quite straight	Strongly curved	Alveolar, strongly recurved	Alveolar, strongly recurved
Chamber subdivisions	None	None	None	None	None	None, somewhat thicker basal layer	Closely-spaced primary and secondary vertical and horizontal partitions	Closely-spaced primary and secondary vertical and horizontal partitions	None	None
Aperture	Early: triangular arch; Mid: 3-pronged opening; Later: longer vertical opening and narrow slit along apertural face	Basal, single arched slit	Cribrate openings in random or double-row in apertural face	Single row of openings in apertural face	Single, sinuous slit with projections (may appear multiple in oblique sections)	Single slit-like opening extending from the base to about a third up the apertural face	Central areal aperture on short neck surrounded by multiple smaller openings across apertural face	Double (occ. triple) row of apertural pores on apertural face	Areal, cribrate	Areal, cribrate, very small openings
Periphery (axial, equatorial)	Rounded-subangular, circular in coiled portion	Hemispherical, circular	Hemispherical, circular	Subangular, almost circular	Subrounded, lobate almost "notched" periphery	Subangular, edge between septa somewhat straight leading to slightly polygonal periphery	Rounded, oval, moderately lobate periphery	Subrounded, outline similar to French Horn	Rounded, oval	Rounded, circular
Dimensions (mm) **Ma = Macrospheric** **Mi = Microspheric** **Eq = Equatorial** **Ax = Axial**	"Large" (1.2-1.4 eq.) "Small" (0.78-0.83 eq.) (see text)	Eq.: <0.4 Ax.: ~0.2	Eq.: ~0.47 Ax.: ~0.27	Pro.: <0.08 Eq.: <0.34 Ax.: ~0.15	Length: 1.27-4.73 Eq.: 0.59-2.48 Ax.: 0.25-0.92	Ma-Pro: 0.05-0.1 Eq.: 1.70-2.70 Ax.: 0.90-1.20	Max-Eq.: ~0.75 Ax.: ~0.15	Eq.: ~1.40	Length: 4.78-6.00 Eq.: 0.8-4.3 Ax.: 0.7-2.3	Eq.: up to 1.35 Ax.: ~0.6
Wall thickness	Thick	Thin	Relatively thick	Relatively thin	Thick	Thick	Thin	Thin	Thick	Thick
Other	Uncertainty over significance of size-related morphotypes (see text for discussion)	Chambers distinctly rectangular in eq. section. The thin wall makes the pseudokeriothecal nature of the wall difficult to observe	Quite similar to *F. gediki*	Very similar to *F. adriatica* (not included herein) which has a single apertural slit but both apertures may be difficult to observe in T/S	Chambers enlarge rapidly in initial coil. Nature of septa (alveolar or solid) still debated (see text). Three similar species grouped here as "ex gr."	Moderate rate of chamber growth	Possible close relationship (synonymy?) with *P. casertana* if wall structure is the same (see text). Notably complex wall for size		Slow-moderate rate of chamber growth. Fewer chambers/whorl and larger than *P. sarvakensis*	More chambers/whorl and smaller than *P. rugosa*

FAMILY	HAUERINIDAE						CORNUSPIRIDAE	MEANDROPSINIDAE	PENEROPLIDAE
Species	***Pseudonummoloculina aurigerica***	***Pseudonummoluculina? ex gr. heimi***	***Pseudonummoloculina? regularis***	***Pseudonummoloculina? cf. irregularis***	***Planinummoloculina gnosi***	***Nummoloculinodonta akhdarensis***	***Vidlalina radoicicae***	***Nummofallotia? apula***	***Peneroplis parvus***
Wall	Porcellaneous						Porcellaneous	Probably 2-layered, inner layer dark, microgranular, outer layer clear, radial hyaline	Porcellanous, imperforate
Basic shape	Rounded biconvex, initially quinqueloculine, then streptospiral, then broad planispiral	Disc-like, even slightly biconcave, initially quinqueloculine, then streptospiral, then planispiral	Disc-like, initially small miolioline then regular planispiral with only slight osscilation	Biconvex, tubular/milioline deuteroloculus followed by streptospiral coiling, only fully planispiral in the last whorl	Biconvex, initially sigmoid/ streptospiral nepionic stage then planispiral, occasionally slightly oscillating	Globular proloculus then a quinqueloculine nepionic stage and then (with a change of plane) planispiral, slightly oscillating, adult stage	Globular proloculus followed by planispiral unsegmented 2nd chamber. Laminations laid down in successive whorls so umbilical area thickens	Planispiral, broad lenticular with distinctive, fibrous umbilical "plug" or "button"	Planispiral, one coil followed by a second which uncoils in classic peneroplid fashion
Uncoil?	No	No	No	No	No	No	No	No	Yes, peneropliform
Number of whorls	1.5-2.5	up to 7 planispiral whorls	up to 7 planispiral whorls	c.5	10-11	up to 4	6-7	c. 3	c. 1-2 before uncoiling
Number of chambers	6-8 (final coil)	2-10 quinquel. then 6-8 but up to 16	3-5	3-5	3-4 / whorl in adult stage	up to 4 / whorl in adult stage	1 post-prolocular chamber only	c. 16-20 (final coil)	c. 7-11 (final coil)
Chamber shape	Low and moderate length	Low and short - moderate length depending on no. of chambers/whorl	Low and moderate length	Low and moderate length	Low and long	Low and long	Tubular, width increases with growth	Equidimensional trapezioid (eq.); V-shape (ax.)	Height remaining constant but breadth increasing rapidly
Nature of septa	Angled backwards	Angled backwards, almost "circular saw" appearance with thickening near roof	Angled backwards	Indistinct, ?subvertical	Indistinct, recurved	Indistinct, recurved	None	Straight, backwards sloping	Curved and recurved backwards
Chamber subdivisions	Ridges on chamber roof expressed on apertural face by notches / crenulations	None	None	None	Basal layer, ridges on distal chamber roof visible as row of notches on septal face from 5th whorl	Rare rows of ridges on distal chamber roof visible as row of notches in gerontic stage	None	None	None
Aperture	Low opening across lower part of whole of apertural face, modified by notches / crenulations	Low, broad opening with a "stocky tooth" but no notches or crenulations	A simple opening (?arch) in apertural face	A simple opening (?arch) in apertural face	A low arch with notches if chamber-roof ribs present	Open aperture with complex or simple tooth depending on section-cut and with notches if chamber-roof ribs present	Simple opening at end of tube	Triangular at base of apertural face	Areal, cribrate
Periphery (axial, equatorial)	Well rounded, circular, slightly lobate	Well rounded, circular	Well rounded, circular	Well rounded, somewhat hexagonal in equatorial section view	Well rounded, circular	Very well rounded, biconvex-globular shape	Circular, axial view lenticular, test sides flat or slightly concave	Subangular-angular, oval	Rounded, drop-shape
Dimensions (mm) **Ma = Macrospheric** **Mi = Microspheric** **Eq = Equatorial** **Ax = Axial**	Pro.: 0.055 Eq.: 0.97-1.3 Ax.: 0.55-0.73	Ma-Pro: 0.056-0.112 Mi-Pro: 0.026-0.053 Ma-Eq.: 0.43-2.06 Mi-Eq.: 0.53-2.16	Eq.: ~1.60 Ax.: ~0.30	Eq.: ~0.60 Ax.: ~0.20	Eq/Ax.: 1.5-3.0	Pro.: 0.12 Eq.: up to 1.5	Pro.: 0.031 Eq.: 0.25-0.43 Ax.: 0.150-0.158	Ma-Pro.: 0.06-0.08 Eq.: 0.3-0.5 Ax.: 0.15-0.25	Length: c. 1.0 Eq.: 0.82
Wall thickness	Thick	Medium	Medium	Thick	Thick	Thick	Thin (thick wall in umbilical area)	Thin	Relatively thick
Other	Differs from *N. akhdarensis* by being less globular, with more chambers, and with notches in most adult chambers	Nummoloculinid with most chambers / whorl in adult forms but can be variable (Conkin & Conkin, 1958 and Piuz & Vicedo, 2020 concept)	Planispiral coiling almost throughout, will little oscillation. Similar to *V. radoicicae* which has a more lenticular axial profile and no septa	Large initial miolioline coil and may not become fully planispiral until the very latest growth stage	Nummoloculinid with most whorls in adult forms	Pillar-like structures in final (gerontic) whorl sometimes. Differs from *P. aurigerica* and *P. gnosi* by only having ribs/notches in the latest chambers	Lenticular axial profile is more typical. Forms with less lenticular profile can be mistaken for *P.*? *regularis*	Revision of the genus is necessary (e.g. relationship between *N. apula*, *N. cenomana* and *N. cretacea*) particularly regarding dimensions	Porcellaneous wall can be difficult to confirm *P. parvus* is one of the smallest *Peneroplis* species

FAMILY	PRAERHAPYDIONINIDAE									SORITIDAE		
Species	***Pseudorhapydionina anglonensis***	***Pseudorhapydionina chiapanensis***	***Pseudorhapydionina dubia***	***Pseudorhapydionina laurinensis***	***Pseudorhipidionina* ex gr. *casertana-murgiana***	***Praetaberina bingistani***	***Praetaberina apula***	***Pseudopeneroplis oyonensis***	***Rajkanella hottingerinaformis***	***Scandonea? phoenissa***	***Scandonea? pumila***	***Perouvianella peruviana***
Wall	Porcellaneous									Porcellaneous		
Basic shape	Inflated lenticular-subglobular planispiral	Initially subglobular planispiral, becoming uncoiled and cylindrical, more or less parallel-sided and smooth	Initially subglobular planispiral, becoming uncoiled and cylindrical, more or less parallel-sided and smooth	Initially subglobular planispiral, becoming uncoiled and cylindrical, somewhat flaring and with depressed sutures	Initially flattened planispiral, becoming peneropliform then flabelliform, slightly flaring seriate portion	Initially subglobular planispiral, followed by an uncoiled peneropliform then cylindrical, slightly flaring portion	Initially subglobular planispiral, followed by an uncoiled peneropliform then cylindrical, slightly flaring portion	Initially streptospiral, then planispiral involute, followed by partially or fully uncoiled portion in peneroplid fashion	Planispiral to slightly streptospiral, lenticular, involute	Initially milioliform/streptospiral then inflated planispiral, involute, biumbilicate	Initially milioliform/streptospiral then subglobular planispiral, involute	Initially planispiral, uncoiling to flattened, flabelliform
Uncoil?	No	Yes, rectilinear and cylindrical	Yes, rectilinear and cylindrical	Yes, rectilinear and flaring cylindrical	Yes, rectilinear, flabelliform	Yes, rectilinear	Yes, rectilinear	Yes, peneropliform	No, or only slightly flared	Occasionally, rectilinear	Not observed*	Yes, flabelliform
Number of whorls	1-2	1.5-2 before uncoiling	1.5-2 before uncoiling	2 before uncoiling	c. 1.5-2 before uncoiling	c. 2.5-3 before uncoiling	c. 2.5 before uncoiling	c. 2.5	c. 3-4.5	<3 before uncoiling	c. 2-3	c. 2-4 before uncoiling
Number of chambers	10-12 total chambers	10-11 total coiled 7 uncoiled	10-11 total coiled 5 uncoiled	up to 16 total coiled 7-11 uncoiled	c. 12-14 (final coil) c.10 (uncoiled)	>30 (final coil) c.10-15 (uncoiled)	c. 13 (final coil) c. 7-13 (uncoiled)	c. 7-8 (final coil) c. 7 (uncoiled)	c. 12 (final coil)	c. 8 (final coil) c. 3 (uncoiled)	c. 5-6 (final coil)	c.13-15 (final coil) c. 6 (uncoil)
Chamber shape	Rounded and elongate	Rounded elongate, inverted and rounded V-shape in uncoiled part	Rounded elongate, inverted and rounded V-shape in uncoiled part	Rounded elongate, inverted and rounded V-shape in uncoiled part	Long, curved and low becoming even longer in uncoiled part	Elongate in coiled portion, elongate and arched uncoiled	Elongate in coiled portion, elongate and arched uncoiled	Ovate-elongate in coiled portion, elongate and arched uncoiled	Broad, short and low, increasing in breadth in last few. U-shaped (axial)	Somewhat reniform, relatively high chamber height	Somewhat reniform, relatively low chamber height	Low, long, curved (eq.); V-shape (ax.)
Nature of septa	Curved backwards, thickened near the periphery	Curved backwards in coiled portion, central peak (convex) in uncoiled part	Curved backwards in coiled portion, central peak (convex) in uncoiled part	Curved backwards in coiled portion, central peak (convex) in uncoiled part	Strongly curved, backwards pointing in spiral part and markedly convex in seriate part	Strongly curved, backwards pointing in spiral part	Strongly curved, backwards pointing in spiral part	Curved backwards	Curved backwards but less curved in last few chambers	Slightly curved, strongly backwards pointing	Curved, strongly backwards pointing	Curved backwards
Chamber subdivisions	Few thin septula, thickened at base	4-5 medium, relatively thick, radial septula per quadrant	5-6 short, thin, radial septula per quadrant	8-9 long, thin, radial septula per quadrant	Septula, radial, extending ~1/3 way in, occasionally bifurcating	Septula (~15/quad.) extending ~1/4 way in. Central chamber with numerous conical pillars	Septula (7-8/quad.) extending ~1/2 way in. Smaller central chamber with fewer cylindrical pillars	Short, radial septula in marginal parts of chambers	Numerous thin, short beans which connect successive septa	None (lack of basal thickening cf. the type species leads to questionable genus assignment)	None (lack of basal thickening cf. the type species leads to questionable genus assignment)	Alternating septula, 2-4 alternating rows of radial and intercameral pillars, soculli (see text fig.)
Aperture	Areal, cribrate	Areal, cribrate	Areal, cribrate	Areal, cribrate	Areal, cribrate with numerous openings	Areal, cribrate with numerous openings	Areal, cribrate with numerous openings	Single row of rounded openings in the median apertural face aligned with previous chambers	Single, rounded. Basal at first then progressively areal and developing a pronounced rim	Areal, cribrate	Areal, cribrate	Areal, numerous between septula and pillars
Periphery (axial, equatorial)	Broadly rounded	Broadly rounded and smooth	Broadly rounded and smooth	Broadly rounded and somewhat "notched" by depressed sutures	Rounded, initial part circular outline	Well rounded, cylindrical-slightly flaring	Well rounded, cylindrical-slightly flaring	Rounded, elongated drop-shape	Well rounded, circular	Well rounded, circular slightly lobate	Very well rounded (hemispherical), circular slightly lobate	Subangular, flabelliform
Dimensions (mm) **Ma = Macrospheric** **Mi = Microspheric** **Eq = Equatorial** **Ax = Axial**	Pro.: 0.020-0.037 Eq.: 0.35-0.50 Ax.: 0.30-0.40	Length: c. 1.34 Pro.: 0.040 Eq.: 0.36	Length: c. 1.0 Pro.: 0.040 Eq.: <0.35	Length: c. 1.5 Pro.: 0.030 Eq.: 0.33	Length: c. 1-1.5 Eq.: c. 0.5	Ma-Pro.: c. 0.10-0.12 Length: 0.7-2.1 Eq.: 0.7-1.0	Ma-Pro.: c. 0.08 Length: 0.7-2.0 Eq.: ~0.7	Pro.: 0.03-0.06 Length: <1.2 Eq.: 0.52	Pro.: 0.06-0.08 Eq.: <1.2 (mostly ~0.9) Ax.: <0.5	Length: <0.80 Eq.: 0.40-0.70 Ax.: 0.16-0.25	Eq.: 0.53 Ax.: 0.35	Ma-Pro.: 0.2-0.33 Length: 2.0-7.0 Eq.: ~0.5-0.7 Ax.: ~0.25
Wall thickness	Medium	Thick	Thick	Thin	Relatively thick	Relatively thin	Relatively thin	Relatively thin	Relatively thick	Relatively thin	Relatively thick	Relatively thin
Other	No uncoiling has been observed hence ? generic assignment. *Moncharmontia* and *Scandonea* are similar but lack septula	Very similar to Eurasian/African homeomorph *P. dubia*	Early coiling may be streptospiral (i.e. = miliolid). Very similar to endemic Central American homeomorph *P. chiapanensis*	The flaring seriate part (with more chambers) separates this species from *P. dubia* and *P. chiapanensis*	*Murgiana*-types have wider seriate chambers than *casertana*-types. *Pseudorhapydionina* has a more cylindrical seriate stage	Differs from other initially-planispiral Praerhapydioninids by the presence of pillars. *Parouvianella* is similar but has a flattened uncoiled portion and the pillars are arranged in rows, not scattered in the central part of the chamber as in *Praetaberina*		Similar to *Peneroplis* but with chamber subdivision. *Pseudorhipidionina* is also similar but has two rows of apertures and longer septula	Externally striate	Genus assignment is questionable and requires a full review	(* limited material studied)	Superficially similar to *Praetaberina* and *Pseudorhipidionina* but not related.