

ORBITOLINA DAVIESI HOFKER, 1966: A FORGOTTEN ORBITOLINIDAE FROM THE THANETIAN OF PAKISTAN AND ITS TAXONOMIC STATUS

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Abstract *Orbitolina daviesi* Hofker, 1966 (family Orbitolinidae) was validly described and thoroughly illustrated from Thanetian limestones of Pakistan. Although its attribution to the genus *Orbitolina* d'Orbigny and any phylogenetic relationships with the Cretaceous taxa have been refuted shortly afterwards, the species has not been taxonomically revised since then. *Karsella hottingeri* Sirel, 1999 was established as new genus and new species from the Thanetian of Turkey, without taking into account J. Hofker's publication. The original description and genus diagnosis of *Karsella* has meanwhile been emended to include the occurrence of a radial zone with septula that follow a zig-zag pattern and associated linear arrangement of the foramina, as well as a complex embryo. *Orbitolina daviesi* clearly displays these features and is here considered a species of the genus *Karsella* Sirel. *Karsella hottingeri* is regarded as a subjective junior synonym of *O. daviesi* Hofker and therefore, the only species of the genus is given as a new combination: *Karsella daviesi* (Hofker). From a suprageneric viewpoint, the two Paleogene genera *Karsella* Sirel and *Cushmania* Silvestri display a complex embryo and might belong to a new subfamily of the Orbitolinidae, phylogenetically different and unrelated to the lower-mid Cretaceous Orbitolininae.

Keywords: Foraminifera, Orbitolinidae, taxonomy, phylogeny, Cretaceous, Paleogene.

INTRODUCTION

In his "Studies on the family Orbitolinidae", Hofker (1966) described a new species as *Orbitolina daviesi* from the Thanetian Harnai Limestone (~ Dungan Formation) of Pakistan (Davies, 1941). As holotype, Hofker designated the megalospheric axial section illustrated in plate 3, figure 3, which is deposited at the Natural History Museum, London. *Orbitolina daviesi* has been thoroughly illustrated showing all the characteristic features for a structural analysis, and an accurate description. The taxonomic position of the Pakistani species within the genus *Orbitolina* d'Orbigny (upper Albian-middle Cenomanian, see Schroeder and Neumann, 1985) and any relationship with the mid-Cretaceous taxa of the Orbitolinidae have been refuted by Schroeder (1975, p. 128). Nonetheless, *O. daviesi* has not been taxonomically revised so far. In 1997, Sirel described "a new complex orbitolinid" as *Karsella hottingeri* n. gen., n. sp. from the Thanetian of the Van region, East Turkey without taking into account the publication of Hofker in which *Orbitolina daviesi* has been described. Cruz-Abad (2018, p. 85) noted the similarities between *O. daviesi* and *K. hottingeri* but refrained from formulating conclusions due to the lack of well-preserved material which was described as "few and badly preserved sections" provided by E. Sirel. Instead, Cruz-Abad (2018, fig. 78F-H) illustrated three specimens of "*Orbitolina*" *daviesi* from the Thanetian of Pakistan provided by L. Hottinger. In his "Illustrated glossary of terms used in foraminiferal research", Hottinger (2006, fig. 41) illustrated two specimens of *Karsella* from the upper Paleocene of Pakistan exhibiting "an architecture strikingly similar to the one of Mid-Cretaceous orbitolinids" including the sub- and supraembryonic zones. It

appears that L. Hottinger's material from Pakistan has been illustrated (with different specimens) as both *Karsella hottingeri* by Hottinger (2006) and "*Orbitolina*" *daviesi* Hofker by Cruz-Abad (2018). *Karsella hottingeri* has been recently revised by Schlagintweit (2020), thereby including *Karsella* within the subfamily Orbitolininae (orbitolinids with a complex embryo), the only post-Cretaceous taxon attributed to this subfamily so far. In the present contribution, the Pakistani (*O. daviesi*) and the Turkish (*K. hottingeri*) taxa are compared and the taxonomic status (generic and suprageneric) of the former is reassessed. In addition, the suprageneric classification of Orbitolinidae displaying a complex embryo is shortly discussed.

DISCUSSION

Taxonomic status of *Orbitolina daviesi* Hofker, 1966

Embryonic apparatus

The genus *Orbitolina* d'Orbigny is characterized by an embryonic apparatus subdivided into three parts, proloculus, subdivided supraembryonic zone (spz), and subdivided subembryonic zone (sbz) (Henson, 1948; Douglass, 1960; Schroeder, 1962; Schroeder and Neumann, 1985). The sbz (below the proloculus) is weakly developed with respect to the spz (above the proloculus) (Schroeder, 1962, p. 185). Directly above the proloculus and in the middle portion, the spz is comparably thin, becoming thicker laterally. Both zones are in planar lateral contact about the middle part of the proloculus, one setting that is also due to the flat-discoidal test morphology (e.g., Schroeder, 1962, fig. 4B). As stated by Schroeder (1962,

p. 179), the proloculus and the subembryonic zone are not in contact by means of an opening or pore. The embryo of “*O.*” *daviesi* is different from that of the Cenomanian orbitolinas and according to Schroeder (1975, p. 128) the Pakistani species can therefore not be assigned to the genus *Orbitolina*. Instead, the embryos of “*O.*” *daviesi* and *K. hottingeri* display the same structure. Due to the rounded apex, the spz envelops laterally the proloculus and displays equal thickness. It consists of numerous, close-set partitions of equal length that are discernible in axial sections (Fig. 1b, d). Both the upper side of the spz and the lower side of the zone below the embryo are convex. The latter is loosely subdivided and surrounds the protoconch at the base, laterally reaching up to the test surface; it is herein interpreted as a peri-embryonic zone (pz) according to the definition of Berthou and Schroeder (1978, p. 72) for the Mid-Cretaceous *Neoiraqia* Danilova, 1963 (Fig. 1i). The pz is distinctly thicker than the spz and subdivided only by a few partitions. A pore opening between the proloculus and the pz is visible in some illustrated specimens (e.g., pl. 2, fig. 10, pl. 3, fig. 5 in Hofker, 1966 for *O. daviesi*; pl. 1, fig. 9 in Sirel, 1997, and fig. 41L in Hottinger, 2006 for *K. hottingeri*). Connections between the megalosphere and the pz (here: peri-embryonic ring; epi-embryonic chambers in Hofker, 1966) by means of several pores is also known from the Lower Cretaceous *Palorbitolina* (see Schroeder, 1963). The subdivision of the large embryonic chamber into a smaller protoconch and a distinctly larger deutoconch by a thin basal ridge/projection is equally recognizable in *O. daviesi* (e.g., Hofker, 1966, pl. 3, fig. 7) and *K. hottingeri* (e.g., Hottinger, 2006, fig. 41K-L). Referring to Schroeder and Neumann (1985, fig. 7: for *Neorbitolinopsis conulus*), the basal ridge can represent a subdivision of the proloculus, whereas the deutoconch comprises the upper part of the embryonic chamber and its partitions. The embryo of *Karsella* was described by Sirel (1997, p. 208) as consisting of a subspherical megalosphere and “periembryonic chambers [...] arranged in a trochoid spire” (Fig. 1A-C). This can be indicative for a reduced juvenile spiral stage. In his “Illustrated glossary of terms used in foraminiferal research”, Hottinger (2006, fig. 41) illustrated two specimens of *Karsella* from the Upper Paleocene of Pakistan exhibiting “an architecture strikingly similar to the one of Mid-Cretaceous orbitolinids” including both sub- and supraembryonic zones (Fig. 1d-e). The terminology used by this author for the embryonic apparatus of *Karsella* is not compatible with the general one used by Schroeder (1962), for example in the upper Albian-lower Cenomanian *Neoiraqia* (Moullade et al., 1979; Schroeder in Schroeder and Neumann, 1985) (Fig. 1i). The embryo of this genus like that of the Eocene *Cushmania* Silvestri, 1925 (Fig. 1e-h, Fig. 3f) show resemblances to that of *Karsella* as already noted by Butterlin and Moullade (1968, p. 10). It is worth mentioning here that M. Moullade, who erected the subfamily Dictyoconinae, assigned *Heterodictyoconus* (= junior synonym of *Cushmania*, e.g. Hottinger and Drobne,

1980) to the Orbitolininae due to its complex embryo (Butterlin and Moullade, 1968). This view was not followed by subsequent authors assigning *Cushmania* to the Dictyoconinae (Hottinger and Drobne, 1980; Loeblich and Tappan, 1987; Kaminski, 2014). The “apical wall” displaying a “subepidermal network” (Hottinger and Drobne, 1980) of *Cushmania* however is well comparable to *Rectodictyoconus* Schroeder, 1964 that on the other hand is included in the Orbitolininae (Loeblich and Tappan, 1987; Kaminski, 2014) (Fig. 3d).

Referring to the chambers enveloping the large embryonic chamber (proloculus-deutoconch) at its lower side and laterally, these can be ascribed either to the subembryonic or peri-embryonic zone (or chambers). The next chamber following below in growth direction is the first post-embryonic one (e.g., Fig. 1i). In L. Hottinger’s (2006) image (Fig. 1d), the subembryonic zone is correctly placed below the large embryonic chamber (proloculus-deutoconch) but the first chamber following the subz is questionable assigned to the peri-embryonic zone. No orbitolinid possesses both sub- and periembryonic zones: it is always one or the other. In some sections, the chambers below the embryonic chamber in *Karsella* appear to be arranged in a trochospire as also indicated by Sirel (1997) (e.g., Fig. 1b-c). In conclusion, the embryo of *Karsella* appears a complex set of structures in which some details are still not fully understood, which is also reflected in a less precise terminology.

Exoskeleton

Both *K. hottingeri* and *O. daviesi* display a thin epiderm and a complex subepidermal network consisting of several orders of horizontal and vertical partitions. The exoskeleton of *Karsella* consists of “several generations of beams and rafters” (Sirel, 1997, p. 208). There may be up to four rafters in adult chambers, and up to three orders of beams, forming a subepidermal network that can be deduced from the original illustrations, which are not of very good quality (Sirel, 1997, pl. 1, fig. 8). Several orders of both horizontal (Fig. 2d) and vertical partitions (Fig. 2c) are conspicuous in “*Orbitolina*” *daviesi*, but no details were included in the original description provided by Hofker (1966).

Endoskeleton

According to Hottinger and Drobne (1980, p. 8), Paleogene Orbitolinidae comprise only two types of endoskeletons: continuous chamber partitions (e.g., *Verseyella* Robinson, 1977, needing suprageneric revision) and separated isolated pillars (e.g., *Dictyoconus* Blanckenhorn). As has already been noted by Schlagintweit (2020), *Karsella hottingeri* does not have pillars in the central zone as indicated in the original description. Instead, *Karsella* is characterized by the presence of a radial zone with radial passages (*sensu* Henson, 1948) and septula in

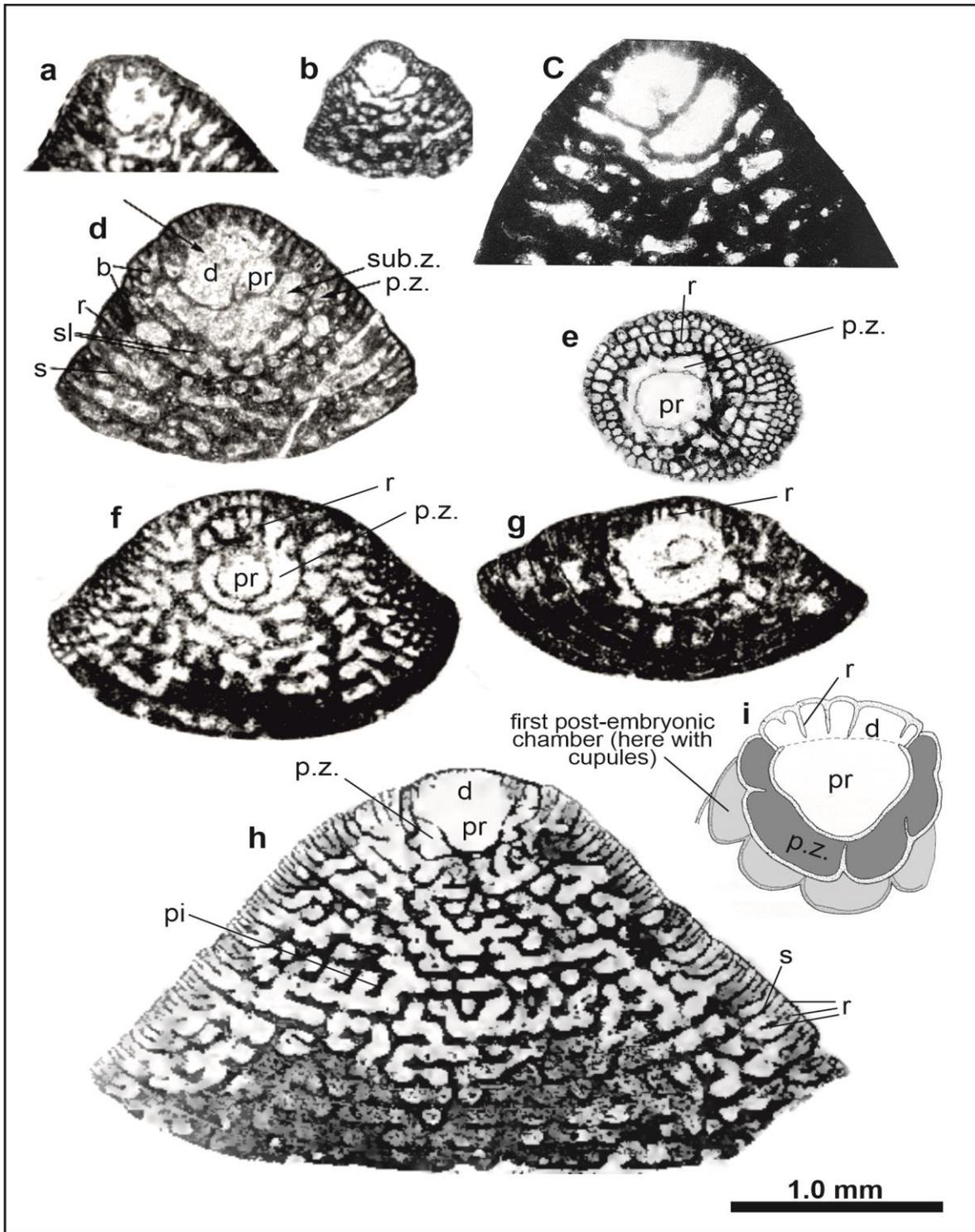


Fig. 1 Paleogene (Thanetian) Orbitolinidae from Turkey (a–b), Pakistan (c–d), and Eocene of Mexico (f), and Florida (e, h). **a–d**, *Karsella daviesi* (Hofker, 1966) comb. nov., axial sections of megalospheric specimens (**a** and **b** from Sirel, 1997, pl. 1, figs. 2, 4 = holotype of *K. hottingeri*; **c** from Hofker, 1966, pl. 3, fig. 9 as *Orbitolina daviesi* n. sp.; **d** from Hottinger, 2006, fig. 41K as *K. hottingeri*). **e–h**, *Cushmania americana* (Cushman, 1919), oblique-transverse and oblique sections of the megalospheric embryo (**e–f**), axial sections of megalospheric specimens (**g–h**) (**e** and **h** from Cole and Applin, 1964, pl. 2, figs. 3, 6; **f–g** from Butterlin and Moullade, 1968, pl. 1, figs. 7 and 5). **i**) Schematic drawing of the megalospheric embryo of *Neoiraqia* Danilova (upper Albian-lower Cenomanian) (modified from Moullade and Peybernès, 1979, fig. 1). Abbreviations: b = beam, d = deuteroconch, pi = pillar, pr = proloculus, p.z. = perieembryonic zone (or chamberlets), r = rafter, s = septum, sl = septulum, sub.z. = subembryonic zone, supra = supraembryonic zone. Arrow in **d**: supraembryonic chamber fide Hottinger (2006).

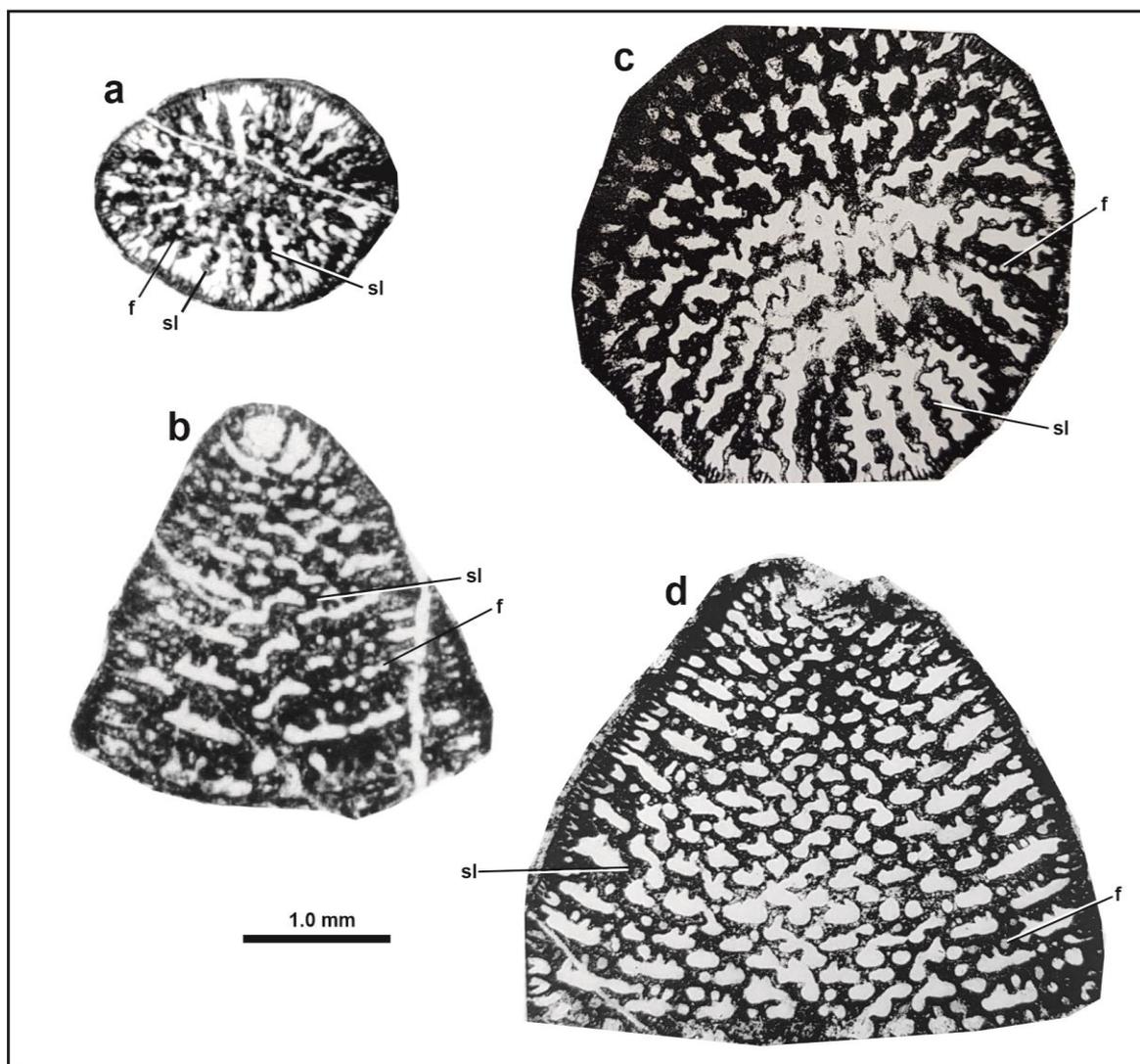


Fig. 2 *Karsella daviesi* (Hofker, 1966) comb. nov., Thanetian of Turkey (a–b) and Pakistan (c–d). **a**, slightly oblique transverse section showing radial zone (from Sirel, 1997, pl. 2, fig. 3). **b**, Axial section (from Sirel, 1997, pl. 1, fig. 9). **c**, Oblique section showing radial zone with undulating (zig-zag-like) septula and associated foramina arranged in radial lines (from Hofker, 1966, pl. 2, fig. 14). **d**, Subaxial section (from Hofker, 1966, pl. 2, fig. 13). Abbreviations: f = foramen, sl = septulum.

a zig-zag pattern associated with a linear arrangement of foramina as a characteristic feature. This pattern is also found in *Orbitolina* (Davies, 1939: Fig. 5; Henson, 1948: Fig. 7; Hofker, 1966: Fig. 1), leading Butterlin and Moulade (1968, p. 10) to conclude that “*Orbitolina*” *daviesi* Hofker displays a structure “curieusement orbitoliniforme”. All other Paleogene Orbitolinidae display pillars in the central zone: *Cushmania* Silvestri, *Daviesiconus* Hottinger & Drobne, *Dictyoconus* Blanckenhorn, and *Fallotella* Mangin (Hottinger and Drobne, 1980; Loeblich and Tappan, 1987). The radial zone with septula in zig-zag pattern is evident in *O. daviesi* (Hofker, 1966, pl. 2, fig. 11, 14) and *K. hottingeri* (Sirel, 1997, pl. 2, fig. 3; Afzal, 2010, pl. 14, fig. 6) (see also 2a, c). These undulating main partitions (septula) are alternating in position between subsequent chambers (Fig. 2d). They reach into the central test part where they are anastomosed and form a distinct network of reduced width. In

shallow tangential sections, the chamber passages between the septula display a rounded outline (Hofker, 1966, pl. 3, fig. 2 for *O. daviesi*). Let us remember that if the septula of Orbitolinidae “would be simple, vertical walls, their alternating position [Remark: between subsequent chambers!] would obstruct the rows of foramina.....therefore, the radial partition must undulate at its foot...” (Hottinger and Drobne, 1980, p. 210). The axes of the foramina are obliquely arranged and visible in axial sections as round pores (Fig. 2b and d). The presence of a well-developed radial zone reaching far into the central test part is obvious in “*Orbitolina*” *daviesi* (Fig. 2c). In the legend of an oblique section (Hofker, 1966, pl. 2, fig. 14), which is re-illustrated here as Figure 2c, Hofker states the occurrence of “radial chamber passages”. In conclusion, *Karsella* Sirel is the only Paleogene taxon displaying a radial zone, a feature that is widely spread among many Lower-middle Cretaceous genera.

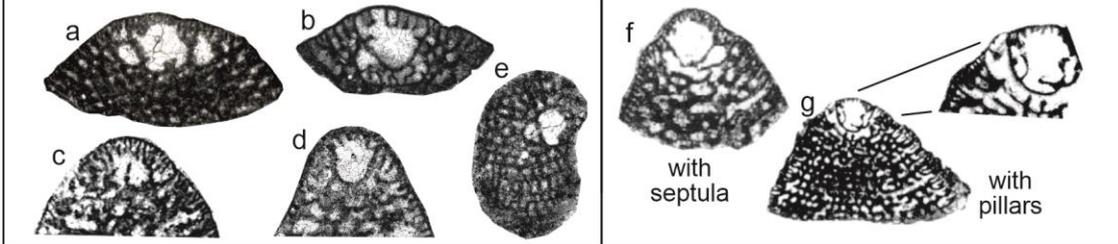
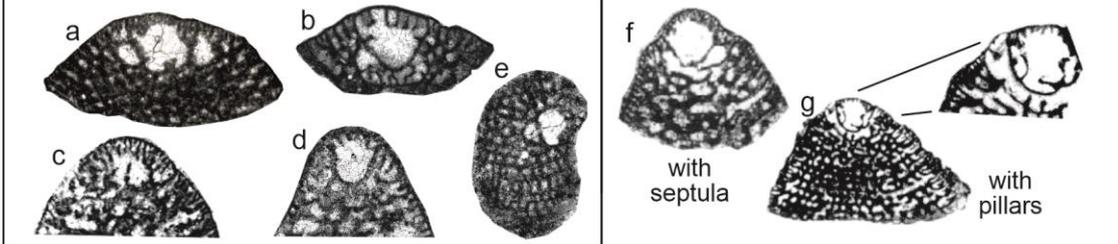
Orbitolininae Martin, 1890	new subfamily?
complex embryo (e.g., septulated deuterocoel, sub-embryonic zone, supra-embryonic zone, peri-embryonic zone/ring)	complex embryo (e.g., septulated deuterocoel, peri-embryonic zone)
<i>Conicorbitolina</i> Schroeder, <i>Eopalorbitolina</i> Schroeder, <i>Palorbitolina</i> Schroeder, <i>Palorbitolinoides</i> Cherchi & Schroeder, <i>Praeorbitolina</i> Schroeder, <i>Mesorbitolina</i> Schroeder, <i>Neorbitolinopsis</i> Schroeder, <i>Neoiraqia</i> Danilova, <i>Orbitolina</i> d'Orbigny, <i>Persiconus</i> Yazdi-Moghadam & Schlagintweit <i>Rectodictyoconus</i> Schroeder	<i>Cushmania</i> Silvestri <i>Karsella</i> Sirel
Upper Hauterivian-Cenomanian	Thanetian-Rupelian
	

Fig. 3 Comparing concept of Cretaceous (subfamily Orbitolininae) and Paleogene Orbitolinidae (new subfamily?) with complex embryo. Examples (without scale): **a**, genus *Palorbitolina* Schroeder (lower Aptian of Croatia), **b**, genus *Mesorbitolina* Schroeder, upper Aptian of Iran, **c**, genus *Rectodictyoconus* Schroeder, lower Aptian of Iran, **d**, genus *Persiconus* Yazdi-Moghadam & Schlagintweit, middle Cenomanian of Iran, **e**, genus *Praeorbitolina* Schroeder, lower Aptian of Iran, **f**, genus *Karsella* Sirel, Thanetian of Turkey (from Sirel, 1997, pl. 1, fig. 4), **g**, genus *Cushmania* Silvestri, middle Eocene of Florida (from Cole, 1942, pl. 6, fig. 2, and detail in 9).

Table 1. Dimensions of *Orbitolina daviesi* Hofker (Thanetian of Pakistan) and *Karsella hottingeri* Sirel (Thanetian of Turkey). Data as indicated in the original descriptions. * measured from the original illustrations, **measured from Hottinger (2006).

dimensions	species	<i>Orbitolina daviesi</i> Hofker	<i>Karsella hottingeri</i> Sirel
test diameter		up to 5.0 mm	up to 3.4 mm
test height		up to 5.0 mm	up to 4.9 mm
diameter embryonic chamber		~0.5 mm	0.23-0.4 mm* (~0.48 mm **)

Dimensions

Except for the test diameter, the dimensions of *O. daviesi* and *K. hottingeri* do not differ significantly (see Table 1). In the absence of consistent biometrical data it can be rather speculated whether the Pakistani species seems to reach larger test diameters. One distinct possibility is that Hofker (1966) based his maximum value on a microspheric specimen that is usually characterized by less conical and therefore broader tests. For the specimen from Turkey (2a), which has a test diameter of ~2.0 mm, there are about 8-9 septula per quadrant. The much larger specimen from Pakistan shows ~14-15 septula per quadrant at a test diameter of ~3.6 mm (2c). The heights indicated by Hofker (1966) and Sirel (1997) are identical. The diameter of the large apical embryonic chamber is comparable too.

Remarks on suprageneric classification

Because of its complex embryo, *Karsella* Sirel has been removed from the Dictyoconinae and assigned to the Orbitolininae by Schlagintweit (2020). Cretaceous orbitolinids with complex embryo have been reported from the upper Hauterivian-lower upper Cenomanian (Clavel et al., 2014; Schroeder and Neumann, 1985; Yazdi-Moghadam and Schlagintweit, 2020) with more than 10

genera (Kaminski, 2014) (Fig. 3). There is no record of Upper Cretaceous (Coniacian-Maastrichtian) Orbitolininae following the end-Cenomanian extinction (Schlagintweit et al., 2016; Cruz-Abad, 2018). Only two Paleogene genera present a complex embryo: *Karsella* Sirel (Thanetian) and *Cushmania* Silvestri (middle Eocene-Rupelian). From a phylogenetic viewpoint, it appears reasonable inferring that both groups were not di-

rectly related to each other because they appear separated by two mass extinctions, namely those from the Cenomanian-Turonian and Maastrichtian-Danian boundaries. In addition, some structural details of the embryos of *Karsella* and *Cushmania* require a further comparative study and clarification with equivalent structures of the Cretaceous orbitolinid counterparts. Despite this, the embryonic structures of the two Paleogene genera appear very similar, and both can belong to a new subfamily, different from the Cretaceous Orbitolininae.

Systematic Description

Phylum Foraminifera d'Orbigny, 1826

Class Globothalamea Pawlowski et al., 2013

Order Loftusiida Kaminski and Mikhalevich, 2004

Suborder Loftusiina Kaminski and Mikhalevich, 2004

Superfamily Orbitolinoidea Martin, 1890 nomen translatum Loeblich and Tappan, 1982 [Orbitolinacea] nomen correctum Kaminski, 2014

Family Orbitolinidae Martin, 1890

?Subfamily Orbitolininae Martin, 1890 nomen translatum

Cushman in Eastman, 1913

Genus *Karsella* Sirel, 1997

Type-species *Karsella hottingeri* Sirel, 1989 by original designation.

Karsella daviesi (Hofker, 1966) comb. nov.

1941 *Orbitolina* sp. – Davies, p. 317 (fide Hofker, 1966).

1966 *Orbitolina daviesi* n. sp. – Hofker, p. 12, pl. 2, figs. 10-14, pl. 3.

1997 *Karsella hottingeri* n. gen., n. sp. – Sirel, p. 210, pl. 1, figs. 1-10, pl. 2, figs. 1-4.

Non 2005 *Karsella* sp. – Tentor and Venturini, fig. 8, 9?, 10-12 [*Schroedericonus turriculus* (Hottinger & Drobne)].

2006 *Karsella hottingeri* Sirel – Hottinger, fig. 41K-L.

2010 *Karsella hottingeri* Sirel – Afzal, p. 115, pl. 14, figs. 5-10, ?11-13?, 14.

2014 “*Orbitolina*” *daviesi* J. Hofker jun. – Hottinger, p. 51, pl. 4.9, fig. 2.

2018 *Karsella hottingeri* Sirel – Cruz-Abad, p. 84, fig. 78A-E (reproduction of Sirel, 1997).

2018 “*Orbitolina*” *daviesi* Hofker – Cruz-Abad, fig. 78F-H.

2020 *Karsella hottingeri* Sirel – Schlagintweit, figs. 1, 2A-B (reproductions of Sirel, 1997, Hottinger, 2006, and Afzal, 2010).

Description: Test large, high-conical to slightly cylindrical with moderately convex base. The megalospheric embryo is situated in a central position at the rounded apex and presents a diameter of up to 0.5 mm. It consists of an irregular ellipsoidal proloculus, a large deuterocoel with partitions (supraembryonic zone) and a few broad peri-embryonic chambers (“subembryonic zone”) that are sporadically subdivided. The neanic stage consists of up to 27 uniserial chambers subdivided into

marginal, broad radial, and reduced central zones. There are 5-7 chambers per the last millimeter of the axial cone length. The marginal zone is complex, displaying several orders of beams and rafters. The main partitions (septula), are triangular in axial section, increase in thickness towards the cone centre and alternate in position between subsequent chambers. In transverse sections, the septula display a zig-zag pattern with associated radially arranged foramina piercing the septa obliquely. The septula form an irregular network displaying oblique stolon axes in the reduced central zone. Wall agglutinated.

Occurrences: *Karsella daviesi* (Hofker) comb. nov. is known from the Thanetian of Turkey (Sirel, 1997), and Pakistan (Hofker, 1966; Hottinger, 2006; Afzal, 2010).

CONCLUSIONS

Based on comparison of the embryonic apparatuses, the presence of a radial zone (an exception in Paleogene Orbitolinidae exhibiting pillars) and a complex exoskeleton, *Karsella hottingeri* Sirel, 1997 is considered a junior synonym of *Orbitolina daviesi* Hofker, 1966. The Pakistani taxon, however, is not a species of *Orbitolina* Orbigny but is assigned herein to *Karsella* leading to the new combination *Karsella daviesi* (Hofker). Both, the Thanetian *Karsella* Sirel, 1997 and Eocene *Cushmania* Silvestri, 1925 might, in accordance with current supra-generic classification of the Orbitolinidae, be removed from the Dictyoconinae and assigned to a group (new subfamily?) of Paleogene Orbitolinidae that display a complex embryo and are phylogenetically separated from the Cretaceous (upper Hauterivian-Cenomanian) Orbitolininae.

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