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A REVIEW OF THE IDENTITY AND BIOSTRATIGRAPHY OF CENOMANIAN 'LARGER' BENTHIC FORAMINIFERA: PART 3 – THE SUPERFAMILY ALVEOLINOIDEA EHRENBERG, 1839

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Abstract. The Alveolinoidea ('alveolinoids' herein) is a superfamily of larger benthic foraminifera (LBF) of the order Miliolida (= with porcelaneous test wall) that are common in the mid-Cretaceous shallow-water carbonate successions of Neotethys. They are encountered in suitable rocks in a broad belt centred around the Mediterranean region and the Arabian Plate but some taxa are found in the central American region. To improve their stratigraphic utility, the identities and distribution of 32 species are critically reviewed based on published records, these taxa having at least possible occurrences in Cenomanian strata. It is shown that misidentifications have overextended the ranges of some taxa, although there are indeed species that have long ranges. Nonetheless, some taxa have short ranges within the Cenomanian that mark them out as potential species to be used, alongside species from other LBF groups, in the development of a biozonation/bioevent scheme for Cenomanian LBF. Alveolinoids are amongst the most morphologically complex mid-Cretaceous LBF, and, as with modern members of the group, mostly lived in the shallow waters of inner carbonate platforms developed in tropical belts. This paleoenvironmental restriction means that their local stratigraphic ranges could often be incomplete compared to the total composite range. Speciations and extinctions within the group seem closely linked to paleoceanographic events including sea-level change, hypertermals and anoxia. As with almost all mid-Cretaceous LBF, work on the taxonomy/identity of alveolinoids is an ongoing task requiring access to pristine material, including types.

Keywords: Foraminifera, Biostratigraphy, Cenomanian, Neotethys, Cretaceous

INTRODUCTION & RATIONALE

The rationale for this paper – part 3 of a series – has previously been discussed by Simmons & Bidgood (2023), Bidgood et al. (2024) and by Simmons et al. (2024; 2025), the latter being parts 1 and 2 of this series. In essence, although larger benthic foraminifera (LBF) are common in mid-Cretaceous sedimentary rocks deposited on carbonate platforms, their biostratigraphic utility is hampered because of uncertainties over identity and stratigraphic range. The seminal publication by Schroeder & Neumann (1985) represents the last major (but partial) synthesis, but since then records in the literature have increased dramatically. New synthesis is thus much needed if LBF are to realise their biostratigraphic potential.

The purpose of this paper (and its associated companion papers) is not higher-level taxonomy, but rather a practical tool for the identification of Cenomanian alveolinoid LBF at genus and species level with the aims of i) providing a meaningful list of features to achieve correct identifications and ii) improving knowledge of their biostratigraphical and paleogeographical distribution.

Like many other LBF, alveolinoids can achieve very large sizes and have considerable internal structural complexity (both remarkable features for single-celled organisms, see Hohenegger, 2011 for a review). Envisioning the three-dimensional structures from two-dimensional views in a thin-section, as Reichel (1936, 1937) did for determining correct identity, can be challenging.

The content of this paper can be summarised as:

- A summary assessment of the diagnostic features providing the identity of known Cenomanian alveolinoid LBF genera and species.
- A critical assessment of the stratigraphic ranges of the taxa, giving most weight to those published records for which the identity has a high probability and the age-calibration is well-founded. The intent is to provide a summary of maximum global stratigraphic range of the taxa studied whilst highlighting differing degrees of certainty in that range. This provides insight into the biostratigraphic utility of each taxon for correlation and chronostratigraphic calibration. Because LBF are environmentally sensitive, local ranges are likely to be truncated compared to global ranges.

The correct identification of alveolinoids to species level requires multiple sections of well-preserved material in order to display key features. Therefore, single photographs of specimens in the literature can be challenging, if not impossible to identify correctly. This coupled with often poor age-calibration means that discussion of species distribution in time and space must be limited awaiting further data, although we intend to return to this issue in a further paper on Cenomanian LBF.

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The 32 taxa discussed herein are (in alphabetical order):
Alveocella wernliana Piuz et al., 2014
Cisalveolina fraasi (Gümbel, 1872)
Cisalveolina lehneri Reichel, 1941
Cisalveolina nakharensis Piuz et al., 2014
Decastroia lata (Reichel, 1936) [formerly *Praealveolina cretacea* subsp. *lata* Reichel 1936 transferred to *Decastroia* herein]
Decastroia miaidinensis Vicedo & Piuz, 2016
Decastroia oblonga Vicedo & Piuz, 2016
Decastroia razini Vicedo & Serra-Kiel, 2011
Decastroia serrakieli Vicedo & Piuz, 2016
Multispirina iranensis Reichel, 1947
Myriastyla grelaudae Piuz et al., 2014
Myriastyla omanensis Piuz et al., 2014
Ovalveolina crassa De Castro, 1966
Ovalveolina maccagnoae De Castro, 1966
Ovalveolina ovum Reichel, 1936
Praealveolina acuta Vicedo & Piuz, 2016
Praealveolina arabica Vicedo & Piuz, 2016
Praealveolina brevis Reichel, 1936
Praealveolina cretacea (d'Archiac, 1837)
Praealveolina debilis Reichel, 1936
Praealveolina iberica Reichel, 1936
Praealveolina osimoi (Zuffardi-Comerci, 1930) emend. De Castro, 1987
Praealveolina pennensis Reichel, 1936
Praealveolina tenuis Reichel, 1933
Reichelia magna Vicedo & Piuz, 2016
Sellialveolina drorimensis (Reiss et al., 1964) emend. Vicedo et al., 2011
Sellialveolina gutzwilleri Vicedo et al., 2011
Sellialveolina quintanensis Vicedo et al., 2011
Sellialveolina viallii Colalongo, 1963
Simplalveolina mardinensis Simmons & Vicedo, 2020
Simplalveolina simplex (Reichel, 1936)
Streptalveolina mexicana Fourcade et al., 1975

These represent, as far as we are currently aware, the entire inventory of alveolinoid species that are known to have at least a possible presence in Cenomanian rocks.

This article firstly introduces aspects of the supra-generic classification of the alveolinoids as a group into Families and Subfamilies. As alveolinoids are complex organisms with complex shell structures a descriptive illustrated glossary of morphological terms is provided in order to standardise features used in establishing identity. We then describe and illustrate the main characteristics of the individual Cenomanian alveolinoid genera.

The main part of the article is a treatment of the 32 alveolinoid taxa, each of which consists of a representative image of the taxon in various orientations which display the diagnostic features of that species. This is followed by a synonym/chresonymy listing (i.e., a list of 'usage' - see below) of the illustrated records of that species around the globe. A suitable source (or sources) for additional images and description is also provided, followed by a discussion on the identity of the taxon and comparisons with similar taxa. This is followed in turn by a statement and assessment of the biostratigraphic range of the species based on the available data, and the quality/accuracy of that data. Finally, there is a statement as to the paleogeographic range of the species.

The article concludes with a discussion of various aspects of the group as a whole (taxonomic, biostratigraphic, paleogeographic and other topics) and the presentation of a range chart for the group.

A NOTE ON HIGHER (SUPRA-GENERIC) CLASSIFICATION

As discussed by Simmons & Bidgood (2023) and Simmons et al. (2024), the supra-generic classification of LBF is, and remains, a work in progress and the validity of the schema such as, for example, Kaminski (2014), the last major supra-generic assessment of agglutinating foraminifera, while currently practical, is open to constant amendment. By following WoRMS.org (Hayward et al., 2025) *Sellialveolina* is assigned to the Rhapydionininae Keijzer, 1945, of the Family Rhapydioninidae Keijzer, 1945; *Myriastyla* is assigned to the Family Myriastylidae Piuz et al., 2014; whereas all the taxa herein are included in the Superfamily Alveolinoidea Ehrenberg, 1839.

Within the Alveolinoidea, the Praealveolinidae family was created by Fleury & Fourcade (1990). Subsequently, within that family, the subfamily Decastroinae was created by Vicedo & Piuz (2016) to accommodate the genera *Decastroia* Vicedo & Serra-Kiel (2011) and *Reichelia.* They also introduced the subfamily Praealveolininae to include the genera *Praealveolina* Reichel, 1933, *Simplalveolina* Reichel, 1964 and *Multispirina* Reichel, 1947.

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

Diagnoses of the genera discussed herein, grouped into a supra-generic structure, are shown in Table 1.

An illustrated glossary of morphological terms used in descriptions of the group is shown in Figure 1 to Figure 3. Sources for the images used in the glossary figures include Hottinger (2006); Piuz et al., (2014); Reichel

Table 1. Taxonomic structure and diagnoses of alveolinoid genera included in this study. Structure after Hayward et al., 2025 ("WoRMS.org" database).

Suborder – Superfamily – Family – Subfamily	**Genera included herein with description**
MILIOLINA **ALVEOLINOIDEA** **ALVEOLINIDAE……………………………………..** Calcareous, porcelaneous. Commonly large, globular or fusiform coiled about an elongate axis. Proloculus followed by flexostyle then quinqueloculine (in microspheric juvenile forms) then planispiral in adult. Chambers numerous and subdivided by secondary partitions or septulae into one or more layers of chamberlets that parallel coiling direction. Numerous apertures in one or more rows.	***Alveocella* –** oval to fusiform test, planispiral throughout with alternate septulae from one chamber to the next, and with postseptal alveoles. Chamber floors are absent in the equatorial area. Aperture 2 or 3 rows of openings extending pole to pole. ***Cisalveolina*** – spherical to ovoid test, a streptospiral early stage with postseptal as well as preseptal passages and with septulae that alternate between chambers. Aperture is a single, large slit but septula extend nearly to the apertural face giving the appearance of subdivision. ***Streptalveolina*** – spherical test, streptospiral throughout with even the final whorl being slightly asymmetrical. Chambers subdivided by partial septulae which are continuous from chamber to chamber. Aperture a row of rounded openings. ***Ovalveolina*** – spherical to ovoid test, regularly planispiral, numerous, widely-spaced, septulae, continuous between chambers and which subdivide only in the back part of the chamber. Chamberlets are simple, commonly pyriform in shape. Preseptal passages large and circular in section. Walls and partitions relatively thick. Aperture a single row of openings without accessory openings.
PRAEALVEOLINIDAE **DECASTROINAE.........** Main feature given by the almost constant presence of medullar and cortical chamberlets, appearing regularly from pole to pole in the adult stage of growth. See Vicedo & Piuz (2016) for further information.	***Decastroia*** – subglobular to axially-elongate, main (cortical) chamberlets larger, forming an upper row and a regular arrangement of 2 or more than 2 rows of secondary (medullar) chambers in the lower part, both extending from pole to pole, with two rows of apertural openings aligned between chambers and with the presence of residual pillars where there are supplementary chamberlets. ***Reichelia*** – possessing multiple spires (up to 5) and with one row of main (cortical) and one row of secondary (medullar) chamberlets. Aperture one or multiple rows, aligned.
PRAEALVEOLININAE…. Main feature given by occurrence of supplementary chamberlets, appearing at the poles, occasionally in the equatorial zone. Septulae aligned chamber to chamber. See Vicedo & Piuz (2016) for further information.	***Multispirina*** – spherical, large, dimorphism prominent, each aperture in the early stage gives rise to separate, intercalated whorls (up to 12 whorls in megalospheric forms, up to 25 in microspheric forms), one row of main (cortical) chamberlets and no secondary chamberlets, preseptal passages large. Aperture a single row of openings at the base of each whorl's apertural face. ***Praealveolina*** – ovoid to fusiform, large, dimorphism prominent, one row of main (cortical) chamberlets and several rows of non-regular supplementary (and not medullar) chamberlets which are connected vertically by radial passages that extend downwards from the preseptal passage. Septulae are aligned chamber to chamber. Aperture a single row of regular openings near the equator but increasing to many rows at the poles.

Suborder – Superfamily – Family – Subfamily	Genera included herein with description
	Simplalveolina – ovoid to subspherical, number of chambers increases from 4 in the first whorl to 13 in the final whorl. Septulae are numerous and are aligned chamber to chamber forming a single layer of main chamberlets with oval section. Preseptal passage circular in section. Basal layer thickens towards the poles to occupy almost the full height of the chamber. Aperture a single row of openings with accessory openings in the sutural groove.
MYRIASTYLIDAE…………………..................... Thick, porcelaneous wall and subspherical to axially elongated shells. Adult chambers are involute and planispirally arranged. The endoskeleton consists of longitudinal ridges (in the direction of growth) supporting each one row of pillars. The pillars are aligned in the direction of growth and alternate in position (staggered rows) from pole-to-pole. Multiple apertures arranged in a single row; supplementary apertures may appear polewards.	***Myriastyla*** – subglobular to axially elongated (ovate), planispiral throughout, the presence of pillar-supporting ridges (rather than complete septula) which are continuous from chamber to chamber and having no 'true' chamberlets or a pre-septal passage. The pillars alternate in position (staggered rows). Multiple apertures in a single row, with supplementary apertures polewards.
RHAPYDIONINIDAE……………...................... Calcareous, porcelaneous. Planispirally or streptospirally coiled, may uncoil later. Embryonal apparatus simple or quinqueloculine, megalospheric proloculus may be followed by flexostyle. Test with central thickening pierced by canals. May include pillars. Aperture multiple.	***Sellialveolina*** –axially compressed alveolinoid, lenticular planispiral test in early stages, becoming peneropliform in later stages. Subdivision of chambers into chamberlets by septulae (which are aligned between chambers) and a perforated basal layer ('floors') with those in the central parts of the chamber tending to develop a crosswise-oblique structure. The preseptal space is relatively wide (¼ to ½ chamber volume) and interrupted by residual pillars.

(1936, 1937, 1947); Schroeder & Neumann (1985); Vicedo & Piuz (2016); Vicedo et al. (2011).

Illustrated summaries of the main diagnostic features of the alveolinoid genera discussed herein are shown in Figures 4-14.

THE ALVEOLINOIDEA, AND TREATMENT OF INDIVIDUAL ALVEOLINOID SPECIES

Herein, we use the informal term 'Alveolinoids' as an informal equivalent 'of the Superfamily Alveolinoidea', to include the taxa listed above within genera placed within the Superfamily Alveolinoidea Ehrenberg, 1839.

The 'alveolinoids' are an interesting group of porcelaneous Foraminifera characterised by large size and internal structural complexity, making them visually fascinating. These two features (separately and together) are causally linked to the organism's relationship with a range of symbionts, similar to other internally-complex LBF. In particular the alveolinoids are similar in form and coiling (though with a different wall structure and architecture) to the Paleozoic fusulinids. The alveolinoids originated in the Early Cretaceous and became common during the mid-Cretaceous to Paleogene interval, where they were important components of the shallower parts of global, warm water, marine carbonate environments. They declined somewhat through the Neogene, but the group is still extant in modern shallow seas.

A full step-by-step review of how the group as a whole is taxonomically classified and subdivided is beyond the scope of this, primarily practical biostratigraphic, atlas. However, a useful overview on the evolution and development of the group can be found in BouDagher-Fadel (2018, p. 335-339). Detailed research on alveolinoids began with the work of Manfred Reichel (1933, 1936, 1937, 1941, 1947), who erected most of the known mid Cretaceous species and whose beautiful 3-dimensional drawings of them are still to be surpassed. The reference by Fleury & Fourcade (1990) is also very useful and detailed, while Hottinger (1960) and Drobne (1977) contain seminal detailed treatment of Paleogene alveolinoids. These contribute to the LBF biozonation schemes developed by Serra-Kiel et al. (1998) and Sirel & Acar (2008).

The inventory of Cenomanian alveolinoids appeared to be complete following the work of Reichel (1933, 1936, 1941, 1947) and De Castro (1966) with few new additions prior to synthesis works within Schroeder & Neumann (1985) and Calonge et al. (2002). However, in the fifteen years or so, work led by Vicent Vicedo and André Piuz based on material mostly from Oman and wider Arabia (Vicedo et al., 2011; Vicedo & Serra-Kiel, 2011; Piuz et al., 2014; Vicedo & Piuz, 2016; Simmons et al., 2020) has established that there is potentially a much greater diversity of Cenomanian alveolinoids than previously thought based on very detailed analysis of internal structural features. This new taxonomy is included herein, but it should be noted that in a practical sense recognition of the new taxa requires access to multiple sections of excellent quality material. With that in mind it is often difficult to use the new species inventory for taxa described in the literature from only one thin-section photograph. It follows that the stratigraphic and palaeogeographic distribution of the full inventory of Cenomanian alveolinoids is challenging, yet it also points to flourishing diversity of alveolinoids in the Cenomanian.

Debate on the patterns of evolution of Cenomanian alveolinoids is still very active. Recently Dousti-Mohajer et al. (2021b) laid out a model for the evolution of alveolinoid species in the Iranian Zagros but this was strongly criticised by Consorti & Vicedo (2022) largely based on misidentification of the species by the former authors, thus rendering their order of first appearances of the various species irrelevant.

In terms of morphology, the Superfamily Alveolinoidea Ehrenberg, 1839 is a large miliolid (porcelaneous) foraminiferal group containing several families (see above). It has been morphologically described as…

"*Test enrolled, commonly about an elongate axis, proloculus may be followed by flexostyle in megalospheric generation, planispiral or streptospiral, or milioline with chambers added in varying planes, may uncoil in the adult and may have septulae or pillars; wall porcelaneous, with basal thickening, subepidermal partitions and pillars; aperture multiple* [except in *Cisalveolina* – our addition]."

Loeblich & Tappan (1987; p. 355-6).

It is the planispiral (or streptospiral) coiling enrolled along an elongate axis (although this axis is shortened in the axially-compressed *Sellialveolina* and in some species of *Cisalveolina* and *Ovalveolina*), together with typical subdivision of chambers by vertical septulae (or by a row of pillars in a few species) into a row, or multiple rows separated by horizontal 'floors', of chamberlets, each with intercameral foramina or an external aperture, that characterises the superfamily as a whole.

Alveolinoid test structure and complexity has required the establishment of a large lexicon of descriptive terminology, aiming towards adopting a consistent terminology over the period of historical study. Figures 1-3 show illustrated glossaries and descriptions of features characteristic to the alveolinoids used herein, many of which are used for discrimination and identity determination at different taxonomic levels. Image sources are from De Castro (1966); Fourcade et al. (1975); Hottinger (2006); Piuz et al. (2014); Reichel (1933, 1936, 1937, 1941, 1947); Schroeder & Neumann (1985); Vicedo & Piuz (2016) and Vicedo et al. (2011).

Further discussion on the specific descriptive terminology of chambers and chamberlets follows below.

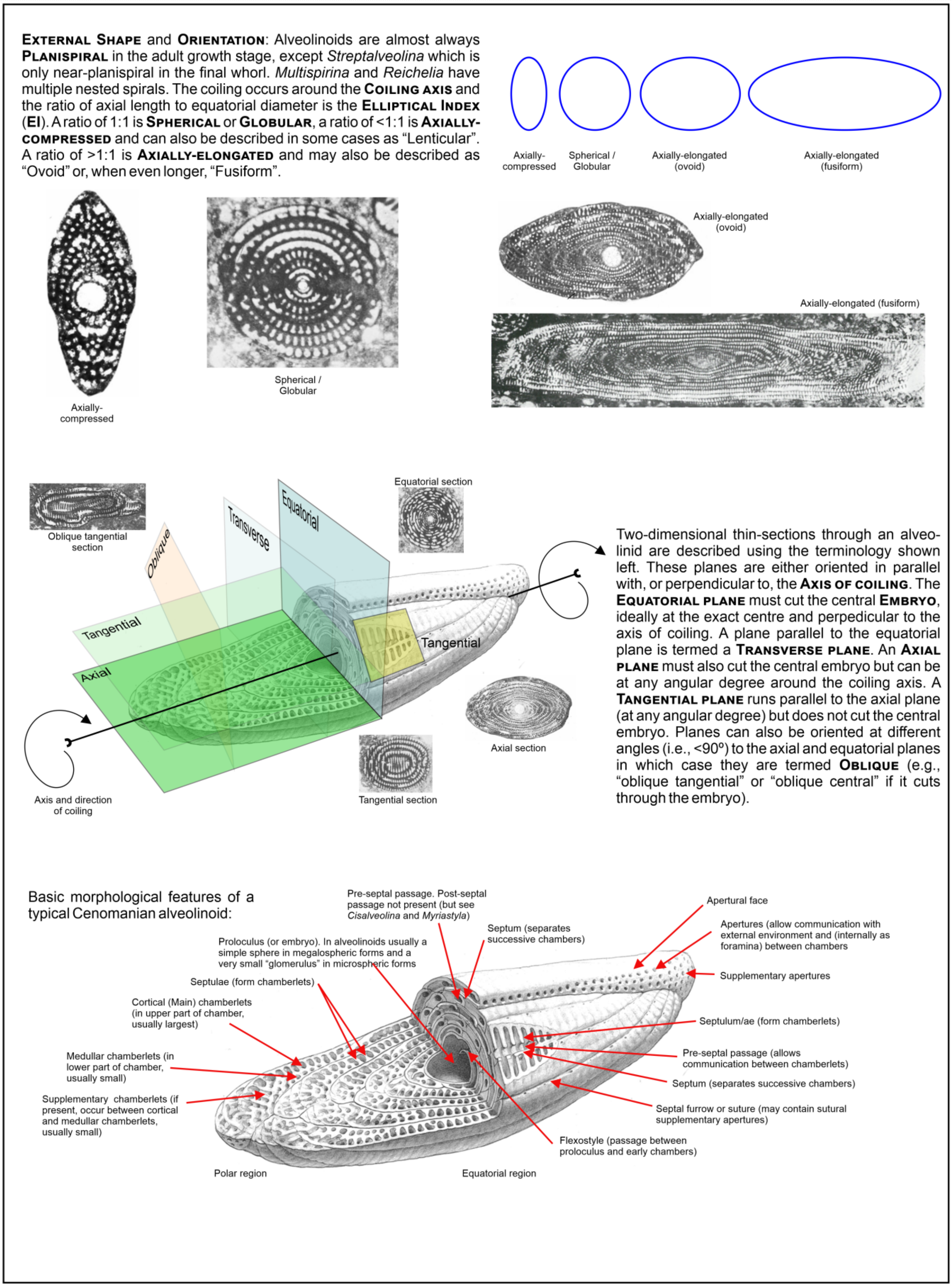
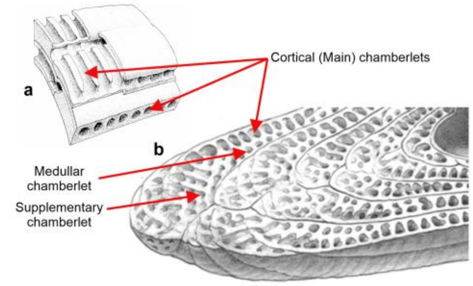
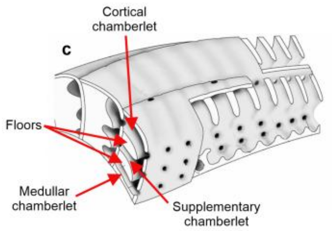


Fig. 1: Alveolinoid glossary and description of structural features (part 1) [See above for image sources].





Chamberlets: segments or subdivisions of a **Chamber** produced during the same instar. In alveolinids these subdivisions are formed by **Septulae** (barriers running perpendicular to the base of the chamber in the growth direction), **Floors** (parallel to and above the base of the chamber in the growth direction) and occasionally **Pillars** (in both orientations in the growth direction and perpendicular to growth direction). The presence of the **Pre-septal passage** (a volumetric space before the chamber-closing septum) ensures that all chamberlets within a chamber are in communication with each other. Chamberlets can occur in discrete rows and also be more "scattered".

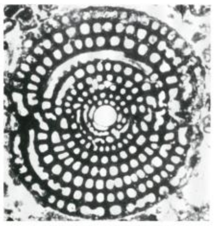
Cortical (or **Main**) **chamberlets**: All alveolinoids have one row of cortical/main chamberlets. Where >1 chamberlet row is present, the cortical chamberlets are the outermost layer (and usually the largest).

Medullar chamberlets: Innermost layer of chamberlets.

Supplementary (or Secondary) chamberlets: Chamberlets not part of a cortical or medullar row but which may be regular (forming their own row) or more scattered.

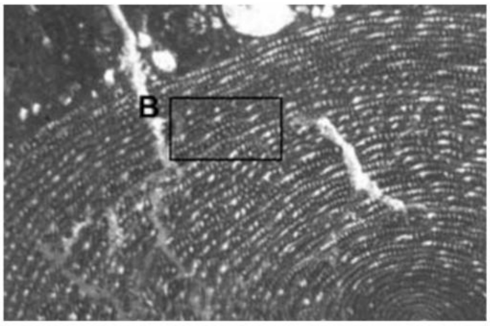
(**a**) - single row of cortical or main chamberlets in *Cisalveolina*.
(**b**) - single row of cortical chamberlets in the equatorial zone of *Praealveolina*, with secondary (i.e., *not* medullar) chamberlets. At first a single layer, then becoming more numerous and scattered near the poles.
© - three complete chamberlet layers (separated by two floors) in *Decastroia* (upper layer = cortical; lower layer = medullar; middle layer = supplementary/secondary). Some descriptions may refer to "two rows of medullar chamberlets" but, strictly speaking, only the *lowest* row is medullary.

The function of chamberlets is unknown but is probably connected with the housing of photosymbionts that has been observed in living alveolinoids and/or to increase the structural strength of the test (internal bracing by septulae and pillars).



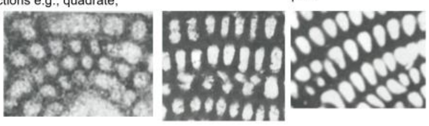
Single row of Cortical chamberlets in *Cisalveolina*

Single row of Cortical chamberlets in equatorial region of *Praealveolina* but with the appearance of Supplementary chamberlets towards the pole

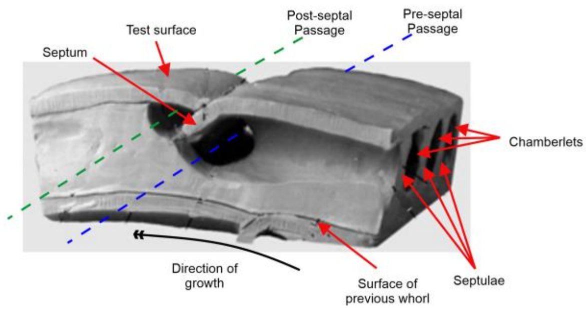


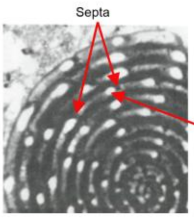
Multiple rows of chamberlets in *Decastroia*. Area "B" shows three chamberlet layers within several chambers (upper row: cortical, middle row: supplementary, lower row: medullar)

Chamberlets (particularly cortical) can have variably-shaped cross-sections e.g., quadrate, elongate/oblong, piriform:

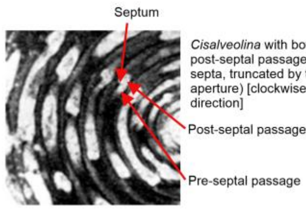


Successive chambers are separated by a **Septum** which in alveolinoids runs perpendicular to the direction of growth. The internal **Septulae** subdivide the chamber and run in the direction of growth. Their relative positions from one chamber to the next can be continuous (mainly) or, sometimes, alternating (e.g., *Cisalveolina, Alveocella*). The septulae can run the complete length of the chamber, or are interrupted at the back (in the sense of direction of growth) of the chamber (i.e., immediately following the previous chamber's septum) or at the front just prior to that chamber's septum. These are termed **Post-septal** and **Pre-septal Passages** respectively. Of the Cenomanian alveolinids, all genera have a pre-septal passage (which can be relatively wide or narrow) but only *Cisalveolina* can be said to display evidence of a post-septal passage. *Myriastyla* does not have true septula and thus cannot be said to have either pre- or post-septal passages.

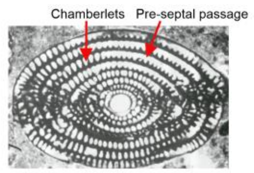




Pre-septal passages in *Praealveolina* (and most Cenomanian alveolinid genera) with no evidence of post-septal passages [clockwise growth direction]



Cisalveolina with both pre- and post-septal passages (note short septa, truncated by the open slit aperture) [clockwise growth direction]



The gradual appearance (from left to right) of the pre-septal passage in axial section of *Praealveolina*, revealed by a cut slightly oblique to the axial plane

Fig. 2: Alveolinoid glossary and description of structural features (part 2) [See above for image sources].

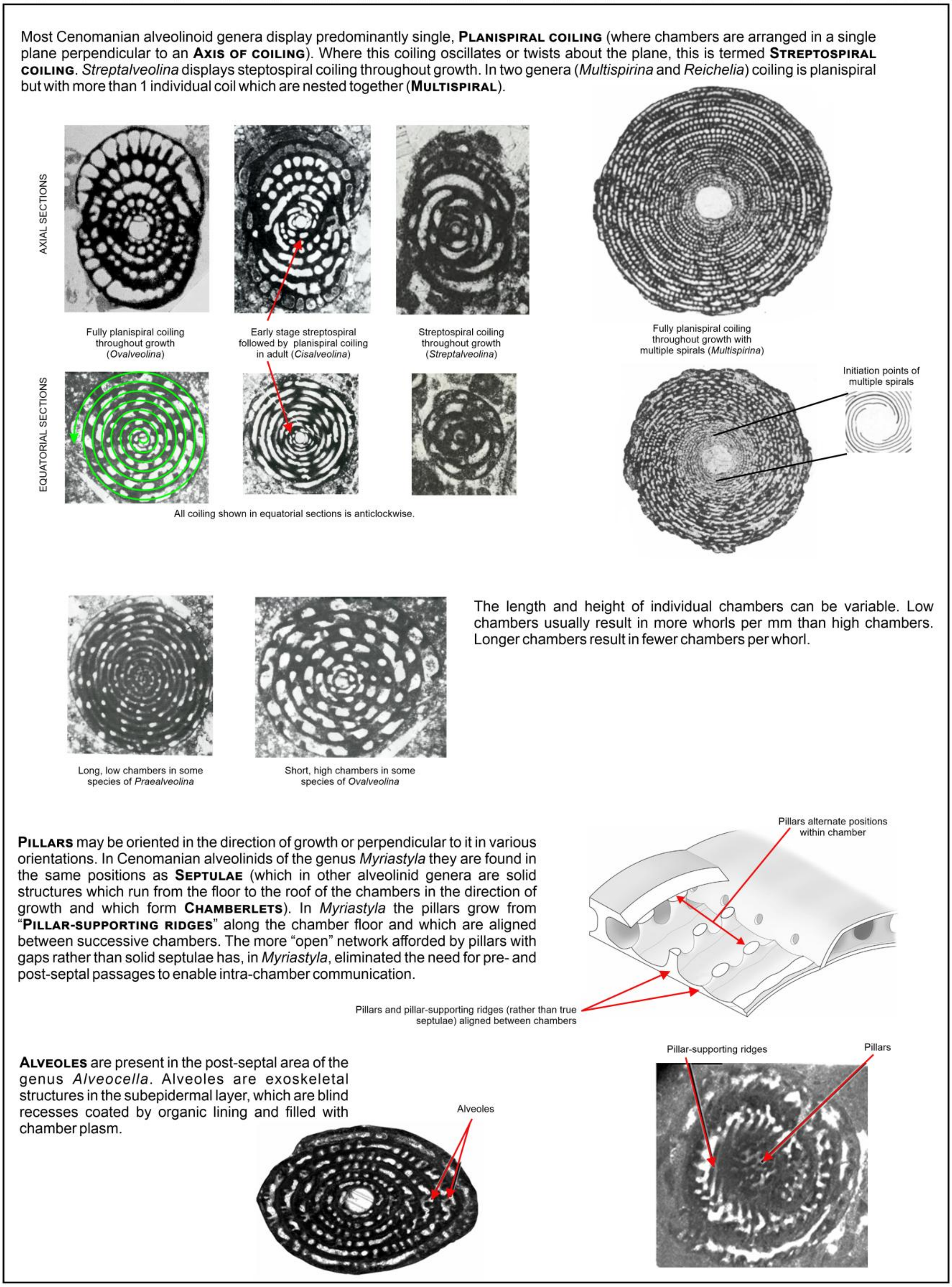


Fig. 3: Alveolinoid glossary and description of structural features (part 3) [See above for image sources].

For an extensive treatment of morphological descriptive terminology of structural elements for foraminifera in general see Hottinger (2006).

A NOTE ON CHAMBERLET TERMINOLOGY

There have been several different and sometimes potentially confusing terms used to define alveolinoid chambers, especially chamberlets (those constructed within individual chambers and separated by vertical septulae and/or horizontal floors).

For those taxa with only a single layer of chamberlets in a chamber (i.e., with septulae but not floors) the descriptions are fairly straight-forward. Reichel (1933 – the first major work on the group as a whole) referred to them as ***primary*** chamberlets (p. 270). Any additional chamberlet layers found (often poleward) in other taxa he referred to as "additional levels of chambers" or ***secondary*** chamberlets.

Some authors (e.g., Hottinger, 2006) freely used terms like ***main*** chamberlets and ***secondary*** / ***supplementary*** chamberlets respectively.

In a major illustrated glossary of terms used in the description of foraminifera, Hottinger (2006) refers to "main chamber lumen" – meaning the volume of the chamber as a whole (i.e., not individual chamberlets) and also "main chamberlet layer", but referring the latter to orbitoidiform types, not alveolinoids.

On the assumption that, in alveolinoids, each chamberlet (irrespective of being primary or secondary) will have a corresponding aperture(s)/foramen(foramina), Hottinger (2006) also distinguished between secondary and supplementary apertures (and therefore, by extension, chamberlets). However, his definitions are more applicable to those foraminifera with a *single* primary aperture and *additional* secondary/supplementary apertures.

Further refinement (or complexity depending upon point-of-view) was provided by Vicedo & Serra-Kiel (2011 and also Vicedo & Piuz, 2016) when describing the new alveolinoid genus *Decastroia* (see Figure 6). This genus can have 2 or more layers of chamberlets in each chamber (separated by one or more floors). Vicedo & Serra-Kiel (2011) termed the uppermost layer of chamberlets as ***cortical*** chamberlets. They termed the lowest layer ***medullar*** chamberlets (see also Vicedo et al., 2011 for a similar treatment of *Sellialveolina*).

In 2016, Vicedo & Piuz used the modified terms "***cortical/main***" and "***medullar/secondary***" but added a third term – ***supplementary*** chamberlets – for those chamberlets that occurred in layers *between* the uppermost (cortical/main) and lowermost (medullar/secondary) layers. Distinct chamberlet rows or layers are primary observed in the equatorial regions of the test of those taxa that possess them. The regular floor structure tends to break down closer to the polar regions of the test and chamberlets (other than the primary/main/cortical ones) appear much more randomly arranged.

We have not used a 'standardised' labelling system herein and have mainly used the terms that the describing authors themselves used. However, sometimes we have clarified terminology where necessary.

STRUCTURE OF THIS PAPER

Ordered by taxonomic grouping, each alveolinoid taxon will be discussed relatively briefly in terms of taxonomic identity and published age ranges. In addition to representative illustrations of the individual taxa provided, one or two suitable source references for good images are also provided.

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

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

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

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

The subsequent systematic section is followed by a discussion of the findings of our critical review of the 32 taxa involved, with a focus on stratigraphic ranges, bioevents, and the potential for biozonation and correlation.

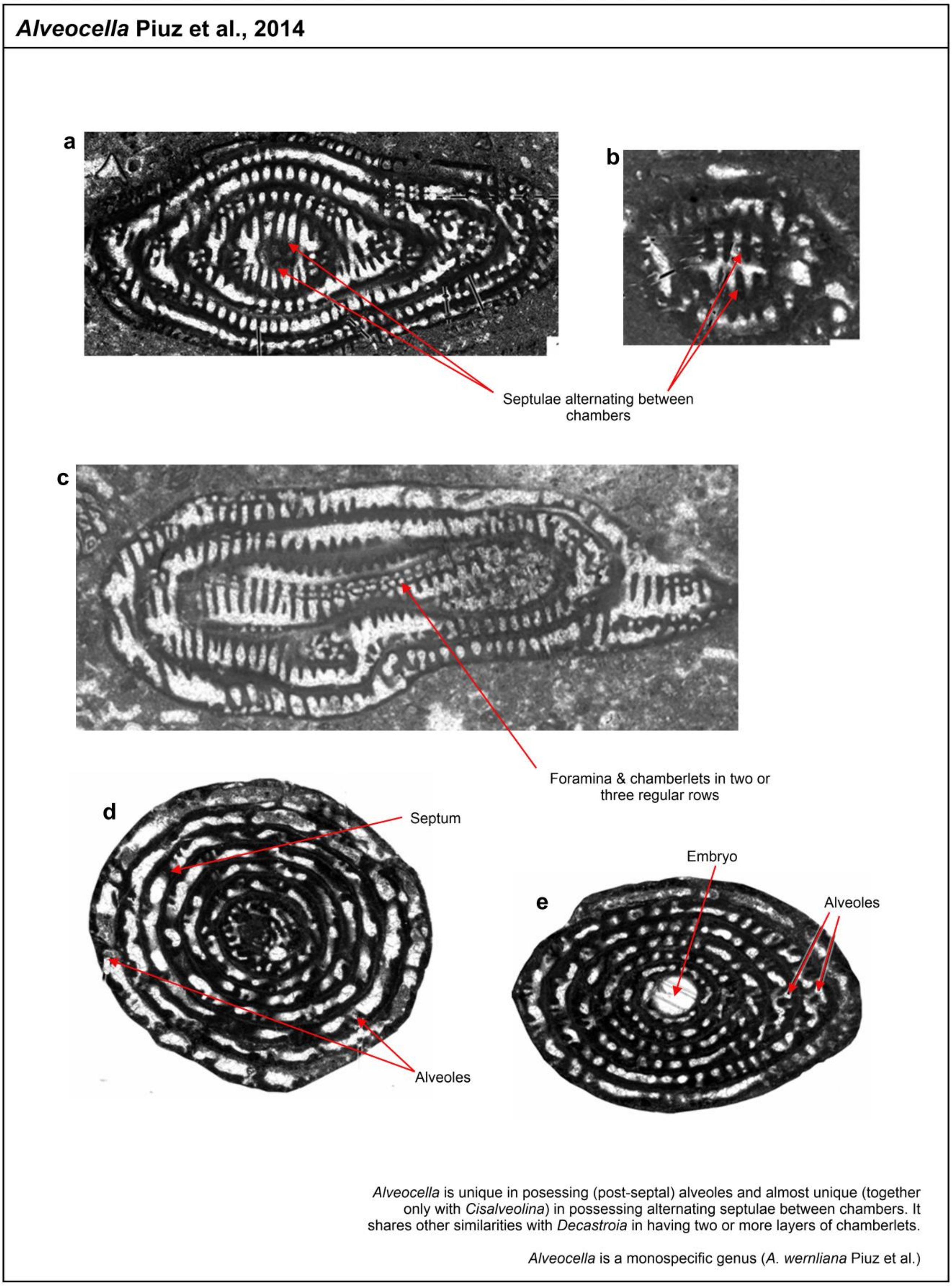


Fig. 4: Characteristics of the genus *Alveocella* [Images from Piuz et al. (2014)].

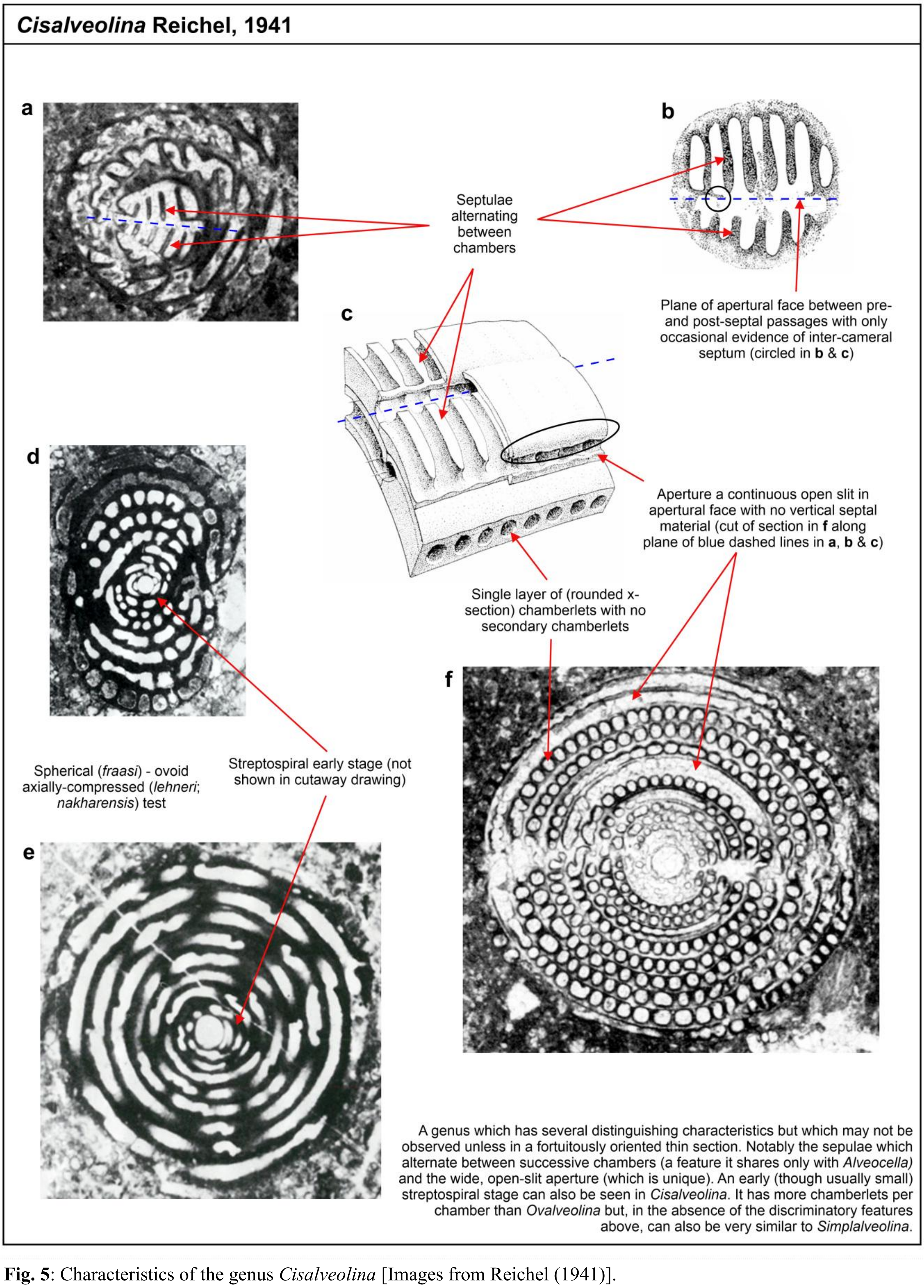


Fig. 5: Characteristics of the genus *Cisalveolina* [Images from Reichel (1941)].

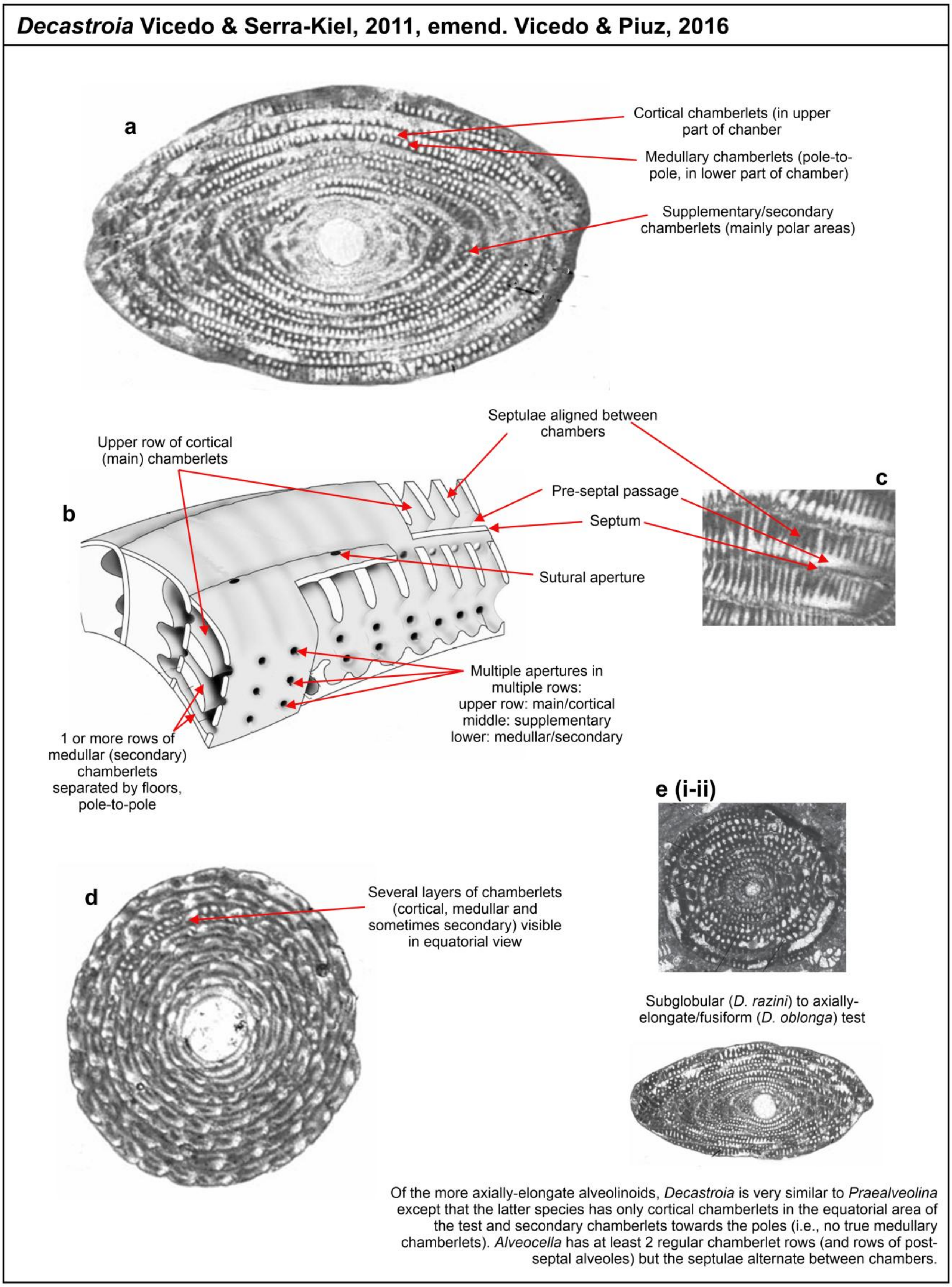
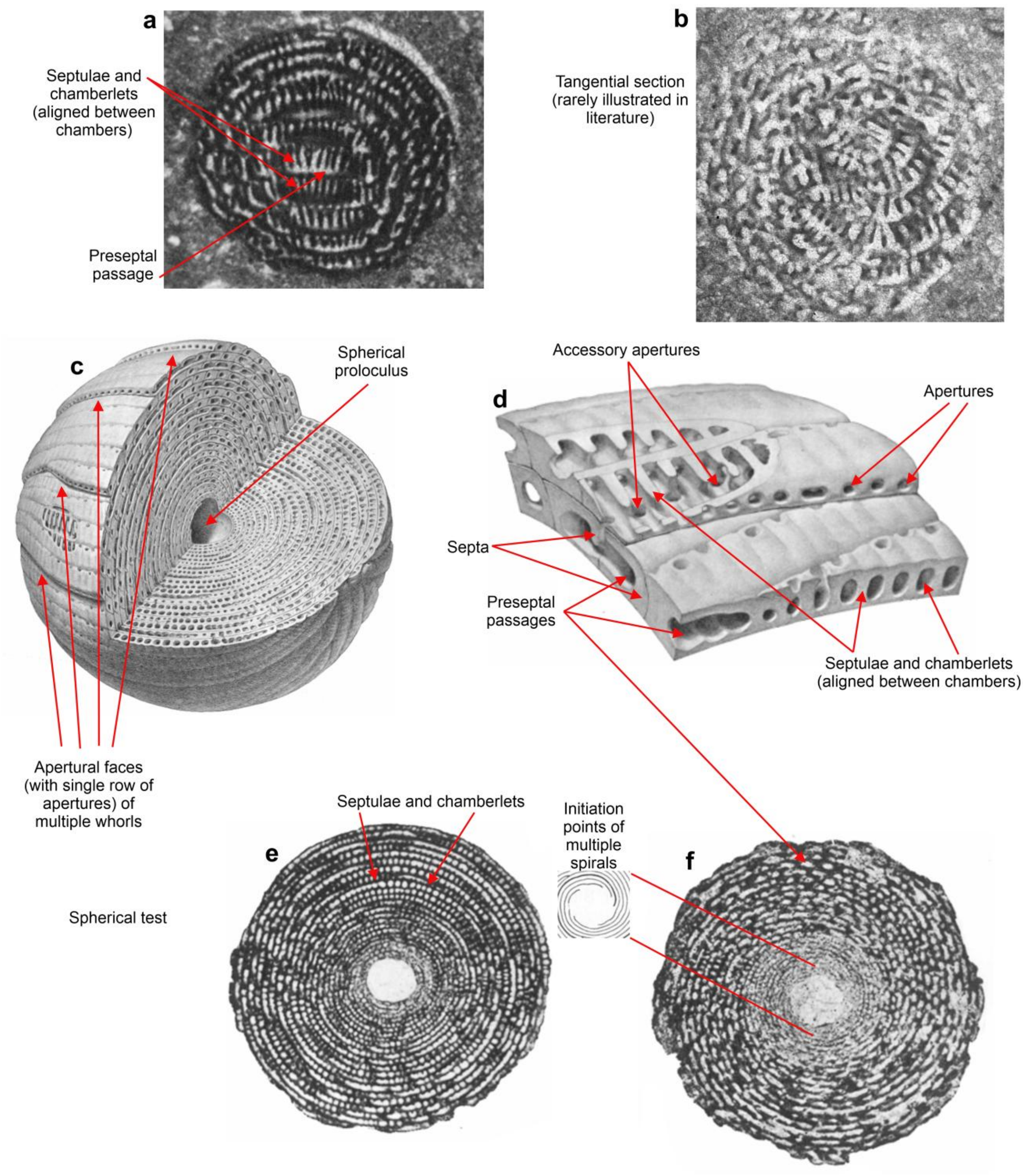


Fig. 6: Characteristics of the genus *Decastroia* [Images from Vicedo & Piuz (2016)].

***Multispirina* Reichel, 1947**



Multispirina, together with *Reichelia*, are the only alveolinid genera to have more than one planispiral coil/spire. *Multispirina* has a single row of chamberlets per chamber, *Reichelia* has at least 2 rows (cortical & medullar) and supplementary chamberlets near the poles. It also has fewer spires (2-5) than *Multispirina* (12-18) and can be more axially-elongate. *Multispirina* is always spherical.

Multispirina is a monospecific genus (*M. iranensis* Reichel).

Fig. 7: Characteristics of the genus *Multispirina* [Images from Reichel (1947); **a, b** Tangential sections courtesy of Mohsen Yazdi Moghadam, Cenomanian of Iran, Sarvak Fm.].

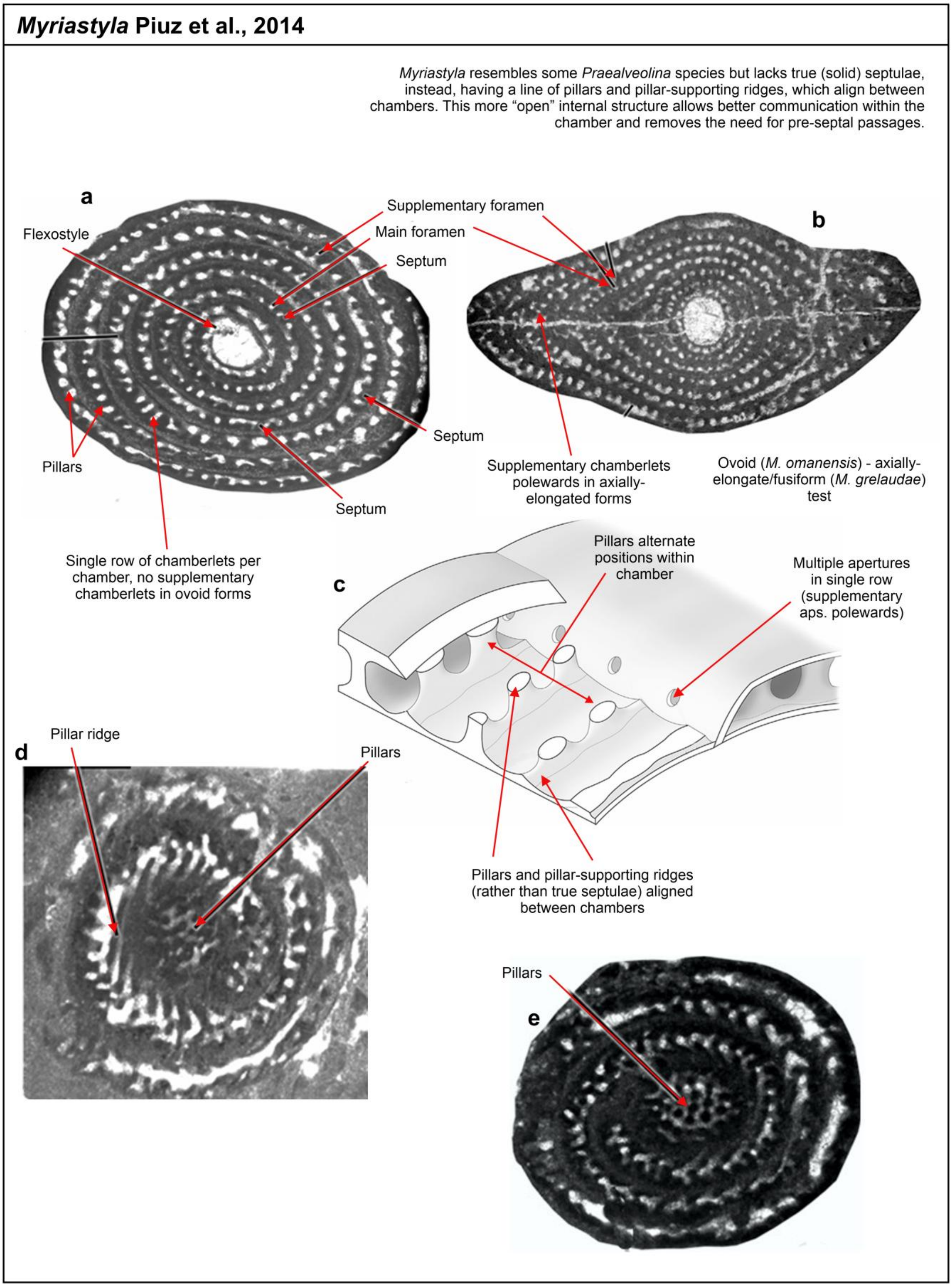


Fig. 8: Characteristics of the genus *Myriastyla* [Images from Piuz et al. (2014)].

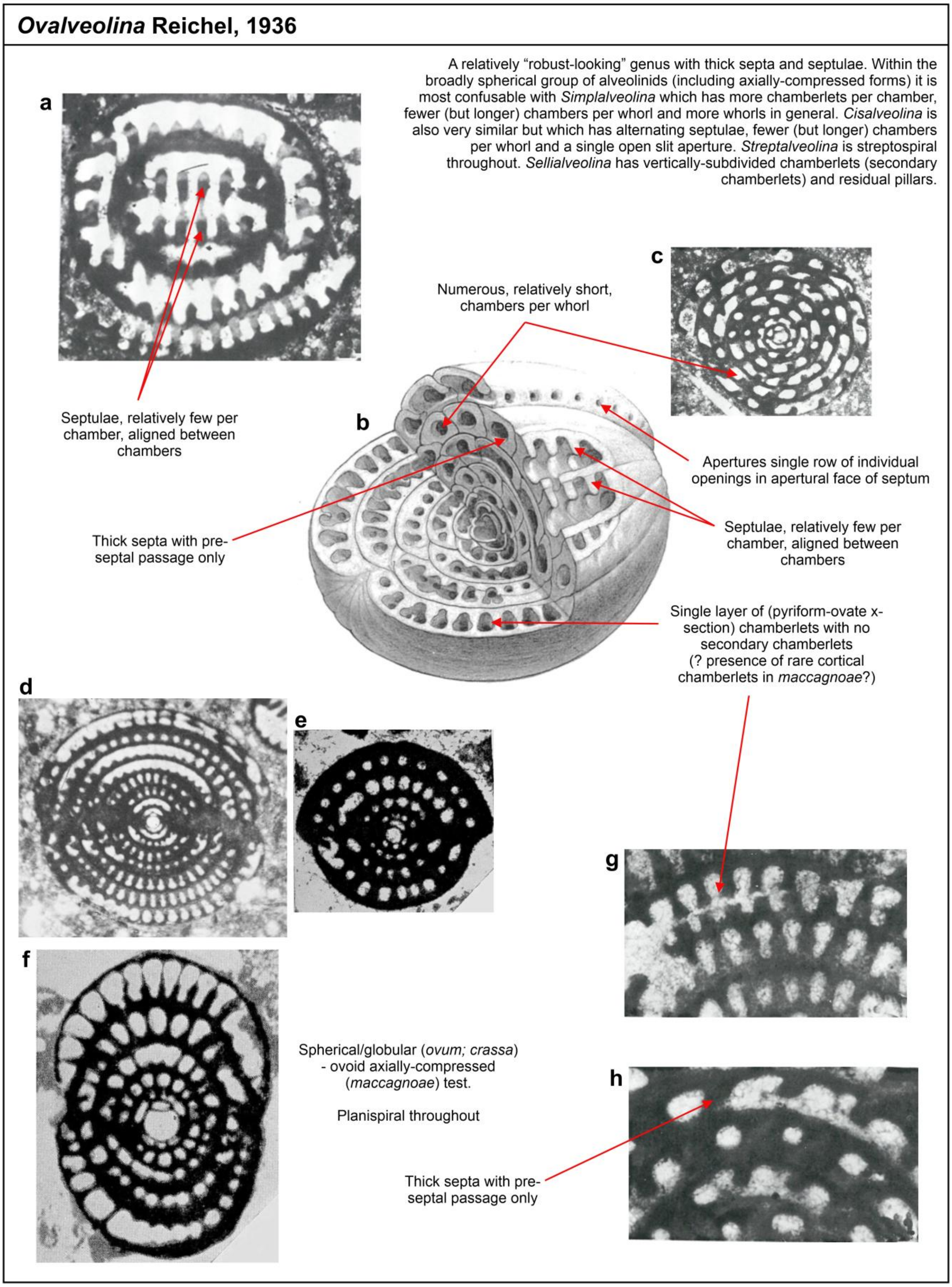


Fig. 9: Characteristics of the genus *Ovalveolina* [Images from Reichel (1936, 1937); Schroeder & Neumann (1985)].

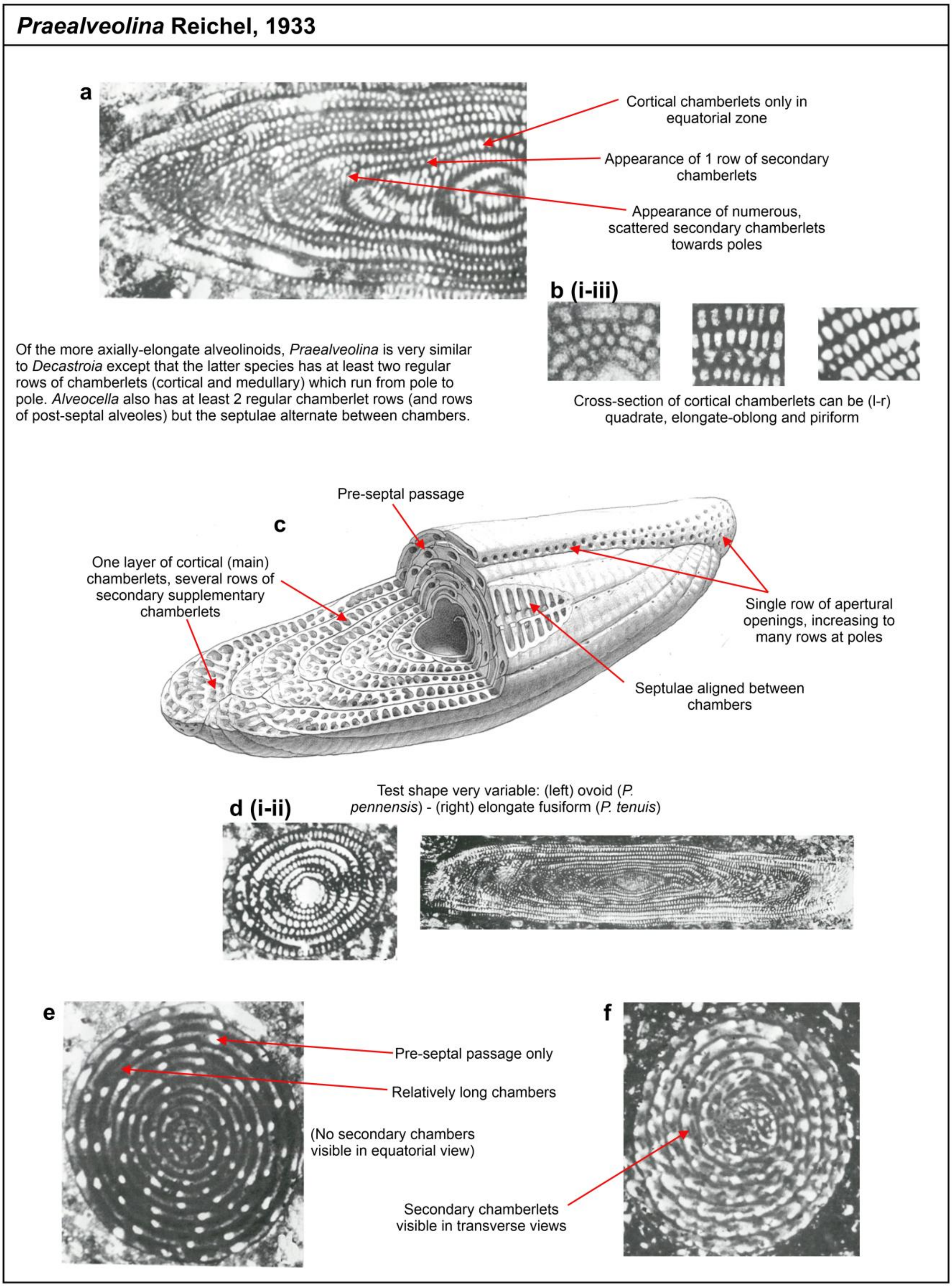
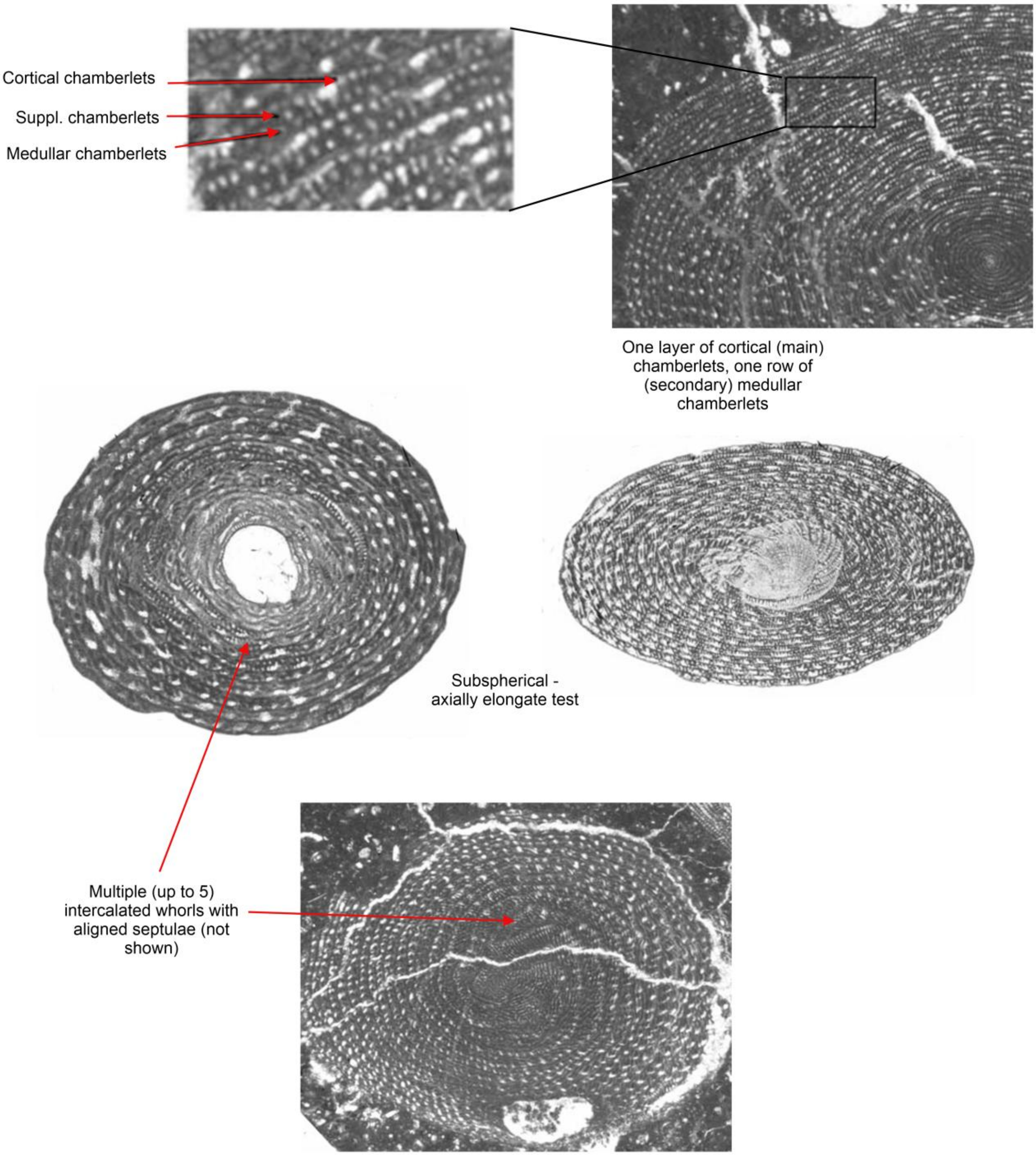


Fig. 10: Characteristics of the genus *Praealveolina* [Images from Reichel (1936, 1937); Schroeder & Neumann (1985)].

Reichelia Vicedo & Piuz, 2016



Reichelia, together with *Multispirina*, are the only alveolinid genera to have more than one planispiral coil/spire. *Multispirina* has a single row of chamberlets per chamber, *Reichelia* has at least 2 rows (cortical & medullar) and supplementary chamberlets near the poles. It also has fewer spires (2-5) than *Multispirina* (12-18) and can also be more axially-elongate.

Reichelia is a monospecific genus (*R. magna* Vicedo & Piuz).

Fig. 11: Characteristics of the genus *Reichelia* [Images from Vicedo & Piuz (2016)].

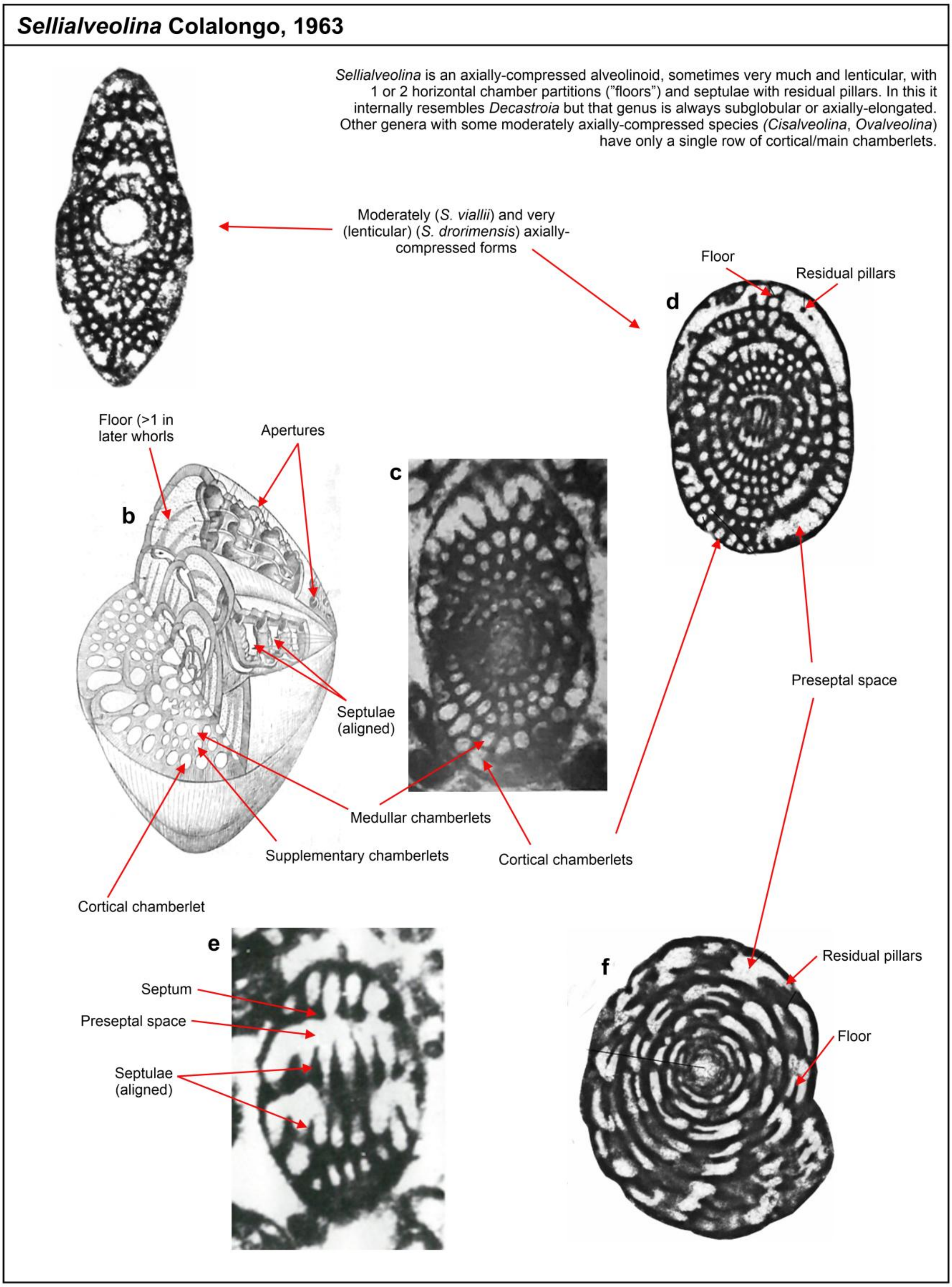


Fig. 12: Characteristics of the genus *Sellialveolina* [Images from Colalongo (1963); Schroeder & Neumann (1985); Vicedo et al. (2011).

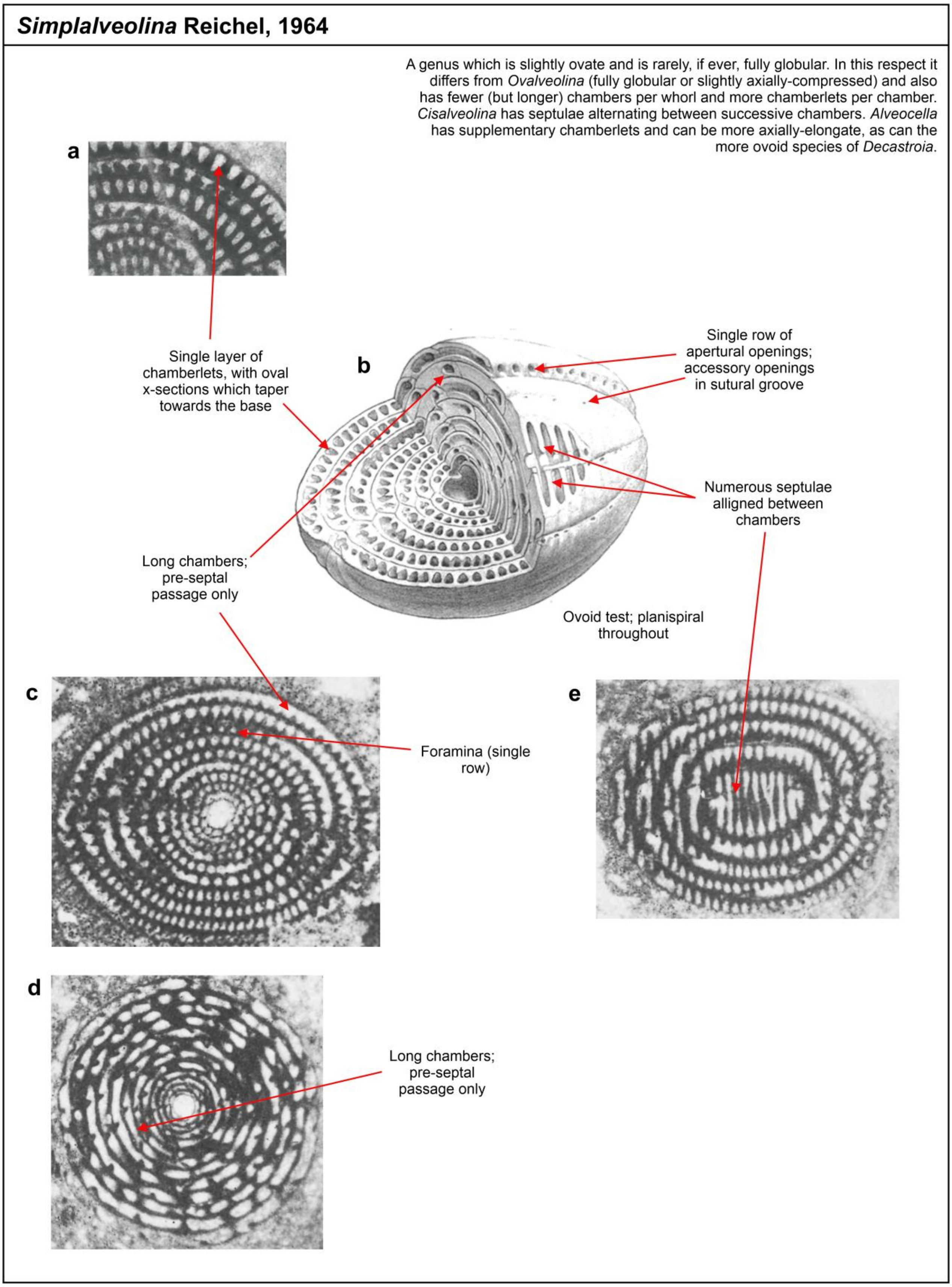


Fig. 13: Characteristics of the genus *Simplalveolina* [Images from Reichel (1936, 1937); Schroeder & Neumann (1985)].

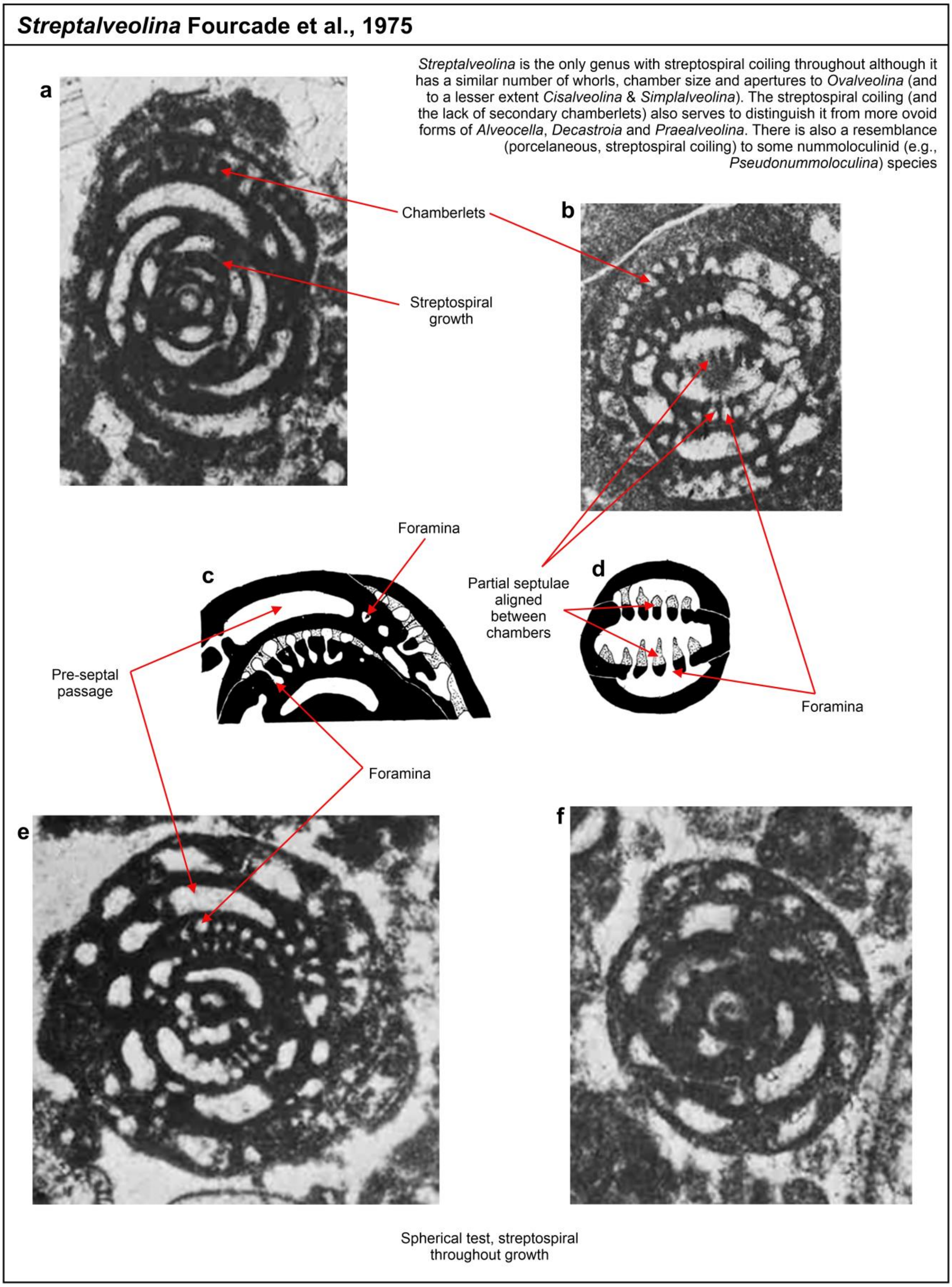


Fig. 14: Characteristics of the genus *Streptalveolina* [Images from Fourcade et al. (1975)].

SYSTEMATICS

Phylum **FORAMINIFERA** d'Orbigny, 1826
Class **TUBOTHALAMANA** Pawlowski, Holzmann & Tyszka, 2013
Order **MILIOLIDA** Delage & Hérouard, 1896
Superfamily **ALVEOLINOIDEA** Ehrenberg, 1839
Family **ALVEOLINIDAE** Ehrenberg, 1839

Genus ***Alveocella*** Piuz et al., 2014

Alveocella was defined by Piuz et al. (2014) with *A. wernliana* as the type (and so far, only) species from lower middle Cenomanian rocks of the Natih Formation, E unit, of Oman (considered by Bromhead et al., 2022, to be upper early Cenomanian, *dixoni* zone, in age). It has not subsequently been recorded elsewhere.

Alveocella is a moderately axially-elongate genus that is similar to *Praealveolina* and other axially-elongate types except that the chamber septulae alternate in position between chambers (as does the subglobular form *Cisalveolina*) and that it also has alveoli, the occurrence of which is a diagnostic feature of this genus. It lacks horizontal chamber subdivisions ('floors' in *Decastroia*) in the equatorial region which also serves to distinguish *Alveocella* from that genus, as well as from *Praealveolina*. However, in respect of alternate septula and alveoli, it is also similar to some younger alveolinoid genera such as *Subalveolina* (Santonian – Campanian) and *Bullalveolina* (Oligocene) (see Reichel, 1936, 1937; Piuz et al., 2014, for details).

See Table 1 and Figure 4 for diagnostic characteristics of the genus.

***Alveocella wernliana* Piuz et al., 2014**
FIGURE 15

T 2014 *Alveocella wernliana* gen. & sp. nov., Piuz et al., p. 349, figs. 3-7; lower middle Cenomanian, Oman Mountains [considered as late early Cenomanian by Bromhead et al., 2022].

Reference Images: Piuz et al., (2014), p. 349, figs. 3-7.

Taxonomy/Identity: For similarities and differences with other taxa see above in the genus description.

Confident Stratigraphic Range: upper early Cenomanian (following Bromhead et al., 2022).

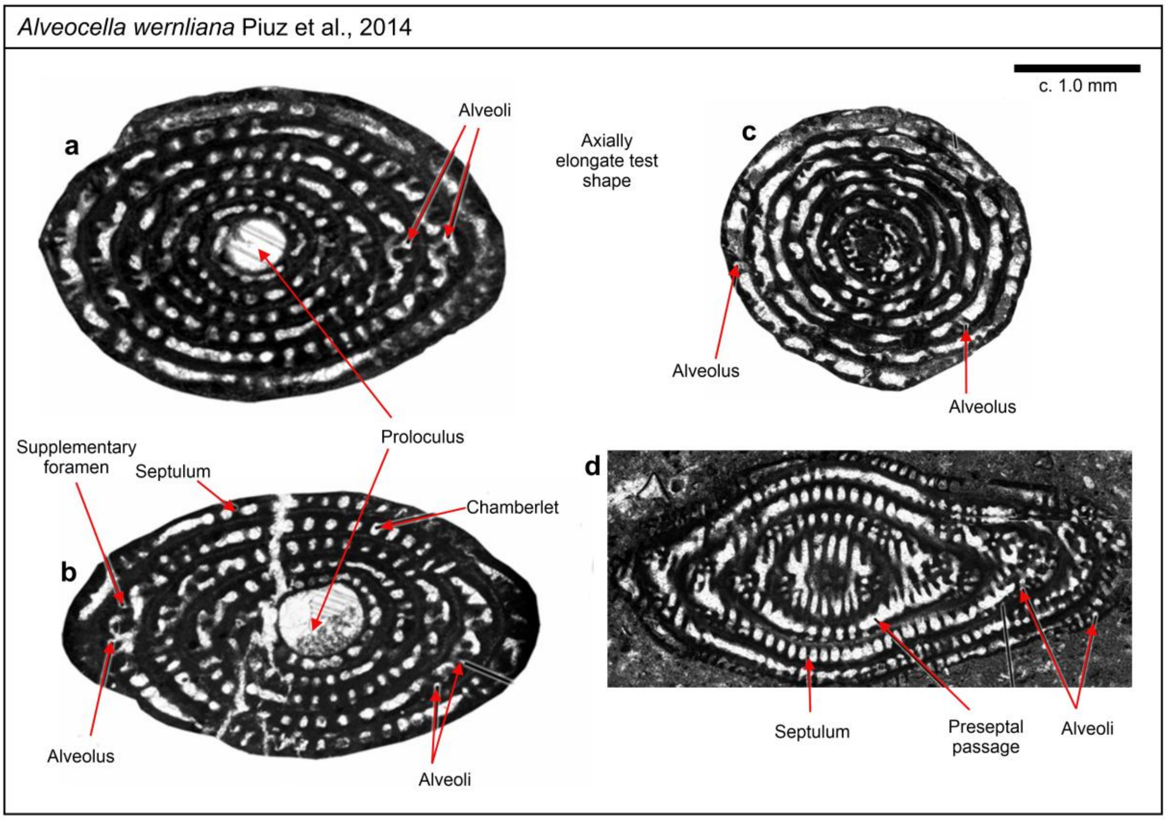


Fig. 15: Representative illustrations of *Alveocella wernliana*: **a.** Axial section (holotype), Piuz et al. (2014, fig. 4.6; lower middle Cenomanian, Oman); **b.** Axial section, Piuz et al. (2014, fig. 4.3; lower middle Cenomanian, Oman); **c.** Near equatorial section, Piuz et al. (2014, fig. 5.11; lower middle Cenomanian, Oman); **d.** Tangential section, Piuz et al. (2014, fig. 6.1; lower middle Cenomanian, Oman). Lower middle Cenomanian age now considered upper early Cenomanian (following Bromhead et al., 2022).

Uncertain Stratigraphic Range: not applicable.

First (and so far, only) described from the lower middle Cenomanian of Oman by Piuz et al. (2014, now thought to be upper early Cenomanian according to Bromhead et al., 2022).

Geographic Distribution: So far recorded only from Oman.

Genus ***Cisalveolina*** Reichel 1941

First described from the Cenomanian of Bingistan, Iranian Zagros, as a new alveolinoid genus by Reichel (1941) with a new species *Cisalveolina fallax* designated as the type species (now understood to be a junior synonym of *Cisalveolina fraasi* (Gümbel, 1872)) alongside a second species *Cisalveolina lehneri*. See Table 1 for diagnosis of the genus.

Cisalveolina is of medium-size (3-5 mm diameter) and is globular to subglobular and rather axially compressed and has an early streptospirally-coiled stage (easily observable in *C. lehneri*) followed by planispiral-involute coiling. According to Reichel (1941), the single characteristic that separates *Cisalveolina* from all other mid-Cretaceous alveolinoid genera is the open nature of the aperture as a long slit in the apertural face, rather than a series of circular, individual openings as in other genera. However, the septula that alternate in position between successive chambers represent a further critical characteristic; they do not extend the whole distance from the base to the roof of the chamber. The septula reach relatively far forward, almost up to the inner side of apertural face, so that in many sections the aperture still appears as divided. The preseptal canal is present but not easily distinguishable. The postseptal canal is relatively large.

Between the three *Cisalveolina* species recognised so far, the principal morphological differences are

C. fraasi – globular/subglobular test, the largest species

C. lehneri – compressed subglobular ('nautiloid') test, the smallest species

C. nakharensis Piuz et al., 2014 – similar to *C. lehneri* in test shape but larger, with a larger megalosphere and by less developed early streptospiral growth.

See Table 1 and Figure 5 for diagnostic characteristics of the genus. Differences between the species are tabulated in Table 2 and in the discussions below.

***Cisalveolina fraasi* (Gümbel, 1872)**
FIGURE 16

1867 *Nummulites cretacea*, Fraas, p. 82, pl. 1, fig. 8; undifferentiated Cenomanian – Turonian boundary beds, Israel [name invalid, junior homonym, new name in Gümbel (1872) - secondary homonym of *Alveolina cretacea* d'Archiac, 1837]

T 1872 *Alveolina fraasi*, n. sp., Gümbel, p. 251; [replacement name for "*Nummulites cretacea* Fraas, 1867"]

1941 *Cisalveolina fallax* n. gen., n. sp. Reichel, p. 257, pl. 15, figs. 1-3; late Cenomanian, Iranian Zagros.

1959 *Cisalveolina fallax* Reichel – Reiss, pl. 1, fig. 15; undifferentiated Cenomanian, Israel.

? 1961 *Cisalveolina fallax* – Hamaoui, p. 17, pl. 3, fig. 1; pl. 9, figs. 26-27; pl. 10, figs. 1-3; undifferentiated Cenomanian – Turonian [most likely late Cenomanian], Israel [possibly *C. lehneri*].

1962 *Cisalveolina fallax* – Hamaoui, pl. 4, figs. 1-2 (?), 4-5, 20; undifferentiated Cenomanian – Turonian [most likely late Cenomanian], Israel.

1962 *Cisalveolina fallax* – Sartoni & Crescenti, p. 205; pls. 34-35; early Turonian [open to reinterpretation as late Cenomanian based on microfaunal assemblage], southern Italy.

1964 *Cisalveolina fallax* – Reichel in Azzaroli & Reichel, p. 4, pl. 1, figs. 1-3, 9; late Cenomanian, Italy

1964 *Cisalveolina fallax* – Devoto, pl. 1, figs. 3, 6; latest Cenomanian, southern Italy.

1965 *Cisalveolina fallax* – Hamaoui in Arkin et al., p. 36, pl. 4, fig. 6; undifferentiated Cenomanian – Turonian [open to reinterpretation as late Cenomanian based on microfaunal assemblage], Israel.

1965 *Cisalveolina fallax* – Paradisi & Sirna, fig. 3; Cenomanian-Turonian boundary, Italy.

? 1965 *Cisalveolina fallax* – De Castro, p. 359, pls. 20-21; late Cenomanian, southern Italy [probably *C. lehneri*].

Non 1965 *Cisalveolina fallax* – Farinacci, fig. 5; late Cenomanian, southern Italy [= *C. lehneri*].

1966 *Cisalveolina fallax* – Luperto Sinni, pl. 10, figs. 2-4; late Cenomanian, southern Italy.

1966 *Cisalveolina fallax* – Vallario, p. 57, pl. 9, fig. 1; late Cenomanian, southern Italy.

1967 *Cisalveolina fallax* – Luperto Sinni, pl. 10, fig. 1; late Cenomanian, southern Italy.

1969 *Praealveolina simplex* – Sampò, pl. 43, fig. 2; undifferentiated Cenomanian, Iranian Zagros

? 1969 *Cisalveolina fallax* – Sampò, pl. 43, fig. 6; pl. 46, fig. 1; undifferentiated Cenomanian, Iranian Zagros [probably *C. lehneri*].

1970 *Cisalveolina fallax* – Radoičić, pl. 1; early Turonian [now understood to be late Cenomanian – Radoičić, 1994], Croatia.

1971 *Nummulites cretacea* Fraas (= *Cisalveolina fallax* Reichel) – Schroeder, figs. 1-3, Cenomanian – Turonian boundary beds, Israel.

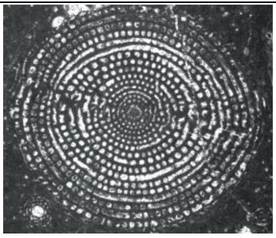
1972 *Cisalveolina fraasi* (Gümbel) – Urlichs, p. 507-508 [recognition that *C. fraasi* is a valid name].

1972 *Cisalveolina falax* (sic) – Radoičić, p. 94, pl. 8, fig. 5; early Turonian [now understood to be late Cenomanian], Serbia.

1973 *Cisalveolina fallax* – Berthou, pl. 8, fig. 2; early late Cenomanian (*Neolobites vibrayeanus* Zone), Portugal.

Non 1973 *Cisalveolina fallax* – El-Naggar & Al-Rifaiy, fig. 6 (14), fig. 7 (2); late Cenomanian, Kuwait [= *Decastroia* sp.].

Table 2: Summary of diagnostic and biometric data for *Cisalveolina* species.

Characteristic	***C. fraasi***	***C. lehneri***	***C. nakharensis***
Original description & provenance	Re-named by Gümbel (1872), originally described from "Cenomanian – Turonian transition beds" (now regarded as late Cenomanian) of modern-day Israel by Fraas (1867) as *Nummulites cretacea.* Type species of *Cisalveolina* (as *C. fallax* Reichel, 1941).	Reichel (1941) from undifferentiated Cenomanian of Tang-i-Moghar, Kuh-i-Bingistan, Iranian Zagros.	Piuz et al. (2014) from lower middle Cenomanian (now regarded as late early Cenomanian), Oman Mountains.
Basic illustration (axial views)	 Consorti (personal collection, late Cenomanian, Central Apennines, Italy - locality of Fabbi et al., 2023)	 De Castro in Schroeder & Neumann (1985, pl. 63, fig. 1; middle Cenomanian, Italy)	 Piuz et al. (2014, fig. 8(6); late early Cenomanian, Oman)
Overall shape (aspect ratio)	Globular (0.80-1.25 **)	Laterally-compressed, subglobular (0.56-0.75 **)	Subglobular (***) (0.61-0.79 ****)
Dimensions (test)	Diameter (meg - equatorial): 2.7 mm (**) (***) Diameter (mic – equatorial): 3.4 mm (**) Diameter (meg – axial): 3.16 mm (*) Diameter (meg – equatorial): 2.9-3.0 mm (*)	Diameter (meg - equatorial): 1.85-1.90 mm (*) (***) Diameter (mic – equatorial): 2.16 mm (*) Diameter (meg – axial): 1.40 mm (*) Diameter (mic – axial): 1.44 mm (*) Diameter (equatorial): 1.10-1.90 mm (**)	Diameter (meg - equatorial): 2.3 mm (***) Diameter (meg – equatorial): 1.61-2.30 mm (****) Diameter (meg – axial): 1.39-1.74 mm (****)
Dimensions (embryo)	Diameter (meg): 0.18-0.288 mm (*) Diameter (meg): 0.14-0.50 mm (**) Diameter: 0.20-0.37 mm (***)	Diameter (meg): 0.18-0.25 mm (*) Diameter: 0.025-0.267 mm (**) Diameter: 0.11-0.14 mm (***)	Diameter: 0.15-0.20 mm (***) Diameter: 0.128-0.212 mm (****)
Coiling	Slightly streptospiral in very early stage ('first whorl' *), regularly planispiral afterwards (**)	Early stage streptospiral/milioline (c. 0.30-0.65 mm), later planispiral (**)	Slightly streptospiral becoming planispiral (***)
No. of whorls	3-11 with lower part of the range in forms with larger proloculi (**) (10-20 in microspheric forms **)	4-13 (higher numbers in specimens with relatively smaller proloculi) (**)	7-8 (***)

Chambers per whorl	2-3 initially, increasing slowly to 8 (**)	2 initially, increasing to 4.5-9 (**)	
Chamberlets per chamber	6 initially to about 18-20 by whorl 7 (**)	1-2 initially to about 10 in final whorl (**)	16-20 by the 4th whorl (***)
Rate of chamber growth	Slow	Slow	Slow
Preseptal canal	Small (**)	Small (**)	
Postseptal canal	Slightly larger (generally) than preseptal canal (**)	Slightly larger (generally) than preseptal canal (**)	Always located in upper half of chamber (***)
Basal layer	Thickens from 0.013-0.25 mm through ontogeny (**)	Absent in early whorls, 0.007-0.020 mm by whorl 5 and 0.015-0.30 mm by the 9th decreasing towards the poles (**)	
Comments	* = data from Reichel (1941) (as *C. fallax*) ** = data from De Castro in Schroeder & Neumann (1985) – contains extensive biometric data *** = data from Piuz et al. (2014)	* = data from Reichel (1941) (as *C. lehneri*) ** = data from De Castro in Schroeder & Neumann (1985) – contains extensive biometric data *** = data from Piuz et al. (2014)	*** = data from Piuz et al. (2014) **** = measurements of Piuz et al.'s (2014) illustrated specimens by the present authors

1974 *Cisalveolina falax* (sic) – Radoičić, p. 139, pl. 15, fig. 2; early Turonian [now understood to be late Cenomanian – Radoičić, 1994], Serbia.
1974 *Cisalveolina fallax* – Saint-Marc, p. 247, pl. 9, figs. 1-2, *non* 3; latest Cenomanian – early Turonian [early Turonian age can be discounted – see Simmons & Bidgood, 2023 for discussion of chronostratigraphic calibration of mid-Cretaceous Lebanese stratigraphy], Lebanon.
1974 *Cisalveolina fallax* – Vila, p. 387, pl. 1, figs. 3-6; late Cenomanian, eastern Algeria [*fide* De Castro in Schroeder & Neumann (1985)].
1975a *Cisalveolina fraasi* – Cherchi & Schroeder, pl. 2, figs. 3-4; late Cenomanian, Sardinia.
? 1976 *Praealveolina simplex* Reichel – Kalantari, pl. 22, fig. 27; undifferentiated Cenomanian, Iranian Zagros.
Non 1976 *Cisalveolina fallax* – Kalantari, pl. 22, figs. 28-29; undifferentiated Cenomanian, Iranian Zagros [possibly *Decastroia* sp.].
1977 *Cisalveolina fraasi* – Chiocchini & Mancinelli, pl. 38, fig. 1; Cenomanian – Turonian boundary interval, southern Italy.
1979 *Cisalveolina fallax* – Mamužić et al., pl. 8, figs. 3-4; undifferentiated Cenomanian, Croatia.
1980 *Cisalveolina fallax* – Fleury, p. 481, pl. 2, figs. 1-5; late Cenomanian – early Turonian (Turonian age doubtful), Greece.
1981 *Cisalveolina fallax* – Saint-Marc, pl. 2, fig. 1; latest Cenomanian – early Turonian [early Turonian age can be discounted – see Simmons & Bidgood, 2023 for discussion of chronostratigraphic calibration of mid-Cretaceous Lebanese stratigraphy], Lebanon.
1981 *Cisalveolina fraasi* – Cherchi & Schroeder, pl. 2, fig. 3; late Cenomanian, Sardinia.
1983 *Cisalveolina fraasi* – Barattolo, pl. 10; undifferentiated Cenomanian, southern Italy.
1985 *Cisalveolina fraasi* – De Castro in Schroeder & Neumann, p. 130, pl. 64, figs. 1-4; pl. 65, figs. 1-4; text-fig. 16; intra-late Cenomanian [not earliest and latest late Cenomanian - explanation of precision not given], global review [note range chart erroneously shows two ranges for this species, the older is actually that of *Cisalveolina lehneri* Reichel, 1941].
1987 *Cisalveolina* sp. – Reitner, pl. 47, fig. 10; late Cenomanian, northern Spain.
1988 *Cisalveolina fraasi* – Sartorio & Venturini, p. 109 (lower), p. 117 [upper – labels on this page transposed]; late Cenomanian, southern Italy.
1988 *Cisalveolina fraasi* – De Castro, p. 410, pl. 5, figs. 1-7; late Cenomanian, Israel with brief global review.
1992 *Cisalveolina fraasi* – Foglia, pl. 2, figs. 1, 3; Cenomanian-Turonian boundary; southern Italy.
1992 *Cisalveolina fallax* – Kalantari, text-fig. 157(1); undifferentiated Cenomanian, Iranian Zagros.

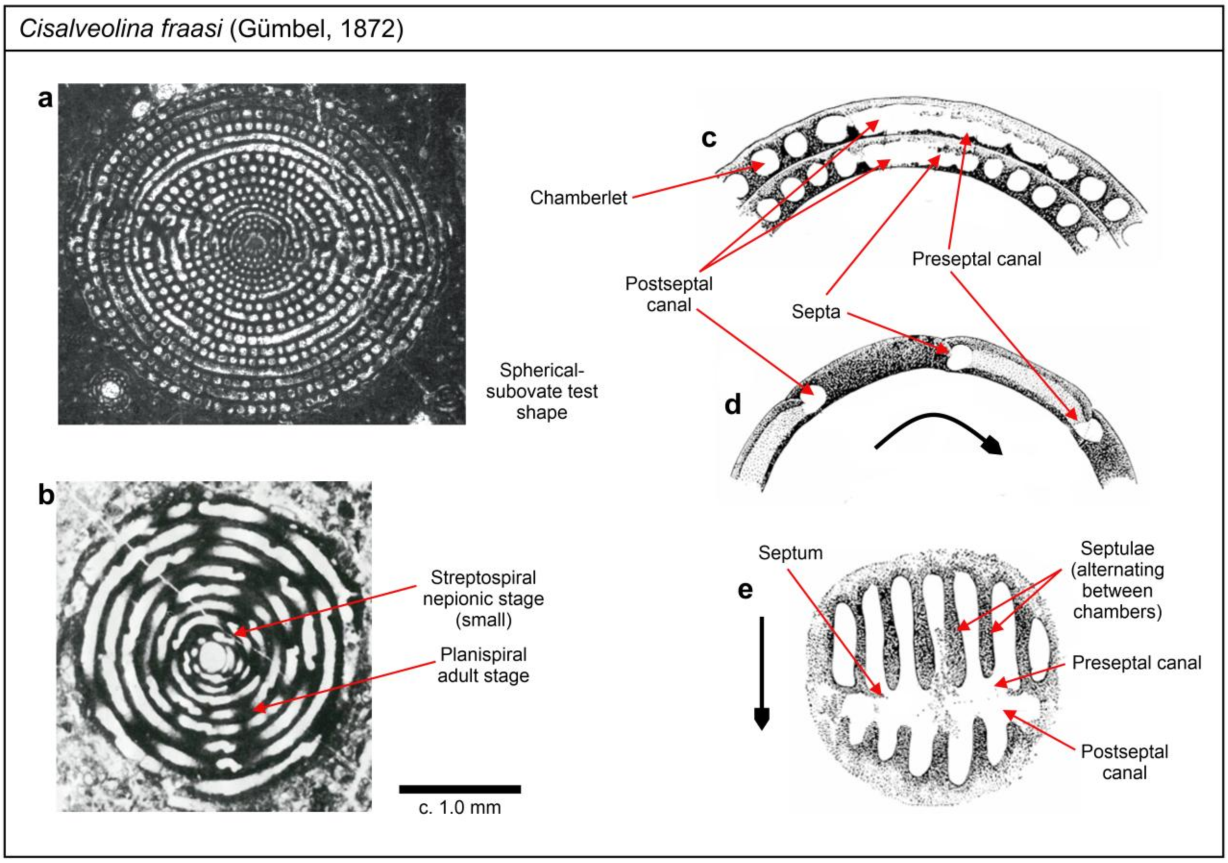


Fig. 16: Representative illustrations of *Cisalveolina fraasi*: **a.** Axial section, (Consorti, personal collection, late Cenomanian, Central Apennines, Italy; locality of Fabbi et al., 2023); **b.** Equatorial section, Schroeder & Neumann (1985, pl. 64, fig. 4; late Cenomanian, Italy); **c.** Oblique axial schematic section, Reichel (1941, fig. 1a); **d.** Equatorial schematic section, Reichel (1941, fig. 2b); **e.** Tangential schematic section, Reichel (1941, fig. 2c); **d-e** black arrow shows direction of growth; scale bar applies to **a-b** only.

1992 *Cisalveolina lehneri* – Kalantari, pl. 75, undifferentiated Cenomanian, Iranian Zagros.

1992 *Praealveolina cretacea* – Kalantari, text-fig. 157; pl. 75; undifferentiated Cenomanian, Iranian Zagros.

1994 *Cisalveolina fraasi* – Chiocchini et al., pl. 19, figs. 1-6; latest Cenomanian [see Frijia et al., 2015 for age revision to intra-late Cenomanian], central Italy.

? 2004 *Cisalveolina fraasi* – Ettachfini & Andreu, figs. 7A-B; late Cenomanian, Morocco.

Non 2004 *Cisalveolina fallax* – Flügel, pl. 72, fig. 2; undifferentiated Cenomanian, UAE [= *Myriastyla omanensis*].

2006 *Cisalveolina fraasi* – Bravi et al., fig. 5a, late Cenomanian, central Italy.

2006 *Cisalveolina fraasi* – De Castro, pl. 3, figs. 10-11; late Cenomanian, southern Italy.

? 2006 *Cisalveolina fraasi* – Ettachfini, pl. 16, figs. 1-2; late Cenomanian, Morocco.

2009 *Cisalveolina fraasi* – Sari et al., pl. 1, figs. 4-?5; late Cenomanian, Türkiye.

Non 2010 *Cisalveolina fallax* – Flügel, pl. 72, fig. 2; undifferentiated Cenomanian, UAE [= *Myriastyla omanensis*].

? 2010 *Cisalveolina fraasi* – Spalluto & Caffau, fig. 14F; undifferentiated middle-late Cenomanian, southern Italy [poorly preserved specimen].

2011 *Praealveolina cretacea* (d'Archiac, 1837) – Amer, fig. 20(2); ?late Cenomanian?, western Iraq.

? 2011 *Cisalveolina* sp. – Amer, fig. 15(4), fig. 21(2); ?late Cenomanian?, western Iraq.

2012 *Cisalveolina fraasi* – Chiocchini et al., pl. 115, figs. 1-7; pl. 116, fig. 1; pl. 117, fig. 1; latest late Cenomanian [see Frijia et al., 2015 for age revision to intra-late Cenomanian], central Italy.

2012 *Cisalveolina fraasi* – Simone et al., fig. 4C; late Cenomanian, southern Italy.

? 2012 *Cisalveolina fraasi* – Lézin et al., fig. 7g; late Cenomanian, Morocco.

? 2012 *Cisalveolina frassi* (sic) – Orabi et al., fig. 3A, M; early and middle Cenomanian, Sinai.

2013 *Cisalveolina fallax* – Al-Dulaimi et al., fig. 10 (2); late Cenomanian, southern Iraq.

2014 *Simplalveolina simplex* (Reichel, 1936) – Afghah & Fadaei, figs. 7d; early, middle and late Cenomanian, Iranian Zagros [age distribution poorly constrained].

2014 *Ovalveolina crassa* (d'Orbigny, 1850) (sic) - Afghah & Fadaei, figs. 7f; early, middle and late Cenomanian, Iranian Zagros [age distribution poorly constrained].

Non 2014 *Cisalveolina frassi* (sic) – Afghah & Fadaei, fig. 7e; early, middle and late Cenomanian, Iranian

Zagros [probably *Simplalveolina simplex* (Reichel, 1936)] [age distribution poorly constrained].
? 2014 *Ovalveolina sp.* – Afghah et al., fig. 10A; early Cenomanian, Iranian Zagros.
Non 2014 *Cisalveolina frassi* (sic) – Afghah et al., fig. 9A; middle Cenomanian, Iranian Zagros [= *S. simplex*].
2015 *Cisalveolina fraasi* – Frijia et al., fig. 7F-G; late Cenomanian (middle part of the *Metoicoceras geslinianum* ammonite zone), central Italy (see also Parente et al., 2008).
2015 *Cisalveolina fallax* – Awadeesian et al., pl. 20 (1-2); undifferentiated middle - late Cenomanian, southern Iraq.
2016 *Praealveolina tenuis* Reichel, 1933 – Assadi et al., fig. 6-14; undifferentiated Cenomanian, Iranian Zagros.
? 2016 *Ovalveolina ovum* (d'Orbigny, 1850) – Assadi et al., fig. 6 a12; undifferentiated Cenomanian, Iranian Zagros.
? 2016 *Cisalveolina fallax* – Kazemzadeh & Loftpoor, plate numbers in Persian; undifferentiated Cenomanian, Iranian Zagros.
? 2016 *Cisalveolina fallax* – Rikhtegarzadeh et al., pl. 2, fig. 4; late Cenomanian, Iranian Zagros.
Non 2016 *Cisalveolina fraasi* – Hart, fig. 10D; undifferentiated Cenomanian, Oman Mountains [= *Alveocella* sp.].
Non 2016 *Cisalveolina fallax* – Assadi et al., fig. 6 a13; undifferentiated Cenomanian, Iranian Zagros [= *C. lehneri*].
2017 *Oalveolina ovum* (sic) – Rikhtegarzadeh et al., pl. 1, fig. 5; undifferentiated Cenomanian, Iranian Zagros
Non 2018 *Cisalveolina* sp. – Boudagher-Fadel, pl. 5.22, figs. 3-4; undifferentiated Cenomanian, India [probably *Ovalveolina* sp.].
? 2019 *Cisalveolina* sp. – Saeedi Razavi et al., pl. 1 [figures numerated in Persian]; undifferentiated Cenomanian, Iranian Zagros [but see unlabelled image in pl. 2 for a clear *Cisalveolina*].
2020 *Cisalveolina fraasi* – Schlagintweit & Yazdi-Moghadam, fig. 3I; late Cenomanian, Iranian Zagros.
2020 *Cisalveolina fraasi* – Yazdi-Moghadam & Schlagintweit, fig. 2G [miscaptioned as 2H]; late Cenomanian, Iranian Zagros.
? 2020 *Cisalveolina* sp. – Ezampanah et al., fig. 7C; late Cenomanian, Iranian Zagros
Non 2020 *Cisalveolina* sp. – Handhal et al., figs. 6b, 7a, 8d, 9c-d; late Cenomanian, southern Iraq [no specimems illustrated are compatable with any species of *Cisalveolina*, 6b might be *Simplalveolina simplex,* others are indeterminate].
2021 *Cisalveolina fraasi* – Schlagintweit & Yazdi-Moghadam, fig. 2H; late Cenomanian, Iranian Zagros.
2021 *Cisalveolina fraasi* – Yazdi-Moghadam & Schlagintweit, fig. 2J; late Cenomanian, Iranian Zagros.
? 2021a *Cisalveolina fraasi* – Dousti-Mohajer et al., pl. 2h; late Cenomanian, Iranian Zagros
? 2021 *Cisalveolina* sp. – Brčić et al., fig. 9(g-h); late Cenomanian, Croatia [see Velić (2007) for unillustrated discussion of range of *C. fraasi* within the late Cenomanian of Croatia].
Non 2021b *Cisalveolina fraasi* – Dousti-Mohajer et al., figs. 8h, 9f; Cenomanian, Iranian Zagros [probably = *C. nakharensis* Piuz et al., *fide* Consorti & Vicedo, 2022].
2022 *Cisalveolina fraasi* – Schlagintweit & Yazdi-Moghadam, fig. 2B; late Cenomanian, Iranian Zagros.
? 2022 *Cisalveolina fallax* – Asghari et al., pl. 1, fig. c; late Cenomanian, Iranian Zagros [poorly preserved specimen].
? 2022 *Cisalveolina* sp. – Al-Dulaimy et al., pl. 3E; late Cenomanian, southern Iraq.
Non 2022b *Cisalveolina fraasi* – Dousti-Mohajer et al., fig. 4f; late Cenomanian, Iranian Zagros [probably = *C. nakharensis* Piuz et al. – same illustration as Dousti-Mohajer et al., 2021b, fig. 9f].
2023 *Cisalveolina fraasi* – Schlagintweit et al., fig. 3i; late Cenomanian, Iranian Zagros.
2023 *Cisalveolina fraasi* – Steuber et al., fig. 4C; late Cenomanian, southern Italy.
2023 *Cisalveolina fraasi* – Fabbi et al., fig. 11f; undifferentiated Cenomanian, Central Apennines, Italy.
? 2023 *Cisalveilina* (sic.) *fraasi* – Shakir & Mousa, pl. 1, fig. R; early Cenomanian, central Iraq [an alveolinoid, but unlikely to be *Cisalveolina*].
? 2023a *Ovalveolina ovum* (d'Orbigny) – Mehrabi et al., fig. 6 D, E; undifferentiated Cenomanian, Iranian Zagros.
? 2023 *Cisalveolina frassi* (sic) – Al-Salihi & Ibrahim, pl. 3A; undifferentiated Cenomanian, southern Iraq.
? 2023 *Cisalveolina lehneri* – Al-Salihi & Ibrahim, pl. 3E; undifferentiated Cenomanian, southern Iraq.
2024 *Cisalveolina fraasi* – Sabouhi et al., fig. 6b; late Cenomanian, Iranian Zagros.
2024 *Cisalveolina frassi* (sic) – Moghaddam et al., fig. 2b; undifferentiated Cenomanian, Iranian Zagros.
? 2024 *Cisalveolina fraasi* – Lazim et al., fig. 2D; undifferentiated Cenomanian – early Turonian [most likely late Cenomanian, Bromhead et al., 2022], southern Iraq.
? 2026 *Cisalveolina* cf. *fraasi* – Schlagintweit & Yazdi-Moghadam, p. 261, pl. 4, figs. 9-10; near middle/late Cenomanian boundary, Iranian Zagros.
2026 *Cisalveolina fraasi* – Schlagintweit et al., pl. 4, figs. 4-5; late Cenomanian, Iranian Zagros.

Reference Images: Schroeder & Neumann (1985), p. 130, pls. 64-65; De Castro (1988), pl. 5, figs. 1-7.

Taxonomy/Identity: This species has a slightly convoluted taxonomic history. First reported in the literature as *Nummulites cretacea* by Fraas (1867), this name was recognised as a homonym by Gümbel (1872) who renamed the taxon (with recognition that it was unrelated to *Nummulites*) as *Alveolina fraasi*. Reichel (1941) introduced *Cisalveolina fallax* which he thought was distinct from *A. fraasi*, the identity of which he was unclear of, but in 1947 considered a possible but highly uncertain synonymy with *Multispirina iranensis* or some species of *Praealveolina*. Schroeder (1971) re-examined the types of *Nummulites cretacea* Fraas (= *Alveolina* *fraasi*) and near-topotypes and confirmed the synonymy with *Cisalveolina fallax*. He considered *N. cretacea* and *A. fraasi nomen oblitum* and retained *C. fallax* as the valid name. However, Urlichs (1972) argued that *A. fraasi* was a valid name and thus the senior synonym of *C. fallax*. Since then, most workers have used the name *Cisalveolina fraasi* as the valid name for the species previously described as *C. fallax* (e.g. Cherchi & Schroeder, 1975a), although occasional use of *C. fallax* still persists (e.g. Al-Salihi & Ibrahim, 2023).

Of the three recognised *Cisalveolina* species, *C. fraasi* is the largest species and is the most spherical/subspherical in overall shape. It differs from *C. lehneri* by having a quite reduced streptospiral initial stage and therefore achieves stable planispiral coiling early in the adult. *C. nakharensis* also has a relatively small streptospiral stage but has a more evident compressed axial profile, rather than being globular.

Ovalveolina ovum (d'Orbigny) is similar although the septulae do not alternate position between chambers. *O. ovum* lacks a post-septal canal and the early streptospiral stage.

Confident Stratigraphic Range: undifferentiated late Cenomanian (common).

Uncertain Stratigraphic Range: not applicable.

Historically, the stratigraphic range of this species has carried some uncertainty (i.e. restricted to or ranging into the early Turonian) because of uncertainties in the age of the type material of both *A. fraasi* and *C. fallax*. For example, Reichel (1941) stated that although the rocks from the type section of *C. fallax* were assigned to the Cenomanian, the associated microfauna suggested they could also conceivably be Turonian. Possible uncertainty persisted with the recognition of this species in "Turonian" strata of Italy (Sartoni & Crescenti, 1962), although by 1964 these occurrences were regarded as late Cenomanian (Reichel in Azzaroli & Reichel, 1964; Devoto, 1964). The notion of a Turonian age was revived by Saint-Marc (1970, 1974, 1981) who considered the species as occurring in the early Turonian in Lebanon. However, the placement of the Cenomanian/Turonian boundary in Lebanon is now considered to be above the position of *Cisalveolina fraasi* (see Simmons & Bidgood, 2023). Nonetheless the notion of *C. fraasi* (and its synonym *C. fallax*) as a Turonian species persisted until at least the synthesis publication and range chart of Arnaud et al. (1981).

De Castro (1983) comprehensively reviewed the range of *C. fraasi* and considered it to be intra-late Cenomanian, a view retained by Schroeder and Neumann (1985) and De Castro (1988) and most workers subsequently. Parente et al. (2007) and Frijia et al. (2015) used carbon and strontium isotopes to restrict the species to a very short range within the *Metoicoceras geslinianum* Zone of the late Cenomanian of some sections in southern Italy. It is unclear if this range is so restricted in other localities where the species occurs (e.g. on the Arabian Plate). For example, Schlagintweit et al. (2026) and other authors have noted that the species occurs over a large part of the upper Sarvak Formation in the Iranian Zagros. Although not precisely biostratigraphically calibrated this evidence suggests a longer range than intra-*Metoicoceras geslinianum* Zone, although still late Cenomanian. Local range of this species will be highly facies-dependent. Without explanation, Hardenbol et al. (1988) show the species as ranging throughout the late Cenomanian except the very earliest. Until more calibrated records such as those of Frijia et al. (2015) become available, the best that can be said about the range of the species is that it is simply "late Cenomanian". Future work may confirm a global extinction within the *M. geslinianum* Zone perhaps associated with paleoclimate and paleoceanographic changes around the onset of Oceanic Anoxic Event 2.

Illustrated records older than late Cenomanian are either dubious concerning the identity of specimens described or dubious regarding age calibration or both (e.g. Orabi et al., 2012; Afghah & Fadaei, 2014; Afghah et al., 2014; Shakir & Mousa, 2023). El Beialy & Al-Hitimi (1994) report the species (unillustrated) from the Ahmadi Formation of subsurface Qatar which is middle Cenomanian (Bromhead et al., 2022). We have observed specimens of *Cisalveolina* in the subsurface of the Iranian Zagros that have the globular morphology of *C. fraasi* but are smaller in dimensions than true *C. fraasi* (Schlagintweit & Yazdi-Moghadam, 2026 illustrate a possible example). These may be ancestral forms, or possibly another species (see illustration of an undetermined alveolinoid by Deville de Periere et al. (2026) (their fig. 3M). They are associated with a microfossil assemblage that is, pending further research, best considered middle Cenomanian. Nonetheless, in summary, it is not believed that *C. fraasi* occurs before or after the late Cenomanian.

Geographic Distribution: Known from Italy, Serbia, Croatia, Sardinia, Greece, Türkiye, Spain, Morocco, Algeria, Egypt, Israel, Lebanon, Iraq, Kuwait and the Iranian Zagros. Records from Iberia are few, although see Berthou (1973) from Portugal and Consorti & Vicedo (2022, based on Schroeder & Neumann, 1985), whilst Petrizzo et al. (2025) report occurrence in Portugal, but without illustration.

Cherchi & Schroeder (1975b) report the species from the late Cenomanian of Tunisia, but without illustration. Philip et al. (2024) repeats published records from North Africa, including Tunisia.

Recorded but not illustrated from the Cenomanian of Dhofar (southern Oman) (Vicedo & Serra-Kiel, 2011) and Yemen (Beydoun et al., 1998).

Cisalveolina lehneri Reichel, 1941
FIGURE 17

T 1941 *Cisalveolina lehneri* n. sp. - Reichel, p. 257, pl. 1, figs. 4-6; undifferentiated Cenomanian, Iranian Zagros.

1947 *Cisalveolina lehneri* – Reichel, pl. 2, fig. 1; undifferentiated Cenomanian, Iranian Zagros [co-occurs with *Multispirina iranensis* Reichel, 1947, suggesting late Cenomanian age].
? 1961 *Cisalveolina fallax* – Hamaoui, p. 17, pl. 3, fig. 1; pl. 9, figs. 26-27; pl. 10, figs. 1-3; undifferentiated Cenomanian – Turonian [most likely late Cenomanian], Israel.
1964 *Cisalveolina lehneri* – Devoto, p. 407, pl. 1, figs. 2, 5, 7; intra-late Cenomanian, southern Italy.
1965 *Cisalveolina lehneri* – Paradisi & Sirna, text-fig. 2; late Cenomanian, Italy.
1965 *Cisalveolina fallax*– Farinacci, fig. 5; late Cenomanian, southern Italy.
1965 *Cisalveolina lehneri* – Farinacci, fig. 5; late Cenomanian, southern Italy.
? 1965 *Cisalveolina fallax*– De Castro, p. 359, pls. 20-21; late Cenomanian, southern Italy.
1966 *Cisalveolina lehneri* – Angelucci & Devoto, text-fig. 5; late Cenomanian, Italy.
1966 *Rabanitina* cf. *basraensis* Smout – Luperto Sinni, pl. 9, figs. 3-4; undifferentiated Cenomanian, southern Italy.
1967 *Cisalveolina lehneri* – De Castro in Bosi & Manfredini, p. 258, pl. 4, fig. 2; late Cenomanian, Italy.
? 1969 *Cisalveolina lehneri* – Sampò, pl. 47, fig. 1; undifferentiated Cenomanian, Iranian Zagros [partial specimen].
? 1969 *Cisalveolina fallax* – Sampò, pl. 43, fig. 6; pl. 46, fig. 1; undifferentiated Cenomanian, Iranian Zagros.
1977 *Cisalveolina lehneri* – Chiocchini & Mancinelli, p. 140, pl. 35, fig. 2; middle – late Cenomanian transition, central-southern Italy.
1980 *Cisalveolina lehneri* – Fleury, p. 481, pl. 2, figs. 6-9; late Cenomanian, Greece.
1985 *Cisalveolina lehneri* – De Castro in Schroeder & Neumann, p. 123, pl. 63, figs. 1-9; text-fig. 15; middle – lower late Cenomanian, global review [range chart mistakenly labelled *Cisalveolina fraasi* (oldest of two occurrences)].
Non 1992 *Cisalveolina lehneri* – Kalantari, pl. 75, undifferentiated Cenomanian, Iranian Zagros [= *C. fraasi*].
1994 *Cisalveolina lehneri* – Chiocchini et al., pl. 17, figs. 9-13; middle Cenomanian, central-southern Italy.
2009 *Cisalveolina lehneri* – Sari et al., pl. 1, figs. 1-3; middle Cenomanian, Turkish Taurides [middle Cenomanian age is based on the presence of *C. lehneri*].
2012 *Cisalveolina lehneri* – Chiocchini et al., pl. 88, fig. 1; pl. 90, fig. 1; pl. 91, figs. 1-7; pl. 95, fig. 1; pl. 96, fig. 1; pl. 97, fig. 1; pl. 98, fig. 1; pl. 99, fig. 1; pl. 100, fig. 1; pl. 102, fig. 1; middle Cenomanian, southern Italy [authors use only a two-fold subdivision of the Cenomanian, range chart would suggest an approximate middle Cenomanian position].
Non 2012 *Cisalveolina* cf. *lehneri* – Orabi et al., fig. 3J; undifferentiated Cenomanian, Sinai, Egypt [specimen is effectively indeterminate].
2016 *Cisalveolina fallax* – Assadi et al., fig. 6 a13; undifferentiated Cenomanian, Iranian Zagros.
2016 *Cisalveolina* cf. *lehneri* – Consorti et al., fig. 4c; undifferentiated Cenomanian, Iberian Ranges, Spain.
? 2016 *Cisalveolina lehneri* – Rikhtegarzadeh et al., pl. 2, figs. 7-8; undifferentiated Cenomanian, Iranian Zagros.
2018 *Cisalveolina lehneri* – BouDagher-Fadel, pl. 5.22, fig. 14; middle Cretaceous, Qatar [record is said to be from Khatiyah Formation which is middle Cenomanian – Bromhead et al., 2022].
2019 *Cisalveolina lehneri* – Parnian et al., fig. 3G (3C in uncertain); middle Cenomanian; Iranian Zagros.
? 2021a *Cisalveolina lehneri* – Dousti-Mohajer et al., pl. 2, fig. g; late Cenomanian, Iranian Zagros.
? 2021b *Cisalveolina lehneri* – Dousti Mohajer et al., fig. 7a; fig. 8g; late Cenomanian, Iranian Zagros.
Non 2021 *Cisalveolina lehneri* – BouDagher-Fadel & Price, pl. 2 figs. C, f; undifferentiated Cenomanian, India [= *Ovalveolina* sp.].
Non 2022 *Cisalveolina lehneri* – Asghari et al., pl. 1, fig. D; late Cenomanian, Iranian Zagros [possibly *C. fraasi*].
2023 *Cisalveolina lehneri* – Fabbi et al., fig. 11e; undifferentiated Cenomanian, Central Apennines, Italy.
? 2023 *Cisalveolina lehneri* – Al-Salihi & Ibrahim, pl. 3E; undifferentiated Cenomanian, southern Iraq [probably *C. fraasi*].
? 2026 *Cisalveolina* cf. *lehneri* – Schlagintweit & Yazdi-Moghadam, p. 261, pl. 4, figs. 11-12; middle Cenomanian, Iranian Zagros.

Reference Images: De Castro in Schroeder & Neumann (1985), p. 123, pl. 63, figs. 1-9; text-fig. 15.

Taxonomy/Identity: *C. lehneri* differs from *C. fraasi* by being more axially compressed (described by Reichel as being the shape of "*Nautilus*"; p. 259) and by having a larger streptospiral stage compared with *C. fraasi*. Individual chambers are longer (in equatorial view) and higher (in equatorial and axial views) that *C. fraasi*.

Confident Stratigraphic Range: intra-middle Cenomanian – intra-late Cenomanian (common)

Uncertain Stratigraphic Range: late Albian – early middle Cenomanian

First described from the undifferentiated Cenomanian of Iran by Reichel (1941). The subsequent interpretation of the stratigraphic range of *C. lehneri* has varied between authors and somewhat dependent on locality. Italian authors (e.g. Devoto, 1964) initially regarded it as a late Cenomanian species. Possible co-occurrence with *C. fallax* (= *C. fraasi*) was suggested by some (e.g. Farinacci, 1965) but can be discounted. More recent views have placed *C. lehneri* in the middle Cenomanian (Chiocchini et al., 2012) or middle Cenomanian to early late Cenomanian (De Castro in Schroeder & Neumann, 1985). Velić (2007) argues that this is an important species for recognising the late early Cenomanian in the Adriatic Platform of Croatia but also reports it from the basal middle Cenomanian. In either case this would appear to be a unique and unusual interpretation, possibly

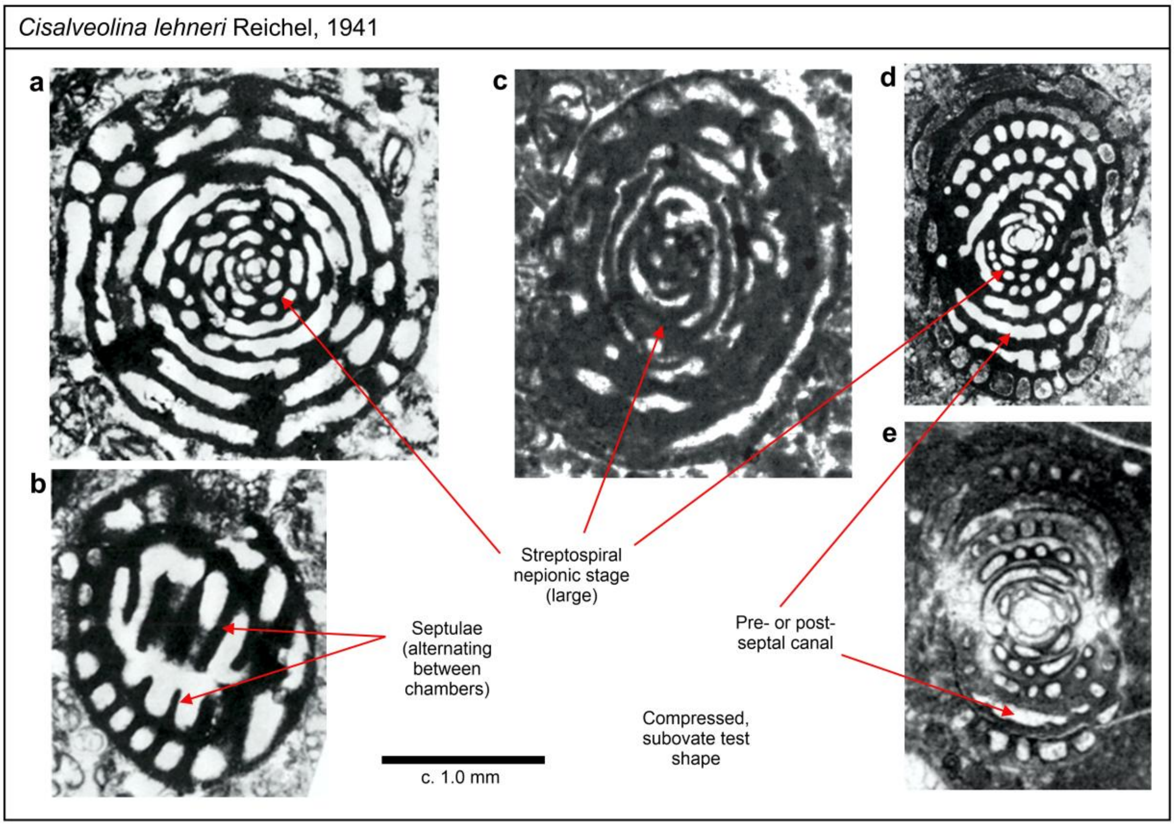


Fig. 17: Representative illustrations of *Cisalveolina lehneri*: **a.** Equatorial section, Schroeder & Neumann (1985, pl. 63, fig. 7; middle Cenomanian, Italy); **b.** Tangential section, Schroeder & Neumann (1985, pl. 63, fig. 6; middle Cenomanian, Italy); **c.** Oblique equatorial section, (Consorti, personal collection, Central Apennines, Italy. Locality of Fabbi et al., 2023); **d.** Axial section, Schroeder & Neumann (1985, pl. 63, fig. 1; middle Cenomanian, Italy); **e.** Axial section, Reichel (1941, pl. 15, fig. 4; Cenomanian, Iran).

the result of the misidentification of other alveolinoid taxa. No illustrations are provided. De Castro (1988) in a short review of the species and in contrast to his 1985 review in Schroeder & Neumann suggested the range could be latest Albian – middle Cenomanian in Italy and occurs in the late Cenomanian outside of Italy (e.g. the Middle East – although middle Cenomanian records are known from there too (e.g. Parnian et al., 2019), although not well age constrained. Zambetakis-Lekkas et al. (2006) without illustration recognise this species in the late Cenomanian of Greece.

In summary, this species is considered to be intra-middle Cenomanian – intra-late Cenomanian in range, with limited overlap with the range of *C. fraasi*. Older or younger range assessments are considered speculative.

Geographic Distribution: Recorded principally from the Arabian Plate (especially the Iranian Zagros and Qatar) and Italy as well as Israel, although some intermediate records are known (e.g. Greece and the Turkish Taurides). As yet, there are no confirmed records from North Africa, only one record from Spain (Consorti et al., 2016) and an uncertain record from Iraq.

***Cisalveolina nakharensis* Piuz et al., 2014**
FIGURE 18

? 1990 *Cisalveolina* sp. A – Smith et al., fig. 6a middle Cenomanian [now considered late early Cenomanian – Bromhead et al., 2022], Oman Mountains.

T 2014 *Cisalveolina nakharensis* n. sp. - Piuz et al., p. 350, figs. 8-9; early middle Cenomanian (now considered late early Cenomanian – Bromhead et al., 2022), Oman Mountains.

2021b *Cisalveolina fraasi* (Gümbel) – Dousti-Mohajer et al., figs. 8h, 9f; late Cenomanian [age may be based on the assumed identification of *C. fraasi*], Iranian Zagros.

2022b *Cisalveolina fraasi* – Dousti-Mohajer et al., fig. 4f; late Cenomanian (age may be based on the assumed identification of *C. fraasi*), Iranian Zagros [same illustration as Dousti-Mohajer et al., 2021b, fig. 9f].

Reference Images: Piuz et al. (2014), p. 350, figs. 8-9.

Taxonomy/Identity: *C. nakharensis* is similar to *C. lehneri* in having a rather axially compressed test whereas *C. fraasi* is more globular. *C. nakharensis* is intermediate in size between *C. lehneri* and *C. fraasi* (2.3 mm max diameter compared with 1.9 mm and 2.7 mm respectively). *C. nakharensis* has a less-well developed early streptospiral stage than *C. lehneri*, which affects only the first two whorls (in which respect it is similar to *C. fraasi*). The proloculus is also intermediate in size between *C. lehneri* and *C. fraasi* (i.e. 150-200 µm). 7-8 whorls are present.

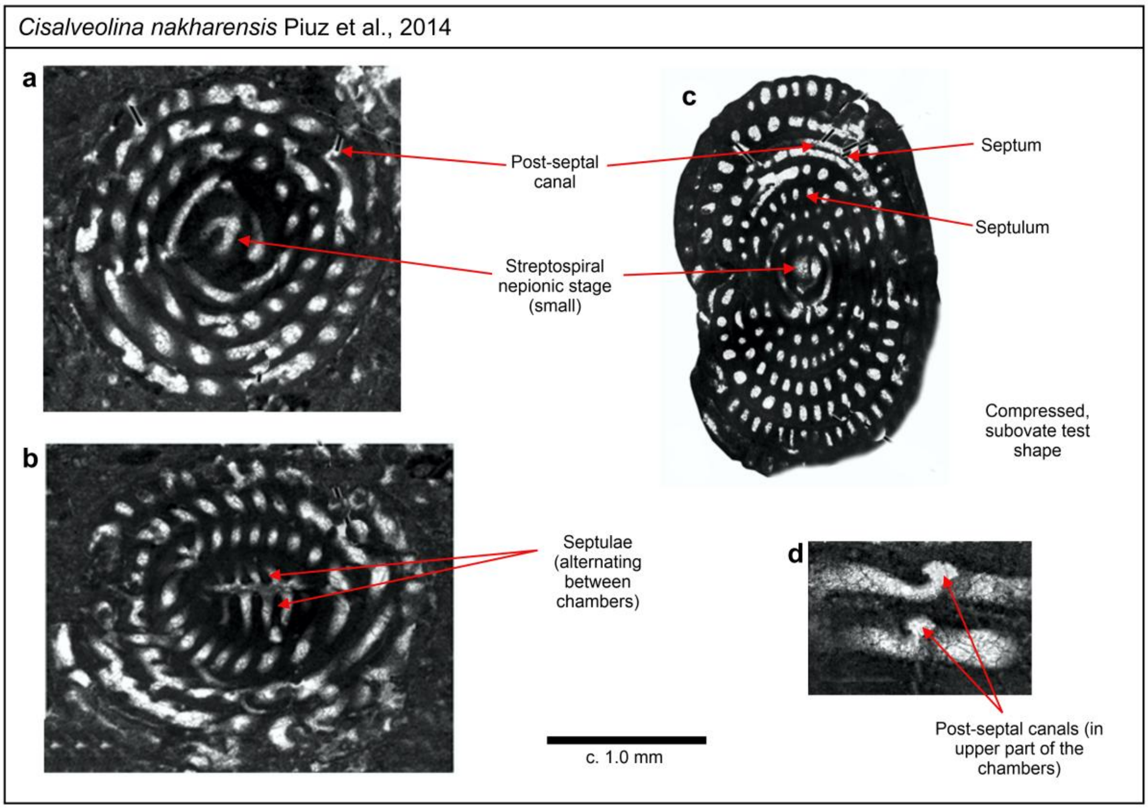


Fig. 18: Representative illustrations of *Cisalveolina nakharensis*: **a.** Equatorial section, Piuz et al. (2014, fig. 9(4)); **b.** Tangential section, Piuz et al. (2014, fig. 9(13)); **c.** Axial section, Piuz et al. (2014, fig. 8(6)); **d.** Enlargement of equatorial view, Piuz et al. (2014, fig. 9(7)). All specimens early middle Cenomanian (now considered late early Cenomanian – Bromhead et al., 2022), Oman Mountains.

Confident Stratigraphic Range: late early Cenomanian

Uncertain Stratigraphic Range: late Cenomanian

Piuz et al. (2014) described this species from the upper part of the Natih Formation (E Member) of Oman and assigned an early middle Cenomanian age. Bromhead et al. (2022) revised the age of this unit to late early Cenomanian based on a synthesis of all chronostratigraphic calibration. Smith et al. (1990) had probably already illustrated this species from similar localities and rock units. We have observed forms similar to this species in the late Cenomanian of the Iranian Zagros, research is ongoing.

Geographic Distribution: So far only recorded from the Arabian Plate (Iranian Zagros and Oman).

Genus ***Decastroia*** Vicedo & Serra-Kiel 2011 emended Vicedo & Piuz 2016

The exclusively Cenomanian genus *Decastroia* was defined by Vicedo & Serra-Kiel (2011), and emended by Vicedo & Piuz (2016), with *Decastroia razini* as the type species, from Cenomanian sediments of Socotra Island (Yemen) between the Gulf of Aden and the Arabian Sea. Three more species; *Decastroia serrakieli*, *Decastroia oblonga* and *Decastroia miaidinensis*, were added to the genus inventory by Vicedo & Piuz (2016), described from the assumed middle, or middle – lower late Cenomanian of the Natih Formation of Oman (see discussion of those species below).

Decastroia is a subglobular to axially-elongate genus extremely similar to *Praealveolina* except having two layers of chamberlets (an upper 'cortical' and lower, and smaller, 'medullar' layer) in the adult stage which extend from the polar regions of the test towards and across the central/equatorial region. *Praealveolina* only has 2 (or more) layers in polar regions which extend towards, but seldom into, the equatorial zone. See Figure 6 for an illustrated description of the genus.

The type species of *Praealveolina* is *P. tenuis* (not *P. cretacea* as stated by Vicedo & Serra-Kiel, 2011, p. 20). *P. tenuis* never displays equatorial supplementary chamberlets (see description of that species here) and is thus distinct from *D. razini*, the type species of *Decastroia*. *Praealveolina lata* shows a form with row(s) of chamberlets – cortical and medullar – which occur in both polar and equatorial regions (see Figure 19 herein) and is thus transferred herein to *Decastroia*.

Praealveolina cretacea is more problematic. According to Vicedo & Serra-Kiel (2011) who examined topotypes of *P. cretacea* from Île Madame, southwest France: "the supplementary chamberlets of *P. cretacea* appear less regularly [our emphasis] in the equatorial region of the shell than in *Decastroia*." The subjective nature of what constitutes "less regularly" is a possible weakness in the overall criteria that uniquely separates

Decastroia from *Praealveolina*.

Defining characteristics of the five species of *Decastroia* are based on degree of axial elongation, size of the megalosphere, 'tightness' or 'looseness' of the primary coiling, and the dimensions and disposition of the cortical, medullar and (if present) supplementary chamberlets (see Table 3).

Having only been recognised recently, records of *Decastroia* in the literature are few. However, some specimens from Neotethys previously assigned to other species (e.g., some species of *Praealveolina* to which it closely resembles) may be attributable to *Decastroia*. These have been included in the synonymies below and in the discussion of *Praealveolina* species.

Scarcity of proven *Decastroia* records in the literature preclude a comprehensive discussion on the evolution of the genus in the context of (presumably) relationship to *Praealveolina*.

***Decastroia lata* (Reichel, 1936)**
FIGURE 19

T 1936 *Praealveolina cretacea lata* n. subsp., Reichel, p. 58, pl. 5, figs. 9-10; pl. 6, fig. 6; Cenomanian, southern France.
1965 *Praealveolina cretacea* var. *lata* – Gibson & Percival, p. 342, pl. 1, fig. 7; undifferentiated Cenomanian, Somalia
? 1969 *Praealveolina cretacea lata* – Sampò, pl. 43, fig. 5; undifferentiated Cenomanian, Iranian Zagros.
1989 *Praealveolina tenuis* – Kuss & Malchus, text-fig. 25; late Cenomanian, Egypt.
2002 *Praealveolina lata* – Calonge et al., pl. 7, fig. 3; Cenomanian, southern France.

Reference Images: Reichel (1936), p. 58, pl. 5, figs. 9-10; pl. 6, fig. 6.

Taxonomy/Identity: A species with very few records in the literature since first described as *P. cretacea lata* n. subsp. by Reichel (1936) who noted that although locally dominant in some beds, it might only be a variety of *P. tenuis* and that "intermediate forms" were also recorded in those beds.

P. lata was differentiated on the 'looseness' of its planispiral coiling. Reichel (1936) states that the size of the proloculus is intermediate between that of *P. brevis* and *P. tenuis*. It appears to have secondary chamberlets in all regions, from 2 layers in equatorial regions to 5-6 rows in polar regions. This necessitates its transfer from *Praealveolina* to *Decastroia*. Chamberlet density (chamberlets/chamber) is also high.

Confident Stratigraphic Range: not applicable.

Uncertain Stratigraphic Range: undifferentiated Cenomanian (?middle – late Cenomanian?).

There are a limited number of verified records of this species, most of which have poor biostratigraphic calibration, although the record of Kuss & Malchus (1989) (as *P. tenuis*) is late Cenomanian. The co-occurrence with *P. tenuis* (Reichel, 1936) hints at a middle – late Cenomanian age.

Geographic Distribution: First described from southern France, there are also records from Egypt, Somalia and possibly the Iranian Zagros.

***Decastroia miaidinensis* Vicedo & Piuz, 2016**
FIGURE 20

1990 *Praealveolina cretacea* – Cherchi & Schroeder, fig. 4; middle – late Cenomanian, Iranian Zagros.
2013 *Praealveolina iberica* – Shahin & Elbaz, pl. 2, fig. 31; undifferentiated Cenomanian, Sinai, Egypt.
T 2016 *Decastroia miaidinensis* sp. nov., Vicedo & Piuz, p. 832, figs. 12-13; middle – early late Cenomanian, Oman Mountains.
2017 *Praealveolina* – Deville de Periere et al., fig. 2D; middle – late Cenomanian, Qatar.

Reference Images: Vicedo & Piuz (2016), p. 832, figs. 12-13.

Taxonomy/Identity: *D. miaidinensis* has the largest megalosphere of the *Decastroia* species, the largest cortical chamberlets diameter and the only species to have supplementary apertures (i.e., in addition to cortical and medullar chambers) in the equatorial region of the test (Vicedo & Piuz, 2016).

The overall shape ranges from subglobular to axially elongate.

Confident Stratigraphic Range: middle to early late Cenomanian.

Uncertain Stratigraphic Range: not applicable.

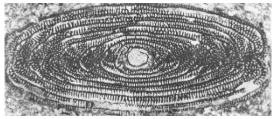
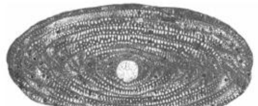
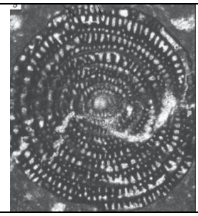
First described from the Natih C and B members in the Oman Mountains (Vicedo & Piuz, 2016), a middle – early late Cenomanian age is interpreted (Vicedo & Piuz, 2016; Bromhead et al., 2022). Sparse records from other parts of Arabia are consistent with this age range.

Geographic Distribution: So far only known from the Arabian Plate.

***Decastroia oblonga* Vicedo & Piuz, 2016**
FIGURE 21

1973 *Praealveolina* (*Praealveolina*) *cretacea* – El-Naggar & Al-Rifaiy, fig. 6(10-11); "very late" Cenomanian, Kuwait.
1973 *Praealveolina* cf. *P.* (*P.*) *tenuis* – El-Naggar & Al-Rifaiy, fig. 6(5); late Cenomanian, Kuwait.
1998 *Praealveolina cretacea* – Whittaker et al., pl. 91, fig. 1; undifferentiated Cenomanian, Qatar.
2004 *Praealveolina cretacea* – Menegatti, pl. 9, figs. 6, 8-9; pl. 10, figs. 1, 2; pl. 13, fig. 3; middle – late Cenomanian, Dubai.
2012 *Praealveolina cretacea* – Orabi et al., fig. 3 (C, F); late Cenomanian, Sinai, Egypt.
2014 *Praealveolina tenuis* – Shahin & Elbaz, figs. 11(9); middle Cenomanian, Sinai, Egypt.

Table 3. Characteristics of *Decastroia* species herein shown in alphabetical order left to right. (meg = Megalospheric form; mic = Microspheric form).

CHARACTERISTIC	*D. LATA*	*D. MIAIDINENSIS*	*D. OBLONGA*	*D. RAZINI*	*D. SERRAKIELI*
Original description & provenance	As *P. cretacea* var. *lata* Reichel (1936 ☼), Cenomanian, France	Vicedo & Piuz (2016, ☼), middle – lower late Cenomanian, Oman	Vicedo & Piuz (2016, ☼), middle Cenomanian, Oman	Vicedo & Serra-Kiel. (2011, ☼), Cenomanian, Yemen	Vicedo & Piuz (2016, ☼), middle Cenomanian, Oman
Basic image (Reference source of image shown thus ☼. All images are holotypes and are not to scale.)					
Other significant illustrative descriptions			Simmons et al. (2020)	Vicedo & Piuz (2016)	
General test shape	Axially elongated	Subglobular to elongate (holotype shown is exceptionally elongate)	Axially elongated	Subglobular to slightly elongate	Axially elongate
Proloculus diameter µm ($_{meg}$ unless stated otherwise)	400-500 (***) / 430-510 (****)	375-500	200-275 $_{meg}$ / 500 $_{mic}$	120-270*	130-230
Max. axial diameter (mm)	6.15 $_{meg}$ (***) / 5.9-6.1 $_{meg}$ (****)	3.1 $_{meg}$ / 4.0 $_{mic}$	3.25 $_{meg}$ / 25.0 $_{mic}$	3.1 $_{meg}$ / >4.0 $_{mic}$	2.7 $_{meg}$ / 6.0 $_{mic}$
Elongation Index	2.5 $_{meg}$ (***) / 2.5-2.6 $_{meg}$ (****)	1.8 $_{meg \& mic}$	2.2 $_{meg}$ / 4.3 $_{mic}$	1.8**	2.0-2.5 $_{meg}$
Whorls (nepionic stage)		0.5-1 $_{meg}$	2-3 $_{meg}$ / 6-7 $_{mic}$	3-4 $_{meg}$ / 6-7 $_{mic}$	2-4 $_{meg}$
Whorls (ephebic stage)	8-10 $_{meg}$ (****)	5-6 $_{meg}$	5-6 $_{meg}$ / 25 $_{mic}$ rather loosely-coiled	3-5 $_{meg}$ / 8-9 $_{mic}$	4-6 $_{meg}$ / 16*** $_{mic}$ tightly-coiled
Cortical chamberlets (axial diameters in µm)	Circular (***), Cellars, 5-6 rows, α<90 (****)	Subcircular to ovoid; 35-37 µm	Subcircular in section, 20-25 µm	18-24 per chamber; circular to sub-rectangular	40-50 per chamber; c. 22 µm
Medullar & supplementary chamberlets	(no info)	Appear early in ontogeny (2^{nd} whorl). Supp. chamberlets occur in equatorial region	Appear after 2-3 whorls. Supp. chamberlets may occur towards equatorial region	Appear after 3-4 whorls (after 7-8 in microspheric forms)	Appear early in ontogeny (2^{nd} whorl)
Comments	Apertures: 2-3 rows (***) / 2 rows (****) (*** Reichel, 1933, 1936-7) (**** Calonge et al., 2002)		Strongly dimorphic	* in Vicedo & Piuz (2016; table 2), 375-500 µm is shown but this seems to be an error and contradicts Vicedo & Serra-Kiel (2011) and in the text (p. 831) ** this seems to be unusually large for a form that is described consistently as 'subglobular' Specimens from Oman are slightly more elongate than those from Yemen	*** in Vicedo & Piuz (2016), 6 is shown in table 2, 16 in text (p.826)

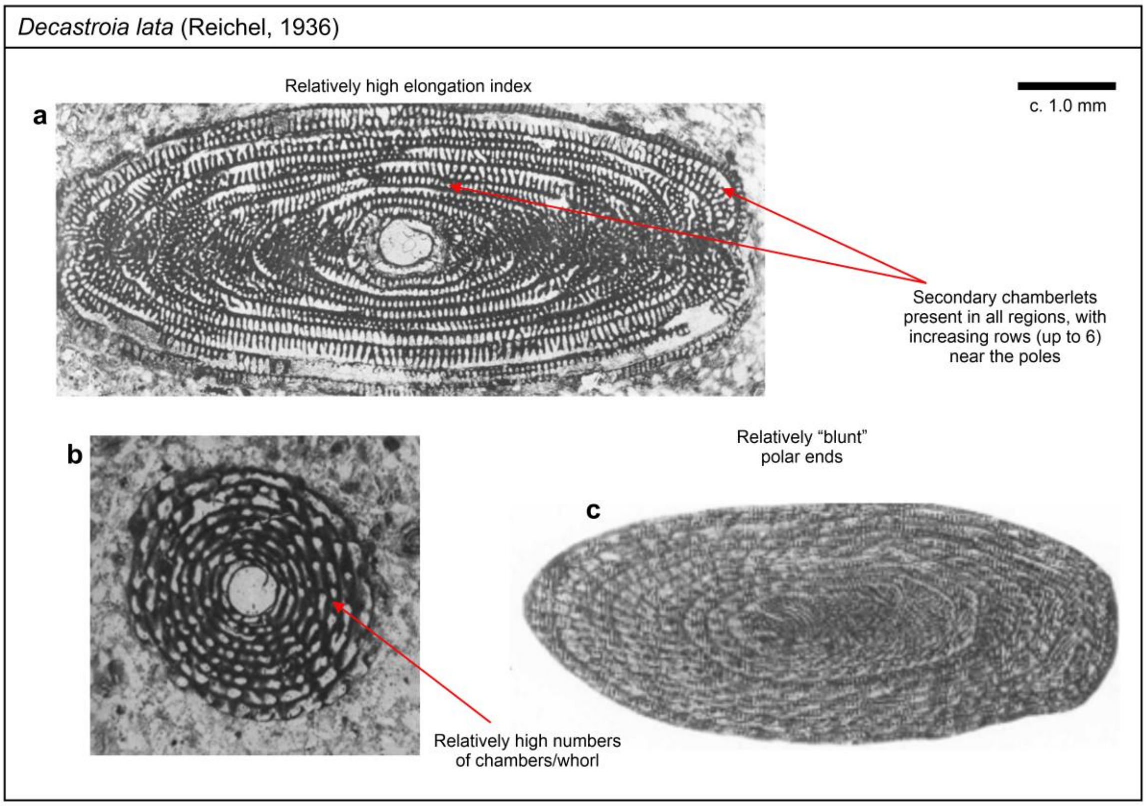


Fig. 19: Representative illustrations of *Decastroia lata*: **a.** Axial section, holotype (refigured by Calonge et al., 2002), Reichel (1936, pl. 6, fig. 6; undifferentiated Cenomanian, southern France); **b.** Equatorial section (image inverted from original), Reichel (1936, pl. 5, fig. 9; undifferentiated Cenomanian, southern France); **c.** Near axial section, Gibson & Percival (1965, pl. 1, fig. 7; undifferentiated Cenomanian, Somalia).

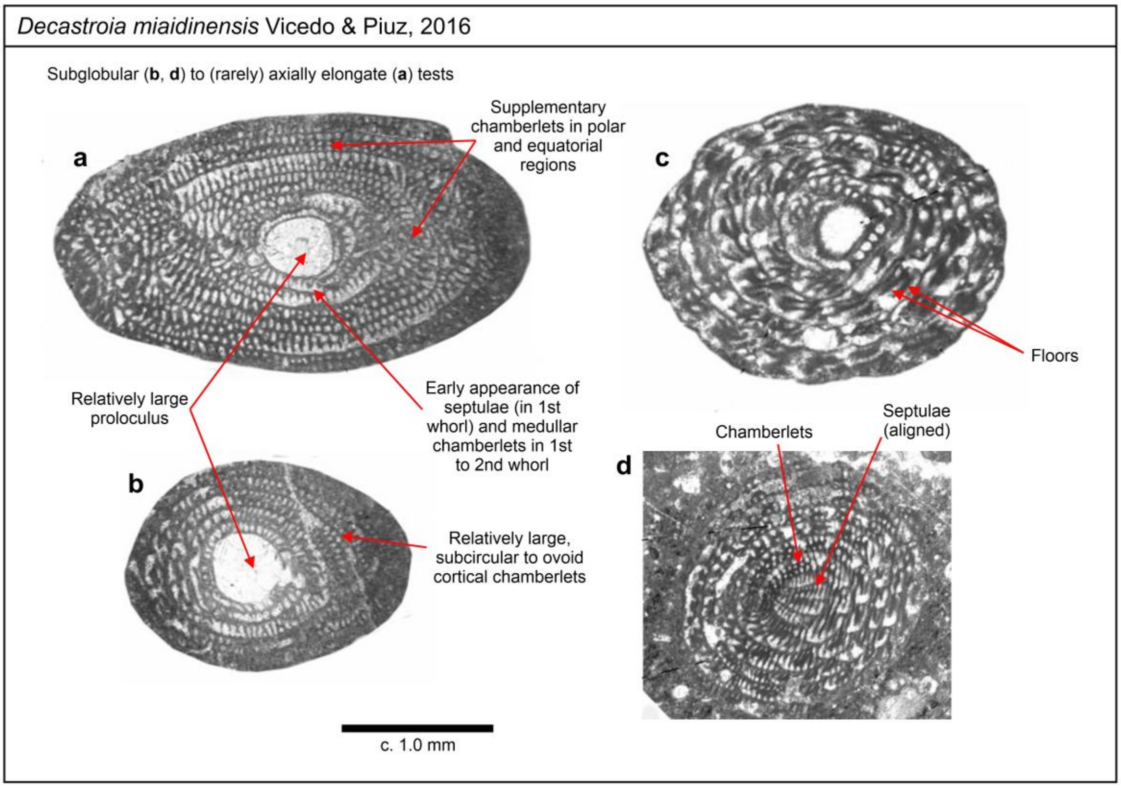


Fig. 20: Representative illustrations of *Decastroia miaidinensis*: **a.** Axial section (holotype), Vicedo & Piuz (2016, fig. 12B; middle – early late Cenomanian, Oman); **b.** Axial, slightly oblique section, Vicedo & Piuz (2016, fig. 12C; middle – early late Cenomanian, Oman); **c.** Oblique near equatorial section, Vicedo & Piuz (2016, fig. 13B; middle Cenomanian, Oman); **d.** Tangential section, Vicedo & Piuz (2016, fig. 13L; middle Cenomanian, Oman).

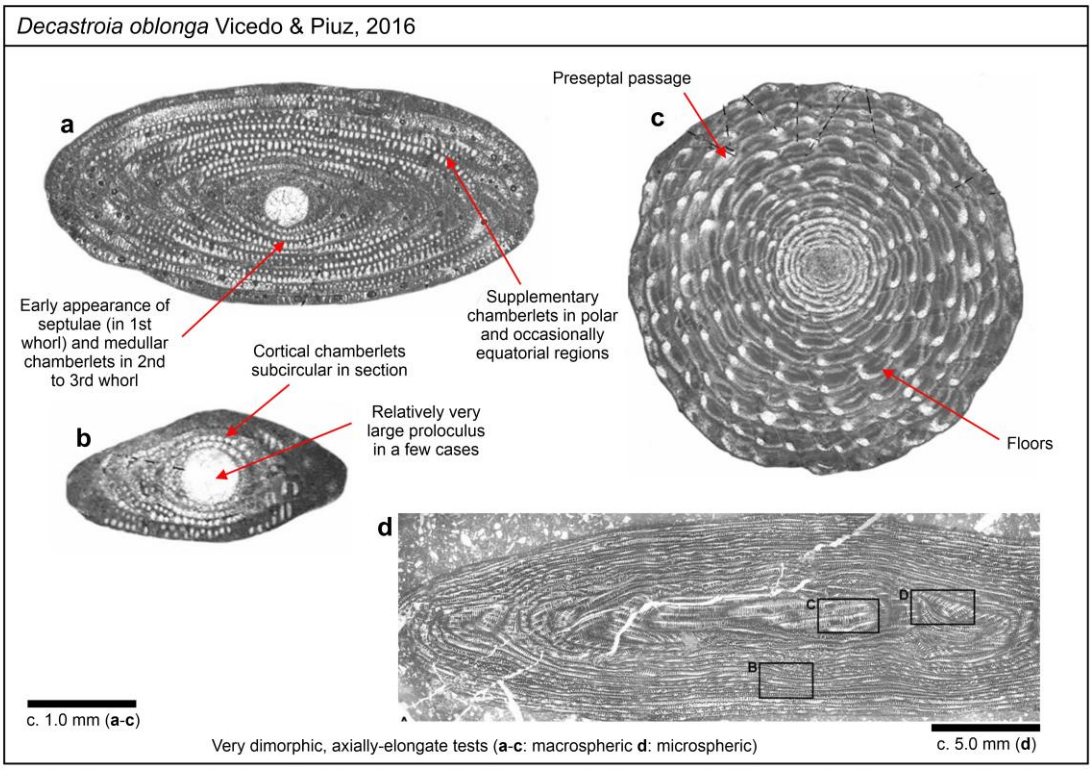


Fig. 21: Representative illustrations of *Decastroia oblonga*: **a.** Axial section (holotype), Vicedo & Piuz (2016, fig. 6A; middle Cenomanian, Oman); **b.** Axial section, Vicedo & Piuz (2016, fig. 6E; middle Cenomanian, Oman); **c.** Subequatorial section, Vicedo & Piuz (2016, fig. 6J; middle Cenomanian, Oman); **d.** Subaxial section (microspheric form), Vicedo & Piuz (2016, fig. 7A; middle Cenomanian, Oman; inset areas B, C & D show aligned septula and presence of cortical and medullar chamberlets).

T 2016 *Decastroia oblonga* sp. nov., Vicedo & Piuz, p. 827, figs. 6-10; middle – early late Cenomanian, Oman Mountains.
2020 *Decastroia oblonga* – Simmons et al., fig. 8(3-7); middle Cenomanian, Turkish Arabian Plate.
2022 *Decastroia* - Ge et al., fig. 4D; late Cenomanian, southern Iraq.
2023 *Praealveolina cretacea* – Shakir & Mousa, pl. 1, fig. O; early Cenomanian, central Iraq.

Reference Images: Vicedo & Piuz (2016), p. 827, figs. 6-10.

Taxonomy/Identity: *D. oblonga* is the most axially-elongate of the *Decastroia* species discussed herein and the largest – only slightly for megalospheric forms but markedly so for microspheric forms – which can attain axial lengths of 25 mm. Rare specimens can have a proloculus with diameters up to 500 µm which Vicedo & Piuz (2016) suggests may be linked to a tri-morphic life-cycle.

Confident Stratigraphic Range: middle – late Cenomanian.

Uncertain Stratigraphic Range: early Cenomanian (doubtful).

First described from the Natih C and B members in the Oman Mountains (Vicedo & Piuz, 2016), a middle – early late Cenomanian age is interpreted (Vicedo & Piuz, 2016; Bromhead et al., 2022). Records from elsewhere in Arabia (e.g. from Kuwait as "*Praealveolina cretacea*" - El-Naggar & Al-Rifaiy, 1973) suggest extension into the latest Cenomanian, although precise biostratigraphic calibration is lacking.

The record from the Mauddud Formation of southern Iraq (Shakir & Mousa, 2023) is problematic as this is undoubtedly early Cenomanian (Bromhead et al., 2022) and records of large, complex alveolinoids are typically absent from this interval. The material is from wells and may represent caved cuttings from higher in the well.

Geographic Distribution: So far described only from the Arabian Plate (Kuwait, Qatar, Dubai, central Iraq, Oman Mountains, Sinai (Egypt) and the Turkish part of the Arabian Plate).

Decastroia razini Vicedo & Serra-Kiel, 2011
FIGURE 22

T 2011 *Decastroia razini* gen. nov. & sp. nov., Vicedo & Serra-Kiel, p. 22, figs. 6-8; undifferentiated Cenomanian, Socotra Island, Yemen.
2016 *Decastroia razini* – Vicedo & Piuz – fig. 11 (A-T); middle – early late Cenomanian, Oman Mountains.

Reference Images: Vicedo & Serra-Kiel (2011), p. 22, figs. 6-8; Vicedo & Piuz (2016), p. 829, fig. 11.

Taxonomy/Identity: *D.razini* is the most subglobular

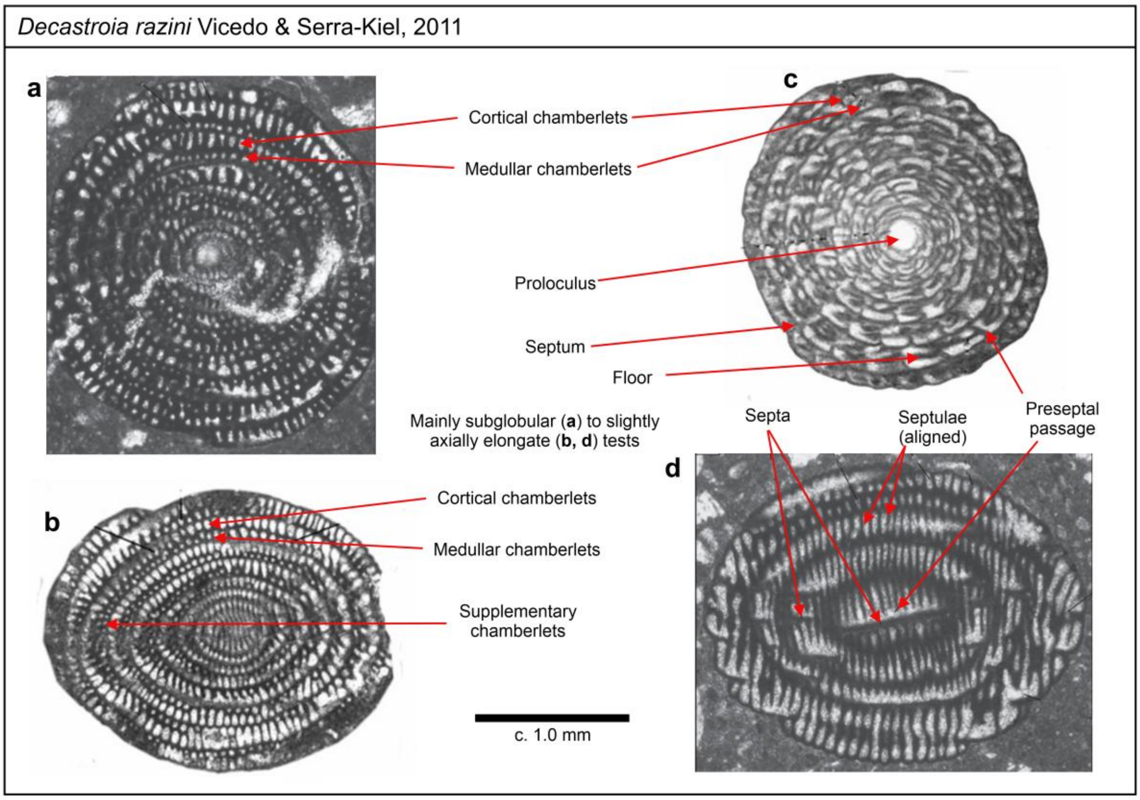


Fig. 22: Representative illustrations of *Decastroia razini*: **a.** Axial section (holotype), Vicedo & Serra-Kiel (2011, fig. 6.9; Cenomanian, Socotra Island, Yemen); **b.** Oblique section, Vicedo & Piuz (2016, fig. 11R; middle Cenomanian, Oman); **c.** Oblique near equatorial section, Vicedo & Piuz (2016, fig. 11E; middle Cenomanian, Oman); **d.** Tangential section, Vicedo & Serra-Kiel (2011, fig. 8.7; Cenomanian, Socotra Island, Yemen).

of the *Decastroia* species and is only slightly axially elongate.

Confident Stratigraphic Range: middle – early late Cenomanian.

Uncertain Stratigraphic Range: not applicable.

First described from the undifferentiated Cenomanian of Socotra Island, Yemen by Vicedo & Serra-Kiel (2011) and subsequently only recorded by Vicedo & Piuz (2016) from the middle – early late Cenomanian of Oman (Bromhead et al., 2022).

Geographic Distribution: So far recorded only from Oman and Socotra Island (Yemen).

***Decastroia serrakieli* Vicedo & Piuz, 2016**
FIGURE 23

1965 *Praealveolina* gr. *P. cretacea* – Hamaoui, pl. 15, fig. 7b; undifferentiated Cenomanian, Israel.
1998 *Praealveolina tenuis* – Whittaker et al., pl. 91, figs. 2-4; undifferentiated Cenomanian, Qatar [states total range in Middle East as middle Cenomanian – middle Turonian although rationale not clear].
T 2016 *Decastroia serrakieli* sp. nov., Vicedo & Piuz, p. 826, figs. 3-5; middle Cenomanian, Oman Mountains.
2018 *Praealveolina cretacea* – Luger, pl. 17, figs. 8-9, 11; middle Cenomanian, Somalia.
2022 *Decastroia* cf. *serrakieli* – Consorti et al., fig. 2H; undifferentiated middle – late Cenomanian, Iranian Zagros.
2022 *Decastroia* cf. *serrakieli* – Yazdi-Moghadam & Schlagintweit, fig. 2H; undifferentiated middle – late Cenomanian, Iranian Zagros.
2023 *Decastroia* cf. *serrakieli* – Schlagintweit & Yazdi-Moghadam, fig. 3H; undifferentiated middle – late Cenomanian, Iranian Zagros.

Reference Images: Vicedo & Piuz (2016), p. 826, figs. 3-5.

Taxonomy/Identity: This species has relatively tightly-coiled whorls. Megalospheric forms are the smallest of the four *Decastroia* species discussed herein, but microspheric forms are relatively the second largest, after *D. oblonga*. Compared to the other axially elongate species (*D. oblonga* and *D. miaidinensis*), the proloculus in *D. serrakieli* is relatively small.

Confident Stratigraphic Range: middle Cenomanian.

Uncertain Stratigraphic Range: late Cenomanian.

First described from the middle Cenomanian of Oman by Vicedo & Piuz (2016) (same age records in Somalia – Luger, 2018), it has been subsequently recorded from the undifferentiated middle – late Cenomanian of the Iranian Zagros, with other records poorly age constrained.

Geographic Distribution: So far recorded only from the Arabian Plate (Qatar, Oman Mountains and Iranian Zagros), Israel and Somalia.

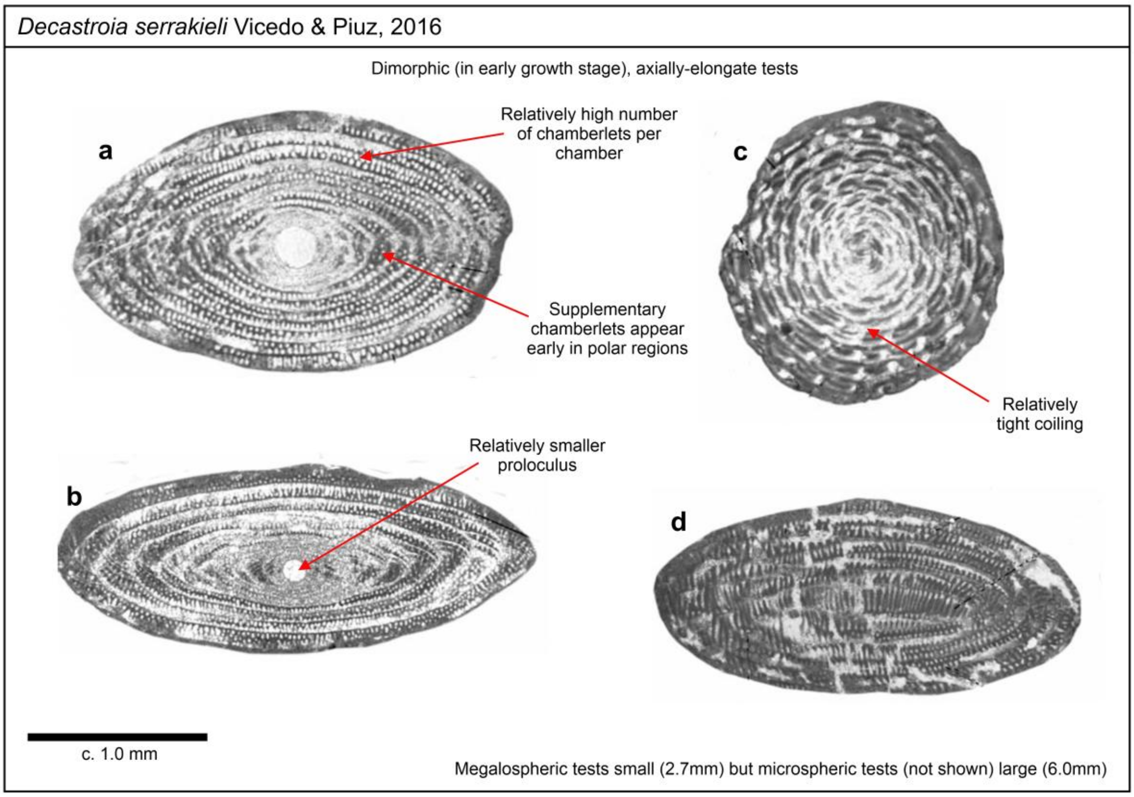


Fig. 23: Representative illustrations of *Decastroia serrakieli*: **a.** Axial, slightly oblique section (holotype), Vicedo & Piuz (2016, fig. 3A; middle Cenomanian, Oman); **b.** Axial section, Vicedo & Piuz (2016, fig. 5D; middle Cenomanian, Oman); **c.** Subequatorial section, Vicedo & Piuz (2016, fig. 3G; middle Cenomanian, Oman); **d.** Tangential section, Vicedo & Piuz (2016, fig. 4D; middle Cenomanian, Oman).

Genus ***Multispirina*** Reichel 1947

See Table 1 and Figure 7 for diagnostic characteristics of the genus.

***Multispirina iranensis* Reichel, 1947**
FIGURE 24

T 1947 *Multispirina iranensis* n. gen., n. sp., Reichel, p. 2, text-figs. 1-5, pls. 1-4; undifferentiated Cenomanian [most likely late Cenomanian from associated fauna and stratigraphic position], Iranian Zagros.
1969 *Multispirina iranensis* – Sampò, pl. 43, figs. 1-4; pl. 46, figs. 1-2; pl. 48, fig. 1; undifferentiated Cenomanian, Iranian Zagros.
? 1973 *Multispirina* sp. – El-Naggar & Al-Rifaiy. fig. 5(12) [*non fide* Hamaoui & Brun, 1974 = *Cycledomia*], fig. 6(9); latest Cenomanian, Kuwait.
1990 *Multispirina iranensis* – Cherchi & Schroeder, fig. 7; middle-late Cenomanian, Iranian Zagros.
1998 *Multispirina iranensis* – Whittaker et al., pl. 73, figs. 4-6; late? Cenomanian, Iranian Zagros.
1998 *Multispirina* sp. nov. – Whittaker et al., pl. 73, fig. 7, pl. 74., figs. 1-5; undifferentiated Cenomanian, Qatar.
2013 *Multispirina iranensis* – Rahimpour-Bonab et al., fig. 8E; undifferentiated Cenomanian, Iranian Zagros.
2013 *Multispieriana* (sic.) *iranensis* – Al-Dulaimy et al., fig. 9(3); late Cenomanian - ?early Turonian, southern Iraq.
2014a *Multispirina iranensis* – Omidvar et al., fig. 3 (6); undifferentiated Cenomanian-Turonian, Iranian Zagros.
2014b *Multispirina iranensis* – Omidvar et al., pl. 2, fig. F; undifferentiated Cenomanian-Turonian, Iranian Zagros.
2016 *Multispirina iranensis* – Kazemzadeh & Loftpoor, pl. 2, fig. 2 or 3 [mis-captioned?]; Cenomanian, Iranian Zagros.
2016 *Multispirina iranensis* – Assadi et al., fig. 6 (a11); late Cenomanian, Iranian Zagros.
? 2017 *Multispirinairanensis* (sic) – Jamalpour et al., pl. 1, fig. e; undifferentiated Cenomanian, Iranian Zagros [possibly *Cisalveolina fraasi* (Gümbel, 1872)].
2018 *Multispirina* sp. – BouDagher-Fadel, fig. 5.21; ? pl. 5.1, fig. 9; undifferentiated Cenomanian, Qatar [possibly *Decastroia* or *Reichelia*].
2019 *Multipirina iranensis* – Kiarostami et al., pl. 1, fig. h; undifferentiated Cenomanian, Iranian Zagros.
Non 2019 *Multispirina* sp. – Naing, fig. 4.10 (f); undifferentiated Albian-Cenomanian, Burma [= radiolarian].
2021a *Multispirina iranensis* – Dousti-Mohajer et al., pl. 2, fig. i; late Cenomanian, Iranian Zagros.
2021b *Multispirina iranensis* – Dousti-Mohajer et al., fig. 8 (i); early late Cenomanian, Iranian Zagros [scale bar appears erroneous].

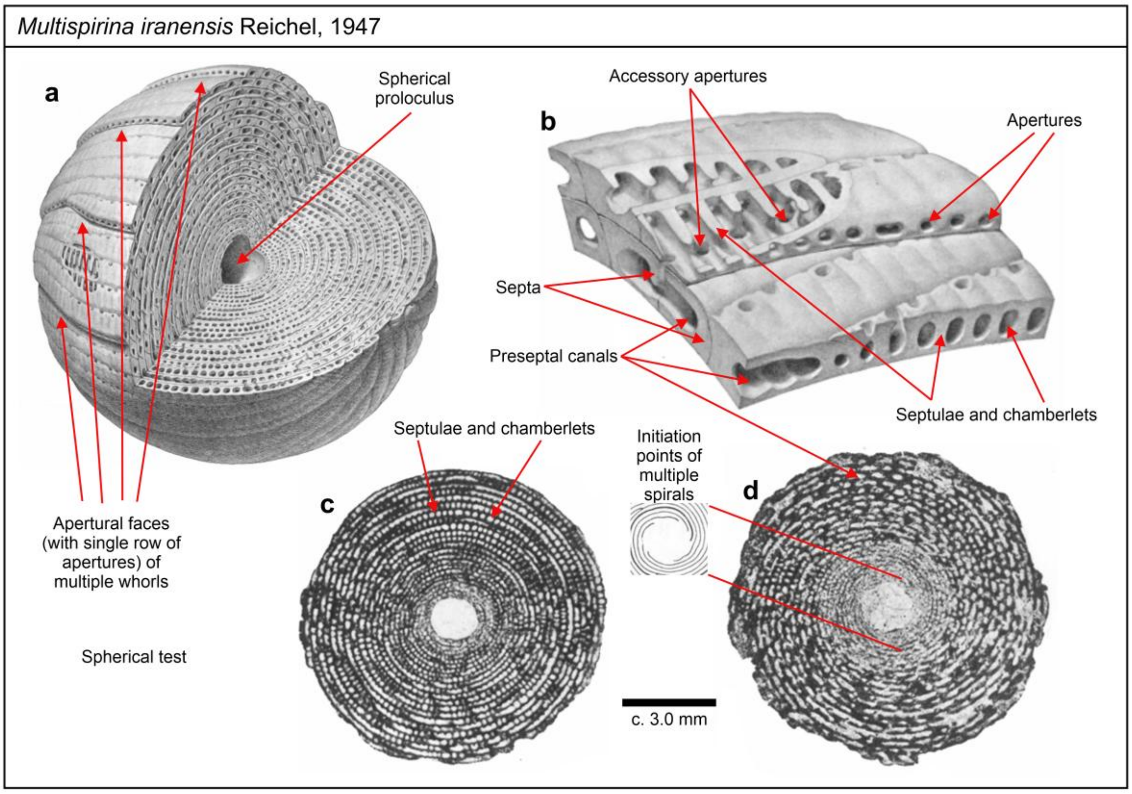


Fig. 24: Representative illustrations of *Multispirina iranensis*: **a.** Schematic cutaway of whole specimen, Reichel (1947, pl. 4, fig. 1); **b.** Schematic enlargement of section across two whorls, Reichel (1947, pl. 4, fig. 2); **c.** Axial section, Reichel (1947, pl. 1, fig. 3, late Cenomanian, Iranian Zagros); **d.** Equatorial section, Reichel (1947, pl. 1, fig. 2, late Cenomanian, Iranian Zagros; inset image taken from text-fig. 2).

? 2021 *Multispirina* sp. – BouDagher-Fadel & Price, pl. 2, fig. a: undifferentiated Cenomanian, Qatar [possibly *Decastroia* or *Reichelia*].

Non 2021 *Multispirina iranensis* – Dehghanian & Afghah, fig. 7 (1); middle Cenomanian, Iranian Zagros [= *Decastroia*].

? 2022 *Multispirina iranensis* – Schlagintweit & Yazdi-Moghadam, fig. 2C; undifferentiated Cenomanian, Iranian Zagros [Doubtful, no multispire visible].

Non 2022 *Multispirina iranica* (sic) – Al-Dulaimy et al., pl. 1, fig. c; middle Cenomanian, southern Iraq [indeterminate alveolinoid, not *Multispirina*]

2023a *Multispirina iranensis* – Mehrabi et al., fig. 6F; undifferentiated Cenomanian, Iranian Zagros.

Non 2023 *Multispirina iranensis* – Al-Salihi & Ibrahim, pl. 1F; late Cenomanian, southern Iraq [indeterminate alveolinoid, not *Multispirina*]

Non 2023 *Multispirina iranica* (sic.) – Jubeir et al., pl. 2, fig. f; undifferentiated Cenomanian, western Iraq [= indeterminate small foraminifera].

Reference Images: Reichel (1947), text-figs. 1-5, pls. 1-4.

Taxonomy/Identity: First and comprehensively described and exquisitely illustrated by Reichel (1947) from the Late Cretaceous (late Cenomanian - ?Turonian) of Iran (now considered late Cenomanian according to Sampò, 1969 and Whittaker et al., 1998). The monospecific genus *Multispirina* is described as…

"Spherical, large, dimorphism prominent, each aperture in the early stage gives rise to separate, intercalated whorls (up to 12 whorls in megalospheric forms, up to 25 in microspheric forms), one row of main (cortical) chamberlets and no secondary chamberlets, preseptal passages large. Aperture a single row of openings at the base of each whorl's apertural face": a combination of descriptive terms from Loeblich & Tappan, 1987 and Vicedo & Piuz, 2016.

…and is therefore almost unique in the alveolinoids (together just with *Reichelia* Vicedo & Piuz 2016), in having multiple, intercalated planispiral coils, rather than a single coil. It also displays low chambers and septula running in the direction of growth and aligned between successive chambers. *Multispirina* differs from the monospecific *Reichelia* in having (a) more spirals (12-18 and even more in microspheric forms) cf. *Reichelia* (2-5); (b) a single row of apertures in the apertural face (cf. 2); (c) a single row of chamberlets (cf. 2) and (d) no supplementary chamberlets polewards, since true 'poles' do not occur in this species. *Reichelia* is subglobular to axially elongated, whereas *Multispirina* displays an almost perfect spherical shape.

As Reichel (1947; text-figs. 1-2) illustrated, the individual whorls are not added sequentially and single whorls split into two whorls at various times during post embryonic growth.

The genus *Decastroia* Vicedo & Serra-Kiel (2011) is also similar except the chambers are horizontally subdivided by 'floors' into an upper (and larger) 'cortical' layer of chamberlets and a lower, smaller, 'medullar' layer. It also lacks the characteristic multiple coils of *Multispirina*.

Confident Stratigraphic Range: late Cenomanian.

Uncertain Stratigraphic Range: middle Cenomanian.

Many records of this species are from undifferentiated Cenomanian strata, but where illustrated occurrence is biostratigraphically calibrated, these records are from the late Cenomanian, although distribution within this substage is uncertain. Middle Cenomanian records (e.g. Bernaus & Masse, 2007; Dawood & Al-Dulaimi, 2023) are unproven, and early Cenomanian records unsubstantiated by illustration can be discounted (e.g. Afghah & Fadaei, 2014).

Geographic Distribution: Central Neotethys. So far recorded with certainty only from the Arabian Plate and almost exclusively the Zagros region. Questionable records are from Kuwait and Qatar, A slight outlier is an unproven record from Israel (Arkin et al., 1965).

Genus ***Ovalveolina*** Reichel 1936

Genus introduced by Reichel (1936) for small, relatively simple alveolinoids with a spherical to ovoid morphology. *Alveolina ovum* d'Orbigny, 1850b is the type species. It has multiple small basal apertures (foramina in previous chambers) disposed in one row. A spherical proloculus is followed by a flexostyle and planispirally arranged set of chambers. Chambers are divided in sub-rectangular chamberlets by means of septula. Septula continuous from chamber to chamber. Preseptal passages are present. According to Loeblich & Tappan (1987) there are no accessory apertures. Externally *Ovalveolina* is similar to *Simplalveolina* and some *Praealveolina,* but *Ovalveolina* is relatively smaller and mainly spherical to ovoid, whereas *Praealveolina* is often ovoid to fusiform (Loeblich & Tappan, 1987). Other differences include than *Ovalveolina* has a thicker basal layer and thicker septula that *Praealveolina*, and a "coarser structure as a whole" (Hottinger, 1974), which – although only loosely constrainable – appears to be the best feature to distinguish both taxa. The septula form a kind of shallow crest or socculi (*sensu* Hottinger, 2006) which continue below the (larger) preseptal passages. A similar form to *Ovalveolina* in the pre-Cenomanian (late Aptian) is *Archaealveolina* Fourcade, 1980. *Ovalveolina* has rounded apertural openings whereas these are slit-like in *Archaealveolina*. The genus resembles *Cisalveolina* except that the septulae adopt the same position relative to one another between successive chambers, rather than alternate, and the apertures are separate openings rather than a broad slit. See Table 1 and Figure 9 for diagnostic characteristics of the genus.

Three *Ovalveolina* species are recognised within the Cenomanian (*Ovalveolina crassa* De Castro 1966, *Ovalveolina maccagnoae* De Castro 1966 and *Ovalveolina ovum* (d'Orbigny, 1850b)) and are comprehensively described in Schroeder & Neumann (1985) with biometric data provided for the former two. The principal differences between them are:

O. crassa – slightly wider than high around the coiling axis; wall thickness ≈ septa thickness (wall is relatively thinner than septa in *O. ovum*); fewer chambers per whorl than *O. ovum*; sub-rectangular to subcircular shaped chamberlets in axial view.

O. maccagnoae – smallest overall size; axially-compressed subglobular ('nautiloid') test (i.e., narrower than high around the coiling axis cf. broadly globular in *O. crassa* and *O. ovum*); *possible* development of cortical chambers.

O. ovum – largest overall size; broadly globular in overall shape; relatively thin-walled compared to septa thickness; pyriform-shaped chamberlets in axial view; more chambers per whorl than other species; pre-septal canal in the higher part of the chamber height.

However, it should be mentioned that several authors, principally Hottinger (1974), have speculated that *O. maccagnoae* should be re-assigned to *Sellialveolina* based on the former's more laterally-compressed outline and other differences, although other authors (e.g., Vicedo et al., 2011) have provided contrary arguments. Hosseinzadeh et al. (2020; p. 3) provides a summary discussion and points out that *Sellialveolina* is a rhapydioninid with two floors of chamberlets – a feature that *O. maccagnoae* does not possess. Thus, we include it within *Ovalveolina* herein.

Ovalveolina? *primigenita* Hosseinzadeh et al., 2020 represents the oldest alveolinoid so far known in the geological record (early Aptian). The occurrence of structures resembling alveoli and few adult supplementary foramina mean that the placement of this species in *Ovalveolina* is questionable.

***Ovalveolina crassa* De Castro, 1966**
FIGURE 25

T 1966 *Ovalveolina crassa* n. sp., De Castro, p. 239 (23)-251 (35); pl. 4-6; middle Cenomanian [? - see stratigraphic range discussion below], southern Italy.
1974 *Ovalveolina crassa* De Castro – Hottinger, pl. 5, figs. 1-4; undifferentiated Cenomanian, Italy.
? 1974 *Ovalveolina crassa* – Saint-Marc, p. 249, pl. 3, figs. 10-11; early Cenomanian, Lebanon.
Non 1976 *Ovalveolina crassa* – Decrouez, p. 108; pl. 20, fig. 12-13; latest Albian – late Cenomanian, Greece [fig. 12 is probably *O. ovum*, fig. 13 is ?*Pseudorhapydionina*].
1977 *Ovalveolina crassa* – Rey et al., p. 380; pl. 3, figs. 1-3; latest Albian, Portugal.
1977 *Ovalveolina* cf. *maccagnoi* – Rey et al., pl. 3, fig. 4 ; latest Albian, Portugal.
1978 *Ovalveolina crassa* – Berthou & Schroeder, p. 70-71; pl. 1, figs. 1-7; earliest Cenomanian, Portugal.

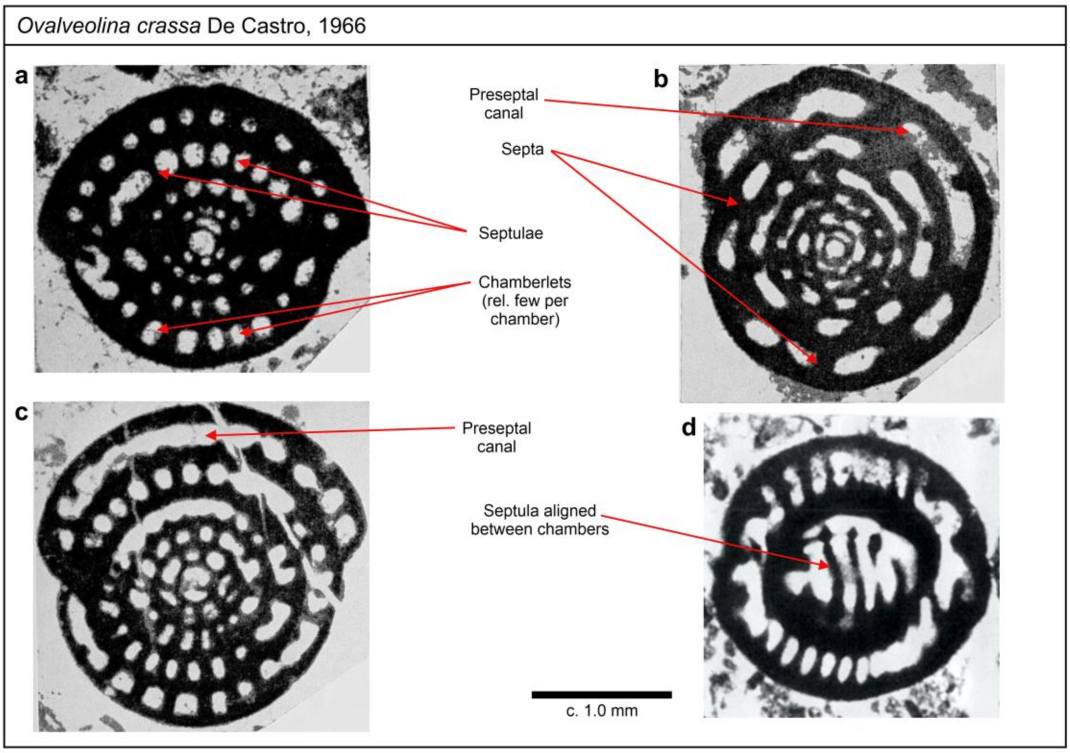


Fig. 25: Representative illustrations of *Ovalveolina crassa*: **a.** Axial section (holotype), De Castro (1966a, pl. IV, fig. 1; ?middle Cenomanian?, Italy); **b.** Equatorial section, De Castro (1966a, pl. IV, fig. 5; ?middle Cenomanian?, Italy); **c.** Oblique axial section, De Castro (1966a, pl. V, fig. 3; ?middle Cenomanian?, Italy); **d.** Tangential section, De Castro (1966a, pl. VI, fig. 5; ?middle Cenomanian?, Italy).

1979 *Ovalveolina crassa* – Rey, pl. 15, figs. 1-3 ; latest Albian, Portugal.

1980 *Ovalveolina crassa* – Fleury, p. 483; pl. 1, figs. 11-14; undifferentiated late Albian – Cenomanian, Greece.

? 1981 *Ovalveolina crassa* – Saint-Marc, pl. 2, fig. 7; early Cenomanian, Lebanon

1985 *Ovalveolina crassa* – De Castro in Schroeder & Neumann, p. 102, pl. 49, figs. 1-12; text fig. 11; early to near top middle Cenomanian, questionably latest Albian; global review.

? 1987 *Ovalveolina* sp. cf. *maccagnoae* – Simmons & Hart, pl. 10.1, fig. 4; middle Cenomanian [now considered late early Cenomanian – Bromhead et al., 2022], Oman Mountains.

1988 *Ovalveolina crassa* – Sartorio & Venturini, p. 104; late Albian, Libya.

1988 *Ovalveolina crassa* – De Castro, p. 405-406, pl. 1, fig. 4; late Albian, southern Italy.

1993 *Ovalveolina* sp. aff. *crassa* – Ettachfini, p. 122, pl. 5, figs. 7-8; undifferentiated early – middle Cenomanian [total range given as late Albian – middle Cenomanian], Morocco.

? 2003 *Ovalveolina crassa* – Schulze, fig. 11g; early Cenomanian, Jordan.

Non 2004 *Ovalveolina crassa* – Schulze et al., fig. 10F (mis-captioned as G); early Cenomanian, Jordan [= *Simplalveolina simplex*].

2009 *Ovalveolina crassa* – Husinec et al., fig. 3 (L-N); Albian – Cenomanian boundary, Croatia.

2012 *Ovalveolina crassa* – Chiocchini et al., pl. 75, figs.1 -7; Albian – Cenomanian boundary, central Italy.

? 2012 *Ovalveolina crassa* – Ghanem et al., fig. 6c (5): early Cenomanian, Syria.

Non 2013 *Ovalveolina crassa* – Ghanem & Kuss, fig. 12 (6-8); early Cenomanian, Syria [probably *Sellialveolina* or similar].

Non 2013 *Ovalveolina crassa* Reichel [sic]– Shahin & Elbaz, pl. 2, fig. 27; late Cenomanian, Egypt, Sinai [= *Decastroia*].

Non 2014 *Ovalveolina crassa* – Afghah & Fadaei, fig. 7a; undifferentiated Cenomanian, Iranian Zagros [= *Simplalveolina simplex*].

Non 2014 *Ovalveolina crassa* - Afghah & Fadaei, figs. 7f; early, middle and late Cenomanian, Iranian Zagros [= *Cisalveolina fraasi* (Gümbel)].

? 2016 *Ovalveolina* sp. – Consorti et al., 2016, fig. 4j; upper Cenomanian, Iberian Peninsula.

Non 2016 *Ovalveolina crassa* – Rahiminejad & Hassani, fig. 3i; earliest Albian, central Iran [probably a glomospirid].

? 2018 *Ovalveolina crassa* – Luger, p. 95, pl. 15, figs. 5-10; pl. 16, fig. 13; latest Albian, Somalia.

2021 *Ovalveolina crassa* – BouDagher-Fadel & Price, pl. 1, fig. c; undifferentiated Cenomanian, western France.

Non 2021 *Ovalveolina crassa* – Dehghanian & Afghah, fig. 7 (5); middle Cenomanian, Iranian Zagros [possibly *Simplalveolina simplex*].

? 2023 *Ovalveolina* cf. *crassa* – Xu et al., fig. 3 (F);

middle Cenomanian, Iranian Zagros.

Reference Images: Schroeder & Neumann (1985), pl. 49, p. 102.

Taxonomy/Identity: *O. crassa* is similar to *O. ovum* in its general subglobular shape but has a demonstrably smaller maximum axial diameter of 1.42 mm (cf. *O. ovum* which has a maximum axial diameter between 1.80-2.20 mm). It also has fewer chambers per whorl (8-9) compared with *O. ovum* (14-16) by the 5th whorl (see Hosseinzadeh et al. 2020; Table 1 therein).

Confident Stratigraphic Range: latest Albian – middle Cenomanian (common around the Albian – Cenomanian boundary).

Uncertain Stratigraphic Range: late Cenomanian.

The species was originally described (De Castro, 1966) from the middle Cenomanian of the southern Apennines, although there is no apparent independent age calibration and the age attribution has been challenged as being older, closer to the Albian/Cenomanian boundary (Rey et al., 1977). De Castro in Schroeder & Neumann (1985) compiled records, mostly from the Mediterranean region, in which he states that *O. crassa* is known possibly from the latest Albian but confidently from the base early to the near-top middle Cenomanian. Late Albian (Vraconian) records are challenged by Berthou & Schroeder (1978). Considered a marker for the base of the Cenomanian in Portugal by Berthou & Lauverjat (1979) and Berthou (1984a, b). In 1988, De Castro was more inclined to accept a late Albian age for *O. crassa*, with more uncertain range extension into the early Cenomanian. There now appear to be sufficient verified records to suggest the oldest records of this species are most likely late Albian with range into the middle Cenomanian. An uncertain record by Consorti et al (2016) is the only significant evidence for extension into the late Cenomanian.

Geographic Distribution: The species has only been confidently described from the peri-Mediterranean region (e.g., Italy, Croatia, Greece, Libya, Morocco) as well as from Portugal. Regional records of *O. crassa* from the Arabian Plate are fairly common (e.g., from the Sarvak Formation of the Iranian Zagros and its regional equivalents but with fewer records than for *O. ovum*) but none can be confidently verified, and many are clearly not this species (see synonymy list). Dousti Mohajer et al. (2021b, 2022a) have reported *O. crassa* from the early Cenomanian of the Iranian Zagros, but not illustrated it, whilst Rabu (1993) reported *O. crassa* without illustration from the early Cenomanian of the Oman Mountains. Roger et al. (1989, 1994) reported it without illustration from the early Cenomanian of Dhofar (southern Oman).

Ovalveolina maccagnoae De Castro, 1966
FIGURE 26

1964 *Sellialveolina viallii* – Ietto, pl. 3; undifferentiated Cenomanian, southern Italy.

T 1966 *Ovalveolina maccagnoi* n. sp., De Castro, p. 252 (36) - 271 (55); pl. 7-10; pl. 11, figs. 1-10, 12-14; pl. 12, figs. 1-6; pl. 13, figs. 1-7; pl.14, fig. 17; middle Cenomanian [?- see stratigraphic range discussion below], southern Italy.

1973 *Ovalveolina maccagnoi* – Hamaoui & Fourcade, tab. 2 (4); undifferentiated Cenomanian, Algeria.

1974 *Ovalveolina maccagnoi* – Hottinger, p. 30, pl. 7, figs. 1-6; undifferentiated Cenomanian, Italy.

? 1974 *Ovalveolina maccagnoi* – Saint-Marc, p. 250, pl. 3, figs. 12-16; early Cenomanian [range shown as early – middle Cenomanian], Lebanon.

? 1974 *Ovalveolina* cf. *maccagnoi* – Saint-Marc, pl. 3, fig. 17; undifferentiated late Albian – early Cenomanian, Lebanon.

? 1976 *Ovalveolina maccagnoi* – Decrouez, p. 109; pl. 20, fig. 11; latest Albian, Greece.

Non 1977 *Ovalveolina* cf. *maccagnoi* – Rey et al., pl. 3, fig. 4 ; latest Albian, Portugal [= *Ovalveolina crassa*].

1980 *Ovalveolina* cf. *maccagnoi* – Fleury, p. 509; text-fig. A3(17-20); pl. 2, figs. 20-29; early – middle Cenomanian, Greece.

? 1981 *Ovalveolina maccagnoi* – Saint-Marc, pl. 2, figs. 8-9; early – middle Cenomanian, Lebanon.

1982 *Ovalveolina maccagnoi* – Mouty & Saint-Marc, pl. 1, fig. 7; earliest Cenomanian [range shown as “Albian – Cenomanian passage” – basal middle Cenomanian], NW Syria.

1985 *Ovalveolina maccagnoae* – De Castro in Schroeder & Neumann, p. 106, pl. 50, figs. 1-9; text fig. 9; latest Albian – near top middle Cenomanian, global review.

Non 1987 *Ovalveolina* sp. cf. *maccagnoae* – Simmons & Hart, pl. 10.1, fig. 4; middle Cenomanian (now considered late early Cenomanian – Bromhead et al., 2022), Oman Mountains [indeterminate but possibly *O. crassa*].

1988 *Ovalveolina maccagnoae* – Velić, pl. 2, figs. 9-10; latest Albian [range extends into earliest Cenomanian], Croatia.

1992 *Ovalveolina maccagnoae* – Foglia, pl. 1, figs. 7-10, 14; early Cenomanian, southern Italy.

1994 *Ovalveolina maccagnoae* – Velić & Vlahović, pl. 1, figs. 1-3; earliest Cenomanian [range suggested as latest Albian – middle Cenomanian], Croatia.

1994 *Ovalveolina maccagnoae* – Chiocchini et al., pl. 14, figs. 1-10; intra early Cenomanian, southern Italy.

? 2006 *Ovalveolina maccagnoi* – Sari, pl. 6.4, figs. 5-7; middle Cenomanian, Turkish Taurides [figs. 5 & 7 resemble *Cisalveolina lehneri* and fig. 6 is *Cisalveolina fraasi*].

? 2007 *Ovalveolina maccagnoae* – Radoičić & Schlagintweit, pl. 3, figs. 7-8; latest Albian, Serbia [internal structure not clear, possibly a *Sellialveolina*].

2009 *Ovalveolina maccagnoae* – Husinec et al., fig. 3(I); earliest Cenomanian [range shown as latest Albian – earliest Cenomanian], Croatia.

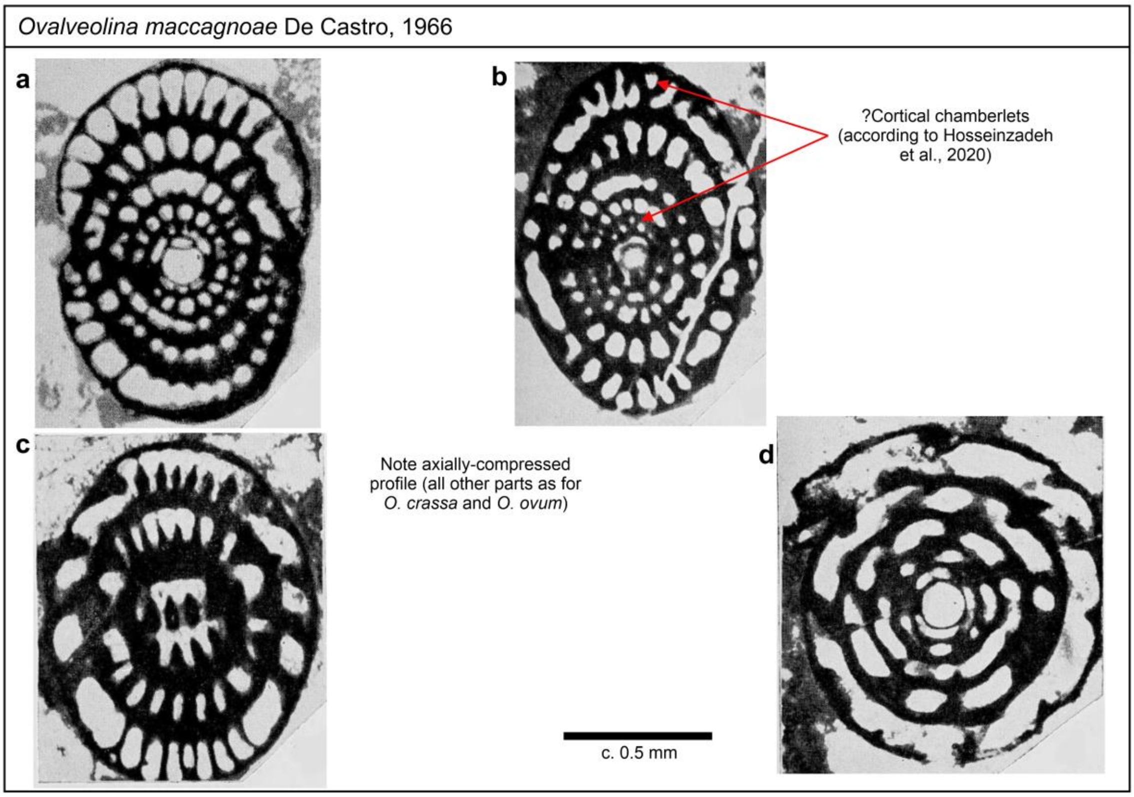


Fig. 26: Representative illustrations of *Ovalveolina maccagnoae*: **a.** Axial section (holotype), De Castro (1966a, pl. VII, fig. 1; ?middle Cenomanian, Italy); **b.** Axial section, De Castro (1966a, pl. X, fig. 1; ?middle Cenomanian, Italy); **c.** Tangential section, De Castro (1966a, pl. IX, fig. 15; ?middle Cenomanian, Italy); **d.** Equatorial section, De Castro (1966a, pl. VIII, fig. 4; ?middle Cenomanian, Italy).

2012 *Ovalveolina maccagnoae* – Chiocchini et al., pl. 80, figs. 1-10; pl. 86, fig. 1; early early Cenomanian, central Italy [pl. 86, fig. 1 is doubtful].
? 2012 *Ovalveolina maccagnoae* – Omaña et al., fig. 5 (4, 6, 9); undifferentiated Cenomanian, eastern Mexico.
? 2013 *Ovalveolina maccagnoae* – Ghanem & Kuss, fig. 13 (11-12); middle Cenomanian (range shown as early – middle Cenomanian), Syria.
? 2019 *Ovalveolina maccagnoae* – Omaña et al., p. 174, figs. 11e, h; undifferentiated middle – late Cenomanian, Mexico.
2020 "*Ovalveolina*" *maccagnoae* – Fleury & Özkan, fig. 9 (6-7); undifferentiated Albian – Cenomanian, Italy.
Non 2020 *Ovalveolina maccagnoae* – Solak et al., fig. 5A-C, undifferentiated early – middle Cenomanian, Turkish Taurides [probably *Sellialveolina viallii*].
? 2021 *Ovalveolina maccagnoae* – Solak, pl. 1, fig. S; early Cenomanian, Turkish Taurides.
? 2021a *Ovalveolina maccagnoae* – Dousti-Mohajer et al., pl. 2, fig. b; middle Cenomanian (range shown as early – middle Cenomanian), Iranian Zagros.
? 2021b *Ovalveolina maccagnoae* – Dousti-Mohajer et al., fig. 8b; middle Cenomanian (range shown as early – middle Cenomanian), Iranian Zagros.

Reference Images: Schroeder & Neumann (1985), pl. 50, p. 106.

Taxonomy/Identity: Close similarity to *Sellialveolina*, especially *S. viallii*, suggests that many records of the two species may have been recorded under the other's name. They also share similar stratigraphic ranges (e.g., De Castro, 1988). Hottinger (1974) discussed the possibility of excluding *O. maccagnoae* from *Ovalveolina*. In *Sellialveolina*, the appearance of a chamber floor subdivides the chamberlets vertically which does not occur in *Ovalveolina*. However, some specimens of *O. maccagnoae* figured by De Castro (1966) develop a few cortical chamberlets according to Hosseinzadeh et al. (2020) (e.g., see Figure 26b herein). Another difference between the two taxa is based on the occurrence of residual pillars, which are present in *Sellialveolina* but absent in *O. maccagnoae*.

An additional part of Hottinger's doubts included the observations that the basal layer and the septulae are much thinner in *O. maccagnoae* than in other *Ovalveolina* species, the preseptal passages are larger and there are "irregularities in the structure" of adult growth stages (Hottinger, 1974, p.30). He suggests that this species could be a relative of *Sellialveolina viallii*. Calonge-Garcia (1993) indicated *O. maccagnoae* is the ancestor of *P.* (=*S.*) *viallii* and its descendant *P.* (=*S.*) *drorimensis*.

Confident Stratigraphic Range: latest Albian – middle Cenomanian (common around Albian – Cenomanian boundary).

Uncertain Stratigraphic Range: not applicable.

Originally described from rocks attributed to the middle Cenomanian in Italy (De Castro, 1966). De Castro in Schroeder & Neumann (1985) compiled records in which he states *O. maccagnoae* is known from possibly from the latest Albian but confidently from the base early to the near-top middle Cenomanian (see Schroeder & Neumann, 1985, table 1). In 1988 De Castro considered the range to be latest Albian – early Cenomanian in Italy, contrary to his previous views. Hardenbol et al. (1998) show a range of latest Albian (*dispar* Zone) to middle Cenomanian, but without explanation. A compilation of viable records suggests a range of latest Albian – middle Cenomanian, with many records from around the Albian/Cenomanian boundary.

Geographic Distribution: With the exception of a record from Syria (Mouty & Saint-Marc, 1982), most viable records of this species are from the peri-Mediterranean region (e.g. Italy, Greece, Croatia, Algeria). A record from Mexico (Omaña et al., 2019) is doubtful. Records from the Arabian Plate are mostly uncertain or unillustrated. Unillustrated records that might extend geographic range include from the intra-early Cenomanian – middle Cenomanian of Sinai (Bachmann et al., 2003)*;* from the late Albian of the subsurface of Tunisia (Bismuth, 1973; Bismuth et al., 1981); from the ?earliest Cenomanian of Spain (Calonge-Garcia, 1996; Calonge et al., 2003; Caus et al., 2009; Consorti et al., 2016). Mülayim et al. (2019) reported it without illustration from the early Cenomanian of south-east Turkey (a part of the Arabian Plate), although note the assigned age is in turn derived as the result of its presence. Reported (but not illustrated) from the undifferentiated early - middle Cenomanian of Crete (Zambetakis-Lekkas et al., 2006).

***Ovalveolina ovum* (d'Orbigny, 1850)**
FIGURE 27

T 1850 *Alveolina ovum*, d'Orbigny, p. 185; Cenomanian (probably middle Cenomanian after Neumann, 1962, Neumann & Fourcade in Schroeder & Neumann, 1985), western France.

1937 *Ovalveolina ovum* (d'Orbigny) – Reichel, p. 70-73; pl. 1, fig. 5; pl. 2, figs. 2-3; pl. 3, fig. 2; pl. 5, fig. 4; pl. 7, fig. 13; pl. 8, figs. 1-4, 9-11; Cenomanian [probably middle Cenomanian after Neumann, 1962, Neumann & Fourcade in Schroeder & Neumann, 1985], Aquitaine, western France.

? 1959 *Ovalveolina ovum* – Dufaure, pl. 1, figs. 4-5; undifferentiated Cenomanian, French Pyrenees.

1961 *Ovalveolina ovum* – Cuvillier, pl. 36, fig. 2; undifferentiated Cenomanian, Aquitaine, western France.

? 1964 *Ovalveolina ovum* – Bozorgnia & Banafti, pl. 82(2); undifferentiated Cenomanian, Iranian Zagros.

1965 *Ovalveolina ovum* – Saint-Marc, p. 137; pl. 5, figs. 1-2; pl. 15, figs. 6-7; undifferentiated Cenomanian, Aquitaine, western France [*fide* Neumann & Fourcade in Schroeder & Neumann, 1985].

? 1965 *Alveolina ovum* (described as *Ovalveolina ovum* in part) – Gibson & Percival, p. 343, pl. 1, fig. 10; undifferentiated Cenomanian, Somalia [possibly *Praealveolina*].

Non 1965 *Ovalveolina ovum* – Gollesstaneh, p. 168, pl. 25, figs. 1-6; pl. 26, figs. 1-6; pl. 27, figs. 1-5; late Aptian – early Albian [a range of morphologies illustrated, including probable *Archaealveolina reicheli* Fourcade, 1980 and *Ovalveolina*? *primigenita* Hosseinzadeh et al., 2020].

1967 *Ovalveolina ovum* – Souquet, pl. 18, figs. 3-4; late Cenomanian, Spanish Pyrenees [*fide* Neumann & Fourcade in Schroeder & Neumann, 1985].

? 1969 *Ovalveolina ovum* – Sampò, pl. 43, figs. 10-11; undifferentiated Cenomanian, Iranian Zagros.

1971 *Ovalveolina ovum* – Pourmotamed-Lachtewechai, p. 84; pl. 17, fig. 2; middle Cenomanian (*jukesbrownei* zone), central France [*fide* Neumann & Fourcade in Schroeder & Neumann, 1985].

1971 *Ovalveolina ovum* – Ramírez del Pozo, p. 299; pl. 77; undifferentiated Cenomanian, Spanish Pyrenees.

Non 1971 *Ovalveolina ovum* – Ramírez del Pozo, p. 299; pl. 83, fig. 2; undifferentiated Cenomanian, Spanish Pyrenees.

Non 1972 *Ovalveolina ovum* – Barr & Weegar, pl. 4, fig. 8; undifferentiated Cenomanian, Libya [= *Reticulinella reicheli* Cuvillier et al., 1969].

1973 *Ovalveolina ovum* – Bilotte, p. 9-12, 14, 16; pl. 2, fig. 8; pl. 5, fig. 3; middle – late Cenomanian, Aquitaine, Western France.

Non 1973 *Ovalveolina ovum* – Berthou, p. 40, 51-54, 63-64; pl. 6, figs. 2-2a; pl. 7, figs. 1-la; middle – late Cenomanian, Portugal [illustrations = *Praealveolina*, ?*O. crassa*, unknown and ?*O. crassa* respectively].

Non 1973 *Ovalveolina ovum* – El-Naggar & Al-Rifaiy, fig. 8 (6, 10-11); late Cenomanian, Kuwait [= *Decastroia*].

? 1974 *Ovalveolina ovum* – Juignet et al., p. 2281; pl. 1, figs. 10, 12-13; middle Cenomanian (*jukesbrownei* zone), central France.

1981 *Ovalveolina ovum* – Tronchetti, p. 94-95, 286-287, 310, 314; pl. 22, fig. 7; middle – late Cenomanian, Provence, southern France [*fide* Neumann & Fourcade in Schroeder & Neumann, 1985].

1984 *Ovalveolina ovum* – Bilotte, pl. 6, fig. 9, pl. 7, figs. 7-8; late Cenomanian, Spanish Pyrenees.

1985 *Ovalveolina ovum* – Neumann & Fourcade in Schroeder & Neumann, p. 109, pl. 51, figs. 1-8; text-figs. 10, 11; global review (total range middle – late Cenomanian; illustrations from middle Cenomanian, western France).

1987 *Ovalveolina ovum* – Simmons & Hart, pl. 10.1, fig. 3; middle – late Cenomanian [would now be regarded as late early Cenomanian – Bromhead et al., 2022], Oman Mountains.

Non 1992 *Ovalveolina ovum* – Kalantari, text-fig. 157 (2); undifferentiated Cenomanian, Iranian Zagros [probably = *Cisalveolina fraasi*].

Non 1993 *Ovalveolina ovum* – Hewaidy & Al-Hitmi, p. 491, pl. 7, figs. 4-6; undifferentiated Cenomanian [would now be regarded as middle Cenomanian – Bromhead et al, 2022], Qatar [probably = *Praealveolina*].

1994 *Ovalveolina* sp. – Radoičić, pl. 1, fig. 4; undifferentiated early – middle Cenomanian, Albania/Kosova border.

? 2005 *Ovalulina* (sic.) *ovum* – Hart et al., fig. 7B; late Cenomanian, Portugal.

? 2008 *Ovalveolina* cf. *ovum* – Ahmadi et al., pl. 4, fig. 5; undifferentiated middle – late Cenomanian, Iranian Zagros.

? 2012 *Ovalveolina ovum* – Kiarostami et al., pl. 3, fig. 21; undifferentiated Cenomanian, Iranian Zagros.

? 2012 *Ovalveolina ovum* – Rahimpour-Bonab et al., fig. 8H; undifferentiated Cenomanian, Iranian Zagros.

? 2013 *Ovalveolina ovum* – Rahimpour-Bonab et al., fig. 8D; undifferentiated Cenomanian, Iranian Zagros.

Non 2013 *Ovalveolina ovum* – Shahin & Elbaz, pl. 2, fig. 28; middle – late Cenomanian, Sinai, Egypt. [= *Decastroia*].

? 2014b *Ovalveolina ovum* – Omidvar et al., fig. 3 (4); undifferentiated Cenomanian - Turonian, Iranian Zagros.

Non 2014a *Ovalveolina ovum* – Omidvar et al., pl. 2, figs. C-D; undifferentiated Cenomanian - Turonian, Iranian Zagros [= *Cisalveolina fraasi*].

? 2015 *Ovalveolina ovum* – Awadeesian et al., pl. 17; late Cenomanian, southern Iraq [possibly *Simplalveolina simplex*].

? 2016 *Ovalveolina ovum* – Kazemzadeh & Loftpoor, pl. 1, fig. 12; undifferentiated Cenomanian, Iranian Zagros.

Non 2016 *Ovalveolina ovum* – Assadi et al., fig. 6 (a12); early Cenomanian [age must be considered imprecise], Iranian Zagros [= *Cisalveolina fraasi* (Gümbel)].

Non 2016 *Ovalveolina ovum* – Hart, fig. 10B; undifferentiated Cenomanian, Oman Mountains [possibly *Myriastyla omanensis* but not *O. ovum*].

2017 *Ovalveolina ovum* – Ahmadi et al., pl. 2, fig. 11; undifferentiated Albian - Cenomanian, Iranian Zagros.

Non 2017 *Oalveolina ovum* (sic) – Rikhtegarzadeh et al., pl. 1, fig. 5; undifferentiated Cenomanian, Iranian Zagros [= *C. fraasi*].

? 2019 *Ovalveolina ovum* – Kiarostami et al., pl. 1, fig. i; undifferentiated Cenomanian, Iranian Zagros.

? 2019 *Ovalveolina ovum* – Özkan & Altiner, fig. 7 (20-21); Cenomanian [considered middle Cenomanian by Simmons et al., 2020], Türkiye [possibly *Simplalveolina* or *Praealveolina*].

2021 *Ovalveolina* sp. – Dehghanian & Afghah, fig. 7 (7); middle Cenomanian, Iranian Zagros.

? 2021 *Ovalveolina ovum* – Dehghanian & Afghah, fig. 7 (6); middle Cenomanian, Iranian Zagros.

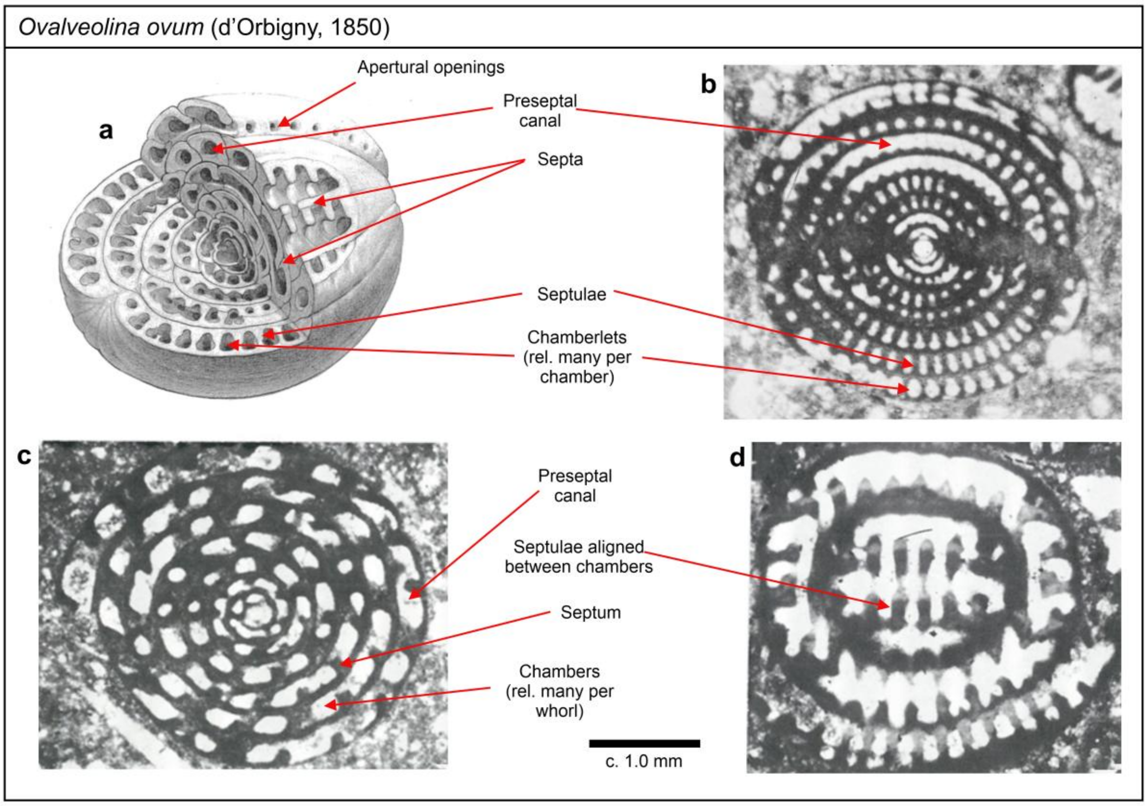


Fig. 27: Representative illustrations of *Ovalveolina ovum*: **a.** Schematic 3D section, Reichel (1936-7, pl. XI, fig. I); **b.** Axial section, Reichel (1936-7, pl. VIII, fig. 1; middle Cenomanian, western France); **c.** Equatorial section, Schroeder & Neumann (1985, pl. 51, fig. 4; middle Cenomanian, western France); **d.** Tangential/subaxial section, Schroeder & Neumann (1985, pl. 51, fig. 2; middle Cenomanian, western France).

? 2021a *Ovalveolina ovum* – Dousti-Mohajer et al., pl. 2a; late Cenomanian, Iranian Zagros.
? 2021b *Ovalveolina ovum* – Dousti-Mohajer et al., fig. 7b; fig. 8a; *non* fig. 9 [not *O. ovum*, possibly *Cisalveolina*]; late Cenomanian, Iranian Zagros.
? 2021 *Ovalveolina ovum* – Saeedi Razavi et al., pl. 1, fig. 5; undifferentiated Cenomanian, Iranian Zagros.
Non 2022 *Ovalveolina ovum* – Asghari et al., pl. 1, fig. e; late Cenomanian, Iranian Zagros. [possibly *Cisalveolina fraasi*].
Non 2022b *Ovalveolina ovum* – Dousti-Mohajer et al., fig. 4a; late Cenomanian, Iranian Zagros. [possibly *Cisalveolina lehneri*].
? 2023a *Ovalveolina ovum* – Mehrabi et al., fig. 6D-E; undifferentiated Cenomanian, Iranian Zagros [possibly *Cisalveolina fraasi*].
2025 *Ovalveolina* cf. *ovum* – Martín-Closas et al., fig 7M-N; late Cenomanian, Spain.

Reference Images: Schroeder & Neumann (1985), text-fig. 10, pl. 51, p. 109.

Taxonomy/Identity: *O. ovum* is very similar to *Simplalveolina simplex* (e.g., globular test, aligned septulae, single row of ovate chamberlets). However, the septulae are thicker and therefore the chamberlets are less numerous per chamber in *O. ovum*, and the chamber/chamberlet height is greater. Also, *S. simplex* shows more thickening of the basal layer towards the poles than *O. ovum* and the pre-septal passages are narrower.

Neumann & Fourcade in Schroeder & Neumann (1985) differentiate *O. ovum* from *O. crassa* by chamber shape: pyriform (pear-shaped) in axial section in *O. ovum* cf. sub-rectangular-subcircular in *O. crassa*, while in transverse section they are shorter and higher in *O. ovum* and the preseptal passage occupies a larger space. *O. ovum* is also generally larger in overall size cf. *O. crassa* (Hottinger, 1974).

O. maccagnoae has a more "nautiloid" external test shape than *O. ovum* which is spherical. In transverse section chamber shape length:height ratio is 3.5 in *O. maccagnoae* cf. 2 in *O. ovum*, highlighting the space occupied by the preseptal passages.

Misidentifications of *O. ovum* are common in the published literature. Many are in fact records of *Simplalveolina* or *Cisalveolina*.

Confident Stratigraphic Range: middle – late Cenomanian (common).

Uncertain Stratigraphic Range: late early Cenomanian.

Originally described from the middle Cenomanian of western France, Neumann & Fourcade in Schroeder & Neumann (1985) compiled records, mostly from France and Iberia, in which they state that *O. ovum* is known from the middle and late Cenomanian (see also Moreau et al., 1978). Hardenbol et al. (1998) show the species ranging from the base of the middle Cenomanian to the base of the *juddi* zone near the top of the late Cenomanian, but without explanation.

The vast majority of viable records of this species are middle or late Cenomanian. The oldest record is that of Simmons & Hart (1987) from Oman that is possibly late early Cenomanian (see also Rabu, 1993).

Geographic Distribution: The species is mostly known from confident records from France and the Pyrenees. There are also confirmed records from the Arabian Plate, although also many misidentifications.

Amongst non-illustrated records, the following are noteworthy. Al-Rifaiy & Cherif (1987) from undifferentiated Cenomanian of Jordan; Bernaus & Masse (2007) from middle Cenomanian, southern Iraq; Berthou (1984b) base middle – earliest late Cenomanian, Portugal; Caus et al. (2009) late Cenomanian, Spain. Reported from the "early Cenomanian" Ahmadi Formation of Qatar (El Beialy & Al-Hitimi, 1994) but the age of this formation is more likely middle Cenomanian (Bromhead et al., 2022). Reported (not illustrated) from the late Cenomanian of central Iran (Vaziri et al., 2005).

Genus ***Praealveolina*** Reichel 1933

Praealveolina is a commonly encountered genus of LBF in shallow marine platform carbonates of the Cenomanian and appears to be exclusive to that stage. It was created by Reichel (1933) using material from France and Spain, with *Praealveolina tenuis* Reichel, 1933 as its type species. New species/subspecies were created in subsequent publications, particularly Reichel (1936).

Praealveolina is the most apparently diverse Cenomanian alveolinoid genus with species variously included/excluded from the genus, as well as extensive use of subgenera and subspecies. The various species included in the genus have the potential to be biostratigraphically very useful (Schroeder & Neumann, 1985; Calonge et al., 2002). However, there have been several attempts to clarify the evolutionary relationships between the various species, often plagued with uncertainties over identity and age-calibration which have sometimes resulted in contradictory interpretations. See Figure 10 for an illustrated description of the genus.

There are nine generally accepted species of *Praealveolina* that occur in the Cenomanian. *P. simplex* Reichel, 1936 is often included, however, that species is herein assigned to *Simplalveolina* (see below). *P. lata* Reichel, 1936 is herein transferred to *Decastroia*. The nine *Praealveolina* species are (in alphabetical order):

- *P. acuta* Vicedo & Piuz, 2016
- *P. arabica* Vicedo & Piuz, 2016
- *P. brevis* Reichel, 1936
- *P. cretacea* (d'Archiac, 1837)
- *P. debilis* Reichel, 1936
- *P. iberica* Reichel, 1936
- *P. osimoi* (Zuffardi-Comerci, 1930) emend. De Castro, 1987
- *P. pennensis* Reichel, 1936

- *P. tenuis* Reichel, 1933

Other *Praealveolina* species that have an, as yet, 'uncertain' status, or which are recorded only very rarely and are poorly known, include *Alveolina maiellana* Silvestri, 1931 recovered from the mid-Cretaceous (possibly Cenomanian) of the Maiella Mountain (Central Italy) the illustrations of which provided by Silvestri (1931) recall a possible *Praealveolina*. *Praealveolina michaudi* Pêcheux, 2002 is the type species of *Caribalveolina* Vicedo, Aguilar, Caus & Hottinger, 2009. *Praealveolina cucumoides* (Silvestri, 1948) (a junior homonym of *Alveolina cucumoides* Chapman, 1908) is a Late Cretaceous form of *Pseudedomia* (see De Castro, 1988, p. 402).

To understand the genus better, it is necessary to review the more important research milestones and publications that concern this group.

After erecting the genus *Praealveolina* in 1933, in a major study on the alveolinoids as a group, Reichel (1936) added a considerable number of species to the genus in the forms of species, subspecies and varieties. He moved the previously established taxon *Alveolina cretacea* d'Archiac, 1837 into *Praealveolina* and created three groups of taxa:

P. cretacea	*cretacea* (type)
(Taxa with secondary chambers	*tenuis*
in A & B forms)	*lata*
	brevis
	debilis
P. iberica	*iberica* (type)
(Taxa with secondary	*iberica* var. *inflata*
chambers in B forms)	*pennensis*
P. simplex	*simplex* (type)
(Taxa with no secondary chambers)	

The species *simplex* was eventually removed from *Praealveolina*. At first, it was placed in a (new) subgenus *Praealveolina* (*Simplalveolina*) by Reichel in Loeblich & Tappan (1964), although it was still being referred to as a *Praealveolina* species by Neumann & Fourcade in Schroeder & Neumann (1985, who also elevated Reichel's subspecies to species rank). This re-assignment was followed by many subsequent authors (e.g., Calonge et al., 2002 and, to quote a recent example, Shakir & Moussa, 2023). This taxon is discussed as *Simplalveolina simplex* herein.

Neumann & Fourcade (1985) did not, however, appear to recognise the taxa *debilis* and *lata*. They also noted that they had observed secondary chamberlets in both A and B forms in *P. iberica* and *P. pennensis*, which rendered Reichel's subdivision void in respect of the *cretacea* and *iberica* subgroupings.

Cherchi & Schroeder (1989) proposed phylogenetic relations between the taxa recognised by Neumann & Fourcade (1985):

Lineage 1: *P. simplex*

Lineage 2: *P. iberica*, *P. pennensis*, *P. brevis*, *P. cretacea* and *P. tenuis*

Lineage 2 was characterised by a general increase in size, increase in axial elongation and increase in number and complexity of secondary chamberlets. Later this was modified further by Calonge (1989, 1994) who suggested that *P. iberica* was a common root to both lineages. Calonge (1994) also split the *P. cretacea* 'group' into 2 branches: *P. cretacea – P. tenuis* and *P. debilis – P. lata* (the two taxa not recognised by Neumann & Fourcade, 1985).

Calonge et al. (2002) revised much of Reichel's (and others') material and included new material of their own from Spain. They recognised a "Lower" and an "Upper Cenomanian Cycle" separated by what they call the "*…main intra-Cenomanian discontinuity… obviously marking a boundary of a third-order sequence*" (Calonge et al., 2002; p. 55).

The Lower Cenomanian Cycle was said to be characterised by a 'sequence' [presumably they mean some sort of evolutionary succession] of two species: *P. iberica* and *P. pennensis*, with some sections including an uppermost level with *P. debilis*.

The Upper Cenomanian Cycle was characterised by *P. brevis* at the base of that succession in *some* areas and which was associated with *P. simplex*. Shortly above the *P. brevis* level, *P. tenuis* appeared in all studied sections (although see below for older records). *P. simplex* was also found associated with *P. tenuis*.

Unfortunately, the important species *P. cretacea* (and its possible successor *P. lata*) was not observed anywhere in the Spanish material studied by Calonge et al. (2002) who were unable to provide a definitive reason for the apparent absence.

Calonge et al. (2002), drawing on studies by Calonge (1989), Caus et al. (1993, 1997) and Mató et al. (1996), discussed the age of the "intra-Cenomanian discontinuity" and the two cycles. The "Lower Cenomanian Cycle" could be calibrated to the *Mantelliceras mantelli* and *Acanthoceras rhotomagense* ammonite zones (early Cenomanian and lower middle Cenomanian respectively) and the "Upper Cenomanian Cycle" to the *Calycoceras naviculare* and *Metoicoceras geslinianum* zones (late but not latest Cenomanian). In terms of planktonic foraminiferal zones, the intra-Cenomanian discontinuity occurs within the *Rotalipora cushmani* zone (intra-middle – late, but not latest, Cenomanian; *sensu* Bidgood & Simmons, 2022). In the uppermost parts of the section the *Whiteinella archaeocretacea* and *Helvetoglobotruncana helvetica* zones are observed (intra-late – earliest Turonian and intra-early – intra-middle Turonian; *sensu* Bidgood & Simmons, 2022).

A carbon-isotope $\delta^{13}C$ peak near the top of some sections is correlated to the *W. archaeocretacea* planktonic foraminifera zone and is coincident with the disappearance of Cenomanian alveolinoids in general and *Praealveolina* spp. in particular.

The carbonate platform facies (of both cycles) are overlain by open shelf sediments of the *H. helvetica* planktonic foraminifera zone.

Calonge (1989) quoted in Calonge et al. (2002), stated that the shallow platform of the Lower Cycle begins at the *Mantelliceras saxbii* ammonite zone and ends at the top of the *Turrilites acutus* zone. In some places in the Iberian Ranges, they stated, remains of *P. tenuis* have been observed in the uppermost dolomitic unit of this cycle suggesting an inception in the upper part of the middle Cenomanian. This is somewhat contradictory to a proposed range chart (Calonge et al., 2002; text-fig. 3) which shows the range of *P. tenuis* in the Iberian ranges to be entirely within the Upper Cenomanian Cycle, which is demonstrably of late Cenomanian in age.

Vicedo & Piuz (2016) introduced two new species, *P. acuta* and *P. arabica*, based on material from Oman. However, at the time of writing these taxa have had relatively few records published from elsewhere.

Following Hayward et al. (2025; the "WoRMS" database) all alveolinoid genera treated herein are placed in the Family Alveolinidae Ehrenberg, 1839. Vicedo & Piuz (2016) erected two new subfamilies in which *Praealveolina* was chosen as type genus of the Subfamily Praealveolininae. *Simplalveolina* and *Multispirina* were also included in this new subfamily by Vicedo & Piuz (2016). The other subfamily created was the Decastroinae with *Decastroia* as the type genus and which also included *Reichelia*. The extremely close similarity between *Praealveolina* and *Decastroia* brings the nature of this higher-level taxonomy into question.

Although some *Praealveolina* species were recognised from the eastern parts of Neotethys from the 1960s (e.g., Israel, Lebanon), a rise in published work from the Middle East – especially Iran – from around the late 1990s/early 2000s has added considerably (though not always reliably) to the literature (see synonymy/chresonymy lists herein).

Dousti-Mohajer et al. (2021b) discussed the evolution of Cenomanian alveolinoids from the Iranian Zagros. That part of their study that refers to *Praealveolina* shows two "evolutionary trends" from two different sections in the Basin, which differ in timing but not so much in actual *order* of first appearances (Dousti-Mohajer et al., 2021b, fig. 5). Their species inventory differs from that of Calonge et al. (2002) in that they do recognise *P. cretacea*, but they do not recognise *P. pennensis*. However, the correct identity of the taxa discussed is doubtful and thus the order of appearance is suspect and chronostratigraphically unconstrained (Consorti & Vicedo, 2022).

In terms of identity, *Praealveolina* is differentiated from other alveolinoids (s.l.) by always being at least slightly fusiform to often very elongated fusiform; having a single spiral coil; with one row of main chamberlets in the equatorial region of the test (showing apertures in a single row along the apertural face) and with supplementary rows of chamberlets towards the axial poles (showing multiple rows of apertures) sometimes extending into the equatorial areas; septula aligned between chambers; and no post-septal passage.

Praealveolina can be very similar to the relatively newly erected genus *Decastroia* Vicedo & Serra-Kiel (2011 emended Vicedo & Piuz, 2016) which has 2 or more complete rows of 'cortical' (= 'main') chamberlets and 'medullar'/secondary chamberlets in polar and equatorial regions of the test. See the section on *Decastroia* for a discussion of this.

As a general remark about species identity in *Praealveolina*, the internal complexity of the shell and variations in external parameters, together with dimorphism, has lent themselves to extensive descriptive and biometric discrimination at species level. Of the authors previously quoted, Reichel (1936) provided lengthy prose descriptions of most species (especially *P. tenuis*). Pertinent biometric/descriptive data from several sources (Reichel, 1933, 1936; Schroeder & Neuman, 1985; Calonge et al., 2002 and Vicedo & Piuz, 2016) for all nine species is extracted and shown in Table 4. Variations and overlap of biometric data, particularly with respect to megalospheric and microspheric generations, demonstrates that correct identity (which requires an 'holistic' approach and is seldom discernible by a single parameter or characteristic) can be difficult to establish except where specimens are well-preserved and fortuitously (or deliberately selected to be meaningful) cut in thin-section. This statement can, of course, be applied to the vast majority of LBF taxa but it is particularly applicable when dealing with *Praealveolina* and related genera. Confusion with species of *Decastroia* is also very possible. Identification of specimens to species level in random thin-section should, at best, be treated with caution. Here we endorse Vicedo & Piuz (2016, recalling Hottinger, 2013) on best practice, when applicable, by recommending a protocol to approach morphometry considering: i) slight biometric changes to draw intraspecific variability in coeval specimens, or ii) significant biometric changes among specimens that are stratigraphically superposed as a criterion to separate species.

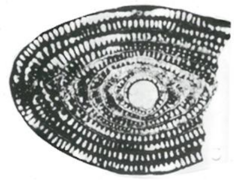
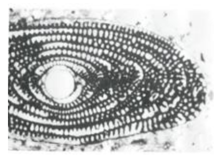
In the individual species treatments below, lengthy diagnoses and descriptions are not given and the reader is referred to the data in Table 4 and the original and subsequent descriptions in those references listed in the paragraph above.

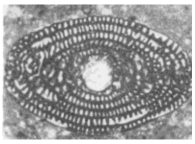
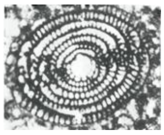
In the absence of a full biometric data set for all nine species, caution should be applied when discussing general morphological trends between *Praealveolina* species. However, if the maximum values shown in Table 4 are used, then the following *general* statements may be made about specific parameters which may *assist* in identification (values are smallest to largest, left to right):

Maximum embryo size:

Acuta → iberica/pennensis → arabica → debilis → brevis → cretacea → tenuis

Table 4: Characteristics of *Praealveolina* species herein shown in alphabetical order left to right. (meg = Megalospheric form; mic = Microspheric form; max = maximum; min = minimum)

CHARACTERISTIC	*PRAEALVEOLINA ACUTA*	*PRAEALVEOLINA ARABICA*	*PRAEALVEOLINA BREVIS*	*PRAEALVEOLINA CRETACEA*
Original description & provenance	Vicedo & Piuz (2016 ☼), middle – early late Cenomanian, Oman	Vicedo & Piuz (2016 ☼), middle – early late Cenomanian, Oman	As *P. cretacea* var. *brevis* Reichel (1936-7 ☼), Cenomanian, southern France	As *Alveolina cretacea* d'Archiac, (1837), Cenomanian, western France
Basic image (Reference source of image shown thus ☼. All images are types (holo-, lecto- or neo-) except *P. tenuis*, and are not to scale.)				
Other significant illustrative descriptions			Schroeder & Neumann (1985)	Schroeder & Neumann (1985)
Proloculus diameter µm ($_{meg}$ unless stated otherwise)	185-215 (*)	230-270 (*)	200-300 (**) / 200-342 / 22 $_{mic}$ (***) / 200-280 (****)	320-340 (up to 430) (* & **) / 20 $_{mic}$ (***) / 339-386 (***) / 270-450 (****)
Axial length (mm)	8 $_{max\ meg}$ / 8 $_{max\ mic}$ (*)	2.1 $_{max\ meg}$ / 3 $_{max\ mic}$ (*)	1.7-4.0 $_{mic}$ (**) / 1.7-3.7 $_{meg}$ / 6.3 $_{mic}$ (***) / 1.3-3.8 $_{meg}$ / 3.8-5.8 $_{mic}$ (****)	4-5 $_{meg}$ / 13-15 $_{mic}$ (**) / 4.5-4.8 $_{meg}$ / 13-15 $_{mic}$ (***) / 3.4-4.8 $_{meg}$ / 7.0-10.0 $_{mic}$ (****)
Equatorial diameter (mm)	1.3 $_{max\ meg}$ / 1.2 $_{max\ mic}$ (*)	1.4 $_{max\ meg}$ / 1.6 $_{max\ mic}$ (*)	1.4-1.8 $_{mic}$ (** & ***)	1.6-2 $_{meg}$ / up to 3 $_{mic}$ (**)
Elongation Index	2.4 $_{meg}$ / 5 $_{mic}$ (*)	1.5 $_{meg}$ / 1.8 $_{mic}$ (*)	1.2-2.2 $_{meg}$ / 3.6-4.0 $_{mic}$ (**) / 1.15-2.2 $_{meg}$ / 3.6-4.1 $_{mic}$ (***) / 1.2-3.2 $_{meg}$ / 2.9-4.8 $_{mic}$ (****)	2.3-2.9 $_{meg}$ / 5 $_{mic}$ (** & ***) / 2.3-2.8 $_{meg}$ / 4.0-5.9 $_{mic}$ (****)
Number of whorls	13-14 $_{meg}$ (*)	7-8 $_{meg}$ / 13-14 $_{mic}$ (*)	6-9 $_{meg}$ / 15-16 $_{mic}$ (** & ***) / 6-9 $_{meg}$ (****)	8-10 $_{meg}$ (**) / mostly 8, max 10 $_{meg}$ (***) / 7-10(11) $_{meg}$ (****)
Chambers per whorl (W_1 = 1st whorl etc.)			4 (W_1) → 12 (W_6) (***)	4 (W_1) → 21 (W_{final}) (***)
Chamberlets per chamber (measured in 4th whorl by ****)		14 per quad. (*)	20 (*) / 19 per mm in final whorl (***) / 12-22 (****)	19-22 per mm by W_6 (***) / 16-21 (****)
Secondary chamberlets (α values are axial diameters in µm)			Appear in 2nd or 3rd whorl in polar regions. 2 layers, sometimes 3 in later whorls (**) / Cellars, 2-3 rows, α<40 (****)	Polar regions from 1st whorl, then found increasingly closer to equator (** & ***) / Cellars, 4-5 rows, α<90 (****)
Shape of chamberlets in axial section			Oval, pear-shaped, narrow at base. 2 x higher than wide in 1st 3 whorls, then 3 x higher (**). Oval (***)	Slightly oval to quadrangular. Narrow and tall where no secondary chamberlets occur (**) / Narrow oval (**)
Apertures			2 at equator, up to 3 at poles (***) / 1-2 rows (****)	Generally 2 layers at equator (rarely 1), 3-4 at poles. Roughly circular cross section (** & ***) / 2 rows (****)
Preseptal canal			Circular-oval, 60-80 µm (**)	Circular-oval, c. 60 µm (**)
Septa			Increases in thickness towards base (**) / Narrow (***)	Fairly thick (** & ***)
Comments	(* Vicedo & Piuz, 2016) Dimorphism observed only in early growth stages.	(* Vicedo & Piuz, 2016)	(* Vicedo & Piuz, 2016) (** Schroeder & Neumann, 1985) (*** Reichel, 1936-7) (**** Calonge et al., 2002)	(* Vicedo & Piuz, 2016) (** Schroeder & Neumann, 1985) (*** Reichel, 1936-7 ☼) (**** Calonge et al., 2002)

CHARACTERISTIC	***PRAEALVEOLINA DEBILIS***	***P. IBERICA***	***P. OSIMOI***	***P. PENNENSIS***	***P. TENUIS***
Original description & provenance	As *P. cretacea* var. *debilis* Reichel (1936-7 ☼), Cenomanian, France	Reichel (1936-7 ☼), Cenomanian, France	As *Alveolina osimoi* Zuffardi-Comerci (1930), Cenomanian, Libya	As *P. iberica* var. *pennensis* Reichel (1936-7 ☼), Cenomanian, France	Reichel (1933), Cenomanian, southern France
Basic image (Reference source of image shown thus ☼. All images are types (holo-, lecto- or neo-) except *P. tenuis*, and are not to scale.)					
Other significant illustrative descriptions	Calonge et al. (2002)	Schroeder & Neumann (1985)	De Castro (1987 ☼) Emended diagnosis and description	Schroeder & Neumann (1985)	Schroeder & Neumann (1985 ☼)
Proloculus diameter µm ($_{meg}$ unless stated otherwise)	200-300 (***) / 210-280 (****)	140-240 (*) / 110-200 / 17 $_{mic}$ (***) / 110-170 (****)	80-200 (*****)	180-240 (** & ****) / 185 (***)	400-600 (*) / 300-570 (***) / 340-580 (****)
Axial length (mm)	Up to 3 $_{meg}$ / up to 10 $_{mic}$ (***) / 1.2-2.3 $_{meg}$ / 3.2-5.4 $_{mic}$ (****)	1-2 $_{meg}$ / up to 3 $_{mic}$ (**) / 1.05-1.12 $_{meg}$ / 2.5-3.0 $_{mic}$ (***) / 0.7-1.3 $_{meg}$ / 1.625-2.8 $_{mic}$ (****)	2.75-3.4 (*****)	1.5 $_{meg}$ / up to 5 $_{mic}$ (**) / 1.45 $_{meg}$ / 5.01 $_{mic}$ (***) / 0.9-1.5 $_{meg}$ / 2.15-3.0 $_{mic}$ (****)	6-8 (12) $_{max\ meg}$ / 14-28 $_{max\ mic}$ (** & ***) / 17-20 $_{max\ mic}$ (*) / 3.5-9.5 $_{meg}$ / 13.0-29.0 $_{mic}$ (****)
Equatorial diameter (mm)	2.8 $_{mic}$ (***)	1 $_{meg}$ (**) / 0.76-1.1 $_{meg}$ / 0.9-0.96 $_{mic}$ (***)	0.67-1.08 (*****)	1 $_{meg}$ / 3 $_{mic}$ (**)	1-2 $_{meg}$ / 2.6 $_{mic}$ (**) / 1.0.-2.1 $_{meg}$ (***)
Elongation Index	1.4-2.5 $_{meg}$ (commonly 1.8-2.0) (***) / 2.5-3.5 $_{meg}$ / 3.8-4.7 $_{mic}$ (****)	1.4 $_{meg}$ (**) / 1.21-1.5 $_{meg}$ / 1.5-1.8 $_{mic}$ (****)	3.3-4.5 (*****)	1.3 $_{meg}$ / 3.1 $_{mic}$ (**) / 1.28-1.4 $_{meg}$ / 2.0-2.13 $_{mic}$ (****)	4-6 $_{meg}$ / 7-9 $_{mic}$ (**) / 3.8-5 (6 in large indiv.) $_{meg}$ / 7.1-9.0 $_{mic}$ (***) / 4.0-5.5 $_{meg}$ / 8.5-9.0 $_{mic}$ (****)
Number of whorls	5-7 $_{meg}$ (***) / 6-7 $_{meg}$ (****)	5-7 $_{meg}$ / up to 10 $_{mic}$ (**) / 5-6, rarely 7 $_{meg}$ / 10 $_{mic}$ (***) / 5-7 $_{meg}$ (****)	8-9 $_{meg}$ / 11-12 $_{mic}$ (*****)	6-7 $_{meg}$ (** & ***) / 6-7(8) $_{meg}$ (****)	9-10 $_{meg}$ (*) / 9-12 $_{meg}$ (**) / 15-16 $_{mic}$ (**) (up to max 23 ***) Whorls tight in equatorial region (**) / 5-7(8) $_{meg}$ (****)
Chambers per whorl (W_1 = 1st whorl etc.)		4 (W_1) → 7 (W_6) (***)	3 (W_1) → 10 (W_9) (*****)	4 (W_1) → 7 (W_4) (***)	4 (W_1) → 23 (W_8) (***)
Chamberlets per chamber (measured in 4th whorl by ****)	13-20 (****)	8-10 (****)	25-35/mm (*****)	15-16 per mm (***) / 10-12 (****)	13-14 per mm (***) / 25-35 (****)
Secondary chamberlets (α values are axial diameters in µm)	Polar regions only (***) / Cellars, 3-4 rows, α<40 (****)	Very rare, 2 rows, α<10 (****) / slightly more common but small (***)	Polar regions only (*****)	In polar regions only, from 3rd or 4th whorl, limited to 2 layers (**) / Rare, 2-3 rows, α<20 (****)	In polar regions only, up to 5-6 layers (**) / Cellars, 4-6 rows, α<40 (****)
Shape of chamberlets in axial section		Taller than wide, gain in height towards poles rather than be divided by floors (***)	Rounded in early whorls, becoming oval from W_3, then more elongate and, after W_8, subrectangular (*****)		
Apertures	1 row (****)	1 row, sometimes doubled at the pole (***) / 1 row (****)	1 row, sometimes doubled at the pole (*****)	1 row often 2 at poles (***) / 1 row (****)	1 row (2 in final whorls of large individuals), up to six in polar regions (***) / 1 row (****)
Preseptal canal		Circular, 50-60 µm (**)	Circular-slightly oval (*****)	Circular, 60-70 µm (**)	Circular-oval, c. 90 µm (**)
Septa	Thick (***)	Thin (**)	Thin (*****)	Thin (**)	Thin (**)
Comments	(*** Reichel, 1936-7) (**** Calonge et al., 2002)	(* Vicedo & Piuz, 2016) (*** Reichel, 1936-7) (**** Calonge et al., 2002)	(***** De Castro, 1987)	(* Vicedo & Piuz, 2016) (**** Calonge et al., 2002)	(* Vicedo & Piuz, 2016) (** Schroeder & Neumann, 1985) (*** Reichel, 1933, 1936-7) (**** Calonge et al., 2002)

Maximum axial diameter (megalospheric forms): *pennensis → iberica/arabica → debilis → brevis → cretacea → acuta → tenuis*

Maximum axial diameter (microspheric forms): *iberica/arabica → pennensis → brevis → acuta → debilis → cretacea → tenuis*

Maximum equatorial diameter (megalospheric forms, position of *brevis* & *debilis* unknown): *pennensis/iberica → acuta/arabica → cretacea/tenuis*

Maximum equatorial diameter (microspheric forms): *iberica → acuta → arabica → brevis → tenuis → debilis → pennensis/cretacea*

Elongation Index (megalospheric forms): *pennensis/iberica/arabica → acuta/lata → cretacea → brevis → debilis → tenuis*

Elongation Index (microspheric forms): *iberica/arabica → pennensis → debilis/brevis → acuta → cretacea → tenuis*

Difference between EI(meg) and EI(mic) – increasing dimorphism: *iberica/arabica → debilis → brevis/pennensis → acuta → tenuis/cretacea*

Number of whorls (megalospheric forms): *iberica/debilis → arabica/pennensis → brevis → cretacea → tenuis → acuta*

These trends are, to a certain perhaps simplistic extent, the general application of 'Cope's Rule' (Rensch, 1948) to praealveolinoid development, although this has not been tested.

As a *general principle*, the compiled range data for those species of *Praealveolina* included in Schroeder & Neumann (1985) has been taken as a starting point and any later modifications to those ranges are discussed. The majority of publications which include records of one or more species of *Praealveolina*, especially in the Middle East, tend to be of simple occurrence reports, with or (often) without illustrated verification or age calibration. Where illustrations are present, they are often single images of random sections which can be difficult to fully verify. The best image from any given set of material is generally selected by authors, but that does not guarantee identity verification, consequently they tend to add little to the determination of stratigraphic limits to species' ranges. Data quality can therefore be variable for *Praealveolina* occurrences in the literature. Only references which materially aid such determination are included in individual species discussions.

Praealveolina acuta Vicedo & Piuz, 2016

FIGURE 28

T 2016 *Praealveolina acuta* sp. nov., Vicedo & Piuz, p. 843, fig. 19; middle – early late Cenomanian, Oman Mountains [age calibration after Bromhead et al., 2022].
? 2016 *Praealveolina cretacea* – Assadi et al., fig. 6 (a10); late Cenomanian, Iranian Zagros [or possibly *P. tenuis*].
? 2018 *Praealveolina* cf. *tenuis* – Luger, pl. 17, figs. 6-7; middle Cenomanian, northern Somalia.
2023b *Praealveolina cretacea* – Mehrabi et al., fig. 15 (A-F, H-J); undifferentiated middle – late Cenomanian, Persian Gulf.
2023a *Praealveolina cretacea* – Mehrabi et al., fig. 6L; undifferentiated Cenomanian, Iranian Zagros.

Reference Images: Vicedo & Piuz (2016), p. 843, fig. 19.

Taxonomy/Identity: First described from the approximate middle to early late Cenomanian of Oman by Vicedo & Piuz (2016), some recent records of *P. cretacea* might be better assigned to this species.

It is morphologically similar to *P. tenuis*, but *P. acuta* is smaller and with a smaller proloculus and acute poles. *Decastroia lata* is also similar but has fewer whorls, a larger equatorial diameter, and supplementary chamberlets from the polar to equatorial regions.

Confident Stratigraphic Range: undifferentiated middle – early late Cenomanian.

Uncertain Stratigraphic Range: not applicable.

Geographic Distribution: Known only from the Arabian Plate and possibly Somalia.

Praealveolina arabica Vicedo & Piuz, 2016

FIGURE 29

T 2016 *Praealveolina arabica* sp. nov., Vicedo & Piuz, p. 839, fig. 18; middle – early late Cenomanian, Oman Mountains [age calibration after Bromhead et al., 2022].
2019 *Praealveolina cretacea* – Özkan & Altıner, fig. 7 (12-13, 17, ?15-16); undifferentiated Cenomanian [probably middle Cenomanian according to Simmons et al., 2020], Turkish Arabian Plate [fig. 7 (14) is possibly a rhapydioninid].
? 2020 *Praealveolina* cf. *arabica* – Simmons et al., fig. 8 (8); middle Cenomanian, Türkiye.

Reference Images: Vicedo & Piuz (2016) p. 839, fig. 18.

Taxonomy/Identity: First described by Vicedo & Piuz (2016) from the middle – early late Cenomanian of Oman.

P. arabica differs from *P. cretacea* (and indeed *P. tenuis*) in having less dimorphism, a smaller overall test size, a smaller proloculus and fewer whorls in adult tests. It also develops secondary chamberlets in the equatorial zone only in the late adult (gerontic) growth stage.

It has less pronounced dimorphism, more chamberlets per chamber and a lower elongation index than *P. brevis*.

Confident Stratigraphic Range: undifferentiated middle – early late Cenomanian.

Uncertain Stratigraphic Range: not applicable.

Geographic Distribution: So far only known from the Arabian Plate.

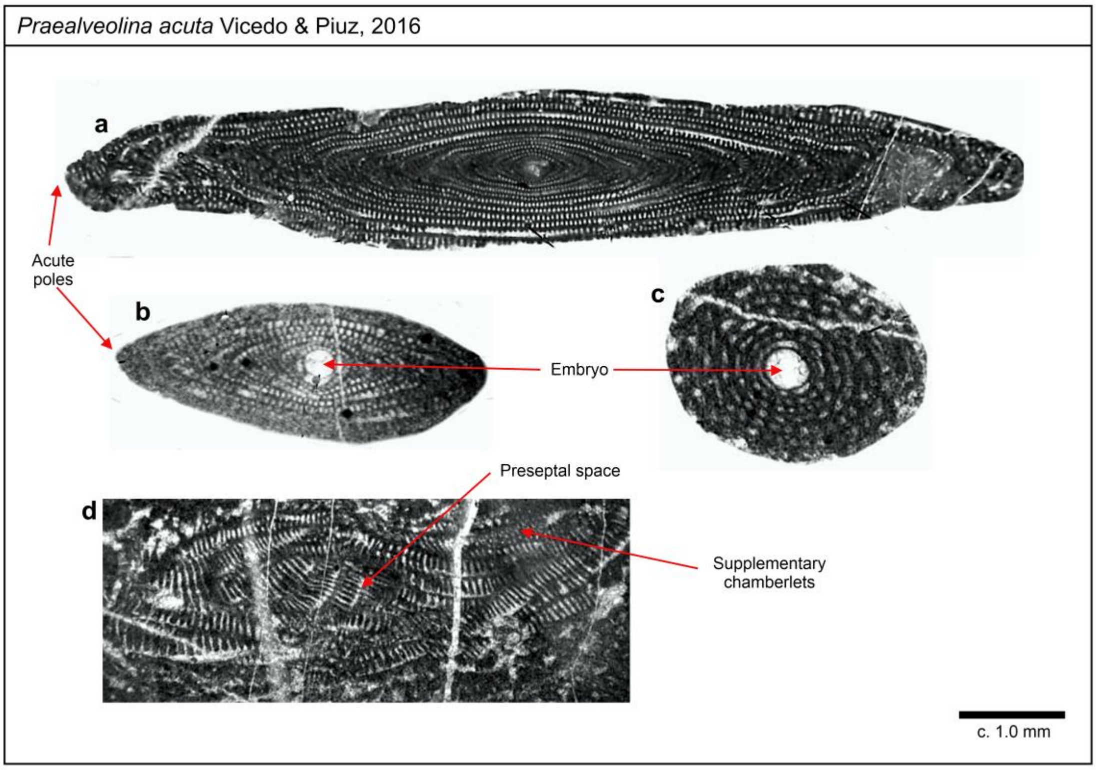


Fig. 28: Representative illustrations of *Praealveolina acuta*: **a.** Axial section (holotype), Vicedo & Piuz (2016, fig. 19G; middle – early late Cenomanian, Oman); **b.** Axial section, Vicedo & Piuz (2016, fig. 19E; middle – early late Cenomanian, Oman); **c.** Oblique near equatorial section, Vicedo & Piuz (2016, fig. 19I; middle – early late Cenomanian, Oman); **d.** Tangential section, Vicedo & Piuz (2016, fig. 19K; middle – early late Cenomanian, Oman).

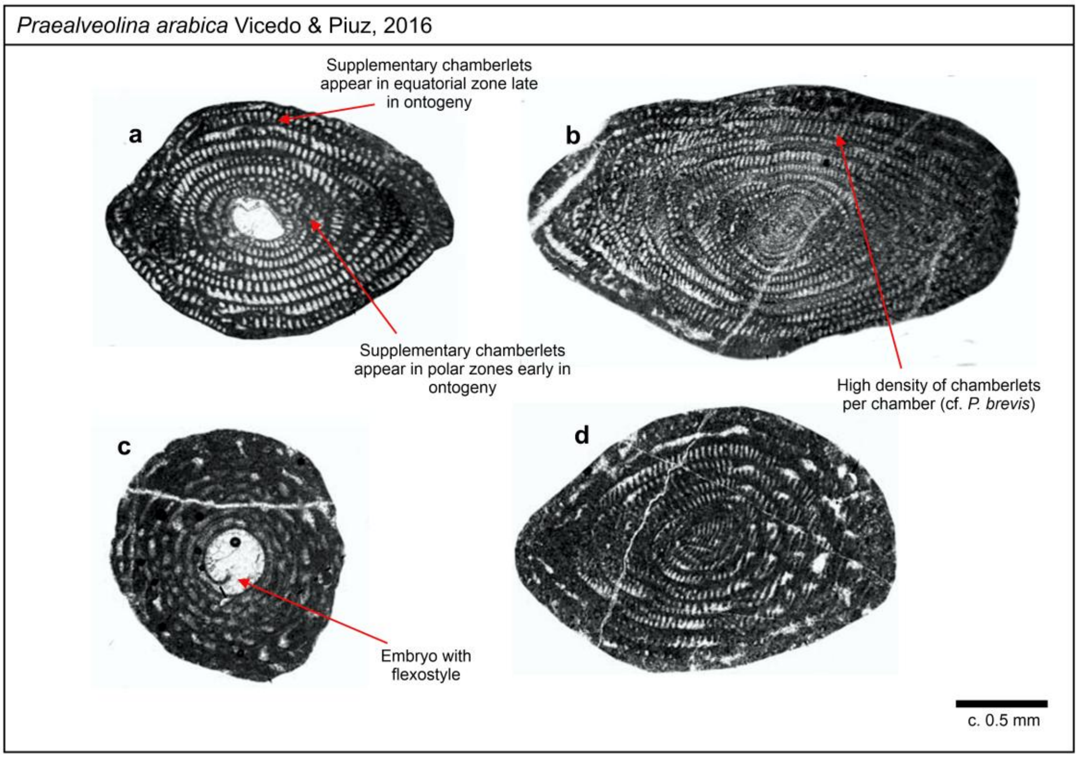


Fig. 29: Representative illustrations of *Praealveolina arabica*: **a.** Axial section (holotype), Vicedo & Piuz (2016, fig. 18C; middle – early late Cenomanian, Oman); **b.** Axial section, microspheric generation Vicedo & Piuz (2016, fig. 18E; middle – early late Cenomanian, Oman); **c.** Oblique near equatorial section, Vicedo & Piuz (2016, fig. 18B; middle – early late Cenomanian, Oman); **d.** Tangential section, Vicedo & Piuz (2016, fig. 18I; middle – early late Cenomanian, Oman).

Praealveolina brevis Reichel, 1936
FIGURE 30

T 1936 *Praealveolina cretacea brevis* n. subsp. – Reichel, p. 60, pl. III, fig. 1; pl. V, figs. 1-2; pl. VI, fig. 3; pl. VII, fig. 14; late Cenomanian, southern France.
? 1961 *Praealveolina* – Cuvillier, pl. 35, fig. 1; undifferentiated Cenomanian, Aquitaine, western France.
Non 1967 *Praealveolina* aff. *brevis* – Souquet, pl. 18, fig. 2; undifferentiated Cenomanian, Spanish Pyrenees [= *P. iberica, fide* Schroeder & Neumann, 1985].
? 1971 *Praealveolina cretacea brevis* – Ramírez del Pozo, p. 299, pl. 78, fig. 1; undifferentiated Cenomanian, northern Spain.
? 1971 *Praealveolina cretacea cretacea* – Ramírez del Pozo, pl. 77; no age stated, northern Spain.
Non 1971 *Praealveolina cretacea brevis* – Ramírez del Pozo, pls. 80-81 late Cenomanian, northern Spain [= *P. iberica, fide* Schroeder & Neumann, 1985].
1973 *Praealveolina iberica* – Berthou, pl. 5, fig. lb; middle Cenomanian, Portugal [*fide* Schroeder & Neumann, 1985].
1973 *Praealveolina cretacea brevis* – Bilotte, pl. 2, fig. 10; [*non* pl. 5, fig. 3 = *P. cretacea*]; late Cenomanian, French Pyrenees
1973 *Praealveolina cretacea brevis* – Bilotte, ?pl. 2, fig. 10; pl. 5, fig. 3; middle – late Cenomanian, French Pyrenees.
1974 *Praealveolina* gr. *cretacea* – Canérot, p. 315, pl. 29, fig. 8; undifferentiated Cenomanian, northern Spain [*fide* Schroeder & Neumann, 1985].
1974 *Praealveolina cretacea brevis* – Hottinger, pl. 17, fig. 2; undifferentiated Cenomanian, Spanish Pyrenees.
? 1974 *Praealveolina* gr. *cretacea* – Juignet et al., p. 2281, pl. 1, fig. 5; middle Cenomanian, France [Note: Schroeder & Neumann (1985) include this image in the synonymy of both *P. cretacea* and *P. iberica*].
? 1975 *Praealveolina* gr. *cretacea brevis* – Christodoulou & Tsaila-Monopolis, pl. 56, fig. 1; undifferentiated Cenomanian, Greece.
1981 *Praealveolina* cf. *iberica pennensis* – Tronchetti, pl. 22, fig. 6; late Cenomanian, Provence, France [*fide* Schroeder & Neumann, 1985].
1984 *Praealveolina cretacea brevis* – Bilotte, pl. 6, fig. 10; late Cenomanian, French Pyrenees.
1985 *Praealveolina brevis* – Neumann & Fourcade in Schroeder & Neumann, p. 117, pl. 56, figs. 1-8; middle – late Cenomanian, western Europe (illustrated from the late Cenomanian of France, including type material).
Non 1987 *Praealveolina* cf. *brevis* – Reitner, pl. 45, fig. 7; undifferentiated Cenomanian, northern Spain [indeterminate, but probably not an alveolinoid].
2002 *Praealveolina brevis* – Calonge et al., pl. 5, figs. 2-8, ?9-10 [because of poor preservation]; late Cenomanian, Pyrenees and topotypes from southern France.
2018 *Praealveolina brevis* – Andrade, pl. 10, fig. 10; late Cenomanian, Portugal.
? 2021a *Praealveolina brevis* – Dousti-Mohajer et al., pl. 2, fig. e; upper late Cenomanian, Iranian Zagros.
? 2021b *Praealveolina brevis* – Dousti-Mohajer et al., fig. 4; fig. 8e; fig. 9e; upper late Cenomanian, Iranian Zagros. [possibly = *Cisalveolina* but alternate septula cannot be observed. Note: same illustration used in both 2021 publications].
? 2022b *Praealveolina brevis* – Dousti-Mohajer et al., fig. 4e; late Cenomanian, Iranian Zagros.
2025 *Praealveolina cretacea* var. *brevis* – Martín-Closas et al., fig 7G-H; late Cenomanian, Spain.

Reference Images: Schroeder & Neumann (1985) p. 117, pl. 56, figs. 1-8.

Taxonomy/Identity: *Praealveolina brevis* is very similar to *P. pennensis* but *P. iberica* and *P. cretacea* are also similar. It is hampered from definitive separation by its relatively imprecise description.

It has a slightly larger proloculus than *P. pennensis* and a more pear-shaped axial cross section of the chamberlets. It also has greater basal thickening of the septa and secondary chamberlets that appear further into the equatorial region than *P. pennensis* as well as more chamberlets per chamber as a whole. *P. debilis* can also have more layers of chamberlets (sometimes 3) in the polar regions compared with *P. pennensis*.

According to Calonge et al. (2002) "*P. brevis* is easily distinguished from *P. cretacea*…by its smaller size and its internal structure exhibiting only one row of apertures and one floor in the equatorial zone, and only one layer of secondary chamberlets developed in the polar region while *P. cretacea* has two rows of apertures and two floors in the equatorial zone…".

Confident Stratigraphic Range: middle – late Cenomanian. Middle Cenomanian records are scarce.

Uncertain Stratigraphic Range: not applicable.

Type material is from the late Cenomanian of southern France (Reichel, 1936; Calonge et al., 2002). Most valid records are from the late Cenomanian (Calonge et al., 2002) but known to occur in the basal part of the middle Cenomanian (Berthou, 1984b) supporting the view of Schroeder & Neumann (1985) that the full range is middle – late Cenomanian (their questionable, base Turonian range extension can be discounted).

Geographic Distribution: The validated records of this species are from Iberia, the Pyrenees and southern France. Records from Greece and the Arabian Plate are questionable.

Praealveolina cretacea (d'Archiac, 1837)
FIGURE 31

1837 *Alveolina cretacea* – d'Archiac, p. 191; "Cretaceous Stage 2" (=Cenomanian), western France. No types designated by d'Archiac. Topotypes designated by Reichel (1936).

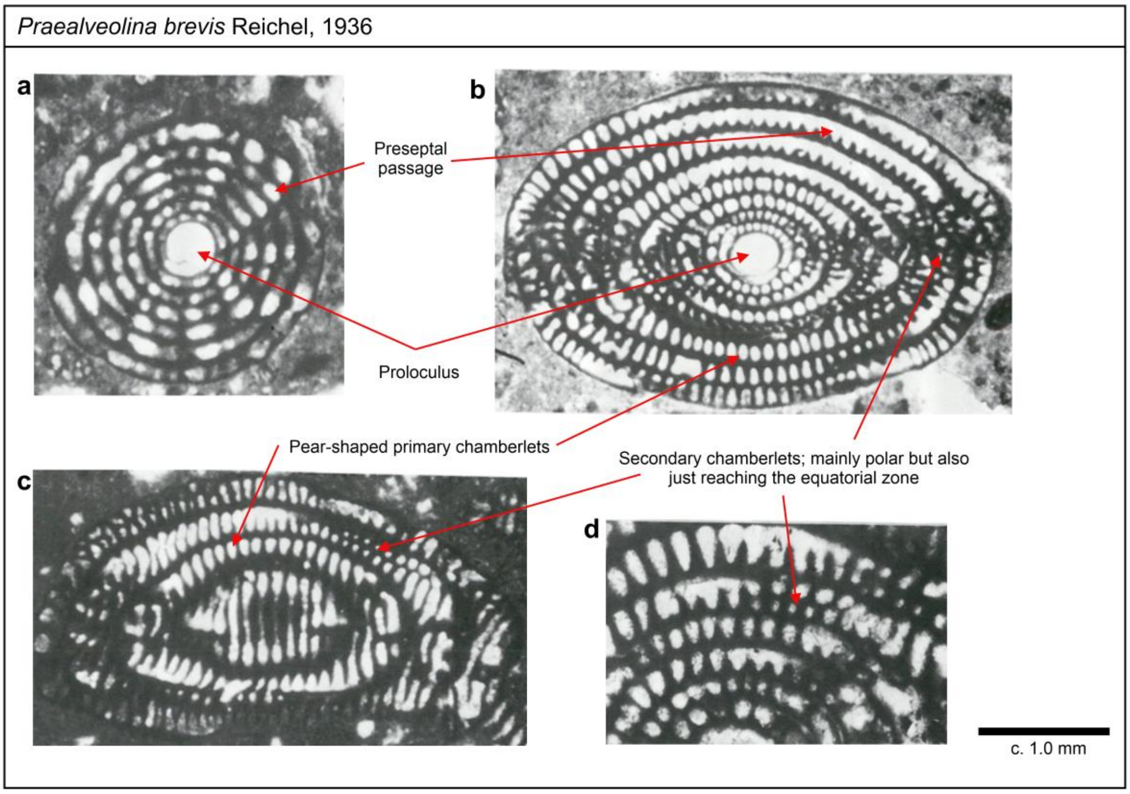


Fig. 30: Representative illustrations of *Praealveolina brevis*: **a.** Equatorial section, Schroeder & Neumann (1985, pl. 56, fig. 3; late Cenomanian, southern France); **b.** Axial section, Schroeder & Neumann (1985, pl. 56, fig. 4; late Cenomanian, southern France); **c.** Subaxial section, Schroeder & Neumann (1985, pl. 56, fig. 6; late Cenomanian, southern France); **d.** Axial section (detail), Schroeder & Neumann (1985, pl. 56, fig. 8; late Cenomanian, southern France). Scale bar is approximate and applies only to **a**-**c**.

T 1936 *Praealveolina cretacea cretacea* – Reichel, p. 52-54; pl. 2, fig. 2; pl. 5, figs. 3-5; pl. 6, fig. 5 [designated as neotype by Schroeder & Neumann, 1985]; pl. 8, fig. 2; undifferentiated Cenomanian, western France.

Non 1936 *Praealveolina cretacea* – Reichel, p. 7, text-fig. 1 undifferentiated Cenomanian, western France [= *P. tenuis, fide* Schroeder & Neumann, 1985].

? 1941 *Praealveolina cretacea* – Reichel, pl. 15, fig. 7; undifferentiated Cenomanian, Iranian Zagros.

? 1965 *Praealveolina* gr. *P. cretacea* – Hamaoui, pl. 9, fig. 10, 13; pl. 12, figs. 5-6; pl. 15, ?figs. 7a-b; undifferentiated Cenomanian, Israel [figs. 7a-b are probably *Decastroia serrakieli*].

1965 *Praealveolina tenuis* – Saint-Marc, pl. 15, figs. 1, 3; Cenomanian (“upper levels”), western France [*fide* Schroeder & Neumann, 1985].

1966 *Praealveolina cretacea tenuis* – Gohrbandt, p. 68, pl. 1, figs. 1-4; middle – late Cenomanian, Libya [*fide* Schroeder & Neumann, 1985].

1966 *Praealveolina* gr. *cretacea* – Hamaoui, pl. 6, figs. 8; pl. 9, fig. 8; undifferentiated Cenomanian, Israel.

Non 1967 *Praealveolina* ex gr. *P. cretacea* – Arkin & Hamaoui, p. 4, pl. 2, fig. 5; undifferentiated Cenomanian, Israel [= *P. tenuis, fide* Schroeder & Neumann, 1985].

1969 *Praealveolina cretacea* – Sampò, pl. 43, fig. 3; undifferentiated Cenomanian, Iranian Zagros.

1971 *Praealveolina cretacea* – Guernet, pl. 46, fig. 2; late Cenomanian, Greece [*fide* Schroeder & Neumann, 1985].

Non 1971 *Praealveolina cretacea cretacea* – Ramírez del Pozo, pl. 77; no age stated, northern Spain [probably = *P. brevis*].

1973 *Praealveolina cretacea* – Viallard, p. 212, pl. 25, fig. 2; pl. 27, fig. 2; Cenomanian, Spanish Pyrenees [*fide* Schroeder & Neumann, 1985].

1973 *Praealveolina cretacea brevis* – Bilotte, [*non* pl. 2, fig. 10 = *P. brevis*]; pl. 5, fig. 3; middle – late Cenomanian, French Pyrenees.

Non 1973 *Praealveolina* (*Praealveolina*) *cretacea* – El Naggar & Al-Rifaiy, fig. 6 (10-11); “very late” Cenomanian, Kuwait [= *Decastroia oblonga*].

1974 *Praealveolina cretacea cretacea* – Hottinger, pl. 16; figs. 1, 3; Cenomanian, Provence, France.

Non 1974 *Praealveolina* gr. *cretacea* – Hamaoui & Brun, p. 23, pl. 26; Cenomanian – “probably” Turonian, Middle East [= *P. tenuis*].

Non 1974 *Praealveolina* gr. *cretacea* – Juignet et al., p. 2281, pl. 1, fig. 5; middle Cenomanian, France [probably *P. brevis*. Note: Schroeder & Neumann (1985) include this image in the synonymy of both *P. cretacea* and *P. iberica*].

Non 1974 *Praealveolina* gr. *cretacea* – Canérot, p. 315, pl. 29, fig. 7 [= *P. iberica, fide* Schroeder & Neumann, 1985].

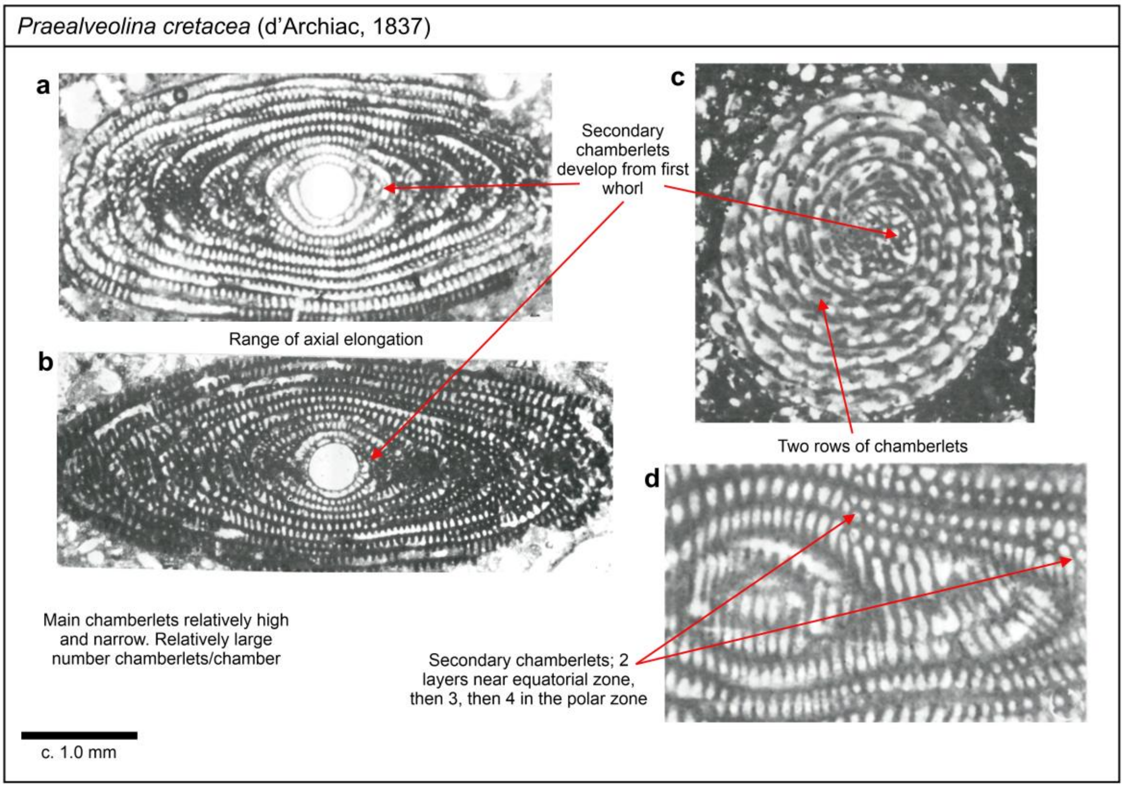


Fig. 31: Representative illustrations of *Praealveolina cretacea*: **a.** Axial section, Schroeder & Neumann (1985, pl. 58, fig. 2; undifferentiated Cenomanian, western France); **b.** Axial section, Schroeder & Neumann (1985, pl. 57, fig. 5; undifferentiated Cenomanian, western France); **c.** Transverse equatorial section, Schroeder & Neumann (1985, pl. 58, fig. 3; undifferentiated Cenomanian, western France); **d.** Axial section (detail), Schroeder & Neumann (1985, pl. 58, fig. 6; undifferentiated Cenomanian, western France). Scale bar is approximate and applies only to **a**-**c**.

? 1976 *Praealveolina cretacea* – Kalantari, pl. 19, fig. 2; pl. 22, fig. 30; undifferentiated Cenomanian, Iranian Zagros.

Non 1977 *Praealveolina* gr. *cretacea* – Prestat, p. 274, pl. 15, fig. 2 [= *P. tenuis, fide* Schroeder & Neumann, 1985].

1979 *Praealveolina* gr. *cretacea* – Deloffre & Hamaoui, pl. 6; pl. 7, fig. 2; middle – late Cenomanian, western France.

Non 1980 *Praealveolina cretacea* – Vila, p. 160, pl. 26, figs. 4-6 [*fide* Schroeder & Neumann, 1985].

1981 *Praealveolina* gr. *cretacea* – Ishak-Ishak, p. 93, pl. 3, figs. 11-12; middle Cenomanian, Syria [*fide* Schroeder & Neumann, 1985].

1981 *Praealveolina* gr. *cretacea* – Tronchetti, pl. 23, figs. 1-3; middle – late Cenomanian, Provence, France [*fide* Schroeder & Neumann, 1985].

Non 1981 *Praealveolina* gr. *cretacea* – Tronchetti, pl. 22, fig. 3 [= *P. tenuis, fide* Schroeder & Neumann, 1985].

? 1982 *Praealveolina cretacea* – Mouty & Saint-Marc, pl. 2, fig. 3; middle – late Cenomanian, NW Syria.

1984 *Praealveolina* gr. *cretacea* – Bilotte, pl. 6, fig. 11; middle Cenomanian, French Pyrenees.

1985 *Praealveolina cretacea* – Neumann & Fourcade in Schroeder & Neumann, p. 118, pl. 57, figs. 1-5; pl. 58, figs. 1-7; pl. 59, figs. 1-7; middle – late Cenomanian (?early Cenomanian), pan-Mediterranean.

? 1987 *Praealveolina cretacea* – Al-Rifaiy & Cherif, pl.2, figs. 12-13; undifferentiated Cenomanian, Jordan.

? 1988 *Praealveolina* gr. *cretacea* – Sartorio & Venturini, p. 108 (lower); middle Cenomanian, Yemen.

1989 *Praealveolina* cf. *cretacea* – Kuss & Malchus, text-fig. 24; late Cenomanian, Egypt.

Non 1990 *Praealveolina cretacea* – Cherchi & Schroeder, fig. 4; middle – late Cenomanian, Iranian Zagros [= *Decastroia miaidinensis*].

Non 1992 *Praealveolina cretacea* – Kalantari, text-fig. 157; pl. 75; undifferentiated Cenomanian, Iranian Zagros [= *Cisalveolina fraasi*].

1992 *Praealveolina* gr. *cretacea* – Sartorio et al., pl. 1, fig. 4, ?5, ?6; undifferentiated early – middle Cenomanian, Italy/Slovenia border.

Non 1998 *Praealveolina cretacea* – Whittaker et al., pl. 90, figs. 3-6; pl. 91, fig. 1; undifferentiated Cenomanian, Qatar [= *Decastroia;* pl. 91, fig. 1 = *Decastroia oblonga*. States total range in Middle East as intra-middle Cenomanian – middle Turonian although rationale not clear].

2002 *Praealveolina cretacea* – Calonge et al., pl. 7, figs. 1-2, 4-5; undifferentiated Cenomanian, western France, topotypes.

2003 *Praealveolina cretacea* – Schulze, fig. 11c; middle – late Cenomanian, Jordan.

2004 *Praealveolina cretacea* – Schulze et al., fig. 10C [=D]; middle – late Cenomanian, Jordan [Figure 10 appears to be mis-captioned, should be image D].

Non 2004 *Praealveolina cretacea* – Menegatti, pl. 9, figs. 6, 8-9; pl. 10, fig. 2; pl. 13, fig. 3; middle – late Cenomanian, Dubai [= *Decastroia oblonga*].

Non 2008 *Praealveolina cretacea* – BouDagher-Fadel, pl. 5.20, fig. 12; undifferentiated Cenomanian, Qatar. [later (BouDagher-Fadel, 2018) revised as *Pseudedomia* (= *Sellialveolina* sp.)].

Non 2011 *Praealveolina cretacea* – Amer, pl. 20, fig. 2; age not specified, Western Desert, Iraq [= *Cisalveolina fraasi*].

? 2012 *Prealveolina* (sic) *cretacea* – Kiarostami et al., pl. 1, fig. 2; Cenomanian, Iranian Zagros.

? 2012 *Praealveolina cretacea* – Ghanem et al., fig. 6e (13?, 22); late Cenomanian, Syria.

? 2012 *Praealveolina cretacea* – Orabi et al., fig. 3 (*non* C, F [=*Decastroia oblonga*], ?I, ?K, ?L); ?fig. 4 (A); late Cenomanian, Sinai, Egypt.

? 2013 *Praealveolina cretacea* – Rahimpour-Bonab et al., fig. 8C; undifferentiated Cenomanian, Iranian Zagros.

? 2013 *Praealveolina cretacea* – Shahin & Elbaz, pl. 2, fig. 29; undifferentiated Cenomanian, Sinai, Egypt.

Non 2013 *Praealveolina cretacea* – Al-Dulaimi et al., pl. 9, fig. 7; late Cenomanian, southern Iraq [possibly = *P. tenuis*].

? 2014 *Praealveolina cretacea* – Afghah et al., figs. ?9B, *non* 12F [possibly = *P. iberica*]; middle – late Cenomanian, Iranian Zagros.

? 2014a *Praealveolina cretacea* – Omidvar et al., pl. 2, fig. E; undifferentiated Cenomanian, Iranian Zagros [possibly = *Decastroia*].

? 2014b *Praealveolina cretacea* – Omidvar et al., fig. 3 (5); undifferentiated Cenomanian, Iranian Zagros [possibly = *Decastroia*].

Non 2016 *Praealveolina cretacea* – Assadi et al., fig. 6 (a10); late Cenomanian, Iranian Zagros [= *P. tenuis* or *P. acuta*].

? 2016 *Praealveolina cretacea* – Kazemzadeh & Loftpoor, pl. 1, fig. 11; undifferentiated Cenomanian, Iranian Zagros.

? 2016 *Praealveolina cretacea* – Rikhtegarzadeh et al., pl. 2, figs. 1-3; undifferentiated Cenomanian, Iranian Zagros.

? 2016 *Praealveolina cretacea* – Ghaseminia et al., fig. 4(I); undifferentiated Albian – Cenomanian, Iranian Zagros.

? 2017 *Praealveolina cretacea* – Rikhtegarzadeh et al., pl. 1, fig. 7; undifferentiated Cenomanian, Iranian Zagros.

? 2017 *Praealveolina cretacea* – Jamalpour et al., pl. 2c; undifferentiated Cenomanian, Iranian Zagros.

2018 *Praealveolina cretacea* – Andrade, pl. 11, figs. 2-3; late Cenomanian, Portugal.

? 2018 *Praealveolina cretacea* – Jamalpour et al., pl. II, fig. 7; undifferentiated Cenomanian, Iranian Zagros.

Non 2018 *Praealveolina cretacea* – Luger, pl. 17, figs. 8-9, 11; middle Cenomanian, Somalia [= *Decastroia serrakieli*].

? 2019 *Praealveolina cretacea* – Parnian et al., fig. 3 (F); undifferentiated Cenomanian, Iranian Zagros.

? 2019 *Praealveolina cretacea* – Kiarostami et al., pl. 1, fig. j; undifferentiated Cenomanian, Iranian Zagros [equatorial section only].

? 2019 *Praealveolina* sp. – Saeedi-Razavi et al., pl. 1, fig. 13; Cenomanian, Iranian Zagros.

Non 2019 *Praealveolina cretacea* – Özkan & Altıner, fig. 7 (12-17); Cenomanian, Turkish Arabian Plate [probable middle Cenomanian – Simmons et al., 2020; = *P. arabica*].

Non 2020 *Praealveolina cretacea* – Haftlang et al., fig. 15f; pl. 2, fig. 22; middle and late Cenomanian, Iranian Zagros [probably = *Decastroia*].

? 2021 *Praealveolina cretacea* – BouDagher-Fadel & Price, pl. 1, fig. d; undifferentiated Cenomanian, France.

? 2021a *Praealveolina cretacea* – Dousti-Mohajer et al., pl. 2, fig. f; middle Cenomanian, Iranian Zagros.

? 2021b *Praealveolina cretacea* – Dousti-Mohajer et al., fig. 8f; fig. 9c; early Cenomanian, Iranian Zagros.

? 2021 *Praealveolina cretacea* – Packer et al., pl. 1, fig. 3; undifferentiated Cenomanian, northern Iraq.

? 2021 *Praealveolina* gr. *cretacea* – Rineau et al., fig. 5A; fig. 7J; late Cenomanian, SE France.

? 2021 *Praealveolina cretacea* – Saeedi-Razavi et al., pl. 1, fig. 7; undifferentiated Cenomanian, Iranian Zagros.

? 2021 *Praealveolina cretacea* – Shapourikia et al., fig. 10i; middle – late Cenomanian, Iranian Zagros.

Non 2021 *Praealveolina cretacea* – Dehghanian & Afghah, fig. 7(2); middle Cenomanian, Iranian Zagros [= *P. tenuis*].

2022 *Praealveolina cretacea* – Asghari et al., pl. 1, fig. f; late Cenomanian, Iranian Zagros.

? 2022 *Praealveolina cretacea* – Al-Dulaimy et al., pl. 2, figs. E-F; early late Cenomanian, SE Iraq.

? 2022 *Praealveolina* ex. grp. *cretacea* – Youssef et al., pl. 19; middle – late Cenomanian, Kuwait [two different species; specimen 4745 = possibly *P. cretacea*, specimen 4628 = *Decastroia*].

Non 2022b *Praealveolina cretacea* – Dousti-Mohajer et al., fig. 4c; middle – late Cenomanian, Iranian Zagros [= *Myriastyla*].

Non 2022 *Praealveolina* gr. *cretacea* – Schlagintweit & Yazdi-Moghadam, fig. 2A; undifferentiated Cenomanian, Iranian Zagros [= *P. tenuis*].

? 2023 *Praealveolina cretacea* – Dawood & Al-Dulaimi, pl. 1, fig. G; early late Cenomanian, southern Iraq.

? 2023 *Praealveolina* gr. *cretacea* – Al-Salihi & Ibrahim, pl. 2, fig. D; early late Cenomanian, southern Iraq [possibly = *Decastroia*].

Non 2023 *Praealveolina cretacea* – Esfandyari et al., fig. 21(s); Cenomanian, Iranian Zagros [indeterminate but not *Praealveolina*].

Non 2023b *Praealveolina cretacea* – Mehrabi et al., fig. 15 (A-F, H-J); undifferentiated middle – late Cenomanian, Persian Gulf [probably = *P. acuta*].

Non 2023a *Praealveolina cretacea* – Mehrabi et al., fig. 6L; undifferentiated Cenomanian, Iranian Zagros [probably = *P. acuta*].

Non 2023 *Praealveolina cretacea* – Shakir & Mousa, pl. 1, fig. O; early Cenomanian, central Iraq [= *Decastroia oblonga*].
? 2025 *Praealveolina cretacea* – Firozian et al., Fig. 5(1h); undifferentiated middle – late Cenomanian, offshore Iran.
? 2025 *Praealveolina cretacea* – Tulub & Hussain, pl. 2, figs. F-G; undifferentiated middle – late Cenomanian, southern Iraq.

Reference Images: Schroeder & Neumann (1985) p. 118, pl. 57, figs. 1-5; pl. 58, figs. 1-7; pl. 59, figs. 1-7.

Taxonomy/Identity: In general size and shape this species appears intermediate between *P. brevis* and *P. tenuis*. It is larger than *P. brevis* and has higher and narrower main chamberlets, although Schroeder & Neumann (1985) caution that this feature is dependent on the presence/absence of secondary chamberlets and some sections can be misleading. There are 2 rows of secondary chamberlets near the equatorial zone progressing to up to 4 rows near the poles. Number of chamberlets/chamber is relatively high.

P. tenuis is larger than *P. cretacea* and also much more axially elongate.

Decastroia lata is also axially elongate, somewhat larger, and appears to have a higher density of chamberlets per chamber.

Confident Stratigraphic Range: middle – late Cenomanian.

Uncertain Stratigraphic Range: not applicable.

This is one of the most widely reported Cenomanian LBF, although has often been used as 'bucket term' for large, relatively complex alveolinoids. Many records in the literature are inadequately illustrated to confirm identity or can now be considered other taxa, including species of *Decastroia*. Nonetheless the notion of a middle – late Cenomanian range (Berthou, 1984; Schroeder & Neumann, 1985) can be supported by verified records. No exclusively early Cenomanian occurrences are known.

Geographic Distribution: Verified records indicate that this species has a widespread distribution, from Portugal, and localities in the western Mediterranean in the west, to the Arabian Plate (e.g. Syria, Iranian Zagros) in the east. It is also known from Libya in North Africa. The type locality is in western France.

Praealveolina debilis Reichel, 1936
FIGURE 32

T(?) 1936 *Praealveolina cretacea debilis* n. sp., Reichel, p.62; figs. 6, 11; undifferentiated Cenomanian, Spain. [holotype according to ICZN 73.1.2].
Non 1973 *Praealveolina* cf. *debilis* – Berthou, pl. 7, fig. 2; middle – (lower) late Cenomanian, Portugal [= *Praealveolina iberica, fide* Schroeder & Neumann, 1985].
Non 1973 *Praealveolina cretacea debilis* – Berthou, pl. 7, figs. 2a, 2b; pl. 30, fig. 2; early – middle Cenomanian, Portugal [probably = *Simplalveolina simplex*].
1974 *Praealveolina cretacea debilis* – Hottinger, pl. 17, figs. 3-4; age not specified but below occurrences of *P. cretacea* and *P. tenuis*.
2002 *Praealveolina debilis* – Calonge et al., pl. 4, figs. 1-9; pl. 5, fig. 1; early – middle Cenomanian, Iberia.
2003 *Praealveolina debilis* – Calonge-García & López-Carrillo, fig. 3B; middle Cenomanian, Spain.
? 2013 *Praealveolina debelis* (sic) – Shahin & Elbaz, pl. 2 (30); undifferentiated Cenomanian, Sinai, Egypt.
? 2014 *Praealveolina debilis* – Shahin & Elbaz, fig. 11 (7); middle Cenomanian, Sinai, Egypt.
2021 *Praealveolina tenuis* – BouDagher-Fadel & Price, pl. 1, figs. e-f; undifferentiated Cenomanian, France
? 2021b *Praealveolina debilis* – Dousti-Mohajer et al., fig. 9d; (upper) early – middle Cenomanian; Iranian Zagros.
Non 2022b *Praealveolina debilis* – Dousti-Mohajer et al., fig. 4d; (upper) middle - late Cenomanian; Iranian Zagros [probably = *Myriastyla*].

Reference Images: Calonge et al. (2002), pl. 4, figs. 1-9; ?pl. 5, fig. 1.

Taxonomy/Identity: This species is not mentioned by Schroeder & Neumann, 1985, nor Vicedo & Piuz, 2016). Even though Reichel (1936) did not specifically designate or mention any holotype for his taxon, his two illustrations (of the same specimen) have to be considered as referred to the holotype (ICZN 73.1.2).

Calonge et al. (2002; p. 57) describe *P. debilis* as "*…always smaller than* P. brevis*, the structural elements are thinner and its equatorial spiral is more loosely coiled*". They also re-illustrated Reichel's holotype (Reichel (1936), fig. 11 therein, Calonge et al. (2002) pl. 5, fig. 1 therein and see also Figure 32a herein) but state that it does not have the same morphology as their specimens of *P. debilis* from Montalbán in Spain.

Confident Stratigraphic Range: late early – early middle Cenomanian

Uncertain Stratigraphic Range: not applicable.

Considered as the third oldest of the *Praealveolina* species according to Calonge et al. (2002) found in ammonite age-calibrated sediments beneath an intra-middle Cenomanian unconformity and above occurrences of *P. pennensis*

Geographic Distribution: Verified records of this species are restricted to Spain. Records from elsewhere are questionable.

Praealveolina iberica Reichel, 1936
FIGURE 33

T 1936 *Praealveolina iberica* n.sp., Reichel, p. 63; pl. 3, fig. 3; pl. 7, figs. 1, 2, 4, 6, 8, 12; undifferentiated Cenomanian, Spain.
1936 *Praealveolina iberica* n.sp. var *inflata,* Reichel, p. 63; pl. 7, fig. 3; undifferentiated Cenomanian, Spain.

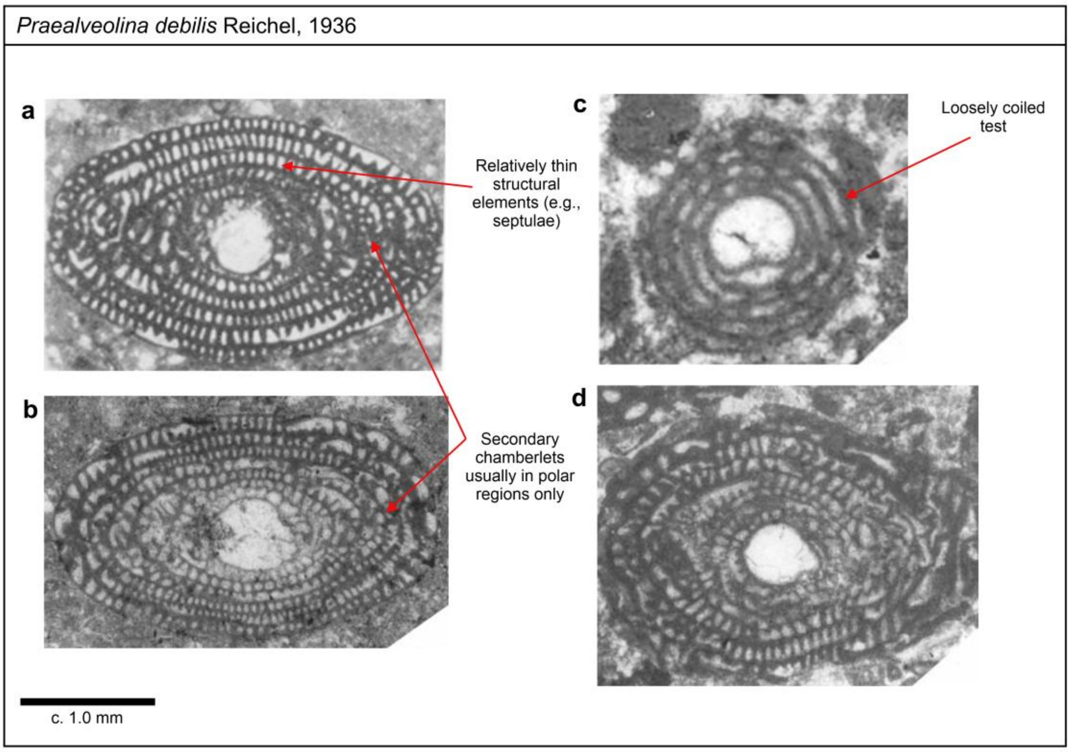


Fig. 32: Representative illustrations of *Praealveolina debilis*: **a.** Axial section, Reichel (?holotype) (1936, fig. 11; undifferentiated Cenomanian, Spain); **b.** Axial section, Calonge et al. (2002, pl. 4, fig. 6; undifferentiated Cenomanian, Spain); **c.** Equatorial section, Calonge et al. (2002, pl. 4, fig. 1; undifferentiated Cenomanian, Spain); **d.** Slightly axial section, Calonge et al. (2002, pl. 4, fig. 9; undifferentiated Cenomanian, Spain).

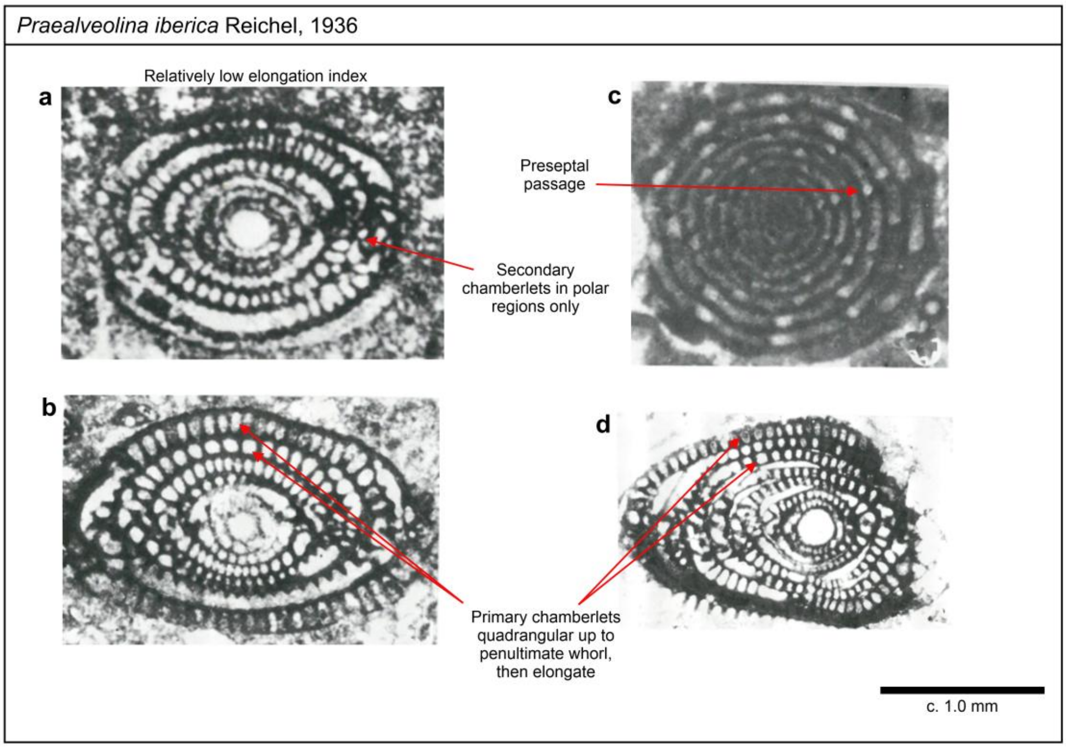


Fig. 33: Representative illustrations of *Praealveolina iberica*: **a.** Axial section, holotype (refigured by Schroeder & Neumann), Reichel (1936, pl. 7, fig. 2; undifferentiated Cenomanian, Spain); **b.** Axial section, Schroeder & Neumann (1985, pl. 53, fig. 6; undifferentiated Cenomanian, Spain); **c.** Equatorial section, Schroeder & Neumann (1985, pl. 53, fig. 9; undifferentiated Cenomanian, Spain); **d.** Axial section (partial), Schroeder & Neumann (1985, pl. 54, fig. 2; undifferentiated Cenomanian, Spain).

Non 1936 *Praealveolina iberica* – Reichel, pl. 3, fig. 4; undifferentiated Cenomanian, Spain [= *P. pennensis*, *fide* Schroeder & Neumann, 1985].
1959 *Praealveolina simplex* – Dufaure, pl. 1, figs. ?6, 7; undifferentiated Cenomanian, France.
? 1965 *Praealveolina* gr. *iberica* – Hamaoui, p. 6; pl. 7, fig. 10; early – middle Cenomanian, Israel.
1966 ?*Praealveolina iberica* – Hamaoui, pl. 2, fig. 8; undifferentiated Cenomanian, Israel.
1967 *Praealveolina* aff. *brevis* – Souquet, pl. 18, fig. 2; late Cenomanian, Spain [*fide* Schroeder & Neumann, 1985].
1971 *Praealveolina simplex* – Ramírez del Pozo, pl. 77; Cenomanian, northern Spain.
1971 *Praealveolina simplex* – Pourmotamed-Lachtewechai, pl. 3, fig. 9; middle Cenomanian, France [*fide* Schroeder & Neumann, 1985].
? 1971 *Praealveolina* gr. *cretacea* – Pourmotamed-Lachtewechai, pl. 3, fig. 8; middle Cenomanian, France [*fide* Schroeder & Neumann, 1985].
? 1971 *Praealveolina iberica* – Ramírez del Pozo, pl. 78; pls. 80-81; late Cenomanian, northern Spain.
Non 1971 *Praealveolina iberica* – Ramírez del Pozo, pl. 80; late Cenomanian, northern Spain [too elongate to be *iberica*].
1973 *Praealveolina iberica* – Berthou, pl. 5, figs. 1, la, le; pl. 6, fig. 4, 4a; early – middle Cenomanian, Portugal [fig. 1b = *P. brevis*, *fide* Schroeder & Neumann, 1985].
1973 *Praealveolina iberica* – Viallard, p. 205; pl. 26, figs. 1, 3; Cenomanian, Spain [*fide* Schroeder & Neumann, 1985].
? 1973 *Praealveolina simplex* – Berthou, pl. 4, fig. lc; early – middle Cenomanian, Portugal.
? 1973 *Praealveolina iberica* cf. *pennensis* – Berthou, pl. 6, fig. 3; early – middle Cenomanian, Portugal [too elongate to be *iberica*].
1974 *Praealveolina* gr. *cretacea* – Canérot, p. 315; pl. 29, fig. 7; Cenomanian, Spain [*fide* Schroeder & Neumann, 1985].
1974 *Praealveolina iberica* – Hottinger, p. 32, pls. 12, 13; Cenomanian – ?Turonian, Pyrenees.
1974 *Praealveolina simplex* – Juignet et al., pl. 1, figs. 2; middle Cenomanian (jukesbrowni ammonite zone), France.
1974 *Praealveolina iberica* – Saint-Marc, p. 253; pl. 9, figs. 4-9 middle Cenomanian, Lebanon.
1978 *Simplalveolina simplex* – Berthou & Schroeder, p. 57, 64, 66; pl. 9, fig. 4 (axial section at the top left of the picture); base middle Cenomanian, (range given as latest early and earliest middle Cenomanian), Portugal.
? 1978 *Praealveolina iberica* – Berthou & Schroeder, p. 57; pl. 9, fig. 4 (pars); base middle Cenomanian, Portugal [too elongate, may = *P. pennensis, fide* Schroeder & Neumann, 1985].
1979 *Praealveolina iberica* – Azéma et al., pl. 41, figs. 6-7; age not stated, Spain [*fide* Schroeder & Neumann, 1985].
1981 *Praealveolina iberica* – Saint-Marc, pl. 2, figs. 2-4; early – middle Cenomanian, Lebanon.
1981 *Praealveolina iberica* – Cherchi & Schroeder, pl. 1, figs. 1-4; reworked Cenomanian clast, Sardinia [note: septulae are unusually thick].
1982 *Praealveolina iberica* – Fourcade & García, pl. 2, figs. 5-6; pl. 3, figs. 2-3; undifferentiated Cenomanian, Spain.
1982 *Praealveolina iberica* – Mouty & Saint-Marc, pl. 2, figs. 4-5; early middle Cenomanian, NW Syria.
1984 *Praealveolina iberica* – Bilotte, pl. 6, fig. 8; early Cenomanian, French Pyrenees.
1985 *Praealveolina iberica* – Neumann & Fourcade, p. 114, pl. 53, figs. 1-11; pl. 54, figs. 1-7; early – middle Cenomanian, Portugal, Spain, France, Lebanon & Israel.
1994 *Praealveolina iberica* – Radoičić, pl. 1, fig. 3; undifferentiated early – middle Cenomanian, Albania/Kosova border.
2002 *Praealveolina iberica* – Calonge et al., pl. 1, figs. 1-14; pl. 2, figs. 1-8; early – middle Cenomanian, Spain.
2003 *Praealveolina iberica* – Calonge-García & López-Carrillo, fig. 3A; early Cenomanian, Spain.
2003 *Praealveolina iberica* – Mancinelli et al., p. 732, fig. 7a-3, h-i; latest Albian – early Cenomanian, southern Italy.
2012 *Praealveolina iberica* – Chiocchini et al., pl. 200, fig. 1-7; undifferentiated late Albian – early Cenomanian, southern Italy.
? 2012 *Praealveolina iberica* – Ghanem et al., figs. 3, 6d (22-23); early Cenomanian, Syria.
Non 2012 *Praealveolina iberica* – Orabi et al., fig. 3E; early, middle & late Cenomanian, Sinai, Egypt [illustration of axially-compressed form, possibly *Sellialveolina*?].
? 2013 *Praealveolina iberica* – Ghanem & Kuss, fig. 12(1-2); early Cenomanian, NW Syria.
Non 2013 *Praealveolina iberica* – Shahin & Elbaz, pl. 2, fig. 31; undifferentiated Cenomanian, Sinai, Egypt [= *Decastroia miaidinensis*].
? 2014 *Praealveolina cretacea* – Afghah et al., figs. 12F (9B = ?*P. cretacea*); middle – late Cenomanian, Iranian Zagros.
? 2014 *Praealveolina iberica* – Afghah & Fadaei, fig. 7b; early Cenomanian, Iranian Zagros.
? 2014 *Praealveolina iberica* – Shahin & Elbaz, fig. 11(8); middle Cenomanian, Sinai, Egypt.
2018 *Praealveolina iberica* – Andrade, pl. 11, fig. 1; late Cenomanian, Portugal.
? 2018 *Praealveolina iberica* – Luger, p. 98, pl. 16, figs. 14-17; pl. 17, figs. 1-5; undifferentiated latest Albian – earliest Cenomanian, Somalia.
? 2019 *Praealveolina iberica* – Özkan & Altıner, fig. 7(18-19); Cenomanian, Turkish Arabian Plate (probable middle Cenomanian – Simmons et al., 2020). [possibly = *Simplalveolina mardinensis* Simmons et al., 2020].
? 2020 *Praealveolina* cf. *P. iberica* – Solak et al., fig. 5D; undifferentiated early – middle Cenomanian, Turkish Taurides.

? 2021a *Praealveolina iberica* – Dousti-Mohajer et al., pl. 2, fig. c; late Albian or early Cenomanian [contradictory statements in text], Iranian Zagros.
? 2021b *Praealveolina iberica* – Dousti-Mohajer et al., figs. 8c, 9b; early – middle Cenomanian, Iranian Zagros.
? 2022b *Praealveolina iberica* – Dousti-Mohajer et al., fig. 4b; undifferentiated Cenomanian, Iranian Zagros.

Reference Images: Schroeder & Neumann (1985), p. 114, pl. 53, figs. 1-11; pl. 54, figs. 1-8.

Taxonomy/Identity: This species (together with *P. pennensis*) has the lowest elongation index of Cenomanian praealveolinoids (s.l.) with the exception of *P.* (= *Simplalveolina* herein) *simplex*.

Schroeder & Neumann (1985) state that, in several cases, *P. iberica* has been identified as *P. simplex* because the secondary chambers – which are few in *P. iberica* and confined to the polar regions – were not observed.

Mancinelli et al. (2003) (after Neumann & Fourcade in Schroeder & Neumann, 1985) noted whilst often confused with *P.* (=*S.*) *simplex*, it differs by "having chamberlets of quadrangular shape which double their height in the last whorl, a maximum of two supplementary chamberlets limited to the polar regions, thicker chamber floors (except in the last whorl), and a larger preseptal passage."

P. pennensis is of broadly similar size and shape. The shape of the chamberlets in *P. pennensis* (oval in the final two whorls, quadrangular in earlier whorls) differs from those in *P. iberica* (much taller than wide, becoming even taller in polar regions).

Confident Stratigraphic Range: base Cenomanian – late Cenomanian.

Uncertain Stratigraphic Range: not applicable.

This is a widely reported Cenomanian LBF, although has often been used as a 'bucket term' for relatively simple praealveolinoids. Many records in the literature are inadequately illustrated to confirm identity or can now be considered other taxa, especially the very similar *Simplalveolina simplex*.

P. iberica is considered to be the oldest of the *Praealveolina* species according to Calonge et al. (2002). It is found in the lower part of the early – middle Cenomanian (type level of Reichel, 1937, from Spain) and is subsequently replaced by *P. pennensis*. Nonetheless verified and age calibrated records from elsewhere (e.g. Andrade, 2018) suggest the species ranges throughout the early, middle and late Cenomanian, a longer range than suggested by Schroeder & Neumann (1985) and Mancinelli et al. (2003). Local ranges will be shorter.

The timing of extinction within the late Cenomanian is unclear, pending better age calibrated records. As noted by Calonge et al. (2002) the inception of the species is close to the base of the Cenomanian, supported by data from Italy (Mancinelli et al., 2003; Chiocchini et al., 2012) where it occurs in beds representing the Albian – Cenomanian transition. A latest Albian age for inception cannot be excluded, but pragmatically, its oldest occurrences form a useful proxy for the base of the Cenomanian.

Geographic Distribution: Widely reported from the western Mediterranean (e.g. Portugal, Spain, southern France, southern Italy), with most records from the Arabian Plate uncertain, although validated from Lebanon, Israel and Syria.

Praealveolina osimoi (Zuffardi Comerci, 1930) emend. De Castro, 1987

FIGURE 34

1914 *Alveolina osimoi* – Parona p. 13, Cenomanian, Libya [*nomen nudem*]
T 1930 *Alveolina osimoi* – Zuffardi Comerci, p. 32-33, pl. 5, fig. 3; (*non* pl. 3, fig. 7; pl. 5, figs. 1, 6 = *Borelis pygmaea* Hanzawa, 1930); undifferentiated middle – late Cenomanian, Libya.
1987 *Praealveolina osimoi* – De Castro, p. 115-119, text-fig. 1, pl. 1, figs. 1-3, pl. 2, figs. 1-6; undifferentiated middle – late Cenomanian, Libya.
? 1988 *Praealveolina* cf. *osimoi* – De Castro, p. 409, pl. 4, figs. 6-9; undifferentiated early to middle Cenomanian, Capri, southern Italy.
? 2018 *Praealveolina osimoi* – Luger, p. 98-99, (*non* pl. 15, figs. 16, 20), pl. 17, figs. 10, 12, 13; middle Cenomanian, Somalia [possibly = *Decastroia* sp.].

Reference Images: De Castro (1987) p. 115-119, text-fig. 1, pl. 1, figs. 1-3, pl. 2, figs. 1-6

Taxonomy/Identity: The species name was initially introduced by Parona (1914) but without description or illustration. This was rectified by Zuffardi Comerci (1930) although she also used the name to include some Oligocene *Borelis pygmaea* from southern Italy. Clarity was introduced by De Castro (1987) who, on the basis of re-examining the types and associated material, emended the species description. The species has been overlooked in the literature on *Praealveolina* occurrences, although Reichel (1933) considered the species as belonging to *Praealveolina*.

According to De Castro (1987) it can be distinguished from the somewhat similar *P. cretacea* and *P. tenuis* by virtue of smaller test and proloculus dimensions of macrospheric forms (see Table 4). *P. osimoi* is very elongate and has an axial elongation index comparable with that of the most elongated *Praealveolina* species, *P. tenuis* and *P. acuta*.

Confident Stratigraphic Range: not applicable.

Uncertain Stratigraphic Range: undifferentiated middle – late Cenomanian.

Geographic Distribution: First described from Libya, the species is also possibly known from southern Italy and Somalia, although these records seem doubtful.

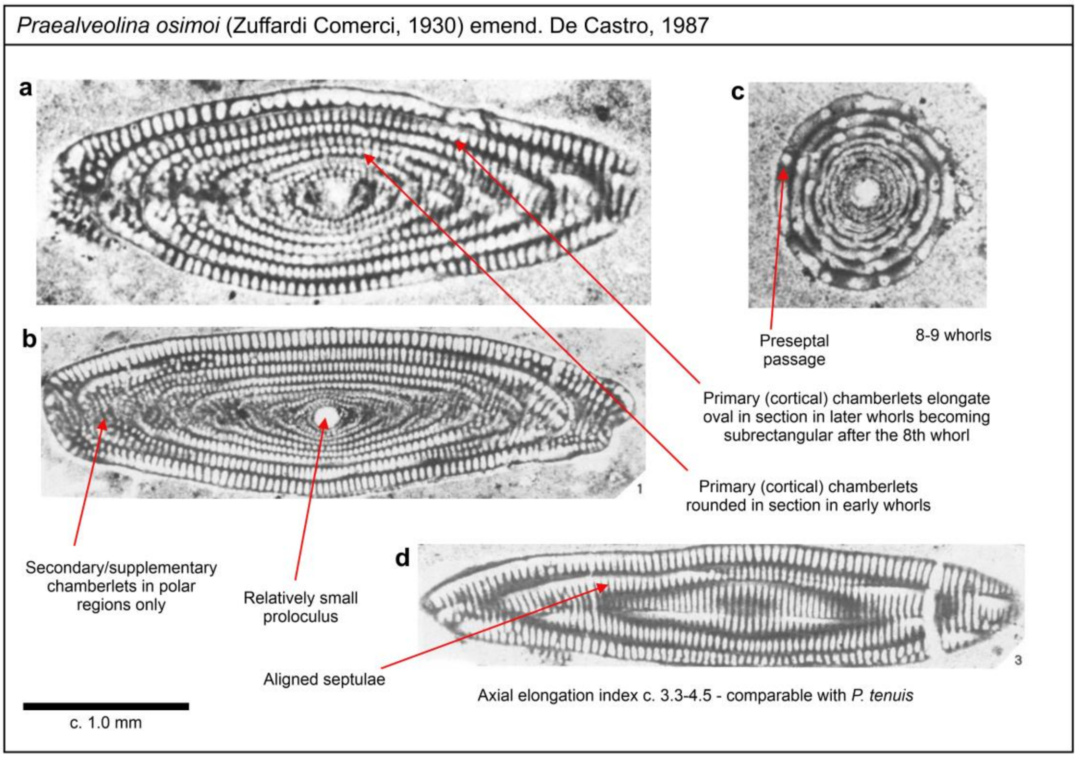


Fig. 34: Representative illustrations of *Praealveolina osimoi*: **a.** Axial section, holotype (designated by De Castro), (1987, text-fig. 1 (a re-illustration of Zuffardi Comerci, 1930, fig. 3); middle-late Cenomanian, Libya); **b.** Axial section, De Castro (1987, pl. 1, fig. 1; middle-late Cenomanian, Libya); **c.** Equatorial section, De Castro (1987, pl. 2, fig. 4; middle-late Cenomanian, Libya); **d.** Tangential section, De Castro (1987, pl. 1, fig. 3; middle-late Cenomanian, Libya).

Praealveolina pennensis **Reichel, 1936**
FIGURE 35

T 1936 *Praealveolina iberica pennensis* nov. subsp., Reichel, p. 65, pl. 2, fig. 5; pl. 7, figs. 5, 7, 9-11; late Cenomanian – ?Turonian, southern France [type locality considered middle – late Cenomanian by Schroeder & Neumann, 1985].

1936 *Praealveolina iberica* – Reichel, pl. 3, fig. 4 [= *P. pennensis*, *fide* Schroeder & Neumann, 1985].

? 1973 *Praealveolina iberica* cf. *pennensis* – Berthou, pl. 6, fig. 3; early – middle Cenomanian, Portugal

1975 *Praealveolina* gr. *cretacea brevis* – Christodoulou & Tsaila-Monopolis, pl. 56, fig. 1; undifferentiated Cenomanian, Greece [*fide* Schroeder & Neumann, 1985].

1978 *Praealveolina iberica* – Berthou & Schroeder, pl. 9, fig. 4 (pars); base middle Cenomanian, Portugal [*fide* Schroeder & Neumann, 1985].

1985 *Praealveolina pennensis* – Neumann & Fourcade in Schroeder & Neumann, p. 116, pl. 55, figs. 1-8; middle – late Cenomanian, Portugal, France and Greece.

2002 *Praealveolina pennensis* – Calonge et al., pl. 2, fig. 9-12; pl. 3, figs. 1-7, ?8-9; early – middle Cenomanian; Iberian Pyrenees [pl. 3, figs. 8-9 fall outside the limits of variability for this species].

? 2003 *Praealveolina* sp. cf. *P. pennensis* – Mancinelli et al., fig. 7j-k; latest Albian – early Cenomanian, southern Italy [too elongated to be *pennensis*].

Reference Images: Schroeder & Neumann (1985), p. 116, pl. 55, figs. 1-8.

Taxonomy/Identity: This species (together with *P. iberica*) has the lowest elongation index of Cenomanian praealveolinoids (s.l.) with the exception of *P.* (= *Simplalveolina* herein) *simplex*.

P. iberica is of broadly similar size and shape. The shape of the chamberlets in *P. pennensis* (oval in the final two whorls, quadrangular in earlier whorls) differs from those in *P. iberica* (much taller than wide, becoming even taller in polar regions).

Lack of understanding of the number and position of the chamberlets has been cited by Schroeder & Neumann (1985) as a reason for confusion between this species and *P. iberica* (even by Reichel himself – see synonymy list) and, sometimes, with *P. brevis*.

Confident Stratigraphic Range: late early – early middle Cenomanian.

Uncertain Stratigraphic Range: not applicable.

Although the type level in southern France is considered to be middle – early late Cenomanian by Neumann & Fourcade in Schroeder & Neumann (1985) who give a total range as middle – late Cenomanian, there is no evidence that the species ranges into the late Cenomanian. Indeed, for Calonge et al., (2002), this is the second oldest of the *Praealveolina* species, found around the early – middle Cenomanian transition and subsequently replaced by *P. debilis*. Records from

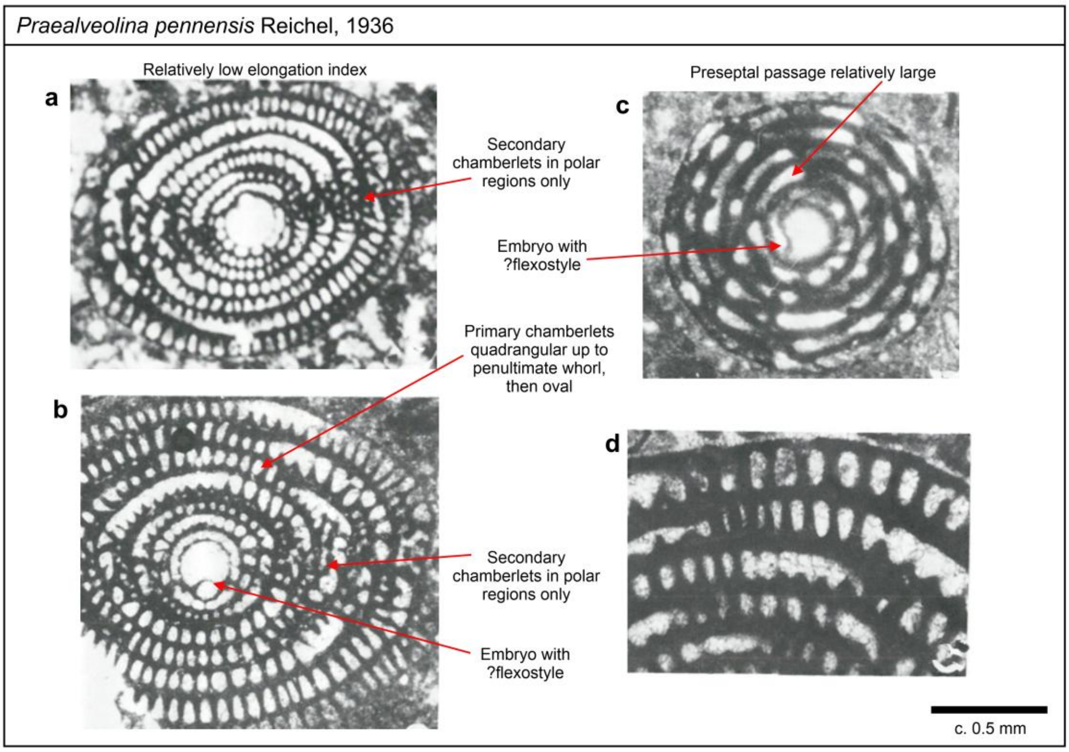


Fig. 35: Representative illustrations of *Praealveolina pennensis*: **a.** Axial section, holo/lectotype (refigured by Schroeder & Neumann), Reichel (1936, pl. 7, fig. 7; middle – late Cenomanian, southern France); **b.** Axial section (partial), Schroeder & Neumann (1985, pl. 55, fig. 5; middle – late Cenomanian, southern France); **c.** Equatorial section, Schroeder & Neumann (1985, pl. 55, fig. 7; middle – late Cenomanian, southern France); **d.** Axial section (detail, juvenile specimen), Schroeder & Neumann (1985, pl. 55, fig. 4, middle – late Cenomanian, southern France).

Portugal occur around the base middle Cenomanian (Berthou, 1984).

Geographic Distribution: Records of this species seem limited to the western Mediterranean (southern France, Portugal, Pyrenees, Greece).

***Praealveolina tenuis* Reichel, 1933**
FIGURE 36

T 1933 *Praealveolina tenuis* n. sp. Reichel, p. 270, text-figs. 1-14; undifferentiated Cenomanian, southern France.
1936 *Praealveolina cretacea tenuis* – Reichel, p. 58, pl. 5, figs. 6-8; pl. 6, figs. 1-2; undifferentiated Cenomanian, southern France.
? 1948 *Praealveolina tenuis* – Silvestri, p. 72, pl. 9(17), fig. 3; age not stated; Somalia.
1961 *Praealveolina tenuis* – Cuvillier, pl. 37, fig. 1; late Cenomanian, Aquitaine, France.
1965 *Praealveolina cretacea* var. *tenuis* – Gibson & Percival, p. 342, pl. 1, figs. 8a, b; undifferentiated Cenomanian, Somalia.
1965 *Praealveolina tenuis* – Saint-Marc, pl. 7, fig. 1; pl. 15, fig. 4; late Cenomanian, Aquitaine, France [*fide* Schroeder & Neumann, 1985].
1965 *Praealveolina* – James & Wynd, fig. 40; undifferentiated Cenomanian, Iranian Zagros.
Non 1965 *Praealveolina tenuis* – Saint-Marc, pl. 15, figs. 1, 3 [= *P. cretacea, fide* Schroeder & Neumann, 1985].
Non 1966 *Praealveolina cretacea tenuis* – Gohrbandt, pl. 1, figs. 1-4 [= *P. cretacea, fide* Schroeder & Neumann, 1985].
1967 *Praealveolina tenuis* – Souquet, pl. 17, fig. 2-4; late Cenomanian, Spanish Pyrenees [*fide* Schroeder & Neumann, 1985].
? 1967 *Praealveolina* ex. gr. *P. cretacea* – Arkin & Hamaoui, p. 4, pl. 2, fig. 5; undifferentiated Cenomanian, Israel.
1970 *Praealveolina* – Moreno de Castro, pl. 2; Cenomanian, Spanish Pyrenees [*fide* Schroeder & Neumann, 1985].
? 1970 *Praealveolina* cf. *cretacea tenuis* – Moreno de Castro, p. 186, ?pl. 1, fig. 2; pl. 2, fig. 2; Cenomanian, Spanish Pyrenees [*fide* Schroeder & Neumann, 1985].
Non 1973 *Praealveolina* cf. *P.* (*P.*) *tenuis* – El-Naggar & Al-Rifaiy, fig. 6(5); late Cenomanian, Kuwait [= *Decastroia oblonga*].
1974 *Praealveolina* gr. *cretacea* – Hamaoui & Brun, p. 23, pl. 26; Cenomanian – “probably” Turonian, Middle East [Turonian age can be discounted]
1974 *Praealveolina cretacea tenuis* – Hottinger, pl. 14, fig. ?5; pl. 15, figs. 1-2; pl. 16, fig. 2; pl. 17, fig. 1; Cenomanian, Portugal and Spanish Pyrenees.
? 1974 *Praealveolina cretacea tenuis* – Saint-Marc, p. 71-72, pl. 8, figs. ?1-2, *non* 3-4 [3 = *Decastroia;* 4 = *Reichelia*]; text-fig. 56; upper middle – late Cenomanian, Lebanon.
1975a *Praealveolina cretacea tenuis* – Cherchi & Schroeder, pl. 2, fig. 2, 9; late Cenomanian, Sardinia.

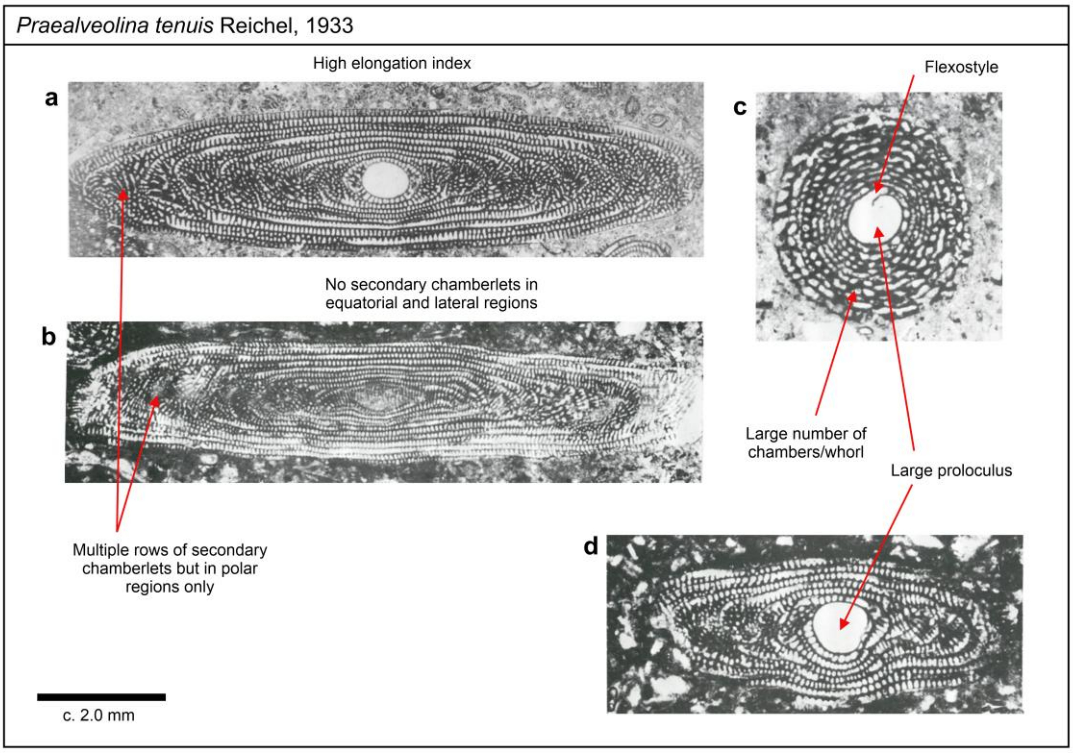


Fig. 36: Representative illustrations of *Praealveolina tenuis*: **a.** Axial section, Reichel (1936, pl. 6, fig. 2; undifferentiated Cenomanian, Portugal); **b.** Axial section (?microspheric form), Schroeder & Neumann (1985, pl. 60, fig. 4; undifferentiated Cenomanian, southern France); **c.** Equatorial section, Schroeder & Neumann (1985, pl. 62, fig. 1; undifferentiated Cenomanian, southern France); **d.** Axial section, Schroeder & Neumann (1985, pl. 61, fig. 2, undifferentiated Cenomanian, southern France).

1977 *Praealveolina* gr. *cretacea* – Prestat, p. 274, pl. 15, fig. 2; late Cenomanian, central Somalia [*fide* Schroeder & Neumann, 1985].

1981 *Praealveolina* gr. *cretacea* – Tronchetti, pl. 22, fig. 3; middle – late Cenomanian, Provence, France [*fide* Schroeder & Neumann, 1985].

1981 *Praealveolina cretacea tenuis* – Cherchi & Schroeder, pl. 2, figs. 1; 9; late Cenomanian, Sardinia.

Non 1981 *Praealveolina cretacea tenuis* – Saint-Marc, pl. 2, fig. 12; late middle – early late Cenomanian, Lebanon [= *Reichelia*].

1984 *Praealveolina cretacea tenuis* – Bilotte, pl. 7, figs. 5-6; late Cenomanian, French Pyrenees.

1985 *Praealveolina tenuis* – Neumann & Fourcade in Schroeder & Neumann, p. 120, pl. 60, figs. 1-6; pl. 61, figs. 1-7; pl. 62, figs. 1-7, text-figs. 13-14; upper middle – late Cenomanian, Neotethys.

Non 1987 *Praealveolina tenuis* – Simmons & Hart, pl. 10.1, fig. 2; undifferentiated middle – late Cenomanian, Oman [= *Decastroia*].

Non 1988 *Praealveolina cretacea tenuis* – Diaz-Otero & Furrazola-Bermudez, pl. 3, figs. 1, 5; pl. 4, figs. 3-8; pl. 6 [= *Caribalveolina michaudi* Pécheux, *fide* Vicedo et al., 2009].

1989 *Praealveolina tenuis* – Kuss & Malchus, text-figs. 26-27; late Cenomanian, Egypt.

Non 1989 *Praealveolina tenuis* – Kuss & Malchus, text-figs. 25; late Cenomanian, Egypt [= *Decastroia lata*].

Non 1990 *Praealveolina tenuis* – Smith et al., fig. 6e; upper middle – late Cenomanian, Oman [= *Decastroia oblonga*].

Non 1993 *Praealveolina tenuis* – Hewaidy & Al-Hitmi, p. 491, pl. 7, figs. 7-10; undifferentiated Cenomanian, Qatar [= *Decastroia*].

1996 *Praealveolina tenuis* – Calonge-García & Sánchez-Real, pl. 1, fig. 2; late Cenomanian, Spain.

? 1998 *Praealveolina cretacea tenuis* – El Sheikh & Hewaidy, p. 509, pl. 2, figs. 14-15; middle – late Cenomanian, northern Egypt.

Non 1998 *Praealveolina tenuis* – Whittaker et al., pl. 91, figs. 2-4; undifferentiated Cenomanian, Qatar [= *Decastroia serrakieli*. States total range in Middle East as middle Cenomanian – middle Turonian although rationale not clear].

2002 *Praealveolina tenuis* – Calonge et al., pl. 6, figs. 1-3, 5-8; late Cenomanian, Spain, Portugal and southern France.

2003 *Praealveolina tenuis* – Schulze, fig. 11d; middle – late Cenomanian, Jordan.

2004 *Praealveolina tenuis* – Schulze et al., fig. 10D [=E]; middle – late Cenomanian, Jordan. [Figures mis-captioned].

Non 2004 *Praealveolina tenuis* – Menegatti, p. 2-38, pl. 10, fig. 1; middle – late Cenomanian, Dubai [= *Decastroia*].

2006 *Praealveolina* sp. cf. *P. tenuis* – Mancinelli &

Chiocchini, p. 102, pl. 5, figs. 1-6; middle Cenomanian, Italy.
2009 *Praealveolina tenuis* – Caus et al., fig. 5(4); late Cenomanian, Pyrenees.
2012 *Praealveolina* cf. *tenuis* – Chiocchini et al., pl. 95, figs. 1-6; pl. 96, fig. 1; pl. 98, fig. 1; middle Cenomanian, southern Italy.
? 2012 *Praealveolina tenuis* – Kiarostami et al., pl. 3, fig. 13; Cenomanian, Iranian Zagros.
? 2012 *Praealveolina tenuis* – Ghanem et al., fig. 6e (?15, ?10, ?18, ?25, *non* 9, 21 [= *Decastroia*]); late Cenomanian, Syria.
Non 2012 *Praealveolina tenuis* – Orabi et al., fig. 3F; middle and late Cenomanian, Sinai, Egypt [= *Decastroia*].
? 2013 *Praealveolina cretacea* – Al-Dulaimi et al., pl. 9, fig. 7; late Cenomanian, southern Iraq.
Non 2013 *Praealveolina tenuis* – Shahin & Elbaz, pl. 2, fig. 32; pl. 3, fig. 1; undifferentiated Cenomanian, Sinai, Egypt [probably = *Decastroia*].
2014 *Praealveolina tenuis* – Shahin & Elbaz, figs. 5(7), *non* 11(9) [= *Decastroia oblonga*]; middle Cenomanian, Sinai, Egypt.
? 2014 *Praealveolina tenuis* – Afghah et al., figs. 9E, 12C; early – middle Cenomanian, Iranian Zagros.
Non 2014 *Praealveolina tenuis* – Afghah & Fadaei, fig. 8c [caption is for 9c]; early – late Cenomanian, Iranian Zagros [indeterminate but not *P. tenuis*].
Non 2016 *Praealveolina tenius* (sic) – Assadi et al., fig. 6 (a14); late Cenomanian, Iranian Zagros [= *Cisalveolina fraasi*].
2018 *Praealveolina tenuis* – Andrade, pl. 10, fig. 11; pl. 11, fig. 3; undifferentiated Cenomanian, Portugal.
? 2018 *Praealveolina* cf. *tenuis* – Luger, pl. 17, figs. 6-7; middle Cenomanian, northern Somalia [possibly = *P. acuta*].
Non 2018 *Praealveolina tenuis* – BouDagher-Fadel, pl. 5.22, figs. 10-11; undifferentiated Cenomanian, Qatar [= *Decastroia*].
? 2019 *Praealveolina tenuis* – Özkan & Altıner, fig. 7(10-11); Cenomanian (probably middle Cenomanian – Simmons et al., 2020), Turkish Arabian Plate
2021 *Praealveolina cretacea* – Dehghanian & Afghah, fig. 7(2); middle Cenomanian, Iranian Zagros.
Non 2021 *Praealveolina tenuis* – BouDagher-Fadel & Price, pl. 1, figs. e-f; undifferentiated Cenomanian, France [probably = *P. debilis*].
2022 *Praealveolina* gr. *cretacea* – Schlagintweit & Yazdi-Moghadam, fig. 2A; undifferentiated Cenomanian, Iranian Zagros.
? 2023 *Praealveolina tenuis* – Dawood & Al-Dulaimi, pl. 1, fig. H; middle Cenomanian, southern Iraq [possibly = *Decastroia*].
Non 2025 *Praealveolina tenuis* – Tulub & Hussain, pl. 2, figs. D-E; undifferentiated middle –late Cenomanian, southern Iraq [doubtful, probably not *P. tenuis* but indeterminate].
2025 *Praealveolina tenuis* – Martin Closas et al., fig. 7 A-D, F, I-J; late Cenomanian, Spain

Reference Images: Schroeder & Neumann (1985), p. 120, pl. 60, figs. 1-6; pl. 61, figs. 1-7; pl. 62, figs. 1-7; text-figs. 13-14.

Taxonomy/Identity: *P. tenuis* is relatively easy to identify because of its large size (the largest of all praealveolinoid species) and largest proloculus. It is also the most axially-elongate praealveolinoid although *P. acuta* (a smaller species with more acute polar regions) can be similar and *P. lata* (now transferred to *Decastroia*) can be slightly less (in his original description Reichel, 1936, suggested that *P. lata* could be a variety of *P. tenuis*).

Confident Stratigraphic Range: late middle (scarce) – late Cenomanian (common).

Uncertain Stratigraphic Range: not applicable.

Alongside *P. cretacea*, this is one of the most widely reported Cenomanian LBF, although has often been used as ‘bucket term’ for very large, relatively complex elongate alveolinoids. Many records in the literature are inadequately illustrated to confirm identity or can now be considered other taxa, including species of *Decastroia*.

The majority of verified records are late Cenomanian, forming the terminal development of *Praealveolina* evolution, but range into the middle Cenomanian is confirmed by a number of records (see also Schroeder & Neumann, 1985). Calonge et al. (2002) drew the range of *P. tenuis* within the late Cenomanian based on material in their studied sections from Iberia. However, they also mentioned that “some remains” of *P. tenuis* had been observed in sections from the uppermost part (weakly dolomitised intervals) of their “Lower Cenomanian Cycle” to which they attributed (calibrated by ammonites) to the intra-middle Cenomanian.

Geographic Distribution: The species is widespread, occurring in Portugal and throughout the circum-north Mediterranean area (Spain, France, Sardinia, Italy), The Levant (Israel, Jordan, Syria) and within the Arabian Plate, Egypt and Somalia, although a number of records are uncertain or dubious.

Genus ***Reichelia*** Vicedo & Piuz 2016

Reichelia was defined by Vicedo & Piuz (2016) with *R. magna* as the type (and so far, only) species, from middle Cenomanian sediments of the Natih Formation, Member C, of Oman. It has not been subsequently recorded elsewhere.

Reichelia is a relatively large, subglobular to axially-elongate genus which is planispirally coiled in multiple spirals, and therefore is similar to the multi-coiled *Multispirina*. *Reichelia* differs from *Multispirina* by having at least two rows of chamberlets (cortical and medullar), plus supplementary apertures in the polar regions, and two rows of apertures in the apertural face. *Reichelia* also has fewer spirals that *Multispirina* (2-5 cf. 12-18). In respect of the two, sometimes three rows of chamberlets, *Reichelia* resembles *Decastroia*, but which only has a single spiral coil. See Table 1 and Figure 11 for diagnostic characteristics of the genus.

Dousti-Mohajer et al. (2021b, p. 11) refers to *Reichelia* as a "…*hybrid genus of* Multispirina *and* Decastroia…" but it is not at all clear in what context this means. It is possibly just a general comment on the overall relative physical appearances of the three genera. Vicedo & Piuz (2016) did, however, include *Reichelia* with *Decastroia* in the same new subfamily they created – the Decastroiainae – thus implying an evolutionary relationship between those two genera but not necessarily with *Multispirina*.

Reichelia magna **Vicedo & Piuz, 2016**
FIGURE 37

1974 *Praealveolina cretacea tenuis* – Saint-Marc, pl. 8, fig. 4 [pl. 8, figs. 1-2 = ?*Praealveolina tenuis*, fig. 3 = *Decastroia*]; upper middle – late Cenomanian, Lebanon.
1981 *Praealveolina cretacea tenuis* – Saint-Marc, pl. 2, fig. 12; late middle – early late Cenomanian, Lebanon.
T 2016 *Reichelia magna* gen. & sp. nov., Vicedo & Piuz, p. 833, figs. 14-16; middle Cenomanian, Oman Mountains.

Reference Images: Vicedo & Piuz (2016), p. 833, figs. 14-16.

Taxonomy/Identity: First described from the middle Cenomanian of Oman by Vicedo & Piuz (2016).

For similarities and differences with other taxa see above in the genus description.

Confident Stratigraphic Range: middle Cenomanian – early late Cenomanian.

Uncertain Stratigraphic Range: not applicable.

Described from the Natih C of the Oman Mountains which is early middle Cenomanian in age (Bromhead et al., 2022).

Geographic Distribution: So far recorded only from Oman and Lebanon.

Genus ***Simplalveolina*** Reichel 1964

First described as a (new) subgenus of *Praealveolina* by Reichel in the Loeblich & Tappan foraminiferal treatise (1964) with *Praealveolina simplex* Reichel 1936 as the type species. *Simplalveolina* displays pre-septal canals and differs from all other planispiral globular-fusiform alveolinoids in having no supplementary (i.e., horizontally-divided) chamberlets, the primary chamberlets being formed by 'vertical' septula running in the direction of growth and aligned between successive chambers in both macro- and microspheric generations.

It is slightly elongated from spherical/subspherical (e.g., compared to the globular *Cisalveolina* which has pre- and post-septal passages and septula alternating between chambers, and the globular *Multispirina* which, like *Simplalveolina*, has aligned septula but has multiple nested planispiral coils). *Simplalveolina* is less elongate/fusiform than most *Praealveolina,* which also has supplementary chamberlets, often disposed in several rows polewards (supplementary chamberlets in *Praealveolina cretacea* (d'Archiac, 1837) appear less regularly in the equatorial region).

Neumann & Fourcade in Schroeder & Neumann (1985) considered the differences to be too small to warrant separation and recommended abandoning *Simplalveolina* and retaining the species in *Praealveolina*. Depending on preservation and/or section orientation through a thin-section, the differences between *Simplalveolina* and some species of *Praealveolina* (e.g. *Praealveolina iberica* Reichel, 1936) can be hard to discern; an observation with which we agree. Loeblich & Tappan (1987) however, retained *Simplalveolina* as a separate genus, a notion we follow here in line with most modern Cretaceous alveolinoid taxonomic studies (e.g., Vicedo & Piuz, 2016).

See Table 1 and Figure 13 for diagnostic characteristics of the genus.

See also the introduction and discussion on the genus *Praealveolina* above.

Simplalveolina mardinensis **Simmons & Vicedo, 2020**
FIGURE 38

2016 *Simplalveolina* gr. *simplex* (Reichel, 1936) – Vicedo & Piuz, fig. 17H-L; middle Cenomanian, Oman Mountains.
? 2019 *Praealveolina iberica* Reichel – Özkan & Altıner, fig. 7 (18-19); Cenomanian, south-east Türkiye.
T 2020 *Simplalveolina mardinensis* n. sp. Simmons & Vicedo (in Simmons et al.), p. 227, figs. 7(1-15), 8(1-2); middle Cenomanian, southeast Türkiye.

Reference images: Simmons et al. (2020), p. 227, figs. 7(1-15), 8(1-2).

Taxonomy/Identity: First described by Simmons & Vicedo (in Simmons et al., 2020) from the Mardin Formation (Cenomanian) of southeast Türkiye. It differs from *S. simplex* in having a smaller proloculus (85-105 μm vs. 110-200 μm), and smaller axial diameter tests with fewer whorls (0.8-1.0 mm & 8-9 whorls vs. 1.3-2.0 mm & 8-12 whorls).

Simmons & Vicedo (in Simmons et al., 2020) state that some specimens in their material with larger proloculi (e.g., Figure 38d) cannot be confirmed as specimens of *S. mardinensis*, or a trimorphic generation, or juveniles of *S. simplex*.

Apart from some specimens previously attributed to *S*. gr. *simplex* by Vicedo & Piuz (2016) from Oman (now thought to be this taxon) and the Turkish type material, this species is yet to be reported from other localities.

Confident Stratigraphic Range: middle Cenomanian.

Uncertain Stratigraphic Range: not applicable.

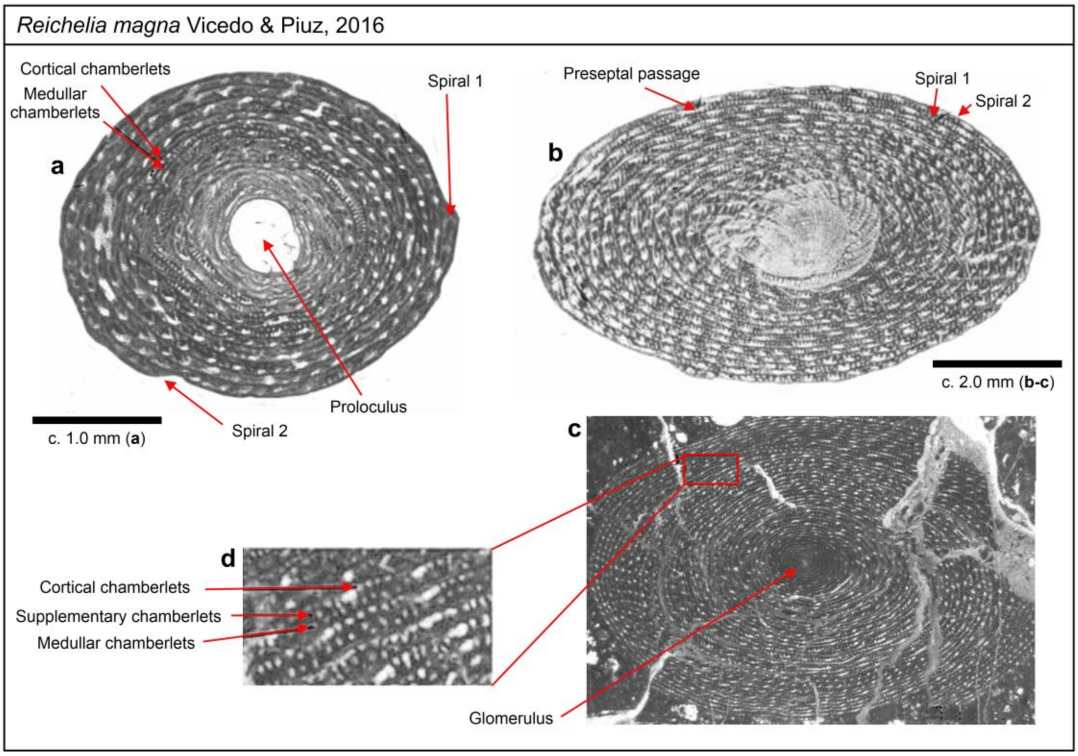


Fig. 37: Representative illustrations of *Reichelia magna*: **a.** Oblique centred section (holotype), Vicedo & Piuz (2016, fig. 14C; middle Cenomanian, Oman); **b.** Oblique non-centred section (microspheric form), Vicedo & Piuz (2016, fig. 15C; middle Cenomanian, Oman); **c.** Oblique centred section (microspheric form), Vicedo & Piuz (2016, fig. 16A; middle Cenomanian, Oman); **d** detail of **c**, Vicedo & Piuz (2016, fig. 16B; middle Cenomanian, Oman).

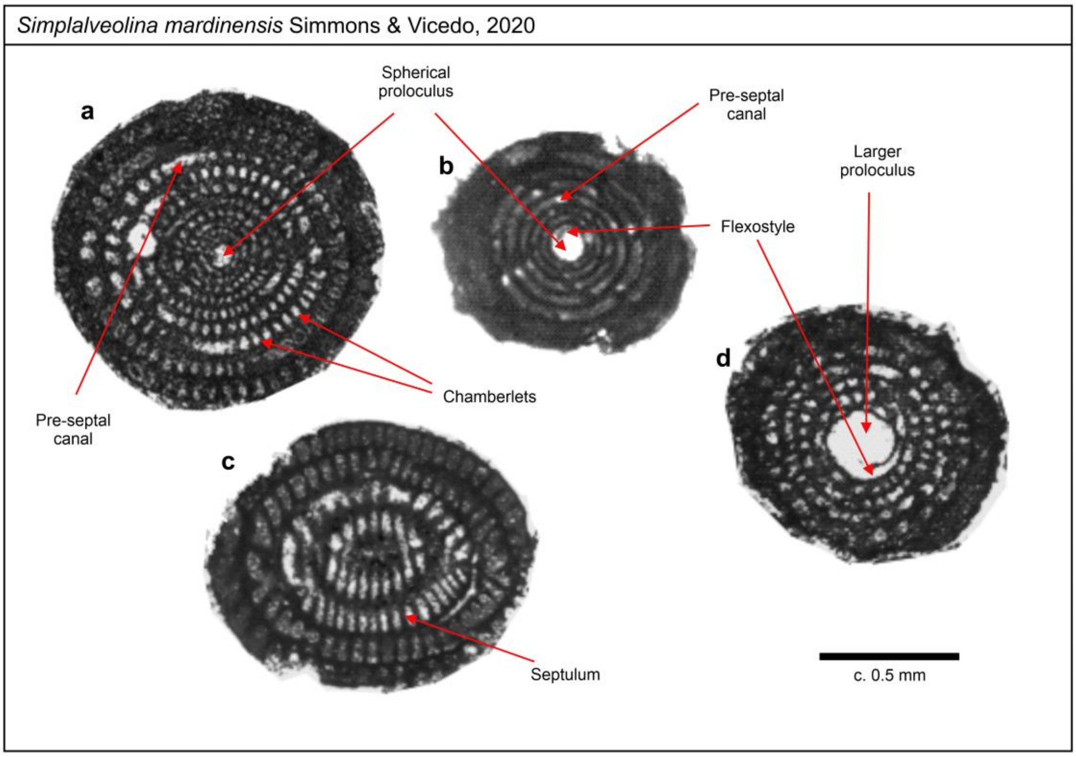


Fig. 38: Representative illustrations of *Simplalveolina mardinensis*: **a.** Axial section, Simmons et al. (2020, fig. 7(2)); **b.** Equatorial section, Simmons et al. (2020, fig. 7(7)); **c.** Tangential section, Simmons et al. (2020, fig. 7(12)); **d.** Equatorial section of ?trimorphic form or juvenile *S. simplex*, Simmons et al. (2020, fig. 8(1)). All specimens middle Cenomanian, Turkish Arabian Plate.

First described from the middle Cenomanian of Türkiye (Derdere Formation), Simmons & Vicedo (in Simmons et al., 2020) also stated that some specimens referred to as *Simplalveolina* gr. *simplex* from the middle Cenomanian of the Natih Formation in Oman (Vicedo & Piuz, 2016) can be assigned to this species. They also speculated that some forms recorded as *Praealveolina iberica* from the Derdere Formation by Özkan & Altıner (2019) and as *S. simplex* by Görür et al. (1991) may be *S. mardinensis* although the illustrations are uncertain.

Geographic Distribution: Central Neotethys. So far recorded with certainty only from Türkiye and Oman. Some records of *S. simplex* from the Iranian Zagros could possibly be assigned *S. mardinensis* (see synonymy list for *S. simplex*) but require additional material to confirm.

Simplalveolina simplex (Reichel, 1936)
FIGURE 39

T 1936 *Praealveolina simplex* n. sp., Reichel, p. 67; pl. 2, fig. 2; pl. 5, fig. 4; pl. 8, figs. 3, 5-9, 12; Cenomanian, western France [middle Cenomanian *fide* Neumann & Fourcade, 1985].
1959 *Praealveolina simplex* – Dufaure, pl. 1, fig. 6-7; undifferentiated Cenomanian, French Pyrenees.
1959 *Praealveolina* cf. *simplex* – Dufaure, pl. 1, figs. 2-3; undifferentiated Cenomanian, French Pyrenees.
1961 *Praealveolina* – Cuvillier, pl. 32, fig. 2; pl. 34, fig. 2; Cenomanian (undifferentiated), western France
? 1961 *Praealveolina* sp. – Hamaoui, pl. 10, figs. 4-5; late Cenomanian-Turonian, Israel [Turonian age can probably be discounted].
? 1963 *Praealveolina simplex* – Neumann, pl. 1, figs. 3-4, 6; pl. 2, fig. 2; early Cenomanian [associated fauna indicates a generalised early – middle Cenomanian age], western France.
1964 *Praealveolina* (*Simplalveolina*) *simplex* – Reichel in Loeblich & Tappan, p. C 510, text-fig. 396-1; Cenomanian [middle], France.
1965 *Praealveolina simplex* – Gibson & Percival, p. 343, pl. 1, fig. 9; undifferentiated Cenomanian, Somalia.
1965 *Praealveolina simplex* – Saint-Marc, p. 138; pl. 5, fig. 1; pl. 6, fig. 1; pl. 15, fig. 5; undifferentiated Cenomanian, western France [*fide* Neumann & Fourcade, 1985]
? 1965 *Praealveolina* aff. gr. *iberica* – Hamaoui, pl. 7, fig. 10; pl. 11, fig. 1; undifferentiated Cenomanian, Israel.
Non 1965 Alveolinid indet. sp. – Hamaoui, pl. 10, fig. 12; pl. 11, fig. 6; pl. 15, figs. 5, 8; undifferentiated Cenomanian, Israel [probably *Praealveolina cretacea*]
Non 1969 *Praealveolina simplex* – Sampò, pl. 43, fig. 2; undifferentiated Cenomanian, Iranian Zagros [*fide* Neumann & Fourcade, 1985].
Non 1971 *Praealveolina simplex* – Ramírez del Pozo, pl. 77 [= *Praealveolina iberica* Reichel, 1936, *fide* Neumann & Fourcade, 1985]
? 1972 *Praealveolina simplex* – Ramírez del Pozo, p. 154, pl. 8, figs. 3-4; undifferentiated Cenomanian, Spain [poorly preserved].
1973 *Praealveolina simplex* – Berthou, pl. 4, fig. 1a-b, 1d (non fig 1c = *P. iberica fide* Neumann & Fourcade, 1985; early?, middle early late Cenomanian, Portugal [no younger than *geslinianum* Zone *fide* Berthou, 1984a, b].
1973 *Praealveolina cretacea debilis* – Berthou, pl. 7, figs. 2a, 2b; pl. 30, fig. 2; early – middle Cenomanian, Portugal.
1974 *Praealveolina simplex* – Juignet et al., p. 2281; pl. 1, figs. 3-4, 6 [non pl. 1, fig. 2 = *P. iberica*]; middle Cenomanian (*jukesbrownei* Zone), Paris Basin, France
Non 1976 *Praealveolina simplex* – Kalantari, pl. 22, fig. 27; undifferentiated Cenomanian, Iranian Zagros [possibly *Cisalveolina fraasi* (Gümbel)].
Non 1978 *Simplalveolina simplex* – Berthou & Schroeder, p. 57, 64, 66; pl. 9, fig. 4; base middle Cenomanian, (range given as latest early and earliest middle Cenomanian), Portugal
1981 *Praealveolina simplex* – Tronchetti, p. 94, 285-286, 291-294, 314, 316; pl. 23, figs. 1-3; [*fide* Neumann & Fourcade, 1985].
1985 *Praealveolina simplex* – Neumann & Fourcade (in Schroeder & Neumann), p. 112, pl. 52, figs. 1-8; text-fig. 12; early – late Cenomanian, global review.
Non 1985 ?*Simplalveolina simplex* – Bilotte, pl. 6, fig. 7; early Cenomanian, French Pyrenees [= *P. iberica*].
1987 *Simplalveolina simplex* – Loeblich & Tappan, p. 365, pl. 380, figs. 7-13; late Cenomanian, France & Spain.
1988 *Praealveolina simplex* – Sartorio & Venturini, p.108 (upper fig.); early Cenomanian, Iranian Zagros.
1992 *Praealveolina simplex* – Kalantari, text-fig. 155 (5); undifferentiated Cenomanian, Iranian Zagros.
1993 *Simplalveolina simplex* – Calonge-Garcia, fig. 3; undifferentiated Cenomanian, Spain.
2002 *Praealveolina simplex* – Calonge et al., pl. 6, fig. 4; late Cenomanian, Spanish Pyrenees [but also known from the middle Cenomanian; Calonge-Garcia & Lopez-Carrillo, 2003].
2005 *Simplalveolina simplex* – Hart et al., fig. 7A-B; late Cenomanian, Portugal.
2008 *Praealveolina* cf. *simplex* – Ahmadi et al., pl. 3, fig. 3; middle - late Cenomanian; Iranian Zagros.
2012 *Praealveolina simplex* – Ghanem et al., fig. 6e (11); late Cenomanian (but shown to range as old as early Cenomanian), Syria.
2014 *Cisalveolina frassi* (sic) – Afghah et al., fig. 9A; middle Cenomanian, Iranian Zagros.
2014 *Ovalveolina crassa* – Afghah & Fadaei, fig. 7a; undifferentiated Cenomanian, Iranian Zagros
? 2014 *Cisalveolina frassi* (sic) – Afghah & Fadaei, fig. 7e; early, middle and late Cenomanian, Iranian Zagros.
Non 2014 *Simplalveolina simplex* – Afghah & Fadaei, fig. 7d; early Cenomanian [age doubtful, more likely late Cenomanian on the basis of associated fauna], Iranian Zagros [= *Cisalveolina fraasi* (Gümbel)].
2016 *Simplalveolina* gr. *simplex* – Vicedo & Piuz, p. 839, fig. 17A-G; *Non* H-L [= *S. mardinensis fide* Simmons et

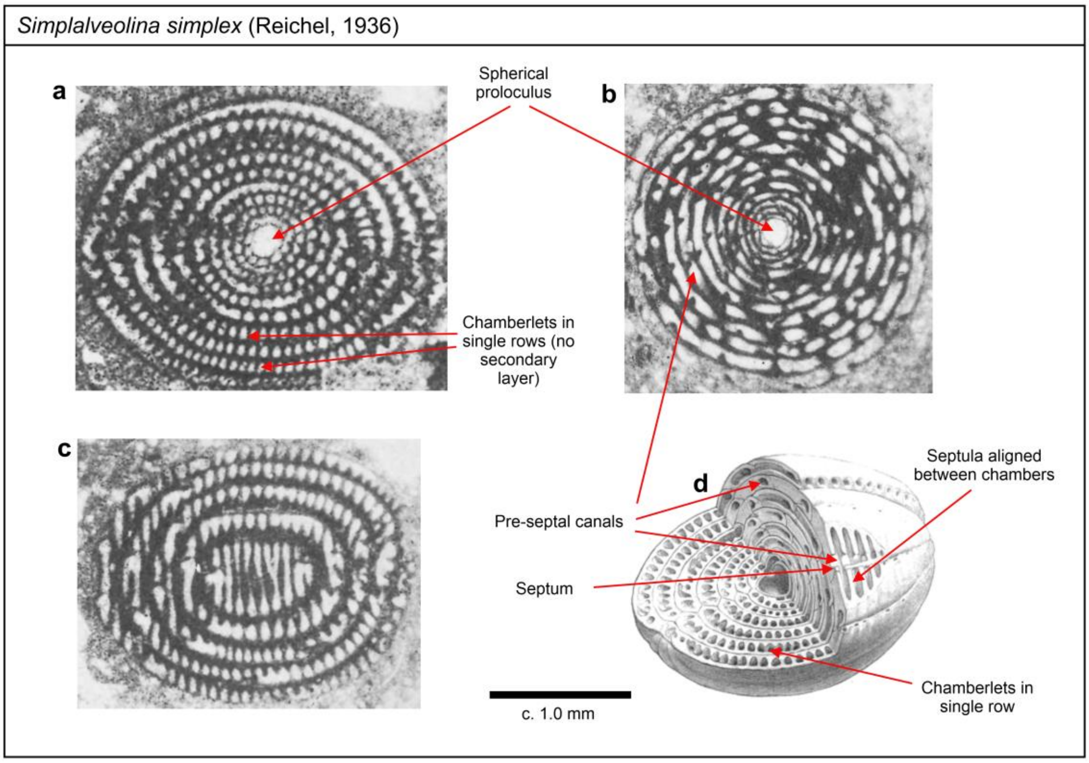


Fig. 39: Representative illustrations of *Simplalveolina simplex*: **a.** Axial section, Reichel (1936, pl. VIII, fig. 5); **b.** Equatorial section, Reichel (1936, pl. VIII, fig. 9); **c.** Tangential section, Reichel (1936, pl. VIII, fig. 7); **d.** Schematic 3D cutaway, Reichel (1936, pl. XI, fig. 2b). Illustrations a – c, middle Cenomanian, western France.

al., 2020]; middle Cenomanian, Oman Mountains.
? 2016 *Praealveolina* ex gr. *P. simplex* – Hart, fig. 10D; undifferentiated Cenomanian, Oman Mountains.
2018 *Simplalveolina* sp. – BouDagher-Fadel, pl. 5.21, fig. 5; pl. 5.22, fig. 8; undifferentiated Cenomanian, France.
Non 2019 *Praealveolina simplex* – Parnian et al., fig. 3D; undifferentiated Cenomanian, Iranian Zagros. [= nezzazatid].
2020 *Praealveolina simplex* – Ezampanah et al., fig. 7E; late Cenomanian, Iranian Zagros.
? 2020 *Praealveolina simplex* – Schlagintweit & Yazdi-Moghadam, fig. 3G; middle-late Cenomanian, Iranian Zagros [similar biometrics to *Simplalveolina mardinensis* Simmons & Vicedo, but only one specimen].
? 2020 *Praealveolina* cf. *simplex* – Yazdi-Moghadam & Schlagintweit, fig. 2I; middle-late Cenomanian, Iranian Zagros.
2021 *Simplalveolina simplex* – BouDagher-Fadel & Price, pl. 1, figs. 7-10; undifferentiated Cenomanian, France.
2021b *Simplalveolina simplex* – Dousti Mohajer et al., fig. 8d; late Cenomanian, Iranian Zagros.
2021 *Ovalveolina crassa* – Dehghanian & Afghah, fig. 7 (5); middle Cenomanian, Iranian Zagros
? 2021 *Praealveolina simplex* – Yazdi-Moghadam & Schlagintweit, fig. 2G; middle-late Cenomanian, Iranian Zagros [similar biometrics to *S. mardinensis*, but only one specimen].
? 2021a *Simplalveolina simplex* – Dousti Mohajer et al., pl. 2, fig. d; late Cenomanian, Iranian Zagros [similar biometrics to *S. mardinensis*, but only one specimen].
? 2023 *Praealveolina simplex* – Schlagintweit et al., fig. 3g; middle-late Cenomanian, Iranian Zagros [similar biometrics to *S. mardinensis*, but only one specimen].
? 2023 *Praealveolina simplex* – Shakir & Mousa, pl. 1, fig. P (?also *Praealveolina* sp., pl. 1, fig. Q); early Cenomanian, central Iraq. [Scale bar must be erroneous].
Non 2024 *Simplalveolina simplex* – Moghaddam et al., fig. 2a; undifferentiated Cenomanian, Iranian Zagros [= ?*Cisalveolina* sp.].
2025 *Simplalveolina simplex* – Martin Closas et al., fig. 7K-L; late Cenomanian, Spain.
2025 *Simplalveolina simplex* – Maksoud et al., fig. 11, A-B; undifferentiated middle – late Cenomanian, Lebanon.
2026 *Simplalveolina simplex* – Schlagintweit & Yazdi-Moghadam, pl. 4, figs. 1-5; middle Cenomanian, Iranian Zagros.

Reference images: Reichel (1936-37), p. 67, pl. V, fig. 4; pl. VIII, figs. 5-9, 12; Pl. XI, fig. 2b.

Taxonomy/Identity: First described from the (most likely middle) Cenomanian of France (Île Madame) by Reichel (1936). The identity is as per the genus. It differs from the only other known species – *S. mardinensis* Simmons & Vicedo 2020; see below – in having a larger proloculus (110-200 µm vs. 85-105 µm) and a larger axial test diameter with more whorls (1.3-2.0 mm & 8-12 whorls vs. 0.8-1.0 mm & 8-9 whorls).

Praealveolina iberica is very similar in overall size and shape and is said to have "possible" supplementary chambers in the polar areas (Neumann & Fourcade in Schroeder & Neumann, 1985; Calonge et al., 2002) whereas true *Simplalveolina* has none. It also has a slightly larger pre-septal canal and a thicker basal layer at the poles. *Praealveolina pennensis* Reichel, 1936 is very similar in size and shape to both taxa but has a more readily visible secondary chamber layer which is not limited to the polar areas. Calonge et al. (2002; table 1) provides useful biometric data to separate *Praealveolina* (with *Praealveolina simplex* included) species.

Confident Stratigraphic Range: middle Cenomanian (scarce) – late Cenomanian (common).

Uncertain Stratigraphic Range: early Cenomanian.

Although this species has been widely reported in the literature, an understanding of its stratigraphic distribution is hampered by potential confusion with, for example, *P. iberica*. It was first described from the Cenomanian of Île Madame, western France by Reichel (1936). This type locality is said to be middle Cenomanian by Neumann & Fourcade in Schroeder & Neumann (1985), but the evidence (co-occurrence with *Ovalveolina ovum* (d'Orbigny, 1850) and *Chrysalidina gradata* d'Orbigny, 1839) is not completely compelling. Calonge et al. (2002) and Caus et al. (2009) considered it restricted to the late Cenomanian in the northern Iberian Peninsula. It is also known from the late Cenomanian of Portugal (Berthou, 1973; Hart et al., 2005; no younger than the *M. geslinianum* ammonite Zone *fide* Berthou, 1984a, b), whilst El Naggar & Al-Rifaiy (1973) mentioned it without illustration from the "very late Cenomanian" of Kuwait. Some of the many records from the Iranian Zagros (see synonymy list) are almost certainly at least in part late Cenomanian.

In addition to the questionable type locality age, confirmed records from the middle Cenomanian are less common but include Juignet et al. (1974) in limestones from the Paris Basin with ammonites from the *A. jukesbrownei* ammonite Zone. Also valid are the records of Berthou (1973) and Berthou & Schroeder (1978) from Portugal (at the base of the middle Cenomanian), and Vicedo & Piuz (2017) (those that are not *S. mardinensis*) from Oman. *S. simplex* has also been recorded from the middle Cenomanian of Lebanon (Saint-Marc, 1974, 1981) without illustration.

Early Cenomanian records are problematic, and we believe that many unillustrated records may be misidentifications of *P. iberica* (Bilotte et al. 1978, Pyrenees; Chiocchini et al. 2008, central Italy; Moullade & Peybernès, 1974, Spain; Roger et al., 1989, southern Oman (Dhofar); Saint-Marc, 1974, 1981, Lebanon). Alternatively, the age of valid records may be doubtful (e.g. Sartorio & Venturini, 1988). Of the illustrated records from the early Cenomanian both those of Neumann (1963) and of Shakir & Mousa (2023) are questionable/unclear, and the early Cenomanian age of Neumann (1963) cannot be proven by any associated fauna. Consequently, we regard early Cenomanian records of this species as uncertain.

Geographic Distribution: Western and Central Neotethys. Recorded with certainty from the Iberian Peninsula to the Arabian Plate and Somalia. Possible *S. simplex* specimens have been noted by us in unpublished material from Morocco.

Genus ***Streptalveolina*** Fourcade et al. 1975

Streptalveolina was defined by Fourcade et al. (1975) with *S. mexicana* as the type (and so far, only) species, from early Cenomanian sediments of central Mexico.

Streptalveolina is the only mid-Cretaceous alveolinoid which is defined as being fully streptospirally coiled although this is more difficult to see in later growth stages and coiling may ultimately be planispiral. It is similar in terms of overall shape (globular to subglobular), chamber size (with simple chamberlets in a single row and aligned septulae) and apertures/apertural face to *Archaealveolina, Ovalveolina*, *Cisalveolina* (that has alternating septulae) and *Simplalveolina*. The streptospiral coiling, in some section orientations, can look similar to that of the genus *Pseudonummoloculina*. The Campanian genus *Praechubbina* Fourcade & Fleury 2001 is similar. However, *Streptalveolina* is distinguished by the single row of simple chamberlets at the base of the septum, which are divided through 'subepidermal' septula. Chamber architecture, especially the relationship between chamberlets and the relative aperture, is extensively described in Fourcade et al. (1975), to which reference should be made for a more detailed treatment. Hottinger et al. (1989) compare other Late Cretaceous alveolinoids with elements of streptospiral coiling (e.g. *Helenalveolina*).

See Table 1 and Figure 14 for diagnostic characteristics of the genus.

Streptalveolina mexicana **Fourcade et al., 1975**
FIGURE 40

T 1975 *Streptalveolina mexicana* gen. & sp. nov., Fourcade et al., p. 111, pls. 1-2, text-fig. 1; early Cenomanian [questionable – see discussion of stratigraphic range], central Mexico.
Non 1987 *Streptalveolina*? sp. – Michaud, pl. 17, fig. 5; Campanian, Mexico, [= *Praechubbina compressa*, *fide* Fourcade & Fleury, 2001].
2002 *Streptalveolina mexicana* – Scott, p. 47-49; pl. 2, figs. 1-9; latest Albian, Texas, USA.
? 2008 *Streptalveolina* sp. – BouDagher-Fadel, pl. 5.20, fig. 9; early Cenomanian [questionable – see discussion of stratigraphic range], Mexico.
? 2021 *Streptalveolina* sp. – BouDagher-Fadel & Price, pl. 2, fig. b; undifferentiated Cenomanian, France.

Reference Images: Fourcade et al., (1975), p. 111, pls. 1-2, text-fig. 1.

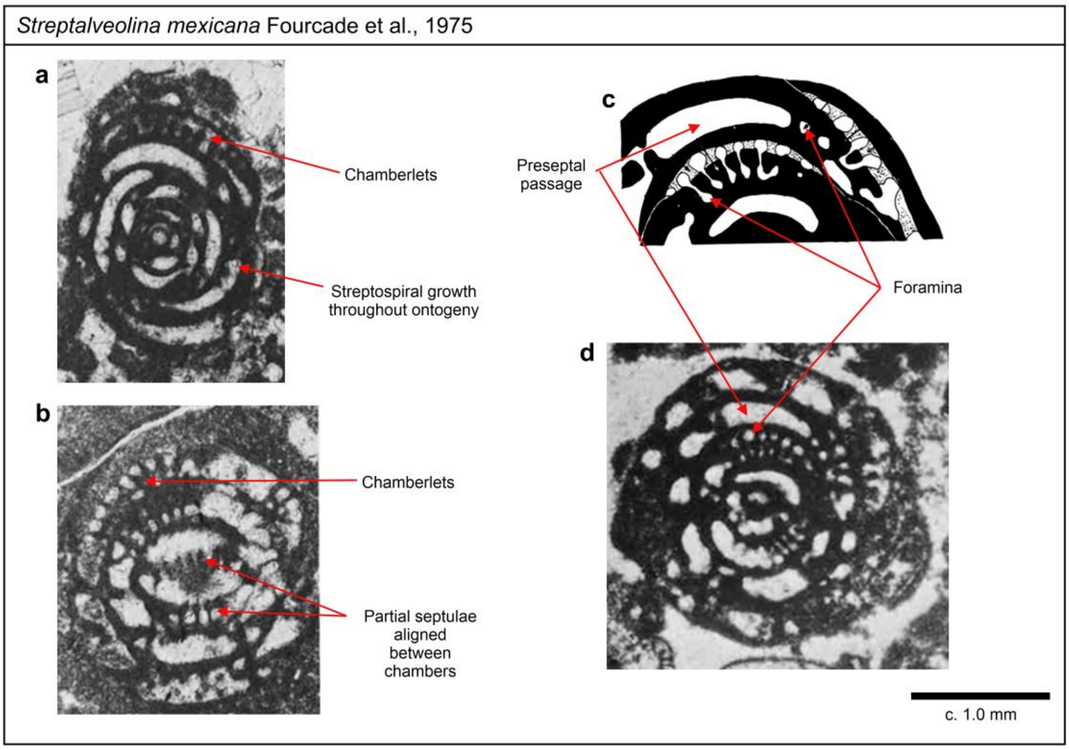


Fig. 40: Representative illustrations of *Streptalveolina mexicana*: **a.** Axial section (holotype), Fourcade et al. (1975, pl. 1, fig. 5; early Cenomanian?, Mexico); **b.** Oblique tangential section, Fourcade et al. (1975, pl. 1, fig. 6; early Cenomanian ?, Mexico); **c.** Schematic oblique section, Fourcade et al. (1975, text-fig. 1); **d.** Oblique section, Fourcade et al. (1975, pl. 1, fig. 1; early Cenomanian?, Mexico).

Taxonomy/Identity: For similarities and differences with other taxa see above in the genus description.

The species *Borelis peybernesi* De Castro in De Castro & Peybernès (1983) from the Albian of the Mediterranean was referred to *Streptalveolina* by BouDagher-Fadel & Price (2021) but this species appears to be streptospiral in the early stage of growth only, before becoming fully planispiral.

Confident Stratigraphic Range: latest Albian

Uncertain Stratigraphic Range: early Cenomanian

The stratigraphic range of this species is discussed by Scott (2002) who reported the species from the latest Albian of Texas. Although the original description of this species is from the supposed early Cenomanian of Mexico (Fourcade et al., 1975), Scott (2002) considered this record to be more likely latest Albian and only questionably early Cenomanian. See also Scott (2022).

Geographic Distribution: First described from central Mexico by Fourcade et al. (1975) and subsequently, though only rarely and unillustrated, from elsewhere in Mexico (e.g. Arzate et al., 1989). Scott (2002) illustrated the species from Texas and reported on a wider distribution in the Gulf Coast region.

BouDagher-Fadel & Price (2021) illustrated a dubious specimen of "*Streptoalveolina* sp." with a provenance of the Cenomanian of the Île Madame in western France.

Family **Myriastylidae** Piuz et al. 2014

Genus ***Myriastyla*** Piuz et al. 2014

Myriastyla was defined by Piuz et al. (2014) with *M. omanensis* as the type species, from lower middle Cenomanian sediments of the Natih Formation, E Member, of Oman (considered by Bromhead et al., 2022, to be upper early Cenomanian, *M. dixoni* ammonite zone, in age). They also defined one more species; *M. grelaudae*, described from the same interval and location.

The essential characteristic that defines *Myriastyla* and differentiates it from other alveolinoid genera bears on the nature of septula that are not solid, 'vertical', sheet-like structures but in this case are "…*longitudinal ridges supporting each a single row of pillars*…" (Piuz et al., 2014, p. 355). Consequently, longitudinal barriers between chamberlets are discrete and (in the upper part of the chamber at least) open, meaning that there are no 'true' chamberlets as implied by Hottinger et al.'s (1989) emended definition of the Alveolinidae. Moreover, there is no pre-septal passage in *Myriastyla* (the only way of ensuring communication between 'true' chamberlets in all other alveolinoids).

Piuz et al. (2014) excluded *Myriastyla* from the Fabulariidae (the only other miliolid group with chambers occupied by pillars rather than septulae) as that family has spherical, concentric, chambers and milioline coiling in the early stage of growth and with a trematophore as aperture, whereas *Myriastyla* is entirely planispiral. In consequence, Piuz et al. (2014) created a new alveolinoid family, the Myriastylidae, to accommodate taxa with such peculiar features.

See Table 1 and Figure 8 for diagnostic characteristics of the genus.

***Myriastyla grelaudae* Piuz et al., 2014**
FIGURE 41

T 2014 *Myriastyla grelaudae* sp. nov., Piuz et al., p. 357, fig. 13; lower middle Cenomanian, Oman Mountains [considered late early Cenomanian – Bromhead et al., 2022].
2021b *Praealveolina debilis* – Dousti Mohajer et al., fig. 9d; early Cenomanian, Iranian Zagros.
? 2021b *Praealveolina iberica* – Dousti Mohajer et al., fig. 9b; early Cenomanian, Iranian Zagros.
2022 *Myriastyla grelaudae* – Consorti & Vicedo, fig. 1, lower-right; Cenomanian, Oman [from type illustrations].

Reference Images: Piuz et al., (2014), p. 357, fig. 13.

Taxonomy/Identity: *M. grelaudae* is more axially elongate in overall shape than *M. omanensis*, which is generally subglobular. It has a larger megalosphere than *M. omanensis* (0.2-0.4 mm cf. 0.1-0.3 mm) and more whorls per unit of diameter (e.g., 8 cf. 6 at a diameter of 1.7 mm).

Confident Stratigraphic Range: upper early Cenomanian (following Bromhead et al., 2022).

Uncertain Stratigraphic Range: not applicable.

First described from the lower middle Cenomanian of Oman by Piuz et al. (2014, now thought to be upper early Cenomanian according to Bromhead et al., 2022).

Geographic Distribution: So far recorded only from Oman and the Iranian Zagros.

***Myriastyla omanensis* Piuz et al., 2014**
FIGURE 42

2004 *Cisalveolina fallax* – Flügel, pl. 72, fig. 2; undifferentiated Cenomanian, UAE.
2010 *Cisalveolina fallax* – Flügel, pl. 72, fig. 2; undifferentiated Cenomanian, UAE.
T 2014 *Myriastyla omanensis* gen. & sp. nov., Piuz et al., p. 355, figs. 11-12; lower middle Cenomanian, Oman Mountains [considered late early Cenomanian – Bromhead et al., 2022].
2022 *Myriastyla omanensis* – Consorti et al., fig. 2J; early/middle Cenomanian boundary, Iranian Zagros.
2022 *Myriastyla omanensis* – Yazdi-Moghadam & Schlagintweit, fig. 2J; early/middle Cenomanian boundary, Iranian Zagros [the same figure as Consorti et al., 2022].
2023 *Myriastyla omanensis* – Schlagintweit & Yazdi-Moghadam, fig. 3I; early/middle Cenomanian boundary, Iranian Zagros [the same figure as Consorti et al., 2022].
? 2026 *Myriastyla* sp. – Schlagintweit & Yazdi-Moghadam, p. 261, pl. 4, figs. 6-8; middle Cenomanian, Iranian Zagros [probably this species].

Reference Images: Piuz et al., (2014), p. 355, figs. 11-12.

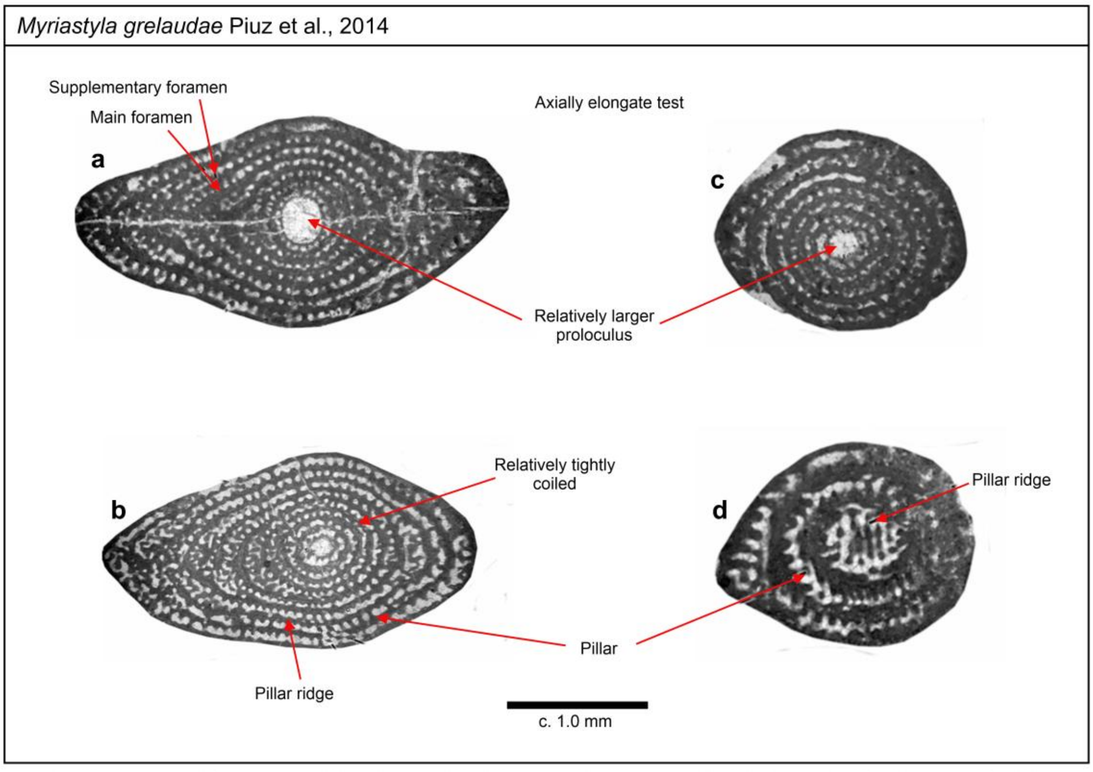


Fig. 41: Representative illustrations of *Myriastyla grelaudae*: **a.** Axial section (holotype), Piuz et al. (2014, fig. 13,4; lower middle Cenomanian, Oman); **b.** Axial, slightly oblique section, Piuz et al. (2014, fig. 13.10; lower middle Cenomanian, Oman); **c.** Near equatorial section, Piuz et al. (2014, fig. 13.13; lower middle Cenomanian, Oman); **d.** Tangential section, Piuz et al. (2014, fig. 13.15; lower middle Cenomanian, Oman). Lower middle Cenomanian ages now considered upper early Cenomanian (following Bromhead et al., 2022).

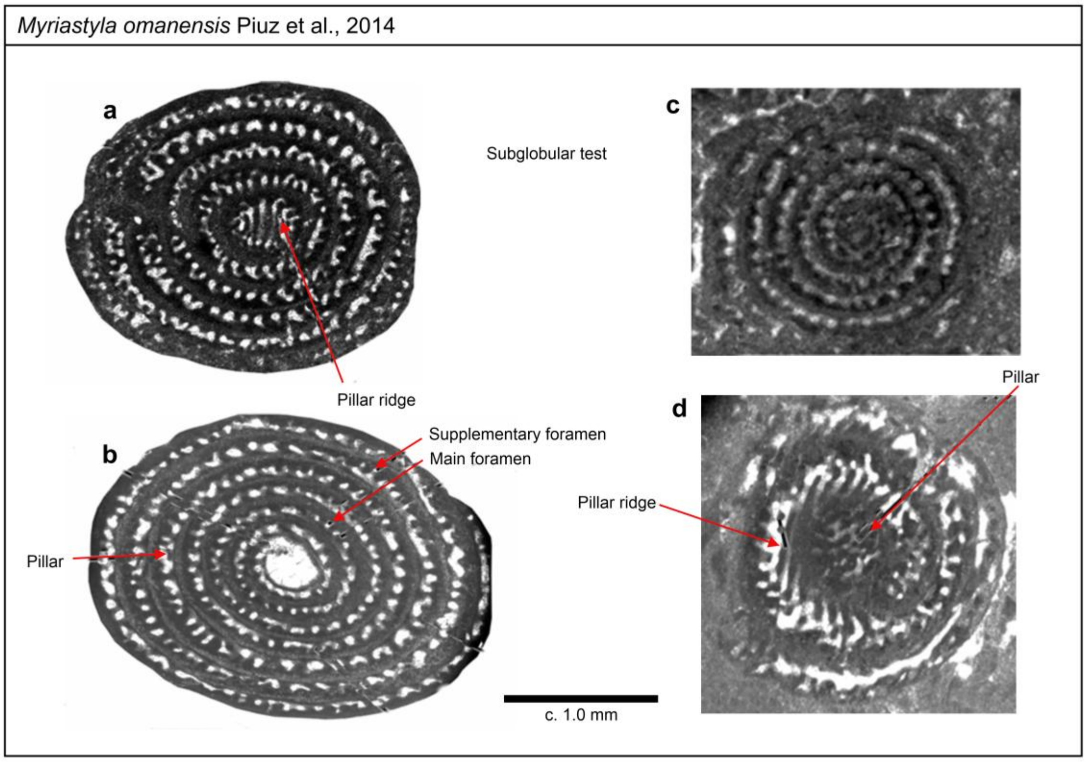


Fig. 42: Representative illustrations of *Myriastyla omanensis*: **a.** Axial section (holotype), Piuz et al. (2014, fig. 11.3; lower middle Cenomanian, Oman); **b.** Axial section, Piuz et al. (2014, fig. 11.2; lower middle Cenomanian, Oman); **c.** Near equatorial section, Piuz et al. (2014, fig. 12.3; lower middle Cenomanian, Oman); **d.** Tangential section, Piuz et al. (2014, fig. 12.6; lower middle Cenomanian, Oman). Lower middle Cenomanian ages now considered upper early Cenomanian (following Bromhead et al., 2022).

Taxonomy/Identity: *M. omanensis* is more subglobular in overall shape than *M. grelaudae*, which is axially elongate. It has a smaller megalosphere than *M. grelaudae* (0.1-0.3 mm cf. 0.2-0.4 mm) and fewer whorls per unit of diameter (e.g., 6 cf. 8 at a diameter of 1.7 mm).

Confident Stratigraphic Range: upper early Cenomanian (following Bromhead et al., 2022).

Uncertain Stratigraphic Range: lower middle Cenomanian.

First illustrated (as "*Cisalveolina fallax*") from the subsurface of the northern United Arab Emirates by Flügel (2004, 2010), it was formally described from the lower middle Cenomanian of the Oman Mountains by Piuz et al. (2014), now thought to be upper early Cenomanian according to Bromhead et al. (2022), and subsequently from close to the early/middle Cenomanian boundary of the Iranian Zagros. Recorded (as sp. but thought probably to be *M. omanensis*) from the lower part of an interval designated as middle Cenomanian by Schlagintweit & Yazdi-Moghadam (2026). As noted by Schlagintweit & Yazdi-Moghadam (2026), species identity is uncertain from the material available, but certainly belongs to the genus *Myriastyla*.

Geographic Distribution: So far recorded only from Oman, the United Arab Emirates, and the Iranian Zagros.

Family **RHAPYDIONINIDAE** Keijzer 1945

Subfamily **RHAPYDIONININAE** Keijzer 1945

Genus ***Sellialveolina*** Colalongo 1963

Sellialveolina represents so far the only Cenomanian rhapydioninid genus (i.e., an alveolinoid with a thick, perforated basal layer and forming chamberlets) that is axially-compressed and lenticular, with 1 or 2 horizontal chamber partitions ('floors') and septulae with residual pillars – see Fleury & Özkan (2020) for a glossary of morphological terms associated with rhapydioninids and Vicedo et al. (2011) for a review of the group. Other genera with moderately axially-compressed species (*Cisalveolina, Ovalveolina*) have only a single row of cortical/main chamberlets. For at least one *Sellialveolin*a species – *S. viallii*, it is somewhat similar to *Ovalveolina maccagnoae* De Castro 1966, but the latter does not possess residual pillars (see below for discussion).

Another confusion genus (into which several occurrences of *S. viallii* and other *Sellialveolina* species have been placed) is *Pseudedomia* Henson, which is morphologically similar but is more axially-compressed and demonstrates uncoiling in the later growth stage (which Colalongo, 1963, did not describe but was demonstrated by De Castro, 1966 – see Hottinger, 1974) and into which a new species (*P. drorimensis*) was placed by Reiss et al. (1964), apparently unaware of Colalongo's 1963 work. Moreover, some *Pseudedomia* species do not have "floors" and thus no secondary chamberlets.

Hamaoui (1965) regarded *Sellialveolina viallii* (the type species of *Sellialveolina*) as belonging in *Pseudedomia* Henson, 1948 and thus *Pseudedomia* being the senior synonym of *Sellialveolina* (see also, for example, Deloffre & Hamaoui, 1979). Fleury & Özkan (2020) briefly discussed the history behind this confusion/error and noted that it persisted in the literature for a long time and still does (e.g., Al-Salihi & Ibrahim, 2023) (*P. drorimensis* was placed in *Sellialveolina* by Fleury, 1980; Vicedo et al., 2011). They also noted, which has never been proven otherwise so far, that true *Pseudedomia* occurs in much younger strata (Campanian-Maastrichtian) compared with *Sellialveolina* (Albian-Cenomanian).

Sellialveolina was comprehensively reviewed and illustrated (including schematically) by Vicedo et al. (2011). They declared it the most primitive rhapydioninid genus known, and the only genus of axially-compressed alveolinoids (i.e. Rhapydioninidae) in the mid-Cretaceous. They listed four species assigned to the genus in the Cenomanian, two of which were new, in two lineages based on material from Western Tethys and Iberia: *Sellialveolina drorimensis*, *Sellialveolina gutzwilleri*, *Sellialveolina quintanensis* (a species we regard as questionable) and *Sellialveolina viallii*.

See Table 1 and Figure 12 for diagnostic characteristics of the genus. Table 5 shows a series of different morphological characteristics for the four species.

Vicedo et al. (2011) stated that *Sellialveolina* originated from the pseudonummoloculinids (see Simmons & Bidgood, 2023 for a treatment of that group) by (i) an increase in shell and embryo size; (ii) an increase in number of chambers per whorl; (iii) adult sexual dimorphism and (iv) an increase in internal complexity. These, they added, followed the same evolutionary trends as other LBF groups that were K-strategists.

This view seems to have been followed by BouDagher-Fadel & Price (2021; fig. 3 therein) but – in apparent self-contradiction – fig. 4 therein shows the Rhapydioninidae evolving from *Pseudedomia*.

Alternatively, Calonge-Garcia (1993) suggested *O. maccagnoae* was the ancestor of *S. viallii* which is the oldest *Sellialveolina* species recorded to date and the oldest rhapydioninid.

Vicedo et al. (2011) implied that the four species of *Sellialveolina* have a distinct stratigraphic distribution: S. *viallii* and *S. quintanensis* in the early Cenomanian, *S. gutzwilleri* in the middle Cenomanian and *S. drorimensis* in the late Cenomanian. This is not confirmed by the review below, with taxa having demonstrably longer ranges. An unnamed small form of *Sellialveolina* was illustrated from the Albian of Greece (Fleury, 1980; Fleury & Özkan, 2020).

Sellialveolina drorimensis (Reiss et al., 1964) emend. Vicedo et al., 2011

FIGURE 43

T 1964 *Pseudedomia drorimensis*, n. sp., Reiss et al., p. 436, pl. 1, figs. 1-12; pl. 2, figs. 1-6; late Cenomanian – ?earliest Turonian, Negev, Israel [associated fauna suggests a late Cenomanian age, latest Cenomanian by stratigraphic position below beds bearing earliest Turonian ammonites].

1965 *Pseudedomia* aff. *P. drorimensis* – Hamaoui, pl. 7, figs. 1-9, 11 [of these, figs. 1, 3-7 & 9 are doubtful; possibly *S. viallii* or incomplete *S. drorimensis*]; pl. 9, figs. 3, ?12 [fig. 12 is doubtful]; undifferentiated Cenomanian, Israel.

1966 *Pseudedomia drorimensis* – Hamaoui, pl. 3, fig. 7; ?pl. 5, fig. 10 [doubtful]; pl. 8, fig. 7; pl. 12, figs. 5-7 [fig. 6 is doubtful]; undifferentiated Cenomanian, Israel.

? 1967 *Pseudedomia drorimensis* – Arkin & Hamaoui, pl. 2, fig. 4; undifferentiated Cenomanian, southern Israel [a rhapydioninid but indeterminate].

? 1967 *Pseudedomia* aff. *P. drorimensis* – Bismuth et al., pl. 11, figs. 16-19; early Cenomanian, Tunisia [possibly = *S. gutzwilleri*].

1970 *Pseudedomia drorimensis* – Saint-Marc, pl. 1, figs. 8-14; basal late Cenomanian, Lebanon [figs. 13-14 are probably *S. viallii*].

? 1970 *Pseudedomia viallii* (Colalongo) – Saint-Marc, pl. 1, fig. 5; middle Cenomanian, Lebanon [other illustrations are *S. viallii*].

? 1970 *Pseudedomia* cf. *drorimensis* – Hamaoui & Saint-Marc, pl. 38, fig. 5; late Cenomanian, Lebanon [a rhapydioninid but indeterminate].

1973 *Pseudedomia drorimensis* – Berthou, pl. 3, fig. 1; *non* pl. 31, figs. 1, 3; *non* pl. 36, fig. 2; late early, middle and late Cenomanian, Portugal [*non* forms are not *Sellialveolina*].

1973 *Pseudedomia* sp. – Hamaoui & Fourcade, pl. 8, fig. 6, 8; undifferentiated Cenomanian, Algeria.

1973 *Pseudedomia* (cf. ? *P. drorimensis*) – Hamaoui & Fourcade, pl. 8, figs. 7, 9; undifferentiated Cenomanian, Algeria.

? 1973 *Pseudedomia* aff. *drorimensis* – Bilotte, pl. 2, fig. 9; undifferentiated Cenomanian, Pyrenees.

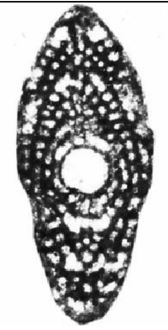
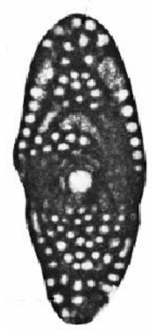
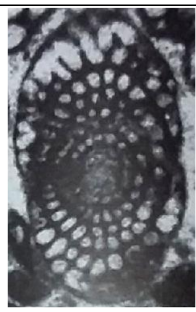
1974 *Pseudedomia drorimensis* – Saint-Marc, p. 245, pl. 10, figs. 8-13 [fig. 7 also resembles *S. drorimensis*]; late Cenomanian (range given as latest early – late Cenomanian), Lebanon [see also Saint-Marc, 1978 (unillustrated)].

Non 1978 *Pseudedomia drorimensis* – Berthou & Schroeder, pl. 9, fig. 4; base middle Cenomanian, Portugal [indeterminate but not *Sellialveolina*].

1979 *Pseudedomia drorimensis* – Deloffre & Hamaoui, pl. 1-8; middle – late Cenomanian, Aquitaine, France [images in pl. 3 are comparable with *S. gutzwilleri*].

1981 *Pseudedomia drorimensis* – Saint-Marc, pl. 2, figs. 13-14; late early – top Cenomanian, Lebanon.

Table 5: Characteristics of *Sellialveolina* species herein shown in alphabetical order left to right. (meg = Megalospheric form; mic = Microspheric form).

Characteristic	***S. drorimensis***	***S. gutzwilleri***	***S. quintanensis***	***S. viallii***
Original description & provenance	Reiss et al. (1964 as *Pseudedomia drorimensis*), late Cenomanian - ?earliest Turonian, Israel	Vicedo et al. (2011, ☼), middle – middle Cenomanian, Spain	Vicedo et al. (2011, ☼), earliest Cenomanian, Spain	Colalongo (1963, ☼), latest Albian – Cenomanian, Italy
Basic image (Reference source of image shown thus ☼. All images are types (holo-, lecto- or neo-) and are not to scale.)				
Other significant illustrative descriptions	Vicedo et al. (2011, ☼)			Vicedo et al. (2011)
Proloculus diameter µm ($_{meg}$ unless stated otherwise)	160-180	110-150	60-110	80-130
Max. Equatorial diameter (mm)	2.4 $_{meg}$ / >3.5 $_{mic}$	1.8-2.0 $_{meg}$ / 1.8-2.1 $_{mic}$	0.9-1.0 $_{meg}$ / 1.3-1.4 $_{mic}$	1.2-1.4 $_{meg}$ / 1.2-1.5 $_{mic}$
Elongation Index ($_{meg}$)	0.2-0.4	0.3-0.4	0.4	0.6
Chambers per adult whorl	17-21	12-14	11-12	10-12
Cortical chamberlets (axial diameters in µm)	20-30	25-30	20-24 (rarely 34-40)	35-50
Medullar chamberlets	Begin in 1st whorl, restricted to central area in early growth stage (Y-shaped septulae, cross-wise oblique)	Begin in 2nd whorl, restricted to central area (Y-shaped septulae)	Begin in 2nd whorl, restricted to central area	Begin in 3rd – 4th whorl, restricted to central area
Preseptal passage	⅓ to ½ chamber volume		¼ to ½ chamber volume	¼ to ½ chamber volume
Comments	Data from Vicedo et al. (2011)	Data from Vicedo et al. (2011)	Data from Vicedo et al. (2011)	Data from Vicedo et al. (2011)

1982 *Pseudedomia drorimensis* – Fourcade & García, pl. 1, figs. 3; ?pl. 3, fig. 3 [indeterminate]; undifferentiated early – middle Cenomanian, Spain.
1982 *Pseudedomia drorimensis* – Mouty & Saint-Marc, pl. 2, fig. 1; middle Cenomanian (range given as middle – late Cenomanian), NW Syria.
Non 1982 *Pseudedomia drorimensis* – Fourcade & García, pl. 1, fig. 4; undifferentiated early - middle Cenomanian, Spain [*fide* Vicedo et al., 2011 = *S. quintanensis*].
Non 1984 *Pseudedomia drorimensis* – Bilotte, pl. 6, figs. 12-15 [=indeterminate]; pl. 7, figs. 1-4 [most likely *Praealveolina*]; early, middle and late Cenomanian, Pyrenees.
1985 *Pseudedomia drorimensis* – Hamaoui in Schroeder & Neumann, p. 138, pl. 67, figs. 1-6; pl. 68, figs. 1-4; (questionable latest early Cenomanian) middle – late Cenomanian (questionable earliest Turonian), global review.
Non 1987 *Pseudedomia drorimensis* – Simmons & Hart,

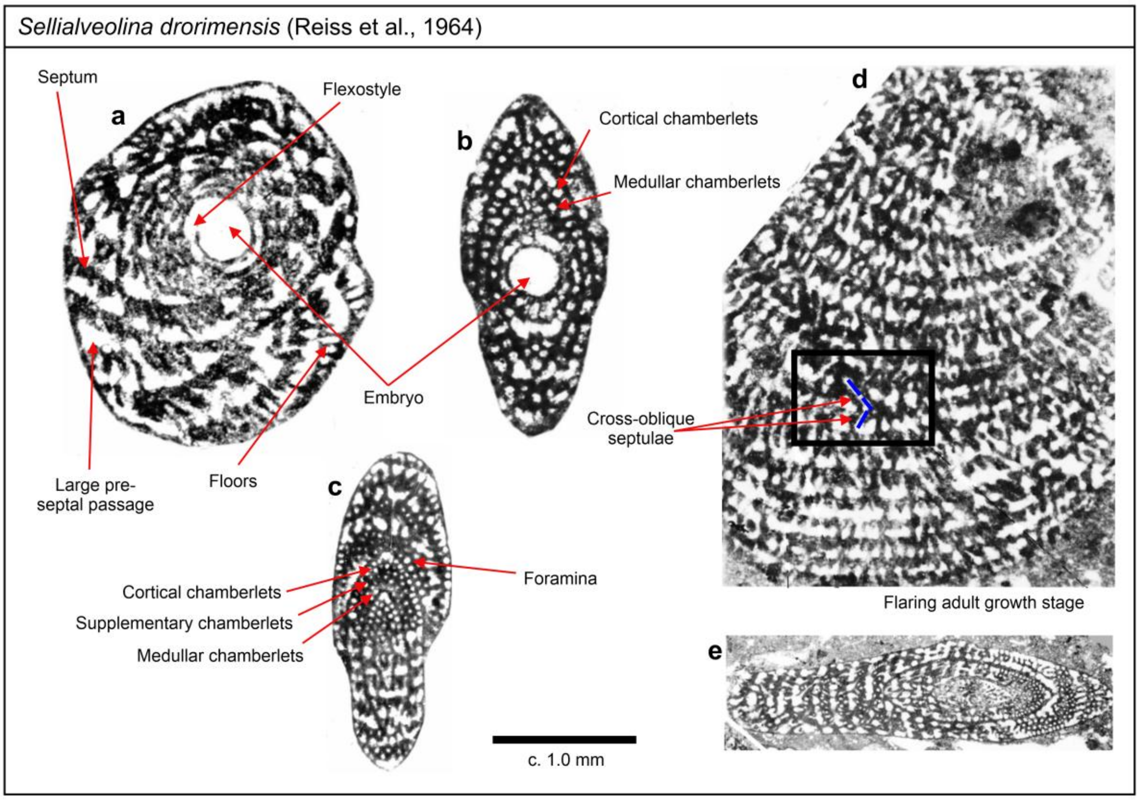


Fig. 43: Representative illustrations of *Sellialveolina drorimensis*: **a.** Equatorial section (topotype), Vicedo et al. (2011, fig. 10(1); late Cenomanian, Israel); **b.** Axial section (topotype), Vicedo et al. (2011, fig. 10(3); late Cenomanian, Israel); **c** .Tangential section (topotype), Vicedo et al. (2011, fig. 10(6); late Cenomanian, Israel); **d.** Equatorial section, showing flaring growth stage (as *Pseudedomia drorimensis*), De Castro (1988, pl. 3, fig. 1; late Cenomanian, Israel); **e.** Tangential section (as *Pseudedomia drorimensis*), De Castro (1988, pl. 3, fig. 5; late Cenomanian, Israel).

pl. 10.1, fig. 1 [= *Decastroia* (top right) and *Praealveolina* (lower left); middle Cenomanian, Oman Mountains [see also Scott, 1990; Smith et al., 1990; Kennedy & Simmons, 1991; Rabu, 1993 (all unillustrated)].

1988 *Pseudedomia drorimensis* – De Castro, pl. 2, figs. 1-10; pl. 3, figs. 1-6; late Cenomanian (- ?earliest Turonian), Israel [topotype: associated fauna suggests a late Cenomanian age, latest Cenomanian by stratigraphic position below beds bearing earliest Turonian ammonites].

? 1989 *Pseudedomia drorimensis* – Kuss & Malchus, text-fig. 28 (? text-fig. 29); late Cenomanian, Egypt.

? 1993 *Sellialveolina* cf. *drorimensis* – Jaillard & Arnaud-Vanneau, fig. 7(11-18) [only figs. 11 & 13 are close to *S. drorimensis*, the others are *Sellialveolina*, some possibly *S. gutzwilleri*]; late Turonian, Peru [see also *Sellialveolina* sp. reported from middle Cenomanian (fig. 7 (19-22))].

? 2002 *Pseudedomia* sp. – Bauer et al., pl. 3, fig. 4; late Cenomanian, Sinai, Egypt.

? 2004 *Pseudedomia* sp. – Bauer et al., pl. 2, fig. 2; late Cenomanian, Sinai, Egypt.

Non 2009 *Sellialveolina* gr. *drorimensis* – Caus et al., fig. 5 (1); middle Cenomanian, Spain [*fide* Vicedo et al., 2011 = *S. gutzwilleri*].

2011 *Sellialveolina drorimensis* – Vicedo et al., p. 49, figs. 10.1 – 10.10; late Cenomanian, Israel.

2012 *Pseudedomia drorimensis* – Ghanem et al., fig. 3; fig. 6e (1-4); middle – late Cenomanian (used as biozonal index), Syria.

Non 2013 *Sellialveolina drorimensis* – Ghanem & Khuss, fig. 14 (1-2); late Cenomanian (used as biozonal index), NW Syria [probably a *Praetaberina*].

? 2018 *Pseudedomia drorimensis* – Andrade, pl. 4, figs. 4-5; pl. 10, figs. 4-5; undifferentiated Cenomanian, Portugal.

Non 2018 *Pseudedomia drorimensis* – Luger, pl. 16, figs. 2-3; middle Cenomanian, northern Somalia [probably a true *Pseudedomia* or another rhapydioninid].

2020 *Sellialveolina* gr. *viallii* – Solak et al., fig. 5(E-I); early – middle Cenomanian, western Taurides, Türkiye [Fig. 5G resembles *S. viallii* but the other illustrations are of *S. drorimensis*].

2020 *Sellialveolina drorimensis* – Fleury & Özkan, fig. 9 (21-25); *non* fig. 13 (26-27) [probably transitional forms or *S. viallii*]; fig. 16 (8); late Cenomanian, France, Lebanon, Algeria & Israel.

Non 2023 *Pseudedomia drorimensis* – Al-Salihi & Ibrahim, pl. 2, fig. E; middle Cenomanian, southern Iraq [= *Decastroia*].

Reference Images: Reiss et al. (1964), pl. 1, figs. 1-12, pl. 2, figs. 1-6; Vicedo et al. (2011), fig. 10.

Taxonomy/Identity: An emended diagnosis of this species was provided by Vicedo et al. (2011). *S. drorimensis* has the strongest adult dimorphism and the most chamberlets per chamber than any other *Sellialveolina* species, and exhibits medullar chamberlets with a "*crosswise-oblique arrangement*" (De Castro, 1988; Vicedo et al., 2011, p. 49 and see Figure 43 herein marked in blue).

Vicedo et al. (2011) provided better illustrative material in the form of topotypes from Israel, than in Reiss et al.'s original description (1964) some of which have been reproduced here.

S. drorimensis is almost twice as large axially and equatorially than *S. viallii* and much more axially compressed, with more chambers per whorl than *S. viallii*.

Confident Stratigraphic Range: late early – late Cenomanian (locally to late Turonian, Peru).

Uncertain Stratigraphic Range: not applicable.

Originally described from what is probably the latest Cenomanian of Israel (Reiss, 1964), there is sufficient evidence (see synonymy list) that the species also occurs in the middle Cenomanian as suggested by Schroeder & Neumann (1985) and Arnaud-Vanneau in Hardenbol et al. (1998) and contrary to the view of Vicedo et al. (2011). Records from Portugal (Berthou, 1973) and Lebanon (Saint-Marc, 1981) extend the range into the late early Cenomanian. More remarkable is the occurrence in the late Turonian of Peru (Jaillard & Arnaud-Vanneau, 1993), where presumably the limited effects of OAE 2 there allowed the species to avoid end Cenomanian extinction as in Neotethys. However, i) most foraminiferal sections provided by Jaillard & Arnaud-Vanneau (1993) point to *Sellialveolina*, although, and in agreement with the authors, to assign them with full certainty to a given species is challenging; ii) the chronostratigraphic arguments provided, especially regarding the Turonian part, are valuable but somehow unconstrained and iii) subsequent studies through the same localities were not able to confirm such occurrences (Navarro-Ramirez et al., 2017; Consorti et al., 2018).

Geographic Distribution: The species is mostly known from the circum-Mediterranean, especially the Levant region. Although not confirmed by illustration from the rest of the Arabian Plate, there are several unillustrated records (e.g., from the late Cenomanian of the Iranian Zagros (Consorti et al., 2015); from the undifferentiated Late Cretaceous and late Cenomanian of Saudi Arabia (Fallatah et al., 2024; Hughes, 2019); from the Cenomanian of Jordan (Schulze, 2003; Schultze et al., 2004); and from the late early Cenomanian – late Cenomanian of Sinai (Bachmann et al., 2003). There is also the outlier record from north-western South America (Jaillard & Arnaud-Vanneau, 1993), which we recommend considering with caution.

Sellialveolina gutzwilleri Vicedo et al., 2011
FIGURE 44

? 1966 *Sellialveolina viallii* – De Castro, pl. 12, figs. 7-10; middle Cenomanian, southern Italy

? 1967 *Pseudedomia* aff. *P. drorimensis* – Bismuth et al., pl. 11, figs. 16-19; early Cenomanian, Tunisia

? 1973 *Pseudedomia* sp. – Hamaoui & Fourcade, pl. 3, figs. 1; pl. 8, figs. 7, 9; undifferentiated Cenomanian, Algeria [possibly more like *S. drorimensis*].

? 1974 *Pseudedomia viallii* (Colalongo) –Bignot & Poisson, pl. 1, figs. 2–9; undifferentiated Cenomanian, Turkish Taurides.

1979 *Pseudedomia drorimensis* – Deloffre & Hamaoui, pl. 3; middle – late Cenomanian, Aquitaine, France

1989 *Pseudedomia drorimensis* Reiss et al. – Calonge, text-fig. 63; undifferentiated Cenomanian, Spain [*fide* Vicedo et al., 2011].

2009 *Sellialveolina* gr. *drorimensis* (Reiss et al.) – Caus et al., text-fig. 5.1; middle Cenomanian, Spain.

T 2011 *Sellialveolina gutzwilleri* n. sp., Vicedo et al., p. 47, figs. 8.1 – 8.17; middle Cenomanian, Spain.

2012 *Sellialveolina viallii* – Chiocchini et al., pl. 87, figs. 6 and 10; early Cenomanian, Italy [other illustrations are of *S. viallii*].

2013 *Sellialveolina gutzwilleri* – Ghanem & Kuss, fig. 13 (1-4, 7) [probably also fig. 5]; middle Cenomanian, NW Syria.

Reference Images: Vicedo et al. (2011), fig. 8.

Taxonomy/Identity: Vicedo et al. (2011) stated that *S. gutzwilleri* is more axially compressed than *S. viallii* (and slightly more compressed than *S. quintanensis*) and has a larger equatorial diameter than both. It has similar degree of axial compression to *S. drorimensis* though is smaller in overall size. It has a subangular periphery compared with the well-rounded periphery of *S. viallii*.

Vicedo et al. (2011) also suggest that the evolutionary position of *S. gutzwilleri* in between the 'simpler' species (*S. viallii* and *S. quintanensis*) and the more 'complex' species, *S. drorimensis*.

De Castro (1988, pl. 1, fig. 9 therein) recognised a 'transitional form' between *Sellialveolina* and *Pseudedomia* in material from Italy. Vicedo et al. (2011) regarded this specimen as having a similar shape to *S. gutzwilleri* and was coeval (middle Cenomanian) with it.

Confident Stratigraphic Range: early – middle Cenomanian (common in middle Cenomanian)

Uncertain Stratigraphic Range: not applicable.

Many records of this species are from the middle Cenomanian (as are the type specimens from Spain - Vicedo et al., 2011), but there are viable records from the early Cenomanian (e.g. Chiocchini et al., 2012 as *S. viallii*).

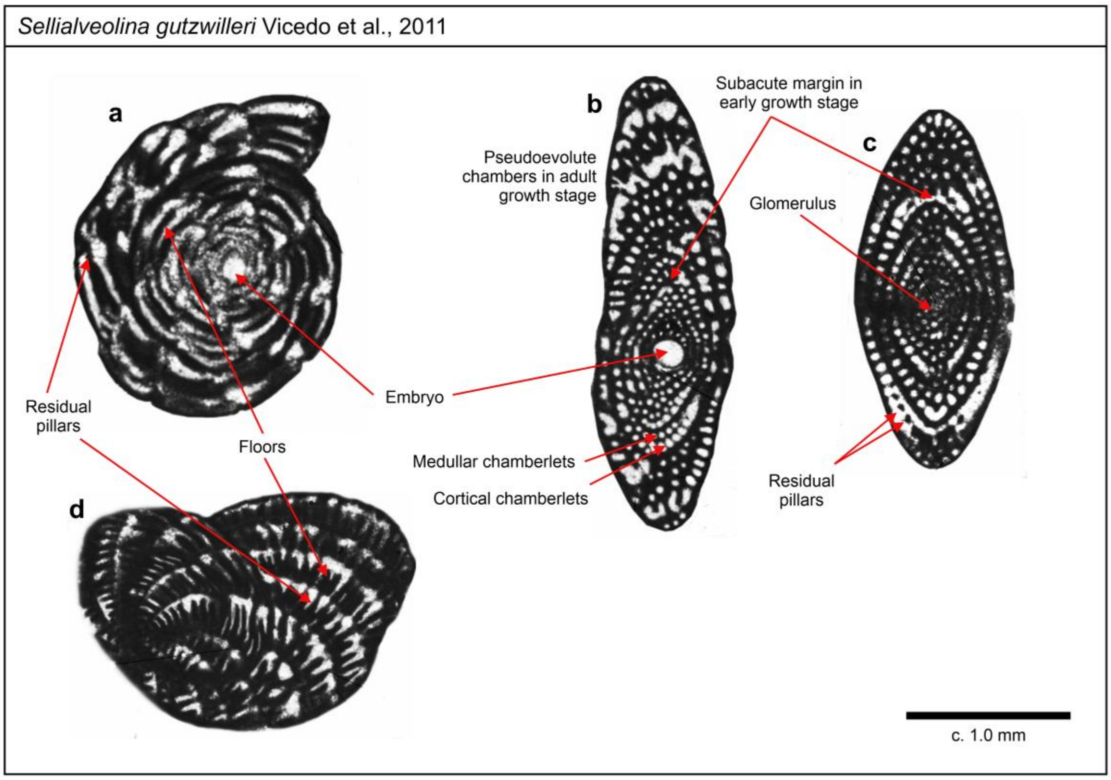


Fig. 44: Representative illustrations of *Sellialveolina gutzwilleri*: **a.** Equatorial section, Vicedo et al. (2011, fig. 8(10); middle Cenomanian, Spain); **b.** Axial section (holotype), Vicedo et al. (2011, fig. 8(13); middle Cenomanian, Spain); **c.** Axial section (microspheric generation), Vicedo et al. (2011, fig. 8(15); middle Cenomanian, Spain); **d.** Oblique section, flaring late growth stage, Vicedo et al. (2011, fig. 8(17); middle Cenomanian, Spain).

Geographic Distribution: The species is known from around the circum-Mediterranean region, perhaps as far east as Syria. There are no other confirmed records from the Arabian Plate.

Sellialveolina quintanensis Vicedo et al., 2011
FIGURE 45

1982 *Pseudedomia drorimensis* Reiss et al. – Fourcade & García, pl. 1, fig. 4; undifferentiated early - middle Cenomanian, Spain

T 2011 *Sellialveolina quintanensis* n. sp., Vicedo et al., p. 44, figs. 6.12 – 6.24; earliest Cenomanian, Spain.

Non 2013 *Sellialveolina quintanensis* – Ghanem & Kuss, fig. 13 (5-6, 8-10); early Cenomanian, NW Syria [probably more advanced species i.e., *S. gutzwilleri* or *S. drorimensis*].

? 2019 *Sellialveolina quintanensis* – Özkan & Altıner, fig. 7 (7-8); undifferentiated Albian – early Cenomanian, Türkiye.

Reference Images: Vicedo et al. (2011), fig. 6(12-24).

Taxonomy/Identity: Vicedo et al. (2011) stated that *S. quintanensis* has a lenticular shape, smaller cortical chamberlets, fewer medullar chambers and which tend to be restricted to the central area of the chambers and a smaller diameter megalosphere with more pronounced dimorphism. It is slightly smaller axially and equatorially than *S. viallii*. However, in our opinion these two taxa are very alike and may not be separated easily, *S. quintanensis* being perhaps just a small morphotype of *S. viallii*. The stratigraphic range and geographic distribution of both taxa overlaps. However, we retain it here pending further research.

Confident Stratigraphic Range: early Cenomanian.

Uncertain Stratigraphic Range: not applicable.

Geographic Distribution: So far only recorded from Spain and possibly Türkiye.

Sellialveolina viallii Colalongo, 1963
FIGURE 46

1960 Praealveolinoids – Radoičić, p. 29, pl. 34; undifferentiated Cenomanian, Serbia [*fide* De Castro in Schroeder & Neumann, 1985].

1962 "*Praealveolina*" – Sartoni & Crescenti, p. 290, pl. 32-33; undifferentiated Cenomanian, southern Italy.

T 1963 *Sellialveolina viallii* n. gen., n. sp. – Colalongo, p. 3-9, text-fig. 2; pl. 29, figs. 1-6; undifferentiated Cenomanian, southern Italy.

Non 1964 *Sellialveolina viallii* – Ietto, pl. 3-4; undifferentiated Cenomanian, southern Italy [= *Ovalveolina maccagnoae* according to De Castro, 1966].

1964 *Sellialveolina viallii* – Devoto, pl. 1, figs. 1, 4; middle Cenomanian, southern Italy.

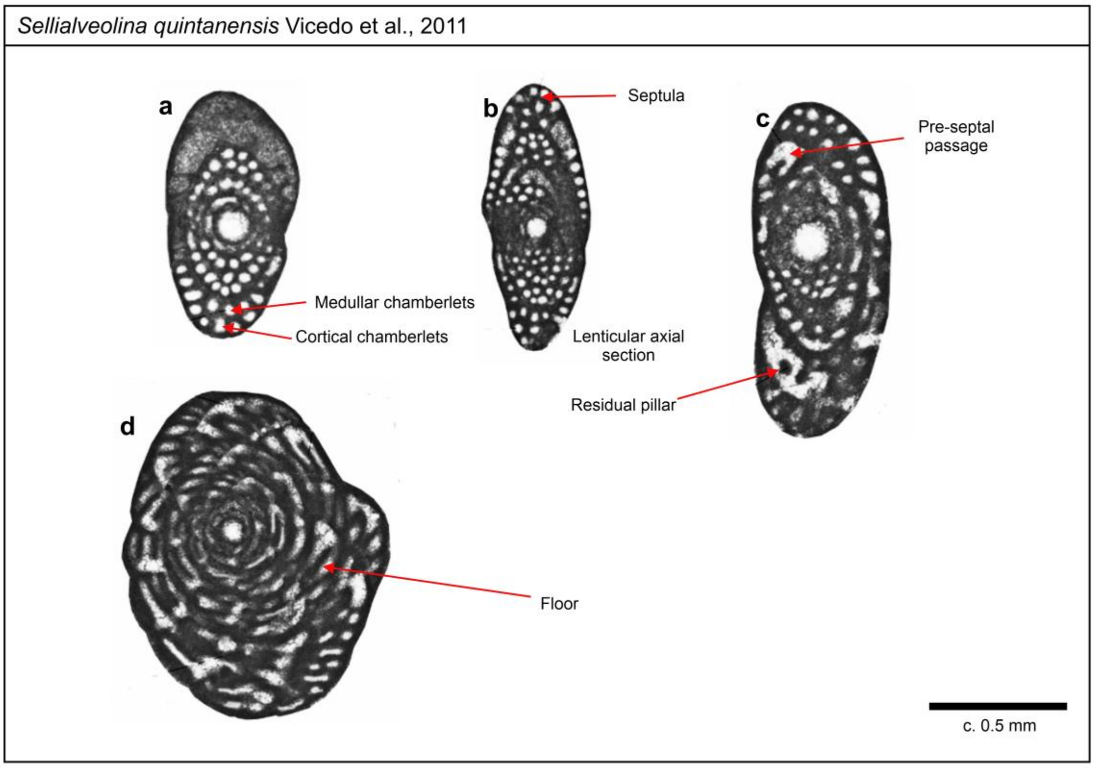


Fig. 45: Representative illustrations of *Sellialveolina quintanensis*: **a.** Axial section, Vicedo et al. (2011, fig. 6(14); earliest Cenomanian, Spain); **b.** Axial section (holotype), Vicedo et al. (2011, fig. 6(16); earliest Cenomanian, Spain); **c.** Oblique centre section, Vicedo et al. (2011, fig. 6(21); earliest Cenomanian, Spain); **d.** Oblique centre section close to equatorial plane, Vicedo et al. (2011, fig. 6(22); earliest Cenomanian, Spain).

1964 *Sellialveolina viallii* – Farinacci & Radoičić, p. 11, pl. 12, fig. 2; undifferentiated Cenomanian, Croatia.
1964 *Sellialveolina viallii* – Sartoni & Colalongo, p. 8, 13, 16, pl. 4, figs. 3-4; late Cenomanian, southern Italy.
1966 *Sellialveolina viallii* – Angelucci & Devoto, text-fig. 4; undifferentiated middle - late Cenomanian, southern Italy.
? 1966 *Sellialveolina viallii* – De Castro, pl. 12, figs. 7-10; middle Cenomanian, southern Italy [possibly = *S. gutzwilleri*].
1967 *Sellialveolina* aff. *S. viallii* – Bismuth et al., pl. 12, figs. 14-15, ?16 [doubtful]; undifferentiated Cenomanian, Tunisia.
1970 *Pseudedomia viallii* (Colalongo) – Saint-Marc, pl. 1, figs. 1-4, 6-7; middle Cenomanian, Lebanon [fig. 5 is probably *S. drorimensis*].
? 1970 *Pseudedomia drorimensis* – Saint-Marc, pl. 1, figs. 13-14; basal late Cenomanian, Lebanon.
1971 *Sellialveolina viallii* – De Castro, text-fig. 17 (1-6); middle Cenomanian, southern Italy.
1971 *Pseudedomia* cf. *viallii* – Fleury, p. 190-192, pl. 2, figs. 1-7; middle Cenomanian, Greece
1973 *Pseudedomia viallii* – Bismuth, p. 195, pl. 4, figs. 4-6; latest Albian, Tunisia [oldest occurrences found in conjunction with *Planomalina buxtorfi* – see De Castro in Schroeder & Neumann, 1985].
1973 *Pseudedomia viallii* – Hamaoui & Fourcade, p. 387-388, ?pl. 8, figs. 2, 4-5 [possibly *S. gutzwilleri*]; pl. 9, figs. 1-8; undifferentiated Cenomanian, Algeria & Tunisia.
1974 *Pseudedomia viallii* – Saint-Marc, p. 243-245, pl. 10, figs. 1-7; middle Cenomanian (range given as early to middle Cenomanian), Lebanon.
? 1974 *Pseudedomia viallii* – Bignot & Poisson, p. 75; pl. 1, figs. 1-9; pl. 3, fig. 7; undifferentiated Cenomanian, Turkish Taurides [possibly *Sellialveolina gutzwilleri fide* Vicedo et al., 2011].
1977 *Pseudedomia viallii* – Chiocchini & Mancinelli, p. 130, 139, pl. 35, fig. 1; middle Cenomanian, southern Italy.
? 1978 *Pseudedomia* cf. *viallii* – Berthou & Schroeder, pl. 8, fig. 1; early Cenomanian, Portugal.
1980 *Sellialveolina* gr. *viallii* – Fleury, p. 511-513, text-fig. A3: 1-16; pl. 2, figs. 10-19; early – middle Cenomanian, Greece.
1980 *Pseudedomia viallii* – Ben Youssef, p. 38, 55, 71, pl. 9, fig. 9; late early – early middle Cenomanian, Tunisia [*fide* De Castro in Schroeder & Neumann, 1985].
1981 *Pseudedomia viallii* – Saint-Marc, pl. 2, figs. 5-6; early – middle Cenomanian, Lebanon.
1982 *Pseudedomia viallii* – Mouty & Saint-Marc, pl. 2, fig. 5; earliest middle Cenomanian, NW Syria.
1982 *Pseudedomia viallii* – Fourcade & García, pl. 1, figs. 5-6; undifferentiated early – middle Cenomanian, Spain.
1984 *Pseudedomia viallii* – Berthou, pl. 1, figs. 5-6; latest Albian and early Cenomanian, Portugal.

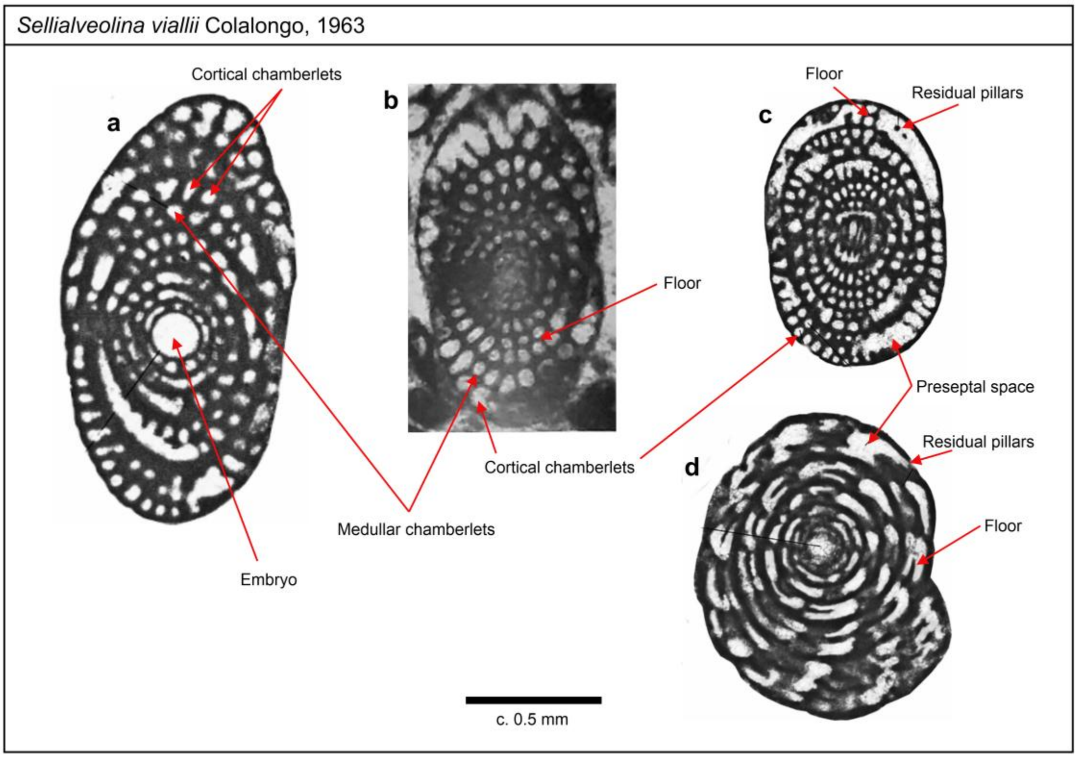


Fig. 46: Representative illustrations of *Sellialveolina viallii*: **a.** Axial section, Vicedo et al. (2011, fig. 6(3); earliest Cenomanian, Spain); **b.** Axial section (holotype), Colalongo (1963, pl. 1, fig. 1; Cenomanian, southern Italy); **c.** Oblique off-centre axial section, Vicedo et al. (2011, fig. 5(14); early Cenomanian, Italy); **d.** Equatorial section, Vicedo et al. (2011, fig. 5(23); early Cenomanian, Italy).

1985 *Sellialveolina viallii* – De Castro in Schroeder & Neumann, p. 133, pl. 66, figs. 1-10, text fig. 17; base middle Cenomanian, southern Italy (full range given as latest Albian (Vraconian) – top middle Cenomanian, global review).
1988 *Sellialveolina viallii* – De Castro, pl. 1, figs. 5-8; early Cenomanian (range given as latest Albian – middle Cenomanian), Italy [fig. 6 is possibly *S. gutzwilleri*; fig. 9 is also of *Sellialveolina* but the species is indeterminate].
1993 *Sellialveolina viallii* – Ettachfini, pl. 4, figs. 5-9, pl. 5, figs. 1-6; early and middle Cenomanian, Morocco.
1994 *Sellialveolina viallii* – Velić & Vlahović, pl. 1, figs. 1-3; early Cenomanian (biozonal marker), Croatia [but shown to range into the latest Albian by Velić, 2007].
1994 *Sellialveolina viallii* – Radoičić, pl. 1, figs. 1, 5; undifferentiated early – middle Cenomanian, Albania/Kosova border.
2000 *Sellialveolina viallii* – Di Stefano & Ruberti, pl. 29, fig. 2; undifferentiated Cenomanian, Sicily, Italy.
2004 *Sellialveolina viallii* – Bravi et al., fig. 5; early Cenomanian, southern Italy.
Non 2006 *Sellialveolina viallii* – Sari, pl. 6.6, figs. 7-9; age indeterminate (present in reworked clast); Turkish Taurides [these are probably more advanced species i.e., *S. gutzwilleri* or *S. drorimensis*; only fig. 9 is possibly *S. viallii*].
2009 *Sellialveolina* gr. *viallii* – Caus et al., fig. 5(2); early Cenomanian, Spain.
2009 *Sellialveolina viallii* – Husinec et al., fig. 3(J-K); earliest Cenomanian, Croatia.
2010 *Sellialveolina viallii* – Spalluto & Caffau, fig. 13(A); early Cenomanian, southern Italy.
2011 *Sellialveolina viallii* – Vicedo et al., p. 44, figs. 5.1-5.23; figs. 6.1-6.11; early Cenomanian, southern Italy & Spain.
2011 *Sellialveolina viallii* – Spalluto, fig. 4d; early Cenomanian, southern Italy.
2012 *Sellialveolina viallii* – Chiocchini et al., pl. 84, fig. 1; pl. 87, figs. 1-5, 7-9; early Cenomanian, Italy [pl. 87, figs. 6 and 10 are *S. gutzwilleri*].
2012 *Sellialveolina viallii* – Simone et al., fig. 4B; early Cenomanian, southern Italy.
? 2012 *Sellialveolina viallii* – Ghanem et al., fig. 6c(1); fig. 6d(21); early Cenomanian, Syria [these are *Sellialveolina* but of indeterminate species].
? 2012 *Sellialveolina viallii* – Orabi et al., figs. 3B, H; early Cenomanian, Sinai, Egypt [these are *Sellialveolina* but of indeterminate species].
2013 *Pseudedomia viallii* – Shahin & Elbaz, pl. 2, fig. 25, *non* fig. 26 [= *Decastroia*]; middle – early late Cenomanian, Sinai, Egypt.
? 2013 *Sellialveolina viallii* – Ghanem & Kuss, fig. 12(3-5); early Cenomanian (range shown to extend into late Albian), NW Syria.
2014 *Pseudedomia viallii* (sic) – Shahin & Elbaz, fig. 6(3); late? Cenomanian, Sinai, Egypt.

Non 2014 *Sellialveolina viallii* (sic) – Afghah & Fadaei, fig. 7c; undifferentiated Cenomanian, Iranian Zagros [probably = *Alveocella*].
Non 2018 *Sellialveolina viallii* – Luger, pl. 15, figs. 17-19; middle? Cenomanian, Somalia [possibly *Reticulinella* but probably not *S. viallii*].
? 2019 *Sellialveolina viallii* – Özkan & Altıner, fig. 7(9); early Cenomanian [Simmons et al., 2020 suggest a middle Cenomanian age for the same strata], Turkish Arabian Plate.
2020 *Sellialveolina viallii* – Fleury & Özkan, fig. 9(9-20 with 17-20 transitional to *S. drorimensis* or *S. gutzwilleri*); fig. 13(25); undifferentiated Cenomanian, Greece, Italy and Türkiye [*non* fig. 9(8), probably = *Ovalveolina maccagnoae*].
Non 2020 *Sellialveolina* gr. *viallii* – Solak et al., fig. 5(E-I); early – middle Cenomanian, western Taurides, Türkiye [Fig. 5G resembles *S. viallii* but the other illustrations are of *S. drorimensis*].
Non 2020 *Sellialveolina viallii* – Mohseni & Javanmard, fig. 5(o); undifferentiated Cenomanian, Iranian Zagros [unknown but not *Sellialveolina*].
? 2021 *Sellialveolina viallii* – Solak, pl. 1, figs. O-R; early Cenomanian, Central Taurides, Türkiye.
Non 2021 *Sellialveolina viallii* – BouDagher-Fadel & Price, pl. 3, figs. a-b; Cenomanian, Xinyu, southern China [a rhapydioninid but not *Sellialveolina*. Possibly *Murciella*].
Non 2021 *Sellialveolina viallii* – Dehghanian & Afghah, fig. 7(9); middle Cenomanian, Iranian Zagros [probably = *Praealveolina* or similar].
2023 *Sellialveolina viallii* – Fabbi et al., fig. 11c; undifferentiated Cenomanian, southern Italy.
? 2024 *Sellialveolina viallii* – Božović et al., fig. 3b; early – middle Cenomanian, Montenegro.

Reference Images: Vicedo et al. (2011), fig. 5; fig. 6(1-11).

Taxonomy/Identity: *S. viallii* is the type species of *Sellialveolina*. Chamberlets are numerous and the preseptal space is large (one third of the distance between septa) and preseptal pillars are frequently present.

In common with a number of authors, De Castro in Schroeder & Neumann (1985; p. 137) comments on the "…*remarkable similarities*…" between *S. viallii* and *Ovalveolina maccagnoae*. The critical difference between the two is at generic level where, in *Sellialveolina*, the appearance of a chamber floor subdivides the chamberlets horizontally which does not occur in *Ovalveolina* (see also the section on *O. maccagnoae* herein). This may not be easy to see in axial sections of *S. viallii* but should be observable in equatorial sections (see Figure 46). However, some specimens of *O. maccagnoae* figured by De Castro (1966) develop a few cortical chamberlets according to Hosseinzadeh et al. (2020) and Fleury & Özkan (2020), but these appear to – if confirmed – be present in early whorls only. The absence of a perforated basal layer and residual pillars in *O. maccagnoae* are additional criteria to exclude it from the rhapydioninids.

Calonge-Garcia (1993) suggested *O. maccagnoae* is the ancestor of *S. viallii* although Vicedo et al. (2011) stated that the genus (with *S. viallii* recorded as the oldest species) evolved from pseudonummoloculinids.

S. viallii differs from the other three Cenomanian species of *Sellialveolina* in the following ways:

S. quintanensis – has a lenticular shape, smaller cortical chamberlets, fewer medullar chambers and which tend to be restricted to the central area of the chambers and a smaller diameter megalosphere with more pronounced dimorphism. It is slightly smaller axially and equatorially than *S. viallii* (Vicedo et al., 2011). We regard these differences as rather minor and although retained here, consider *S. quintanensis* to be of questionable status.

S. gutzwilleri – is more axially compressed than *S. viallii* (and *S. quintanensis*) and has a larger equatorial diameter than both. It has a subangular periphery compared with the well-rounded periphery of *S. viallii* (Vicedo et al., 2011).

S. drorimensis – is almost twice as large axially and equatorially than *S. viallii* and much more axially compressed, with more chambers per whorl than *S. viallii*.

Confident Stratigraphic Range: latest Albian – middle Cenomanian (common in early Cenomanian).

Uncertain Stratigraphic Range: not applicable.

Whilst this species is commonly encountered in the early Cenomanian (e.g. Vicedo et al., 2011) and may be used as a *local* biozonal index for such (e.g. Cruz-Abad et al., 2017), there are sufficient records (see synonymy list) to support the assertion of De Castro in Schroeder & Neumann (1985) and De Castro (1988) that the full range of this species is latest Albian – middle Cenomanian. Bismuth et al. (1981) regarded the species (unillustrated) as a marker for the latest middle Cenomanian in Tunisia. Arnaud-Vanneau in Hardenbol et al. (1998) show the extinction of *S. viallii* at the top of the middle Cenomanian.

Scarce supposed late Cenomanian records of this species (e.g. Sartoni & Colalongo, 1964; Shahin & Elbaz, 2014) can most likely be discounted as being poorly chronostratigraphically calibrated.

Geographic Distribution: The majority of records of this species are from the circum-Mediterranean area (e.g. Spain, Italy, Greece, Croatia, Morocco, Tunisia), with occurrences as far east in the Arabian Plate as Lebanon and Syria. Reports from the Iranian Zagros cannot be confirmed.

Non-illustrated reports that slightly extend the geographic distribution include from the Cenomanian of southwest Slovenia (Šribar & Pleničar, 1990) and from the early – middle Cenomanian of Crete (Zambetakis-Lekkas et al., 2006).

STRATIGRAPHIC RANGE: CONFIDENCE AND UNCERTAINTY

The determination of the stratigraphic range of a species or genus carries a degree of uncertainty. At the very least stratigraphic range assessments can be judged to be confident or uncertain. This is reflected in the text below and is coded by line ornament in Figure 47 to reflect degrees of confidence in our assessments and interpretations. It should be noted that even confident ranges have a degree of uncertainty, with assignment to a substage typically implying the assignment is undifferentiated, unless clearly stated otherwise. In other words, if a taxon is known from the late Cenomanian, but with no information on where in the late Cenomanian it has an inception or extinction, the range is shown as throughout the stage. To imply anything else would be a false impression of known biostratigraphic precision. Further discussion on the philosophy of certainty in biostratigraphic evaluation can be found in Simmons & Bidgood (2023) and in Simmons et al. (2024). In this work we have used three broad categories to depict stratigraphic range confidence: Confident and common – a wide, solid, green line on range charts. A relatively large number of (correctly) illustrated records (or if unillustrated, from a generally reliable source) with at least plausible age-control. Confident but scarce – a narrow, solid, green line on range charts. At least one, but relatively fewer records but which fit the same criteria as above. Uncertain – a series of orange '?' on range charts. Occurrences that lie outside of the 'confident' ranges that are neither confirmed in terms of identity nor age-control but cannot be completely dismissed (e.g., an illustrated record with poor age-control or an unillustrated record from a generally reliable source with good age control). As can be readily understood, subjectivity plays a role here, and the boundaries between one category and other are inevitably gradational. Records which exist of named species occurring in rocks outside of these ranges, but which are based on very uncertain (i.e. dubious) identity and/or age control are not shown. To use *Simplalveolina simplex* as an example, it has been commonly recorded from late Cenomanian strata (many records with identities confirmed by illustration) (= a wide, solid green line on Figure 47), but also occasionally been recorded from middle Cenomanian strata (= a thin, solid green line on Figure 47). On the other hand, the early Cenomanian records of *S. simplex* have a degree of uncertainty regarding identity or have not been illustrated at all. This is represented by a series of orange '?' on Figure 47. We freely acknowledge that these are the results of our own (subjective) assessment of the various data points we have observed and examined and agree that others may come to different conclusions.

Moreover, the stratigraphic ranges of benthic fossils such as LBF will vary geographically because of facies control or because of differential biogeographic dispersal of a taxon in time (i.e., due to endemism or depending on

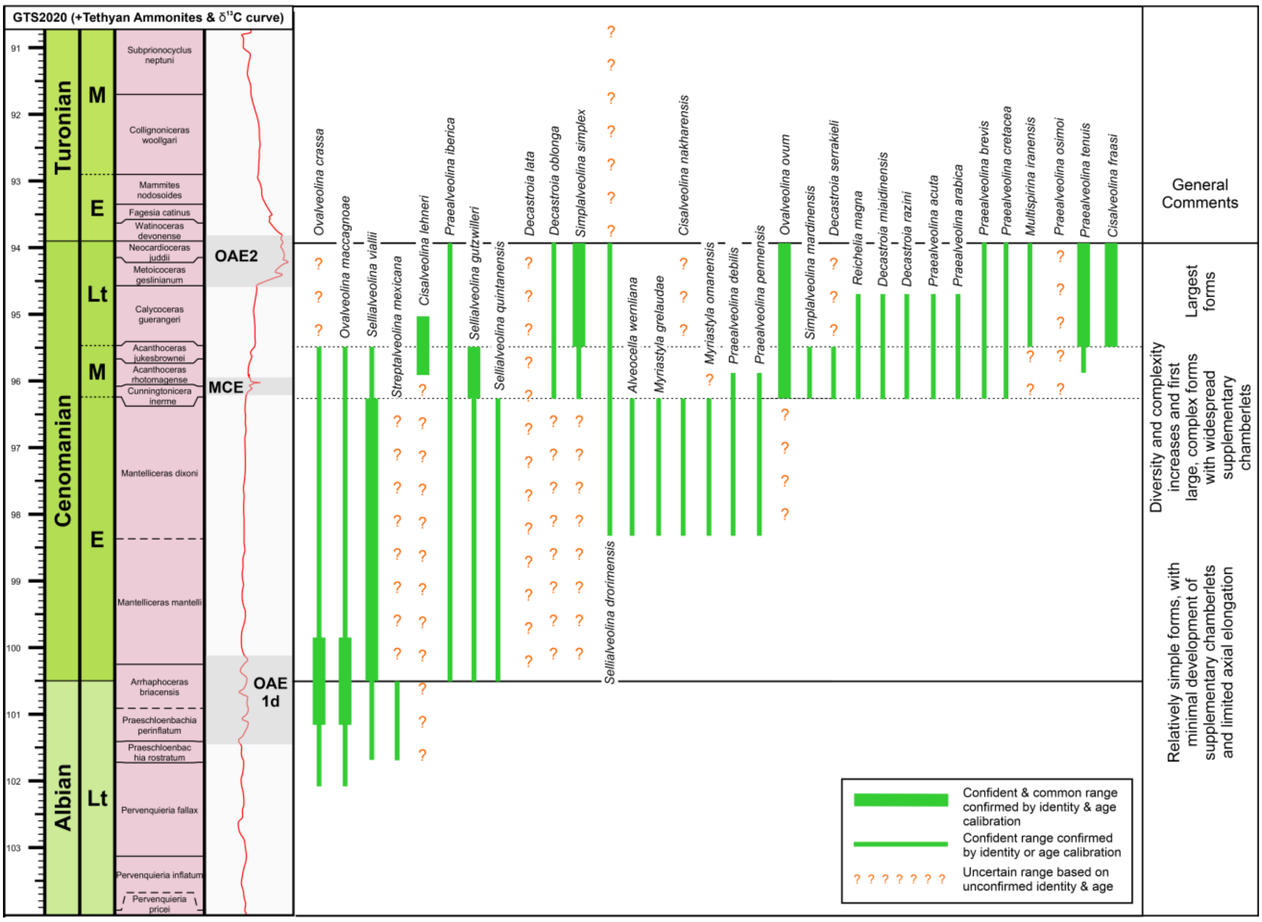


Fig. 47: Range chart of alveolinoids discussed herein.

palaoceanographic factors) (see discussion of *Moncharmontia* by Schlagintweit & Yazdi-Moghadam, 2021). This is very likely to be true for environmentally niche-restricted taxa such as alveolinoids that appear to have thrived (and still thrive) to the shallowest parts of carbonate platforms (Hallock, 1999; Hottinger, 2000; Hohenegger, 2011; BouDagher-Fadel, 2018). This implies that constructing a composite stratigraphic range for an individual species is dependent on many locational/observation factors which build up from a series of local stratigraphic occurrences. In this paper we are particularly concerned with establishing the maximum global range of a taxon, noting variations in certainty for that range. A taxon may have a localised range very different from its combined global composite range. There may also be interesting variations in range relating to the progressive migration of a taxa throughout its geographic distribution (i.e. dispersal from its location of evolution). This is a subject to which we will return in a future paper.

DISCUSSION

Alveolinoids are amongst the largest and more structurally complex of the LBF. They reached extremes of specific diversity with *Alveolina* d'Orbigny and *Glomalveolina* Hottinger in the late Paleocene – Eocene, a time period for which they have established value for biostratigraphy (Hottinger, 1960; White, 1992, 1994; Pignatti & Papazzoni, 2017). Although the Cenomanian taxa are perhaps not quite as diverse, there is an increasing understanding that as the variation of structural detail becomes better understood (e.g. Vicedo & Piuz, 2016), there is arguably a large number of species. As in the modern day, Cenomanian alveolinoids were constrained under precise environmental circumstances in shallow-waters, and which might also have resulted in endemism, with forms known only or mostly from the Mediterranean margin of northern Neotethys, and others from the Arabian Plate. A few taxa are known from the American province.

Evaluation of the distribution of Cenomanian alveolinoids in time and space is challenging because so many records are difficult to identify precisely and/or precise age-calibration is lacking. For example, if to consider *Cisalveolina fraasi*, removal of all uncertain records leaves mostly occurrences records in the Arabia/Zagros and the peri-Adriatic regions that are mostly "undifferentiated late Cenomanian". Did *C. fraasi* arise first in the Middle East and disperse towards the Mediterranean? How rapid was dispersal? Was extinction synchronous? These questions are hard to answer with the data at hand.

As documented in the preceding sections of this paper, stratigraphic ranges of individual taxa are not always well understood. Nonetheless, even without being able to identify individual species, some general comments on Cenomanian biostratigraphy can be made. The earliest part of the Cenomanian (approximately equivalent to the *mantelli* ammonite zone) is characterised by relatively simple alveolinoids, for example, *Praealveolina iberica* with minimal development of supplementary chamberlets and limited axial elongation. Close to the early/middle Cenomanian boundary diversity and complexity increases, and the first larger *Praealveolina* and *Decastroia* species occur with widespread supplementary chamberlets, axial elongation (i.e. a clearly fusiform shape) and larger size. Transition from *Praealveolina* to *Decastroia* may have occurred via forms like *D. lata* – originally and until now regarded as a *Praealveolina* but assigned by us to *Decastroia*. Most of the very largest alveolinoids (e.g. *Praealveolina tenuis*, *Cisalveolina fraasi*, and *Multispirina iranensis*) appear to be most characteristic of the late Cenomanian. Certainly, as with many Cenomanian LBF groups, diversity increases from close to the base of the middle Cenomanian.

Other than in northwest South America, where - apparently - the effects of Ocean Anoxic Event 2 (OAE 2) were minimal (Navarro-Ramirez et al., 2017; Consorti et al., 2018), alveolinoids suffered significant extinction by the end of the Cenomanian. If this happened at the stage boundary or before it (intra-*M. geslinianum* ammonite zone) is unclear. There is evidence that in southern Italy and Portugal (Berthou, 1984; Parente et al., 2008; Frijia et al., 2015; Petrizzo et al., 2025) that extinction occurred early, soon after the onset of OAE 2 in the *M. geslinianum* zone. If this is the case everywhere it is unclear due to the lack of precise biostratigraphic calibration, although Dr. Gianluca Frijia (pers. comm., 2025) believes it likely to be the case based on sections from the Arabian Plate with unpublished carbon isotope proxy data. On the other hand, we know of sections from the same region where alveolinoids occur close to the apparent base Turonian. In any case, in Neotethys, alveolinoids, adapted to oligotrophic conditions, are absent from Turonian strata, presumably badly affected by the paleoceanographic changes such as eutrophic conditions associated with OAE 2, sea-water temperature changes or ocean acidization (Hart, 2007; Petrizzo et al., 2025). Alveolinoids do not make a widespread return until the late Coniacian – Santonian (Hottinger et al, 1989).

There are arguments that the alveolinoids show endemism within the Cenomanian. Certainly, the gradient of specific diversity seems to be high on the Arabian Plate and there are taxa described from there that have not yet been found elsewhere (Vicedo & Serra-Kiel, 2011; Piuz et al., 2014; Vicedo & Piuz, 2016). As displayed by the distribution model of modern LBF (Förderer et al., 2022) high endemism coincides with high diversity, and this is likely to be such a case. Likewise, some forms from the circum-Mediterranean region are unknown from the Middle East (Calonge et al., 2002 and data herein). However, more detailed taxonomic work is required, since as this study shows a great many of the alveolinoid records in the literature cannot be precisely identified. Studies comparable to those executed on Omani material (e.g. Vicedo & Piuz, 2016) need to be undertaken elsewhere as there are very few records from central Africa, and virtually none (to our knowledge) from southern Africa, Asia and the Pacific regions. These would also provide evolutionary insights that at present are unclear as a result of limited biostratigraphic and paleogeographic understanding of taxa. Whilst, in some ways comparable to the Global Community Maturation cycles of Hottinger (2001), size and complexity of alveolinoids seems as a general rule to have increased throughout the Cenomanian, there are exceptions, and it is not clear to what degree evolution is driven by sea-level changes and oceanographic changes (e.g., changes in marine water temperatures).

CONCLUSIONS

We have critically reviewed the available literature (several hundred references) for the alveolinoid taxonomic group (i.e., the superfamily Alveolinoidea), and have critically applied both identity and age criteria for LBF taxa that are present in the Cenomanian. Thirty-two separate Cenomanian LBF alveolinoid species have been treated herein. We have constructed a biostratigraphic range chart for these taxa based on our assessment of data points as being confirmed (i.e., with correct or at least plausible identification and age-calibration) which will subsequently form the basis for a more comprehensive Cenomanian biozonation. Whilst some taxa are long-ranging throughout the Cenomanian and adjoining stages, others have restricted ranges within the Cenomanian, providing stratigraphic utility for correlation. It should be borne in mind that as benthic foraminifera are adapted to specific ecological niches, local ranges can (and often will be) more restricted than global composite ranges, providing some local stratigraphic utility if understood to be a biofacies phenomenon rather than a chronostratigraphic one.

Many of these alveolinoid LBF taxa require further study (and re-examination of type material and/or access to new/additional material) to improve our taxonomic understanding, and the evolutionary and biogeographic relationships between them.

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