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On the Eocene Pediculariinae (Gastropoda, Ovulidae) *Olianatrivia riberai* Dolin L., Biosca-Munts & Parcerisa, 2013 and *Perispatula costagranosa* Checchi, Zamberlan & Alberti, 2013

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ABSTRACT The species *Olianatrivia riberai* Dolin L., Biosca-Munts & Parcerisa, 2013 on the one hand, and *Perispatula costagranosa* Checchi, Zamberlan & Alberti, 2013 on the other, are reconsidered on the basis of a new examination of the available material. A systematic comparison of morphological characters, performed here for the first time, together with geostratigraphic considerations, leads us to conclude that these two taxa represent two clearly distinct species. *P. costagranosa* is therefore reinstated as a valid species after having been placed in synonymy with *O. riberai* without proper justification in 2018. However, this re-evaluation, combined with a study of the internal shell structure using X-ray tomography, does not allow the two species to be separated at the generic level. Consequently, *P. costagranosa* is assigned to the genus *Olianatrivia* as *Olianatrivia costagranosa* (Checchi, Zamberlan & Alberti, 2013) comb. nov.

KEY WORDS Ovulidae, Pediculariinae, Eocene, *Olianatrivia*, *O. costagranosa*, *O. riberai*, *Perispatula*, Spain, Italy

INTRODUCTION

In 2013, by chance, two species belonging to an entirely new genus were published almost simultaneously. One originates from Catalonia (Spain) and dates from the boundary between the upper Bartonian and the lower Priabonian (transition from the Middle to the Late Eocene). The other, from the Vicenza region (Italy), dates from the boundary between the upper Ypresian and the lower Lutetian (transition from the Early to the Middle Eocene).

The genus of the first species was named *Olianatrivia*, in reference both to the locality that gave its name, Oliana anticline, where the original deposit is situated, and to the morphological convergence of this shell with those of certain *Triviinae* (DOLIN L. *et al*., 2013: 782). The genus of the second species, on the other hand, was described under the name *Perispatula*, in reference to the characteristic spatula-shaped protuberances that border the shell along its entire periphery (CHECCHI *et al*., 2013: 29).

Their respective author groups logically associated them with the genus *Cypropterina* De Gregorio, 1880 (type species: *Cypraea ceciliae* De Gregorio, 1880, by monotypy)

because of its highly distinctive, cabochon-like shape, its very flattened ventral sole, and its nearly circular outline. Accordingly, this genus was placed directly within the Pediculariinae, treated as a subfamily of the Ovulidae Fleming, 1822 for *Olianatrivia*, and within the family Pediculariidae Gray, 1853 for *Perispatula*. This constitutes the only divergence between the two treatments, although it is not a substantive one, as it merely reflects the long-standing controversy regarding the validity of the Pediculariidae as a distinct family versus the placement of its representatives as a subfamily within the Ovulidae (see CHECCHI *et al*., 2013 for further details). At present, according to Molluscabase ((https://www.molluscabase.org/) [accessed 23.ii.2026]), which has undergone several updates on this matter (CELZARD & GÓMEZ-GARCÍA, 2025), members of the Pediculariidae are now classified within the subfamily Pediculariinae, and this is the view followed here.

Where the two author groups converge again is in recognizing the necessity of erecting a new genus, as the characteristics of these two species are truly unique. The genus is indeed distinguished from all others by shells with an oval outline, a low and bumpy dorsal profile, and very strong, bead-like dorsal ribs terminating in long, spatulate protuberances. These, radiating outwards in a fan-like arrangement, border the entire perimeter of the shell and represent the continuation of extremely pronounced teeth that extend across the whole surface of a very flattened ventral sole. Thus, in parallel, two distinct genera were described, each presumed to be monotypic.

Subsequently, DOLIN L. & AGUERRE (2018: 110) declared *P. costagranosa* to be an "*objective synonym [same type species]*" of *Olianatrivia*, without further comment. At most, we can read in the original description of *O. riberai* that Dolin "*had already observed specimens from the Veronese area (Italy) and from Béarn (France)*" (DOLIN L. *et al*., 2013: 782). This author had most probably examined *P. costagranosa* in the case of the Italian specimens (we ourselves have not yet seen French material), but without paying attention to the differences discussed in the present paper. That being said, the assertions made by these authors are incorrect: the taxa *O. riberai* and *P. costagranosa* are not objective synonyms [same name-bearing type and not same "type species"] since each of these species possesses its own name-bearing type (ICZN, 1999: Art. 61.3.4).

In the present study, we therefore sought to revisit this synonymy, which is not justified at the specific level by either morphological criteria or the geostratigraphic considerations of which we are aware. We also attempted, through X-ray tomography studies, to better define the genus of these species by considering *Olianatrivia* and *Perispatula* as a priori distinct, before reaffirming their synonymy at the generic level.

Abbreviations:

D:	Shell diameter (mm)
DD:	Shell dorso-ventral diameter (mm)
H:	Shell height (mm)
MGVM:	Museu de Geologia « Valenti Masachs » (UPC), Manresa (Spain)
MNHN.F:	Muséum National d'Histoire Naturelle, Paleontology Collection (Paris)
PC:	Private collections

TYPE LOCALITIES AND TYPE STRATA

O. riberai and *P. costagranosa* are two southern European Eocene species. The former was discovered in a marly limestone matrix at

the boundary between the upper Bartonian and the lower Priabonian near the locality of Odèn (Catalonia, Spain), and the latter in upper Ypresian / lower Lutetian volcanodetrital levels of the Rossi quarry in Monte di Malo (Vicenza, Italy). These two localities, separated by nearly 900 km in a straight line, were connected during the Eocene (MERLE, 2008) and could therefore have been inhabited by the same gastropod species. Indeed, ASTIBIA *et al*. (2018) had already identified species in common when comparing Eocene molluscan faunas from Pyrenean regions of Spain with those of the Tethyan (Italy and the Alps) and Northern (Paris Basin and Normandy) domains (ASTIBIA *et al*., 2016), thereby confirming the role of the Pyrenean region as a connection between these paleobiogeographic provinces.

In contrast, *O. riberai* and *P. costagranosa* differ in age by approximately 10 Ma, the former dating from the late Middle Eocene, the latter from the transition between the Early and Middle Eocene. Although the duration of a fossil species may very exceptionally reach about 10 Ma, as in the case of the bivalve *Gryphaea dilatata* J. Sowerby, 1816 (HALLAM, 1959), the average duration of a marine animal species is closer to about 4 Ma according to synthetic estimates derived from the fossil record (RAUP, 1991). Although purely empirical, this average – established from approximately 17,500 fossil taxa – should therefore encourage particular caution when examining two morphospecies that appear very similar but lived some 10 Ma apart.

MATERIAL AND METHODS

Three specimens of *O. riberai* were kindly loaned to us by the Museu de Geologia "Valenti Masachs" (Manresa, Spain) for the duration of this study. These include the holotype MGVM 2585 (**Pl. 1, fig. A**), the paratype MGVM 2586, designated as juvenile (but more likely subadult, **Pl. 1, fig. B**), and the fragmentary paratype MGVM 2587 (**Pl. 1, fig. D**). Photographs of paratype MNHN.F.A48090, preserved at the MNHN, were also consulted and are presented here (**Pl. 1, fig. C**).

At the same time, four specimens of *P. costagranosa* were also provided to us for study. They come from private collections, as we were not granted permission to borrow the types deposited at the Museo Civico "G. Zannato" in Montecchio Maggiore (Italy). The illustrations of the type material are nonetheless presented here (**Pl. 2**, **fig. A, B**) to clearly demonstrate that the specimens studied are in every respect similar to the holotype and paratype and cannot in any way be attributed to another species. Three of the *P. costagranosa* specimens examined are adults (**Pl. 3, fig. A-C**), and one even exhibits two spectacularly long spatulate protuberances, positioned opposite each other and aligned along the shell's axis (**Pl. 3, fig. B**). The fourth specimen is genuinely juvenile, providing the first glimpse of what the shell's development must have been like (**Pl. 3, fig. D**).

All specimens were subjected to conventional morphological examination under a binocular microscope, but were also systematically scanned in 3D using an X-ray tomograph (EasyTom 130 kV, RX Solutions, France) in order to visualize their internal structure (**Pl. 4-6**). First, images were acquired by slowly rotating the specimens in increments of a quarter of a degree in the X-ray beam. These preliminary images allowed assessment of the specimens' overall outlines at low resolution and enabled the generation of visuals in the form of false-color 3D solids. Examples are provided in **Pl. 2** (**fig. C-N**). Although fine details are not clearly visible – particularly of the spatulate outgrowths, which are poorly

differentiated from each other using this method – it is nevertheless easier to distinguish what immediately separates *O. riberai* (light orange) from *P. costagranosa* (light blue). We therefore considered it useful to present these images in **Pl. 2** (**fig. C-N**) before going into detail about their differences in the Discussion section.

The software was then used to generate virtual sections of the specimens along all three spatial axes. The images were subsequently processed to optimize the contrast of the different phases present without any loss of information. However, the holotype of *O. riberai* proved to be completely filled with very fine, cemented sediments, making it difficult to distinguish the shell from its infill. When sediments are coarse and/or loosely compacted, it is generally possible to differentiate the phases by carefully examining a large number of images, based on differences in continuity. Thus, at equivalent contrast, the sediments appear fragmented, whereas the shell exhibits a continuous structure (CELZARD & ALBERTI, 2025). In the case of the holotype of *O. riberai*, the sediments were extremely compact, complicating interpretation. Fortunately, all other specimens of each species exhibited much better contrast.

We also performed a few radiographs, of which only two examples are illustrated here (**Pl. 2, fig. O-P**). These images were obtained by superimposing tomographic slices with a certain degree of transparency. This approach allows visualization of some anatomical details within the shell volume, although at a depth that remains very limited.

SYSTEMATICS

Class: Gastropoda Cuvier, 1795
Subclass: Caenogastropoda Cox, 1960
Order: Littorinimorpha
Golikov & Starobogatov, 1975
Superfamily: Cypraeoidea Rafinesque, 1815
Family: Ovulidae Fleming, 1822
Subfamily: Pediculariinae Gray, 1853
Genus: *Olianatrivia* Dolin L., Biosca-Munts & Parcerisa, 2013
(Type species: *Olianatrivia riberai* Dolin L., Biosca-Munts & Parcerisa, 2013 by monotypy)

Synonymy: *Perispatula* Checchi, Zamberlan & Alberti, 2013 (Type species: *Perispatula costagranosa* Checchi, Zamberlan & Alberti, 2013 by monotypy)

DISCUSSION

The reader is referred to the original publications for detailed descriptions of *O. riberai* and *P. costagranosa*. This section is instead devoted to highlighting the differences between them – these species having never been systematically compared before – based on **Pls. 1-3**. While the similarities are obvious in terms of overall morphology, surface ornamentation, and size (all specimens illustrated in **Pls. 1-3** are at the same scale, except for areas framed in white), which led to the synonymy proposed in 2018, several characteristics remain clearly distinct.

The first key difference concerns the number of spiral cords on the dorsum: always 12 in *O. riberai*, but consistently 10 in *P. costagranosa*. Consequently, the beaded cords of the former are much thinner than those of the latter, with intercostal spaces approximately twice as wide as the cords themselves in *O. riberai*, but roughly as wide as the cords in *P. costagranosa*. Another consequence is that, since each dorsal cord ends in a spatulate protuberance at the edge of the shell, *O. riberai* bears 24 closely spaced spatulae around the periphery, compared with 20 in *P. costagranosa*. In the latter, the spatulae are well differentiated and

spaced apart, on average broader at their tips than at the base, and have profiles that are either square or dovetail-shaped. In contrast, in *O. riberai*, the spatulae are narrower at the tips, closer together, and on average more triangular in profile. From a ventral view, the spatulae are also considerably longer in *P. costagranosa* than in *O. riberai*. These fundamental differences, observed consistently across all examined specimens, alone justify their separation at the specific level.

The beaded patterns running along the spiral cords on the dorsum of *O. riberai* transform into varices and become more spaced out along the flanks as they approach the level of the spatulae (**Pl. 1, fig. E**). In contrast, in *P. costagranosa* the beads remain closely arranged and gradually attenuate toward the tips of the spatulae (**Pl. 3, fig. G**; see also the original drawing, Fig. 4, in CHECCHI *et al*. 2013: 31). It may also be noted that, although in both species each surface of the ventral half-sole delimited by the aperture is remarkably flattened, the base is significantly concave in transverse section in *O. riberai*, whereas it is markedly flatter in *P. costagranosa*.

Having unambiguously distinguished the two species *O. riberai* and *P. costagranosa*, it is useful to consider the features that unite them at the generic level. First, it may be noted that the two species evidently develop their characteristic peripheral spatulate outgrowths only at the adult stage. This is illustrated by the juvenile specimen of *P. costagranosa* (**Pl. 3, fig. D**), which lacks them entirely, and by the subadult specimen of *O. riberai* (**Pl. 1, fig. B**), whose periphery is flanked only by spikes extending from the dorsal cords, which are likely to be spatulae in the process of developing. One may also note the strong lateralization of the shell in the juvenile specimen of *P. costagranosa* (**Pl. 3, fig. D**), whose general appearance is strongly reminiscent of modern Pediculariinae. This observation supports the placement of these genera within this subfamily, as already suggested in the original descriptions of these species.

All illustrated specimens (**Pls. 1-3**) thus share the same type of surface ornamentation – both on the dorsum and on the ventral sole, as well as the same pattern of callosities – occurring both at the base of the shell on the one hand, and along its periphery on the other hand. For both species, the aperture is central, straight or slightly arched, and exhibits the same asymmetry in terms of dentition. The teeth on the outer lip radiate in pairs toward the peripheral spatulae, except for the two terminal ones. In contrast, the teeth on the inner lip remain simple (one per spatula), except in the most central part of the ventral sole, so that there are always between 2 and 5 fewer teeth on the inner lip than on the outer lip (see also the radiographs in **Pl. 2, fig. O-P**).

Another feature shared by both species, and which may be regarded as an additional character defining the genus, is that the bead-like bumps running along the dorsal cords extend to the tips of the peripheral spatulae. These tips, viewed from the dorsum, are concave and margined (**Pl. 1, fig. E**; **Pl. 3, fig. G**), so that the beads (*O. riberai*) or the varices (*P. costagranosa*) are particularly prominent there. Viewed from the base, the spatulae are slightly striated and lack beaded patterns, whereas these are clearly present and aligned along the teeth on the base (**Pl. 1, fig. F**; **Pl. 2, fig. D, J**; **Pl. 3, fig. E**).

To better characterize the morphological features at the generic level, we made use of tomography. Indeed, whereas the aperture of the adult specimens of *P. costagranosa*

examined here is exposed, with a clearly visible fossula (**Pl. 3, fig. E-F**), this is not the case for *O. riberai*. All specimens illustrated in **Pls. 1** and **3** were scanned, but **Pls. 4-6** present only a selection of representative images. These show sections at different depths within the shells, depending on the elements of interest to be observed, and along different axes: longitudinal sections (plane passing between the two extremities), dorso-ventral sections (plane separating the dorsum from the base), and transverse sections (plane perpendicular to the longitudinal axis).

Plate 4 thus presents longitudinal sections, which clearly highlight the concavity (in the sagittal plane) of the ventral sole of *O. riberai* compared with that of *P. costagranosa*, which is very flat. This difference in geometry is also reflected in the internal structure of the last whorl of the shell (compare **Pl. 4, fig. A-B** with **Pl. 4, fig. C-F**). The difference in the density of the teeth on the outer lip, arranged in pairs (**Pl. 4, fig. D**), and on the inner lip, predominantly simple (**Pl. 4, fig. F**), is also clearly visible (see again **Pl. 2, fig. O-P**), as is the lateralization of the shell in the juvenile specimen of *P. costagranosa* (**Pl. 4, fig. G-H**).

Plate 5 presents dorso-ventral sections that clearly reveal the differences in the morphology of the spatulae of *O. riberai* and *P. costagranosa* at the level of the base (compare **Pl. 5, fig. A, D**, and **F**) and further within the shell thickness (compare **Pl. 5, fig. B, E,** and **G**). The difference in transverse concavity of the ventral sole between the two species can also be seen (compare **Pl. 5, fig. A** and **C** with **fig. D** and **F**), as well as the dentition of the holotype of *O. riberai*, which is much clearer than with any standard photographic method (**Pl. 5, fig. B**). Here again, the lateralization of the shell of the juvenile *P. costagranosa* is evident (**Pl. 5, fig. H**).

Finally, **Plate 6** shows transverse sections at different positions along the longitudinal axis highlighting the siphonal canal (**Pl. 6, fig. A, E, I**), the fossula (**Pl. 6, fig. C, G, K**), the whorls (**Pl. 6, fig. F, J, M**), and, once again, the extreme transverse concavity of *O. riberai* (**Pl. 6, fig. B, D**), whereas it is weak to negligible in *P. costagranosa*.

The general characteristics shared by *O. riberai* and *P. costagranosa*, which therefore define the genus, are summarized in **Table 1**. The same table also compiles the features that unambiguously distinguish the two species.

In conclusion, we can reasonably assert that the synonymy proposed in 2018 is valid only at the generic level, but cannot be applied at the specific level. *Olianatrivia* (published 7 December 2013) takes precedence over *Perispatula* (published 15 December 2013). In fact, CHECCHI *et al*. (2013: 33) stated that *Olianatrivia* appeared while the article on *Perispatula* was still in press. Consequently, *P. costagranosa* is reinstated as a valid species as *Olianatrivia costagranosa* (Checchi, Zamberlan & Alberti, 2013) comb. nov.

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Diagnostic characters	Shared (generic level)	Differentiated (specific level)	
		O. riberai	***P. costagranosa***
General morphology	Small size (1.5-2.0 cm in length), low-convex profile, cabochon shape, with a radiating appearance around the periphery		
Dorsal spiral cords	Very strong, beaded along their entire length	12 thin cords	10 wide cords
Intercostal spaces		Twice as wide as the spiral cords	Equal to the width of the spiral cords
Bead-like patterns	Beads closely spaced and nearly contiguous, on dorsal cords (extending to the surface of the peripheral outgrowths) and along the teeth	Spacing out and transforming into varices on the flanks, at the level of the spatulate outgrowths	Decreasing in size without changing appearance at the level of the spatulate outgrowths
Peripheral outgrowths	In adult shells, spatula-shaped, extending from dorsal spiral cords and ventral teeth; concave and margined on top, striated underneath	24 spatulae, closely packed, narrower at the tips, on average more triangular in profile	20 spatulae, more spaced apart, with square or dovetail profile
Ventral sole	Very flattened on either side of the aperture	Strongly concave both longitudinally and transversely	Flat longitudinally, slightly concave transversely
Aperture	Central, straight or slightly curved		
Adapical ridge / terminal fold	Merged with the teeth of the inner lip		
Dentition	Very strong, prominent, extending across the entire ventral surface, asymmetrical relative to the aperture, radiating in pairs (mostly on the outer lip, less on the inner lip), and thickening toward the spatulae	13 to16 teeth on the inner lip; 18 teeth on the outer lip	11 to 12 teeth on the inner lip; 15 to 18 on the outer lip
Terminal canals	Deep and tubular*, exhalant canal curved*		
Fossula and angulation	Smooth and slightly hollowed fossula*, pronounced angulation*		
Shell growth	No spatulae at the juvenile stage; peripheral spikes at the subadult stage; juvenile shell lateralized, adult shell symmetrical		

* Not always directly visible in *O. riberai*, but confirmed by tomographic studies.

Table 1. Key diagnostic criteria shared by the genera *Olianatrivia* and *Perispatula*, and those distinguishing the species *O. riberai* and *P. costagranosa*.

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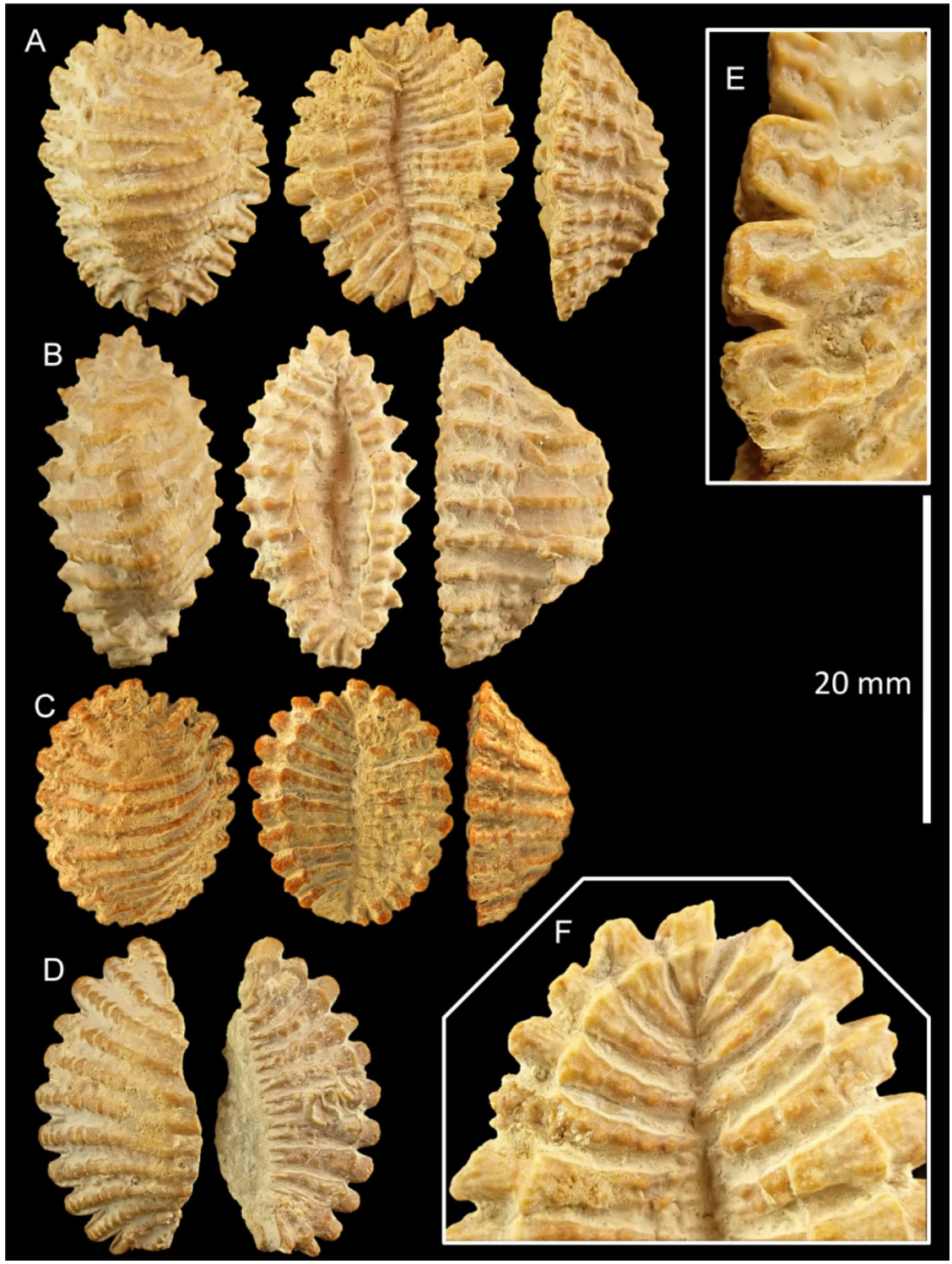

Plate 1. **A-F.** *Olianatrivia riberai* Dolin L., Biosca-Munts & Parcerisa, 2013; Odèn (Catalonia, Spain), upper Bartonian / lower Priabonian. **A.** Holotype MGVM 2585 (H 19.3, D 14.6, DD 8.1). **B.** Paratype (subadult) MGVM 2586 (H 21.1, D 11.3, DD 11.0). **C.** Paratype MNHN.F.A48090 (H 15.3, D 12.6, DD 7.0). **D.** Paratype (fragmentary) MGVM 2587 (H 19.5). **E.** Detail of the labrum of the holotype, showing the structure of the spatulate protuberances. **F.** Detail of the ventral sole of the holotype, showing the beaded patterns on the teeth, as well as the underside of the spatulae.

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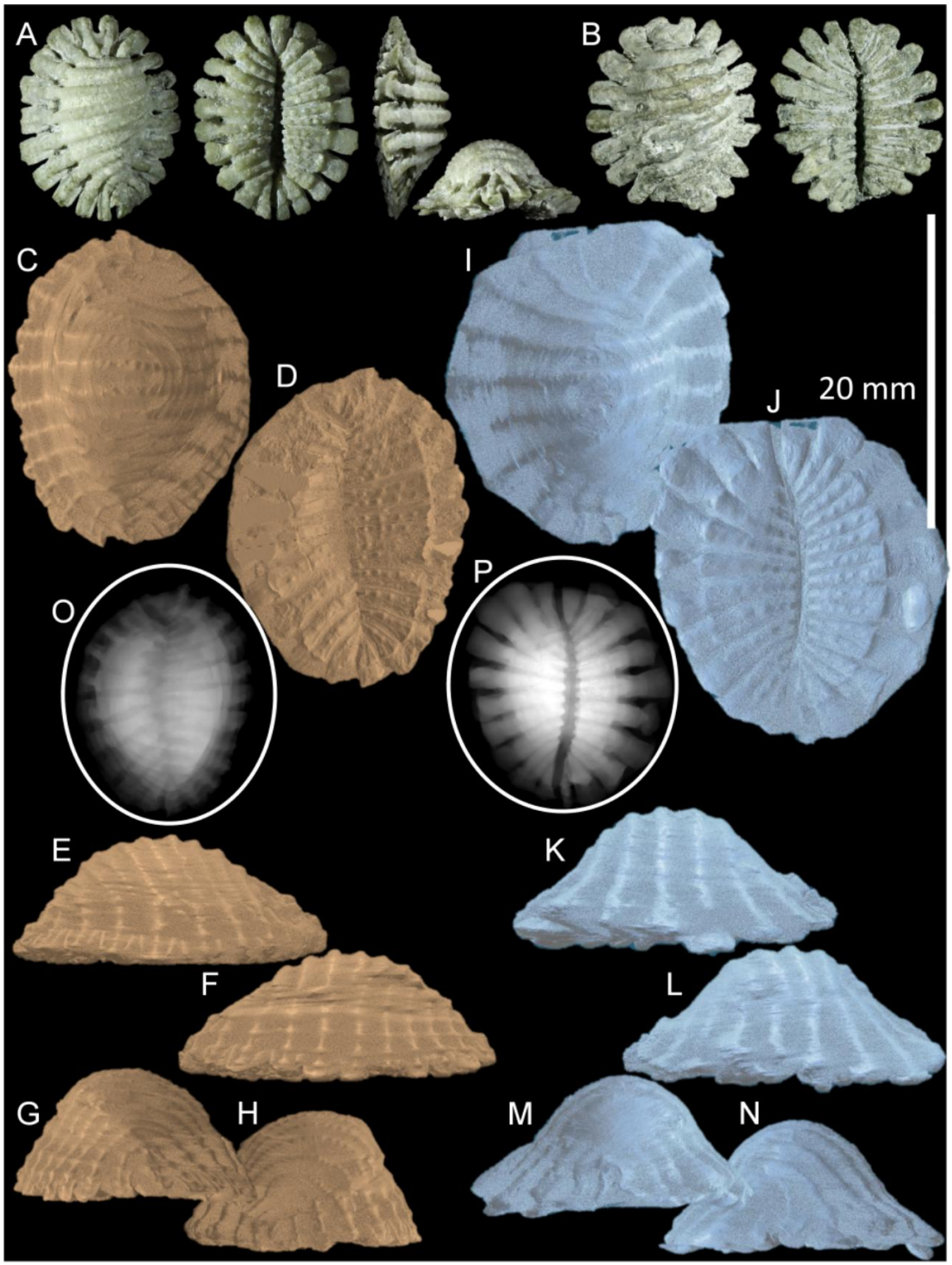

Plate 2. **A-B.** *Perispatula costagranosa* Checchi, Zamberlan & Alberti, 2013; Monte di Malo (Vicenza region, Italy), upper Ypresian / lower Lutetian. **A.** Holotype MCZ 4007-I.G.352743 (H 12.3, D 9.7, DD 4.8). **B.** Paratype MCZ 4008-I.G.352744 (H 11.7, D 10.5, DD 5.7). **C-H.** Low-resolution tomography showing the shells as false-color 3D solids from different viewpoints: dorsal (**C**), ventral (**D**), left lateral (**E**) and right lateral (**F**), anterior (**G**) and posterior (**H**) ends of the holotype MGVM 2585 of *Olianatrivia riberai*. **I-N.** Same as **C-H**, respectively, but for specimen A of Plate 3 of *P. costagranosa*. **O-P.** Radiographs of the holotype MGVM 2585 of *Olianatrivia riberai* (**O**) and of specimen A of Plate 3 of *P. costagranosa* (**P**).

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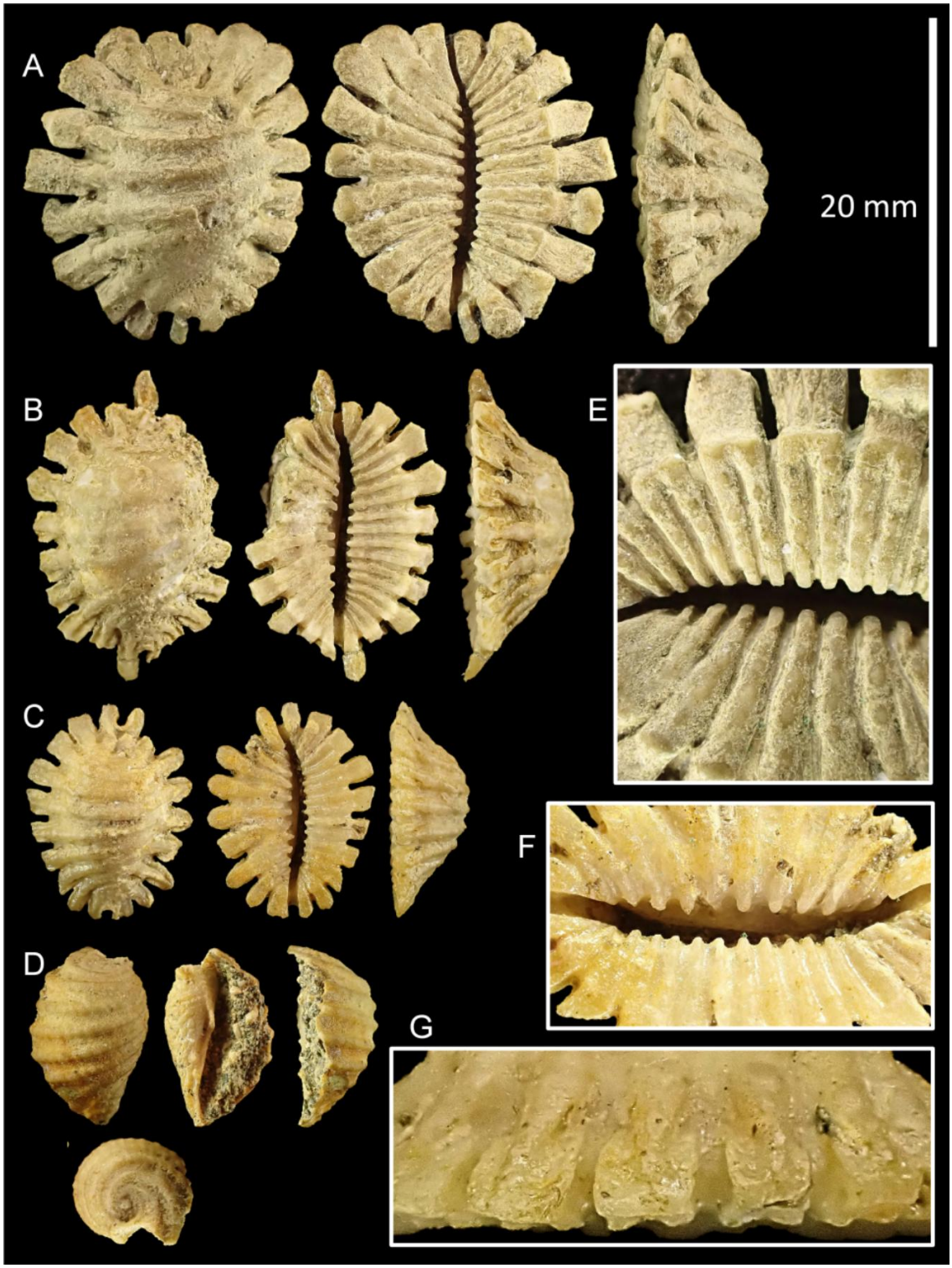

Plate 3. **A-G.** Specimens (PC) of *Perispatula costagranosa*; Monte di Malo (Vicenza region, Italy), upper Ypresian / lower Lutetian. **A.** H 19.5, D 17.7, DD 8.3. **B.** H 19.3, D 12.5, DD 6.7. **C.** H 13.0, D 10.3, DD 4.9. **D.** Juvenile specimen: H 10.8, D 6.9, DD 4.8. **E.** Detail of the ventral sole of specimen A, showing the aperture and the beaded patterns on the teeth. **F.** Detail of the aperture and the fossula of specimen C. **G.** Detail of the labrum of specimen C, showing the structure of the spatulate protuberances.

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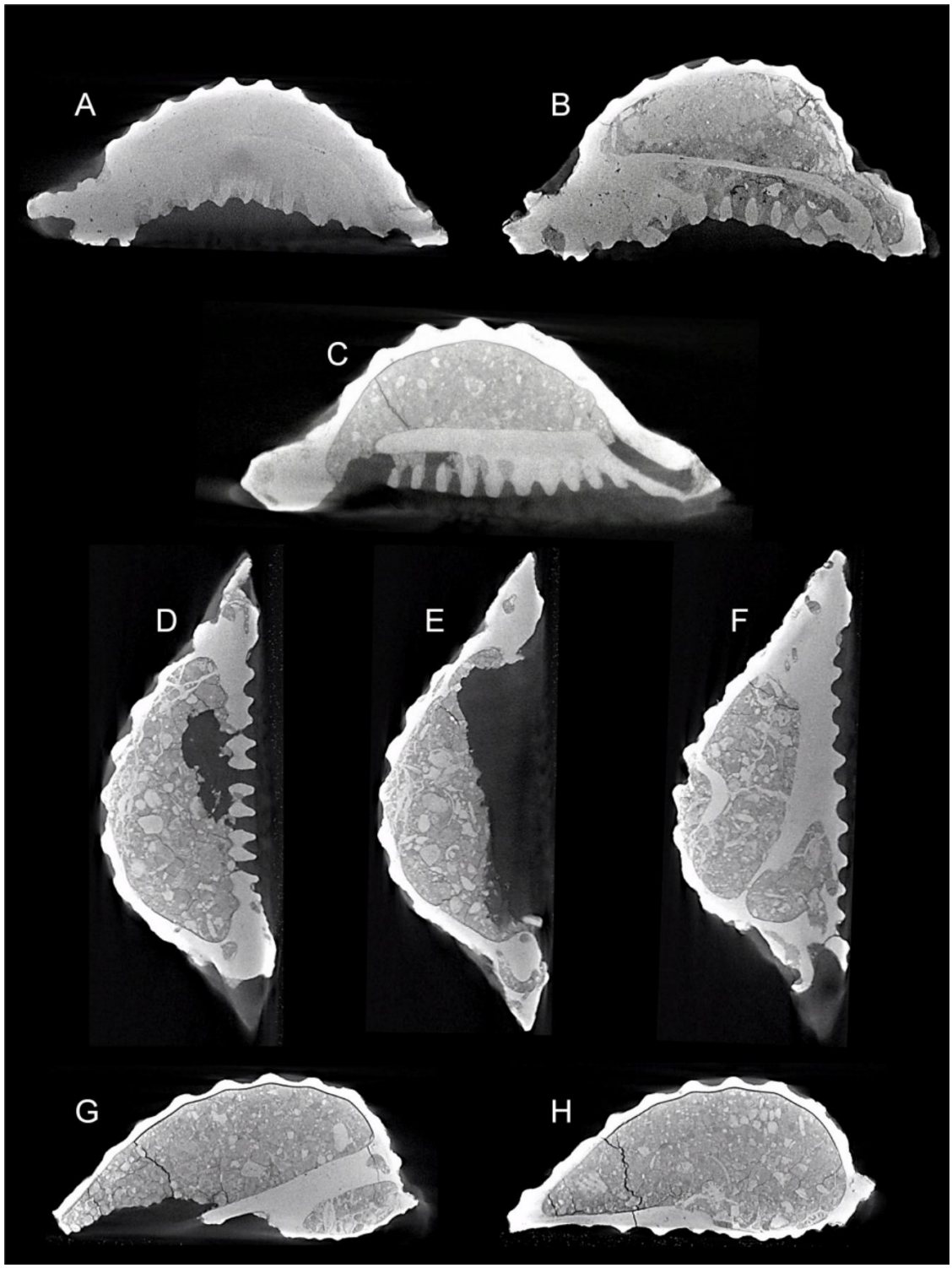

Plate 4. **A-H.** Longitudinal sections (not to scale) obtained by X-ray tomography at different depths within the shells of: **A.** Holotype MGVM 2585 of *O. riberai*; **B.** Paratype (subadult) MGVM 2586 of *O. riberai*; both showing the pronounced concavity of the ventral sole along the shell axis; **C.** Specimen A of Plate 3 of *P. costagranosa*; **D-F.** Specimen C of Plate 3 of *P. costagranosa*, at the level of the labral teeth (in pairs) (**D**), the central aperture (**E**), and the columellar teeth (mostly simple) (**F**); **G-H.** Juvenile specimen D of Plate 3 of *P. costagranosa* at two different depths, showing the lateralization of the shell.

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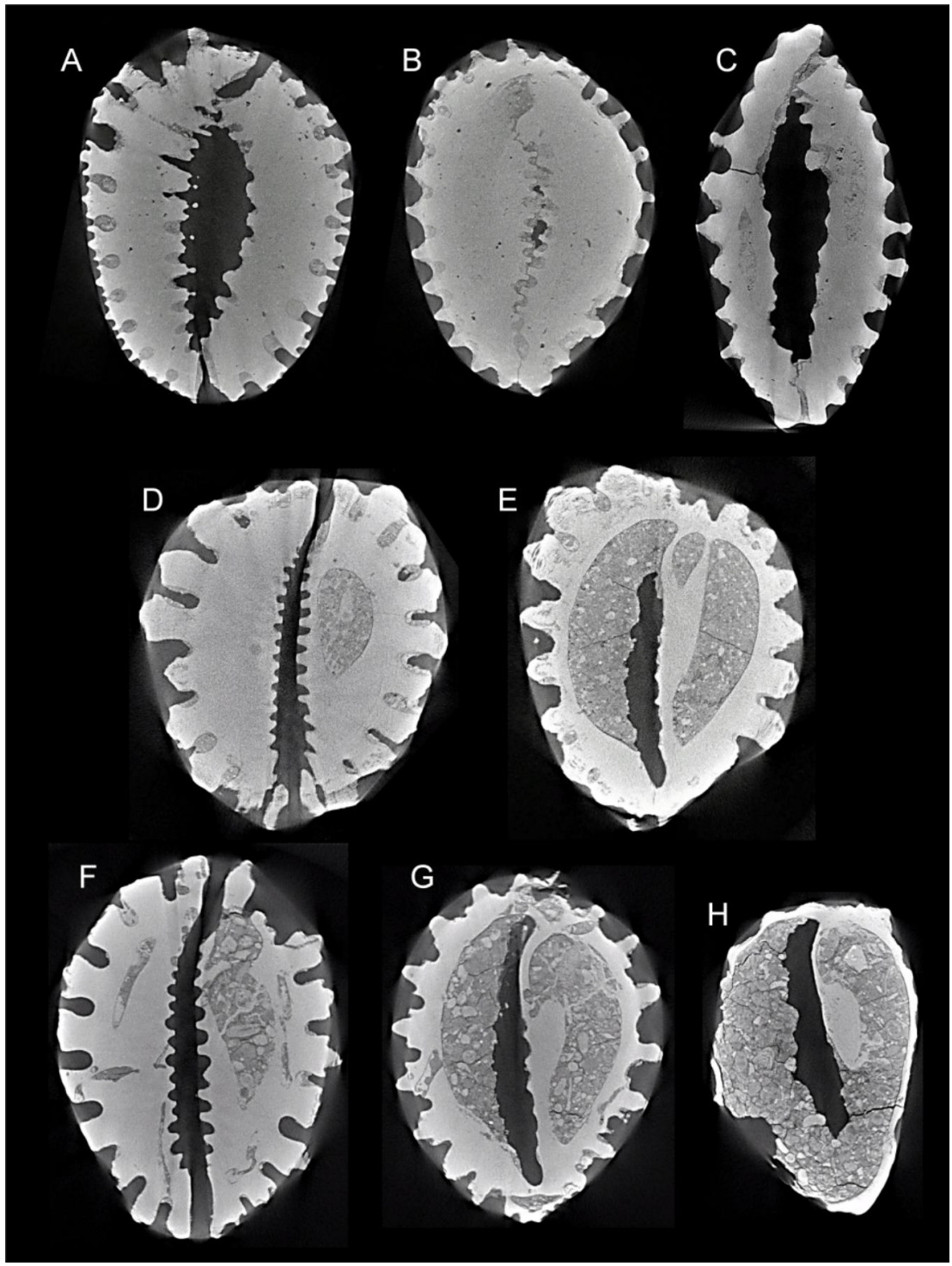

Plate 5. **A-H.** Dorso-ventral sections (not to scale) obtained by X-ray tomography at different depths within the shells of: **A-B.** Holotype MGVM 2585 of *O. riberai*, showing the difference between labral and columellar teeth as well as the characteristic profile of the spatulae at the level of the ventral sole (**A**), and revealing the aperture slightly above the base (**B**); **C.** Paratype (subadult) MGVM 2586 of *O. riberai* at the level of the base, showing peripheral projections that are pointed but not yet spatulate; the transverse concavity of the base is also clearly visible (**A** and **C**); **D-E.** Specimen A of Plate 3 of *P. costagranosa* at the level of the base (**D**) and slightly above it (**E**); **F-G.** Same as **D-E**, but for specimen C of Plate 3; **H**. Juvenile specimen D of Plate 3.

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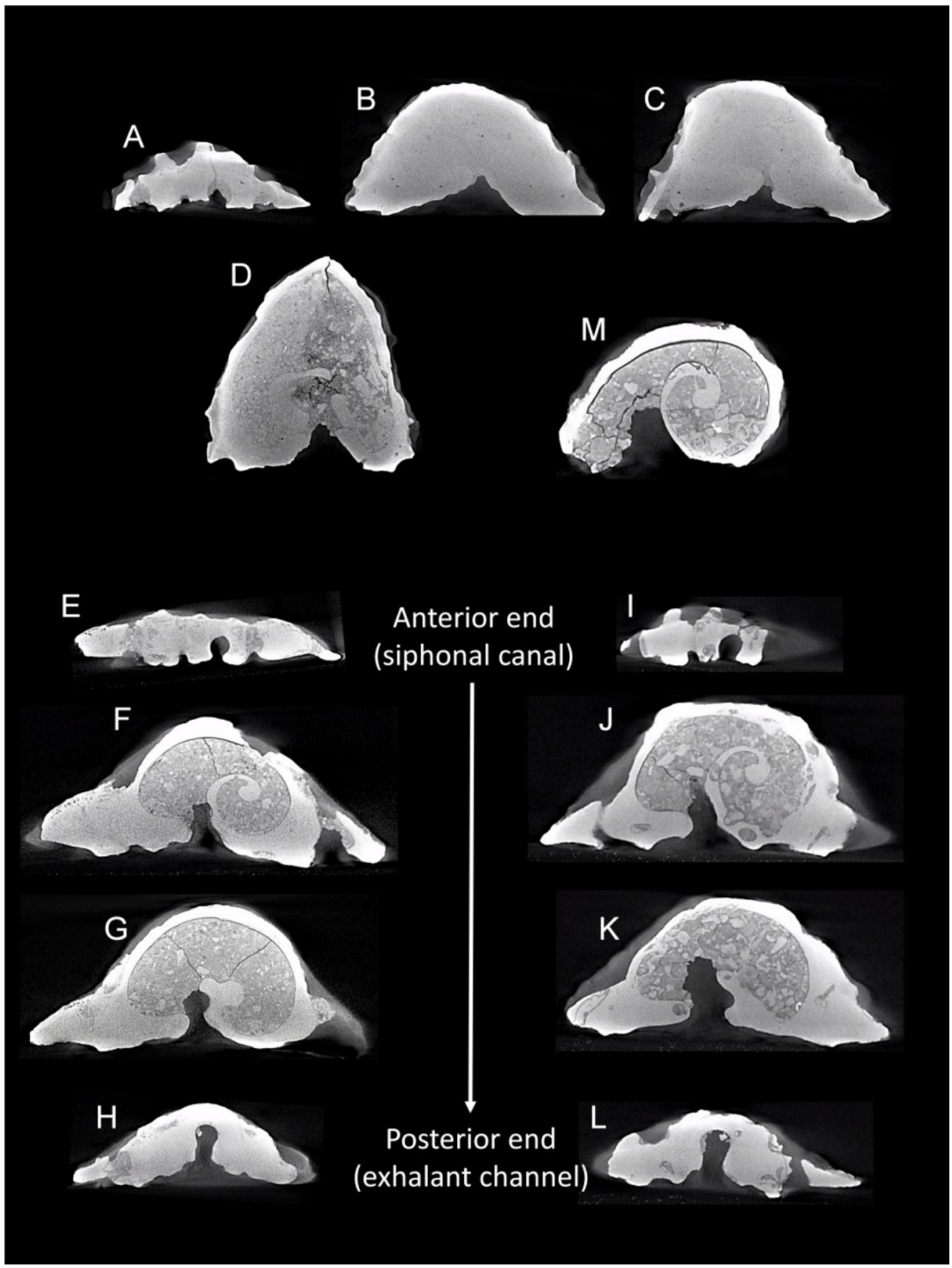

Plate 6. **A-M.** Transverse sections (not to scale) obtained by X-ray tomography at different depths within the shells of: **A-C.** Holotype MGVM 2585 of *O. riberai*: at the anterior tip with the siphonal canal at the center (**A**), at the anterior third showing the transition from dorsal beads to widely spaced varices on the flanks (**B**), and at the posterior third showing the fossula (**C**); **D.** Paratype (subadult) MGVM 2586 of *O. riberai* at the center of the shell. **E**-**H**. Sequence of sections of specimen A of Plate 3 of *P. costagranosa*, from the anterior tip showing the siphonal canal at the center (**E**) to the posterior tip showing the exhalant canal at the center (**H**), passing through the first anterior third showing the whorls (**F**) and the second third showing the fossula (**G**). **I**-**L**. Same as **E**-**H**, respectively, but for specimen C of Plate 3. **M**. Juvenile specimen D of Plate 3.