Fossilized gill soft tissues in Mesozoic freshwater unionoid bivalves: reinvestigation and new evidence of the evolution of adaptation to the freshwater environment

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Large freshwater unionoid bivalves today are a globally distributed and diverse group, with a history dating back to the Triassic. Their evolutionary success largely depends on their reproductive behavior, today, they all take maternal care via brooding their embryos, which is only possible in the modified (advanced) eulamellibranch gills, facilitating survival in freshwaters. It can be expected that such an essential trait could have originated in the last common ancestor of advanced Unionida lineages sometime after Carnian, Late Triassic, where unionoids with filibranch gills were known, and before the Middle Jurassic, when advanced unionoids already existed. The gill anatomy of unionoids, because of their calcified gill filaments, enhances exceptional preservation of associated soft gill tissues. New Late Triassic unionoid materials from Poland with gill tissues preserved, *Silesunio parvus*, *Tihkia silesiaca*, *Tihkia*? sp., together with other Mesozoic materials from archival collections from Cretaceous of United Kingdom ("*Unio porrectus*") and Brazil (*Anodontites freitasi*) provide new insights into gill evolution in Unionida. The traits observed during surface investigation supported a filibranch trait in the gill anatomy of *S. parvus* and *Tihkia*? sp. indicating the origin of evolving advanced gills took place after the Triassic. Yet, the eulamellibrach anatomy was confirmed only in Late Cretaceous *A. freitasi*. The preservation of the gills in the remaining specimens studied does not provide new data on the origins of advanced gills in unionoids and its more detailed timing.

Key words: Unionida, brooding, soft tissues, gill anatomy, freshwater, Triassic, Cretaceous, Mesozoic.

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Introduction

Unionoid bivalves (order Unionida) are now an important and highly diverse member of freshwater ecosystems, with almost 1000 living species, from which up to 40% are threatened with extinction (Lopes-Lima et al. 2018; Graf and Cummings 2021). They also have a long evolutionary history dating back to the Triassic (Skawina and Dzik 2011). Their evolutionary success and risk of future extinction might at least partially relate to the fact that larvae of all living species are today obligate parasites of fish (e.g., Bauer and Wachtler 2001), with a few exceptions including no-host development or an amphibian as a host (e.g., Watters and O'Dee 1998). Unionoids take maternal care of their offspring by brooding in the cavities of modified eulamellibranch gills, a character which is independently shared with at least some members of other freshwater bivalve families, e.g., Sphaeridae, Cyrenidae, and some Dreissenidae (Morton and Puljas 2013; Graf 2013; Mansur et al. 2019). Both larval parasitism, and maternal brooding, are widely accepted as adaptations for dispersion and survival in freshwaters. Unfortunately, although unionoid fossils are known from the freshwater deposits of all regions of Pangea since the Triassic prior to the onset of the continental breakup (ca. 200 million years ago; Seton et al. 2012), the questions of how and when these crucial adaptations evolved and how they impacted the evolution of this bivalve group remain to be fully understood.

The parasitic character of the larvae and their brooding in eulamellibranch gills are independent features yet both crucial for the unionoid life cycle (and today present in all the Recent representatives). One may thus hypothesize that these traits existed in the Middle Jurassic last common ancestor of modern lineages of Unionida (Boucot and Poinar 2010; Skawina and Dzik 2011; Graf et al. 2015; Bolotov et al. 2016, 2017; Huang et al. 2018; Skawina 2021). Unfortunately, early evolution of larva in Unionida may remain undetermined, likely because of low fossilization potential of the larva (the oldest fossil unionoid glochidia were discovered in the Miocene by Gross and Piller 2018). The gill anatomy of adult Unionida, on the other hand, has a better preservation potential than their larvae, because of the presence of chitinous gill supports with calcium concretions ("calcified rods" formed from calcium phosphate), a feature present also in the gills of marine trigoniids, closest living relatives and possible ancestors of Unionida (Ridewood 1903; Silverman et al. 1989; Whyte 1991; Richard et al. 1991; Wilby and Whyte 1995; Torrens et al. 2000; Hinzmann et al. 2015). These concretions are known to serve as a source of calcium for mineralization of unionoid offspring shell in calcium-poor freshwater habitats (Silverman et al. 1985, 1987, 1989). Both Trigoniida and Unionida share similarities in general anatomy, shell microstructure, and gill physiology, e.g., ciliary patterns (Tevesz 1975; Morton 1987; Graf and Cummings 2006). Filibranch gill anatomy is present in both fossil and living trigoniids, while only the oldest unionoids share this character with their trigoniid ancestors. All the living members of the Unionida today share the eulamellibranch anatomy of their gills, additionally modified for brooding (Klug et al. 2005; Graf and Cummings 2006; Skawina and Dzik 2011; Skawina 2021).

Eulamellibranch gills have transverse interfilamentar tissue junctions, which connect gill filaments (of which gill supports are their skeleton) side by side within the demibranchs (see for definition in Carter et al. 2012; Knight et al. 2014). Such arrangement allows for a "basket" shape anatomy of the demibranchs to form. In contrast, in filibranch gills, the gill filaments are connected by the ciliary connections only, the so-called "ciliated discs" of interlocking cilia, which facilitate the mechanical disconnection and reconnection of single filaments, and the shuffled arrangement of filaments; see SOM 1: A–G, Supplementary Online Material available at http://app.pan.pl/SOM/app70-Skawina_Ghilardi_SOM.pdf; see Ridewood 1903; Knight et al. 2014; Freitas et al. 2022). The filibranch anatomy of the gills does not exclude larval brooding behavior, but the incubation of embryos is in the mantle (infrabranchial) cavity, not within the gills (Morton 1978; Mackie 1984).

Although the eulamellibranchy provides the crucial ability for unionoids to live in freshwaters to brood the embryos inside their gills, and all Recent members of Unionida share this trait, the oldest putative eulamellibranch gills in this group are currently known from the Senonian, Upper Cretaceous of Brazil (single specimen in Simone and Mezzalira 1993). The Jurassic age of other examples of soft tissue gill preservation in unnamed fossils and unnumbered unionoids was once mentioned by Richard et al. (1991: 1753): "Fossil records contain phosphatized impressions in unionid gills from sample dating back to the Jurassic period. Apparently these fossil bivalves contained calcium concretions and calcified chitinous rods (B. Runyger, British Museum of Natural History, personal communication)." Finally, the phosphatized gills in unionoids were more recently described in two specimens of *Silesunio parvus* from the Upper Triassic of Poland (Skawina 2010; Skawina and Dzik 2011), but these gills share their filibranch gill anatomy with trigoniid ancestors, and no transverse tissue connections were observed.

In this paper, a new Late Triassic material is described for the first time. This includes new findings of: Carnian *Silesunio parvus*, Norian *Tihkia*? sp. and Norian–Rhaetian *Tihkia silesiaca* specimens. These specimens join the two previously described specimens of *S. parvus* (ZPAL Ab. III/2168 and ZPAL Ab. III/2208) and are the only known specimens with the potential to provide data about gill microstructure. This material provides an exceptional opportunity to constrain the early evolution of eulamellibranchy and reproductive behavior in Unionida in the Triassic, at the time when crucial adaptations to the successful dispersal in freshwaters worldwide probably emerged or were already established. This material also allows to observe the anatomy of these crucial soft tissue organs in a sequence of a dozen million-year time intervals. The paper also contains a reinvestigation of younger Mesozoic (Cretaceous)

Fig. 1. Late Triassic Unionida *Silesunio parvus* Skawina & Dzik, 2011, with preserved gills, from Carnian, Krasiejów, Poland. **A**. ZPAL Ab. III/2209. → A_1, preserved larger fragments of demibranchs visible in dorsal-middle areas both valves of the bivalve; A_2, right-valve gills with 22 parallel gill supports, likely collapsed in the middle, preserved as paired dark-brown linear structures continuing into deposit-color lines; A_3, left valve gills with brownish demibranchs fragmented into sections, gill supports are shuffled and tangled, transported within the valve and thus coming from outer or inner demibranchs, or from both. **B**. ZPAL Ab. III/2214. B_1, probably a complete inner and outer demibranchs in three-dimensional preservation; gill supports of demibranchs start near the area of umbo and continue up to near the posterior end of the bivalve.; one (outer?) demibranch is translocated toward the ventral part; the gills in the center of the shell are preserved as brownish linear structures, otherwise in the color of the deposits. B_2, brownish (collapsed in the middle?) gill supports visible as fine paired linear structures, shuffled and tangled within the demibranch; underneath the layer, the gill supports likely belonging to the inner demibranchs visible. **C**. ZPAL Ab. III/2216. C_1, interpreted parts of inner and outer demibranch, arranged in opposite directions while the lines of attachment of gill supports of each demibranch are slightly shifted from each other. Some of the gill supports are shifted according to their neighbors ones (black arrows). C_2, indicated with white arrows examples of collapsed middle part of each gill support visible as deposit color-line surrounded by brownish parallel lines. **D**. ZPAL Ab. III/2215. D_1, two partially preserved demibranchs, and one (outer?) translocated toward the ventral part of a bivalve, gill supports brownish, collapsed, in majority parallel to each other. D_2, detail showing translocated demibranchs; no tissue junctions between adjacent filaments are visible. **E**. ZPAL Ab. III/4409. E_1, brownish, mostly parallel lines of believed gill supports covering the middle part of the left valve of the bivalve. E_2, brownish linear structures devoid of the collapsed central part of each line, thus different from the other examples.
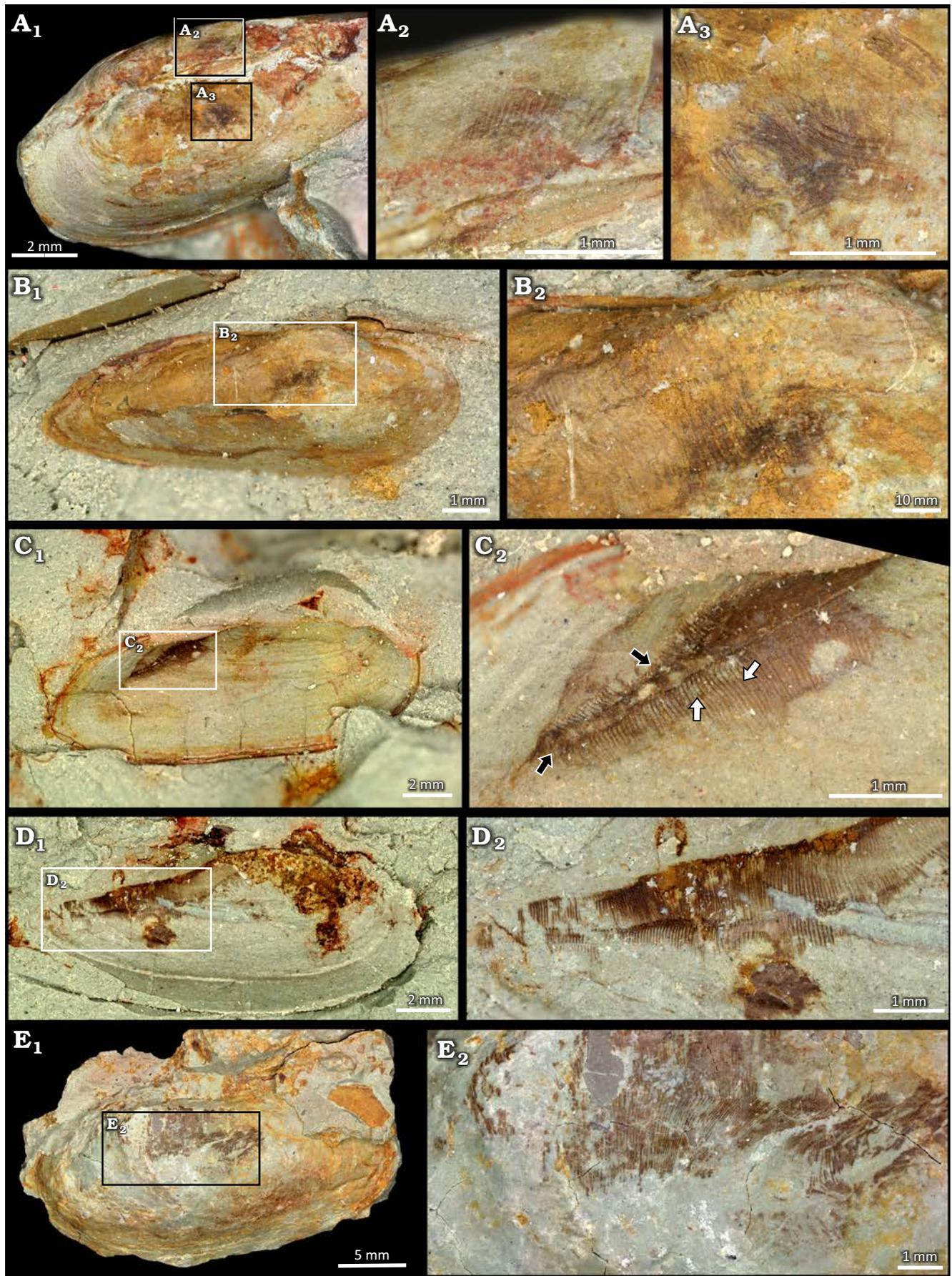
specimens bearing fossilized gills, unnamed specimen(s) from the Lower Cretaceous of the United Kingdom and *Anodontites freitasi* from Upper Cretaceous of Brazil, which provide additional information about the evolution of eulamellibranchy in Unionida during the Mesozoic.

Institutional abbreviations.—IG, Geological Institute of the State of São Paulo, São Paulo, Brazil; NHMUK, Natural History Museum, London, United Kingdom; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Material and methods

Locality descriptions.—Three localities, Krasiejów, Poręba, and Lipie Śląskie-Lisowice, with freshwater Keuper (Upper Triassic) strata in Silesia and the Kraków-Częstochowa Upland of SW Poland are known for spectacular vertebrate fossils like dipnoan and ganoid fishes, large temnospondyl amphibians, and aquatic and land reptiles of different lineages, including phytosaurs, dicynodonts, archosauromorphs, carnivorous archosaurs and turtles (e.g., Dzik et al. 2000, 2008; Dzik and Sulej 2007; Sulej et al. 2012).

Locality Krasiejów, near Opole, SW Poland preserves fossils of middle–late Carnian age. *Silesunio parvus* occurring in lacustrine deposits therein, preserves juvenile sculpture on the post-larval shell, calcified shells or internal molds with muscle attachment scars, and those with phosphatized gills (e.g., Skawina and Dzik 2011; Skawina 2013). The features mentioned above are variably preserved in the fossiliferous interval studied (about 1 m thick), however, the specimens with phosphatized gills were discovered only within a thin "yellow basal mudstone layer" on the very bottom of the profile (Skawina 2013: fig. 4).

Locality Poręba, near Zawiercie, Kraków-Częstochowa Upland, SW Poland, preserves fossils of the Norian age. This locality is famous for the occurrence of the *Proterochersis porebensis* turtle (Szczygielski and Sulej 2016). The fluvial strata at Poręba are about 6 m thick, comprising yellowish conglomerates with bones, and grey mud- and claystones interbedded with sandstones (Sulej et al. 2012; Szczygielski and Sulej 2016). Bivalves are occasionally found as shell imprints, calcified shells, and internal molds with preserved muscle scars. Specimens with preserved gills were only discovered as internal molds. These molds were concentrated due to Recent weathering and rainwater washing across the exposed strata.

Locality Lipie Śląskie-Lisowice near Lubliniec, SW Poland preserves fossils of the late Norian–Rhaetian age. The locality is chiefly known for its large dicynodonts and the large predatory archosaur *Smok wawelski* (Dzik et al. 2008; Niedźwiedzki et al. 2012; Kowal-Linka et al. 2019). The locality is currently flooded clay-pit but at the time of collection it was approximately 12 m thick section exposing fluvial deposits consisting mostly of grey silt- and mudstones interbedded with sandstones. Unionoid bivalves *Tihkia silesiaca* are preserved as internal molds with preserved muscle attachment scars, and poorly preserved shell imprints (Skawina and Dzik 2011). The phosphatized gills were only found on two specimens, partial internal molds pressed with the rock with a poorly preserved shell palimpsest on it.

The provenance and age of Mesozoic unionoid bivalves from the UK, mentioned by Richard et al. (1991) in the collection hosted by NHMUK is unclear. Re-examination of this collection led to the re-discovery of a drawer of selected internal molds of Mesozoic trigoniids (a dozen of specimens) and unionoid (single specimen) with preserved gill tissues (thank to analyses of Noel J. Morris, NHMUK and Martin A. Whyte, Sheffield University; AS personal communication with Katie Collins, 2024). Some trigoniids in the material in question, like *Laevitrigonia gibbosa*, NHMUK PI MB 2424, came from the Upper Jurassic limestones, in the Isle of Portland, Dorset, UK (see Wilby and Whyte 1995; Torrens et al. 2000; see SOM 2). However, the single internal mold originally labeled as *"Unio porrectus"*, NHMUK PI MB 2396, had limited information regarding the locality of origin. The specimen's collection number and accompanying notes (including names of Martin A. Whyte, who also mentioned an unnamed single fossil Early Cretaceous unionoid in Whyte 1991), and original taxonomical assignment indicate its origin from the lowermost Lower Cretaceous of Wealden Group, comprising non-marine mudstones and sandstones (Newton 1910; Radley 2006; Radley and Allen 2012).

The Late Cretaceous (Senonian) *Anodontites freitasi*, IG 1033-I comes from the Adamantina Formation, Bauru Group, containing terrestrial vertebrates like titanosaur *Gondwanatitan*; Kellner and Azevedo 1999; Bandeira et al. 2016; Aureliano et al. 2021). This specimen has been discovered in a brown sandstone cropping out at the railway line, 16 km from Adamantina toward Flórida Paulista city (Simone and Mezzalira 1993). It has been described and illustrated previously by Simone and Mezzalira (1993). The age of these strata is unclear (e.g., Simone 1994; Nava and Martinelli 2011; Ghilardi et al. 2011; Silva Junior et al. 2022), but is most likely Senonian. IG 1033-I is preserved as an internal mold.

Methods.—The surface of specimens were examined under optical magnifiers and Keyence digital microscope, with acquired digital images analysed further on the screen). The lack of tissue connections between gill supports, thus filibranchy, was inferred when no visible interlamellar tissue junctions were observed. Such junctions are assumed to have been visible if present according to experimental taphonomy and comparison with other fossil material (Skawina 2010; Knight et al. 2014; SOM 1). Likewise, the presence of shuffled gill supports possible due to the disconnection of interlocking cilia, could also be visually detected if present (e.g., Klug et al 2005). The presence of the tissue connections between gill supports, thus eulamellibranchy, was inferred by observing the interfilamentar tissue junctions themselves and the parallel arrangement of gill supports as a result of these tissue junctions.
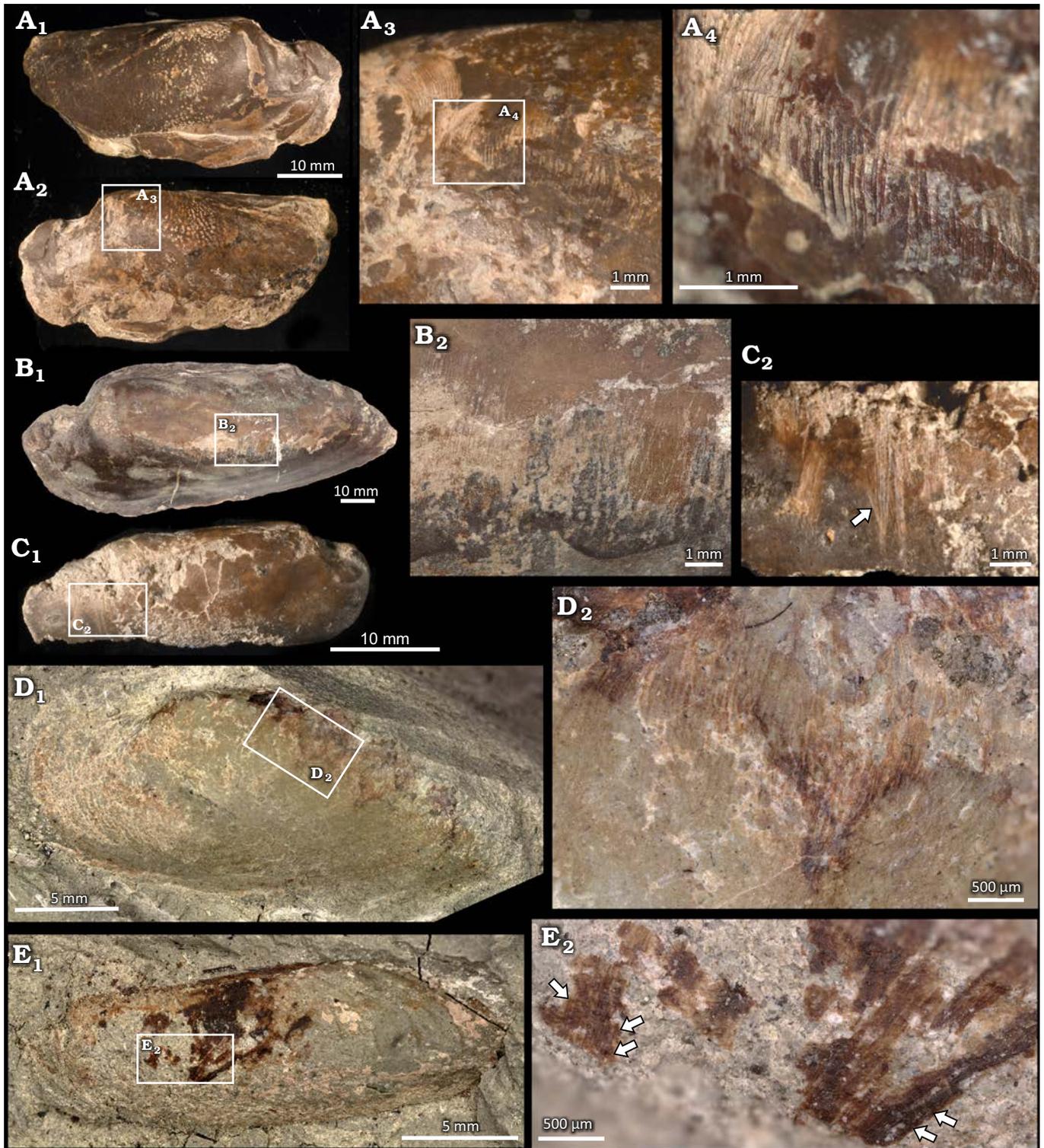
Fig. 2. Late Triassic Unionida *Tihkia*? sp. from Norian, Poręba, Poland (A–C) and *Tihkia silesiaca* Skawina & Dzik, 2011, from Norian–Rhaetian, Lipie Śląskie-Lisowice, Poland (D, E). **A**. ZPAL V. 39/496, internal mold. A_1, right lateral view; A_2, left lateral view, with brownish three-dimensionally preserved linear structures, likely a few fragments of torn demibranchs; A_3, A_4, details with paired brownish linear structures interpreted as gill supports; the gill supports are here collapsed in the middle. **B**. ZPAL V. 39/473, internal mold. B_1, left lateral view with multiple parallel linear structures; B_2, detail of parallel linear structures. Linear structures interpreted as gill supports are preserved brighter than the sediment. **C**. ZPAL V. 39/474, partially preserved, damaged internal mold. C_1, whitish linear structures interpreted as gill supports forming what resembles a demibranch; C_2, a fragment of which looks partially rotated from the natural position, from the surface into the depth of the specimen (arrowed). **D**. ZPAL V. 33/298, left valve imprint with darker and lighter brownish linear structures corresponding to gill supports; these form a poorly preserved larger fragment of a demibranch in middle-dorsal area of the specimen (D_1); D_2, single gill supports are interpretable, collapsed in the middle, note the tangled arrangement. **E**. ZPAL V. 33/305, poorly preserved left valve imprint with a dark brownish area of poorly preserved, phosphatized gill supports (E_1); E_2, detail with single gill supports recognizable (arrows).

Results

Carnian (Triassic).—Two specimens (ZPAL Ab. III/2168 and 2208) were already described in Skawina (2010) and Skawina and Dzik (2011). Five new specimens (ZPAL Ab. III/2209, 2214–2216, 4409), all preserved as partial molds with shell imprints (probably a kind of shell "palimpsest") have been discovered since then. Only ZPAL Ab. III/2209 (Fig. 1A) has both valves nearly shut close, while remaining has either a single valve, or two valves preserved in a butterfly position (Fig. 1B–E) (Skawina and Dzik 2011: fig. 1; SOM 1: G–J herein). None of them form a complete internal mold. The gill supports of demibranchs are preserved as brownish linear structures three-dimensionally preserved or flat, partially as color imprints (see Fig. 1A$_2$, B, SOM 1: G–J). The demibranchs are recognizable as more (Fig. 1A$_2$, B–D) or less (Fig. 1A$_1$, A$_3$, E) complete fragments. They are located in the center and dorsal part of the shell area, expanding to the posterior part of the bivalve, which corresponds to their expected anatomical position (see SOM 1: A). In ZPAL Ab. III/2214–2216 parts of both the inner and outer demibranch are visible. Gill supports are preserved as most commonly brownish, paired linear structures with a mid-deposit color line that likely corresponds to decay-driven collapsed gill supports, which are torn in the mid-line (compare with SOM 1: D, F). Only ZPAL Ab. III/4409 bears brownish flat linear structures with no change in color in the middle (Fig. 1E). No signs of connections between gill supports are recognizable in all these specimens, while some fragments of filaments are shuffled or tangled (e.g., Fig. 1A$_1$, A$_3$, C$_2$).

Norian (Triassic).—All the specimens of *Tihkia*? sp. are preserved as internal molds. Those are: the best preserved ZPAL V. 39/496 (Fig. 2A$_1$–A$_3$), and ZPAL V. 39/473 and ZPAL V. 39/474. Both latter specimens show whitish repeated parallel lines typical for the demibranch position (Fig. 2B, C). ZPAL V. 39/496 preserves a few fragments of a demibranch comprising of dark-brown paired, parallel linear structures, in the middle and dorsal area. These structures are similar in shape to equivalent structures in *S. parvus* and of Recent decaying material (SOM 1: D, F). No morphological observation of tissue connections is visible in this material.

Norian–Rhaetian (Triassic).—The specimens of *Tihkia silesiaca* with fossilized gills are poorly preserved. Two specimens, ZPAL V. 33/298 and ZPAL V. 33/305, have brownish areas in the middle or dorsal-middle of the shells. ZPAL V. 33/298 is a left valve. It has visible darker and lighter brown linear structures interpreted as gill supports, which are corresponding to the expected position of demibranchs (Fig. 2D). The lighter brown part expands toward the posterior part of the specimen; here, some filaments are translocated/shuffled (Fig. 2D$_2$). The second specimen is a right valve ZPAL V. 33/305. It preserves an agglomerate of brown linear structures that is difficult to interpret, however, single structures are distinguishable (Fig. 2E). The poor preservation of these specimens does not allow for inquiries about the possible presence or absence of interfilamentar tissue junctions of filaments.

Early Cretaceous.—NHMUK PI MB 2396 is an internal mold, originally labeled as "*Unio porrectus*". It displays an agglomerate-like area in the postero-middle part of the left side (Fig. 3A–D). The area, ca. 20 mm long and 10 mm wide, consists of delicate whitish linear structures similar to gill supports and situated in the area of the expected demibranch position. The preservation state of this structure prevents more detailed morphological analysis or discussion of the presence/absence of interfilamentar tissue junctions of filaments. The specimen has its muscle attachment scars visible. The presence of a few minute attachment scars inside the umbonal cavity, and absence of a strong, commonly single pedal elevator in the apex of each umbonal cavity which is typical for Trigoniida (Newell and Boyd 1975; Graf and Cummings 2006; Skawina and Dzik 2011) suggests unionoid affinities of this specimen (Fig. 3A$_5$, A$_6$).

Late Cretaceous (Senonian).—The specimen of *Anodontites freitasi*, IG 1033-I, is an internal mold. The fossilized fragment of a demibranch is preserved on the middle-dorsal area of the left side of the specimen. This structure is about 10 mm long and 5 mm wide. It is preserved as a whitish net-like of vertical and horizontal linear structures. The horizontal structures may correspond to gill supports, while the vertical structures indicate the presence of the interfilamentar tissue junctions preserved in this specimen.

Discussion

Phosphatized soft tissues were previously occasionally reported from mollusks (e.g., mantle, muscles in cephalopods; Allison 1988; Wilby and Briggs 1997; Wilby et al. 2004), while only a few such structures were discovered in fossil bivalves (gills, muscles, sometimes labial palps; e.g., Harper and Todd 1995; Klug et al. 2005; Knight et al. 2014; Klug et al. 2022). Preservation of gills has been reported more frequently from the fossil group traditionally called the palaeoheterodonts thus Unionida + Trigoniida (e.g., Graf and Cummings 2006; Carter et al. 2011) than from other bivalve taxa. The accepted explanation is that this group have chitinous gills supports calcified, that can serve as nucleation center and source of mineral precursors which facilitate early mineralization and protect gill tissue against post-mortem decomposition (Ridewood 1903; Silverman et al. 1985; Silverman et al. 1989; Whyte 1991; Skawina 2010). Unfortunately, gill preservation in freshwater bivalves occurs rarely (Whyte 1991; Simone and Mezzalira 1993; Skawina and Dzik 2011) in comparison to trigoniids (e.g., Klug et al 2005). Also, all or most of the trigoniids with fossilized soft tissues are preserved as internal molds. Wilby and Whyte (1995) proposed that the enclosure of decaying soft tissue within the tightly closed shell was a necessary prerequisite to establish an environment enabling
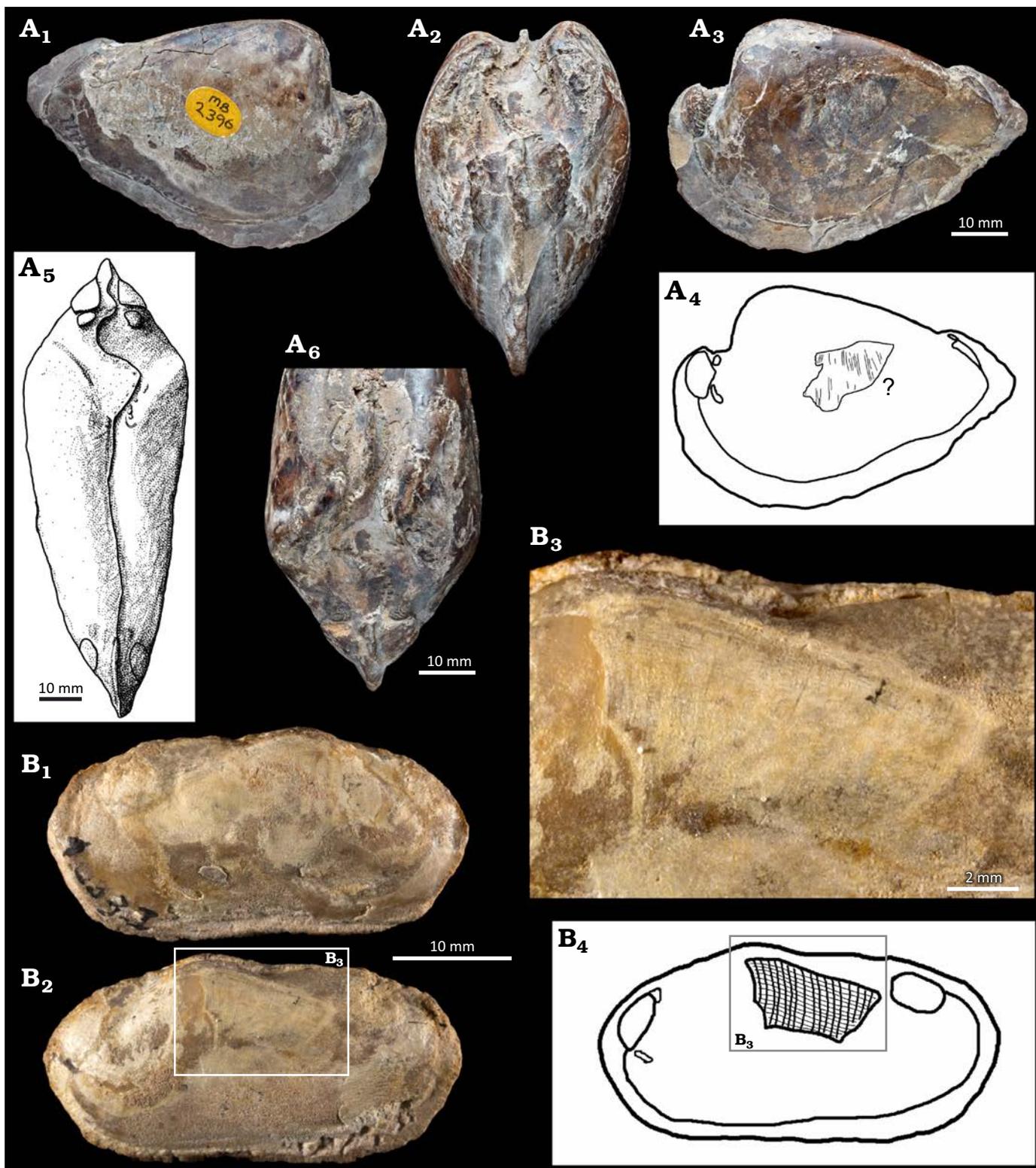
Fig. 3. Cretaceous Unionida with partial gill preservation. **A**. "*Unio porrectus*" J. De C. Sowerby, 1828, NHMUK PI MB 2396, Lower Cretaceous, Wealden Group, Isle of Portland, UK. A_1, internal mold in right lateral view; A_2, anterior view with hinge line and anterior set of muscle scars visible; A_3, left lateral view, on this side an about 20 mm long and 10 mm wide area linear structures resembling gill supports of a demibranch visible; A_4, drawing of supposed part of demibranch; drawing (A_5) and photograph (A_6) of dorsal view. The presence of a few minute muscle attachment scars in the area of the umbo suggests a relation with Unionida. **B**. *Anodontites freitasi* Mezzalira, 1974, IG 1033-I, Upper Cretaceous of Adamantina Formation, Bauru Group, Senonian, Brazil. B_1, internal mold in right lateral view; photograph (B_2) and drawing (B_4) of left lateral view in the dorsalo-middle part of this side about 10 mm length and 5 mm wide, a brighter structure is visible; B_3, a detail with area interpreted as preserved gills. The hypothesized mineralized gill supports form a net-like structure (lines are transversely connected), indicating eulamellibranch anatomy.

soft tissue mineralization. This proposition is not supported fully by the fossil record of freshwater bivalves. Although a single Norian specimen and both Cretaceous specimens studied herein are internal molds, the well-preserved gills of Carnian *S. parvus* and poorly preserved tissues of Rhaetian *T. silesiaca* occur in the specimens with open shells (or not fully opened like in ZPAL Ab. III/2209). It is possible that osmotic freshwater conditions could influence the decay and impact on early mineralization processes, or some other yet unknown traits of these particular "taphonomic window" localities were involved.

Most of the fossilized demibranchs in the specimens from the Polish Upper Triassic preserved two brownish linear structures with a break in-between. This character as interpreted by comparison with modern decaying material, could have appeared within 150 hours postmortem, providing no subsequent disturbance occurred (Skawina 2010: fig. 1; SOM 1: D–F). After this time, ciliated tissue decays and interfilamentar junctions should be visible at least in some areas of the preserved demibranchs, proving that interfilamentar junctions were initially present. Such preservation of interfilamentar junctions connecting gill demibranchs was indeed observed in the specimen of Late Cretaceous *A. freitasi*, as well as in unrelated Cretaceous inoceramid (Knight et al. 2014). However, no similar structures were observed in Carnian and Norian bivalves, and their preservation of Rhaetian and Early Cretaceous specimens did not allow for their clear interpretation. The materials studied herein, including new specimens with the oldest preserved unionoid gills, confirm the filibranch anatomy of the Carnian, Late Triassic Unionida. The same can be assumed for Norian unionoids based on morphological analyses (no interfilamentar junctions observed in preserved gills). There is thus a clear similarity between the gill anatomy of Triassic Unionida and the gill anatomy of their closest marine relatives, Trigoniida. Although filibranchy does not fully exclude it, it represents an incomplete state of maternal care in the evolution of Unionida in freshwaters. Future research, including more fieldwork and careful screening of museum collections, is needed to provide more evidence on evolution of the reproductive behavior and maternal care in Unionida.

Conclusions

A new Late Triassic fossil material of Unionida with extraordinarily preserved gill tissues is described from Poland (*Silesunio parvus*, *Tihkia silesiaca*, *Tihkia*? sp.), together with a reinvestigation of Cretaceous fossils from archival museum collections from United Kingdom ("*Unio porrectus*") and Brazil (*Anodontites freitasi).*

The preserved anatomy of gills may provide paleobiological information about the possibility of fossil behavior, brooding embryos in maternal gills (if anatomy is advanced, eulamellibranch), which is accepted as an adaptation to freshwater habitats and may support the evolutionary success of this group of bivalves.

The visible features of the gills of Late Triassic unionoids (*S. parvus* and *Tihkia?* sp.) do not support the advanced anatomy, while eulamellibranchy was confirmed in the specimen of Late Cretaceous *A. freitasi*. The preservation of gills in remaining specimens is not allowing for considerations about their anatomy, thus inferring about the detailed timing of origins of the crucial anatomical adaptations to life in freshwaters.

Author's contributions

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