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Umbonal musculature and relationships of the Late Triassic filibranch unionoid bivalves

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Exceptionally well-preserved Late Triassic unionoids from Silesia, Poland, show prominently ornamented juvenile shells and umbonal muscle attachments that are similar to *Margaritifera*, which are anatomically the least derived among extant unionoids. Their phosphatized (originally chitinous and impregnated with calcium phosphate) gill supports lacked transverse connections, and occasionally some of them were separated from others, being thus at the filibranch grade, like their trigonioid ancestors. Several separate small foot elevator attachments in these unionoids indicate Trigonodidae adaptation to marine or brackish water, in which the original trigonioid strong single attachment was already split into two in the Early Triassic. The ribbing of juvenile shells suggests a change to deeper infaunal life for juvenile stages, and generally less efficient near-surface locomotion, with a wedge-like foot, in adults. Much later the unionoids became eulamellibranchial, which promoted the brooding of the fish that their larvae parasitize. To accomodate the classification of the order under this scenario of evolutionary changes, a new suborder Silesunionina is proposed for its filibranch members. It includes the **Silesunionidae fam. nov.**, with the location of umbonal muscles similar to that in the extant underived unionoids, and the **Unionellidae fam. nov.**, with umbonal muscles attached to the external wall of the umbonal cavity. The early Late Triassic (Carnian) ***Silesunio parvus* gen. et sp. nov.** and latest Triassic (Rhaetian) ***Tihkia*(?) *silesiaca* sp. nov.** are proposed.

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INTRODUCTION

The order Unionida (= Unionoida and Unioniformes, see the taxonomic section below) comprises the largest, biogeographically most widespread, and commercially most important freshwater bivalves (Graf & Cummings, 2006; Bogan & Roe, 2008). They have played their biological role for at least two hundred million years, since the Late Triassic, but their early phylogeny and relationships remain obscure. It is clear, based both on morphology and molecular evidence, that their closest marine extant relative is the relict Australian trigoniid *Neotrigonia*. The Triassic mostly brackish-water bivalves classified in the family Trigonodidae (= Pachycardiidae) are widely believed, based mostly on their hinge structure, to link the marine trigoniids with freshwater unionoids (Newell & Boyd, 1975). This picture is somewhat complicated by the inclusion of the freshwater anthracosiid bivalves into the order Unionida. They have been known since the Carboniferous, a time when the morphological features of the trigoniids that make them similar to the trigonodids (thick shell and massive hinge teeth) or the unionoids (V-shaped umbonal sculpture) were hardly developed. The question of which of these fossil bivalves the unionoid clade was actually rooted in thus emerges. The fossil material of freshwater bivalves rarely offers enough anatomical information to solve such dilemmas, but

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*Corresponding author. E-mail: dzik@twarda.pan.pl in recently discovered localities in southern Poland, Late Triassic freshwater unionoid bivalves with preserved gills, umbonal muscle attachment scars, and juvenile shell ornament have been found (Dzik & Sulej, 2007). Here, we use evidence on these aspects of the anatomy to propose an evolutionary scenario of the origin and early diversification of the unionoid bivalves that can be matched with their molecular phylogeny.

In the following sections we present new data on the Triassic unionoids and review the available evidence on the distribution of the umbonal sculpture in the Mesozoic unionoids, and the diversity of the umbonal musculature in the Palaeozoic trigonioids and anthracosiids, as well as in their possible Triassic relatives. This will be used to restore the succession of events leading from the Silurian emergence of the trigonioids to the late Mesozoic diversification of advanced unionoids.

MATERIAL AND METHODS

The early Late Triassic (Carnian; about 230 Myr old) rocks exposed at the Krasiejów clay pit in Silesia, southern Poland, have yielded numerous fossils of small unionoid bivalves. The fossiliferous stratum is mostly a red, fine-grained mudstone or claystone that was deposited in a vast lake covering a significant part of the central European Germanic Basin, presumably during the Lehrberg episode of sea-level rise, in a climate with dry seasons (Dzik & Sulej, 2007). Most of the specimens are preserved in claystone as imprints or natural casts of the shell surface. Although the original aragonitic shell wall is not preserved in such fossils, the imprints provide a lot of information on the external shell ornamentation owing to the fine grain of the sediment. This also applies to the umbonal parts of the shell, with ornamentation specific for the early postlarval developmental stages. Limestone concretions occurring within the claystone frequently represent internal shell moulds that show muscle scar impressions, including the adductors, pedal retractors and protractors, umbonal muscles, and the pallial line. Also, some aspects of the hinge are reproduced in negative on the moulds, as if visible from its ventral side. Rarely, in limestone grainstone intercalations, bivalve shells have been recrystalized into calcite. They show details of the hinge teeth.

The most spectacular aspect of the natural casts of the Krasiejów bivalve is that phosphatized gills have been preserved under some diagenetically dissolved shells that are open, in ‘butterfly style’, or have displaced valves (Dzik & Sulej, 2007; Skawina, 2010).

In a nearby clay pit at Lipie Śląskie-Lisowice, deposits of the latest Triassic (Rhaetian; about 205 Myr old) are exposed, with numerous fossils of a large unionoid bivalve (Dzik, Niedźwiedzki & Sulej, 2008; Gorzelak, Niedźwiedzki & Skawina, 2010). The rocks there are grey and generally more coarsely grained, suggesting deposition in a wet climate. The bivalves are mostly preserved as natural casts of closed valves in marly limestone concretions within a claystone lens. Rarely, internal moulds with preserved muscle attachment scars can be found, partially covered with the imprint of the shell as a palimpsest. They bear scars of adductors, pedal retractors and protractor, and also groups of small umbonal muscle impressions. Unlike in Krasiejów, natural casts of opened shells are very rare. In a couple of specimens phosphatized gills are preserved.

Grzegorz Racki found specimens with shell preserved in calcite in calcareous grainstone blocks dumped at Marciszów, near Zawiercie (racki, 2010). Their original location in the rock section and geological age remain unknown, but they are certainly younger than the strata exposed at Krasiejów, and are probably coeval with those at Lisowice.

Material from all Polish sites is stored in the Institute of Palaeobiology, Polish Academy of Sciences, in Warsaw, Poland (ZPAL).

Additional materials include fossil freshwater and brackish-water bivalves from the collections of the Natural History Museum (NHM), London, UK, Leicester University (LEIUG), UK, examined by the junior author, and the Museum für Naturkunde, Berlin (MfN), examined by the senior author. They provided specimens of Carboniferous *Anthracosia* and Triassic *Unionites* from various European localities, with preserved muscle scar impressions. Their locations are given in the descriptions below.

GILL STRUCTURE

The supports of the trigonioids and unionoids are impregnated with calcium phosphate that readily crystallized during fossilization (Whyte, 1992). Unlike *Neotrigonia*, all extant Unionida bear eulamellibranch gills, i.e. with filaments connected by transverse junctions (e.g. Graf & Cummings, 2006). Experimental decay of gills of *Unio* exposes chitinous gill filament supports with such junctions, even in very decayed tissue, and so their presence should thus be expected in fossilized specimens. Yet, in the Krasiejów freshwater bivalves the phosphatized gill supports lack such junctions (Fig. 1; Skawina, 2010). In places where skeletons of the superimposed gill blades are exposed, the complete depth of the supports is visible, thereby excluding the possibility that the junctions have been overlooked. Potentially, the filaments in such an ancient Late Triassic form could be connected only by soft tissue, without a chitinous

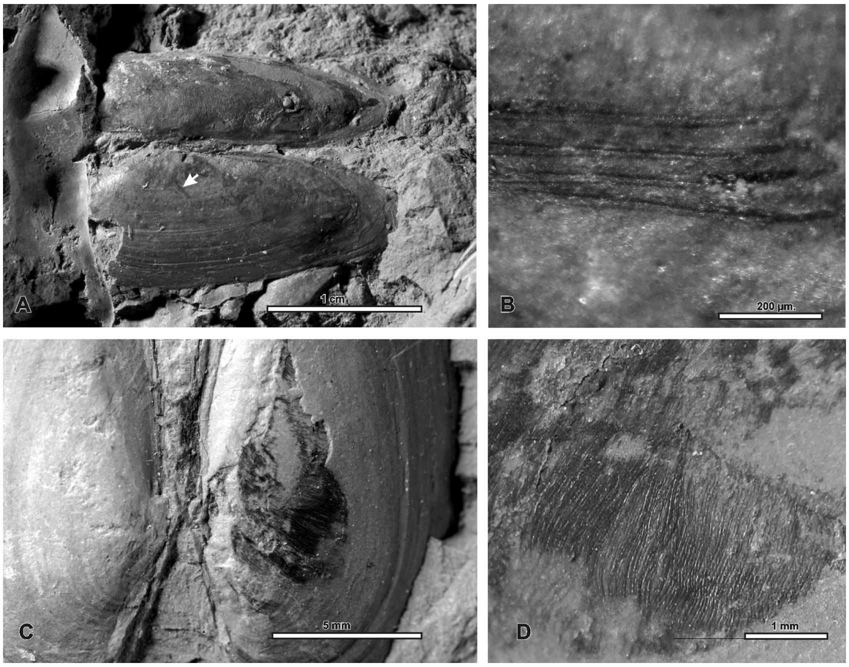

Figure 1. Phosphatized gill supports in ***Silesunio parvus* gen. et sp. nov.** from the early Late Triassic lacustrine deposits at Krasiejów, Southern Poland. A, general view of specimen ZPAL AbIII/2208 with valves in 'butterfly position'; gills visible as darker striated structures owing to staining with dark iron minerals. B, displaced sets of gill supports show bending independent of each other owing to the lack of interconnections (which proves a filibranch organization). C, D, specimen ZPAL AbIII/2168 with a more typical preservation of gill blades.

internal skeleton. This seems to be excluded by the occasional divergence and deformation of particular supports, independent of their neighbours in folded parts of the gills. Interfilamentous junctions of the eulamellibranch-grade gills are fossilized, as shown by their preservation in the Late Cretaceous phosphatized gills of the mycetopodid (thus a member of the hyriid clade) *Anodontites freitasi* (Lopes de Simone & Mezzalira, 1993). Most likely, the Triassic bivalves from Krasiejów had filibranch-grade gills. These make them similar to roughly coeval marine trigonioids with fossilized gills (see Torrens *et al.*, 2000; Klug, Hagdorn & Montenari, 2005).

Although the filibranch trigonioid gill anatomy differs from that of the extant Unionida, the ctenidial ciliary pattern of *Neotrigonia* resembles that of the unionoids (Tevesz, 1975), and members of both orders posses chitinous gill supports partially impregnated with calcium phosphate (occurring in specialized cells; Ridewood, 1903; Morton, 1987; Silverman, 1988; Silverman *et al.*, 1989; Whyte, 1992).

The close affinity of the marine *Neotrigonia* and freshwater unionoids is generally accepted (Waller, 1998; Graf & Ó Foighil, 2000; Hoeh, Bogan & Heard, 2001; Giribet & Wheeler, 2002). This is supported by: the hinge structure and shell musculature (Newell & Boyd, 1975); the ultrastructure of sperm, with unique, multiple, unfused proacrosomal vesicles in mature spermatozoa (Healy, 1996); and molecular phylogenetic evidence (Hoeh *et al.*, 1998). Among plesiomorphic aspects of the trigonioids, the byssal organ in juveniles (Gould, 1969), their aragonitic nacreous shell, free mantle margins, and striated teeth of the hinge were inherited by the unionoids (Graf & Cummings, 2006). The Margaritiferidae, comprising the least-derived extant unionoids, still do not have siphonal cavities separated by the posterior mantle fusion, being on the level of *Neotrigonia* (Gould & Jones, 1974; Graf & Cummings, 2006), although in both a division of the mantle cavity is functionally achieved by the pallial ridges (Gould & Jones, 1974; Smith, 1980). The Triassic unionoids from Silesia show ridges on the shell that possibly correspond to the incipient separation of apertures.

As an expression of its somewhat advanced evolutionary status, *Neotrigonia* lacks a typical veliger, and does not rely on planktotrophy to fuel prejuvenile ontogeny (Ó Foighil & Graf, 2000), whereas all recent members of the Unionida are characterized by freshwater habitat (Graf & Ó Foighil, 2000; Graf & Cummings, 2006) and ovoviviparity, with larvae obligately (with a few exceptions, e.g. Allen, 1924) parasitizing the gills, fins, or skin of a specific host fish or amphibian (Howard, 1951; Watters & O'Dee, 1998; Wächtler, Dreher-Mansur & Richter, 2001). The larvae must infect an appropriate fish host to complete their development and metamorphosis (Lefevre & Curtis, 1908; Kat, 1984; Bauer, 2001; Wächtler, Dreher-Mansur & Richter, 2001).

The early Late Triassic bivalve from Krasiejów may thus represent a connecting link between bivalve orders, still having gills similar to its marine trigonioid ancestor but with shell morphology and freshwater habitat typical of the unionoids. No evidence is available regarding possible brooding chambers in its gills (marsupia) or parasitic larval stages (glochidia), but the juvenile shell morphology indicates an early postlarval development similar to extant unionoids.

JUVENILE SHELL SCULPTURE

All extant members of the Unionida have parasitic larvae (glochidium, lasidium, or haustorium; see Parodiz & Bonetto, 1963; Wächtler *et al*., 2001). It may thus be expected that this was also the case with its last common ancestor, living before the Mid Jurassic, when advanced unionoids undoubtedly already existed. Nevertheless, the oldest fossil larvae – glochidia – are found geologically as late as the Pleistocene (Brodniewicz, 1968), and are thus not informative regarding the question of when the Unionida acquired parasitic larvae.

In all recent unionoids, a juvenile digs itself into well-aerated sediments after leaving the fish (reaching depths from a few up to 30 cm; Piechocki & Dyduch-Falniowska, 1993; Wächtler *et al*., 2001; Schwalb & Pusch, 2007), to grow there to a size of up to 2 cm in length (Bauer, 2001; Strayer, 2008). The shell of such juveniles usually bears prominent ridges (Modell, 1942), in contrast to mature, usually smooth, unionoid shells, but similar to many advanced trigonioids. This led to the suggestion that the nodose juvenile shell ornament is a plesiomorphic trait inherited after the trigonioid ancestor (Graf & Cummings, 2006). Some authors propose that such sculpture derives from the trigonioid ancestor (Watters, 1994). It is thus very confusing to note that the beak sculpture of young shells in the least anatomically derived extant unionoids, *Margaritifera*, shows concentric growth lines that are just a little more prominent than the growth lines on the rest of the shell (Fig. 2B). A very similar umbonal ornamentation is shown by the unnumbered NHM specimen from the early Eocene of Soisson, France, labelled '*Unio*

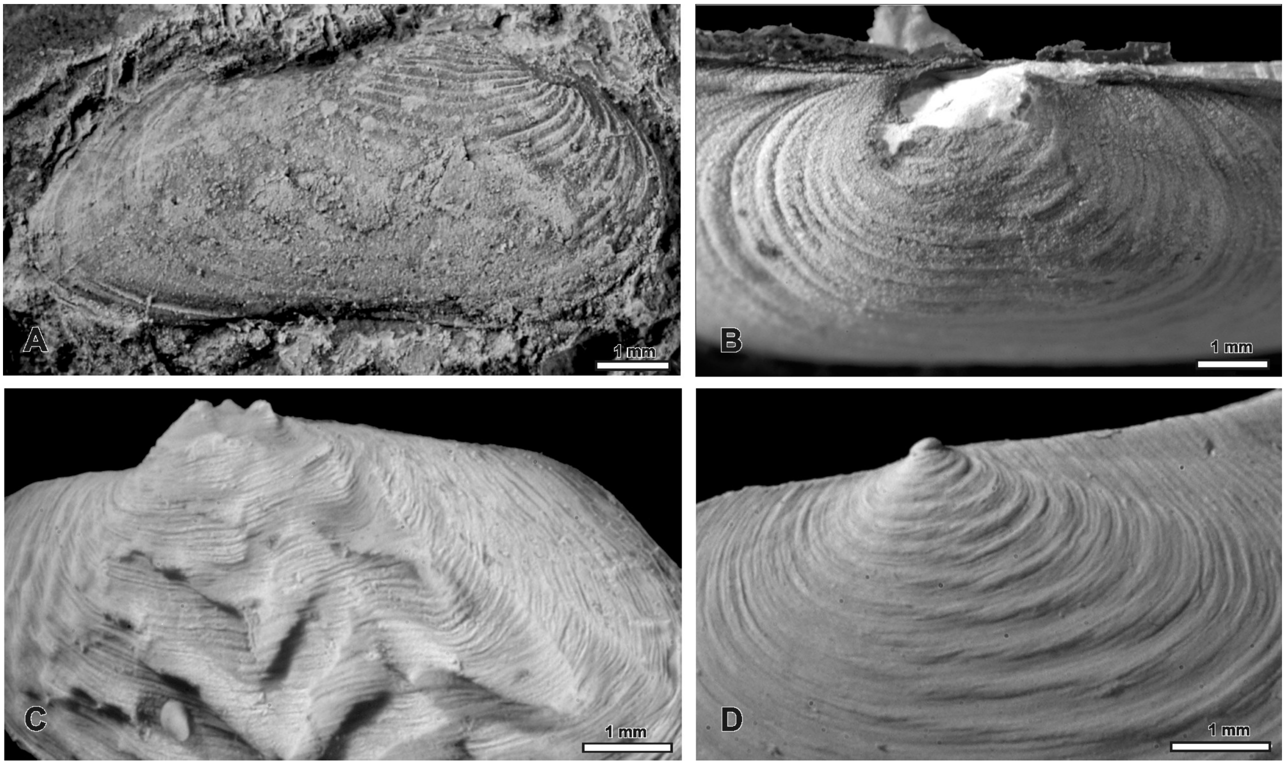

Figure 2. Beak sculpture on the shell of various unionoids. A, juvenile holotype specimen ZPAL AbIII/2210 of ***Silesunio parvus* gen. et sp. nov.** from the early Late Triassic of Krasiejów. B, juvenile recent *Margaritifera margaritifera* from a stream in Germany (specimen collected and supplied by Reinhard Altmüller). C, recent *Unio tumidus* from Krutynia River, Poland. D, *Anodonta anatina* from the same site.

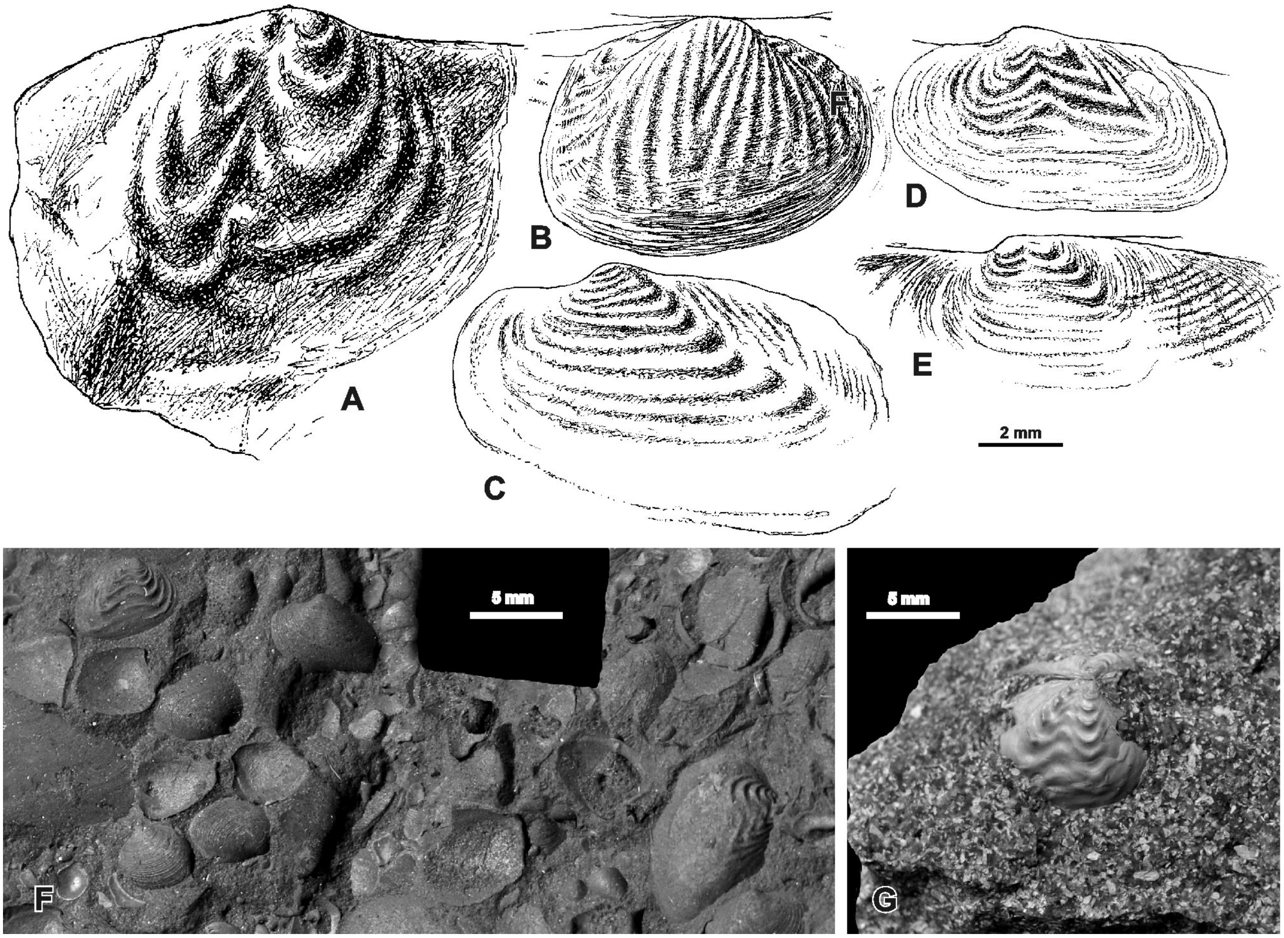

Figure 3. Beak sculpture of the unionoids. A, '*Unio*' *andersoni* Hudson, 1963, specimen LEIUG 110395, from the Mid Jurassic (Bathonian) Kildonnan Member of the Lealt Shale Formation, Scotland. B, *Parreysia* from the Pliocene of Sivalik, India (unnumbered specimen associated with specimen NHM 83043). C, '*Unio wateleti* Deshayes', 18, unnumbered NHM specimen from the early Eocene of Soisson, France. D, '*Unio*' *solandrei* Sowerby, 1826, specimen NMH 72606 from the late Eocene Headon Beds at Hardwell, England. E, '*Unio*' *valdensis* (Mantell, 1844), specimen NHM HGR 52 392828 from the Early Cretaceous (Hauterivian?) Wealden beds at Brook village, Isle of Wight. F, '*Unio*' *gualterii* Sowerby, 1836 from the Wealden Hastings Sandstone at Royal Tunbridge Wells, England, specimen MB.M. 6915. G, '*Unio*' *menkei* Koch & Dunker, 1837, diluvial erratic boulder from Kreuzberg, Berlin, specimen MB.M. 6907. (A–E, camera lucida drawings).

wateleti Deshayes' (Fig. 3C), which shows that this morphology is likely to be plesiomorphic. In fact, juvenile ornamentation with virtually concentric prominent ribs characterizes the unionoids as being as old as the Early Cretaceous (Aptian–Albian) *Protelliptio hamili* (McLearn, 1929) from the Blairmore Formation of Alberta (Yen, 1946) and *Protelliptio douglasi* (Stanton, 1903) from the Kootenai Formation of Montana (Yen, 1950). Delvene & Araujo (2009: figs 3, 4) illustrated an Early Cretaceous unionoid with apical shell ribbing closely similar to recent *Margaritifera*, but unlike the associated '*Margaritifera*' *idubedae* (Palacios y Sànchez, 1885), as classified.

That this is not a reversal from the original state is supported by the apical shell morphology of the Triassic unionoid from Krasiejów. There, growth lines are also strictly parallel with the mantle margin, but much more prominent than in the more advanced ontogenetic stages (Fig. 2A). Nineteen such concentric riblets were counted in specimen ZPAL AbIII/2210, they are 0.08 mm apart near the umbo and 0.16 mm near the end of this growth stage. The growth increments following it are generally irregular and obscure, but in places their rather rhythmic distribution suggests daily increments, with a distance of 0.13 mm separating each of them. The ornamentation of the juvenile shell appears to be highly inherited, and is therefore a reliable character for species-level taxonomy (e.g., Ortmann, 1912; McMichael & Hiscock, 1958; Good, 1998). More general aspects of the juvenile shell ornament have long been recognized to have systematic significance at the family or subfamily level, although it is rarely known in the fossil material (McMichael, 1957); for example, Haas (1969a, b) defined the subfamily Hyriinae by its radial beak sculpture. Although common in mollusks, secretion of elevated ribs at locations that migrate along the growing mantle margin (a necessary prerequisite of V-shaped or zigzag patterns) is not trivial, and requires precise morphogenetic control (Savazzi & Yao, 1992; Watters, 1994). The coincidence between the change in behaviour of a growing unionoid and its shell ornamentation suggest that it is of some functional importance. It has been proven by experiments with mature shells of strongly ornamented unionoid species that the ribs oblique to the shell margin help to anchor them in the sediment while digging (Watters, 1994), in the same way as terrace lines are proposed to work in arthropods (Vinther & Briggs, 2009). If so, their evolutionary transformation was under selection control, and should be more or less directional (Watters, 1994). The main source of skepticism regarding the taxonomic value of shell ornamentation in the unionoids is its rather chaotic distribution within many families of the order. Genera believed to be closely related may have a smooth beak or have V-shaped, zigzagged, or radial ornamentation. This could hardly have originated randomly (although secondary losses are likely), and it is the duty of palaeontologists to trace routes of transformation from one sculptural pattern to another. Unfortunately, the published evidence is too scarce to propose an evolutionary scenario of such changes at the moment.

The Hyriidae are the most basal among the Unionida, with prominent zigzag-shaped beak sculpture that sometimes also occurs on the adult shell (Haas, 1969a, b; Watters, 1994). Their extant members have glochidial larvae (Graf & Cummings, 2006), but are more derived than the margaritiferids in having full mantle fusion and the marsupia only in the inner demibranchs (Hoeh *et al*., 2001). It is generally believed that their fossil record starts from the early Late Triassic Chinle Formation, and that these are the oldest unquestioned freshwater unionoids (Reeside, 1927; Good, 1989, 1998; Watters, 2001). Among the Late Triassic unionoids, beak ornamentation occurs in '*Diplodon*' *gregoryi* Reeside, 1927 from the Shinarump conglomerate (basal Chinle Formation) of Arizona, and in '*Diplodon*' *dockumensis* Simpson, 1896 and *Archiparreysia haroldi* (Reeside, 1927), which are both from the Dockum Group of Texas. '*Diplodon*' *gregoryi* and *Antediplodon pennsylvanicus* (Pilsbry, 1921) from the Norian Stockton Formation of Pennsylvania have radial ribs over the whole shell surface, which is a rather unexpected state in the earliest unionoids. In '*D.*' *dockumensis*, delicate radial riblets are restricted to the juvenile stage and, together with the shell morphology, are consistent with its unionoid nature, but this pattern could have easily developed independently of that known in later hyriids.

The most puzzling of the Triassic unionoids is *Archiparreysia haroldi*. In a much-retouched photograph oblique ribs cross each other at an angle, a pattern known in recent hyriines (Modell, 1942), but Modell (1964: 106) classified his new genus in the quadruline unionids. However, the presence of either the Hyriinae or Quadrulinae in the Triassic requires confirmation with more reliable material, because of a gap in the record covering all of the Jurassic period. A pattern of the apical shell ornamentation somewhat similar to that in the Triassic '*Diplodon*?' *haroldi* characterizes the Early Cretaceous *Teruella*. It may be derived, however, from the unionid pattern of the kind known in roughly coeval *Sulcatapex*: i.e. the oblique ribs being transformed into rows of tubercles, as suggested by the morphology of the apex (Mongin, 1978: fig. 7). Their homology remains to be carefully traced.

Until now, the oldest finding of an undoubted unionoid with oblique ribs on the juvenile shell is '*Unio*' *andersoni* Hudson, 1963 from the Mid Jurassic (Bathonian) Kildonnan Member of the Lealt Shale Formation, Scotland (Hudson, 1963). At the tip of the shell LEIUG 110395 (Fig. 3A) there is a series of five or six zigzag-shaped ribs, covering about 6 mm of the shell height. In the anterior half of the shell they are almost parallel with the growth increments, except for some undulation; in the midlength they rise adapically into an A shape, and form a lobe in the posterior part of the shell. Among the few early unionoids with apical sculpture that are known well enough to be compared against, the Early Cretaceous (Barramian–Albian) '*Unio*' *heilonjiangensis* (Sha & Fürsich, 1993) is morphologically intermediate between the umbonal ornamentation of the Triassic species from Krasiejów (or *Margaritifera*) and that in '*U.*' *andersoni*. Pan & Sha (2009) described a Mid Jurassic unionoid that they classified in the recent unionid genus *Cuneopsis*, but neither its juvenile shell ornamentation nor umbonal musculature is known to support such a classification.

The pattern observed in the Recent European species of *Unio* is more advanced, and can be derived from that in '*U.*' *andersoni*, except for a tendency for more prominent undulations in the anterior lobe. This pattern is typical of *Vetulonaia* species from the Late Jurassic (Kimmeridgian) Morrison Formation of Colorado (Branson, 1935; Holt, 1942). The Early Cretaceous Wealden (Barremian) '*Unio*' *gualterii* Sowerby, 1836, from Royal Tunbridge Wells, UK (specimen

MB.M 6915; Fig. 3F), '*Unio*' *menkei* Koch & Dunker, 1837, from Obernkirchen, Germany (MB.M 6907), and a diluvial erratic boulder from Kreuzberg, Berlin (Fig. 3G), also belong to unionids with prominent W-shaped apical ornamentation. *Sulcatapex cretaceus* Yen, 1946 from the Early Cretaceous (Aptian–Albian) Cloverly Formation of Wyoming (Yen, 1946) and '*Unio*' *solandrei* Sowerby, 1829 from the late Eocene Headon Beds of England (NHM 72606; Fig. 3D) are similar, except in that their juvenile shells are more elongated. In the latter species and '*Unio*' *valdensis* Mantell, 1844 (specimen NHM NGR 52 392828; Fig. 3E) from the Wealden (Hauterivian?) of the Isle of Wight, England, the ornamented juvenile is only about 3 mm high. '*Margaritifera*' *idubedae* from the Weald (Barremian?) of Spain (Delvene, 2005) differs from the Mid Jurassic species and from *Vetulonaia* in the somewhat wider extent of the posterior lobe. Mongin (1961) and Delvene & Araujo (2009) classified this species as *Margaritifera* because it has mantle attachment scars. This interpretation requires that the lack of W-shaped beak ornamentation in *Margaritifera margaritifera* (Linnaeus, 1758) results from an evolutionary reversal. The alternative, which we prefer, is that the mantle attachment scars are plesiomorphic (Smith, 1982), and were retained by '*U.*' *valdensis* despite its more advanced shell ornamentation.

The complex W-shaped juvenile ribbing pattern is well exemplified by a species of *Parreysia* from the Pliocene of Sivalik, India (unnumbered specimen associated with specimen NHM 83043). The ribbing extends for about 5 mm of the shell height: it was thus restricted to the juvenile developmental stage, as in *Unio*, but its homology is not apparent (Walker *et al.*, 2001). The V-shaped ribs in the shell at mid-length point to the shell venter instead of the apex: opposite to the orientation in '*U.*' *andersoni* and its relatives. *Parreysia* has marsupia on all four gill blades (Ortmann, 1910), which is a plesiomorphic trait for the Unionidae (that may have marsupia only in outer demibranchs). Several Late Cretaceous (Maastrichtian) unionids with a similar sculpture that frequently extends to mature stages (e.g. Whitfield, 1903, 1907; Watters, 2001) may represent the same clade.

However, they may also belong to the extinct family Trigonioididae, with exactly the same pattern of mature shell ornamentation, which Watters (2001: 293) has already suggested for *Yeniella paraholmesiana* (Yen, 1954), a possible synonym of *Nipponaia asinaria* Reeside, 1957. The trigonioidids with W-shaped ribs are known since the Mid Jurassic (Guo, 1998). Separation of the anterior pedal retractor attachment from that of the anterior shell adductor is the diagnostic character of the Trigonioididae, distinguishing them from extant unionids (Sha, 1992; Sha & Fürsich, 1993; Barker, Munt & Radley, 1997). Thus, to solve the question of the relationship between W-shaped ribbing in the unionoids and trigonioidids, one has to refer to their musculature.

UMBONAL MUSCULATURE

Except for the oyster-like genera *Acostacea* and *Pseudomulleria* that are secondarily monomyarian (Yonge, 1978), the Unionida retained the plesiomorphic state of two well-defined adductors, with the anterior retractor scar immediately behind the anterior adductor (slightly dorsal), and isolated pedal protractor scar below. The posterior set of muscle scars is variously impressed. The mantle attachment scars are also plesiomorphic, known only in *Neotrigonia* and recent Margaritiferidae (Smith, 1982), but are also in found in Early Cretaceous unionoids with V-shaped beak sculpture (Delvene & Araujo, 2009), and are developed in the Triassic species from Marciszów and Krasiejów.

Specific for the unionoids is a group of minute muscles attached to the shell wall within the umbonal cavity. They are referred to as the pedal elevator (Graf & Cummings, 2006). Their most widespread location is on the anterior slope near the main hinge tooth in a linear longitudinal row diverging slightly forwards. They may differ in number and disposition in left and right valves. Such muscle attachment scars occur in anatomically underived *Margaritifera* and in the Hyriidae, but are also found in several genera of the Unionidae (*Lampsilis*, *Elliptio*, or *Pyganodon*). The evidence that this pattern is very ancient is offered by the Triassic material from Silesia. In the early Late Triassic species from Krasiejów, the umbonal muscle scars occur more or less irregularly over the anterior and interior walls of the umbonal cavity. They are more numerous, more scattered, and more variable in distribution than in the extant unionoids. The strongest impressions are almost always left by a series of a few scars situated near the top of the umbonal cavity (which is rather shallow), and arranged along a line curved posteriorly towards the ligament. In a few specimens from the latest Triassic of Lisowice the umbonal musculature is represented by a set of about four muscle scars arranged linearly at the top of the umbo, especially deep at the left valve. An anterior pedal retractor, split into a series of attachments in front of the beak, also occurs in the Early Cretaceous (Barremian–Albian) '*Unio*' *heilonjiangensis* (Sha & Fürsich, 1993). This is also the location of the attachments in the co-occurring trigonioidids (Sha, 1992: 260).

It seems thus that patterns of umbonal muscle distribution in extant unionoids other than those similar to *Unio* are derived. In *Unio*, the umbonal muscle attachment scars are located mostly at the inner slope of umbones, in a more posterior location than in *Margaritifera*.

Only two umbonal impressions occur in *Spatha* (?= *Mutela*), interpreted as visceral muscle attachments (LR Cox, 1969; Haas, 1969a, b). The usually single attachment of the robust and strong pedal elevator at the top of the umbonal cavity of the African family Iridinidae is an apomorphy (Graf & Cummings, 2006; Van Bocxlaer & Van Damme, 2009). The oldest iridinids are known from the Late Cretaceous (Graf & Cummings, 2006; Van Bocxlaer & Van Damme, 2009). Although such scars show some similarity to that of the pedal elevator in *Neotrigonia*, molecular data indicate that this must have been a secondary derived character (Graf & Cummings, 2006).

Similarly misleading is the location of the umbonal musculature in the advanced unionid *Anodonta*. A cluster of muscle scars is situated there at the external side of the shell near its tip. A similar pattern is also known in *Astarte* (Pojeta, 1971) and the Ordovician *Babinka* (McAlester, 1964) or *Thoralia* (Morris, 1980). In all of these cases, such a pattern probably resulted from a secondary disappearance of the umbonal cavity in the extremely flattened shells.

Unlike unionoids, the pedal elevator muscle of trigonioids operates a muscular and massive T-shaped foot. It inserts in the apex of the shell umbonal cavity and, because of the massive asymmetric hinge, it happens that the imprint on the left valve is more conspicuous than that of the right (Newell & Boyd, 1975; Johnston, 1993). Already in the Early Devonian *Eoschizodus* only a single, robust pedal elevator scar occurs in each umbo. If the freshwater unionoids truly originated from the marine trigonioids, a stage with a transitional pedal elevator pattern must be identified. That this is truly possible is shown by the Permian trigonioid *Scaphellina*, in which the elevator attachment was split into two separate scars within each umbonal cavity, but not as deep as in typical trigonioids (Newell & Boyd, 1975). *Scaphellina* is a derived bivalve unlikely to be related to the unionoids, but there are also Triassic forms with such musculature.

The umbonal cavity in the thick-shelled *Pachycardia* from the Late Triassic (Carnian) of Frommer Bach in the Dolomites, Italy (unnumbered NHM specimen) has two apices, suggestive of double umbonal attachments of the pedal elevator. Although coeval with the early unionoids, and thus too late in geological time, this genus is traditionally considered the probable ancestor of the unionoids, based on the similarity of their hinges. Even more convincingly, split muscle scars are visible in the umbonal cavity of the shell mould NHM 36375 (Fig. 4F), probably representing a juvenile *Trigonodus* from the Mid Triassic (Ladinian) of Rottweil, Württemberg, Germany. In this case both the age and morphology meet our expectations regarding the ancestry of the unionoids.

PUTATIVE PRE-JURASSIC UNIONOIDS

Among the potential unionoids of the Triassic, the best known is the type species of *Unionites*, *Unionites muensteri* Wissmann, 1841. Exquisitely preserved specimens from the Late Triassic Heiligkreutz Beds of Alto Adige, Italy show details of their external shell morphology, without any distinction between the juvenile and mature shell ornamentation (NHM 36373). The muscle attachment scars are well represented in internal moulds from the St Cassian Beds of the same region (NHM 36374 and NHM L 4058). A characteristic feature of their musculature is the separation of the elongated probable anterior pedal retractors from the adductors. They are located on a thickening of the shell below the anterior lunule, between the beak and the adductors, displaced adaxially close to the toothless hinge (Fig. 4G–I). Although the location of these scars is not very different from that of the umbonal muscles in the unionoid from Krasiejów, such homology seems unlikely. Similarly isolated is the position of the anterior pedal retractor attachments in the Early Cretaceous *Trigonioides*, although they are of a more generalized, rounded shape. This homology is further supported by the anterior pedal retractor scars in the Late Carboniferous anthracosiids from England. In *Carbonicola subconstricta* (Sowerby, 1812) a rounded scar is located behind each adductor (NHM NL 1769 and 1770; Fig. 4C, E), but in another specimen (NHM NL 1766; Fig. 4D) the scars are split in two. A series of a few separate small scars in continuity with the adductors occur in *Carbonicola aquilina* (Sowerby, 1840) from Rotterham in Yorkshire, England (Fig. 4A, B). Numerous scars of the anterior pedal retractor were already developed in the earliest known trigonioid *Silurozodus*. There is thus continuity between this state, probably the least derived, and that of *Unionites*. We concur with Geyer *et al.*'s (2005) conclusion that *Unionites* is a geologically late anthracosiid. The picture is somewhat obscured by findings of *Unionites* in the Early Triassic marine strata, where they co-occur not only with the trigonioid bivalves, but also with ammonoid cephalopods, indicating an open-sea environment (Kumagae & Nakazawa, 2009). Actually, most findings of *Unio*-like Triassic bivalves in the Germanic Basin are in strata that originated in marine or brackish conditions. Most surprisingly, the whole bivalve fauna of the South German Schilfsandstein ('reed sandstone'), equivalents of which underlie the Krasiejów red mudstone, is fully marine, despite

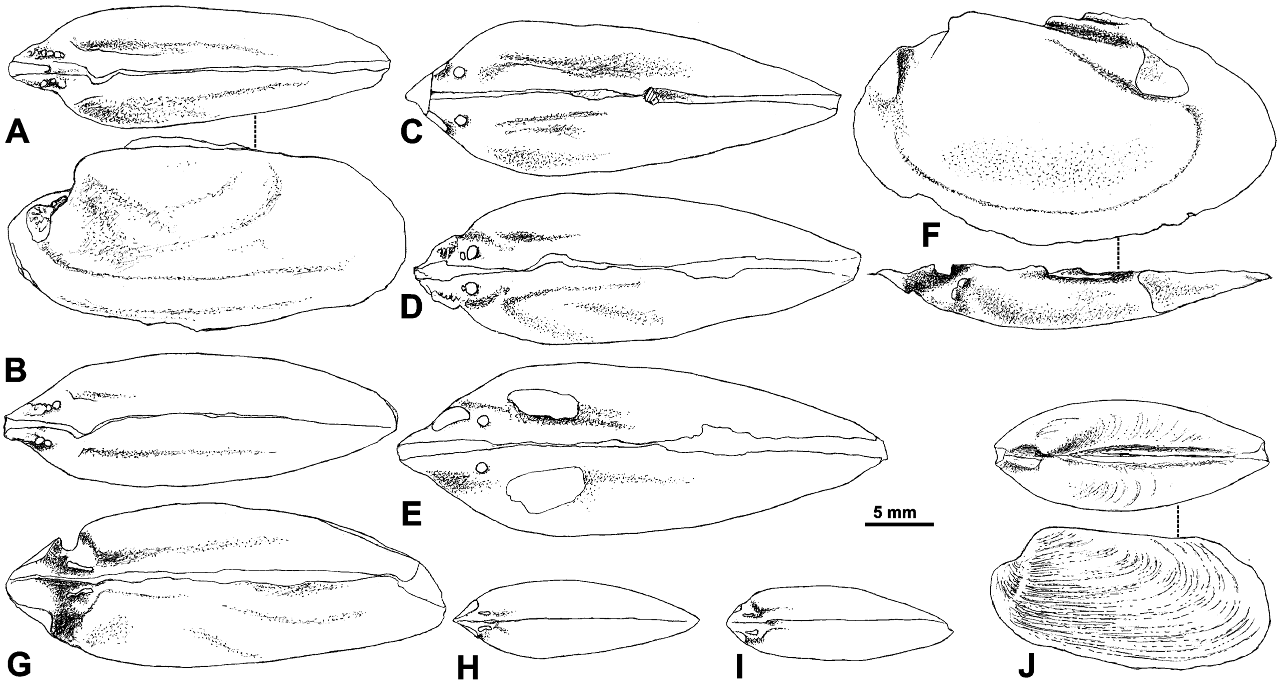

Figure 4. Development of dorsal musculature in the anthracosiids and trigonodids; camera lucida drawings. A, B, *Carbonicola aquilina* (Sowerby, 1840), internal moulds NHM 2217 and 2216 from the Late Carboniferous at Rotterham in Yorkshire, England. C–E, *Carbonicola subconstricta* (Sowerby, 1812) internal moulds NHM NL 1770, 1766, and 1769. F, shell internal mould NHM 36375 of probable juvenile *Trigonodus* [labelled ?*Myophoria ovata* (Goldfuss, 1837) var.], from the Mid Triassic (Ladinian) of Rottweil, Württemberg, Germany. G–J, *Unionites muensteri* Wissmann, 1841; internal moulds NHM 36374 and NHM L 4058 from the Late Triassic St. Cassian Beds (G, H) and the Heiligkreutz Beds of South Tirol, Italy (I), and specimen from the latter locality with shell preserved (J), held under the same collection number NHM 35373.

the presence of possible *Unionites* (Linck, 1968, 1971). Probably the anthracosiids were euryhaline animals.

Neither *Unionites* nor the anthracosiids show scars of the pedal elevator muscle in their beak region. There is thus no direct evidence, except for their brackish or even marine habitat, of a relationship with the trigonioid bivalves. The oldest findings of the Trigoniida are from the Late Silurian (Liljedahl, 1992), and the single umbonal attachment scar was already well developed in the Early Devonian (Johnston, 1993). If the anthracosiids were derived from the trigonioids, this could have happened well before the formation of their strong umbonal attachment for the pedal elevator. It is possible that the anthracosiids were replaced during the Triassic by the unionoids in freshwater habitats, and *Unionites* was a Late Triassic 'living fossil', the last member of its generally Palaeozoic clade.

However, the real pattern of relationships among the freshwater pre-Jurassic bivalves may not be so simple. An additional complication was introduced by the Mid Triassic (Anisian; Wilson & Edgecombe, 2003) possible unionoid fauna from the Wianamatta Shales, exposed in the area of Sydney, Australia. These are generally small and very variable bivalves. Numerous specimens with a size below 1 cm in length are generally of robust appearance and are relatively thick shelled; the largest ones are elongated, laterally compressed, and relatively thin-shelled. It is possible to arrange them into an ontogenetic series, with rare, small, thin-shelled specimens at the start of the series (Fig. 5A–I), and equally rare robust specimens of size exceeding 1 cm at the end (Fig. 5J–X). Etheridge (1888) distinguished four species in the assemblage, but boundaries between them are not easy to determine. He proposed the new genus *Unionella* for the robust minute forms, with *Unionella bowralensis* Etheridge, 1888 as the type species, but the other two of his species co-occurring in the same beds are 'fairly similar' (McMichael, 1957: 233). For the fourth species, *Unio dunstani* Etheridge 1888, with compressed and elongated relatively larger shells (up to 37 mm in length), McMichael (1957) proposed another genus *Protovirgus*. Some doubts regarding the generic-level (perhaps even species-level) distinction between these forms have arisen because of the unusual and almost unique, if these are truly unionoids, pattern of the umbonal musculature.

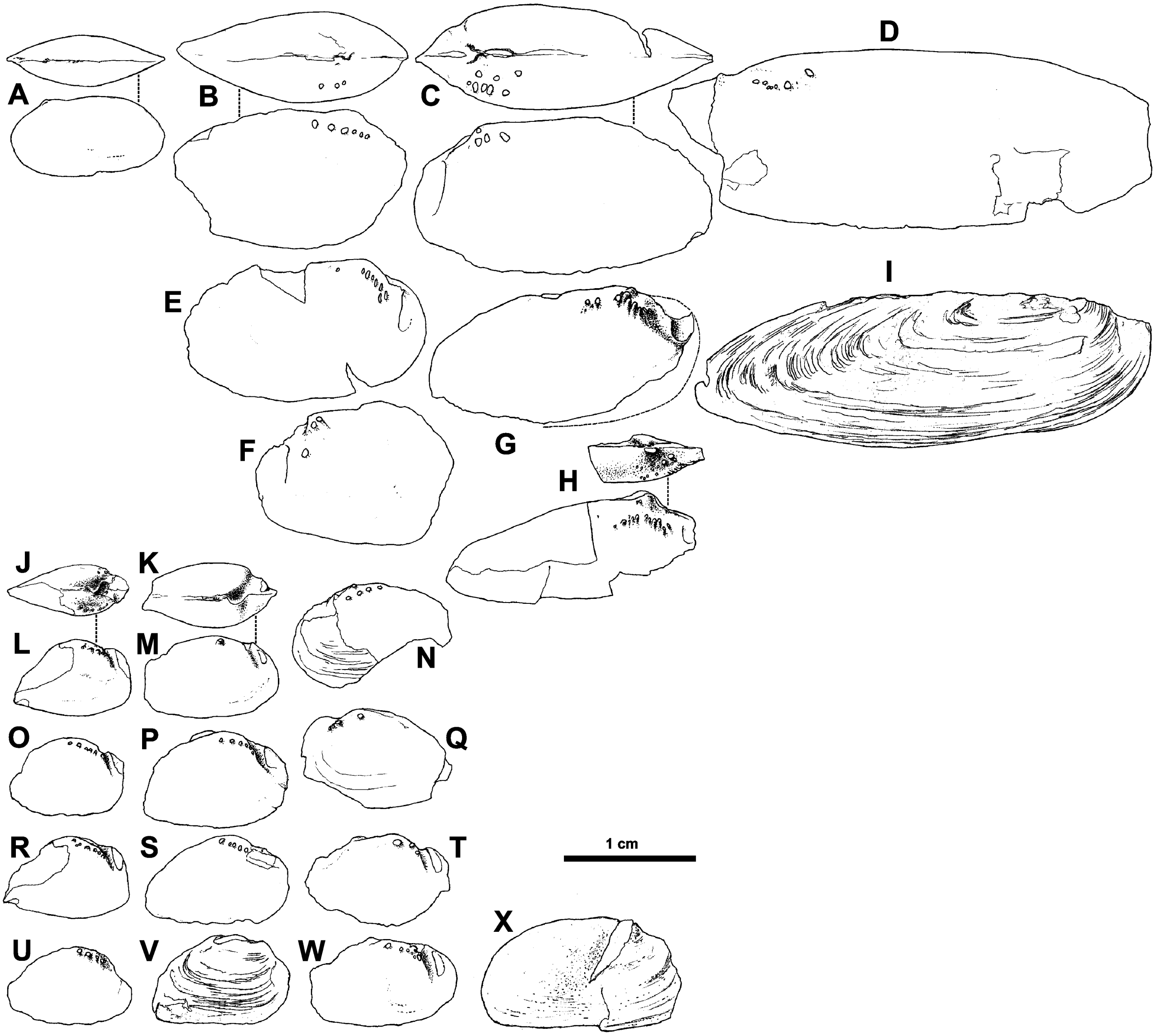

Figure 5. Possible unionoids from the Mid Triassic (Anisian) Wianamatta Shales at Sydney, Australia; camera lucida drawings of NHM specimens under collective numbers. A–I, *Protovirgus dunstani* (Etheridge, 1888). J–X, *Unionella bowralensis* Etheridge 1888.

All the recognizable morphotypes in the collection have a variable, but essentially the same, location of a linear series of small muscle attachment scars that occupy not the region between beaks and adductors or hinge line, but the external wall of the beaks. There is no evidence of the anterior pedal retractor being separated from the valves adductor attachment area, and this contradicts the suggestion of McMichael (1957: 234) that *Unionella* is a member of the Anthracosiidae. Its musculature instead resembles that of *Anodonta*, but its shells have well-developed beaks.

The Wianamatta bivalves are similar in the distribution of their umbonal muscles to the nuculoids (e.g. Bradshaw, 1978), but their hinge, although unknown in detail (Etheridge, 1888), was definitely heterodont, as shown by the undulations on the ventral side of the hinge (see Fig. 5B, J, K). Also, the Early Cambrian bivalve *Pojetaia runnegari* possesses dorsal musculature as two robust scars attached to the external slopes of the umbo (Runnegar & Bentley, 1983). Such umbonal area musculature is believed to serve as visceral retractors attached to the visceral floor (e.g. Bradshaw, 1978; Bailey, 1986), or foot-associated muscles for elevating the foot (e.g. Driscoll, 1964; LR Cox, 1969; Liljedahl, 1992; Johnston, 1993). Cummings & Bogan (2006) thought that umbonal muscles (they call them 'additional dorsal muscles') help to secure the dorsal position of the body inside the shell. There are thus two possible explanations of the external position of the umbonal muscles in the *Unionella–Protovirgus* group of freshwater bivalves: either (1) this is a plesiomorphic condition, and they are unrelated to the unionoids or trigonioids; or (2) this is an early case of secondary migration of the foot elevator attachments after they split into several separate attachments. There is no way to solve this question with the evidence available at the moment, but because of the Mid Triassic age of the Wianamatta fauna the most parsimonious solution seems to be the latter possibility. There would then be a relationship between the Krasiejów and Wianamatta unionoids, and also a similar grade of evolutionary advancement regarding the gill structure (unknown in the *Unionella–Protovirgus* group).

TAXONOMIC IMPLICATIONS

The unionoids are unknown from before 230 Mya, i.e. the Late Triassic. The principle of parsimony requires that until there is strong reason to believe that this results from incompleteness of the fossil record, we have to assume that their ancestor is among Mid or Early Triassic trigonioids. All of the unionoids are freshwater species, but among the Triassic trigonioids, which are generally fully marine species, the Trigonodidae are from brackish water. Almost all the trigonioids have a single strong foot elevator attachment in each of the very robust shell umbones, whereas the unionoid foot elevator attachment is split into a linear series of scars along the admedial slope of the umbo. But the Triassic members of the Trigonodidae have double foot elevator attachments, although located as in *Neotrigonia* or other typical trigonioids. It is thus tempting to accept Newell & Boyd's (1975) idea that among the brackish water Mid Triassic Trigonodidae is the direct ancestor of the unionoids (possibly *Trigonodus*). The double umbonal muscle scars would then be ancestral to the state characterizing the Mid–Late Triassic freshwater bivalves with a cluster of variably developed umbonal muscle attachments. The cluster tends to be located in the anterior portion of the beak, either on its external surface in *Unionella*-like forms (probably representing an extinct lineage) or on its admedial slope in *Tihkia*-like forms (and later true unionoids).

This traditional picture of the ancestry of the Unionida has a few weak points. The first is posed by the Carboniferous to Permian brackish and freshwater Anthracosiidae that lack clear foot elevator attachments. The single strong attachment of the foot elevator is known to have already developed in the trigonioid lineage in the Early Devonian (Johnston, 1993). If the anthracosiids have anything to do with the Triassic unionoids, one must accept an independent origin of the multiple foot elevator attachments of the unionoids (*de novo* from its absence in the anthracosiids) and the double attachment in *Trigonodus*. They would not be homologous.

In fact, this is supported by the location of the umbonal muscles in the rudists, which is the likely out-group to the palaeoheterodont (Trigoniida + Unionida; see Graf & Cummings, 2006) clade (Skelton & Smith, 2000). In the Late Jurassic free-living megalodontid rudist *Pachyrisma* from the Kimmeridgian of Błaziny, Poland, examined by us, there is a series of muscle attachments on the admedial side of the umbo extending to the anterior foot retractor attachment (exactly as in underived unionoids), but at the same time the tip of the umbo shows a sharp depression, suggestive of the presence of a weak *Neotrigonia*-like elevator. Hence, it is possible that the trigonioid and unionoid patterns of umbonal musculature are results of a divergent evolution from an ancestor equipped with both sets of muscles. It may be noteworthy that a strong umbonal muscle attachment within the umbonal cavity, associated with other linearly arranged attachments, was also identified in an Early Ordovician nuculoid (Dzik, 1994: fig. 24A–C). This may be a plesiomorphic feature for most bivalves.

Another uncertainty emerges when the evolutionary origin of the prominent juvenile shell ornament of the unionoids is considered. In most cases the change from this juvenile morphology to a smooth shell surface is sudden, presumably connected with a transition from the deep infaunal life in juvenile stages to the shallow infaunal locomotion of adults. The ontogeny would then recapitulate the evolutionary change suggested by the weakening of the foot elevator attachment: from an anchor-like muscular foot, enabling deep penetration of the sediment, to a wedge-like foot used for a less efficient near-surface horizontal locomotion. The early Late Triassic *Silesunio* gen. nov. has well-developed prominent concentric ribs restricted to the early stages of ontogeny, similar to those in the Early Cretaceous *Protelliptio* and recent *Margaritifera*. If the concentric ribbing of these juvenile shells is truly homologous, then it originated before the eulamellibranch grade gills, and, implicitly, before the brooding of larvae and the subsequent parasitizing of fish. The Margaritiferidae have brooding chambers in all four gill blades (as in some Unionidae; Graf & Cummings, 2006), which is probably a plesiomorphic state. If this is the case then the advanced Unionidae, with brooding chambers only in the outer blades, and the Hyriidae, with chambers only in the inner blades, originated from a four-blade ancestor with V-shaped ribbing of the juveniles. This could have happened after the Jurassic, but the presence of the Late Triassic '*Diplodon*' species with radial or V-shaped juvenile or mature shell ornamentation resembling that of the Hyriidae is puzzling. Watters (2001) already suggested, because of the lack of such forms in the Jurassic, that this is a homoplasy with the post-Jurassic Hyriidae.

The separation of the anterior pedal retractor from the anterior adductor attachment area in the late Palaeozoic Anthracosiidae and in the Mid Jurassic–Late Cretaceous Trigonioididae is another case of apparent homoplasy. The trigonioidids had M-shaped shell ribbing (similar to juvenile ornamentation in some advanced Unionidae) that extended to mature developmental stages. A similar extension or disappearance of juvenile shell ornamentation took place independently and repeatedly in several lineages of advanced unionoids. The origins of the trigonioidids remain a mystery.

It appears that in the evolution of freshwater bivalves, like in any other animal group, particular evolutionary inventions that can be used as major diagnostic characters emerged sequentially in different geological epochs (Fig. 6). Unavoidably, a better knowledge of the course of evolution must result in the emergence of 'connecting links' and the obliteration of clear-cut boundaries between taxonomic units based on sets of diagnostic characters.

We believe that the new evidence on Late Triassic freshwater bivalves, although still incomplete and tentative, should be included in concepts of high-rank unionoid taxa. It is proposed here to use the filibranch versus eulamellibranch grades to diagnose paraphyletic units of suborder rank. The pattern of the anterior pedal retractor and elevators is used to define families of the earliest unionoids. The trigonodids would then be characterized by the presence of double pedal elevators in each valve beak. Anthracosiids would include possible unionoids with weak elevators, but with the anterior pedal retractors separated from adductors. The family rank taxon for *Unionella*-like forms would be based on pedal elevators on the external wall of the beak, and that for *Tihkia*-like forms would be based on pedal elevators on the internal wall of the beak. There seems to be no reasonable alternative to such an approach until more anatomical evidence on the early unionoids is made available.

CLASS BIVALVIA LINNE, 1758

ORDER UNIONIDA STOLICZKA, 1871

Emended diagnosis: Freshwater bivalves characterized by linearly arranged pedal elevator attachments in the beak region, but having plesiomorphic nacreous internal shell layer, and, in underived forms, transversely ribbed cardinal teeth of the hinge.

Nomenclatorial remark: We prefer Unionida, rather than Unionoida or Unioniformes (Bogan & Roe, 2008), because the ending -ida, not -oida, is generally applied to the genus-derived roots of ordinal-rank names in other molluscan classes and many animal phyla, but the vernacular name 'unionoids' is here applied to members of the order to allow a distinction from the family rank taxon Unionidae.

SUBORDER **SILESUNIONINA NOV.**

Diagnosis: Freshwater unionoids with filibranch-type gills and presumably free-living larvae.

Remark: The defined suborder is apparently paraphyletic: it occupies a transitional position between the ancestral Trigoniida and more advanced members of the Unionida.

Families included: Trigonodidae Modell, 1942 (= Pachycardiidae Cox, 1961), possibly Anthracosiidae Amalitzky, 1898, probably Unionellidae fam. nov., and Silesiunionidae fam. nov.

FAMILY **UNIONELLIDAE NOV.**

Diagnosis: A series of pedal elevator attachments linearly arranged on the external wall of the shell beak cavity.

Genera included: Unionella Etheridge, 1888, *Protovirgus* McMichael, 1957.

FAMILY **SILESUNIONIDAE NOV.**

Diagnosis: A series of pedal elevator attachments linearly arranged on the anterior wall of the shell beak cavity. Anterior pedal retractor attachment unified with that of the valves adductor.

Genera included: Silesunio gen. nov., probably *Tihkia* Sahni & Tewari, 1958.

GENUS ***SILESUNIO* NOV.**

Type species: Silesunio parvus gen. et sp. nov.

Etymology: The genus name refers to the geographic region of the findings of type species of unionoid bivalves (Silesia).

Diagnosis: As for the type species.

***SILESUNIO PARVUS* GEN. ET SP. NOV.**

(FIGS 1, 2A, 7–9)

Holotype: ZPAL Ab/III 2210 (Fig. 2A).

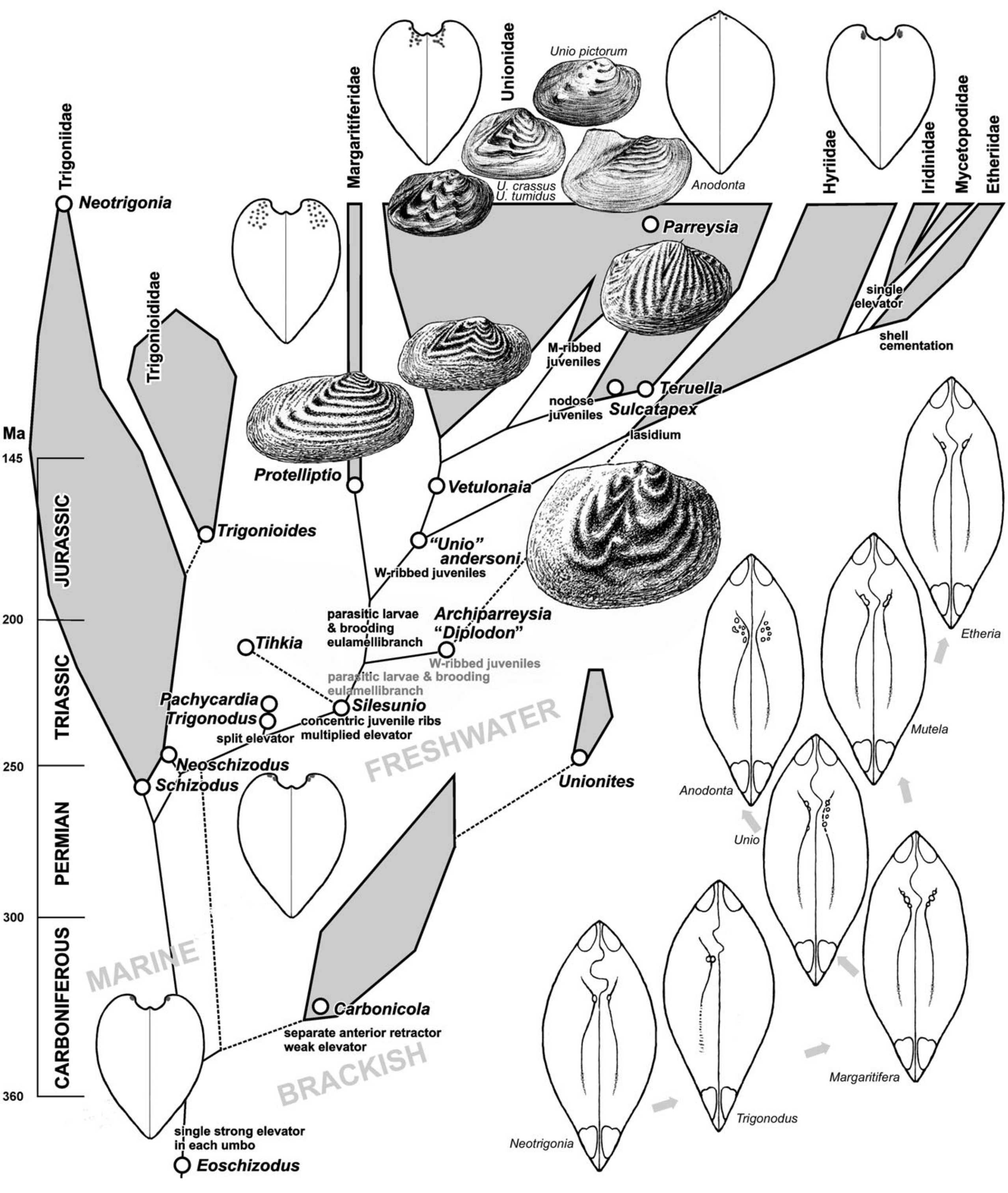

Figure 6. The proposed most parsimonious (in terms of as late as possible origin of evolutionary novelties) scenario of evolutionary transformations leading from the trigonioids to the main groups of the unionoids. Juvenile shell ornamentation of some unionoids and diagrammatic representation of probable changes in the foot elevator muscle attachments are shown. Note that the Etheriidae in the traditional meaning is probably polyphyletic (Bogan & Hoeh, 2000). Alternative interpretations with single and double origin of W-shaped juvenile ribs are represented by solid and broken lines, respectively.

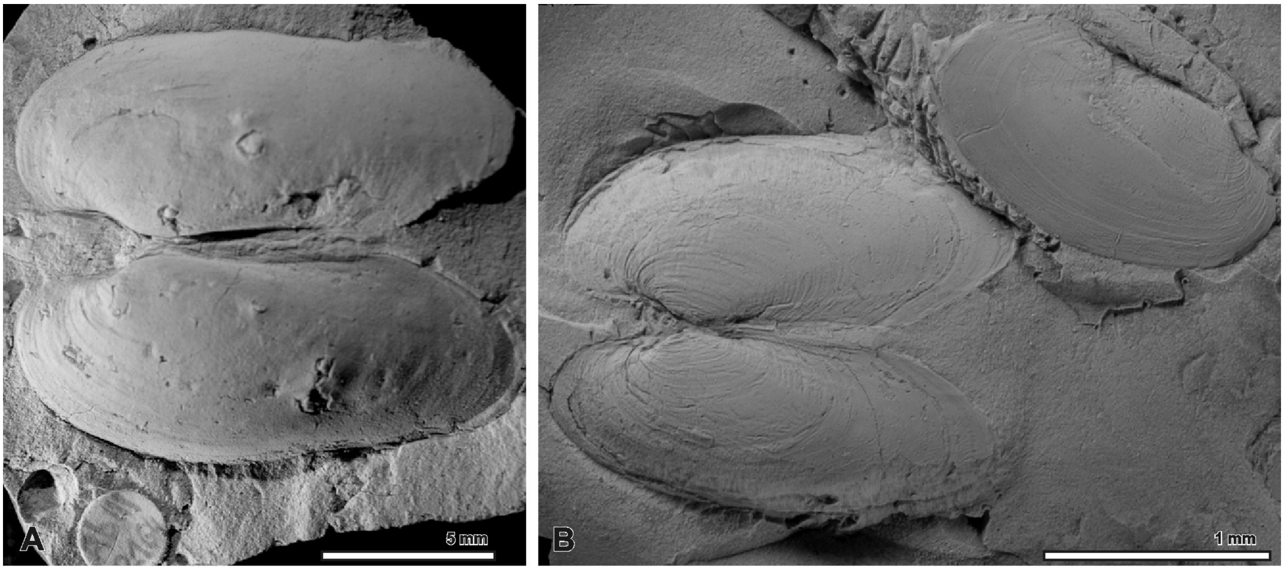

Figure 7. ***Silesunio parvus*** **gen. et sp. nov.** from the early Late Triassic of Krasiejów: 'butterfly style' opened valves. A, ZPAL AbIII/2164; B, ZPAL AbIII/2167.

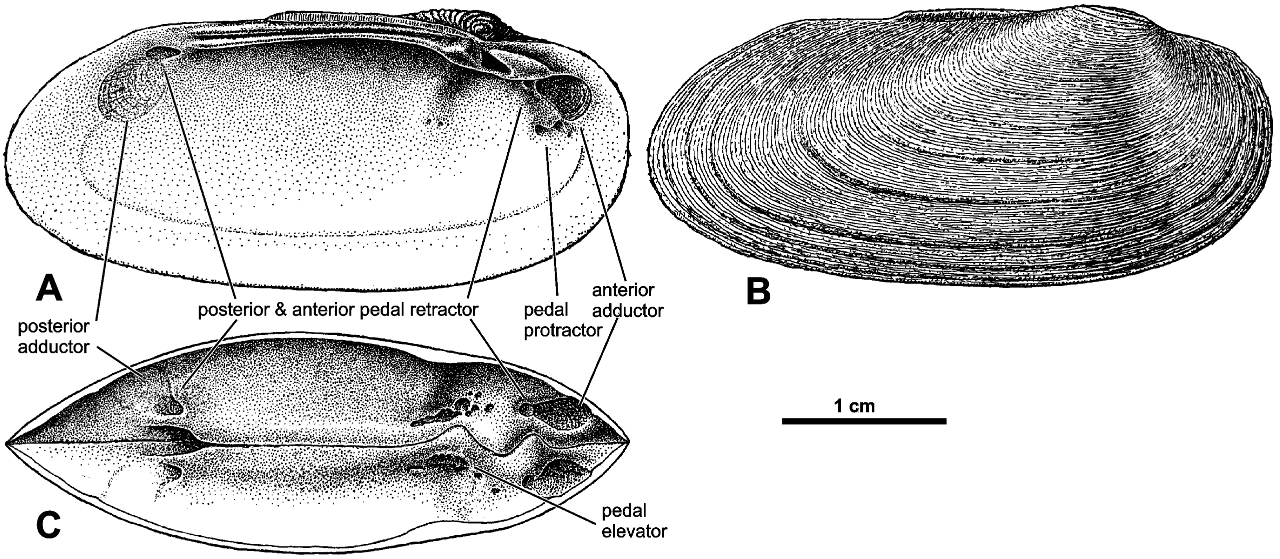

Figure 8. ***Silesunio parvus*** **gen. et sp. nov.** from the early Late Triassic of Krasiejów: restoration of the interior of left valve (A), external view of right valve (B), and ventral view of the hinge and dorsal muscle attachments (C).

Type locality: Krasiejów, Opole Silesia, southern Poland.

Type horizon: Lacustrine grey claystone and red finely grained mudstone bed within red-coloured fluviatile series of Late Carnian calcareous mudstones (Dzik & Sulej, 2007).

Etymology: The species name refers to the small size of specimens (latin *parvus*, meaning little, tiny).

Diagnosis: Elongated shell of small size does not exceed 50 mm and generalized morphology, with juvenile stage bearing concentric ribs parallel with the mantle margin. Umbonal muscles tend to disperse over the anterior slope of the beaks.

Material: Several hundred specimens of various preservation in the ZPAL collection; five of them with preserved gills.

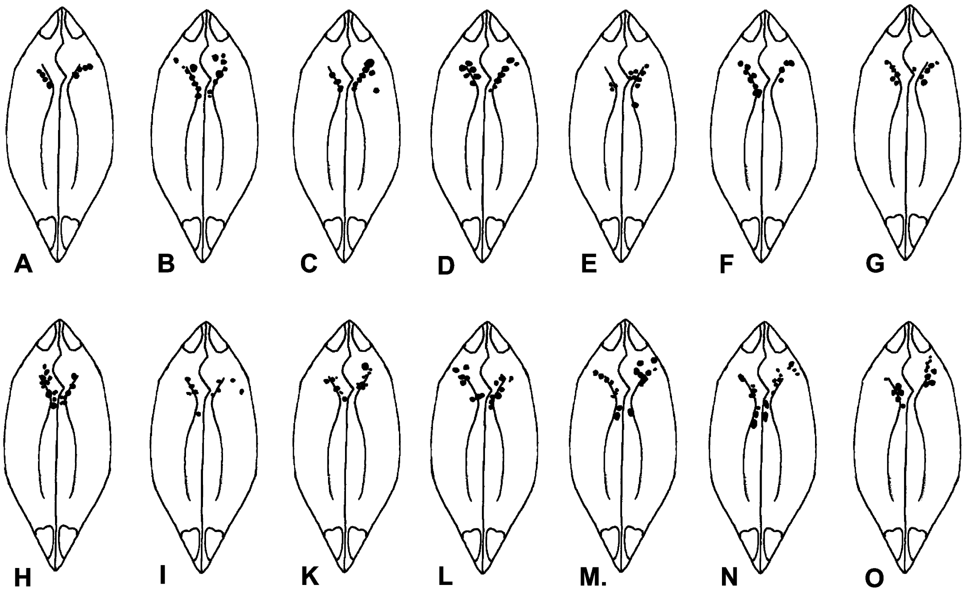

Figure 9. Diagrammatic presentation of variability in disposition of the umbonal musculature in ***Silesunio parvus* gen. et sp. nov.** from the early Late Triassic of Krasiejów; camera lucida drawings. Specimens ZPAL AbIII: A, B, 2161–2162; C, D, 2165–2166; E, 2176, F, 2185; G, 2199; H–O, 2199–2205.

Description: Shell length usually more than two times its height (ratio ranging from 1.9 to 2.9). Its largest inflation is approximately at the midlength of the valve. Shell wall moderately thick, with greatest thickness in the region of the cardinal teeth. The umbones are prominent, located at about 1/4–1/5 of the length of the shell from its anterior end. Umbonal musculature is clearly recognizable on both valves. Separate small scars are distributed on the top, anterior slope, and over the interior side of each umbo, varying in number from 2 to 16 on each valve.

Remarks: Although the length of imprints of bivalve shells in the Krasiejów lacustrine bed vary from 10 to 50 mm, most specimens are open valves of lengths below 20 mm. Apparently this is a result of high juvenile mortality in the time-averaged fossil assemblage, to which dead shells were steadily contributed. Moulds of mostly closed shells forming calcareous concretions are generally larger than their imprints in clay, and their length vary from over 20 to 50 mm. These fossils probably originated as a result of a catastrophic covering of a living population with suspended sediment. Mature shells can be distinguished from juveniles by the thickening of the shell margin and condensation of growth increments.

Specimens of this species are similar to *Tihkia silesiaca* sp. nov. in shape, position of the main muscle scars, and in distribution of concentric growth lines on the shell, but differ in much larger mature size and dispersed, highly variable umbonal muscle scars, in a more swollen shell, more anteriorly located umbo, as well as better developed pallial line, and sometimes visible mantle muscle scars on the surface of the shell. Some of these differences result from the relatively thicker shell wall. This species differs from species of *Tihkia* in small size of mature specimens. It is almost coeval with the Maleri Formation fauna, which is generally similar to that of Krasiejów, despite the large geographic distance between them (Dzik & Sulej, 2007).

Antediplodon lewisi Richards, 1948 from the Norian Stockton Formation of Pennsylvania at Montclare near Phoenixville, Montgomery County, Pennsylvania (Richards, 1948), shows shell shape and size (44 × 17 mm) similar to *S. parvus* sp. nov. With a lack of information on beak ornamentation or musculature, the generalized shell outline cannot be used as the only basis for species identification.

Genus *Tihkia* Sahni & Tewari, 1958

Type species: *Tihkia corrugata* Sahni & Tewari, 1958

Original diagnosis: 'The shell is thick and varies in shape from broadly oval to narrow sub-quadrate. Anteriorly, the shell is broadly, and posteriorly somewhat narrowly rounded or sub-angular. The length is in all cases greater than the height, relative proportions varying within wide limits. The beaks are anteriorly situated but are not terminal; they are inconspicuous and curved inwards and very slightly forward. The umbo is comparatively flat and smooth but is not otherwise distinguished from the rest of the shell by any distinctive character. The lunule is present and there is a well defined opisthodetic ligament' (Sahni & Tewari, 1958: 4101).

Remarks: Among Triassic unionoids of this kind the diagnostic umbonal musculature and gill structure is known only in two populations from Silesia. Shells of the Rhaetian species, of generalized appearance, are closely similar to those from India, Tanzania, and Zambia, but differ in geological age: about 10 Myr from *T. corrugata* and perhaps 20 Myr from *Tihkia karooensis* (Cox, 1932). Until at least umbonal musculature is known in these Gondwanian forms, their generic level identification with the Polish species remains only a hypothesis. The generic affiliation of the Rhaetian species from Silesia is based on the assumption that its compact set of umbonal muscles near the umbo tip is a generic rank distinction, and that it may be shared with the Gondwanian species of Tihkia.

Species included: Tihkia corrugata Sahni & Tewari, 1958 from the Late Triassic (late Carnian or early Norian) Maleri Formation of the Hyderabad State and the region of Tihki, Vindhya Pradesh, India (Sahni & Tewari, 1958), *T. karooensis* (Cox, 1932) from the supposedly Mid Triassic Manda Beds of Tanzania and Ntawere Formation of Zambia (Cox, 1932), and *T. silesiaca* sp. nov. from the early Rhaetian of the Upper Silesia, Poland.

TIHKIA(?) SILESIACA SP. NOV.

(FIGS 10, 11)

Holotype: ZPAL V.33/286 (Fig. 10H, I).

Type locality: Lipie Śląskie-Lisowice, Opole Silesia, Poland.

Type horizon: Dark-grey marly claystone lens within fluviatile fine sandstone unit of early Rhaetian age.

Etymology: After the region of Silesia.

Diagnosis: Elongated shell of medium size, reaching 80 mm, and generalized morphology, with juvenile stage bearing concentric ribs parallel with the mantle margin. A set of about four small muscle scars tightly arranged in a line near the top of the umbo.

Material: About 100 specimens in the ZPAL collection; two of them with preserved gills.

Description: Shell length almost three times its height. Its largest inflation is at 1/3–1/4 of its length from the anterior end. The shell wall is relatively thin, except for the region of cardinal teeth. The umbones are rather prominent, situated approximately one-third of the width from the anterior end. In at least one specimen, ZPAL V.33/305, dark mineralized gills of morphology similar to those in *S. parvus* sp. nov. are visible, although not well enough preserved to prove that they are filibranch. The presumably juvenile specimen from Marciszów (Fig. 10A–D) shows juvenile ornamentation that is similar to that in *S. parvus* sp. nov., although less prominent. Its umbonal musculature is indistinguishable from that of the Lisowice specimens.

Remarks: Specimens are preserved mainly as internal moulds or internal moulds of closed shells in marly limestone concretions, with the shell preserved as palimpsest on their surface or, rarely, as impressions of opened shells in claystone. The species differs from *S. parvus* sp. nov. in a proportionally much thicker shell wall, larger mature size of a less swollen shell, not so anteriorly situated umbo, compact distribution of the umbonal muscle scars, and rather indistinctly impressed pallial line, with no detectable mantle muscle scars (this may have resulted from a less perfect preservation). *Tihkia silesiaca* sp. nov. resembles the type species of the genus *T. corrugata* Sahni & Tewari, 1958 (Sahni & Tewari, 1958) from the Late Triassic Maleri Formation in size, shape, and shell surface ornamentation, but differs in slightly less swollen shell and a thinner wall. The differences in known aspects of the shell morphology are not great, but no data on umbonal musculature are available for the Indian species. It seems rather unlikely that they are similar in this respect because of the significant time span separating them (probably about 20 Myr). The same applies to *T. karooensis* (Cox, 1932) from the Manda Beds at Gingama, Songea District of Tanzania. The hinge structure remains unknown, although one of the type specimens shows slightly displaced valves partially exposing the hinge region that seems similar to that of the Indian species. Some juvenile specimens in the type series are only slightly corroded at their apices, but no juvenile shell ornamentation is visible. Even less corroded specimens in the same NMNH collection from Ntawere Village, 5 km north of Katumbi, upper Luangwa River valley, Zambia, also seem to have smooth apices. C. B. Cox (1969) suggested a Mid Triassic age for both the Ntawere Formation (early Anisian) and the Manda Formation (late Anisian) based on vertebrates unknown outside Gondwana, where all the marine stratotypes of the Triassic units are located. This date has been accepted by Nesbitt

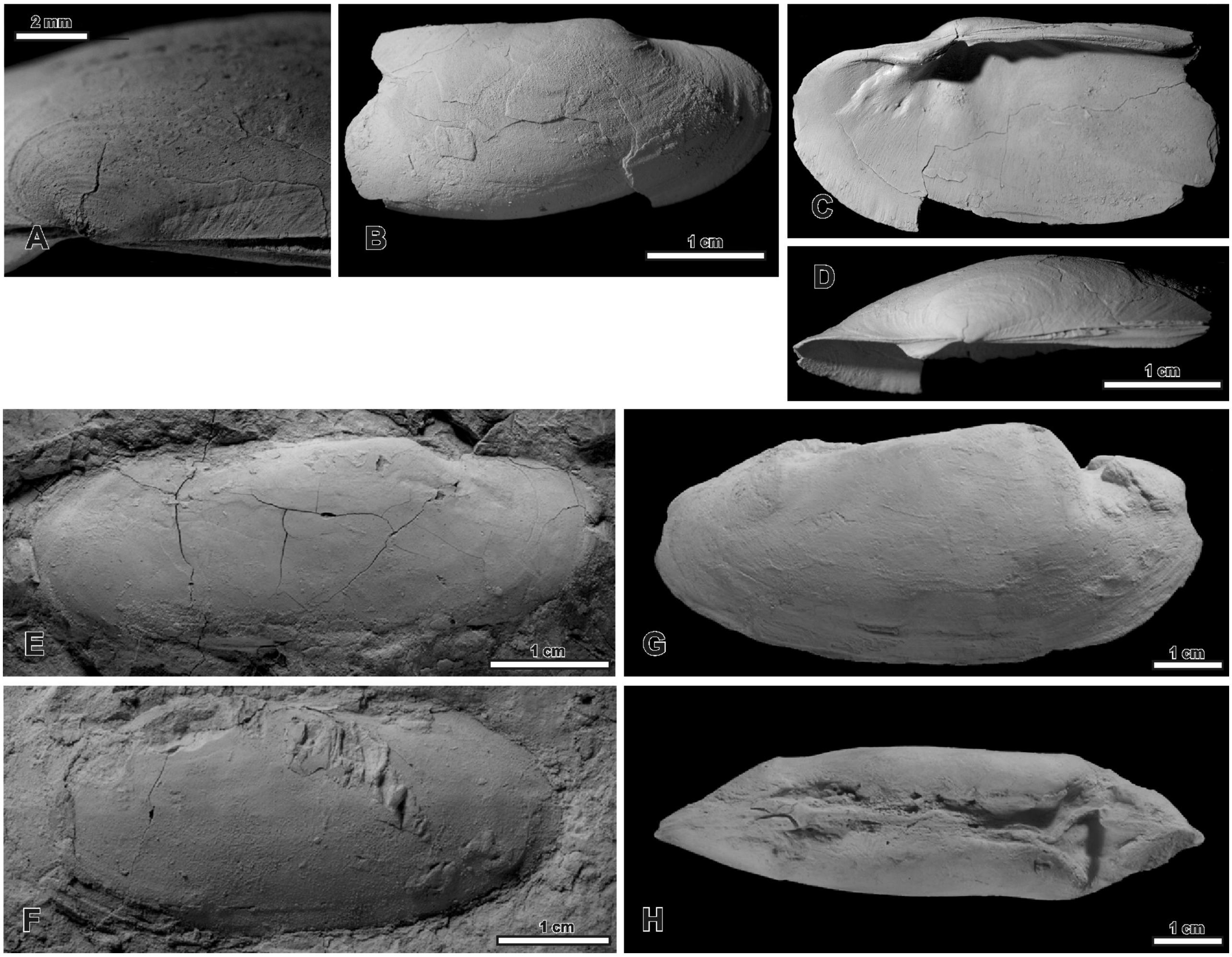

Figure 10. ***Tihkia silesiaca* sp. nov.** from the latest Triassic of Silesia (A–D) and Lisowice (E–H; external views of isolated valves and the natural mould). A–D, right valve with wall transformed into sparitic calcite ZPAL V33/310 from Marciszów: A, magnification of umbo showing concentric juvenile ribs; B–D, external, inner, and dorsal views of the specimen. E–F, moulds of right valve ZPAL V33/299 and left valve ZPAL V33/301 from Lisowice. G–H, holotype, mould of articulated valves ZPAL V.33/286 in lateral and dorsal views, respectively.

et al. (2010), although their identification of *Silesaurus*, shared with the Krasiejów fauna, which can be directly correlated with the Alpine Carnian, instead suggests a Late Triassic age of the Manda Formation bivalves.

SUBORDER UNIONINA STOLICZKA, 1871

Emended diagnosis: Unionoids characterized by eulamellibranch gills, ovoviviparity, and larvae that parasitize fish.

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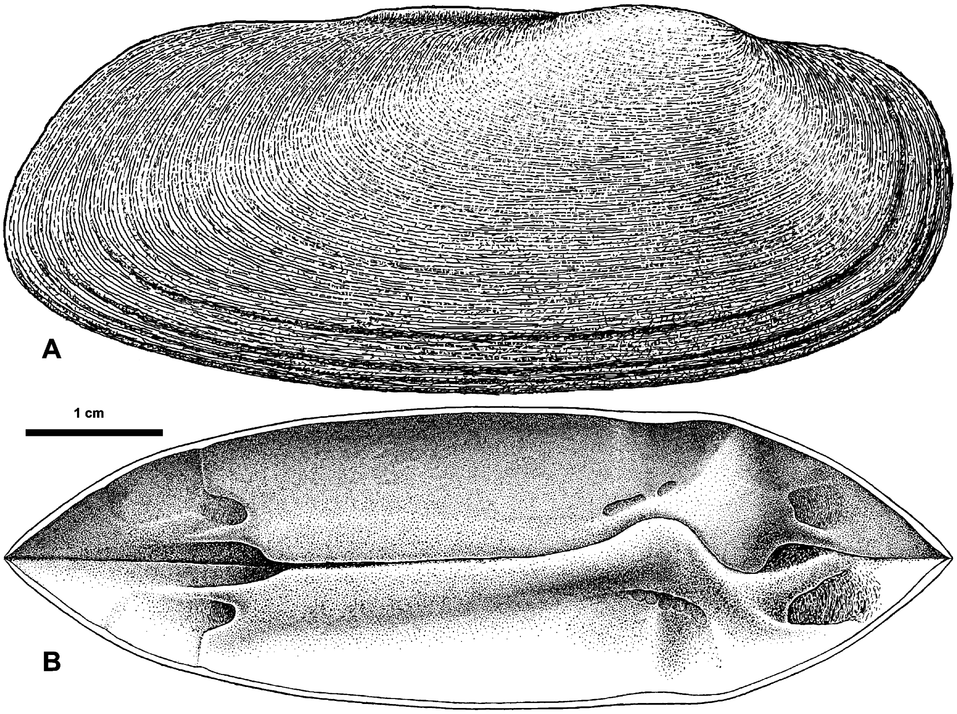

Figure 11. ***Tihkia silesiaca* sp. nov.** from the latest Triassic of Lisowice: restoration of the external view of right valve (A) and dorsal muscle attachments (B).

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