

Ornate Bairdiidae (Ostracoda) in 3 dimensions:
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of *Triebelina* van den Bold, 1946, *Nodobairdia*
Kollmann, 1963 and *Mirabairdia* Kollmann, 1963

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Ornate Bairdiidae (Ostracoda) in 3 dimensions: exploring carapace morphology and pore canals of *Triebelina* van den Bold, 1946, *Nodobairdia* Kollmann, 1963 and *Mirabairdia* Kollmann, 1963

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ABSTRACT

Marine ostracods of the family Bairdiidae Sars, 1888 have an evolutionary history starting from the Ordovician with an explosive diversification of ornate forms during the Triassic. Representatives of the family are notoriously homeomorphic, which makes their taxonomy a major challenge of modern ostracodology. Their classification has thus been problematic since the 1970s. Here we present the first CT-scan investigation of recent and fossil ornate Bairdiidae valves in order to characterize and evaluate the taxonomic significance of unexploited characters, such as pores and pore canals. Thanks to 3D tomography, we explore the distribution of pores at the surface and the pathway of pore canals within the valve wall of the recent genus *Triebelina* van den Bold, 1946 and the Triassic genera *Nodobairdia* Kollmann, 1963 and *Mirabairdia* Kollmann, 1963. In *Triebelina indopacifica* van den Bold, 1946, we describe an unexpected system of double pore canals, so far unknown in ostracods. We confirm that pore systems in *Triebelina* have largely intramural positions. In the Triassic Bairdiidae (*Nodobairdia mammilata* Kollmann, 1963 and *Mirabairdia pernodosa* Kollmann, 1963), we recognize simple unrimmed and massively nodular pores as well as marginal pores. Lateral normal pores of the Triassic specimens appear to be mostly in intra-solum positions. Although still exploratory and at the limits of the tomographic resolution, these observations provide new evidence to reject the formerly proposed synonymy of Triassic genera with *Triebelina*, which obstructed the establishment of a phylogenetic classification.

KEY WORDS

Ostracods,
ornate Bairdiidae,
morphology,
normal pore canals,
CT-scan,
3D analysis.

RÉSUMÉ

Bairdiidae ornés (Ostracoda) en 3 dimensions : exploration de la morphologie de la carapace et des canaux de pores de *Triebelina van den Bold*, 1946, *Nodobairdia Kollmann*, 1963 et *Mirabairdia Kollmann*, 1963. Les ostracodes marins de la famille des Bairdiidae Sars, 1888 ont une histoire évolutive remontant à l'Ordovicien avec une diversification explosive des formes ornées au cours du Trias. Ils sont notoirement homéomorphes, leur taxinomie fait partie des enjeux majeurs de l'ostracodologie moderne, et leur classification pose problème depuis les années 1970. Ici, nous effectuons la première étude par tomographie de valves de Bairdiidae ornés récents et fossiles pour caractériser et évaluer l'importance taxinomique de caractères inexploités, tels que les pores et les canaux de pores. Grâce à la tomographie 3D, nous explorons la distribution des pores en surface et le trajet des canaux sous-jacents dans la paroi des valves de *Triebelina van den Bold*, 1946 récents ainsi que *Nodobairdia Kollmann*, 1963 et *Mirabairdia Kollmann*, 1963 du Trias. Chez *Triebelina indopacifica van den Bold*, 1946, nous décrivons des systèmes de canaux doubles jusqu'alors inconnus chez les ostracodes. Nous confirmons que les systèmes de pores de *Triebelina* sont largement en position intra-murale. Chez les Bairdiidae du Trias (*Nodobairdia mammilata Kollmann*, 1963 et *Mirabairdia pernodosa Kollmann*, 1963), nous reconnaissons des pores simples sans bordure et massivement nodulaires ainsi que des pores marginaux. Les pores normaux latéraux des spécimens du Trias semblent être principalement en position intra-solum. Bien qu'encore exploratoires et aux limites de la résolution tomographique, ces observations fournissent de nouvelles preuves pour rejeter la synonymie autrefois proposée des genres du Trias avec *Triebelina*, qui a fait obstacle à l'établissement d'une classification phylogénétique.

MOTS CLÉS
Ostracodes,
Bairdiidae ornés,
morphologie,
canaux de pores
normaux,
CT-scan,
analyse 3D.

INTRODUCTION

Representatives of the ostracod family Bairdiidae Sars, 1888 have been components of marine ecosystems since the Ordovician. In spite of their omnipresence since more than 450 Ma, the taxonomy of recent and fossil Bairdiidae remains problematic, mostly by pervasive homeomorphies that have largely complicated the concepts of genera and species. The emblematic genus *Bairdia* M'Coy, 1844 was described from the Carboniferous of England, and for more than a century it was reported through the entire Phanerozoic up the Recent (Forel *et al.* 2021a). Through the long evolutionary history of Bairdiidae, the Triassic (c. –252 Ma to –201 Ma; Cohen *et al.* 2013 [updated 2023]) was a major turning point with the diversification of ornate forms, most of which did not cross the Triassic-Jurassic boundary (e.g. Kollmann 1960, 1963; Kristan-Tollmann 1970, 1971; Bolz 1971a, b; Kozur 1971a, b; Forel & Crasquin 2022; Forel *et al.* 2022a, b). Ornate bairdiids are less diverse today, and the phylogenetic link between Triassic and extant taxa remains unresolved.

The taxonomic validity of the genera *Glyptobairdia* Stephenson, 1946 and *Bairdoppilata* Coryell, Sample & Fields, 1935 was debated for about 25 years (Stephenson 1947; Triebel 1948; Key 1954; van Morkhoven 1958, 1962; Rome 1960; Kollmann 1960, 1963; Bolz 1969, 1971a, b; Kristan-Tollmann 1969, 1970, 1971; Maddocks 1969; van den Bold 1974). Discussions focused on the importance of the ornamentation and supplemental dentition, the functions of these structures, and whether they might represent a homoeomorphic feature. Because of its close association with

soft anatomical traits of living animals, it is now recognized that bairdoppilatan dentition may be a shared-derived trait, which is potentially indicative of a phyletic lineage. Successful important breakthroughs have partially disentangled the modern “*Bairdia* dynasty” (Malz 1988) with the establishment and/or revision of the genera *Aponesidea* Maddocks *in* Maddocks & Iliffe, 1986, *Bairdoppilata* Coryell, Sample & Fields, 1935, *Glyptobairdia* Stephenson, 1946, *Havanardia* Pokorný, 1968, *Mydionobairdia* Titterton & Whatley, 1988, *Neonesidea* Maddocks, 1969, *Papillatabairdia* Bentley, 1982, *Paranesidea* Maddocks, 1969, *Pterobairdia* McKenzie & Keij, 1977, and *Triebelina van den Bold*, 1946, based on characters of soft parts, appendages, male copulatory organs, masticatory apparatus, and carapaces. However, other representatives remain to be investigated.

On the other hand, the higher taxonomy of fossil Bairdiidae has not significantly changed since the 1960s when Sohn (1960) and Kollmann (1960, 1963), respectively, proposed classification schemes of Palaeozoic and Triassic taxa, obtaining low consensus. Kollmann (1960) considered *Glyptobairdia* as the recent representative of a lineage, *Carinobairdia*, already present in the Triassic. Within the still pending questions, it is worth mentioning the Subfamily Bairdoppilatinae, established by Kristan-Tollmann (1969), to which she assigned numerous Triassic genera that display supplemental dentition (Table 1). The main objection came from Bolz (1971a, b) who considered that coarse sculpture developed convergently in different Triassic taxa, and that all systematic schemes based on sculpture elements are merely artificial. He proposed that most of the Triassic genera listed

TABLE 1. — Summary of Triassic ornate Bairdiidae Sars, 1888 and their diagnostic characters.

Genus	Type species	Age and type area	Alternative scheme 1	Alternative scheme 2
<i>Abrobairdia</i> Chen in Chen & Shi, 1982	<i>A. bitubera</i> Chen in Chen & Shi, 1982	Changhsingian, China	na	na
<i>Alatobairdia</i> Kristan-Tollmann, 1971	<i>A. foveolata</i> Kristan-Tollmann, 1971	Rhaetian, Austria	na	<i>Alatobairdia</i> Kozur (1991)
<i>Carinobairdia</i> Kollmann, 1963	<i>C. triassica</i> Kollmann, 1963	Rhaetian, Austria	pars <i>Lobobairdia</i> pars <i>Triebelina</i> (<i>Nodobairdia</i>) Bolz (1971a, b), Kozur (1973)	pars <i>Bolzibairdia</i> Kozur (1991)
<i>Ceratobairdia</i> Sohn, 1954	<i>C. dorsospinosa</i> Sohn, 1954	Roadian, Texas	<i>Havanardia</i> Bolz (1971a)	pars <i>Petasobairdia</i> Kozur (1991)
<i>Cornutobairdia</i> Kristan-Tollmann, 1970	<i>C. reticulata</i> Kristan-Tollmann, 1970	Rhaetian, Austria	<i>Triebelina</i> (<i>Triebelina</i>) Bolz (1971a, b)	<i>Triebelina</i> Kozur (1971a)
<i>Dicerobairdia</i> Kollmann, 1963	<i>D. bicornuta</i> Kollmann, 1963	Rhaetian, Austria	<i>Triebelina</i> (<i>Triebelina</i>) Bolz (1971a, b)	<i>Triebelina</i> Kozur (1971a) pars <i>Paraglyptobairdia</i> Kozur (1991)
<i>Edithobairdia</i> Forel in Forel <i>et al.</i> , 2019	<i>E. polyacantha</i> (Kristan-Tollmann, 1978)	Carnian, Italy	na	na
<i>Eisobairdia</i> Kristan-Tollmann, 1978	<i>E. infracostata</i> Kristan-Tollmann, 1978	Carnian, Italy	na	na
<i>Lobobairdia</i> Kollmann, 1963	<i>L. salinaria</i> Kollmann, 1963	Rhaetian, Austria	<i>Lobobairdia</i> Bolz (1969, 1971a, b)	pars <i>Praelobobairdia</i> Kozur (1991)
<i>Margarobairdia</i> Kristan-Tollmann, 1978	<i>M. margaritifera</i> Kristan-Tollmann, 1978	Carnian, Italy	na	na
<i>Medwenitschia</i> Kollmann, 1963	<i>M. ornata</i> Kollmann, 1963	Rhaetian, Austria	<i>Triebelina</i> (<i>Triebelina</i>) Bolz (1971a, b)	<i>Triebelina</i> Kozur (1971a, 1991)
<i>Mirabairdia</i> Kollmann, 1963	<i>M. pernodosa</i> Kollmann, 1963	Ladinian, Italy	<i>Triebelina</i> (<i>Nodobairdia</i>) Bolz (1971a, b)	<i>Triebelina</i> (<i>Mirabairdia</i>) Kozur (1971a)
<i>Neobairdiolites</i> Kollmann, 1963	<i>N. placklesensis</i> Kollmann, 1963	Rhaetian, Austria	<i>Bairdiolites</i> Kristan-Tollmann (1970)	na
<i>Nodobairdia</i> Kollmann, 1963	<i>N. mammilata</i> Kollmann, 1963	Ladinian, Italy	<i>Triebelina</i> (<i>Nodobairdia</i>) Bolz (1971a, b)	<i>Triebelina</i> Kozur (1971a) pars <i>Bolzibairdia</i> Kozur (1991)
<i>Parurobairdia</i> Kristan-Tollmann, 1969	<i>P. bicostata</i> Kristan-Tollmann, 1969	Carnian, Austria	<i>Bairdia</i> Bolz (1971a, b)	<i>Triebelina</i> Kozur (1971a)
<i>Petasobairdia</i> Chen in Chen & Shi, 1982	<i>P. bicornuta</i> Chen in Chen & Shi, 1982	Changhsingian, China	na	pars <i>Praelobobairdia</i> Kozur (1991)
<i>Ptychobairdia</i> Kollmann, 1960	<i>P. kuepperi</i> Kollmann, 1960	Rhaetian, Austria	<i>Triebelina</i> (<i>Ptychobairdia</i>) Bolz (1971a, b)	<i>Triebelina</i> Kozur (1971a)
<i>Urobairdia</i> Kollmann, 1963	<i>U. austriaca</i> Kollmann, 1963	Norian, Austria	<i>Bairdia</i> Bolz (1971a, b)	<i>Bairdia</i> Kozur (1971a)

in Table 1 should be subsumed within the genus *Triebelina*. The school of Kozur (1973, 1991) created several tribes and 11 new bairdiid genera that were either synonymized with previously known genera or never used by later workers. Since these discussions, no improvement has been done on such an important issue, and the two conceptions of ornate Bairdiidae classification are alternatively used in the literature (e.g. Urlichs 1972; Sohn 1987; Mette & Mohtat-Aghai 1999; Hillebrandt *et al.* 2013; Monostori & Tóth 2014; Forel & Grădinaru 2020).

In the following, we have chosen to adopt the generic scheme initiated by Kollmann (1960, 1963) in order to keep things as simple as possible and to avoid artificial over-splitting. In recognition of the high level of homeomorphy in Bairdiidae, Triassic occurrences of “*Triebelina*” are cited by their original generic identifications, corresponding to the traditional scheme initiated by Kollmann (1960, 1963). Van den Bold (1974)

stated that the modern representatives may have arisen several times from less ornate stock. If so, then Bolz’s (1971a, b) long-ranging concept of *Triebelina* may be paraphyletic.

Triassic bairdiids are morphologically diverse, and more characters should be investigated for potential taxonomic significance, including opaque patches and normal and marginal pores. Wang *et al.* (2020) and Forel *et al.* (2021b) have shown the high potential of 3D investigations to clarify the taxonomic attribution and taphonomy of fossil carapaces lacking soft parts. Such methods have so far neither been used for recent taxa nor for comparative morphology of recent and fossil taxa.

Here we carry out the first exploration of normal pores and associated canals in Recent and Triassic ornate Bairdiidae by means of X-ray computed tomography, describe their characteristics and distribution, and discuss their significance for comparative morphology and systematics.

TABLE 2. — Summary of pore types observed on Bairdiidae Sars, 1888 from the literature.

Taxa	Type A'	Tunnel-shaped	On node or papilla	Type A''
<i>Aponesidea</i> Maddocks <i>in</i> Maddocks & Iliffe, 1986	×	×	—	—
<i>Bairdia</i> M'Coy, 1844 (fossil)	×	×	—	—
<i>Bairdoppilata</i> Coryell, Sample & Fields, 1935	×	×	—	—
<i>Glyptobairdia</i> Stephenson, 1946	×	×	—	—
<i>Havanardia</i> Pokorný, 1968	×	×	—	—
<i>Margarobairdia margaritifera</i> Kristan-Tollmann, 1978	×	×	—	—
<i>Mydionobairdia</i> Titterton & Whatley, 1988	×	×	—	—
<i>Neonesidea</i> Maddocks, 1969	×	×	—	—
<i>Nodobairdia mammillata</i> Kollmann, 1963	×	×	×	—
<i>Papillatabairdia</i> Bentley, 1982	×	×	×	—
<i>Paranesidea</i> Maddocks, 1969	×	×	—	—
<i>Pterobairdia</i> McKenzie & Keij, 1977	×	×	—	—
<i>Triebelina</i> van den Bold, 1946	×	×	—	—
Family Bythocyprididae Maddocks, 1969	×	×	—	×
Family Pussellidae Danielopol <i>in</i> Maddocks, 1976	×	×	—	×

PORES IN BAIRDIIDAE

The valves of ostracods are crossed by normal pore canals (NPC) through which setae (also called sensory hairs, sensory bristles, sensillae) are connected to nerve cells of the underlying epidermal layer and act as touch receptors, photoreceptors, chemoreceptors or mechanoreceptors. Normal pore systems are taxonomically useful and important for determining phyletic relationships among ostracods (e.g. Müller 1894; van Morkhoven 1962; Hartmann 1967; Sandberg & Plusquellec 1969; Hanai 1970; Sylvester-Bradley & Benson 1971; Rosenfeld & Vesper 1977; Pokorný 1978; Keyser 1980, 1982, 1983; Okada 1982, 1983; Tsukagoshi & Ikeya 1987; Kamiya 1989; Maddocks 1990, 1992; Tsukagoshi 1990; Ishizaki 2001; Holmes & Chivas 2002; Park & Ricketts 2003; Ishii *et al.* 2005; Olempska 2008; Danielopol *et al.* 2018; Lord *et al.* 2020). Several types of NPC have been described, but only type A is found in Bairdiidae (single pore with seta, which is further divided into type A', without a rim or with a narrow rim, or A'', surrounded by a broad funnel-shaped rim, summarized in Table 2; Puri & Dickau 1969; Puri 1974).

NPC and associated setae are retained through the ontogeny of Bairdiidae, and more are added at each molt; in *Neonesidea oligodentata* Kajiyama, 1913, they increase from 10 in A-7 to 2,145 in the adult (Smith & Kamiya 2002), making them almost impossible to map. Newly added NPC are distributed between those inherited from the previous instar in the central area of the valves and they are densely crowded along the free margin. The ontogenetically older pores are less numerous, larger, and may have more distinct walls, while those arising later in ontogeny are smaller and have narrower or no walls (Maddocks 2015). All pores so far illustrated for living Bairdiidae are of A' type, tunnel-shaped, either rimless or with a narrow rim-wall (Fig. 1). In reticulate taxa the pores are intra-mural, emerging on the muri between reticules. The A'' type or funnel pore, with a broad surrounding disk or funnel-shaped plaque (Sylvester-Bradley & Benson 1971), so far has only been observed in the families Bythocyprididae Maddocks, 1969 and Pussellidae Danielopol *in* Maddocks, 1976.

For Triassic ornate Bairdiidae, Kristan-Tollmann (1978) stated that the median field of *Nodobairdia mammillata* Kollmann, 1963 from the Carnian of Italy appears to be coarsely reticulate. Figure 1M shows pores of type A' in the dorsal areas between the large nodes. Additional pores may be obscured beneath the smaller nodular or granular elevations. Kristan-Tollmann (1978) also illustrated simple, unrimmed pores (type A') in *Margarobairdia margaritifera* Kristan-Tollmann, 1978 (Fig. 1N).

MATERIAL AND METHODS

Traditionally, pores of ostracods are studied by reporting their position on line drawings of the general outline of the valves, thus illustrating in 2 dimensions the 3-dimensional distribution of pore systems (e.g. Smith & Kamiya 2002; Ozawa *et al.* 2014). In the material studied for the present contribution, some pores are visible on SEM photos (Figs 3-5), but the complex surface of ornate bairdiids makes it hard to map their distribution. Such work is further complicated for fossil taxa where the reticulate surface is often filled with sediments. X-ray computed tomography has the potential to overcome these difficulties and open new perspectives by its ability to trace pore canals within the valve wall.

STUDIED MATERIAL

All information regarding the bairdiid specimens studied here is summarized in Appendix 1.

Three *Triebelina* specimens have been picked from recent sediments collected in French Polynesia, South Pacific, by the first author by snorkelling in the two main bays of the Moorea Island, Society Archipelago (Fig. 2A, B). Two adult left valves of *Triebelina indopacifica* van den Bold, 1946 (Figs 3; 4) and one juvenile right valve referred to *Triebelina* sp. (Fig. 5) have been studied. The largest valve of *Triebelina indopacifica* is quite corroded (Fig. 3), with meandering tracks at the surface and cavities of clotted morphology inside the wall of the valve; these cavities never cross it entirely, which clearly differentiates them from pore canals. A carapace of

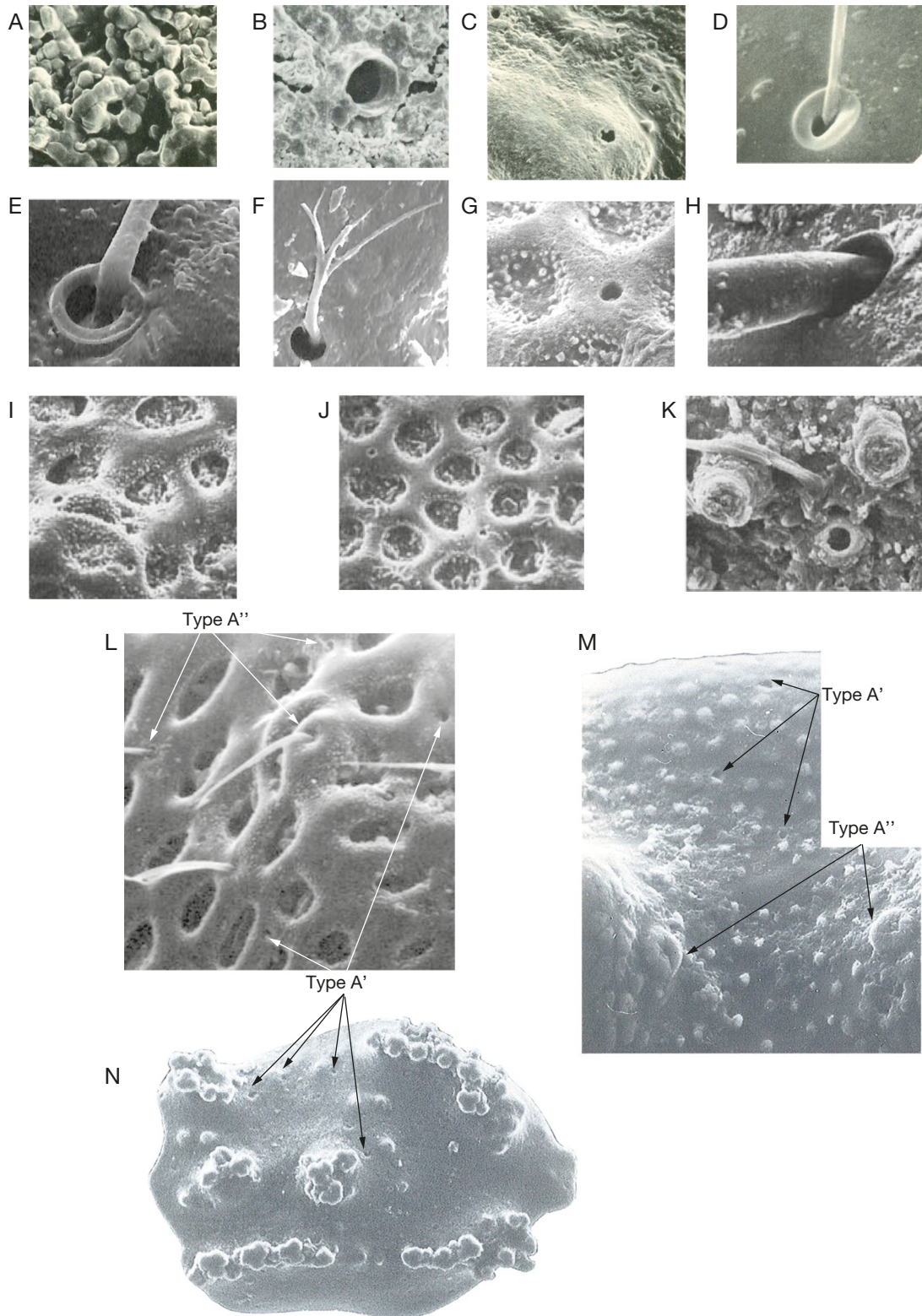


FIG. 1. — Summary of pores in Bairdiidae published in the literature: **A**, A' pore in the Pennsylvanian species *Bairdia* sp. from Oklahoma (Puri & Dickau 1969: pl. 6, fig. 4); **B**, A' pore in *Neonesidea obscura* (Müller, 1894) (Puri & Dickau 1969: pl. 3, fig. 3); **C**, A' pore in *Glyptobairdia coronata* (Brady, 1870) (Puri & Dickau 1969: pl. 6, fig. 3b); **D**, A' pore in *Bythocypris bosquetiana* (Brady, 1866) (Puri & Dickau 1969: pl. 2, fig. 2); **E**, A'' pore in *Triebelina? pustulata* Keij, 1974 (Maddocks & Wouters 1990: fig. 19); **F**, A' pore in *Triebelina? pustulata* Keij, 1974 (Maddocks & Wouters 1990: fig. 18); **G**, A' pore in *Havanardia havanensis* Pokorný, 1968 (Malz & Lord 1988: pl. 3, fig. 6c); **H**, A' pore in *Paranesidea? confusa* Titterton & Whatley, 1988 (Titterton & Whatley 1988: pl. 5, fig. 7); **I**, **J**, A' pores in *Triebelina sertata* Triebel, 1948 (**I**, Titterton & Whatley 1988: pl. 9, fig. 14; **J**, Titterton & Whatley 1988: pl. 9, fig. 6); **K**, A'? pore in *Mydionobairdia schyroconcha* (Maddocks, 1969) (Titterton & Whatley 1988: pl. 9, fig. 17); **L**, A' and A'' pores in *Mydionobairdia schyroconcha* (Maddocks, 1969) (Krutak 1982: pl. 7, fig. 2); **M**, A''? pores in *Nodobairdia mammillata* Kollmann, 1963 from the Carnian, Late Triassic, of Italy (Kristan-Tollmann 1978: pl. 8, fig. 4); **N**, A' pores in *Margarobairdia margaritifera* Kristan-Tollmann, 1978 from the Carnian, Late Triassic, of Italy (Kristan-Tollmann 1978: pl. 5, fig. 4). No scale bar.

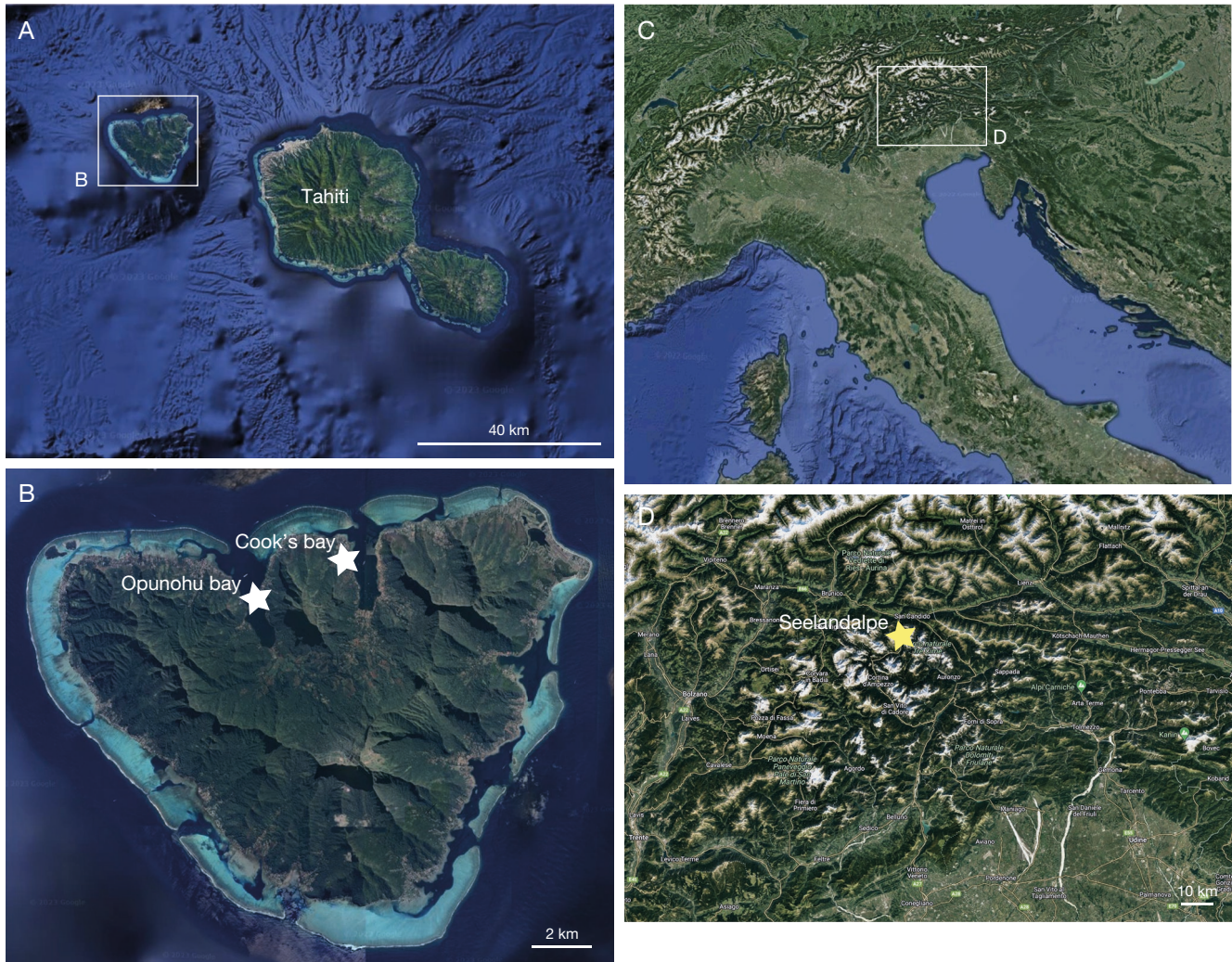


FIG. 2. — Geographic positions of ostracod sampling areas (see Appendix 1): **A**, general satellite view of the Society Archipelago, French Polynesia; **B**, insight into Moorea Island, Society Archipelago; **C**, general satellite view of the Alps; **D**, insight into Seelandalpe in South Tyrol (Cassian Formation, Cassian, Late Triassic). Stars indicate sampling positions.

Triebelina sp. was accidentally disarticulated during scanning preparation, and only the right valve has been studied. The three recent specimens are stored in the MNHN micropaleontology collections under collection numbers MNHN.F.F67777-MNHN.F.F67779.

Three fossil specimens were picked from sample MHI 2053 (Muschelkalkmuseum Hagdorn Stadt Ingelfingen, Ingelfingen) from the Carnian, Late Triassic of Seelandalpe, Tyrol (e.g. Fürsich & Wendt 1977; Fig. 2C, D) for analysis. One left valve and a complete carapace of *Nodobairdia mammilata* have been observed (Figs 6-8; 10; 11). One left valve of *Mirabairdia pernodosa* Kollmann, 1963 was broken during preparation for tomography so hampering the complete description of its morphology. Nevertheless, the largest fragment, corresponding to its ventral half, is shown anyway to make comparisons and insights into this rare species (Fig. 10).

The surface of the carapace of *Nodobairdia mammilata* did not need any cleaning, but it was filled with sediment that has been virtually removed. Conversely, the inner and

outer surfaces of the isolated valve were slightly encrusted with sediments and have been virtually cleaned. In terms of preservation, two major features are observed in the isolated left valve of *Nodobairdia mammilata* Kollmann, 1963 (Fig. 6):

- thin parallel cracks, oriented anteroventrally and running through the thickness of the valve, may be cleavage planes related to recrystallization. The cracks are clearly distinguished from pores by their length and orientation (Fig. 6H, I);
- the entire surface is covered by a thin layer of slightly darker grey colour on the scans, more porous than the underlying texture, which may be related to weathering. It is also visible on the inner surface, although to a lesser extent (Fig. 6I). All ornamental features described below, as well as pore canals, are located in the underlying denser material. When cleaning the surface, this layer has not been removed, as it is sometimes interfingered with the underlying material;

- this thin layer is not observed in the carapace, which appears to be in an overall better condition with the exception of the broken postero-dorsal node and cracks at the second

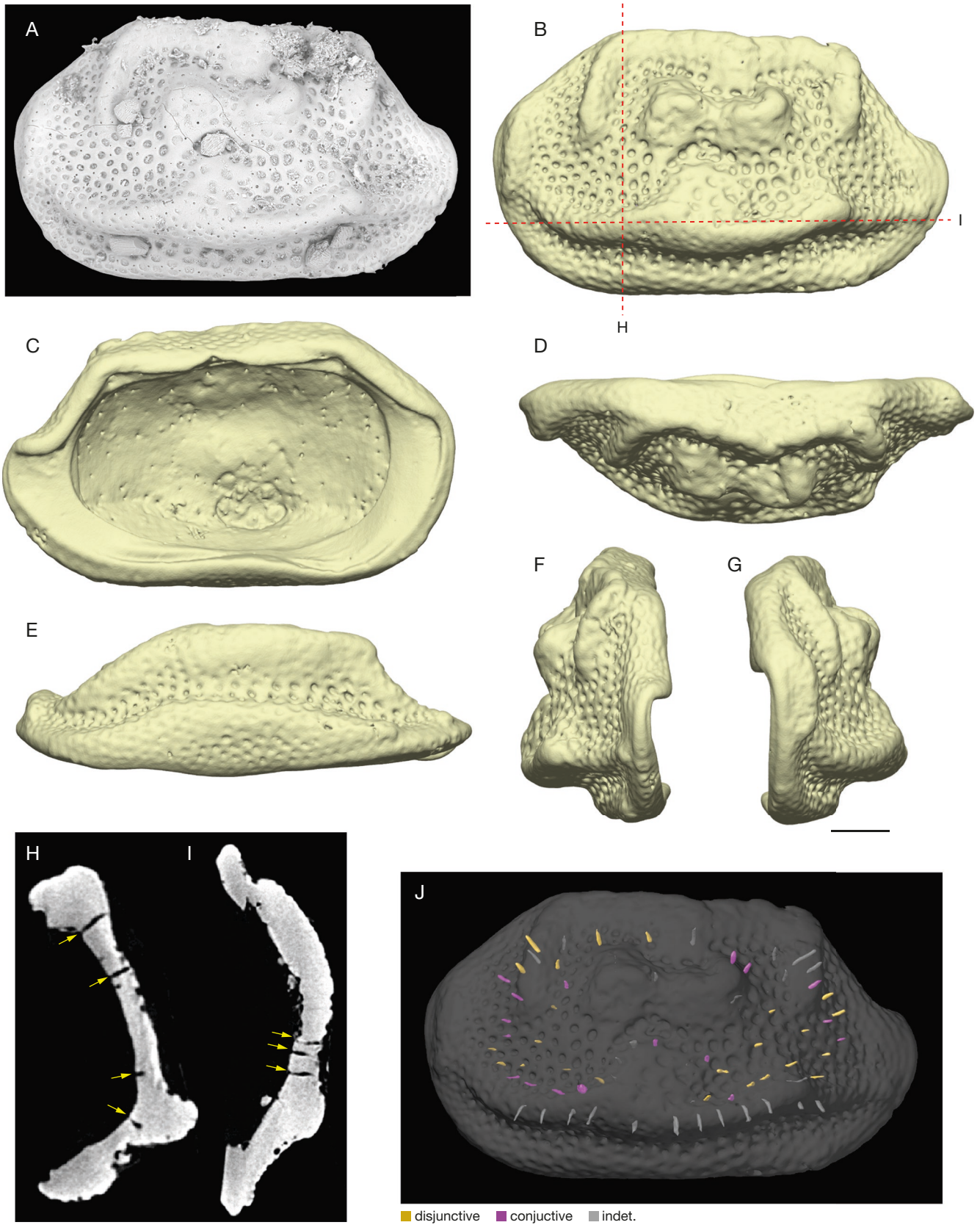


FIG. 3. — *Triebelina indopacifica* van den Bold, 1946, largest adult left valve, possibly gerontic (MNHN.F.F67777): **A**, SEM image; **B-G**, 3D reconstructions; **B**, outer view with red dotted lines showing the position of individual scans in **H** and **I**; **C**, inner view; **D**, dorsal view; **E**, ventral view; **F**, posterior view; **G**, anterior view; **H, I**, individual scans with yellow arrows showing pores, position on the valve shown in **B**; **H**, coronal view; **I**, axial view; **J**, translucent 3D reconstruction showing position of pore canals through the valve wall and position of pores regarding micro-ornamentation. Scale bar: 100 μ m.

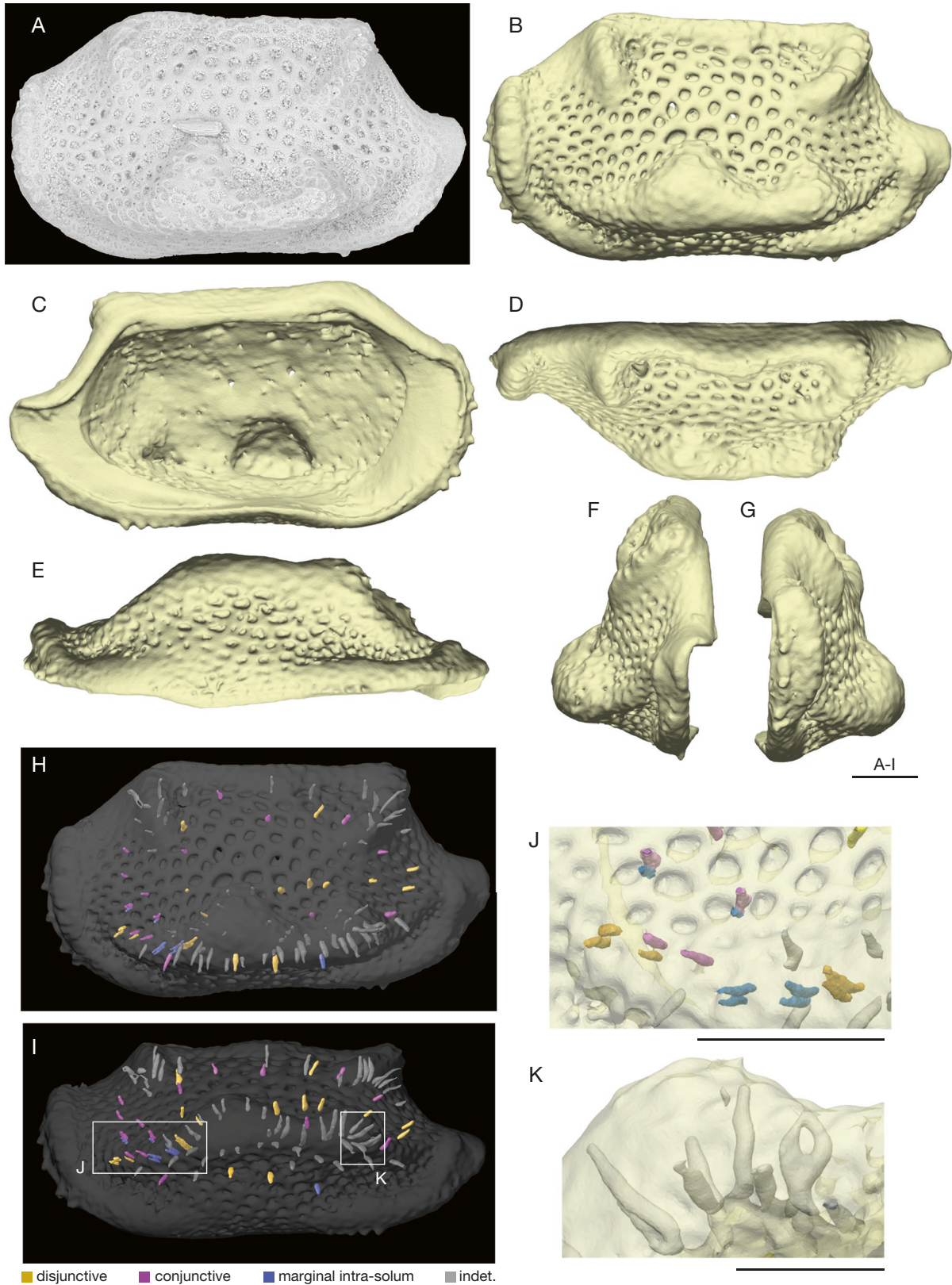


FIG. 4. — *Triebelina indopacifica* van den Bold, 1946, smallest adult left valve (MNHN.F.F67778): **A**, SEM image; **B-G**, 3D reconstructions: **B**, outer view; **C**, inner view; **D**, dorsal view; **E**, ventral view; **F**, posterior view; **G**, anterior view; **H, I**, individual scans with **yellow arrows** showing pores, position on the valve shown in **B**; **H**, translucent 3D reconstruction showing pore canals through the valve wall and position of pores regarding micro-ornamentation; **I**, subventral view of the valve, white boxes show the position of insights **J** and **K**; **J**, anterior extremity of the ventral ridge showing series of double pore systems; **K**, subventral view of the posterior extremity of ventral ridge showing anastomosed pore canal. Scale bars: A-J, 100 µm; K, 50 µm.

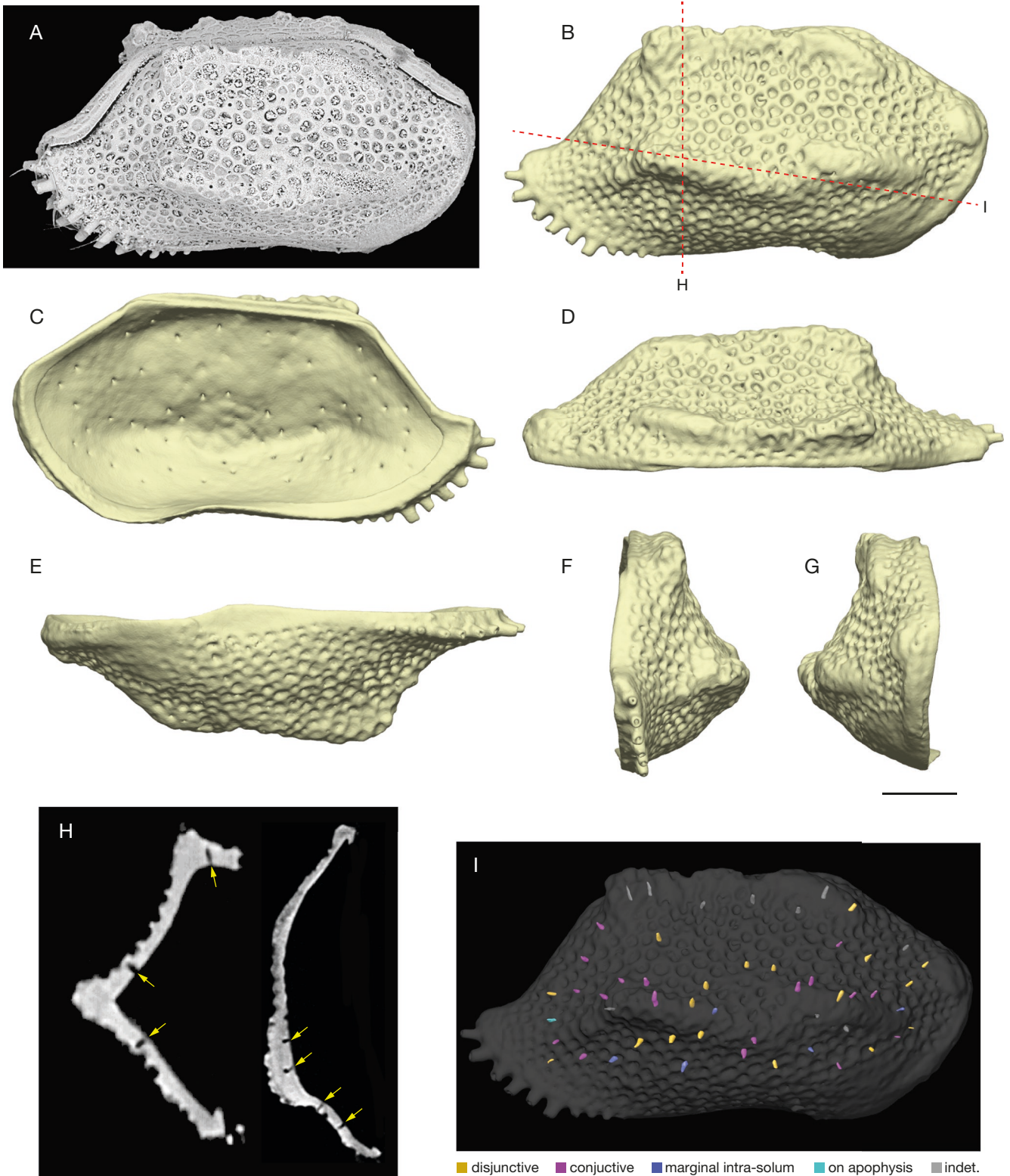


FIG. 5. — 3D reconstructions of *Triebelina* sp., juvenile right valve (MNHN.F.67779): **A**, SEM image of the carapace that was disarticulated during preparation; **B-G**, 3D reconstructions; **B**, outer view with **red dotted lines** showing the position of individual scans in **H** and **I**; **C**, inner view; **D**, dorsal view; **E**, ventral view; **F**, posterior view; **G**, anterior view; **H, I**, individual scans with **yellow arrows** showing pores, position on the valve shown in **B**; **H**, coronal view; **I**, axial view; **J**, translucent 3D reconstruction showing pore canals through the valve wall and position of pores regarding micro-ornamentation. Scale bar: 100 μ m.

subdorsal node of the left valve (Fig. 7A-F). The three fossil specimens are stored in the Muschelkalkmuseum Hagdorn Stadt Ingelfingen, Ingelfingen collections under collection numbers MHI 2053/1-MHI 2053/3.

IMAGING

All specimens were investigated with XRadia CT-400 tomography (XRadia, Concord, California, United States) at the Slovenian National Building and Civil Engineering Institute, Ljubljana, Slovenia. For each scanned specimen, the spatial resolution per pixel (in μm) is provided in Appendix 1, using a 20 X magnification optical objective. The voltage and current were respectively set to 80 kV and 7 W. 1 600 projection images at an exposure time of 28 to 30 seconds per projection were captured through the charge-coupled device (CCD) camera. Post-production of the data files was carried out at the Centre de Recherche en Paléontologie-Paris (CR2P). The original RGB TIFF image stack was optimized using ImageJ software (1.52a, NIH). After cropping, reorienting the specimens and working on the contrast, we obtained a stack of 8-bits TIFF virtual slices (the resolution in pixels and the isometric voxel size are listed in Appendix 1). The Mimics Innovation Suite software (24.0 Research Edition, Materialise) was used to perform the 3D reconstruction (segmentation and 3D rendering). All details are summarized in Appendix 1.

ANALYSIS OF PORES

Differential absorption of X-rays by the various components of the samples provides contrasted images, corresponding to variations in voxel colour from black to white depending on the density and nature of the materials. The Mimics segmenting software, by pixel colour selection, has enabled us to discriminate between the different structures of the samples and virtually eliminate sediment covering the surface and/or filling the inside of the valves on the 3D reconstructions. Thanks to 3D tomography, some observational issues related to diagenesis of both recent and fossil specimens investigated here (diagenetic dissolution, overgrowth and recrystallisation) have thus been overcome. Although SEM observations of the surface of *Triebelina* illustrate rimmed and unrimmed pores (Fig. 1E, F, I, K; Appendix 1), the resolution of the micro-tomography performed here does not allow to precisely reconstruct this state of character. Our analysis remains descriptive. Close observation of SEM images (e.g. Figs 4A; 5A) shows that pores of different sizes occur in recent ornate Bairdiidae, but some of the smallest pores are invisible on scans because of resolution or sediment infilling. As a consequence, we refrain from using quantitative tools because of the incompleteness of the record of pores at the surface of the studied specimens.

3D reconstructions are accessible in Appendices 2-7.

ABBREVIATIONS

Institutions

MHI	Muschelkalkmuseum Hagdorn Stadt Ingelfingen, Ingelfingen;
MNHN	Muséum national d'Histoire naturelle, Paris.

Others

AMS	adductor muscle scars;
LV	left valve;
NPC	normal pore canals;
RV	right valve.

MORPHOLOGICAL RESULTS

TRIEBELINA INDOPACIFICA VAN DEN BOLD, 1946

The present 3D reconstructions illustrate the major morphological characters of *T. indopacifica*. The two largest valves have a wide calcified inner lamella and are adult (Figs 3C; 4C). In both specimens, the AMS are located within the cavity underlying the swelling of the ventro-lateral ridge but are weathered and cannot be satisfactorily observed.

The RV (Fig. 5) is small, thin-walled, and has a narrow calcified inner lamella; it is an instar. The AMS pattern is plain, consisting of eight elongate scars organised in four parallel diagonal rows (Fig. 5C). The species identification of this juvenile is uncertain.

NODOBAIRDIA MAMMILLATA KOLLMANN, 1963

External structures

The type material of *Nodobairdia mammillata* (type species of *Nodobairdia* Kollmann, 1963) was incrustated with sediments that limited the observations, but allowing the recognition of its diagnostic features (Kollmann 1963). The 3D investigation offers the unique opportunity to virtually remove all sediment masking inner and outer morphology and characters of the valves. Based on the size diagram in Forel & Moix (2020), the dimensions of the isolated LV studied here (Appendix 1) may correspond to a submature A-1 stage (Fig. 6), while the carapace corresponds to a younger juvenile, possibly of A-3 stage (Fig. 7A-F).

The diagnostic features of *Nodobairdia mammillata* include three aligned subventral nodes, two dorsal nodes at LV and four subdorsal nodes at both valves, the anterior and posterior ones being oblong (Kollmann 1963). In this species, the antero-dorsal and postero-dorsal nodes at LV are reduced in submature stages and adults, and the subventral nodes coalesce in adults (Kollmann 1963). These features are observed in our largest LV (Fig. 6A), confirming its submature stage, while the strong antero-dorsal node and unfused subventral nodes of the carapace (Fig. 7A, B) confirm that it represents a younger stage. The coalescence of the ventral row of nodes in the largest LV confirms the *N. mammillata* attribution and differentiates it from *N. verrucosa* Kollmann, 1963.

The 3D investigation of the LV shows that the wall is actually thickened between the two dorsal nodes (Fig. 6A-C). The convexity in the lateral outline is formed by a dorsal ridge that seems to develop quite late during the ontogeny, as it is less prominent in the carapace (Fig. 7A-C). The macro-ornamentation features are covered with verrucae (Figs 6A; 7A, B) that are also visible for instance in Kristan-Tollmann (1978, 1986) and Dépêche & Crasquin-Soleau (1992). The median surface, which is delimited by the subventral and

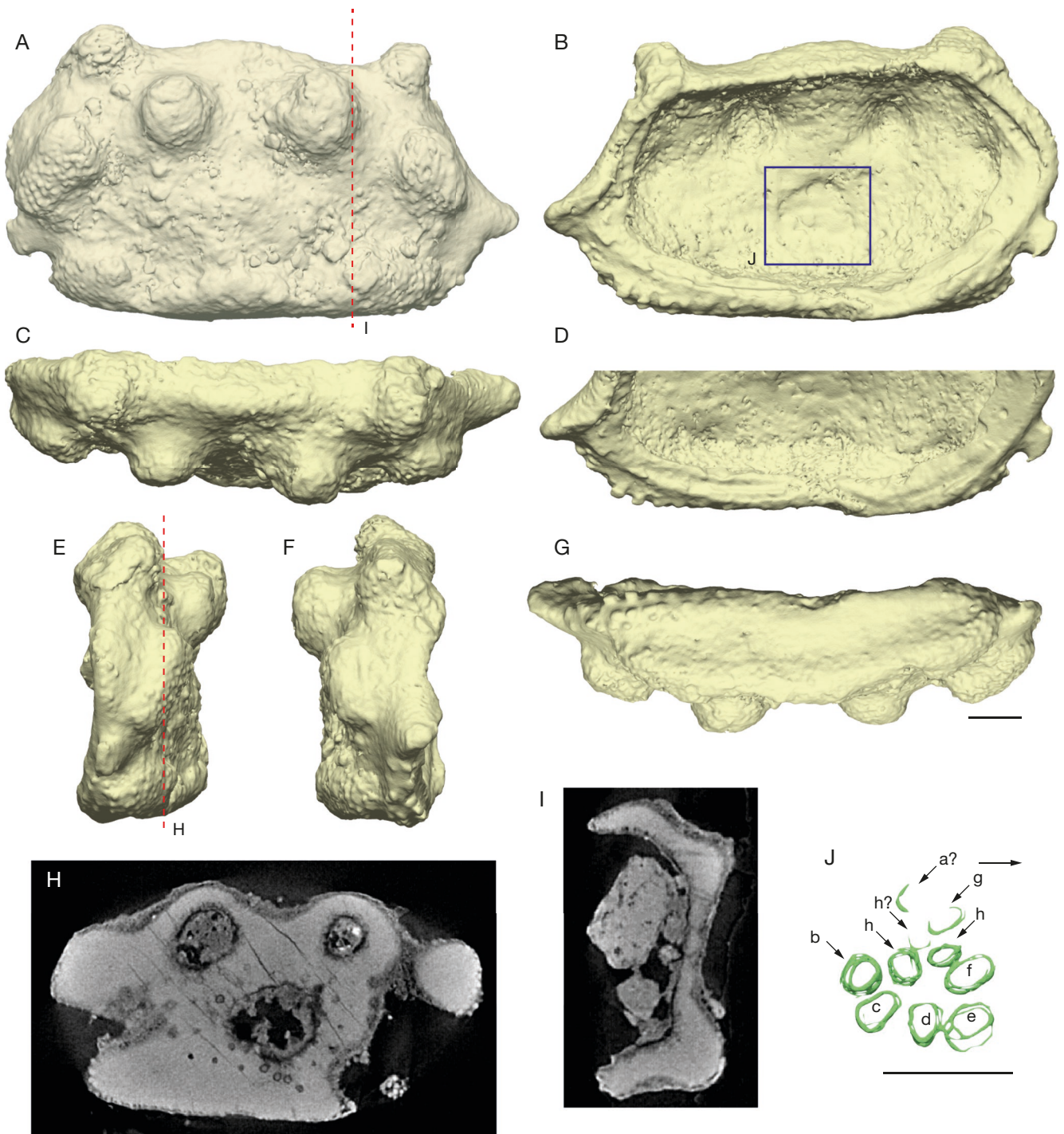


FIG. 6. — *Nodobairdia mammillata* Kollmann, 1963, left valve (MHI 2053/1): **A–G**, 3D reconstructions: **A**, outer view with **red dotted line** showing the position of individual scan in **I**; **B**, inner view with blue box shows the position of AMS and insight in **J**; **C**, dorsal view; **D**, subventral inner view with insight on the ventral area; **E**, anterior view with **red dotted line** showing the position of individual scan in **H**; **F**, posterior view; **G**, ventral view; **H**, **I**, individual scans, position on the valve shown in **A** and **E**; **H**, sagittal view; **I**, coronal view; **J**, reconstruction of the AMS with individual scars noted **a** to **h**, **arrow** points to anterior. Scale bars: 100 µm.

subdorsal structures, displays a reticulum made of round, large and deep fossae; they are more developed in the isolated LV and mainly seen on individual scans (Fig. 6H, I). The three subventral nodes delimit a flat and smooth ventral surface (Figs 6G; 7D). The anterior extension, termed “nose”, was taken as a subgeneric marker of *Triebelina* (*Nodobairdia*) by Bolz (1971b), who considered it as antero-ventral marginal denticles interconnected by a calcitic layer, i.e., a frill. This

structure appears to be hollow in the isolated LV (Fig. 8A, B), but it is impossible to confirm whether a radial pore canal is present. A tiny opening seems to be present at the extremity of the nose in the LV of the carapace, but the definition of the scan does not allow further precision. In both LV, the postero-ventral margin is thickened and bears three parallel rows of full spines that are more strongly developed in the largest LV; they also develop anteriorly and are interrupted

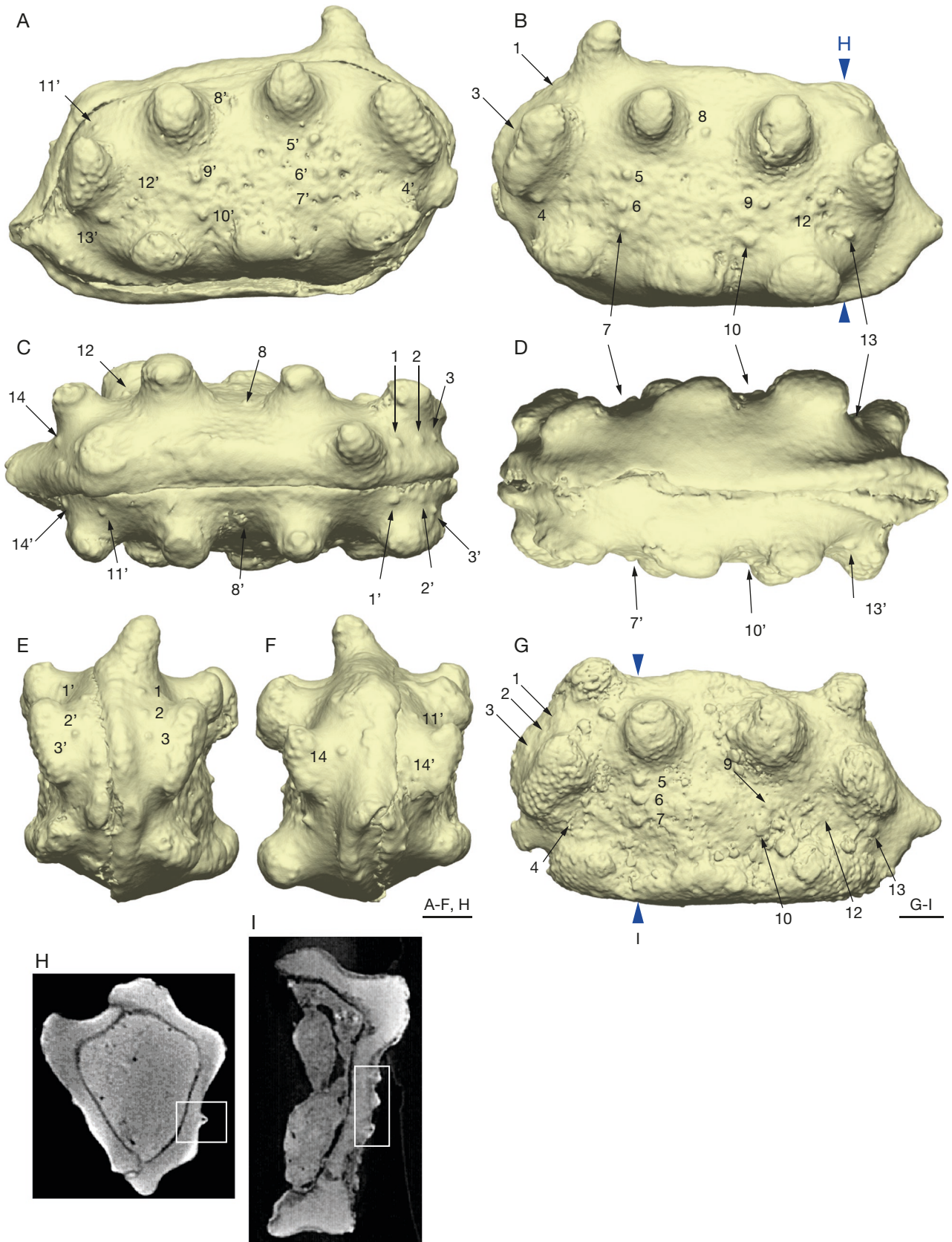


FIG. 7. — 3D reconstructions of *Nodobairdia mammillata* Kollmann, 1963 showing the distribution of nodule-like Aⁿ pores, labelled 1 to 14 at LV and Aⁿ to 14ⁿ at RV: **A-F**, juvenile carapace (MHI 2053/2); **A**, right lateral view; **B**, left lateral view with blue arrows showing the position of individual scan in **H**; **C**, dorsal view; **D**, ventral view; **E**, anterior view; **F**, posterior view; **G**, left lateral view of the submature LV (MHI 2053/1) with blue arrows showing the position of individual scan in **I**. Scale bars: 100 µm.

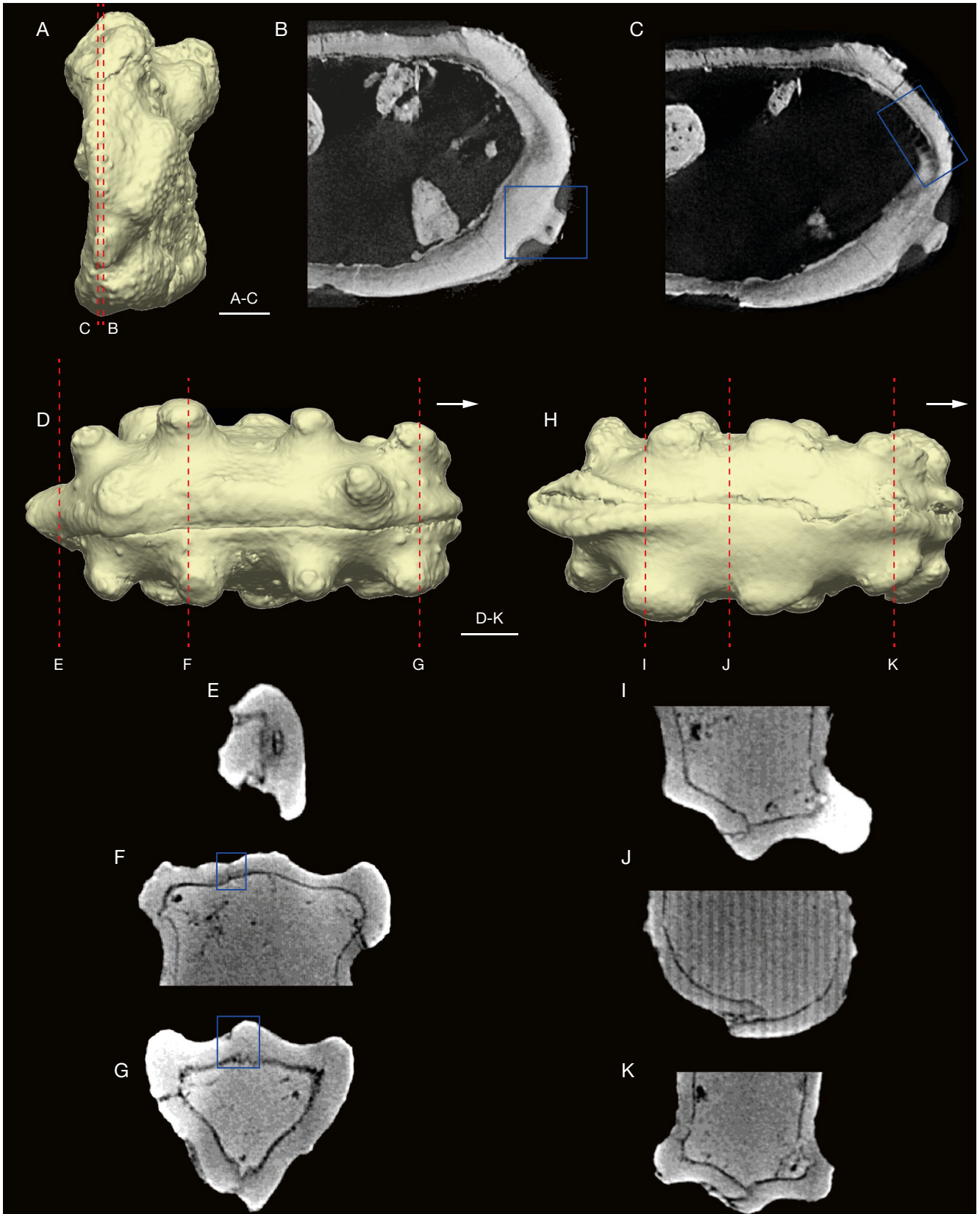


FIG. 8. — 3D reconstructions and individual scans of *Nodobairdia mammillata* Kollmann, 1963: **A-C**, isolated LV (MHI 2053/1); **A**, anterior view of the with **red dotted lines** showing the position of individual scans in **B** and **C**; **B**, **C**, individual scans, position on the valve shown in **A**; **B**, sagittal section with **blue box** showing the hollow nose at the anterior margin; **C**, sagittal section with **blue box** showing the bairdopillate teeth; **D-K**, juvenile carapace (MHI 2053/2); **D**, dorsal view with **red dotted lines** showing the position of individual scans (coronal sections) in **E-G** with dorsal contact of the valves; **E**, posterior end; **F**, posterior half; **G**, anterior end; **H**, carapace in ventral view with **red dotted lines** showing the position of individual scans coronal section in **I-K** with ventral contact of the valves; **I**, posterior end; **J**, posterior half; **K**, anterior end. Scale bars: 100 μ m.

by the oral concavity (Fig. 6G). The thickened portion of the carapace is separated from the actual margin by a narrow flat area (Fig. 7D).

The lateral surface of *Nodobairdia mammillata* also displays at least 14 nodules that are distributed in a recognizable pattern at each valve (Fig. 8). These nodules have never been described, but they are visible in specimens from the Norian-Rhaetian of Australia (Dépêche & Crasquin-Soleau 1992), Ladinian, Carnian and Rhaetian of Hungary (Monostori & Tóth 2014) as well as Carnian of Sicily (Crasquin *et al.* 2018). They are symmetrical between the valves and are here labelled from 1 to 14 in the LV and from 1' to 14' in the RV. All of them are recognized in the juvenile carapace (Fig. 7A-F) and submature LV (Fig. 7G), indicating that they may be fully acquired quite early in the ontogenetic development of the species. They are further described and discussed below.

Internal structures

The calcified inner lamella of the largest LV extends from the antero-dorsal margin to slightly higher than the posterior border; in lateral view it is very reduced along the ventral margin and shows maximum of width along the antero-ventral margin (Fig. 6B). The vestibule is very narrow. The inner surfaces are carved by:

- four subdorsal cavities corresponding to the subdorsal nodes, in both valves. In the isolated LV, the cavities are shallower below the anterior and posterior nodes, corresponding to a thickening of the nodes themselves (Fig. 6B);
- two dorsal cavities corresponding to the dorsal nodes, in the left valves. They are very reduced in the submature LV, corresponding to particularly thick areas of the valve;
- three deep ventral cavities in the carapace and an elongate lineation ventrally, with the three main cavities corresponding to the three aligned ventral nodes, nearly coalescing in the isolated LV (Fig. 6D). Overall, the submature LV displays thicker structures compared to those of the younger carapace;
- the circular AMS spot is located in a shallow cavity around mid-length and slightly below mid-height in the isolated LV (Fig. 6B). It is composed of at least nine subcircular to subrectangular individual scars organized into three rows: a ventral arcuate row of four scars, a median row (apparently incomplete) of three scars, and an upper row of two scars (Fig. 6J). Other scars (frontal, mandibular) are not observed. The AMS pattern of *Nodobairdia* was never reported so far. Kristan-Tollmann *et al.* (1980) labelled the individual scars of Triassic ornate forms from a to g, surrounding a central h scar that can be doubled or tripled (see Forel & Chitnarin 2023 for summary). The h-scars are typically arranged horizontally next to each other, the inner one being larger than the outer one: this pattern is observed here in the *N. mammillata* LV with a possibly triple h-scar (Fig. 6J). This observation is of major importance, as changes in the number of scars h are associated with the typical Triassic evolutionary stage of the AMS (Kristan-Tollmann *et al.* 1980). The d-scars are also generally divided into three to five small scars, but only one is observed here. The scars recognized here, from a to triple h, display the same position

and relative size compared to other ornate Bairdiidae that have been so far studied (Forel & Chitnarin 2023: fig. 5); they are considered homologous.

Kollmann (1963) mentioned a hinge composed of a simple bar in the RV, protruding at the anterior and posterior ends, and a corresponding furrow in the left valve, which is the usual condition in Bairdiidae. Kristan-Tollmann (1971) described the hinge as a long, straight and smooth bar with triangular anterior and posterior lists and corresponding furrow. The preservation of the hinge in both specimens does not allow any precise observation, but the scans of the carapace reveal the details of the dorsal contact of the valves: the RV is nested in the LV at the posterior end (Fig. 8D, E), the overlap of LV on RV develops until the mid-part of postero-dorsal node, is interrupted along dorsal border (Fig. 8D, F) and resumes from the anterior part of the antero-dorsal node to the anterior margin (Fig. 8D, G).

The carapace also allows observation of the ventral contact of the valves, which we here describe following the terminology used in Adamczak (1976) and Olempska (1999). As mentioned above, the RV is posteriorly nested into LV. The contact develops into a sort of contact groove (Fig. 8H, I) that progressively reduces and flattens until the anterior end of the posterior subventral node, where the ventral contact consists of RV being overlapped by LV (Fig. 8H, J). An anterior contact groove progressively redevelops around mid-part of the median subventral node until the anterior end of the anterior subventral node (Fig. 8H, K).

Auxiliary (bairdoppilate?) teeth and sockets are poorly developed on the carapace, possibly being less expressed in juveniles, but they are visible anteriorly on the isolated LV, more clearly on individual scans than on reconstruction (Fig. 8A, C). Kristan-Tollmann (1971) mentioned six to eight small teeth in the RV; five sockets are clearly seen in the studied LV, three additional being more questionable because of preservation.

EXPLORING PORE SYSTEMS

Pores of different sizes are visible on all scanned specimens, but some are at the limit of the resolution of the CT-scan. The present investigation is, therefore, preliminary, and we hope that the use of other methods, such as nano-CT or synchrotron light, will be of major significance to describe these minute structures with more precision.

TRIEBELINA INDOPACIFICA

Marginal pores

In *Triebelina* sp., six large marginal spines are visible along the postero-ventral margin (Fig. 9A, B). They are hollow, but no setae are associated with them. A tiny pore is also visible at the base of each spine (Figs 5A; 9B), which houses the marginal setae (eyelash setae of Maddocks 2013). The associated radial pore canals cannot be tracked through the entire thickness of the valve wall because of low resolution. The two adult specimens of *Triebelina indopacifica* are overall more

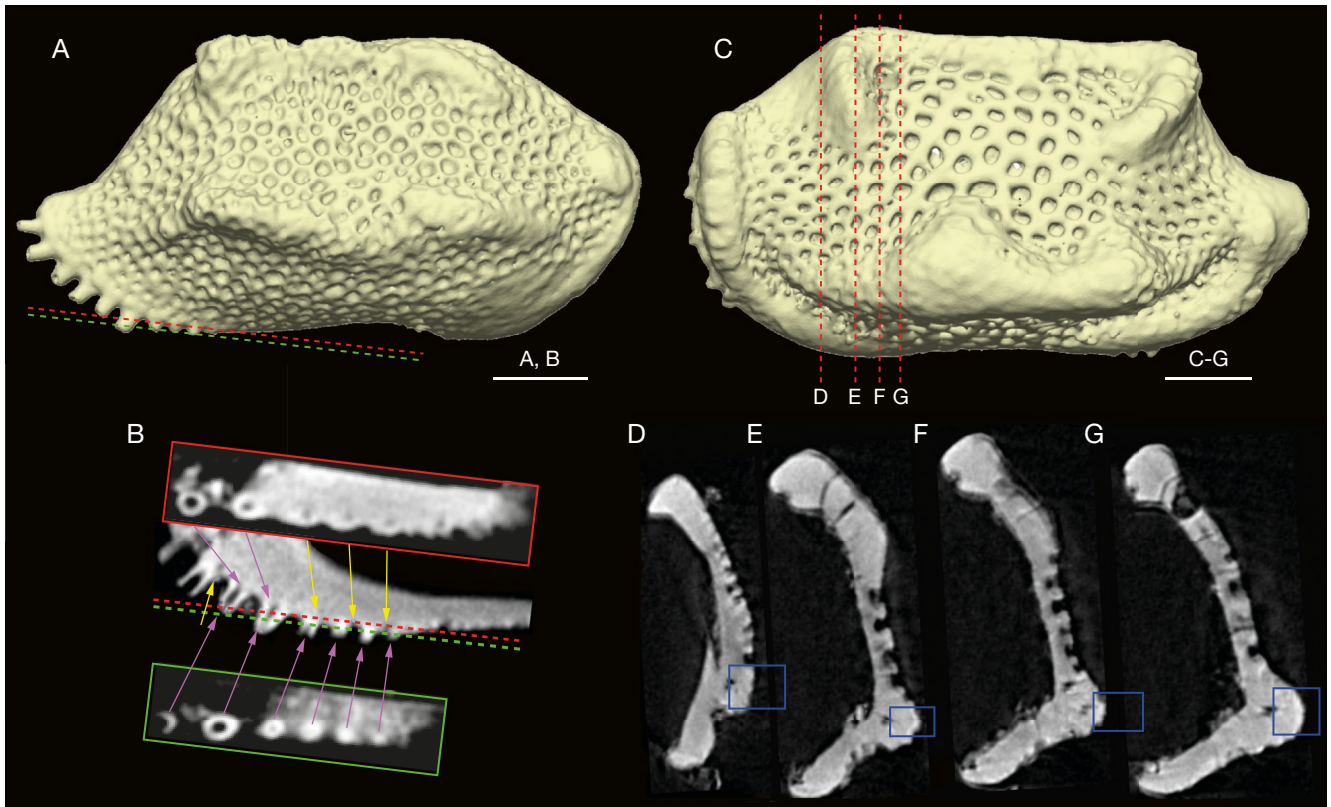


FIG. 9. — **A, B**, Spines-related pores of *Triebelina* sp.; **A**, outer view with red and green dotted lines showing the position of individual scans in **B**; **B**, individual scans showing two axial sections of the postero-ventral margin framed in red and green and a central sagittal section of the same area, spines are shown by pink arrows and spines-related pores are shown by yellow spines; **C-G**, double pore systems of *Triebelina indopacifica* van den Bold, 1946; **C**, outer view with red dotted lines showing the position of individual scans in **D-G**; **D-G**, successive coronal sections showing double pore systems in blue boxes. Scale bars: 100 μ m.

worn, and marginal spines are less well preserved, although they have been illustrated on the type material (van den Bold 1946: fig. 7). Four broken marginal spines occur along the antero-ventral margin of the smaller LV, and minute structures along the posteroventral margin (Fig. 4).

Lateral normal pores

In all three *Triebelina* specimens, lateral NPC cross the entire thickness of the valve perpendicularly to the surface (Figs 3H, I; 5H, I). They are not uniformly distributed, as they are closely associated with macro-ornamentation and less abundant in uniquely micro-ornamented zones (Figs 3J; 4H; 5J). On the scans and 3D reconstructions, these macro-ornamentation related canals are rarely observed to cross the thickest portion of ornamentation features, while they are more abundant on the SEM images (Figs 3A; 4A; 5A). These differential observations are, therefore, related to the resolution of the CT-scan, small pore canals being undetected. The following preliminary description consequently focuses on the largest pore canals clearly observable through scans.

Two rows of pore canals border the ventral ridge of all specimens and the median bulge in the case of *T. indopacifica* (Figs 3J; 4H; 5J). Dorsally, they are also distributed into two rows along the horizontal ridge as well as the anterior and posterior lateral vertical elements. In areas lacking macro-ornamentation, pores are mainly located at the anterior and

posterior ends of the lateral surface, where the crests and ventral ridge interrupt, but this pattern is strongly biased by the resolution limits of the CT-scan. The smallest LV of *T. indopacifica* displays numerous pore canals through the thickest parts of the macro-ornamentation, mainly through the posterior portion of the ventral ridge, while they are less numerous near the AMS (Fig. 4H, I). Overall, a certain polarity of the distribution of canals for all the three valves studied is visible, with denser distribution along the ventral margin compared to the dorsal area.

The smaller LV of *T. indopacifica* displays a unique set of nine double pore systems aligned in two rows above the anterior termination of the ventral ridge (Fig. 4H-J). At the time of writing, we are not aware of any previous work reporting such systems of double pore canals in ostracods. These canals are relatively narrow, and they cross the valve thickness while being very closely positioned, nearly touching each other. The possibility that they may correspond to artifacts is precluded, as their respective walls are clear and coherent in axial, coronal and sagittal views. One anastomosed pore canal is also seen at the posterior end of the ventral ridge of the same LV (Fig. 4I, K). Such unique pore systems, their relation to setae and calcification, and taxonomic significance should be appropriately investigated in the future. Overall, the area of the ventral ridge in *T. indopacifica* here appears as the richest in terms of diversity of pore canal morphologies.

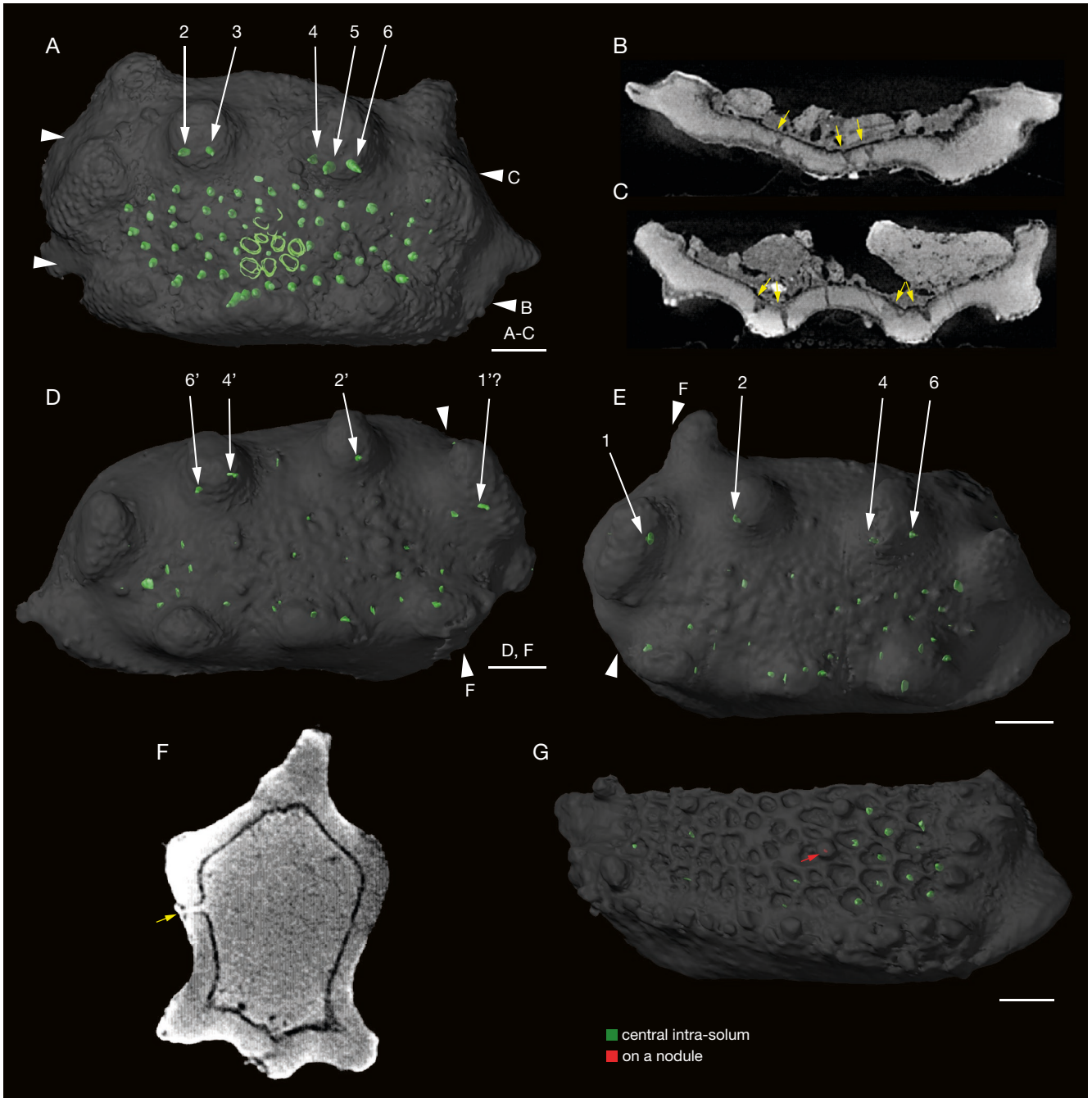


Fig. 10. — Normal pore systems in Triassic Bairdiidae Sars, 1888: **A-F**, *Nodobairdia mammillata* Kollmann, 1963: **A**, translucent 3D reconstruction of the adult LV (MHI 2053/1) showing the position of pores regarding micro-ornamentation with recognizable pore systems labelled from 2 to 6 and **white arrows** showing the position of individual scans in **B**, **C**; **B**, ventral coronal view; **C**, subdorsal coronal view; **D**, translucent 3D reconstruction of the RV of the complete carapace (MHI 2053/2) showing the position of pores regarding micro-ornamentation with recognizable pore systems labelled from 1' to 6' and **white arrow** showing the position of individual scans in **F**; **E**, translucent 3D reconstruction of the LV of the complete carapace showing the position of pores regarding micro-ornamentation with recognizable pore systems labelled from 1 to 6 and **white arrow** showing the position of individual scans in **F**; **F**, axial view; **G**, translucent 3D reconstruction of *Mirabairdia pernodosa* Kollmann, 1963 (MHI 2053/3) showing position of pore canals through the valve wall and position of pores regarding micro-ornamentation. Scale bars: 100 µm.

The position of pores regarding reticulation is shown in Figs 3J; 4H; 5J. The reticulation at the surface of all macro-ornamental areas (dorsal, ventral and median ridges) is blurred and it is impossible to determine the relationship of pores to reticulation. In other areas, pores in all three *Triebelina* specimens are intramural. Further analysis of juvenile speci-

mens will be of importance to compare the ontogeny of pore systems with the ontogenetic history of calcification. The study of complete carapaces will clarify how pore canals are organized in the two valves of these highly asymmetrical ostracods, if the asymmetry of the valves also corresponds to an asymmetry of the pore systems.

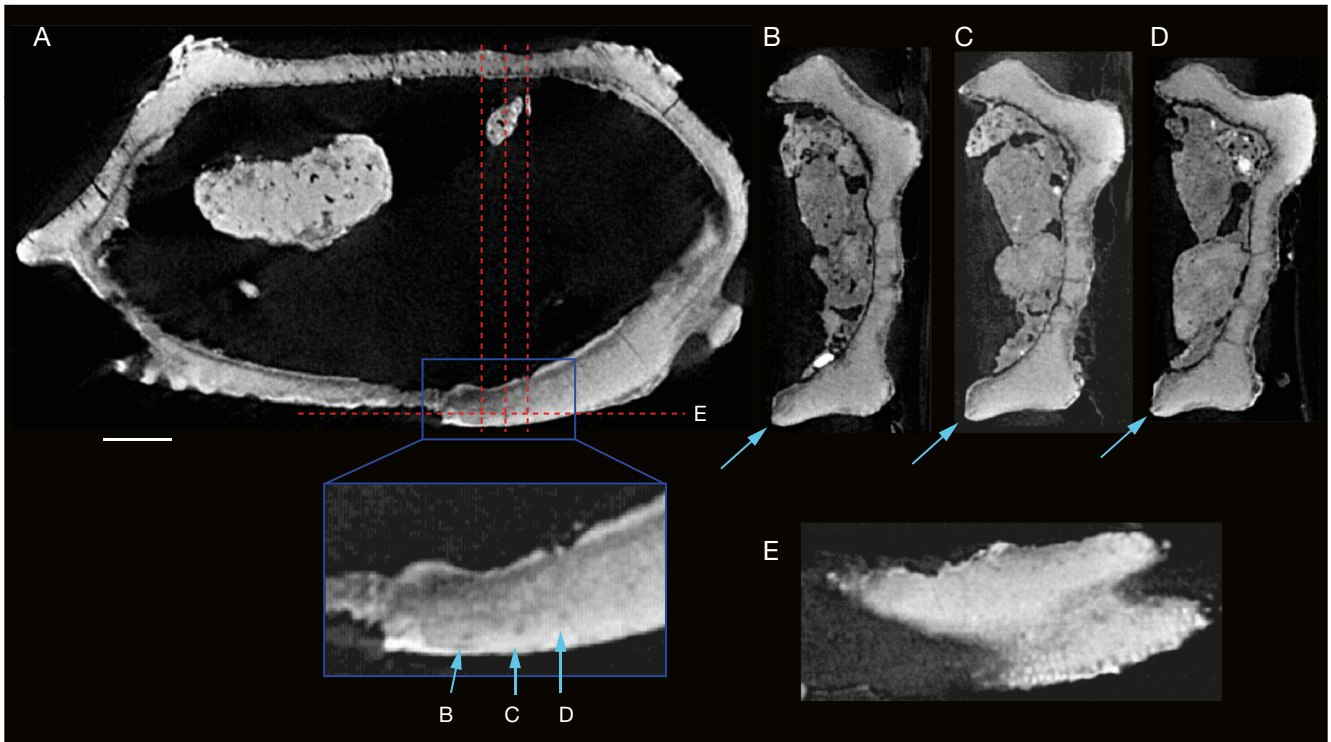


FIG. 11. — Individual scans showing eyelash pores in the LV of *Nodobairdia mammillata* Kollmann, 1963 (MHI 2053/1): **A**, sagittal section with **blue box** showing enlarged ventral margin and **red dotted lines** indicating the position of scans in **B-E**; **B-D**, successive coronal sections; **E**, axial section. Scale bar: 100 μ m.

TRIASSIC BAIRDIIDAE

The virtual cleaning of all specimens has revealed the presence of canals in different areas of the valves. In some areas, dissolution occurred and can be easily recognized as corresponding to groups of holes of different sizes underlain by disturbed sediment. The two specimens of *N. mammillata* are the most significant with the most abundant pores being preserved. We recognize three types of pores: NPC, pustule-related pores, and marginal pores that may have carried eyelash setae. Most of them are filled with sediment that is clearly recognizable from the valve wall by its distinct contrast (Fig. 10B, C, F).

Normal pores

They are spread over the surface of each valve. Three main distribution zones are recognized: in association with macro-ornamentation (nodes and ridge), in association with micro-ornamentation on the median surface (reticulation) and through nodules. They are all straight, conical with the larger opening inside. Only a few canals cross the heaviest parts of the subdorsal and subventral ornamentation of *N. mammillata* (Fig. 10A). In the largest LV, they are located in the ventro-marginal region of the two median nodes, where they are aligned and organized in a radiating pattern (Fig. 10A, C). In the carapace, they occur at all subdorsal nodes at both valves (Fig. 10D, E).

Pore canals associated with subdorsal nodes are labelled from 1 to 6 at LV and 1' to 6' at RV, all being in recognizable positions regarding nodes (Fig. 10A, D, E). The smallest specimen lacks the systems 3/3' and 5/5', possibly indicating that

they may appear later in the ontogeny of the species. Among the few works that discussed pores in Bairdiidae, Maddocks (2013) mentions that pores of different sizes occur in adults, the largest being those that appeared earlier in the development of the species. In the present case, pore systems 4, 5 and 6 in the adult LV (Fig. 10A) are large and roughly similar in size. Additional tiny structures are visible within the subdorsal nodes but the resolution hampers on the determination of their nature. Specimens of *N. mammillata* illustrated in Kristan-Tollmann (1978) show unrimmed pores of type A' located between the subdorsal nodes (Fig. 1M). These structures are not observed in any of the two specimens studied, most likely because of preservation and/or resolution.

In *N. mammillata* and *M. pernodosa*, pores are more densely seen in association with reticulation in the median area (Fig. 10A, D, E, G). This pattern differs from what has been observed in *Triebelina* where pores appear less abundant in this area. However, in the three Triassic specimens studied, the pores appear to be intrasolar, which probably means that the supposed sola are compound with poorly developed second-order muri within. *M. pernodosa* displays one pore canal going through a nodule (Fig. 10G). The study of complete and better preserved *Mirabairdia* specimens will be necessary for further discussion and comparison.

Nodular pores

The lateral surface of *N. mammillata* displays at least 14 nodules in a symmetrical pattern between RV and LV (Fig. 7). The 3D tomography reveals that these nodules are actually

hollow and penetrated by tiny pore canals that can only be fully studied with higher resolution scans (Fig. 8H, I). They can easily be recognized in several of the published specimens, for instance in Dépêche & Crasquin-Soleau (1992). It is uncertain whether the pores illustrated by Kristan-Tollmann (1978) from the Carnian of Italy (Fig. 1M) correspond to these nodular pores; she illustrated such pores at the base of the two median subdorsal nodes, where they are not seen in the present analysis. This disparity needs to be verified with high resolution investigation of well-preserved specimens. The level of significance of this pattern for *N. mammillata* also remains to be investigated. Other species such as *Nodobairdia verrucosa* Kollmann, 1963 seem to also display such structures, but until type specimens are re-analysed, it is hard to determine whether the pattern of nodular pores is of specific or supra-specific significance.

Marginal pores

The largest LV of *N. mammillata* displays a series of narrow canals aligned along the anteroventral margin (Fig. 11). These structures are elongate in coronal view and small round cavities in axial view. They cannot be tracked along their entire length through the valve thickness because of their small diameter that is close to the resolution limit of the CT-scan. However, their position perpendicular to the valve margin and their regularly spaced disposition reminds radial pore canals.

DISCUSSION AND CONCLUSIONS

The taxonomy of fossil ostracods is not an easy task, and its disconnection with modern forms is particularly responsible for the numerous, fundamental, disagreements. Advocates for the standardization of definitions in ostracod species have recently emphasized the need for modern techniques, including SEM and 3D imagery (Lord 2020; Forel *et al.* 2021a). 3D techniques offer unique opportunities to evaluate taphonomic alteration, to analyse the homologies of morphological structures, and to apply these insights to an improved phylogenetic classification (Wang *et al.* 2020; Forel *et al.* 2021b). Here we use 3D tomography to study the morphology of recent and fossil ornate Bairdiidae and to go beyond their ornamentation and surface, and accessing to the poorly visible pores and pore canals. This preliminary analysis reached the resolution limit of the CT-scan images on several aspects. However, it suggests that CT-scan has a considerable potential for improving the studies on ostracods taxonomy, particularly on those that frequently display homeomorphy.

Several phylogenetic relationships have been proposed among ornate Bairdiidae, including a lineage extending from the Permian genus *Ceratobairdia* to Triassic *Ptychobairdia*, Late Cretaceous *Alatanesidea pokornyi* Colin & Lauerjat, 1978 up to the Pliocene to recent genus *Havanardia* (Jellinek 1994). A similar evolutionary line was proposed by Forel & Crasquin (2022) focusing on the Permian and Triassic interval, with *Ceratobairdia* deriving from the Early Permian genus *Petasobairdia*, which gave rise to *Parurobairdia* in the Late

Permian and *Ptychobairdia* at the end of the Early Triassic. However, these proposals remain debatable. Consensus on this field will be only be reached with more detailed studies on underexploited characters with potential taxonomic significance, including pores and pore systems.

This contribution represents a first attempt on exploration of pores of Triassic Bairdiidae and proposes important observations that will need to be further investigated in the future. Pore canals in *Nodobairdia* and *Mirabairdia* are associated with micro-ornament in the median field, whereas they are associated with macro-ornament in *Triebelina*. Apparently intrasolar pores have been observed in Triassic genera, whereas pores of recent *Triebelina* are intramural. These interpretations require further verification and careful delineation of associated homologies. The relationship of pore systems to macro- and micro-ornament requires more investigation.

In Recent *Triebelina*, for the first time, we have traced the course of normal pore canals through the valve, including possible double and anastomosed canal systems. The ontogeny of these systems should be investigated to understand its relationship to valve calcification.

We consider that these new morphological data could thoughtfully support taxonomic distinctions at the generic level among living and Triassic ornate bairdiids. They offer no justification for merging the Triassic representatives into the genus *Triebelina*. Rather, they offer promise for eventual delineation of the phylogenetic relationships among living and fossil ornate Bairdiidae.

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APPENDICES

APPENDIX 1. — Summary of information of studied material (all dimensions without spines and dorsal nodes). Abbreviations: **LV**, left valve; **RV**, right valve.

Locality	Species	Age	Figures	Nature	Slices				3D reconstruction			
					Seconds per projection	Voxel size (µm)	resolution (pixels)	Number of slices		Length (µm)	Height (µm)	Repository
French Polynesia, Society, Moorea, Opunohu bay	<i>Triebellina indopacifica</i> van den Bold, 1946	Recent	Fig. 4	LV	28	1.03	812 × 308	552	712	416	MNH.N.F. F67777	Appendix 2
	<i>Triebellina indopacifica</i> van den Bold, 1946	–	Figs 5; 10	LV	30	1.03	524 × 750	350	672	356	MNH.N.F. F67778	Appendix 3
	<i>Triebellina</i> sp.	–	Figs 6; 10	RV	28	1.03	220 × 714	394	579	287	MNH.N.F. F67779	Appendix 4
French Polynesia, Society, Moorea, Cook (Pao-Pao) bay	<i>Nodobairidia marmillata</i> Kollmann, 1963	austriacum Zone Carnian, Late Triassic	Figs 7-9; 11	LV	30	1.17	940 × 594	435	947	556	MHI 2053/1	Appendix 5
Cassian Formation, Seelandalp close to Schluderbach, South Tyrol, sample MH12053	<i>Nodobairidia marmillata</i> Kollmann, 1963	–	Figs 8; 9; 11	carapace	30	1.03	460 × 904	614	LV: 810 RV: 759	LV: 448 RV: 418	MHI 2053/2	Appendix 6
	<i>Mirabairidia pernodosa</i> Kollmann, 1963	–	Fig. 11	broken LV	28	1.03	824 × 920	633	765	258	MHI 2053/3	Appendix 7

APPENDIX 2. — 3D reconstructions of *Triebelina indopacifica* van den Bold, 1946 (MNHN.F.F67777): https://doi.org/10.5852/cr-palevol2024v23a11_s1

APPENDIX 3. — 3D reconstructions of *Triebelina indopacifica* van den Bold, 1946 (MNHN.F.F67778): https://doi.org/10.5852/cr-palevol2024v23a11_s2

APPENDIX 4. — 3D reconstructions of *Triebelina* sp. (MNHN.F.F67779): https://doi.org/10.5852/cr-palevol2024v23a11_s3

APPENDIX 5. — 3D reconstructions of *Nodobairdia mammillata* Kollmann, 1963 (MHI 2053/1): https://doi.org/10.5852/cr-palevol2024v23a11_s4

APPENDIX 6. — 3D reconstructions of *Nodobairdia mammillata* Kollmann, 1963 (MHI 2053/2): https://doi.org/10.5852/cr-palevol2024v23a11_s5

APPENDIX 7. — 3D reconstructions of *Mirabairdia pernodosa* Kollmann, 1963 (MHI 2053/3): https://doi.org/10.5852/cr-palevol2024v23a11_s6