

Gill Structure and Relationships of the Triassic Cycloid Crustaceans

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ABSTRACT Unusually well-preserved fossils of a *Halicynine*-like cycloid crustacean frequently occur in the early Late Triassic lacustrine clay bed at Krasiejów in Opole Silesia, southern Poland. Its gill-like structures form a horseshoe-shaped pair of units composed of numerous calcified blades with reverse U-shaped cross-section. Originally, these were parallel slits opening on the ventral surface of the carapace. Lobation of the posterior margin of the carapace, of unusually large mature size for the group, make the animal different from other members of Halicynidae, and the new name *Opolanka decorosa* gen. et sp. nov. is proposed for it. More completely preserved specimens of cycloids from Vosges, France, and Madagascar show that the slit openings were located above radially arranged coxae of the walking appendages and a reduced abdomen. The disposition and arrangement of the cycloid gills suggest at least close analogy, and possibly homology, with the “respiratory areas” of the Branchiura, serving mostly as ion-exchange organs. It is proposed that they originated, in connection with the body size increase and adaptation to fresh-water environment, as radially arranged infoldings of the respiratory areas cuticle, with strongly calcified rigid dorsal parts suspended from the carapace. At least three ecologically and anatomically distinct lineages were represented in the order Cyclida, which was probably initially confined to marine environments and gradually adapted to life in continental waters. New taxa Schraminidae fam. nov. (with *Schramine* gen. nov.) and Americlidae fam. nov. (with *Americlus* gen. nov.) are proposed. *J. Morphol.* 269:1501–1519, 2008. © 2008 Wiley-Liss, Inc.

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Three generally Palaeozoic arthropod groups have recently appeared to ignore the “almost mystic” Permo-Triassic boundary and continue their occurrence almost until the end of the Mesozoic: the freshwater euthycarcinids, marine pelagic concavicularid thylacocephalans (Schram et al., 1999; Lange et al., 2001), and the mostly shallow-water marine cycloids (Fraaije et al., 2003) suggested as pre-Jurassic ecological analogues of crabs. Except for one early Mid Triassic fauna in France (Gall and Grauvogel, 1967), findings of post-Carboniferous cycloids (the term coined after the superfamily Cycloidea Glaessner, 1928) are rare and most species are based on few specimens.

Herein, a relatively large sample of a *Halicynine*-like cycloid is described from the early Late Triassic tetrapod locality Krasiejów in Silesia, Poland. The cycloids are associated there with numerous conchostracans and characean oögonia. Thus, little doubt remains that the environment of sedimentation was freshwater (Dzik and Sulej, 2007), similar to that of the French locality (Gall, 1985). Adult cycloids from Krasiejów exceed 6 cm in carapace width, which makes them the largest known members of the group, truly comparable in shape and size with recent crabs. Several specimens show three-dimensionally preserved gill-like structures within their carapaces. These structures, known already in the Carboniferous (Schram et al., 1997) and Mid Triassic (Gall and Grauvogel, 1967) species, do not resemble any earlier known crustacean gills and may be of importance in interpreting the relationships of cycloids.

I present here the available evidence concerning the morphology of this species from Krasiejów. Uncertainties resulting from incomplete preservation are discussed in light of additional data from the Mid Triassic *Halicynine* from Vosges, France, preserved in non-carbonate shale, and an Early Triassic species from Madagascar, preserved three-dimensionally in early diagenetic concretions. All the available information on the morphology, ecology, and stratigraphic distribution of cycloids will then be used to interpret their evolutionary relationships.

Abbreviations

The specimens from the early Late Triassic of Krasiejów are housed at the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw (abbreviated ZPAL) and at the Laboratory of Paleobiology of the Opole University (UOBS). The Mid Triassic material from Grès à Voltzia of Vosges is

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still in the private collection of Léa Grauvogel-Stamm (LGS) but is intended to be deposited at the Zoological Museum of Strasbourg University. The Early Triassic specimens from Madagascar are housed at the Museo civico di Storia naturale in Milan (MSNM).

CARAPACE MORPHOLOGY OF THE KRASIEJÓW CYCLOID

The crab-like cycloid with an oval carapace having a diameter more than 6 cm is one of the most common large invertebrates at Krasiejów. The cycloids are not easy to encounter, however, because the soft early Late Triassic clay in which they occur is not laminated and tends to split across such weakly sclerotized fossils. The fossils are most common near the base of the lacustrine fossiliferous horizon, being associated there with numerous conchostracans, rare coleopteran elytra, and plant detritus (Dzik and Sulej, 2007). Thus, their palaeoecological context closely resembles that of *Halicynne ornata* Trümpy, 1957 from the Grès à Voltzia in Vosges (Gall and Grauvogel, 1967; Gall, 1985). The main difference is that the clay at Krasiejów is strongly calcareous and, instead of secondary phosphatization, the main factor controlling preservation of fossils there is their original and secondary mineralization with calcium carbonate.

Taphonomy

Most of the specimens collected at Krasiejów are probably dead animals, as suggested by frequent preservation of internal gill-like structures that are apparent derivatives of the ventral cuticle. As shown by cycloids from other localities of the Triassic, the exuviation suture extended along the posterior margin of the carapace and molted appendages and sternites are then displaced to the anterior end of the carapace. Such anteriorward orientation of appendages is known also in the Krasiejów material. Isolated carapaces without any other associated structures may represent parts of exuvia.

Cycloid carapaces and appendages from Krasiejów usually preserve their mineralized walls. Additionally, calcium carbonate precipitated during early diagenesis of the fossils. Round millimeter-size nodules tend to develop over the carapace, their nucleation centers being within the carapace wall. Frequently, their rows mark the distribution of otherwise poorly preserved appendage. The carapace itself is composed in places with rosette-like plates. They probably reflect the process of calcification of the organic matrix expanding from more or less regularly distributed centers of mineralization. Whether this occurred *in vivo* or rather during early diagenesis when calcium ions migrated

within a weakly calcified skeleton, is difficult to decide.

Calcite acicular radiate structures (rosettes) occur in fossil and recent myodocopid ostracodes (Bate and Sheppard, 1982; Siveter et al., 1987). They probably originate as calcareous nodules within the cuticle matrix as a result of crystallization from an amorphous calcium carbonate gel (Sohn and Kornicker, 1969). Their growth was thus spatially limited by surfaces of the carapace wall. Originally the nodules were composed of monohydrocalcite ($\text{CaCO}_3 \cdot \text{H}_2\text{O}$) and calcite. In such myodocopids, it is not quite clear whether they originate *in vivo* or diagenetically after death of the organism (Olempska, 2005).

Carapace Dorsal Morphology

The carapace morphology of the Krasiejów cycloid shows most of the aspects typical of the Triassic species of *Halicynne*. Details of its morphology are obliterated in most specimens by crushing and overprinting by internal gill structures. The dorsal surface of the carapace is best preserved in an incomplete specimen, ZPAL Ab III/1369, probably owing to its predepositional fragmentation (Fig. 1A–C). It shows a triangular rachis with a series of medial transversely widened tubercles, and oblique furrows delimiting narrow elevations in its posterior part. The oblique belts apparently correspond to posterior segments of the head, which seem to extend as far posteriorly.

The furrows ending with bulbs seem to correspond to apodemes connected with the musculature of the head appendages and their disposition is to some degree similar to that restored as plesiomorphic for decapod crustaceans by Secretan (1972, 1973).

Two triangular lobes, corresponding to the lateral lobes of Busse and Horn (1978), flank the rachis on its both lateral sides anteriorly, as shown by specimen ZPAL Ab III/1367 (Fig. 1D–F). All the rachis and the vaulted area of the carapace that surrounds it are covered with rather large, randomly distributed tubercles.

The center of the vaulted area is finely radially furrowed, except for its anterior part (Fig. 1A,B). At the bottom of the furrows, shallow pits are arranged linearly. The main furrows seem to correspond to blades of the gill-like structures beneath, although no direct evidence of this is available as the carapace is exfoliated in all specimens with those structures well preserved. The furrows gradually shallow and are replaced by more numerous and finer striae at the slope of the carapace. They disappear near the marginal flat area.

The margin has no abrupt boundary and externally is delimited by a narrow thickening of the carapace along its edge. This part of the carapace is thicker and was probably strongly mineralized,

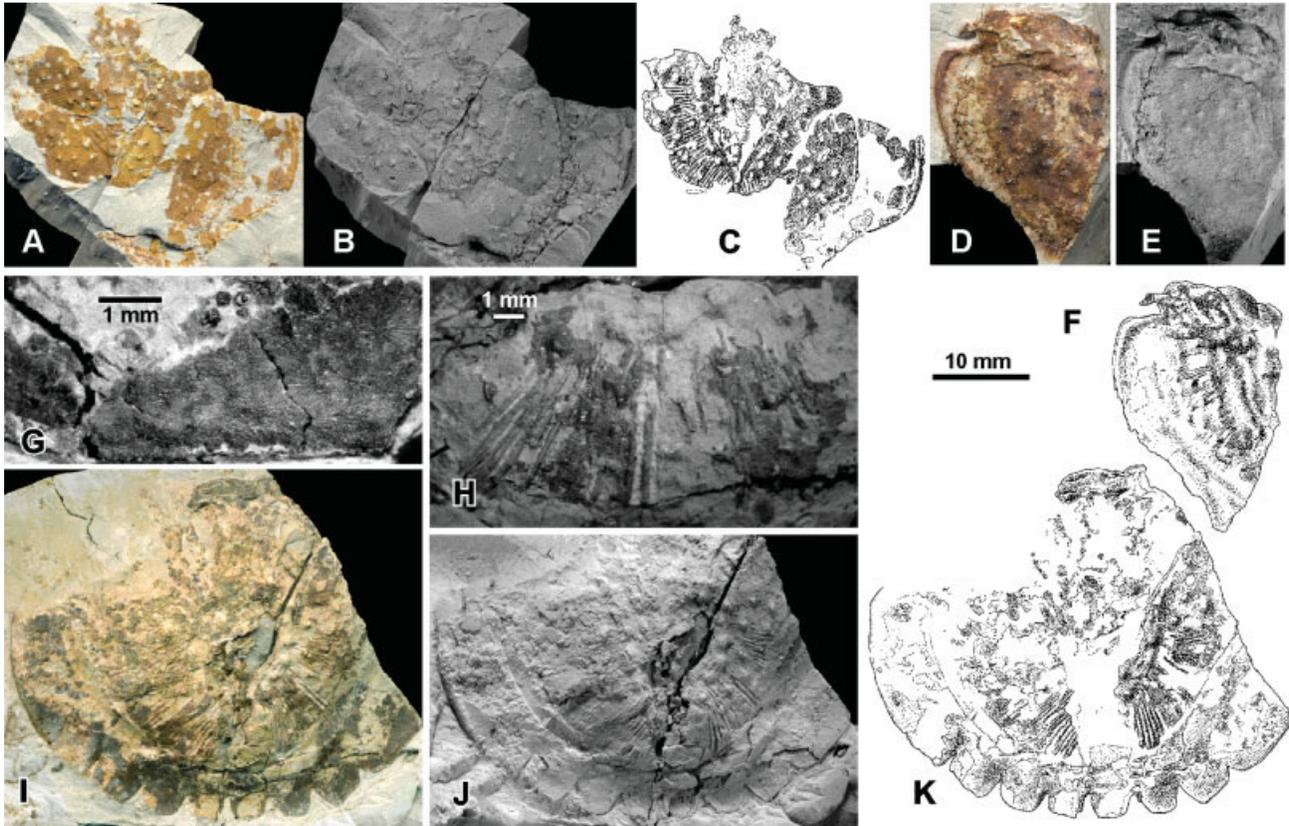


Fig. 1. Carapace morphology of *Opolanka decorosa* gen. et sp. nov. from the early Late Triassic of Krasiejów, Poland; specimens photographed uncoated, coated with ammonium chloride and their *camera lucida* interpretive drawing. **A–C**: Crushed carapace ZPAL Ab III/1369 showing details of external morphology and lobation. **D–F**: Obliquely deformed left part of the carapace ZPAL Ab III/1367 showing surroundings of the ocular sinus. **G–K**: Holotype ZPAL Ab III/1363 with partially exfoliated carapace showing rosette-like calcification centers on the carapace wall (G), extent of ventral calcification (doublure; I–K), and dorsal surfaces of the gill pouches (H).

as suggested by a plate-like distribution of mineralization rosettes in specimen ZPAL Ab III/1363 (Fig. 1G).

Six lobes delimited by narrow incisions on the carapace margin are developed along its posterior end, the external ones being somewhat wider than others (Figs. 1I–K and 2J,K). They do not show any apparent variability within the sample, but are absent in the smallest of known specimens ZPAL Ab III/1368 (Fig. 2A–E). This specimen differs from most of the remaining ones in being more elongated along its axis. It seems unlikely that it represents another species, as specimens of small size are elongated even if their posterior margin is clearly lobate (Fig. 2G–I). There seems to be an allometric change in ontogeny both in respect to proportions of the carapace (see Fig. 3) and the contour of its posterior margin.

Head Region and Appendages

In a few specimens, a dorsoventrally compressed structure is visible, probably representing the labrum. A furrow separates it from the carapace, but in the axial part there is apparently a continuation

between these skeletal units (Figs. 1I,K and 4C–E). Laterally the furrow deepens and there could have been a suture. The exact shape of the ventral margin of the labrum is not traceable.

Along the sides of the labrum, the carapace extends into an almost vertical wall expanding ventrally to demarcate a lateral notch, perhaps for the antennae. Structures possibly representing antennae are preserved in specimen ZPAL Ab III/2155 (Fig. 4A,B). A more posteriorly located notch in the carapace, with a ventrally curved frontal part, probably held the eyes.

Some remnants of the strongly calcified and spiny walking appendages are preserved in specimen ZPAL Ab III/2159 (Fig. 4F–H). Details of their morphology are hard to determine, but there are four subequal pairs of them recognizable.

Gill-Like Structures

Similar to other *Halicynne*-like cycloids, large gill-like structures are present on both sides of the body. They occupy two fields along both sides of the rachis and comprise together a horseshoe shape. Until recently their exact organization

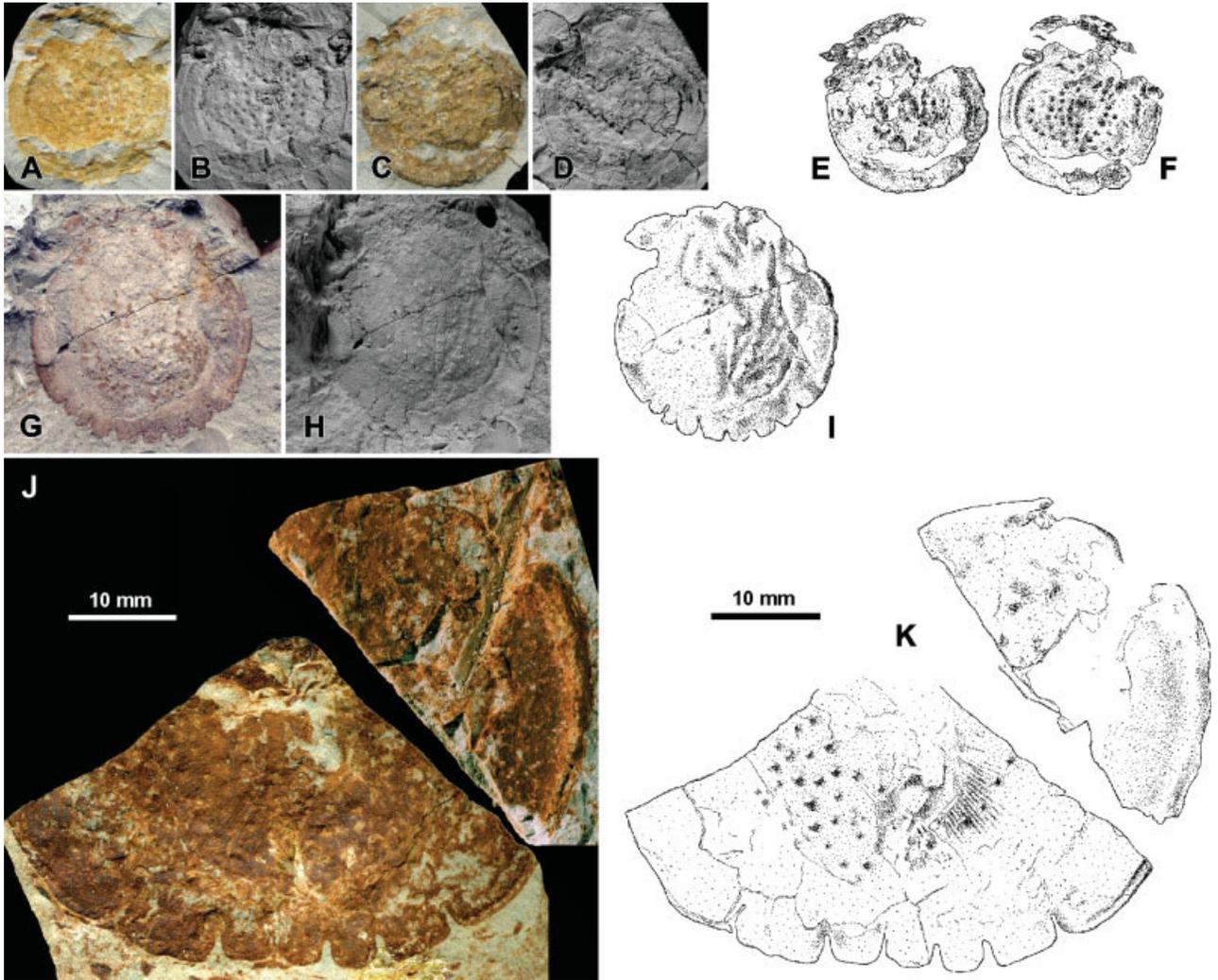


Fig. 2. Ontogenetic differences in carapace morphology of *Opolanka decorosa* gen. et sp. nov. from the early Late Triassic of Krasiejów, Poland; specimens photographed uncoated, coated with ammonium chloride and camera lucida interpretative drawings. **A–F**: Part and counterpart of juvenile specimen ZPAL Ab III/1368 lacking lobation of the posterior carapace margin. **G–I**: Juvenile specimen UOBS 00093 with posterior lobation but still elongate outline. **J,K**: The largest found specimen ZPAL Ab III/1181.

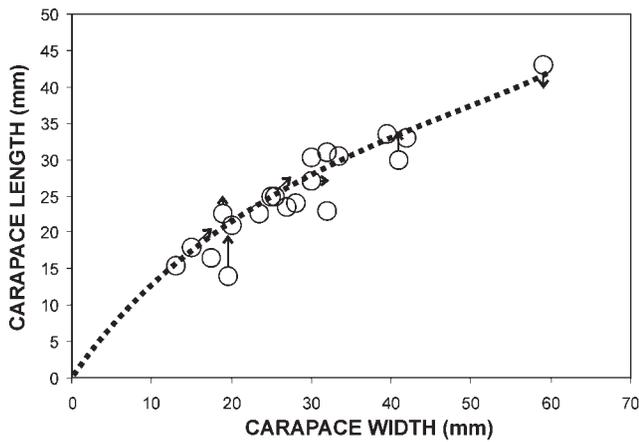


Fig. 3. Plot showing changes in carapace morphology in ontogeny of *Opolanka decorosa* gen. et sp. nov. from the early Late Triassic of Krasiejów, Poland; probable original dimensions of specimens deformed or incomplete are indicated by arrows.

remained unclear (Gall and Grauvogel, 1967; Schram et al., 1997), but specimens from Krasiejów clearly show that these are a series of, at least dorsally, heavily calcified units with a U-shaped cross section that opens ventrally. Their exact number is difficult to determine because the whole set is never exposed completely in the material at hand. Probably this varied, as in different specimens the units may be either rather sparsely (Fig. 1H,I), or densely (Fig. 5A–F) distributed. They are estimated to range from about 50 to 80 in number.

The fields with the blades are separated from the clearly demarcated margin of the well-calcified ventral doublure of the carapace by a rather wide area of weakly calcified ventral cuticle. Ventral margins of the gill blades, although rarely exposed, are irregular (Fig. 6C), suggestive of a continuation into a weakly mineralized ventral part. There is no reason to suggest that they were

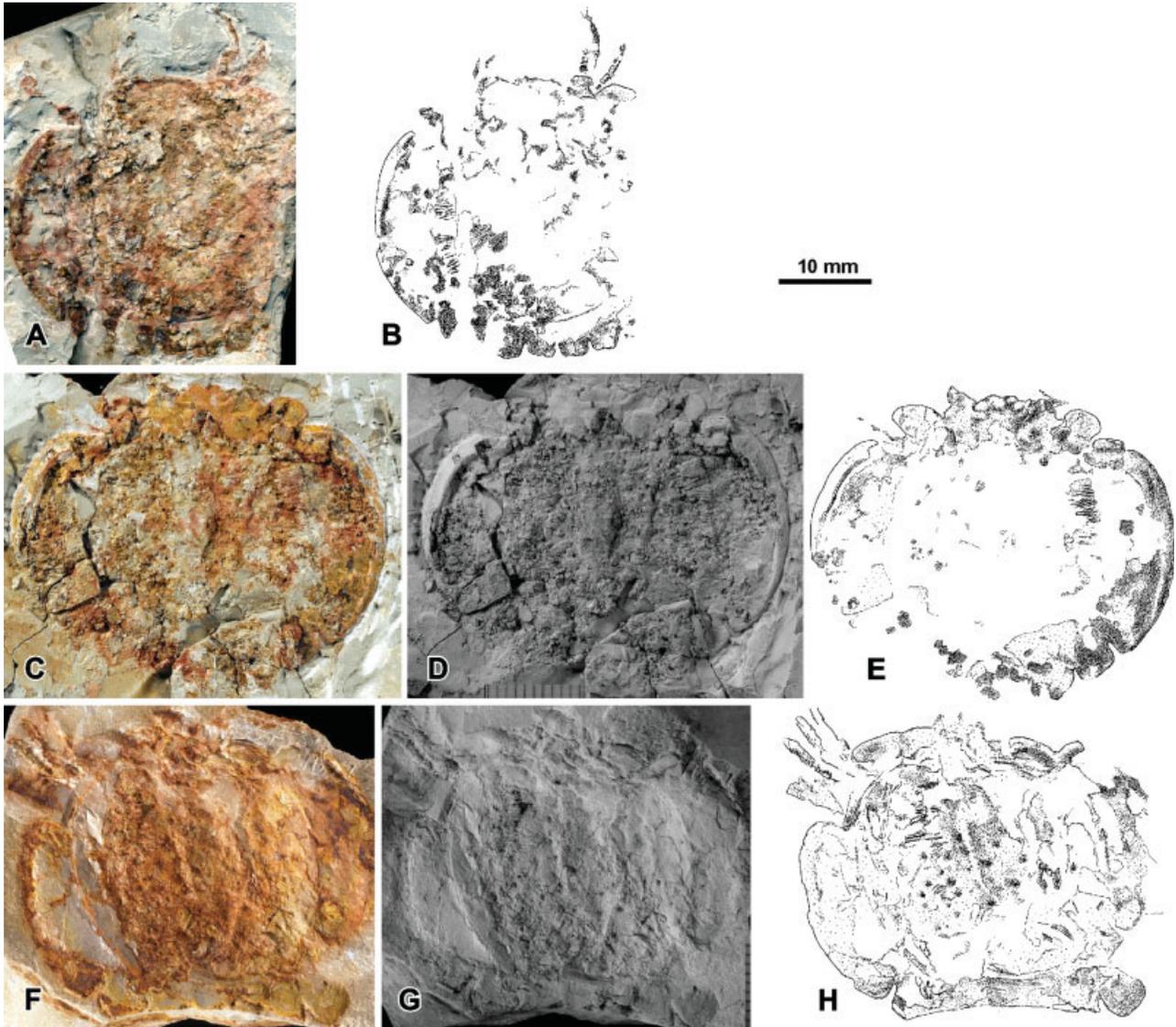


Fig. 4. Head region and appendages of *Opolanka decorosa* gen. et sp. nov. from the early Late Triassic of Krasiejów, Poland; specimens photographed uncoated, coated with ammonium chloride and *camera lucida* interpretative drawings. **A,B**: Probable antennule and second antenna of specimen ZPAL Ab III/2155. **C,D**: Specimen ZPAL Ab III/2153 with preserved head region showing unfolded eye and folded antennal lobes. **F–H**: Specimen ZPAL Ab III/2159 with poorly preserved walking appendages.

enclosed in a chamber with a narrow opening, making the whole structure similar to the book lungs of chelicerates, as suggested by Gall and Grauvogel (1967). Instead, their form suggests that they opened with slits over the ventral surface of the carapace. The cuticle there was thin and one may hypothesize that its infolding and regular arrangement was due to the connection of stronger cuticularized and mineralized dorsal parts of each slit with the furrows on the carapace, by apodemes (Fig. 6E).

VENTRAL MORPHOLOGY OF TRIASSIC CYCLOIDS

The adaxial margin of the gill fields in the Krasiejów cycloid encompasses an area at least roughly cor-

responding to the rachis of the carapace (Fig. 6B). The furrows demarcating the rachis supported apodemes probably connected with ventral structures of the body. There are some remnants of the sternal cuticle visible in section in specimen UOBS 02027 (Fig. 5A–F) but its exact structure is not determinable.

To develop a better understanding of the anatomy of the Late Triassic cycloid it is necessary to refer to material of a geologically older age, preserving structures inadequately represented in the Krasiejów material.

Mid Triassic *Halicynne* from Vosges

The stratigraphically and anatomically closest cycloid is that from the early Mid Triassic (Ani-

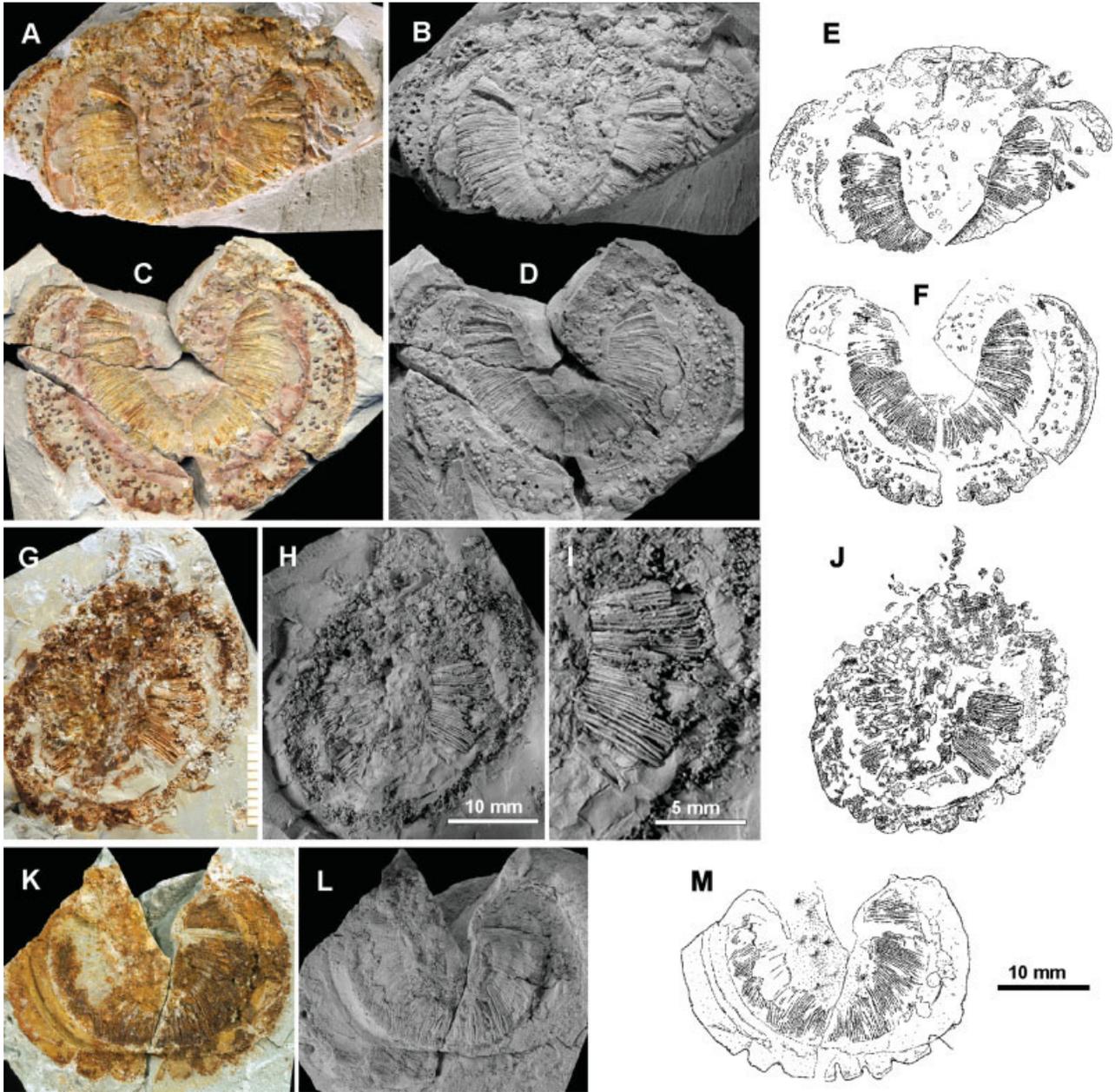


Fig. 5. Gill structures in the respiratory area of *Opolanka decorosa* gen. et sp. nov. from the early Late Triassic of Krasiejów, Poland; specimens photographed uncoated, coated with ammonium chloride and *camera lucida* interpretative drawings. **A–F**: Part and counterpart of specimen UOBS 02027 showing well preserved anterior part of the gills. Note carbonate concretions over the carapace margins. **G–J**: Specimen ZPAL Ab III/2154. **K–M**: Specimen ZPAL Ab III/2158.

sian) Grès à Voltzia in Vosges, eastern France. Specimens of the cycloid *Halicynne* from this famous palaeontological locality with unusually good preservation (*Konservat Lagerstätte*) show soft parts of the body (Gall and Grauvogel, 1967). They probably underwent early diagenetic phosphatization; but the shale containing fossils is decalcified, and the original structure of the carapace is not well preserved. The associated fossils and sedimentary context shows that the fossils were deposited in a freshwater deltaic environment (Gall, 1985).

I examined the original collection of *Halicynne* from the Vosges and confirmed the interpretation of preserved skeletal structures offered by Gall and Grauvogel (1967). No mouth appendages are preserved in any of the numerous specimens from Vosges. They were thus very different from the walking appendages, being either reduced or weakly sclerotized. The differences from the Krasiejów cycloid relate to differences in size and preservation. For instance, the gill blades, well visible in LGS 59 (Gall and Grauvogel, 1967, pl. G:1) are

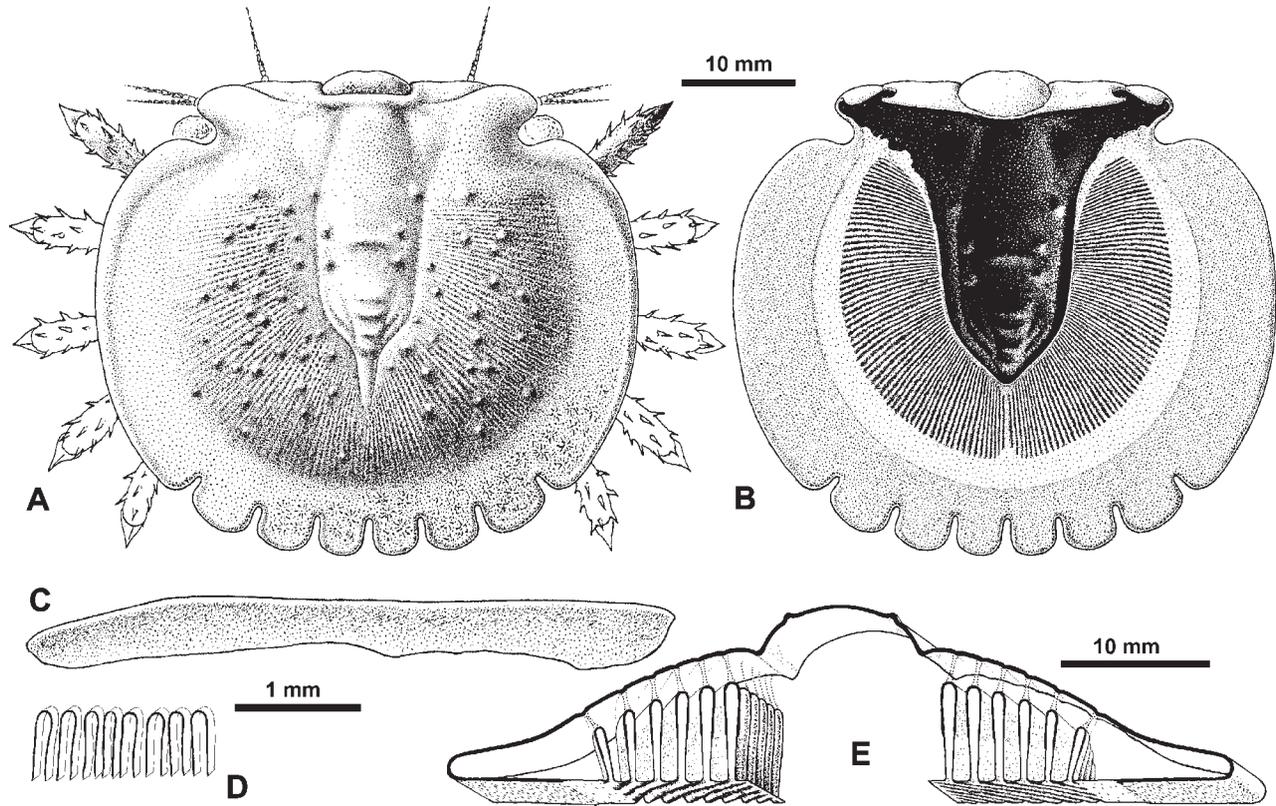


Fig. 6. Restoration of *Opolanka decorosa* gen. et sp. nov. from the early Late Triassic of Krasiejów, Poland. **A:** Dorsal view of the carapace with hypothetical arrangement of appendages. **B:** Ventral view of the carapace and respiratory area. **C, D:** Single unit of the gills in lateral view and diagrammatic presentation of units in UOBS 02027 (see Fig. 5A–F) based on *camera lucida* drawings. **E:** Restored arrangement of calcified parts of the gills within the carapace.

as densely distributed as if the gill slits share their separating walls. Some data known already to those authors can be now interpreted in view of the evidence on other cycloids published since then. Thus, the two flagellate appendages composed of numerous joints preserved in the anterior part of the body of a specimen with anteriorly displaced walking appendages (Gall and Grauvogel, 1967, pl. C, D; probable exuvium) have to be interpreted rather as the biramous antenna than an exopod. In no other cycloid has the presence of an exopod been confirmed (Schram et al., 1997, 2006).

Possible abdomen. Two cylindrical structures, preserved either as coalified (LGS H 36; Gall and Grauvogel, 1967, pl. E) or three-dimensionally mineralized (LGS H 11; Gall and Grauvogel, 1967, pl. F:2, also LGS H 21, 45, and 60) are associated with the posterior part of the gut in the Vosges *Halicyna*. These possible gonads extend well behind the area covered with coxae up to the carapace margin and show that there was a free abdomen of some length.

Coxae. The latter specimen also shows a distinct boundary separating bases of walking appendages (coxae). Their arrangement is semiradial, closely similar to that in the Carboniferous cycloids (Woodward, 1894, 1905; Hopwood, 1925;

Schram et al., 1997, 2006). The former specimen shows that there were five pairs of appendages with at least four more joints (that is five together), the terminal dactylus being narrower, sharp and with denticulated concave edge. All appendages are of virtually the same size and morphology. Another unnumbered detached appendage in the collection shows densely distributed strong spines covering the preceding joints. How these basal and distal parts of the appendages articulated, cannot be determined with this material.

The answer to this question is offered by the geologically somewhat older Triassic specimens from Madagascar.

Early Triassic Cycloids from Madagascar

Three-dimensionally preserved cycloids occur in concretions in the *Claraia* and fish beds of the Middle Sakamena Group of Madagascar reported by Brambilla et al. (2002) and Pasini and Garasino (2003, 2007). The age of the strata has been determined as Olenekian based on the conchostracan *Euestheria truempyi* Kozur and Seidel, 1983 found in a concretion from an unspecified locality in the same area near Ambilobé (Shen et al., 2002). There is an intercalation of fresh-water and

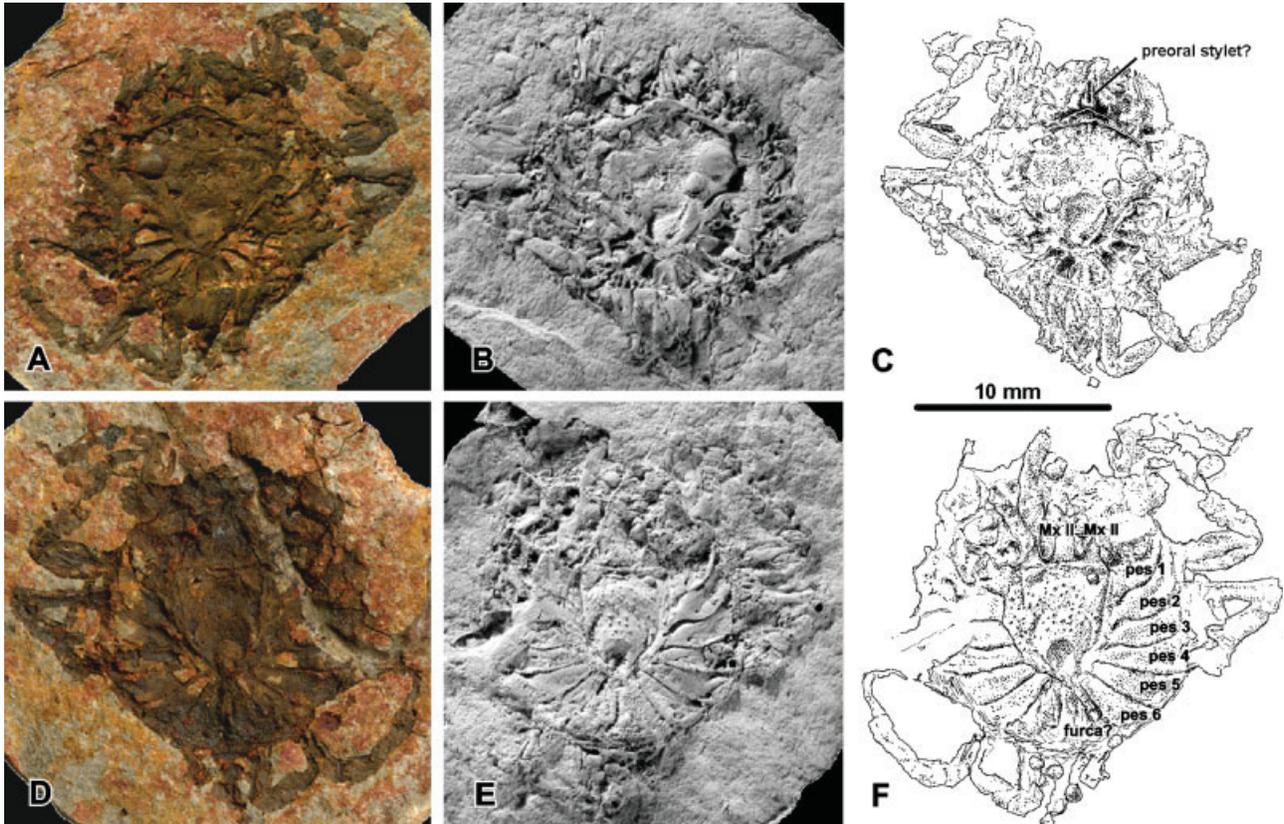


Fig. 7. *Schramine gondwanae* (Brambilla et al., 2002) from the Olenekian of the Middle Sakamena Group at Mahatsara on Ifasy River in Madagascar; counterpart (A–C) and part (D–F) of holotype MSNM i13280 photographed uncoated, coated with ammonium chloride and *Camera lucida* drawings. Oval objects scattered over this and other fossils from the Early Triassic Madagascar are larval and early postlarval bivalve shells and rare bellerophonitid gastropod conchs.

marine environments there, and the cycloids may have come from either of these environments. The rock is devoid of calcium carbonates or phosphates (Besairie, 1972) and skeletal structures are removed, represented by empty cavities or replaced with silica and iron oxides. Delicate cuticular structures may then be three-dimensionally preserved in empty carapaces. It was proposed that this situation is of early diagenetic origin (Beltan, 1996).

Abdomen. The most instructive of the Madagascar specimens is MSNM i13280, the holotype of *Halicynne gondwanae* Brambilla et al., 2002 from Mahatsara on the Ifasy River. It is presumably a detached ventral part of an exuvium deposited in anoxic sediment, perhaps poisoned with hydrogen sulfide. Numerous larval and early postlarval bivalve shells covering the cuticle suggest this. Apparently, larvae died shortly after settling on the specimen, which was probably the only hard object on the muddy bottom.

The latex cast of the part (Fig. 7E,F) shows an exquisitely preserved sternite, coxae, and somewhat displaced and deformed distal parts of appendages. The boundaries between six pairs of coxae and the sternite are distinct and clear cut. The

sternite is covered with sharp tubercles. In its posterior part an oval depression developed, probably as a result of the collapse of the proximal segment of the abdomen. The furcal rami may be the poorly recognizable and deformed, indistinctly annulated structure behind the sternite, which is armed with a row of setae along its admedial margin.

Appendages. A transverse ridge that separates the anterior triangular part of the sternum of MSNM i13280 from its polygonal posterior part may represent artificial breakage in the concretion. In front of it there are oval areas that probably represent bases of the collapsed maxillae. No other mouth appendages are preserved. There is a wrinkled zone between the coxae and movable parts of appendages. Appendages are poorly preserved and the number of joints is hard to determine.

Appendage joints are better preserved in the otherwise rather obscure juvenile paratype specimen MSNM i22868 (see Fig. 8). Basal joints are armed along their ventral margins with dense rows of spines. Terminal joints (dactyli) are narrow and acute, gently curved. Only three free joints of the appendages are discernible, which means that together with the coxae only four joints are pres-

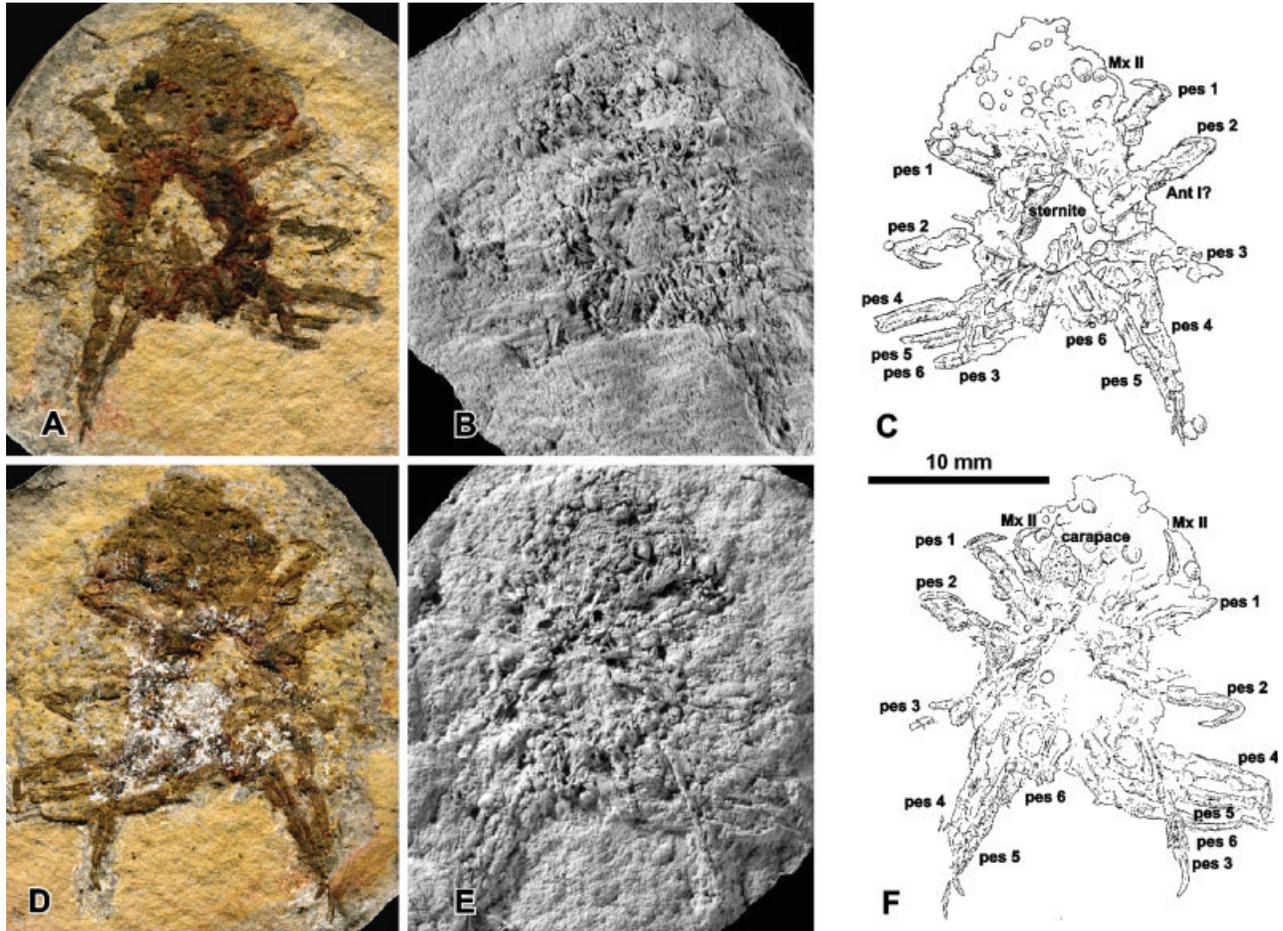


Fig. 8. *Schramine gondwanae* (Brambilla et al., 2002) from the Olenekian of the Middle Sakamena Group at Mahatsara on Ifasy River in Madagascar; part (A–C) and counterpart (D–F) of juvenile specimen MSNM i22868 photographed uncoated, coated with ammonium chloride and *Camera lucida* interpretative drawings.

ent, one less than in *Halicyne*. Altogether seven pairs of appendages are represented, including probable maxillipedes and second maxillae. The specimen probably represents an exuvium split and opened along the posterior margin of the carapace. The dorsal surface of the carapace, preserved as displaced between anterior appendages, is ornamented with fine tubercles.

The latex cast of the counterpart of MSNM i13280 (Fig. 7B,C) shows the ventral parts of the coxae in internal view and the smooth interior of the sternite. A finely annulated probable antenna (or exopod) can be seen near the second walking appendage. Most interestingly, the acute anterior end of the sternite is well represented. There are no mouth appendages extending in front of it but, instead, there is an elongate structure with an acute anterior end and a medial furrow. It may represent a preoral stylet. The cuticle around it is strongly folded, preventing identification of any other anatomical details.

Gills. In this respect specimen MSNM i26555, the holotype of “*Halicyne*” *mamoroi* Pasini and Garassino, 2007 from the Mamoro site near the Mamoro River, is more complete. This complete specimen is either partially decomposed, or caught in the process of molting, as suggested by all its appendages being anteriorly oriented. The gill structures with vertically oriented blades are represented on the counterpart (Fig. 9E,F).

If compared with the geologically younger Grès à Voltzia *Halicyne* and the Late Triassic Krasiejów species, the gill area on the specimens from Mamoro is more posteriorly located and narrower but this may as well be an effect of post-mortem decay. Longitudinally extended structures in the middle of the carapace are difficult to interpret and only in front of them are bases of walking appendages recognizable. They are three-dimensionally preserved and rows of spines are discernible along their ventral sides.

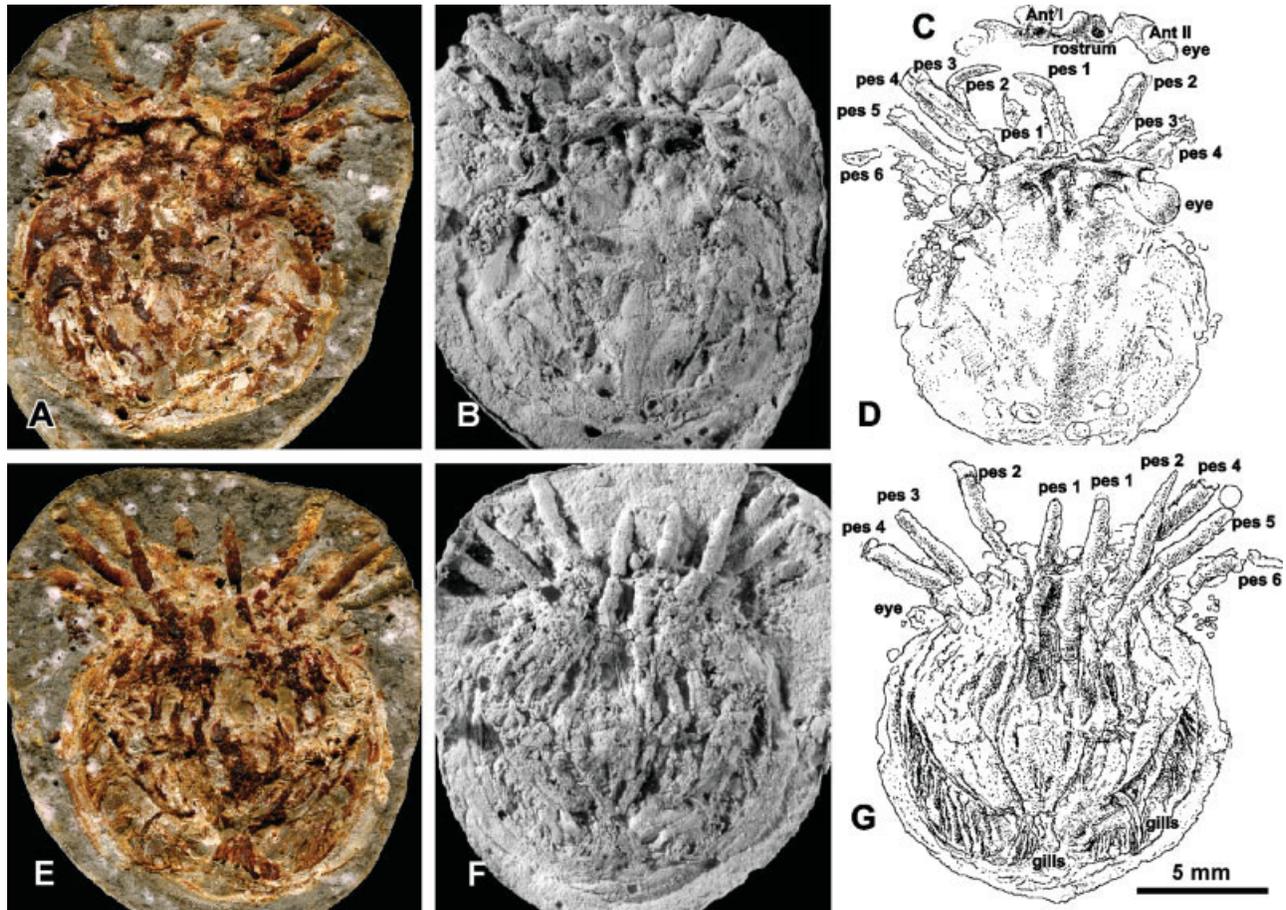


Fig. 9. *Schramine mamoroi* (Pasini and Garassino, 2007) from the Olenekian of the Middle Sakamena Group at Mamoro in Madagascar; part (A–D) and counterpart (E–G) of holotype MSNM i26555 photographed uncoated, coated with ammonium chloride and *Camera lucida* drawings.

Head. Even more morphologic details can be seen on the latex cast of the part MSNM i26555 (Fig. 9B–D). Large probable eyes are represented, with the vertically bent anterior margin of the carapace showing a sinus which probably originally held the second antenna (Fig. 9C). In the middle of the frontal area, a narrow, vertically dipping, probable labrum is bordered by two indistinct openings possibly corresponding to the poorly preserved basal joints of antennae. However, the interpretation of this part of the fossil is highly tentative.

More apparent is the morphology of the distal parts of appendages, altogether six homonomous pairs (possibly including second maxilla or maxillipeds). They do not differ in form from those in “*Halicynne*” *gondwanae*. The dorsal surface of the carapace can be seen in this specimen, with an indistinct medial elevation discernible in the posterior part of the carapace. Oblique striation on the left side of the carapace closely resembles that in later species of *Halicynne*.

A partial restoration of the venter of MSNM i13280 can be attempted with data on paratype

MSNM i22868 incorporated (see Fig. 10). Specimens of “*Halicynne*” *gondwanae* and “*H.*” *mamoroi* are too incomplete to decide whether they represent separate species or are conspecific. Seven pairs of strong appendages make at least the former species basically different from the Grès à Voltzia cycloid, which is definitely a species of *Halicynne*. However, some differences are apparent in respect to the type material of *Halicynne ornata* Trümpy, 1957 from the Anisian upper dolomite of the middle Muschelkalk of Badenia, Germany (see Fig. 11). The type species of the genus, *Halicynne agnota* (Meyer, 1838) from the Ladinian Trigonodus dolomite at Rottenmünster near Rottweil, Germany, differs even more.

The body plan of “*Halicynne*” *gondwanae* appears similar to that of the Early Carboniferous “*Halicynne*” *montanaensis* Schram et al., 2006, with its six pairs of appendages derived from subradially arranged coxae, and an additional pair emerging from the head region (Schram et al. 2006). A question arises whether these differences do not prevent classification of all these species in the same

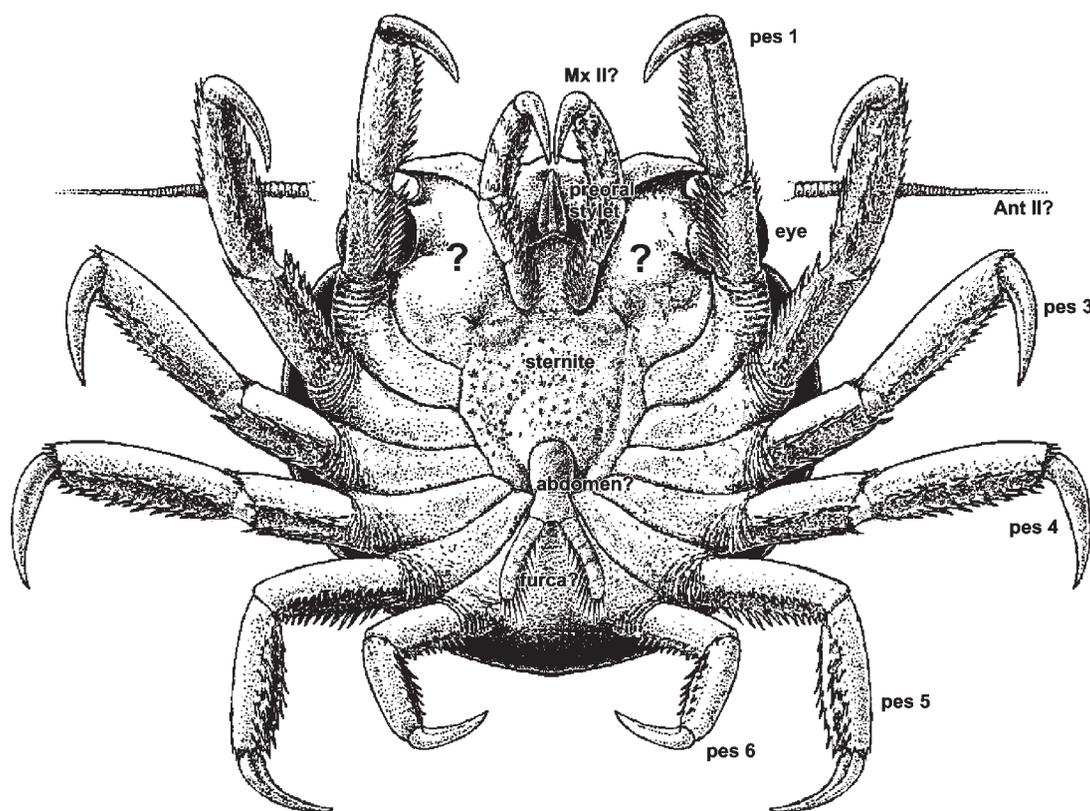


Fig. 10. Restoration of the ventral side of *Schramine gondwanae* (Brambilla et al., 2002) from the Olenekian of Madagascar in ventral view, based mostly on MSNM i13280.

genus. They differ not only in morphology but in their geological age. A review of stratigraphic distribution of particular body plans is thus helpful.

REVIEW OF CHRONOLOGICAL DISTRIBUTION OF THE CYCLOIDS

The youngest cycloid is *Maastrichtiocaris rosstrata* Fraaije et al., 2003 nom. corr. (the ending *-caris* denotes feminine gender and the species name has to be such) from the late Maastrichtian of Maastricht, The Netherlands (Fraaije et al., 2003). Its relationships to other cycloids are hard to trace (see Fig. 11). No other cycloid shows presence of anterolateral foramina or similar lobation of the carapace, although its elevated rim may remotely resemble that of the Late Triassic *Mesoprosope*. Such a rim, but a different arrangement of lobes, characterizes the enigmatic *Stagmacaris* from the Kimmeridgian of Örlingen Valley near Ulm, Germany (Schweigert, 2006).

The significantly older *Juracyclus posidoniae* Schweigert, 2007 from the Toarcian Posidonia shale of Gomaringen near Tübingen in Württemberg, Germany does not help in finding the evolutionary roots of post-Triassic cycloids. In distribution of lobes, centrally located rostrum and tuberculated crests on both its sides differs from all

known cycloids. The only specimen of *Juracyclus* rather resembles a partially preserved decapod carapace and a more complete specimen is needed to support its cycloid affinity.

Halicyne and Relatives

The Late Triassic cycloid from Krasiejów is similar to somewhat older species of *Halicyne* in carapace morphology, especially at juvenile stages, prior to development of its characteristic lobation. Of special significance in this regard is the semiradial fine furrowing of the carapace, possibly corresponding to the "gill" blades beneath, which is a feature of both the late Anisian *Halicyne ornata* and early Ladinian *H. agnota* (Meyer, 1847; Woodward, 1870, pl. 23:8; Schweigert, 2007, fig. 1:2). The other specimen from the same stratum and locality illustrated in Meyer (1847), Woodward (1870, pl. 23:7) as *H. laxa* (Meyer, 1838) may be a preservational variant, and restudy is needed to determine its distinct status as a species. The name *H. laxa* may not be available for it for the reason given by Hopwood (1905, p. 308).

In the specimen from the lower Keuper described by Müller (1955), only the axial part of the carapace is exposed from the rock matrix, and it is too incomplete to show specific diagnostic

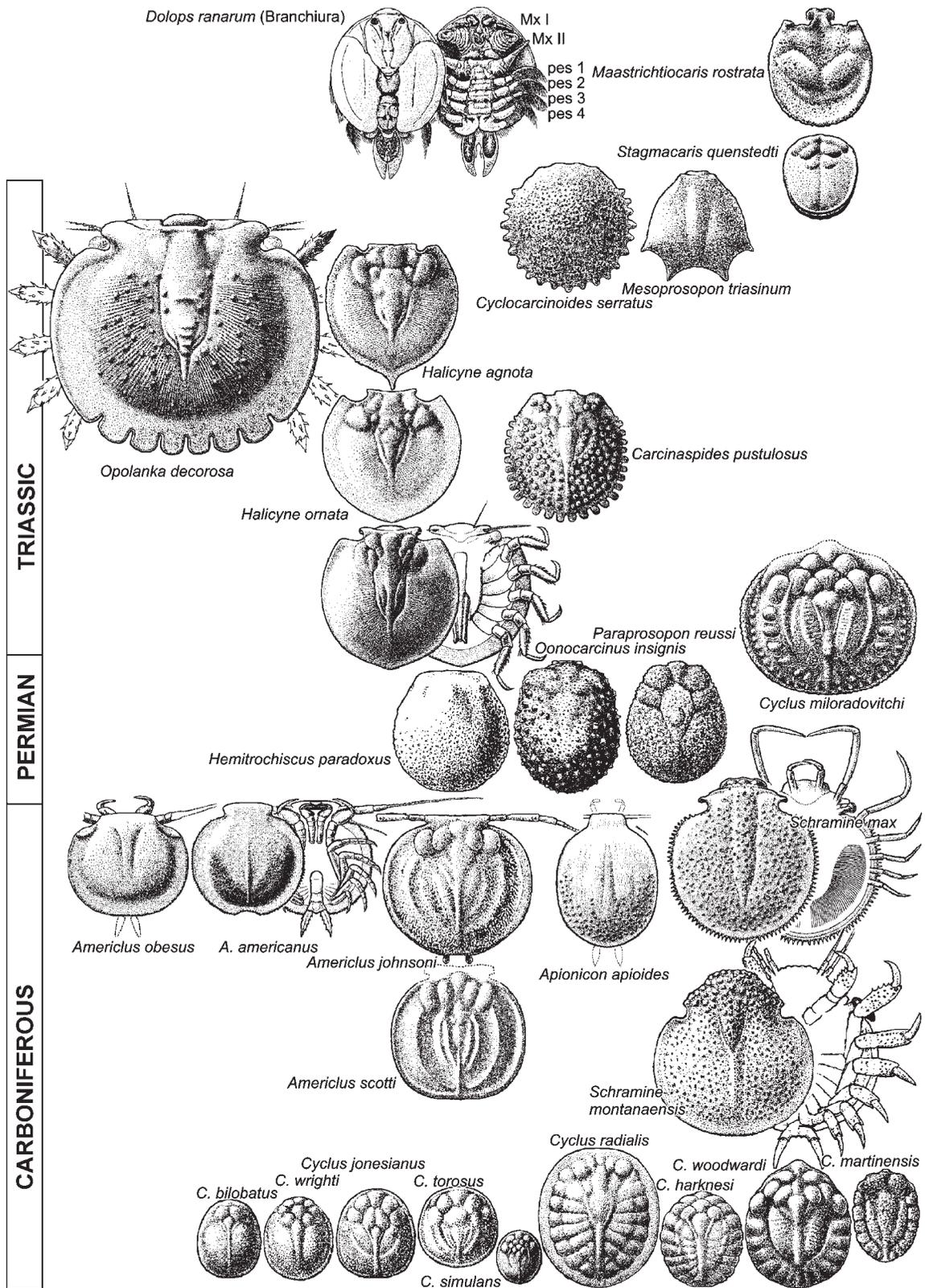


Fig. 11. Stratigraphic distribution of members of the order Cyclida (data from Meyer, 1847; Schauroth, 1854; Schafhütl, 1863; Woodward, 1870, 1893, 1894, 1905; Gemmellaro, 1890; Reed, 1893, 1908; Stolley, 1915; Trümpy, 1957; Kramarenko, 1961; Goldring, 1967; Schram et al., 1997, 2006; Fraaije et al., 2003; Schweigert, 2006, 2007). Drawings of specimens not to scale but show size differences between related forms.

characters. It is hard to tell it apart from the more completely preserved *Halicynne ornata* Trümpy, 1957 from the upper dolomite of the middle Muschelkalk of Badenia, Germany.

Halicynne silesiensis Alexandrowicz, 1973 from the Röt marine strata with *Myophoria costata* near Siewierz, Upper Silesia (Alexandrowicz, 1973), apparently belongs to the same lineage with the Vosges material of Gall and Grauvogel (1967), and it is difficult to detect any character distinguishing these species in the published descriptions. Perhaps a less triangular shape of the rachis and the more convex carapace distinguish the French form. Probably the geologically oldest record of this lineage is from the middle Bundsandsstein (Karlshafen/Trendelburger Beds) of Hessen, Germany, where *H. ornata* co-occurs with the conchostracan *Isaura* along with plant remains. Although marine bivalves occur in the overlying sandstone, the environment of *Halicynne* was apparently freshwater (Busse and Horn, 1978). The European species of *Halicynne* may form a lineage characteristic for marginal parts of the Muschelkalk Germanic Basin.

The Krasiejów species, although living in the same area, apparently represents another direction of evolutionary change, towards widening and enlarging the size of the carapace. The roots of its lineage are definitely close to the Vosges *Halicynne*, as suggested by similarity in the form of the carapace rachis, but with the available evidence it is not possible to determine the time of separation.

Oonocarcinus and Relatives

Lobation of the carapace that extends along its whole margin, along with a strong tuberculation of the carapace, characterizes *Carcinaspides pustulosus* (Schafhäutl, 1863) found in a limestone of the Isar Valley (in the alpine part of Bavaria); it was the only fossil from there (Schafhäutl, 1863). Most likely this means that it is from the "Wettersteinkalk" and therefore of Mid to early Late Triassic age (G. Schweigert, personal communication, 2007), and thus similar to that of Krasiejów.

The lack of the marginal flat area and striation of the carapace, shared by the Krasiejów form with species of *Halicynne*, makes *Carcinaspides pustulosus* similar rather to *Cyclocarcinoides serratus* (Stolley, 1915) from the gray Norian limestone at Siriuskogel near Ischl, Salzkammergut, Austria (Stolley, 1915). *Mesoprosopon triasinum* Stolley, 1915 from the same locality bears only four prominent spinose protuberances at the posterior margin of the carapace.

Cycloids such as *Carcinaspides*, characterized by thick robustly ornamented and high vaulted carapace, resemble the Permian *Oonocarcinus insignis* Gemmellaro, 1890 from the olisthostromal limestone block at Sosio, Sicily, Italy. The rock is prob-

ably of Wordian age (Feldmann et al., 2004). Gemmellaro (1890) subdivided his Sosio material of *Oonocarcinus* into three species, differing in the size and prominence of tubercles on the carapace: *O. insignis*, with prominent tubercles and length of five specimens ranging from 22 to 33 mm, *O. geinitzi*, represented by four specimens of 7–10 mm length with delicate tuberculation, and the even finer ornamented 7 mm long *O. anceps*. Possibly, these differences are only due to ontogenetic changes within a single species.

Lobation and ornamentation of the morphologically indistinguished carapace of *Hemitrochiscus paradoxus* Schauroth, 1854 from the late Permian Zechstein dolomite of Pösneck, Germany (Schauroth, 1854) is even more obscure. The original drawing in Schauroth (1854, pl. 22:1) does not allow us to be sure of the identity of the fossil, but the figure of the same species in Geinitz (1861; original not seen, reproduced in Glaessner, 1969) shows a fossil similar to *Cyclocarcinoides*.

Yet another species from Sosio, *Paraprosopon reussi* Gemmellaro, 1890, bears two pairs of distinct cephalic lobes. To some degree it is morphologically intermediate between Permian *Oonocarcinus* and some Carboniferous species of *Cyclus*, suggesting such an origin for the lineage. *Cyclus communis* Rogers, 1902 from the Late Carboniferous Iola Limestone at Kansas City (Rogers, 1902) may serve as a possible connecting link.

Palaeozoic "Halicynne"

"*Halicynne*" *gondwanae* from the Early Triassic of Madagascar, redescribed earlier, is thus the only source of data on the anatomy of cycloids more ancient than the Mid Triassic *Halicynne*. Its seven pairs of strong appendages with only four joints are similar to the oldest cycloid with known appendages, "*Halicynne*" *montanaensis*, from the Namurian Bear Gulch Limestone, Montana. Schram et al. (2006, p. 7) noted that "the radial lamellae [...] are not preserved" but on their figure 1:2 a series of dark parallel lines are reproduced, drawn also on figure 2:2. If they have anything to do with gills, the number of slits was much smaller in "*H.*" *montanaensis* than in the Westfalian Mazon Creek "*Halicynne*" *max* Schram et al., 1997 or the Triassic *Halicynne*. If the homology of appendages proposed by Schram et al. (2006) is correct, "*H.*" *max* is transitional to the Mid Triassic *Halicynne* in reductions seen in the walking appendages, both in respect to their total number and in the number of joints (the latter probably even further advanced).

Flat carapace "Cyclus"

"*Cyclus*" *americanus* Packard, 1885, from the Essex biota of the Mazon Creek area of Illinois, the best known cycloid (Schram et al., 1997), has the

same number of appendages as noted earlier, but the first pair of thoracic appendage more resembles maxillae than walking appendages, and it probably lacked "gills". It shares a relatively flat and weakly ornamented carapace with *Halicyne*, but the walking appendages are subdivided into eight joints, twice as many as in "*Halicyne montanaensis*" and "*H. gondwanae*". Carboniferous forms with prominent lobation of the carapace, such as the late Westphalian "*Cyclus johnsoni*" (Woodward, 1894) and early Westphalian "*C. scotti*" (Woodward, 1893, 1894) may be transitional to species of *Cyclus* s.s.

Cyclus s.s.

Carapace vaulting and mineralization comparable with *Oonocarcinus* and relatives characterized the true species of *Cyclus*, a taxon that is the first cycloid to appear in the fossil record. Trümpy (1957) already suggested that the flat-carapace Carboniferous forms represent a genus different from *Cyclus* s.s., with its highly vaulted and ornamented carapace. Their distinctive aspect is a prominent lobation of the carapace, frequently extending backward from the head region to the thorax. The last true *Cyclus* is probably *Cyclus miloradovitchi* Kramarenko, 1961, from the Early Permian *Schwagerina* horizon at the Sim River, the Urals (Kramarenko, 1961). Its specimens were found associated with trilobites and a diverse assemblage of other marine animals. It is stratigraphically preceded by *C. packardii* Rogers, 1902 from the Late Carboniferous Iola Limestone at Kansas City (Rogers, 1902).

Other members of the genus occur in Early Carboniferous marine strata. The type species, *Cyclus radialis* (Phillips, 1836), comes from the Viséan Carboniferous Limestone at Bolland, Yorkshire, and is known to be associated with fenestellid bryozoans (Goldring, 1967, p. 317). *Cyclus martiniensis* Goldring, 1967 was found together with corals in the Viséan Hotwells Limestone at Mendip Hills, England. Similar species are known also in the marine Early Carboniferous of Kazakhstan (Tschernyshev, 1933).

Some evidence concerning the appendages of true *Cyclus* is offered by the specimen MSNM i26230 from the Olenekian of the Middle Sakamena Group at Ambitambonoagna, Madagascar (identified as *Halicyne gondwanae* by Pasini and Garassino, 2003). Ammonoids occur in other concretions from the same locality (Pasini and Garassino, 2003) making a marine habitat possible for this form. Unlike other Madagascan cycloids, this specimen is preserved strongly compressed in shale, with low relief. The part of MSNM i26230 (Fig. 12; Pasini and Garassino, 2003, Figs. 5 and 6) under low light exposes transverse furrows on the carapace separating at least five lobes. Their disposition is unlike the radial arrangement of coxae in cycloids and the whole structure is located

above the appendages. These are thus furrows of a lobate carapace typical of *Cyclus* s.s. The counterpart shows transverse (also in respect to the furrows), longitudinal, indistinct wrinkles probably corresponding to surface ornamentation of the carapace. They do not have any expression on the internal mold, which indicates that the original carapace wall was rather thick. The homonomous organization of appendages, with the six pairs of walking legs of similar size and morphology, may represent the ancestral status for the group. The exact number of appendage joints cannot be determined because of their poor preservation, but it is apparent that there were at least six joints (including coxae). It cannot be excluded that appendages of *Cyclus?* sp. were of as complex articulation as those of the Late Carboniferous "*Cyclus americanus*". A pair of probable minute antennules with delicate annulation is also recognizable in the specimen from Ambitambonoagna. Nevertheless, the Triassic age makes extrapolation of anatomical data to Early Carboniferous members of the lineage rather tenuous.

Although the probable *Cyclus* from Ambitambonoagna is the only direct source of information on the number of thoracic appendages in the genus, some evidence on the Early Carboniferous cyclid tagmosis can be inferred from their carapace morphology. Lobation of the cyclid carapace apparently corresponds to their body segmentation. Reed (1908) proposed a notation for bosses and ridges on the carapace of *Cyclus*, but he did not aim to identify the segmentation pattern to which they correspond. Also, the nomenclature used by Busse and Horn (1978) for homologous structures in *Halicyne* did not address this question. In such a situation, one has to compare the lobation pattern of *Cyclus* with the observations on early decapods by Secretan (1972, 1973). This seems to be substantiated by the suggestion of Newman (1983) that the 5-6-5 (or 5-7-4) body plan of maxillopodan crustaceans derived from that of the 5-8-6 plan of Eumalacostraca. The most elaborate pattern is represented by *Cyclus radialis* and *C. woodwardi* (Reed, 1908; Woodward, 1894; Goldring, 1967; Schram et al., 1997). It consists of a series of variably distributed paired head lobes presumably corresponding to the head appendage series including the second maxilla, invariably followed by six almost homonomous lobes. They are apparently connected with the six pairs of thoracic appendages identified in all other more completely preserved cyclids, from Carboniferous to Early Triassic. Such was probably the status typical for the early cyclids.

TAXONOMIC NOMENCLATURE OF THE CYCLOIDS

It follows from the above review, that at least three separate branches can be distinguished in

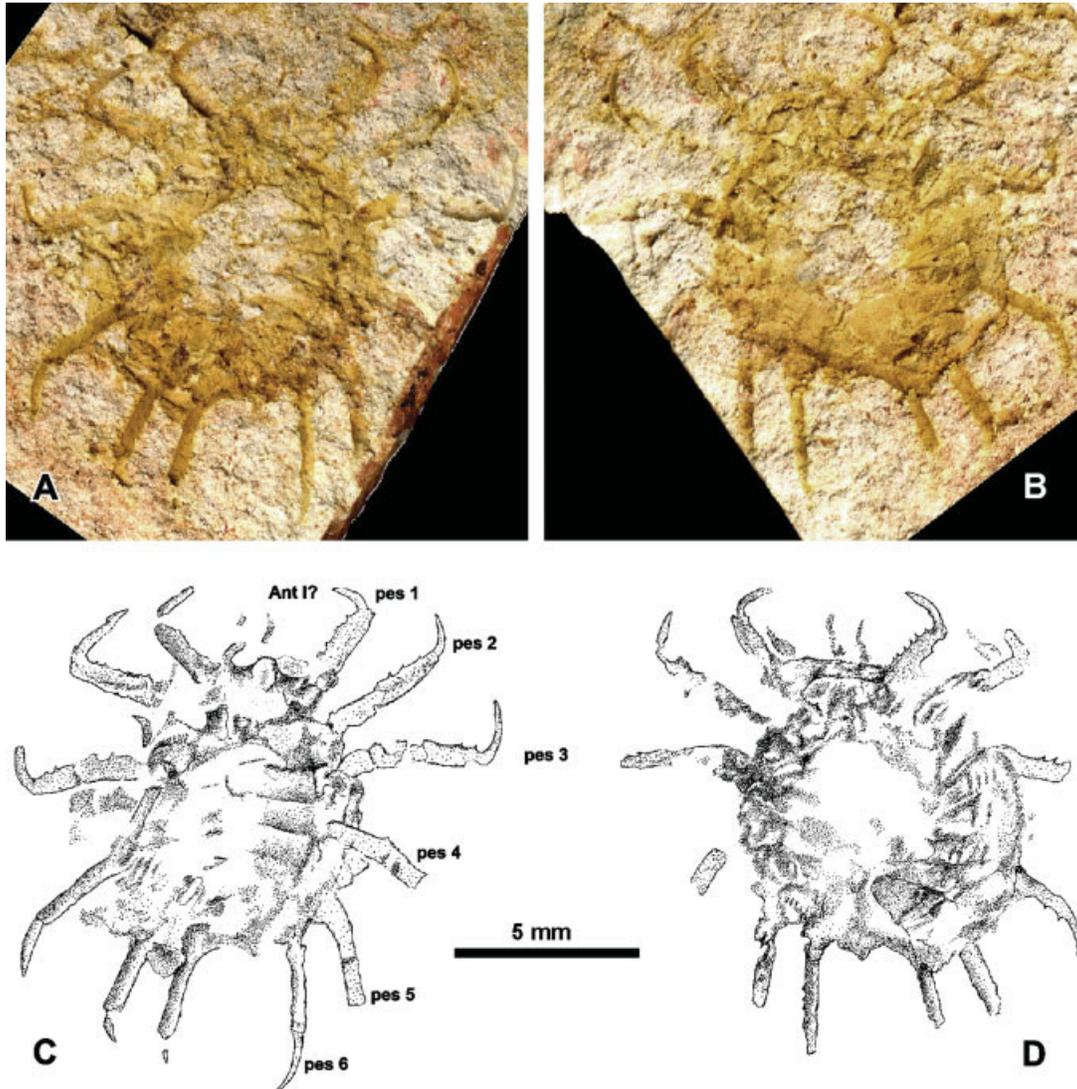


Fig. 12. Probable *Cyclus* from the Olenekian of the Middle Sakamena Group at Ambitambo-noagna, Madagascar; specimen MSNM i26230 (Pasini and Garassino, 2003), photographs and camera lucida drawings of part and counterpart.

the diversity of the cycloids, differing not only in morphology, but also in regard to environmental preferences. As is usual for taxa with a relatively good fossil record, they may originate sequentially each from the other and are possibly paraphyletic in cladistic terms.

The branch to which the Krasiejów cycloid belongs is characterized by weakly sclerotized and probably highly modified mouth appendages, five pairs of walking appendages, and internal book gills or lungs with numerous parallel slits on either side of the venter. The carapace is gently convex. These cycloids lived in fresh waters, being commonly associated with conchostracans. In terms of taxonomic nomenclature, this is the family Halicy-nidae Gall and Grauvogel, 1967 comprising *Halicyne* Meyer, 1847, and *Opolanka* gen. et sp. nov.

The species "*Halicyne*" *montanaensis*, "*H.*" *max*, and "*H.*" *gondwanae* deserve separate generic and family names, for which *Schramine* gen. nov. and *Schraminidae* fam. nov. are here proposed. Although they share "gill" blades with the Halicy-nidae, they otherwise are less derived. They preserved the more plesiomorphic condition of six walking appendages, which show gradation in of size and geniculation, and a prominent second maxilla of an underived morphology.

A true marine environment was probably preferred by members of the family Cyclidae Packard, 1885, which are characterized by a well-mineralized, highly-vaulted carapace with usually robust tuberculation, and six pairs of walking appendages. In the Early Carboniferous, this branch is represented by numerous species of *Cyclus* de

Koninck, 1841, a genus which continued into the Permian. Probably the group of Early Carboniferous species, with simple lobation of their smooth carapace without segmentation, is distinct enough to deserve a separate generic name, but restudy of the original material is necessary before it is done. Most likely, the Late Permian to Cretaceous forms with massive carapaces, classified in families Mesoprosopidae Glaessner, 1969 and Hemitrochiscidae Trauth, 1918, continue the same branch. Possibly this post-Triassic lineage owes its morphology, unusual for the cycloids, to a diminution in mature size. No data on appendages of the Mesoprosopidae and Hemitrochiscidae are available.

Transitional at least in morphology, but possibly also in ecology, is the third branch with "*Cyclus*" *americanus* as the best-known species. Carapaces of these cycloids are generally flat and smooth or finely tuberculated. They bear six pairs of walking appendages, but only the first of them is geniculate (maxillipedes, as interpreted by Schram et al., 1997), diminishing in size posteriorly. The mouth appendages are small but have an undervived morphology, similar to walking appendages (Schram et al., 1997). Although an origin of this branch separate from the marine, strongly vaulted *Cyclus* is likely, the great difference in carapace morphology requires their classification in at least a separate genus and family. *Americlus* gen. nov. and Americlidae fam. nov. are here proposed for them.

Thus, it appears that the cycloids differ not only in the shape of their carapaces, but also in more important aspects of their body plans: number of walking appendages, degree of specialization of mouth appendages, and probably in the presence or lack of the unique "gill" apparatus. They deserve splitting not only into several family rank taxa. The superfamily rank of Cycloidea Glaessner, 1928 was raised to an order by Schram et al. (1997). Another question would be the placement of the order (or perhaps suborder) within the higher rank classification of the crustaceans.

EVOLUTIONARY RELATIONSHIPS OF THE CYCLOIDS

On the basis of cladistic analysis of the morphological data, Schram et al. (1997) classified the subclass Halicyna Gall and Grauvogel, 1967, with its only order Cycloidea Glaessner, 1928, as the sister taxon of the Copepoda. The main basis for this is the large size of the first antenna in *Americlus americanus*, a characteristic feature of copepods.

The antennae of *Schramine montanaensis*, the oldest cycloid with known appendages, although poorly preserved, are not so prominent and seem to protrude anteriorly (Schram et al., 2006). This disposition seems to be even more apparent in the species of *Cyclus*? from Madagascar. Although geo-

logically late, this latter taxon preserved segmentation of the carapace typical of the much older members of *Cyclus* s.s., and there is no reason to believe that its sensory appendages had lost their plesiomorphic status. The similarity of cycloids to copepods may thus not be an original and persistent feature.

The aspect of the cycloid morphology of possibly crucial importance to interpretation of their affinities is the "gill" apparatus. No such structure is known in the present-day Crustacea, in which gills usually developed in a direct connection with appendages (Boxshall, 2004). The similarity to chelicerate book lungs, suggested by Gall and Grauvogel (1967), appears remote at best, based on the evidence now available on the Triassic *Halicynelike* cycloids, and apparently has resulted from their similar function (see Jeram, 1990; Reisinger et al., 1991).

There are, however, gill structures in crustaceans once proposed to be close relatives of the cycloids, which may have provided a basis for evolutionary development of the *Halicynelike* gills. These are the respiratory areas on the lower surface of the branchiuran carapaces, represented by a pair or two of well-defined oval fields with thinner cuticle, supplied with branching blood vessels (Sutherland and Wittrock, 1986; Overstreet et al., 1992). They function also as ion exchange organs (Haase, 1975), perhaps as an adaptation of branchiurans to the freshwater environment. The new data from Krasiejów suggest that the gill structures of Halicynidae are serial infoldings of the ventral cuticle in ventral oval areas on the carapace, similar to the branchiuran respiratory areas. Infoldings increased the area of contact of blood with the surrounding water. This may be an evolutionary response to the apparent freshwater life environment of Halicynidae.

The tagmosis of Maxillopoda, in which Branchiura and Copepoda are classified, may have originated from the 5-8-8 plan of the malacostracans (Newman, 1983). The reduction was apparently achieved by precocious maturity of a larval form (paedomorphosis). The recent branchiurans are highly derived crustaceans adapted to parasitism and most of their plesiomorphic features seem to be lost as a result of secondary simplification, making identification of their ancestry difficult.

The least derived of the recent branchiurans is *Dolops*, the only member of the group lacking suckers, of Gondwanan distribution (Huggins, 1970). Its first maxilla bears hooks used to grasp the host skin and anchor to it (Avenant et al., 1989), instead of being transformed into suckers typical of other branchiurans. Another unique character of this branchiuran is the sperm transfer that involves the employment of spermatophores. According to Fryer (1958, 1960), spermatophore formation indicates that Branchiura and Copepoda

are not closely related and that the phylogenetic position of Branchiura among recent crustaceans is isolated.

The hook-like appearance of the maxillules in *Dolops* may be used to link morphologically the branchiurans with the pentastomids, a relationship with strong molecular support (e.g. Abele et al., 1989; Lavrov et al., 2004). This also implies that the polarity of morphological change within Pentastomida was opposite to that proposed by Walossek and Müller (1994; Waloszek et al., 2005).

Only the African species of *Dolops*, *D. ranarum*, lacks respiratory areas (Avenant et al., 1989, p. 144). In one of the most derived branchiurans with a reduced carapace, *Chonopeltis*, the carapace reduction is restricted to parts outside of the respiratory area (see Van As and Van As, 1999a,b). This seems to prove its high functional importance in the physiology of these organisms.

The conical preoral structure identified in the Madagascan "*Halicyne*" *gondwanae*, may also support branchiuran affinities and a parasitic mode of life of the cycloids. It may be a homologue of the evertible preoral spine of *Argulus*, which is used by recent branchiurans to penetrate the host body integument (Gresty et al., 1993). Paired gonads of branchiurans are located laterally on the abdomen, and may penetrate into the furcal lobes (Avenant et al., 1989), resembling the proposed interpretation of tubular structures associated with the intestine in *Halicyne*.

Already Hopwood (1925, p. 305) proposed classifying the cycloids within Branchiura, interpreting the lateral ridges on the carapace of some species of *Cyclus* as signs of fusion of lateral cephalic lobes. The mud-filled gut was interpreted by him as the evidence of a benthic lifestyle, but the streamlined appearance of the carapace is a possible adaptation to ectoparasitism on fishes "on occasion."

The evolutionary scenario that emerges from the above-presented data seems to support this idea. The Cyclida, with their original number of six homonomous thoracic appendages lacking exopods, presumably originated from ancestral maxillopodans. The Late Cambrian *Bredocaris admirabilis* Müller, 1983, with a disc-shaped cephalic shield and seven pairs of thoracic appendages identified in the largest found instars (0.85 mm long; Müller and Walossek, 1988) is the only geologically older form with such a possible body plan. Its unsegmented and legless abdomen continues smoothly into a furca. The first maxilla bears a rudimentary exopod, and the second maxilla is of the same morphology as the thoracic appendages. Müller and Walossek (1988) considered specialization of the first thoracic appendages into maxillipeds in the coeval *Skara minuta* as similar to that seen in Copepoda (actually the term Maxillopoda refers to this feature) but the ancestor of the Cyclida is expected not to show any such specializations.

In the subsequent Late Palaeozoic evolution towards the condition seen in *Halicyne*, the cycloids modified their maxillae (and the first thoracopod in *Americlus americanus*) into a grasping apparatus and developed a preoral spine. It is not possible to decide whether the observed reduction of the thoracic appendage number was a result of reduction of the maxillipeds or rather the posteriormost walking pair. The uniform appearance of the walking appendages in *Halicyne* and *Opolanka* gen. nov. suggests that only juveniles might have been parasitic, if at all. The increase of mature size in *Opolanka* gen. nov. makes the crab-like ecology, suggested by Schram et al. (1997) also for earlier cycloids, likely.

The argulid branchiurans, with only four thoracic appendages and a weak sclerotization of the carapace shield, are almost certainly secondarily simplified. Thus the biramosity of their appendages does not imply their plesiomorphic status.

DIAGNOSES OF NEW TAXA

Class Crustacea Pennant, 1777

Subclass Branchiura Thorell, 1864 (*Halicyna* Gall and Grauvogel, 1967)

Order Cyclida (Schram et al., 1997) *nom. corr. ex* Cycloidea (Glaessner, 1928; in Schram et al., 1997)

Family Schraminidae, fam. nov.

Diagnosis. Six pairs of thoracic appendages (including enlarged maxillipeds) with four joints; gently convex, tuberculated carapace.

Genus *Schramine* gen. nov.

Type-species. *Halicyne max* (Schram et al., 1997)

Derivation of name. After Frederick R. Schram, in recognition of his works on Paleozoic cycloids and other fossil crustaceans.

Diagnosis. As for the family.

Family Americlidae, fam. nov.

Diagnosis. Six pairs of thoracic appendages (including enlarged maxillipeds) with up to eight joints; flat and almost smooth carapace.

Genus *Americlus* gen. nov.

Type species. *Cyclus americanus* Packard, 1885

Derivation of name. Composition from parts of specific and generic names of the type species.

Diagnosis. As for the family.

Family Halicynidae Gall and Grauvogel, 1967 (*nom. corr. ex* Halicynae Gall and Grauvogel, 1967)

Emended diagnosis. Five pairs of thoracic appendages with five joints; mouth appendages modified; gently convex carapace.

Genus *Opolanka* gen. nov.

Type species. *Opolanka decorosa* gen. et sp. nov.

Derivation of name. "Opolanka" is a woman from Opole Silesia.

Diagnosis. *Halicyne*-like cyclid with lobate posterior margin of the carapace.

Opolanka decorosa gen. et sp. nov.

Holotype. ZPAL Ab III/1363 (Fig. 1G–K).

Type horizon and locality. Late Carnian lacustrine claystone at Krasiejów, Opole Silesia, southern Poland.

Derivation of name. Allusion to a similarity in form of the posterior part of the carapace to decorations of the female national dress in the Opole region.

Diagnosis. as for the genus.

Comparison: *Opolanka decorosa* gen. et sp. nov. differs from all other cyclids in its posteriorly lobate large carapace. Its probable closest relative *Halicyne ornata* lacks also tuberculation of the carapace and its rachis is more triangular.

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