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Taxonomy and paleoecology of the Maastrichtian-Paleogene benthic foraminifer *Valvulineria orali* (Inan, 2003) comb. nov.

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ABSTRACT - Specimens classically cited in foraminiferal literature as *Cocoarota orali* Inan, 2003 are here instead considered as *Valvulineria orali* (Inan, 2003) comb. nov. This species is widely distributed in Upper Cretaceous (upper Maastrichtian) to Paleogene (lower Lutetian) shallow-water carbonates in the Neo-Tethyan realm, from Spain to Pakistan. The species was previously considered as possessing a free way of life. Material from the Danian-Thanetian of the Kambühel Formation of the Northern Calcareous Alps, Austria, and from the Danian-Selandian of the Şahinkaya Member of the Eastern Pontides, Turkey, evidences a facultative(?) epibiont life style in peri-reefal environments. The observed test plasticity is likely due to adjustments to variable substrate surfaces and supports the interpretation of an epibiont life style. The systematic placing of the species is discussed herein based on synonymies and taxonomical differences with the genera to which it has been previously attributed.

Keywords: Taxonomy; Rotaliida; epibiont foraminifera; paleoecology.

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1. INTRODUCTION

The calcareous benthic foraminiferan species *Cocoarota orali* Inan, 2003 possesses a long stratigraphic range that crosses the K-Pg boundary, encompassing the late Maastrichtian to Lutetian (Inan, 2003). Its relatively simple architecture and morphological variability with respect to size and chamber shape suggest that its ability to survive the K-Pg mass extinction was arguably connected to an opportunistic behaviour (Hottinger, 2001), typical of r-strategists (Consorti and Rashidi, 2019). The species was originally referred to the genus *Cocoarota* based upon, among other features, the occurrence of a prominent umbilical plug. The type-locality/stratum of *C. orali* are upper Danian shallow-water carbonates from the Sivas area of central Anatolia, Tukey. Furthermore, the species has a wide paleogeographic distribution, having been so far reported from Spain, Austria, Slovakia, Turkey, Iran and Pakistan (see synonymy, and this work). In this contribution we aim to cast doubts on the generic placement of this species that, in our opinion, and in agreement with Buček and Köhler (2017) and Serra-Kiel et al. (2020), should be regarded as a member of the genus *Valvulineria* Cushman. Based on a critical literature research and new material from different localities, we also aim to provide some taxonomical, morphological as well as ecological aspects of this species, indicating its facultative epibiont life style in peri-reefal depositional environments.

2. STRATIGRAPHY AND MATERIAL

The present study is based on thin sections from upper Maastrichtian to Thanetian shallow-water carbonates of Austria and Turkey from the stratigraphic sections reported in figure 1. Further samples in thin section from Iran and Spain are also used and illustrated for the purposes of the present work, to which a brief stratigraphic setting is reported in the followings.

2.1 AUSTRIA

The specimens illustrated here in figure 2 are from Danian-Thanetian carbonates of the Kambühel Formation (Fig. 1) at its type-locality in southeastern Austria (Tollmann, 1976; Tragelehn, 1996; Sanders et al., 2019). The Kambühel Formation represents a Maastrichtian-Upper Paleocene carbonate platform that developed along the southern rim of the Northern Calcareous Alps. At

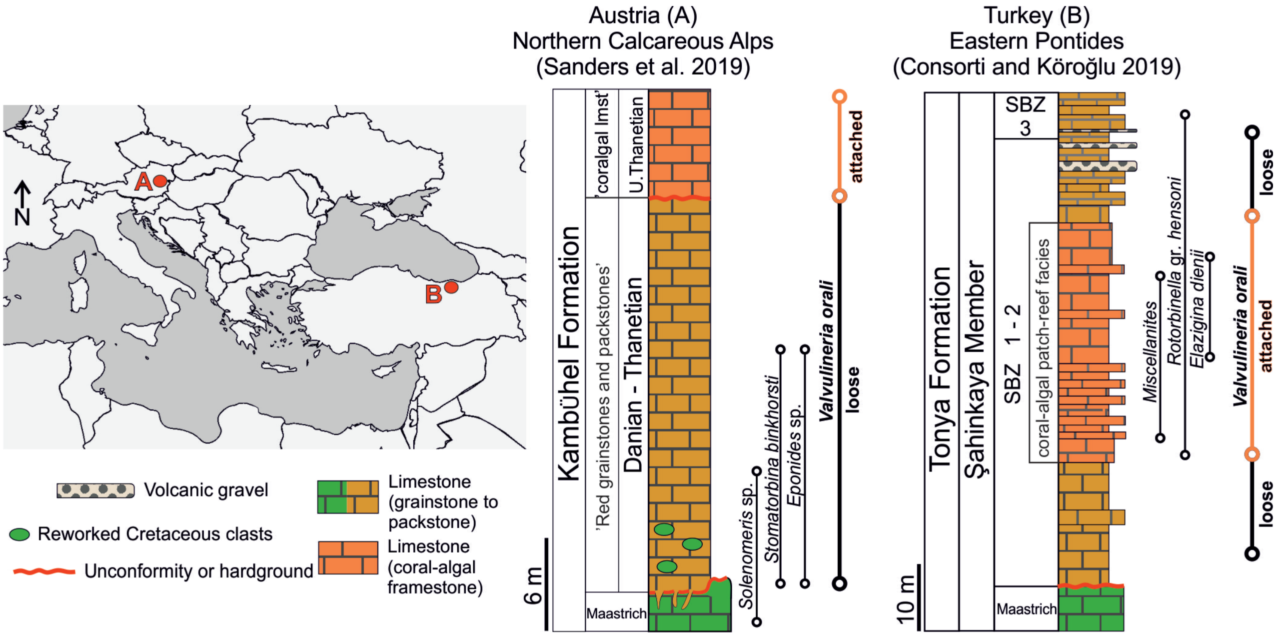

Fig. 1 - Lithostratigraphic columns of the Kambühel Formation (A) and the Tonya Formation (B) sections studied herein, with facies distribution of *Valvulineria orali* showing evidences of epibiont (attached) life style.

Kambühel hill, the K/Pg boundary is represented by an iron-stained hardground that formed during subaerial exposure, followed by rocky shore-zone deposits (e.g., beach rocks) (Sanders et al., 2019). The typical microfacies of these rocks consists of grainstones with coralline algae, bryozoans, rhynchonellid brachiopods, intraclasts, and lithoclasts. The benthic foraminiferan assemblage includes *Stomatorbina binkhorsti* (Reuss), *Cibicidoides succedens* Brotzen, encrusting *Solenomeris*, and *Valvulineria orali* (Inan) nov. comb. (Schlagintweit et al., 2018; Schlagintweit and Rigaud, 2019). The youngest sediment unit cropping out at Kambühel hill, Thanetian in age, consists of coralgal limestones (with textures encompassing floatstones, bafflestones and rudstones). The algal flora consists of both green (Dasycladales) and red algae (crustose corallinaceans, Solenoporaceae). In this section specimens are usually found loosely dispersed in the matrix, but in peri-reefal limestones (coral-algal association), *V. orali* may be found fixed to hard substrates by its spiral side often in association with coralline red algae (Figs. 2 a,d), or carbonate grains (Figs. 2 f-h). In these cases, the spiral side adopts to the surface of the substrates; no cement between the test and the substrates has been observed. Beside *V. orali*, there are other calcareous foraminifera attached to bryozoans (Fig. 2b).

2.2 TURKEY

The material comes from the Şahinkaya Member, NE Sakarya Zone of the Eastern Pontides, Turkey (Fig. 1). *Valvulineria orali*, cited as *Cocoarota orali* Inan, has been observed in Danian to Selandian (SBZs 1 and 2) high-energy shoal facies and coral-algal patch-reef facies (Consorti and Köroğlu, 2019, Fig. 2); the latter is likely placed into the mesophotic zone of the carbonate platform, at a relatively shallow depth. The shoal microfacies consists of grainstone-packstone mostly with rounded fragments of coralline algae, echinoderms and benthic foraminifera. The patch-reef shows bindstone to floatstone textures with sparse corals, both isolated and colonial, along with crustose red algae and microbial films that trapped the sediment. The benthic foraminiferal assemblage includes *Planorbulina cretae* (Marsson), *Rotorbinella hensoni* (Smout), *Ornatononion moorkensii* Hottinger, *Miscellanites primitivus* (Rahaghi), *Miscellanites minutus* (Rahaghi), *Miscellanites globularis* (Rahaghi) and *Elazigina dienii* (Hottinger). In this section specimens are usually found loose in the matrix, however the patch-reef limestones of the Şahinkaya Member offered hard substrates for attaching *V. orali* that may be found fixed on green and red algae (Figs. 3a, 4 a-c), as well as small carbonate grains (Fig. 4d).

2.3 IRAN

The specimens illustrated come from the Patorgi section of the Sistan Suture Zone (Schlagintweit et al., 2020), eastern Iran, the Mount Chah Torsh section of Central Iran (Schlagintweit and Rashidi, 2019; Schlagintweit et al., 2019, 2020), and the Qorban section of southwestern Iran (Benedetti et al., 2020; Consorti et al., 2020; Schlagintweit et al., 2020). In the Patorgi section, *V. orali* occurs in grainstones with miliolids, *Idalina sinjarica* Grimsdale and remains of dasycladaleans, and bioclastic packstones with abundant red algae, corallinaceans, *Polystrata alba*

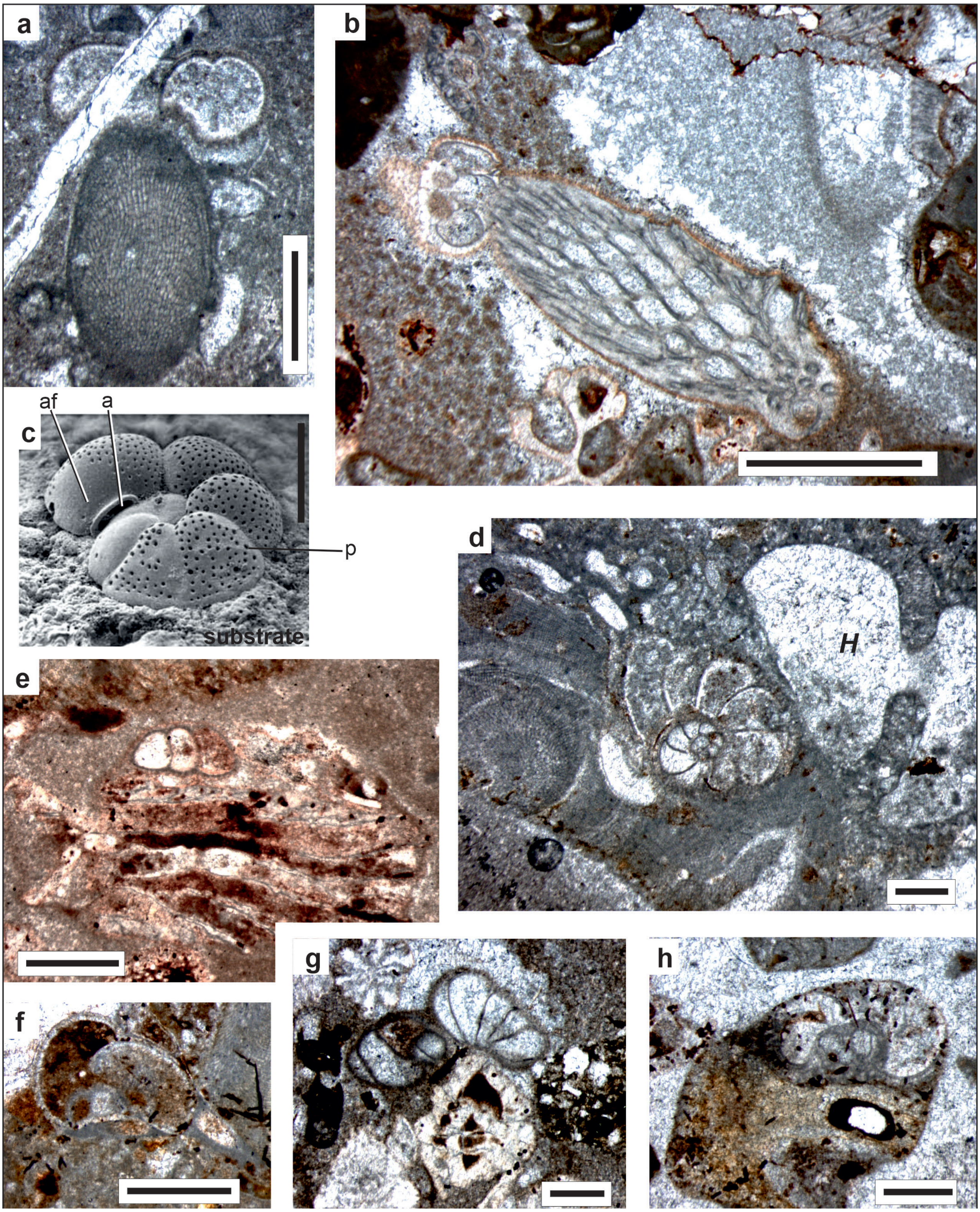

Fig. 2 - *Valvulineria orali* (Inan) from the Paleocene of Austria with evidence of epibiont (attached) life style. a) attached to a coralline alga. b) unknown foraminifera attachedto a bryozoan. c) Recent *Paracibicides edomica* Perelis and Reiss (modified from Hottinger, 2006b, fig. 1f; af: apertural face, p: pores, a: aperture), figured as an example in comparison with epibiont *Valvulineria orali*. d) associated to coralline algae and large agglutinated *Haddonia* (*H*). e-h) attached to diverse (bio-) clasts. Note the attached spiral side adhering to the convex substrate surfaces. Scale bar 0.5 mm for all figured specimens.

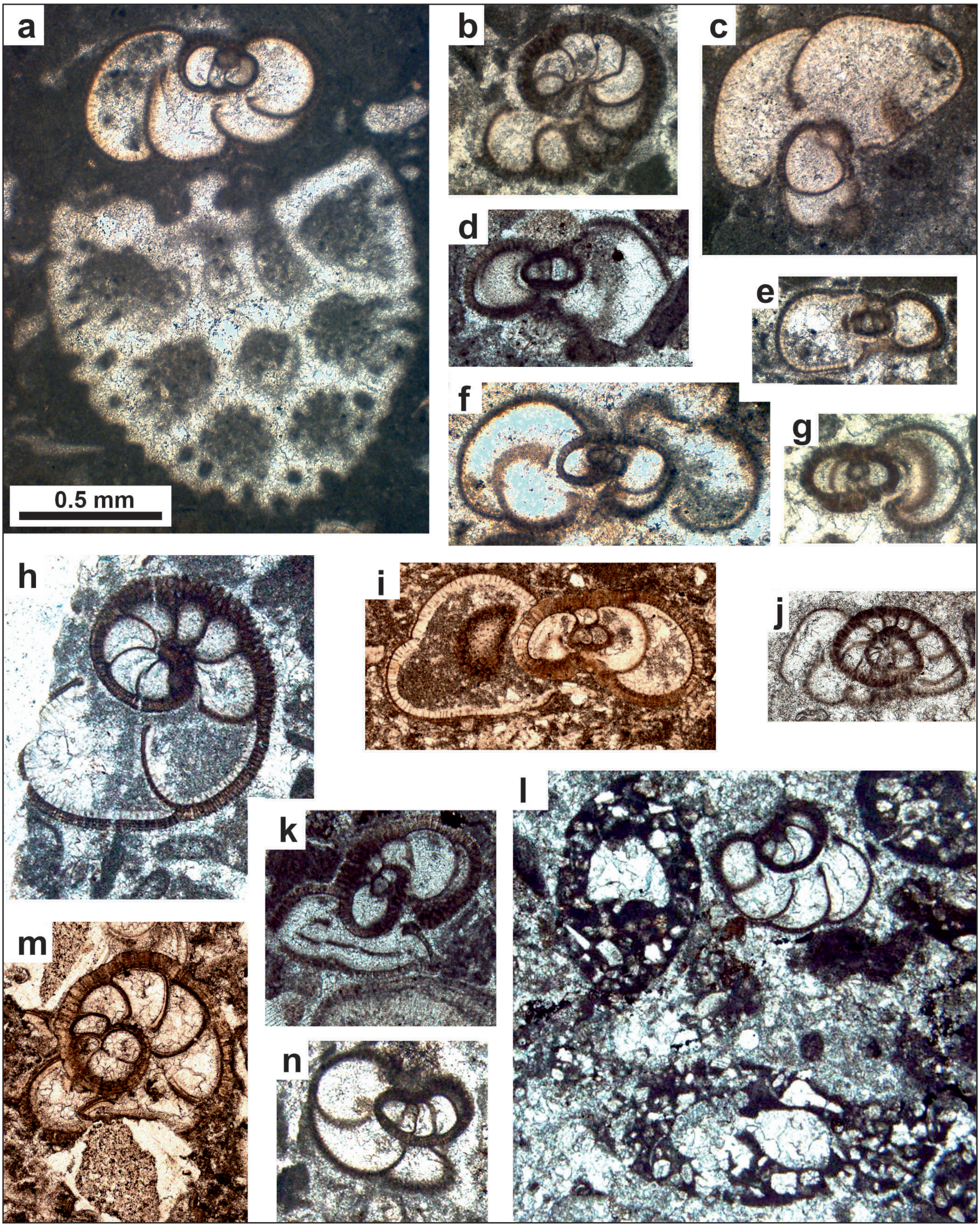

Fig. 3 - *Valvulineria orali* (Inan) from the Paleocene of the Eastern Pontides, Turkey (a-c, e-g), Iran (d, h j, k, l, n), and Spain (i, m). **a**, oblique section together with dasycladale *Broeckella belgica* Morellet & Morellet. b, h, j, equatorial sections, partly slightly oblique. c, f, k-n, oblique sections. d-e, g, subaxial sections. i, axial section. Evidences of epibiont life style in a, d, k and m. Scale bar 0.5 mm for all figured specimens.

(Pfender) Denizot, and bryozoans (Figs. 3 d,k). The age is Selandian or Thanetian. From the Mt. Chah Torsh section, *V. orali* has been observed in Danian limestones together with specimens of the agglutinated miliolid *Haymanella* Sirel and green algae (Fig. 3l). From the Qorban section, *V. orali* is reported from dasycladalean grainstones, bioclastic grainstones associated with *Mardinella daviesi* (Henson), *Schroedericonus turriculus* (Hottinger and Drobne), small-sized miliolids and dasycladaleans. The age is Thanetian (see Benedetti et al., 2020).

2.4 SPAIN

The two specimens illustrated (Figs. 3 f,m) are from Cantabria, northern Spain, and have been collected during work for the geological map 1:50 000 Santander (Hoja 35 http://info.igme.es/cartografiadigital/datos/magna50/pdfs/d0_G50/Magna50_35.pdf; Ramírez del Pozo et al., 1976), particularly from the lithostratigraphic units 30 (T^{A}_{11-2}) and 32 (T^{Aa}_{21}) shown as a frame element of the map. Samples are stored in the Ramírez del Pozo collection at the Insituto Geológico y Minero de España at Tres Cantos, Madrid under the numbers 9-04GS A0 2169 (lower Paleocene) and 19-04GS A0 2185 (lower Eocene, Ilerdian).

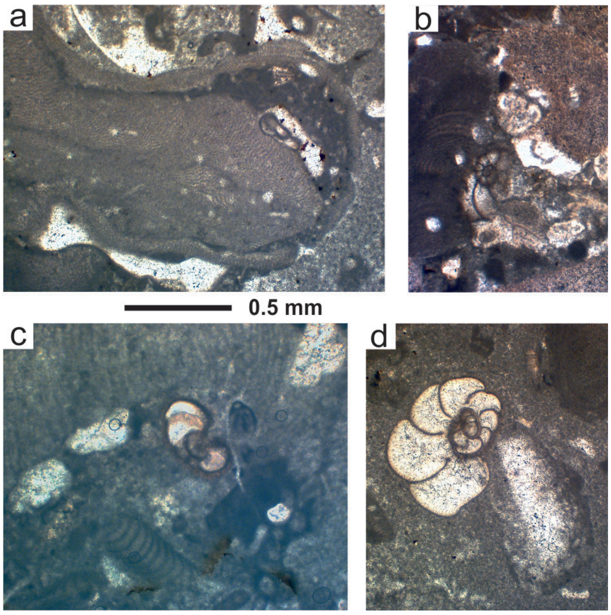

Fig. 4 -*Valvulineria orali* (Inan) from the Paleocene of Turkey (Eastern Pontides) with evidences of epibiont (attached) life style on red algae (a-c) and a carbonate grain (d). Scale bar 0.5 mm for all figured specimens.

3. SYSTEMATIC PALEONTOLOGY

Phylum Foraminiferida d'Orbigny, 1826
Class Globothalamea Pawlowski et al., 2013
Subclass Rotaliana Mikhalevich, 1980
Order Rotaliida Delage & Hérouard, 1896
Superfamily Discorboidea Ehrenberg, 1838
Family Cancrisidae Chapman, Parr & Collins, 1934
Genus ***Valvulineria*** Cushman, 1926
Type-species *Valvulineria californica* Cushman, 1926

Remarks: An updated description of the holotype of *Valvulineria californica* Cushman deposited at the Smithsonian Institution can be found in Revets (1996). It states as follows: "Test unequally to equally biconvex, low trochospiral, spiral side nearly flat, tending towards concavity, evolute, umbilical side convex, involute, with a clearly depressed central umbilicus, periphery broadly rounded, strongly lobulate, 2.5 whorls; chambers spherical, strongly inflated, rapidly increasing in size, 7 chambers in final whorl; sutures gently arcuate, strongly depressed, becoming flush, spiral suture clearly depressed, somewhat undulate; aperture elliptical, umbilical extra-umbilical, restricted to lowermost part of leading chamber face, continuing into the umbilicus, hidden under an umbilical folium, successive folia partially coalescing, but leaving a relict foramen in previous chambers, relict apertures gradually closed off; wall optically granular, finely perforate."

Unlike *Valvulineria*, *Cibicides* (type-species: *Cibicides refulgens* de Montfort, 1808) is plano-conconvex, the periphery is angular and carinate; aperture is low interiomarginal. *Anomalina* (type-species: *Anomalina ariminensis* d'Orbigny in Fornasini, 1902) is slightly trochospiral or planispiral, planoconvex, with an umbilical plug. Unlike *Valvulineria*, the holotype of *Cocoarota cocoaensis* Cushman, 1928 (type-species of the genus *Cocoarota*) re-described by Revets (1996) clearly shows a prominent umbilical plug. We rely on the latter character to shift the species *Cocoarota orali* Inan from the genus *Cocoarota* to the genus *Valvulineria*.

Valvulineria orali (Inan, 2003)
Figs. 2-4

1972 *Anomalina* sp.-Borza et al., pl. 24, fig. 1, pl. 25, figs. 1-4.
1998 Rotaliid gen. et sp. indet.-Sirel, pl. 63, figs. 1-19.
2003 *Cocoarota orali* n. sp. Inan, 201-202, pl. 1, figs. 1-14.
2005 *Cibicides* sp.-Afzal et al., pl. 1, fig. 12.
2005 *Planorotalites pseudomenardii*-Afzal et al., pl. 2, fig. 4.
2015 *Valvulineria* aff. *patalaensis* Haque-Sirel, pl. 10, figs. 1-19.
2017 *Globanomalina pseudoiota*-Al-Dulaimi and Al-Dulaimi, pl. 7, fig. 6
2017 *Valvulineria* aff. *patalaensis* Haque-Sirel and Deveciler, pl. 5, figs. 8-11.
2017 *Valvulineria* sp. - Buček and Köhler, pl. 26, figs. 1, 3.
2017 *Cibicides* sp. - Buček and Köhler, pl. 26, fig. 2.
2018 *Valvulineria* aff. *patalaensis* Haque-Sirel, p. 164, pl. 57, figs. 1-19.
2019 *Cocoarota orali* Inan-Consorti and Rashidi, figs.

8H, 8K.

2019 *Cocoarota orali* Inan-Consorti and Köroğlu, fig. 8o-p.

2020 *Valvulineria bacetai* n. sp. Serra-Kiel and Vicedo, p. 45, fig. 23L'-N'; P'-R'.

Description: Test small free or attached with a rounded periphery, flared, low trochospiral to almost planispiral; slightly asymmetrical or faintly plano-concave. There are up to 3 whorls of chambers. The umbilical side is occupied by delicate, thin folia. Wall perforated by relatively wide pores; usually coloured in thin section and double-layered; the outer layer with a blackish to brown color, the inner layer yellowish or bright orange; both layers always are lamellar perforated. Lamellar thickening is evident in earlier chambers rather than the outermost ones due to the superposition of lamellae during ontogeny. Chambers gradually increase in size; last chambers inflated, markedly more voluminous and/or irregular in shape. Chamber sutures always arched and slightly depressed. Aperture consists of a slit placed centrally in interiomarginal position. Spherical proloculus with a diameter ranging from 50 to 80μm. Shell diameter ranges from 0.45 mm to 1 mm, shell thickness 0.3 mm to 0.5 mm. First whorls composed of 4 chambers, last whorl of 7 to 8 chambers.

Differences: Comparison among fossil taxa referred to *Valvulineria* is extremely difficult if looking only at the figured types. This is especially hampered by the preparations used by the different authors: for instance, isolated specimens in Nakkady (1950), Drooger (1952), Haque (1956), Hillebrandt (1962) *vs.* specimens in thin section of Inan (2003) or Serra-Kiel et al. (2020), which make problematic a thoughtful comparison of some diagnostic features such as shell texture or internal structures. Furthermore, the list of accepted fossil *Valvulineria* species is somewhat broad (see WoRMS catalogue at https://www.marinespecies.org/foraminifera/aphia.php?p=taxdetails&id=112100). Additionally, to re-study all the deposited type material goes beyond the aims of the present contribution. Assessment is further hindered by the size variation observed among the specimens collected herein as well as the ones observed throughout the literature, supporting the idea that size should not be a discriminant character. In this regard, we suspect that Inan (2003) focused only on specimens comprised into a certain size-range (i.e., specimens consisting of 1 to 1.5 whorls), leaving apart larger shells like the one figured in plate 1 fig. 5 therein. A thoughtful size sorting has been instead made among the two *Valvulineria* species recognized by Serra-Kiel et al. (2020), that furthermore come from different time frames: *Valvulineria patalensis* from the Danian; *Valvulineria bacetai* (= here considered a junior synonym of *V. orali*) from the Thanetian. Instead, we consider *V. bacetai* of Serra-Kiel et al. (2020) in fig. 23O' closer to a *Cibicidoides*, thus not included in our synonymic list. The three species defined by Haque (1956; *V. hillsi* and *V. patalaensis* from the lower Eocene; *V. ranikotensis* from the Paleocene), and the Paleocene *Valvulineria koenigswaldi* Drooger, 1952, *Valvulineria palmi* Drooger, 1952, *Valvulineria alpina* Hillebrandt, 1962 and *V. esnehensis* Nakkady, 1950, among others (see also LeRoy, 1953), have been mostly defined based on external characters of the shell. Therefore, through the original descriptions, there is no chance to understand whether the double layered shell characterizing *V. orali* occurs. Based on comparable characters, we can state that, unlike *V. hillsi*, *V. esnehensis* and *V. patalaensis*, the septa of *V. orali* are always broadly arched; *V. ranikotensis* instead shows more regularly arched septa but, unlike *V. orali*, its shell is markedly plano-convex. Unlike *V. orali*, *V. palmi*, *Valvulineria critchetti* LeRoy and *Valvulineria aegyptiaca* LeRoy are very small (mean diameter 0.12 mm, 0.29 mm and 0.45mm, respectively). *V. alpina* looks closer to *V. orali* by morphometry, size ranges (see Hillebrandt, 1962, plate 8, figs. 7, 8); number of chambers for the last whorl; and for having a well-rounded periphery; but unlike *V. orali*, shell shape is biconvex. *V. scrobiculata* (Schwager) also looks very close to *V. orali* especially by the occurrence of highly inflated last chambers and rounded periphery, shell dimension is however somewhat reduced (mean diameter 0.42 mm). *V. koenigswaldi* resembles to *V. orali* by its faint planispiral arrangement, inflated last chambers, biometry (7 to 9 chambers in the final whorl, max. diameter 0.85 mm) and arched, almost centered, elongated aperture; but unlike *V. orali* folia looks quite smaller. Based on such brief survey through these Paleocene peri-Mediterranean species, and concerning the occurrence of a relatively wide size variation within *V. orali*, we may suspect a potential synonymy with *V. scrobiculata*, *V. alpina*, or *V. koenigswaldi* that should be checked with closer attention in a further taxonomical effort. Ecologically, the fossil species may have occupied different habitats; most of them were found in shales or marls, whereas *V. orali* is always reported from shallow-water limestones, with evidences of an attached way of life on peri-reefal hard substrates.

Remarks: In her description of *Cocoarota orali*, Inan (2003) stated about the occurrence of an 'umbonal boss' (= umbilical plug, see Hottinger, 2006a). This feature likely represents one of the main constraints used for placing the species within the genus *Cocoarota*. However, no umbilical plug seems to occur in both Inan's specimens and the ones studied herein. The umbilicus is instead observed as occupied by some sort of thin folia such as those of the genus *Valvulineria* and reported like 'apertural flap' by Loeblich and Tappan (1987) or 'umbilical folium' by Revets (1996). Likewise, thin folia can be observed in *Valvulineria bacetai* of Serra-Kiel et al. (2020) as well as *Valvulineria* aff. *patalaensis* in Sirel (2018). Our conclusive observations allow us to consider *Cocoarota orali* and *Valvulineria bacetai* as synonyms. Both taxa are validly published in accordance with the rules of the International Code of Zoological Nomenclature (ICZN), thus they can be categorized with Inan's species having the priority and grouped under the new combination *Valvulineria orali* (Inan). The rather wide size variability observed from the studied localities, coupled with the diagnostic features summarized herein, would also suggest the that small specimens identified by Serra-Kiel et al. (2020) as *Valvulineria patalaensis* Haque and by Sirel (2018) as *Valvulineria* aff. *patalaensis* Haque can be included in the variability of *Valvulineria orali* (Inan). However, a definitive conclusion cannot be drawn since a detailed taxonomical comparison among all fossil *Valvulineria* species so far described in the literature is still not available, thus further studies should be carried out.

4. PALEOECOLOGY

Test morphology of benthic foraminifera is conceived to adapt into microhabitats and related to the functional unit of behavioral strategies. These are associated to ecological requirements such as e.g., food catchment, sheltering from predators or photosynthesis in symbiont-bearing species. These assessments have been largely tested by studying recent species and are based on some parameters including the test shape (symmetrical vs. asymmetrical, lenticular, discoidal, incrusting, among others), the presence, distribution and characters of pores, and ornamentation (Corliss, 1991; Jorissen, 1999; Hottinger, 2006b; Hohenegger, 2009 and references cited therein). The foraminiferal test thus plays a key role for understanding its functional morphology and, particularly in fossil examples, represents a critical tool linking each species to its own microhabitat (see e.g. Dubika et al., 2015; McLoughlin et al., 2018; Consorti et al., 2020). Such an approach is here briefly discussed for *V. orali*.

The shells of *Valvulineria orali* are low trochospiral to almost planispiral, asymmetrical in shape. Pores are relatively wide and well distributed along the dorsal and lateral sides. Chambers of the last whorl grow exponentially through ontogenesis, whereas their outline, generally sub-globular with well-rounded periphery, is occasionally aberrant. Furthermore, *Valvulineria orali* is found on hard/firm substrates (mostly represented by red algae) using the spiral side of the shell as attached surface (Figs. 2 a,d, 4 a-c). These features point to an epibiont behavior analogous to that of some recent cibicidids such as *Cibicides lobatulus* (Walker and Jacob) studied by Dubika et al. (2015) as well as *Paracibicides edomica* Perelis and Reiss or *Caribbeanella elatensis* Perelis and Reiss in Hottinger (2006b). In particular, our study in thin section agrees with the outcomes showed by Dubika et al. (2015, see Figs. 2-4) while studying the epibiont behaviour of *Cibicides lobatulus*. However, since *V. orali* is commonly recovered as a reworked grain in high energy facies, it is quite uncertain if the epibiont life style was constantly adopted, or rather represented a temporary adaptation to certain ephemeral ecological requirements once hard substrates were easily available. Like several recent examples (e.g., Jorissen et al., 1992), its microhabitat preferences may have changed in response to fluctuating environmental circumstances, making it an opportunistic species able to rapidly re-adapt into different niches.

5. CONCLUSIONS

The double layered, low trochospiral benthic foraminifer with rounded periphery usually found in Maastrichtian-Paleocene limestone successions from Pakistan to Spain, previously reported as *Cocoarota orali* Inan, is here re-described and taxonomically revised as *Valvulineria orali* (Inan). Whereas it has been previously considered as possessing a free way of life, or being able to crowd over different substrates, we provide herein some evidences of a facultative epibiont life style. In fact, *Valvulineria orali* is particularly abundant into certain stratigraphic levels dominated by peri-reefal coral-algal (association with corals, red and green algae), mesophotic patch-reefs or indurated microbial films, suggesting a preference to hard or firm substrates in which an attached life-style would be a plausible, probably temporary, adaptation strategy.

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