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ANNULAR CHAMBERS IN CRETACEOUS ORBITOLINIDAE (LARGER BENTHIC FORAMINIFERA): AN OVERVIEW

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Abstract Annular chambers, if present, are usually confined to ultimate chambers within some Orbitolinidae, and were therefore regarded of subordinate importance not being included in the family diagnosis. However, this peculiar chamber type in some agglutinated conical foraminifera forms almost the entire post-embryonic part of the test. This may either be due to the general plan of test construction (e.g., in genus *Coskinolinella* Delmas & Deloffre, species *Pseudorbitolina schroederi* Luger) or represent a special test adaptation to changing environmental conditions during transgressive events (e.g., in genus *Palorbitolinoides* Cherchi & Schroeder). An emendation of the diagnosis of the family Orbitolinidae is here proposed to include tests that may consist completely or almost exclusively of post-embryonic annular chambers. As a result, the genus *Coskinolinella* Delmas & Deloffre, up to now treated as a genus of uncertain status or deleted in foraminiferal classifications, is now included in the family Orbitolinidae. Uniserial chambers with distinct concave apertural faces (appearing as stacked-cones) have erroneously been interpreted as annular chambers in the case of the late Albian-early Cenomanian *Heterocoskinolina bariensis* Luperto Sinni & Reina and therefore misassigned to *Coskinolinella*. Besides the different chamber arrangement, such an assignment would also contradict the established latest Aptian–early late Albian *Coskinolinella* lineage (*C. daguini*-*C. santanderensis*-*C. navarrensis*), and its palaeogeographically restricted occurrence.

Keywords: Foraminifera, morphology, terminology, taxonomy, Cretaceous

INTRODUCTION

Orbitolinidae is a family of Cretaceous-Paleogene larger benthic foraminifera displaying an agglutinated conical test of variable apical angle. The various external but taxonomically unrelated morphologies have been classified by Henson (1948, fig. 12). The initial part may display a coiled spire as in most of the dictyoconids or some orbitolinids (e.g., *Praeorbitolina* Schroeder). The main test part consists of co-axial series of chambers (= rectilinear or uniserial chamber arrangement or chambers in a straight line; Hottinger, 2006) that may be discoidal (planiseptal sensu Rat, 1963), bent towards the cone base (convex or spheriseptal sensu Rat, 1963) or towards the apex (concave) (Figure 1a–e). With changing chamber morphology during ontogeny, further types can be distinguished (see Rat, 1963; Arnaud-Vanneau, 1980, fig. 209). In the glossary of Hottinger (2006, p. 6), annular chambers have been defined simply as ring-shaped chambers that may be subdivided as in *Cycloclypeus* Carpenter, 1856 or the Orbitolinidae (e.g., beams, rafters, septules; Hottinger, 2006, figs. 19 and 71 with explanations). In the latter group, annular chambers are added obliquely (= in three dimensions) around a large umbilicus. The diameter of the annular chambers increases continuously during ontogeny so that the resulting test morphology becomes conical. Annular concentric (or cyclical) chambers instead refer to two dimensions (within a single plane; discoidal-annular in Hottinger, 2006, fig. 80) such as known from for example *Cyclorbiculina* Silvestri, *Mardinella* Meriç & Çoruh or *Cyclolina* Orbigny (e.g., BouDagher-Fadel, 2018, fig. 1.18). In the adult parts of dictyoconids (e.g., *Palaeodictyoconus actinostoma* Arnaud-Vanneau & Schroeder) annular chambers are comparably more rarely recorded than in the Orbitolininae (Fig. 1f–j). In these typically low conical forms, the ultimate chambers thin out completely towards the test center and lack a central zone (e.g., Douglass, 1960; Loeblich & Tappan, 1987, e.g., genus *Mesorbitolina* Schroeder, 1962). Among the different types of annular chamber morphologies summarized by Rat (1963), an orbitolinid test composed exclusively of annular post-embryonic chambers is not included. With respect to the different test morphologies, some of these could not be accomplished without having annular chambers, e.g., those with adult parts bent upwards (Henson, 1948, reflexed types, fig. 12k-l). According to Arnaud-Vanneau (1980, p. 81), annular chambers may in some cases be regarded as forming a final gerontic stage. Concerning annular chambers within the Orbitolinidae Martin, 1890, it should be noted that tests consisting of completely annular chambers are not included in the diagnosis of the family that only refers to an “early stage trochospiral to pseudoplanispiral, then rectilinear with broad, low chambers” (Loeblich & Tappan, 1987, p. 156). In the present contribution, taxonomic problems and implications associated with annular chambers are discussed based on selected case studies concerning the genera *Palorbitolinoides* Cherchi & Schroeder, 1980, *Coskinolinella* Delmas & Deloffre, 1961, and *Pseudorbitolina* Douvillé, 1910.

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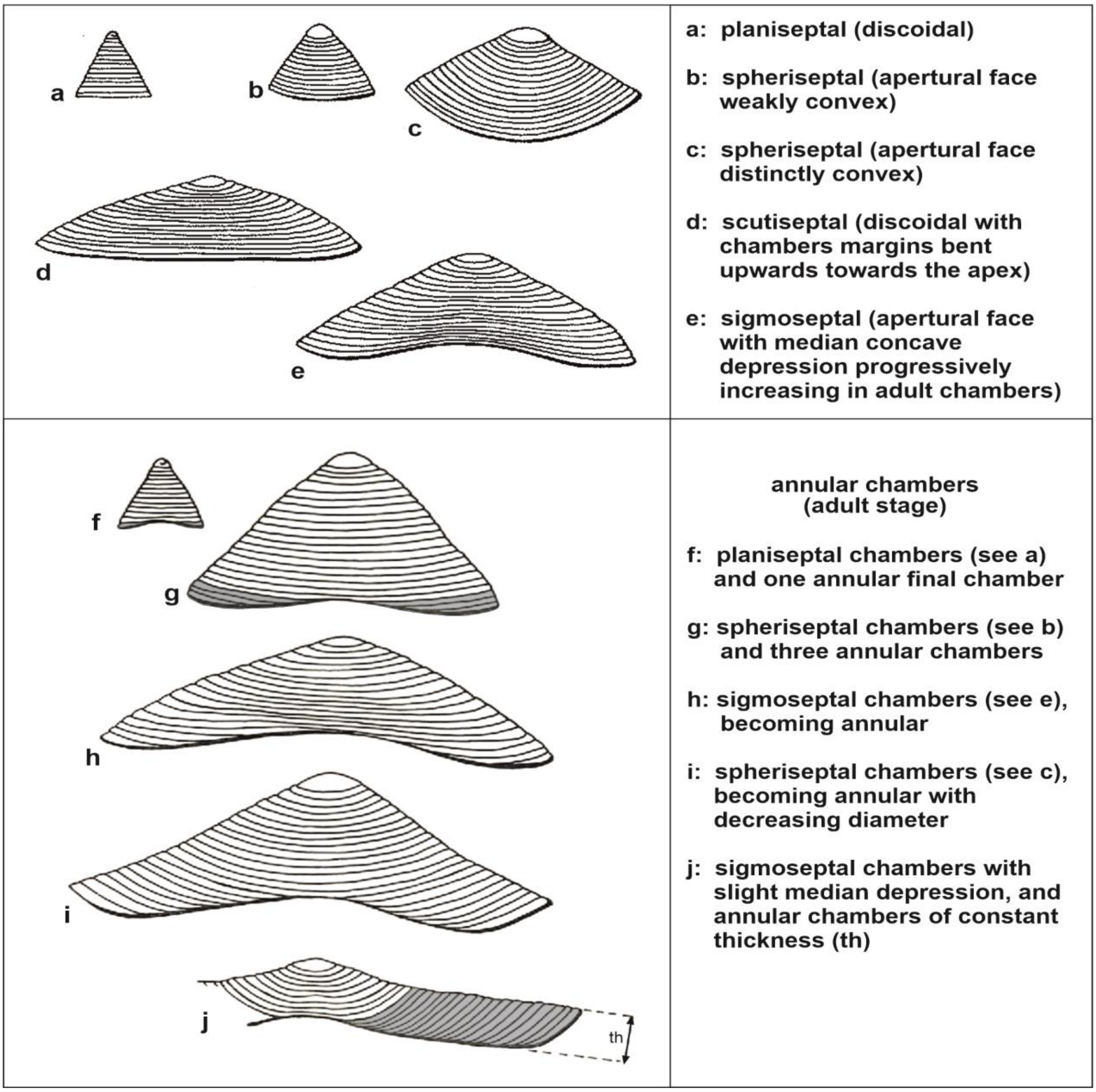

Fig. 1 Examples for the terminology of chamber morphology (modified from Rat, 1963). Annular chambers in f-g and j are marked in gray.

2. MATERIAL AND METHODS

The material used in the present study either refers to illustrations in the literature or to own thin-section material. The specimens of *Palorbitolinoides hedini* Cherchi & Schroeder, 1980 are from the middle Albian Kazhdumi Formation of southeastern Iran where distinctive horizons with monospecific assemblages of this species are related to sequence stratigraphic events, respectively the regional Arabian maximum flooding surface (MFS) K100 sensu Sharland et al. (2001); Schlagintweit et al., (2022). The material used for *Pseudorbitolina schroederi* Luger, is from the late Maastrichtian Tarbur Formation of southwestern Iran (see Schlagintweit, 2022). Specimens of *Coskinolinella daguini* Delmas & Deloffre are from the latest Aptian of Cantabria, northern Spain (see Schlagintweit et al., 2016). The specimen of *Coskinolinella santanderensis* Ramírez del Pozo is from the early Albian of Cantabria, northern Spain (Ramírez del Pozo collection, IGME, Tres Cantos).

3. TAXONOMIC PART

Phylum Foraminifera Orbigny, 1826
Class Globothalamea Pawlowski et al., 2013
Order Loftusiida Kaminski & Mikhalevich, 2004
Suborder Orbitolinina Kaminski, 2004
Superfamily Orbitolinoidea Martin, 1890
Family Orbitolinidae Martin, 1890
Subfamily Orbitolininae Martin, 1890
Genus ***Palorbitolinoides*** Cherchi & Schroeder, 1980
***Palorbitolinoides hedini* Cherchi & Schroeder, 1980**
Fig. 2a-d

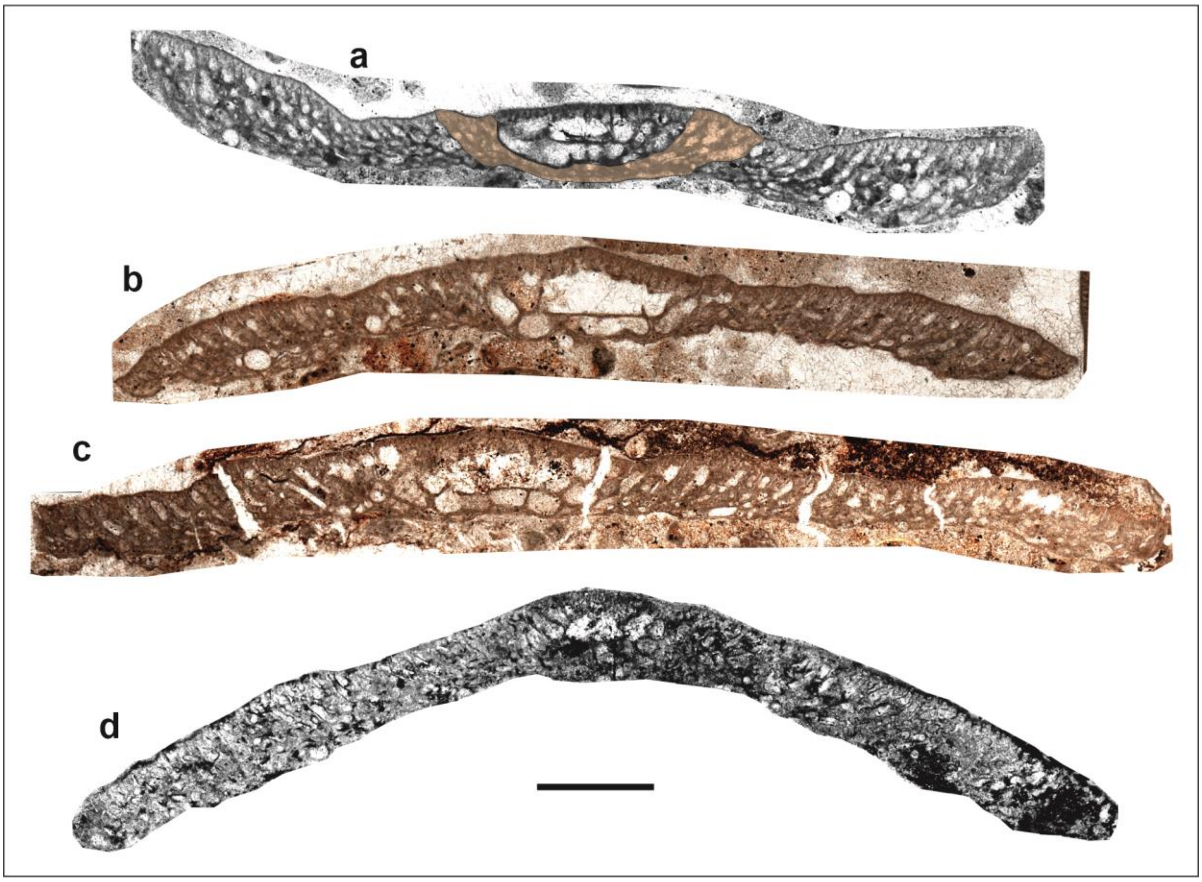

Fig. 2 Annular chambers in *Palorbitolinoides hedini* Cherchi & Schroeder from the middle Albian Kazhdumi Formation of southwestern Iran. **a** Reflexed conico-concave test (Henson, 1948, fig. 12k–l). Early uniserial post-embryonic chambers marked in orange. **b–c** Low conico-concave test (Henson, 1948, fig. 12i–j) completely formed by annular post-embryonic chambers, so that the embryo base marks the test base. **d** High covexo-concave test (Henson, 1948, fig. 12r); compare to the specimen of *Pseudorbitolina schroederi* Luger shown in Fig. 3d.

*1980 *Palorbitolinoides hedini* n. gen., n. sp. – Cherchi & Schroeder, p. 385, pl. 1, figs. 1-5.

Remarks: The following statements refer to the type-species *Palorbitolinoides hedini* Cherchi & Schroeder, 1980, first described from lower Albian strata of Tibet, but known to range younger (Schlagintweit et al., 2022). The genus is defined exclusively on the structure of the megalospheric embryo (Cherchi & Schroeder, 1980). As in other orbitolinids, gross external test morphology is variable in *P. hedini* and is therefore not of taxonomic significance (Figure 2). The specimens studied herein are from distinctive beds of the middle Albian Kazhdumi Formation of southwestern Iran (Zagros Zone) (Schlagintweit et al., 2022). Morphologically, they are mostly low-conical to almost discoidal, corresponding to the convexo-concave and conico-concave types with or without reflexed chamber margins (Henson, 1948, fig. 12). In some specimens, the large-sized apical embryo is followed by a few uniserial chambers with distinct convex apertural faces due to the embracement of the embryo (Figure 2a, d). The rest of the test consists of annular chambers (compare Fig. 1j). However, there are also specimens where the embryo is immediately followed by annular chambers (Figure 2b–c). In these mostly flat discoidal specimens, the base of the embryo corresponds to the base of the test. The test of the holotype specimen of *P. hedini* shown in pl. 1, fig. 5 of Cherchi & Schroeder (1980) is comparably thick (about 2.5 times the height of the embryo) with numerous chambers with convex apertural faces in most chambers. In the latest part, the chambers are sigmoseptal (Figure 1e), and the presence of any annular chambers is not discernible and unclear.

Subfamily Dictyoconinae Schubert, 1912

Remarks: Due to the simplicity of the embryo (see Hofker, 1965 for details), *Coskinolinella* is herein included within the Dictyoconinae.

Genus ***Coskinolinella*** Delmas & Deloffre, 1961

Coskinolinella daguini Delmas & Deloffre, 1961

Fig. 3a-d, f

*1961 *Coskinolinella daguini* n. gen., n. sp. – Delmas & Deloffre, p. 167, text-fig. 1, pl. 1, figs. 1-8.

Coskinolinella santanderensis Ramírez del Pozo,

*1971 *Coskinolinella santanderensis* n. sp. – Ramírez del Pozo, p. 254, pl. 62, fig. 1.

Fig. 3g-h

Remarks: The type-species *Coskinolinella daguini* was described by Delmas & Deloffre (1961) from upper Aptian-lower Albian carbonates recovered from subsurface drillings performed in the Aquitaine Basin of

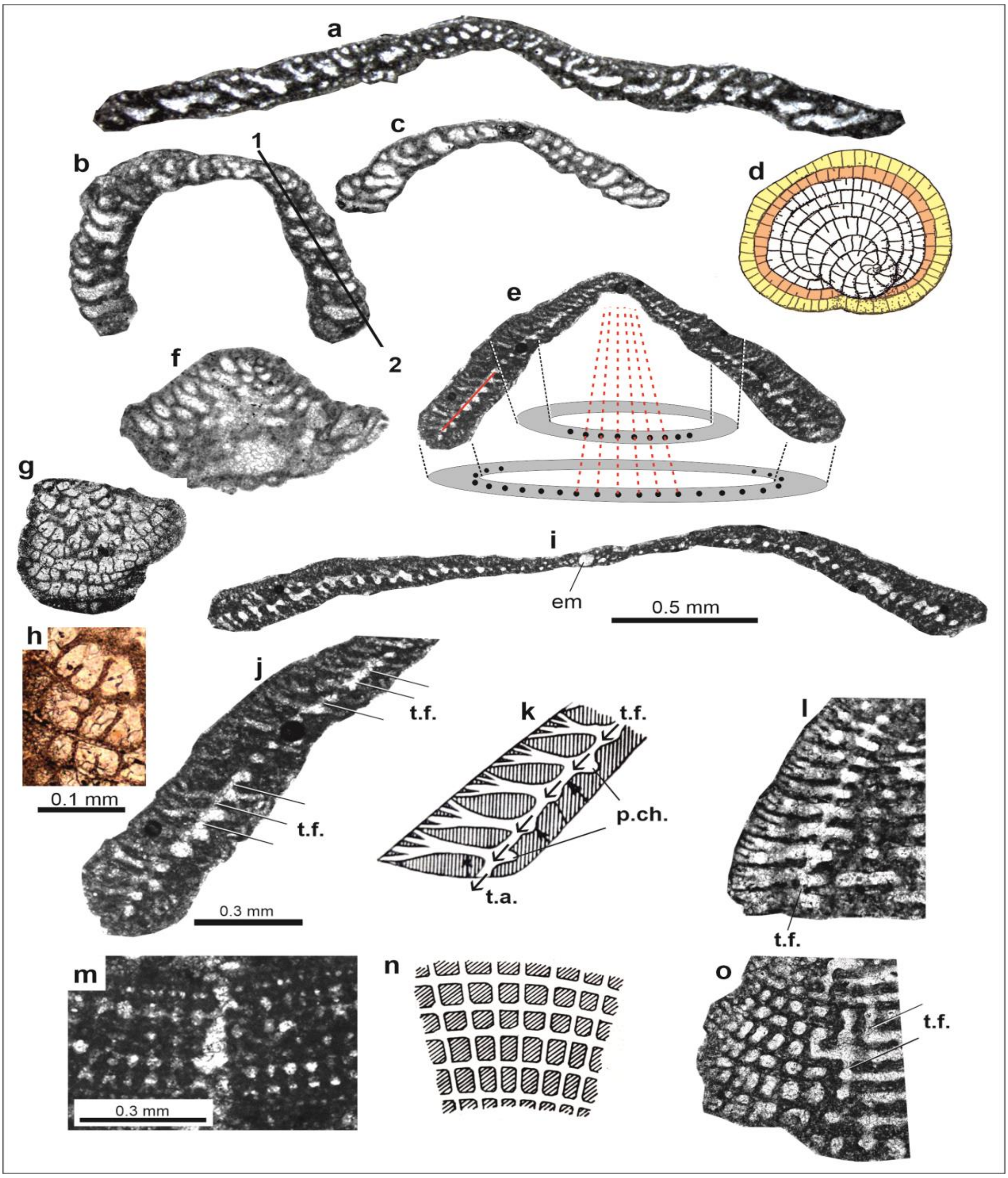

Fig. 3 Annular chambers in *Coskinolinella daguini* Delmas & Deloffre (upper Aptian Reocín Formation of Spain; **a–-c, d?, f**), *Coskinolinella santanderensis Ramírez del Pozo* (early Albian of Spain; **g-h**), *Pseudorbitolina schroederi* Luger (upper Maastrichtian Tarbur Formation of Iran; **e, i–j, k, m-n:** reconstruction of Henson, 1948), and some comparisons with *Gusicella minima* (Henson) (upper Maastrichtian Tarbur Formation of Iran; **l, o**). **a** subaxial section. Note the presence of foramina (left side) of unknown distribution pattern throughout the test. **b–c** oblique sections. **d** Drawing of the dorsal side of an isolated specimen with two annular chambers highlighted in colours (modified from Hofker, 1965, fig. 1, without scale, illustrated as *C. daguini* it might in fact belong to *C. santanderensis*). **e** subaxial section. Note the concentric arrangement of foramina (radial tubular apertures *sensu* Henson, 1948) in line between subsequent chambers in the middle part of the annular chambers (solid red left in the test, dotted red in the reconstructed part). **f** tangential section; approximate position shown in **b** (1------2). **g-h** tangential section showing intercalary beams. **i** axial section of a megalospheric specimen (em = embryo). **j** Detail from Fig. 3e (axial section) showing aligned tubular apertures (= tubular foramina, t.f.) sensu Henson (1948). **k** Schematic drawing modified from Henson (1948, fig. 16a) showing aligned tubular foramina (t.f., arrows towards test base) and primary chambers (p.ch.) in axial section (arrows); t.a. aperture at test base. **l** Part of the test in axial section showing aligned tubular foramina at the transition marginal to central zone. **m–n** Tangential sections showing aligned main partitions (**m:** thin-section, **n:** reconstruction from Henson, 1948, fig. 16e). **o** Part of the test in tangential section showing from left to right the cellular subepidermal network, and aligned vertical main partitions and tubular foramina.

southwestern France and assigned with hesitation to the Orbitolinidae (Figure 3a–c, e). Based on isolated specimens and oriented thin-sections, Hofker (1965) provided the following test morphology: Following a flat initial spire of about two whorls, there are a few discoidal chambers that cover the lower part of the spire which in turn are followed by annular chambers that make up the main part of the test (see Hofker, 1965 for clear details and illustrations). Cherchi (1985) indicated up to 15 to 20 annular chambers in *C. daguini*. The gross outer test morphology of *Coskinolinella* is low conical and may display a wavy profile of the test surface making the observation of the continuity of a single chamber extremely difficult (Fig. 3a). Such morphotypes have been related to microspheric specimens by Cherchi (1985). It is worth mentioning that such uneven morphologies are also reported from the modern *Cycloclypeus*, a rotaliid with annular neancic chambers, in cases related to test teratologies (Briguglio et al., 2016, e.g. Appendix 1).

The marginal part of the chamber may show different degrees of subdivisions allowing for the distinction of three different species. *C. daguini* (radial main partitions, Fig. 3f), *C. santanderensis* Ramírez del Pozo, 1971 (radial main + intercalary partitions, Fig. 3g) and *C. navarrensis* Ramírez del Pozo, 1971 (radial main + intercalary partitions + horizontal partitions) that form a lineage with increasing test complexity in the late Aptian-late Albian interval with overlapping species ranges (Cherchi, 1984, 1985). The radial main partitions are well visible in the type specimens (e.g., Delmas & Deloffre, 1961, fig. 1.6-7, pl. 1, fig. 8). In the *Treatise on Invertebrate Paleontology*, Loeblich & Tappan (1964) included *Coskinolinella* into the family Dicyclinidae with a discoidal or depressed conical test displaying cyclical chambers and furthermore into the subfamily Dicyclininae including, i.e. taxa with *chambers partially subdivided by radial transverse partitions*. Later, Loeblich & Tappan (1987, p. 697) treated *Coskinolinella* as a genus of uncertain status and disagreed again with the placement within the Orbitolinidae due to *the absence of any internal chamber subdivisions*. Loeblich & Tappan (1987) only referred to the work of Delmas & Deloffre (1961) and omitted the well-illustrated works of Hofker (1965) and Cherchi (1984, 1985). It is worth to mention, that the two-layered wall observed from several orbitolinids (Douglass, 1960; Hofker, 1966; Cherchi & Schroeder, 1978 ; Cruz-Abad, 2018) has also been observed in *Coskinolinella santanderensis* (Fig. 3h). According to Douglass (1960, p. 252), the outer layer consists of hyaline calcite with variable amounts of silica grains. In the recent classifications of Kaminski (2004, 2014), *Coskinolinella* is also excluded, obviously following Loeblich & Tappan (1987). Recently, Tasli & Solak (2019) assigned the species *Heterocoskinolina bariensis* Luperto-Sinni & Reina, 1992 to the genus *Coskinolinella* based on rich material from the late Albian of Turkey. The adult chamber arrangement was considered as annular (Tasli & Solak, 2019, fig. 3B) and the internal structure as identical to *Coskinolina* Delmas & Deloffre. Therefore, the new combination *C. bariensis* (Luperto-Sini & Reina) was introduced as a fourth species of the genus. The taxonomic revision of Tasli & Solak (2019) is rejected herein, instead classifying the chambers of *Heterocoskinolina bariensis* as a succession of rectilinear conical chambers (stacked-cone structure) and not being ring-shaped (Figure 4a). The axial section shown Fig. 6.1c of Tasli & Solak (2019) shows that the chambers are not annular but are rectilinear (stacked-cones) with the septa pierced by multiple foramina in the central test part referred to as *perforated plates* (Figure 4b–c).

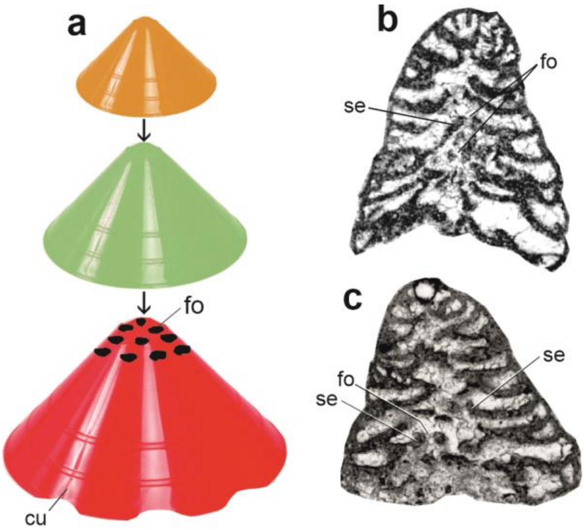

Fig. 4 **a** Schematic reconstruction of *Heterocoskinolina bariensis* Luperto-Sinni & Reina displaying stocked-cone structure of three chambers with septal infoldings (cupules = cu) converging towards the central area with cribrate foramina (fo). **b–c** Axial sections re-illustrated from Tasli & Solak (2019, figs. 8.4c and 6.1c, modified), late Albian of Turkey. Abbreviations: fo = foramen, se = septum.

The irregular appearance of the central zone results from the infoldings of the septa (cupules) that converge towards the test axis. Transverse sections near the test base may appear as being annular due to a central concave depression in some specimens (Tasli & Solak, 2019, figs. 5.1c, 5.3e, 8.4b). Apart from the different interpretation of the test structure, there are also phylogenetic and palaeobiogeographical aspects that would make the occurrence in the Turkish Taurides very surprising. These aspects however were not discussed by Tasli & Solak (2019). The occurrence of a form without rafters (*H. bariensis*) would contradict the *Coskinolinella* lineage with the late Albian *C. navarrensis* (with rafters) as end member as established by Cherchi (1984, 1985). It is also noteworthy that the occurrences of *Coskinolinella* give evidence for a palaeogeographical restricted distribution in the western Neotethys such that any occurrences in its central part and on the southern margin would be surprising. For example, Ghanem & Kuss (2013) reported *Coskinolinella* from the Albian of Syria. The specimen illustrated in Fig.11.10 as *C. navarensis* represents a trochospiral form with open umbilicus (*Trochospira*? sp.). The other specimen illustrated as *C.* cf. *santanderensis* (Fig. 11.21 therein) is undiagnostic (undeterminable tangential section of any larger benthic foraminifera). Also, the illustrations of Arnaud-Vanneau & Premoli Silva (1995) from the Albian of the Central Pacific (pl. 4, fig. 6: *C. daguini*, pl. 4, fig. 7: *C. navarensis*) are by no means convincing and appear undeterminable not even to genus level. In conclusion, the overall test construction with its prominent stage of annular chambers as well as the coiled initial part would, in my opinion, include the *Coskinolinella* within the Orbitolinidae, thus confirming the view of Cherchi (1984, 1985).

Subfamily Dictyorbitolininae Schroeder, 1990 (in Schroeder et al., 1990)
Genus ***Pseudorbitolina*** Douvillé, 1910

Remarks: The taxonomic status of *Pseudorbitolina* has been treated controversely in the literature: Meandropsinidae (Henson, 1948), Soritidae subfamily Meandropsininae (Loeblich & Tappan, 1964), Orbitolinidae (Galloway, 1933, Loeblich & Tappan, 1987: subfamily Dictyoconinae), Incertae sedis (Neumann, 1978). One reason for Henson (1948, p. 103) not placing *Pseudorbitolina* into the Orbitolinidae was the non-alternating main partitions and foramina. These features compare *Pseudorbitolina* to the Dictyorbitolininae as defined by Schroeder in Schroeder et al. (1990) (Schlagintweit, 2022). As the test construction of annular chambers throughout does not represent an exclusion criterion, *Pseudorbitolina* is herein assigned to the Dictyorbitolininae thus becoming its second upper Cretaceous representative together with *Gusicella* Schlagintweit & Rashidi, 2021 (Fig. 3l, o).

***Pseudorbitolina schroederi* Luger, 2018**
Fig. 3e, i, j-k, m-n
*2018 *Pseudorbitolina schroederi* n. sp. – Luger, p. 72, pl. 7, figs. 6-9.

Remarks: *Pseudorbitolina schroederi* was described by Luger (2018) from the Maastrichtian of Somalia. Other occurrences, sometimes assigned to *Pseudorbitolina marthae* Douvillé, are from the Maastrichtian of Qatar (Henson, 1948), SE Turkey (Meriç, 1974), Iraq (Radoičić, 1979), and Iran (Schlagintweit, 2020). Morphologically, *P. schroederi* is characterized by a convexo-concave test displaying annular-concentric chambers mainly throughout the complete ontogeny (Figure 3e, i). As in specimens of *Palorbitolinoides hedini* (Figure 2b–c), axial sections of *P. schroederi* may show an embryo that is directly followed by annular chambers Fig. 3i). Henson (1948, p. 102–103) remarked that (1) *the apertures of consecutive chambers are in alignment*, (2) the radial partitions *typically arranged in radial rows* and that *each layer contains a chamber which is tubular, undivided, completely cyclical*. Note that only the ultimate opening of the foraminiferan shell cavity towards the outer ambient environment is termed here tubular aperture, while those inside refer to tubular foramina (see Hottinger, 2006) (Fig. 3k). The test structure of *Pseudorbitolina* has been illustrated by Henson (1948, fig. 16) in several schematic drawings (e.g., Figure 3k, n), and also clearly evidenced in the thin-section specimens from the upper Maastrichtian Tarbur Formation (Fig. 3e, h, k). In the Upper Cretaceous orbitolinid *Gusicella minima* (Henson) equivalent aligned tubular foramina, sensu Henson (1948), are present and arranged in a concentric ring at the transition between marginal to central zones (see Schlagintweit & Rashidi, 2021 for details) (Fig. 3l, o). As in *Pseudorbitolina*, the radial main partitions as well as the tubular foramina of *Gusicella* are arranged in alignment between subsequent chambers. In contrast to *Pseudorbitolina*, *Gusicella* additionally has multiple foramina within the pillared central zone. This conical form with uniserial chambers has been assigned to the subfamily Dictyorbitolininae Schroeder in Schroeder et al. (1990) as the first Upper Cretaceous taxon of this group (Schlagintweit & Rashidi, 2021). The Dictyorbitolininae includes Orbitolinidae that display foramina arranged in a ring at the outer margin of the central zone, with an alignment paralleling the vertical main partitions (beams) (Schroeder in Schroeder et al., 1990, p. 196). They are arranged perpendicular to the septum (*verticaux par rapport au plancher* = perpendicular to the floor, meaning septum), in continuity paralleling the cone mantel line like in *Gusicella* and *Pseudorbitolina*. Although also called *ouvertures marginal* by Schroeder in Schroeder et al. (1990), they differ from the marginal apertures (and foramina) of the Paleogene taxa where these are arranged obliquely to the septum (i.e., *about 45^o with the mantel line of the cone*). Following Henson (1948), the *marginal foramina* of the Dictyorbitolininae should be termed tubular foramina as they are in vertical continuity (= linear arrangement) from one chamber to the next. In the Paleogene forms, they alternate regularly from one chamber to the next one, are laterally displaced to each other, not in linear continuity, but they also form a single circular row as discerned in transverse sections (Hottinger & Drobne, 1980, p. 211).

4. EMENDED DIAGNOSIS OF ORBITOLINIDAE

The case studies demonstrate that a test construction that includes annular chambers needs to be included into the diagnosis of the Orbitolinidae. The family is here emended as follows (emendments to Loeblich & Tappan, 1987 in bold letters): .....early stage **may be** trochospiral to pseudoplanispiral, then **with** rectilinear, **or rarely, annular** chambers…. The definition of the early stage should also be emended as several orbitolinids (e.g., *Palorbitolina* Schroeder, 1963, *Neoiraqia* Danilova, 1963) do not exhibit a coiled initial part, but instead an apical embryo followed by rectilinear chambers.

5. CONCLUSIONS

Annular chambers have repeatedly been reported from orbitolinids forming the final adult part of the test. The example of *Palorbitolinoides hedini* presented herein indicates that the test of orbitolinids may completely be composed of annular post-embryonic (neanic) chambers, a circumstance that necessitates an emendation of the Orbitolinidae in that respect. It also concludes that due to this chamber arrangement in *Coskinolinella* Delmas & Deloffre and *Pseudorbitolina schroederi* Luger it not *per se* exclude their belonging to the Orbitolinidae. However, there are still pending some further structural details (e.g., embryo of *Pseudorbitolina*), that would allow a full and inclusive description and evaluation of the suprageneric status. For the moment being, *Coskinolinella* and *Pseudorbitolina* are best treated as representatives of the Orbitolinidae. The alignment of the main radial partitions as well as foramina in *Pseudorbitolina schroederi* refer this taxon to the subfamily Dictyorbitolininae Schroeder that so far excludes taxa displaying completely annular chambers. Finally, annular chambers may be mimicked by rectilinear conical chambers (stacked-cones) as in *Heterocoskinolina bariensis* Luperto-Sinni & Reina.

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