AGGLUTINATED CONICAL FORAMINIFERA (ORBITOLINIDAE, COSKINOLINIDAE) FROM THE UPPER CRETACEOUS (CAMPANIAN) OF GREECE, WITH DESCRIPTION OF PARACOSKINOLINA KLOKOVAENSI S N. SP.

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Abstract An assemblage of agglutinated conical foraminifera including Lepinococus chiocchinii Cruz-Abad et al., Calveziconus localvezae Caus & Cornella, Paleodictyoconus sp., and Paracoskinkelina klokovaensis n. sp. are described from the upper lower-middle Cretaceous of Klokova Mountain of the Gavrovo-Tripolitza Zone, SW continental Greece. With the presence of one rafter in the marginal zone, the new species P. klokovaensis compares to the Lower Cretaceous species Paracoskinkelina arcuata (Arnaud-Vanneau) that is distinguished by its cylindroconical test morphology and much larger size. The assemblage occurs in inner platform carbonates associated with other foraminifers such as dicyclinclinds, and Accordiella conica Farinacci. Representatives of the genus Paracoskinkelina were so far only reliably reported from the Upper Berriasian–Albian interval. This new record suggests that the genus either survived the larger benthic foraminifera extinction event associated with the Cenomanian – Turonian boundary anoxic event, or may be an example of an Elvis taxon or homoplasy.

Keywords: Late Cretaceous, Larger Benthic Foraminifera, Dictyoconinae, taxonomy, biostratigraphy

INTRODUCTION

Larger agglutinated conical foraminifers (Orbitolinidae, Coskinkelinae) are widespread in Lower Cretaceous shallow-water platform carbonates (e.g., Arnaud-Vanneau, 1980; Clavel et al., 2014). Records from the Upper Cretaceous (post-Cenomanian) are restricted to a distinctly reduced number of genera and species (Genovés, 1968; Moullade and Viallard, 1973; Neumann, 1978; Bilotte, 1974; Luperto Sinni and Martin-Chivelet, 1999; Schlagintweit et al., 2016; Lugier, 2018; Schlagintweit and Rashidi, 2021). In the Adriatic-Dinaric carbonate platforms, occurrences of Upper Cretaceous orbitolinids are known, where these have been described in open nomenclature (Fleury, 1970; Luperto Sinni, 1976). From the “lower Senonian” of Greece, Orbitolinid foraminifers have been described and illustrated by Fleury (1970). Referring to the locality Mount Kloko, and their description in open nomenclature, they have been grouped as “K orbitolinidés”. Fleury (1970, p. 36) noted that the observed forms could not be assigned to any known species. In fact, three different forms were described as Orbitolinidae gen. ind., Coskinkelina sp., and Dictyoconus sp. This assemblage of agglutinated conical foraminifers is herein taxonomically reassessed, including a description of Paracoskinkelina klokovaensis n. sp. It contributes to the still relatively poor knowledge of this group of larger benthic foraminifera from Upper Cretaceous shallow-water carbonates, and their distribution within the peri-Mediterranean realm.

GEOLOGICAL SETTING

The Gavrovo–Tripolitza Platform (Dercourt, 1964) belongs to the external Hellenides and crops out in the western part of continental Greece, the Peloponnese, and some islands (Zambetakis-Lekkas and Alexopoulos, 2007, Fig. 1). Composed mainly of Upper Cretaceous and Eocene shallow-water carbonates, these sedimentary rocks form the mountains of Varassova and Klokova in south Akarnania, as well as the Gavrovo massif (Ori Valtou) further north, and a discontinuous chain of smaller massifs at the Peloponnese western edge, from Skolís to Pylos-Methoni (Auboin et al., 1958; Fleury, 1970, 1980; Bernier and Fleury, 1980; Mavrikas, 1993). In a greater paleotectonic context, the Gavrovo-Tripolitza Zone represents “an Adria-derived” (Nirta et al., 2020) or “South Adriatic” unit (Zelic et al., 2010), so that the successions and their fossil biota can be compared with Apulia, and the “Senonian” occurrences of orbitolinids there (Luperto Sinni, 1976). The material studied herein comes from Klokova Mountain in Akarnania, a region of west-central Greece. The locality has been studied in detail by Fleury (1970), distinguishing eight lithologic units. Orbitolinid foraminifers have been observed in the lower-middle part (~60 m vertical range in Klokova section) (Fleury, 1970, Fig. 1) (Fig. 2). The orbitolinid assemblage occurs in biomicritic (occasional fenestral) limestones, indicating inner platform facies. Accompanying benthic foraminifers include Accordiella conica Farinacci, dicyclyclins and Sensalveolina aubouini Fleury (Fig. 3). The succession studied by Fleury (1970, p. 93, figs. 28-29, 1980) is exposed on the southern side of Klokova Mountain along the road between Nafpaktos and Messolonghi. It is also the type-locality of Sensalveolina aubouini (Fleury, 1984). The levels with “Orbitolinidés K”
Fig. 1 Geographic sketch map showing the location of Klokova mountains on the opposite side of the Gulf of Corinth facing Patra. This is the type-locality of *Paracoskinolina klokovaeansis* n. sp. (for Klokova) have been placed into the upper Santonian-Lower Campanian by Fleury (1980, fig. 8, p. 44). Based on Orbitolinid and other larger benthic foraminifera, they can be assigned to the uppermost lower-middle Campanian (see subchapter Biostratigraphy following the systematic descriptions for details).

**MATERIAL AND DEPOSATORY**

The four thin sections containing the illustrated specimens from Klokova Mountain (material from Fleury, 1970, 1980) are hosted by the Paleontology Museum, Department of Geology of Babeș-Bolyai University, Cluj-Napoca, Romania, under the official depository numbers 24307 to 24310 (Table 1). The two specimens illustrated from Brač Island, Croatia, are the property of the Croatian Geological Survey and their repository is currently in the Geological-Paleontological Department of the Croatian Natural History Museum, Demetrova 1, Zagreb, Croatia.

**SYSTEMATIC MICROPALeONTOLOGY**

The classification follows Kaminski (2014).

Phylum Foraminifera d’Orbigny, 1826

Class Globothalamea Pawlowski et al., 2013
Order Loftusiida Kaminski & Mikhalevich, 2004
Suborder Orbitolinina Kaminski, 2004
Superfamily Coskinolinioidea Moullade, 1965
Family Coskinolinidae Moullade, 1965

**Remarks:** While the family Coskinolinidae is placed in the order Loftusiida by Kaminski (2014), it is included in the order Textulariina by Cruz-Abad et al. (2017).

Genus *Lepinoconus* Cruz-Abad, Consorti & Caus, 2017
* Lepinoconus chiocchini* Cruz-Abad, Consorti & Caus, 2017
Fig. 4a, d, g, j

1970 *Coskinolina* sp. – Fleury, p. 36, pl.1, figs. 5-7.
1976 *Urgonina* sp. – Luperto Sinni, p. 312, pl. 37, figs. 1-6.
1976 *Paracoskinolina* sp. – p. 313, Luperto Sinni, pl. 38, figs. 1-3.
1976 *Abradia mosa* (Hofker) – p. 316, Luperto Sinni, pl. 41, figs. 1-12.
1993 Orbitolinidés K – Mavrikas, pl. 1, fig. 10.
*2017 Lepinoconus chiocchini* gen. et sp. nov. – Cruz-Abad et al., p. 348-350, pls. 1-2 (with synonymy)

<table>
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<th>Inventory number</th>
<th>Field Number</th>
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<td>273-GKL39-3357</td>
<td>Bucur &amp; Schlagintweit</td>
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<td>24308</td>
<td>276-GKL43X-3845</td>
<td>Bucur &amp; Schlagintweit</td>
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<td>24309</td>
<td>276-GKL43-511</td>
<td>Bucur &amp; Schlagintweit</td>
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<tr>
<td>24310</td>
<td>276-GKL43-1780</td>
<td>Bucur &amp; Schlagintweit</td>
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**Remarks:** For a detailed description of this monospecific genus see Cruz-Abad et al. (2017). The thick wall (with pseudo-keriotheca) and the aligned pillars are clearly discernible in the Greek specimens (Fig. 4A, D, J). The broken transverse section shown in Fig. 4D has a diameter of ~1.1 mm, slightly larger as the maximum test diameter indicated by Cruz-Abad et al. (2017) as 1.0 mm. Apart from the occurrences in Greece, Italy, and ?Albania (see synonymy in Cruz-Abad et al., 2017), a further occurrence can be added from Brač Island, Croatia, also in association with *Calveziconus lecalvezae* and *Paracoskinolina klokovaeansis* and at an equivalent stratigraphic position (Gušić and Jelaska, 1990; Cvetko-Tešović et al., 2001).

Superfamily Orbitolinioidea Martin, 1890
Family Orbitolinidae Martin, 1890
Subfamily Dictyoconinae Schubert, 1912

**Remarks:** Schubert (1912, p. 207) introduced the name *Dictyoconinae* for a “group” (Gruppe) of agglutinated foraminifers comprising the five genera: *Lituonella*...
Schlumberger in Schlumberger and Douvillé, 1905, Coskinolina Stache, 1875, Chapmania Silvestri, 1904, the eponymous Dictyoconus Blanckenhorn, 1900, and Lituola Lamarck, 1804, and suggested that this “row” of taxa represented a stratigraphic succession. With reservation, Schubert (1912) added Conulites Carter, 1861 and Conulina d’Orbigny, 1831. Without going into details about the taxonomic status of these genera, only Dictyoconus is left as a member of this “group”. Others are partly junior synonyms of other genera (e.g. Litoconella and Coskinolina), and belong to other families and orders (e.g. Chapmania). Obviously, the work of Schubert (1912), written in German, was overlooked by Moullade (1965) when he established the new subfamily Dictyoconinae. Shortly afterwards, the priority of the name introduced by Schubert (1912) was recognized by Moullade (1966, p. 35). Although both, Schubert (1912) and Moullade (1965) are included in the reference list of Loeblich and Tappan (1987), confusingly, they choose to retain the name Dictyoconinae Moullade, 1965. While some workers correctly used Schubert as author of the subfamily (e.g. Arnaud-Vanneau, 1976; Decrouez and Moullade, 1974), many have not questioned Loeblich and Tappan (1987) and follow their incorrect taxonomy (e.g. Mancinelli and Chiocchini, 2006; Vecchio and Hottinger, 2007; Clavel in Granier et al., 2013; Kaminski, 2014; Vicedo et al., 2014; Schlagintweit et al., 2016; Serra-Kiel et al., 2016; Villalonga et al., 2019).

Genus Paleodictyoconus Moullade, 1965
Paleodictyoconus cf. senonicus Moullade & Viallard, 1973
Figs. 3 pars, 4b-c, e-f

1970 Dictyoconus sp. – Fleury, pl. 1, 1?, 4.
?1976 Paleodictyoconus sp. – Luperto Sinni, p. 315-316, pl. 39, figs. 1-6, pl. 40, figs. 1-4.
1985 Paleodictyoconus senonicus Moullade & Viallard – Bilotte, p. 358, pl. 16, figs. 1-5.

**Fig. 2** Upper Cretaceous successions of Klokova Mountain, SW Greece (see Fleury, 1970, fig. 1, for details) with the distribution of some benthiic foraminifers (A-B: Senalveolina aubouini Fleury, sample GKL 43; C-D Accordiella conica Farinacci, sample GKL 43x, without scale). Note: the lower/middle Campanian boundary is approximately placed at the LAD of *K. tergestina* (Friija et al., 2015, fig. 15). For microfacies of sample GKL 39 see Figure 3.
Remarks: Although Moullade and Viallard (1973, p. 340, footnote) noted similarities of the specimens illustrated by Fleury (1970) as *Dictyoconus* sp. with *Paleodictyoconus senonicus*, they refrained from a concluding assessment because the Greece material lacks axial sections showing the pronounced initial spire, a circumstance also accounting for some reservations expressed herein (cf.). *P. cf. senonicus* has been observed in association with *P. klokovaensis* in the same samples (Fig. 3). The dimensions of *P. senonicus* are larger (height up to 1.5 mm, diameter up to 1.15 mm), there are 1 to 2 rafters (according to Moullade and Viallard, 1973), the test diameter is not increasing continuously from apex to base as in *P. klokovaensis*, but may decrease later resulting in a bell-shaped outline in axial sections (e.g. Moullade and Viallard, 1973, pl. 1, figs. 1, 5, 8). The pillars of *P. senonicus*, with a tendency to anastomization, are alternating between subsequent chambers (Fig. 4C, F). Last but not least, there are 8-9 chambers per last 0.5 mm axial length, meaning that the chamber height of *P. cf. senonicus* is reduced compared to *P. klokovaensis*.

Remarks: Bilotte (1985) reported *P. senonicus* from the lower Campanian of the French Pyrenees. For the orbitolinid occurrences in southern Italy, the exact stratigraphic position is still uncertain (Luperto Sinni, 1976, p. 303, “restano…datati con molta precision”). At the type-locality, *P. senonicus* occurs in levels with *Lacazina elongata* Munier-Chalmas & Schlumberger below and above. This species is reported from the upper Santonian–lower Campanian (Gräfe, 2005, fig. 4).

Genus *Calveziconus* Caus & Cornella, 1982

*Calveziconus lecalvezae* Caus & Cornella, 1982

Fig. 4h-k

1976 *Paleodictyoconus* sp. – Luperto Sinni, pl. 39, figs. 1-6, pl. 40, figs. 1-4
1981 *Calveziconus lecalvezae* n. gen., n. sp. – Caus and Cornella, p. 27-34, ps. 1-2.
1985 *Calveziconus lecalvezae* Caus and Cornella – Bilotte, p. 358, pl. 17, figs. 1-12.
1988 *Calveziconus lecalvezae* Caus and Cornella – Caus et al., pl. 2, fig. 4.
1988 *Calveziconus lecalvezae* – Gusić and Jelaska, pl. 2, fig. 8 pars.
1990 *Calveziconus lecalvezae* – Gusić and Jelaska, pl. 8, fig. 2, pars. 3, pl. 9, fig. 1.
1992 *Calveziconus lecalvezae* Caus and Cornella – Pleničar and Šribar, pl. 4, fig. 6.
2001 *Calveziconus lecalvezae* Caus and Cornella – Cvetko-Tešovic et al., p.608, fig. 9A.
2007 *Calveziconus lecalvezae* Caus and Cornella – Velić, pl. 25, figs. 1-4.
2010 *Calveziconus lecalvezae* Caus and Cornella – Zambetakis-Lekkas, fig. 4.2.
Aglutinated conical foraminifera (orbitolinidae, coskinolinidae) from the Upper Cretaceous (Campanian) of Greece

Calveziconus lecalvezae Caus and Cornella – Sokač et al., pl. 19, figs. 7-10.
2013 Calveziconus lecalvezae Caus and Cornella – Molina et al., fig. 8.6 and fig. 8.8 pars.
2015 Calveziconus cf. lecalvezae Caus and Cornella – Fríjia et al., fig. 8L.
2016 Calveziconus cf. lecalvezae Caus and Cornella – Moro et al., fig. 5c, f, o, p, t, and u.
2019 Calveziconus lecalvezae Caus and Cornella – Villalonga et al., p. 20, pl. 1, figs. 1-6, pl. 2, figs. 1-11.
2020 Calveziconus lecalvezae Caus and Cornella – Sha et al., fig. 9d, f, ?g.

Remarks: Rare sections, not allowing a detailed description, have been observed in the orbitolinid assemblage of Klokova Mountain. The species has a wide palaeogeographic distribution from Spain, Slovenia, Croatia, Greece, to India (see synonymy). In the original description, Calveziconus has been compared with the genera Orbitolinopsis Henson, Neorbitolinopsis Schroeder, and Abrardia Neumann & Damotte. Instead, striking structural matches with the Lower Aptian Irgia Henson can be stated. These comprise the medium-high conical test, a simple, slightly eccentric embryo, a marginal zone with several beams and one rafter, and a reticulate central zone. From the Maastrichtian Simsima Formation of
Qatar, Whittaker et al. (1998) reported “Calveziconus” sp. nov. showing a complex marginal zone (with up to four orders of rafters, pl. 42, fig. 3 therein) and pillars in the central zone (pl. 42, figs. 4-5 therein); this form is different from *Calveziconus* Caus & Cornell. More sections are needed for a better characterization of the Middle East form.

Genus *Dictyoconella* Henson, 1948

**Type species:** *Dictyoconella complanata* Henson, 1948

*Dictyoconella complanata* Henson, 1948

Fig. 41

*1948 Dictyoconella complanata* n. gen., n. sp. – Henson, p. 25, plate 6, figs. 2-3, 16, pl. 10, fig. 14.

1998 *Dictyoconella complanata* Henson – Whittaker et al., pl. 47, figs. 4-6.

2021 *Dictyoconella complanata* Henson – Schlagintweit and Rashidi, p. 7, figs. 2a-b pars, 3-4 (with synonymy).
Remarks: A single specimen (~ 4 mm in diameter) in a slightly oblique section parallel to the plane of test compression. *D. complanata* has so far been reported from Maastrichitian strata; the occurrence in the Campanian of Greece extends its stratigraphic record and also the previously assumed palaeogeographic restriction to the Arabian Plate (see Schlagintweit and Rashidi, 2021).

Subfamily Dictyorbitolininae Schroeder in Schroeder et al., 1990
Genus *Paracoskinolina* Moullade, 1965
Type species: *Coskinolina sundinlandensis* Maync, 1950
*Paracoskinolina klokoavaensis* n. sp.
Figs. 3 pars, 5a-j, 6a

1970 *Dictyoconus* sp. – Fleury, p. 37, pl. 1, figs. 2-3.

Origin of the name: Referring to the type-locality of the new species: Mount Klokova in western Greece.
Holotype: Subaxial section shown in Fig. 5a.
Paratypes: Specimens illustrated in Fig. 5b-j.
Horizon and locality: late early-middle Campanian of Mount Klokova, SW Greece.
Description: Medium- to high-conical test displaying smooth surface and plane to slightly convex base. The test height may slightly exceed the diameter, often the latter accounts for about 2/3 of the former. A small initial spire is barely visible (Fig. 5a, i); the embryo has not been observed. Each adult rectilinear chamber (up to 16 in adult specimens) is subdivided into a marginal and central zone. The exoskeleton of the marginal zone consists of one horizontal partition (rafter) (e.g. Fig. 5b) and 1 to 2 intercalary beams between the vertical main partitions (beams). The latter are straight and slightly but continuously widening inwards and exceed the length of the intercalary beams distinctly (about 4 times). The pillars of the central zone are aligned between subsequent chambers as visible in axial sections (Fig. 5b). In oblique section, they appear slightly offset against each other (Fig. 5e). The pillars are widened at the base and top and may have a string-of-pearls appearance (Fig. 5a). There are ~5 pillars in axial section for a test diameter of 0.5 mm. The foramina of the central zone are, like the pillars, aligned; the outermost foramina (towards the marginal zone) are arranged in a circle (Fig. 5d, left side). The wall is finely agglutinated.

Dimensions (in mm):
Test diameter: 0.85-1.1 mm
Test height: 0.75-1.2 mm
Number of chambers per last 0.5 mm cone axis: 6-7
Apical angle: ~28 to 55 degrees

Remarks: From the upper Albian-Cenomanian shallow-water carbonates of the Argolis Peninsula of Greece, Decrouez and Moullade (1974) described four new Orbitolinidae, which amongst them *Paracoskinolina fleuryi*. This taxon does not possess aligned pillars, instead alternating main partitions, and is therefore excluded from the genus *Paracoskinolina* Moullade (see emended genus diagnosis of Arnaud-Vanneau, 1980). Although nothing is known about the embryo and the internal structure displayed in transverse sections, this taxon lacks horizontal partitions and has been tentatively transferred to *Cribellopsis* Arnaud-Vanneau by Yazdi-Moghadam and Schlagintweit (2021). The form described as *Dictyoconus walnutensis* (Carsey) subspecies *pyrenaicus* by Moullade and Peybernès (1975) from the lower–middle Albian of northern Spain is similar to the Campanian species from Greece to some extent (e.g. dimensions, one rafter). Schroeder (1985) clarified that this Spanish taxon does not belong to *Dictyoconus* Blanckenhorn because of the aligned pillars in the former. In addition, Schroeder (1985, p. 46) concluded that “*Dictyoconus* pyrenaicus should be transferred to *Paracoskinolina* or an allied form due to the aligned pillars and foramina. In fact, the transverse section provided by Moullade and Peybernès (1975, pl. 1, fig. 1) nicely shows the concentric arrangement of the foramina, a diagnostic feature of the Dictyorbitolininae sensu Schroeder et al. (1990). Some morphological differences, such as a more inflated test and differing apical angle (50-70 degrees, acc. to Schroeder, 1985), of *Paracoskinolina pyrenaicus* (Moullade and Peybernès) comb. nov. are worth mentioning.

Comparisons: The new species has been described and illustrated by Fleury (1970) as *Dictyoconus* sp. Contrasting with *Paracoskinolina Moullade*, *Dictyoconus* Blanckenhorn has pillars in the central zone that alternate in position between subsequent chambers (e.g., Davies, 1930, 1939; Arnaud-Vanneau, 1980; Loeblich and Tappan, 1987). Having a single rafter in the chamber marginal zone, *P. klokoavaensis* can be compared with *P. arcuata* Arnaud-Vanneau, 1976 and *P. reicheli* (Guillaume, 1956) (Fig. 6). *P. arcuata* is morphologically different with its cylindro-conical test also displaying larger dimensions (e.g., height > 3 mm) (Arnaud-Vanneau, 1976, 1980). *P. reicheli* (Guillaume) is slightly larger as *P. klokoavaensis* and with up to four intercalary beams (e.g. Guillaume, 1956, pl. 1, fig. 6), its marginal zone is more complex. The other species, *P. maynci* (Chevalier, 1961), *P. sundinlandensis* (Maync, 1950), and *P. coogani* Scott, 2002 lack rafters in the marginal zone. Note that many other “*Paracoskinolina*” have already been taxonomically revised or are still in need of revision (e.g., Cherchi and Schroeder, 1982; Schlagintweit, 2020; Yazdi-Moghadam, 2021). These include those described before the taxonomic clarification of the genus provided by Arnaud-Vanneau (1980).

Biostratigraphy: The levels with “Orbitolinidés K” (for Klokova) have been placed into the upper Santonian-Lower Campanian (Fleury, 1980, fig. 8, p. 44). Fleury (1980) respectively established a zone “Cs B 5 à “Orbitolinidés K” et Montcharmontia apenninica s.s.” In some sections, these orbitolinids appear some metres above the
Fig. 6 Comparison of Paracoskinolina species with one horizontal partition in the marginal zone:  

<table>
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<tr>
<th>Species</th>
<th>$P.\ klokovaensis$</th>
<th>$P.\ reicheli$</th>
<th>$P.\ arcuata$</th>
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<tr>
<td>D</td>
<td>0.85-1.1</td>
<td>1.12-1.53 (1.28)</td>
<td>0.60-1.25</td>
</tr>
<tr>
<td>H</td>
<td>0.75-1.2</td>
<td>1.05-1.42 (1.16)</td>
<td>0.85-3.25</td>
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<tr>
<td>D/H</td>
<td>0.58-0.92</td>
<td>0.65-0.95 *</td>
<td>0.2-0.7 *</td>
</tr>
<tr>
<td>n</td>
<td>6-7</td>
<td>5-6</td>
<td>5-7</td>
</tr>
<tr>
<td>h</td>
<td>0.065-0.085</td>
<td>0.1-0.11</td>
<td>0.08-0.10</td>
</tr>
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Stratigraphy: lower-middle Campanian, upper Hauterivian-lower Aptian.

Stratigraphy of the two Lower Cretaceous species according to Clavel et al. (2014).

Fig. 7 Central Mediterranean area (modified from Google Earth) with occurrences of Campanian Orbitolinidae-Coskinolinidae.  

1: Zambetakis-Lekkas and Alexopoulos (2007)  
2: Fleury (1970, 1980, this work)  
3: Mount Biokovo (Sokač et al., 2012)  
4: Brač Island (Gušić and Jelaska, 1990; Cvetko-Tešović et al., 2001)  
5-7: Moro et al. (2016)  
8: Luperto-Sinni (1976)  
9: Frijia et al. (2015)  
10: Cruz-Abad et al. (2017).
The genus *Paracoskinolina* was so far recorded from the upper Berriasian (Bucur et al., 2020) to the middle-upper Albian interval (Maync, 1955; Scott, 2002). The occurrence of an individual species in the Upper Cretaceous was already reported for the genera *Falsurgonina* Arnaud-Vanneau, 1980 (*F. parva* Luperto Sinni & Martin-Chivete), *Orbitolinopsis* Henson, 1948 (*O. senonics* Gendrot, 1968), and *Paleodictyoconus* Moullade, 1965 (*P. senonics* Moullade & Viaillard, 1973). As already noted previously, also *Calveziconus* Caus & Cornella, 1982 might belong to this group, showing striking similarities with the lower Aptian *Iraqia* Henson. Concerning *Orbitolinopsis senonics*, Gendrot (1968, p. 680) noted the presence of a pseudo-keriothecal wall structure *sensu* Douglass (1960) visible only in extreme thin sections. Poorly discernible in the detailed view provided by Gendrot (1968, pl. 6, fig. 6), such a feature has so far not been described from any other species of the genus (e.g., Arnaud-Vanneau, 1980). The four species appear several million years after the larger benthic foraminifera extinction event associated with the Cenomanian–Turonian boundary anoxic/eutrophication event (e.g., Parente et al., 2008). This phenomenon of “reappearance” after longer gaps (or “ghost ranges”; Wills, 2007) may be related to morphological convergence (homeomorphism) (see also Elvis taxa; Fara, 2001) or iterative evolution reflecting common functional constraints. The repeated evolution of peculiar shell morphologies (e.g., digitate) for example are known from planktonic foraminifera during the Cretaceous and Cenozoic (Coxall et al., 2007). Iterative evolution as the main mode of morphological variation in Mesozoic imperforate larger benthic foraminifers has been recently discussed by Septfontaine (2020). This phenomenon appears to be present also in the long-lasting and complex history of the Orbitolinidae stretching from the upper Berriasian to the Paleogene (lower Oligocene) including two main-mass extinctions (Ce/T and K/T). The functional significance of individual test morphologies and structures in the Orbitolinidae (e.g., Hottinger and Drobne, 1980) is poorly constrained and needs further studies.

The distribution pattern of the conical agglutinated taxa reported from the Upper Cretaceous of Greece herein within the Central Mediterranean realm is shown in figure 7. The occurrence of comparable assemblages seems to be characteristic for distinct levels in the lower-middle Campanian of the Adriatic-Dinaric Carbonate Platform (Italy, Slovenia, Bosnia, Croatia, Greece).

**CONCLUSIONS**

The taxonomic assessment of the assemblage of conical agglutinated foraminifera (*Coskinolinaidae, Orbitolinidae*) from the Gavrovo–Tripolitza Platform of the external Hellenides (Greece), first described by Fleury (1970) demonstrates that the following taxa are present: *Leptococconus chiochinnii* Cruz-Abad, Consorti & Caus, *Paleodictyoconus cf. senonics* Moullade & Viaillard, *Calveziconus lecalvezae* Caus & Cornella, *Dictyoconella complanata* Henson, and *Paracoskinolina klokoavaensis* n. sp. The age of this assemblage can be revised to the uppermost lower-middle Campanian. *Paracoskinolina klokoavaensis* represents the first record of the genus *Paracoskinolina* Arnaud-Vanneau in the Upper Cretaceous, thus representing either a survivor of the Cenomanian–Turonian boundary extinction or the reappearance of a peculiar morphological trait. Displaying a comparably complex exoskeleton (one rafter and several orders of intercalary beams), *P. klokoavaensis* can be considered a rather advanced (or complex) representative of the genus. The occurrence of comparable assemblages of agglutinated conical larger benthic foraminifers seems to be characteristic for distinct levels in the lower-middle Campanian of the Adriatic-Dinaric Carbonate Platform (Italy, Slovenia, Bosnia, Croatia, Greece).

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**REFERENCES**

Carter, H.J., 1861. Further observations on the structure of Foraminifera and on the larger fossilized forms of Sind, etc. Journal of the Bombay Branch of the Royal Asiatic Society, 6: 31-76.
Cruz-Abad, E., Consorti, L. & Caus, E., 2017. Lepinocous chiocchinii gen. n., sp. n., a conical aggluti- nated foraminifera from the Upper Cretaceous of Ita-


