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A New Pleurocystitid Blastozoan from the Middle Devonian of the Eifel (Germany) and Its Phylogenetic Importance

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A new pleurocystitid blastozoan from the Middle Devonian of the Eifel (Germany) and its phylogenetic importance

ELISE NARDIN and JAN BOHATÝ

Rich echinoderm fauna from the Middle Devonian of the Eifel (Rhenish Massif, Germany) has yielded specimens of the rare recumbent pleurocystitid rhombiferans. *Regulaecystis testudineus* sp. nov. extends the stratigraphic range of the pleurocystitids to the Eifelian (Middle Devonian). Specimens show a strongly inflated and ornamented theca, which is unusual for the European pleurocystitids. Phylogenetic analysis of all described pleurocystitid genera suggests a close relationship of *Regulaecystis* with the other Devonian genera. Results indicate that the degree of inflation and of ornamentation of the theca can be interpreted as convergences within the pleurocystitids due to environmental conditions (such as surface consistency, hydrodynamism). *R. testudineus* sp. nov. was living as a strict epibenthic vagile organism; lying on muddy soft to firm substrates in quiet to agitated shallow warm water environments.

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Introduction

Recent intensive fieldwork in the Nims Member of the Junkerberg Formation (Eifelian, Middle Devonian) from the Prüm Syncline (Eifel, Germany) has revealed an abundant invertebrate fauna, among which rare specimens of the first recorded recumbent pleurocystitid rhombiferans in the Middle Devonian of the Eifel (Rhenish Massif). The three-dimensional preservation of the new specimens allows the clear and complete observation of all morphological details. The occurrence of the new species *Regulaecystis testudineus* sp. nov. enlarges the stratigraphic range of the family Pleurocystitidae from the Floian (Early Ordovician) to the Eifelian (Middle Devonian). The older species *R. pleurocystoides* Dehm, 1932 from the Lower Devonian Hunsrückschiefer (Germany) is compressed and secondarily flattened, making morphological features difficult to distinguish clearly. The atypical morphology of *Regulaecystis testudineus* sp. nov. broadens the morphological variability shown by the Devonian pleurocystitid species (*Coopericystis devonica* [Paul, 1974] from the Middle Devonian of Great Britain; *Henicocystis darraghi* Jell, 1983 and *Hillocystis atracta* Jell, 1983 from the Early Devonian of Aus-

tralia; *Turgidacystis graffhami* Parsley and Sumrall, 2007 from the Early Devonian of Oklahoma). The description of the new species and the revision of the Devonian European genera of pleurocystitids will discuss the palaeoecology and the evolutionary trends within the family Pleurocystitidae.

Institutional abbreviations.—BMNH, Natural History Museum, London, UK; GIK, Institute für Geologie und Mineralogie der Universität zu Köln, Germany; GSM, British Geological Survey, Kenworth, UK; MB-E, Museum für Naturkunde, Berlin, Germany; SMF-HS, Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany; USNM, Smithsonian Institution National Museum of Natural History, Washington, D.C., USA.

Other abbreviations.—Plate circlets: B, basal; IL, infralateral; L, lateral; R, radial; O, oral.

Geological setting

The three fossiliferous sites are located in the Prüm Syncline, Eifel (Rhenish Massif, Germany) (Fig. 1). Studied materials

were collected in the marly or argillaceous strata, intercalated with limestone beds, of the Nims Member (lower part of the Grauberg Subformation) of the upper part of the Junkerberg Formation (upper middle Eifelian, Middle Devonian), which can be attributed to the uppermost *Tortodus kockelianus* Conodont Biozone.

Locality 1 is the SW-housing subdivision and roadwork extension "Wiesenweg" of the village Gondelsheim (UTM 50°13'58.89"N / 6°29'52.33"E; 6 km NE of Prüm). Fossils (GIK-2278, GIK-2279, GIK-2281) were three-dimensionally preserved and isolated within the component-dominated marl beds (packstone). The fine-grained matrix enclosing abundant clasts and the presence of algae suggest a relatively quiet shallow water environment with a firm substrate and a moderate terrigenous sediment influx.

Locality 2 is the agricultural area "Acker Gondelsheim", directly west of the locality 1 (UTM 50°13'58.146"N / 6°29'42.64"E; 5.75 km NE of Prüm). Fossils (GIK-2277) are exposed as isolated cobbles that were washed out from the topsoil after ploughing activities. Both localities yielded diverse associated fauna: brachiopods, bryozoans (see Ernst 2008), tabulate corals, well-preserved crinoids (see Bohatý 2005; 2006; 2009b; 2011), and rare isolated thecae of the blastoid *Hyperoblastus eifelensis* (Roemer, 1852).

Locality 3 is the slope of the former planned roadwork extension of the federal road B51 "Schurf 3", in the south of Brühlborn (UTM 50°12'21.26"N / 6°27'39.97"E; 2.5 km NNE of Prüm). Fossils (GIK-2276, GIK-2280) were collected in the wackestone layers marked with sparse bioclasts and abundant macrofauna (brachiopods, bryozoans, crinoids, corals, and stromatoporoids; see Ernst 2008). The depositional environment is interpreted as relatively shallow water, with moderate to high current activity, and restricted terrigenous influx.

Material and terminology

All illustrated specimens are housed in the collections of the GIK and the SMF-HS. Two additionally studied specimens are deposited in private collections (non-figured) and are accessible through contact with the second author. Additional specimens of pleurocystitids from the BMNH, the USNM, the MB-E, and the GSM have been studied for comparison. The specimens of the new species have been prepared using air-abrasive techniques. Photographs of NH_4Cl whitened rhombiferans were arranged using digital image editing software. Morphological terminology follows Kesling (1967) and Paul (1968, 1984).

Systematic palaeontology

Subphylum Blastozoa Sprinkle, 1973

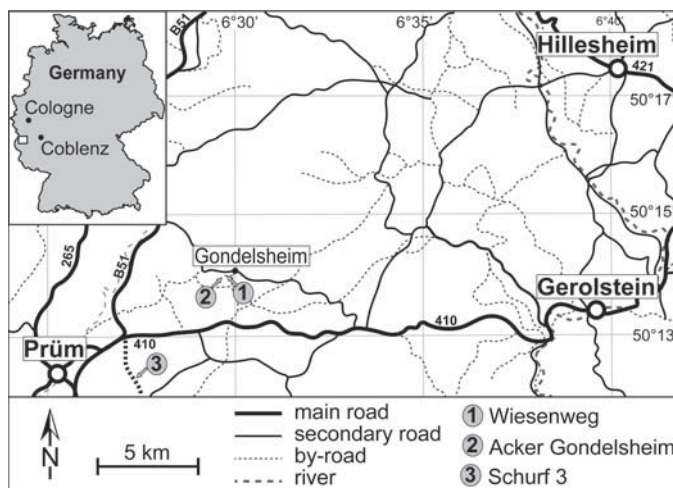Class Rhombifera Zittel, 1879 emended Paul, 1968

Fig. 1. Geographical location of the fossiliferous sites near Prüm, Eifel (Rhenish Massif, Germany).

Order Dichoporita Jaekel, 1899

Superfamilly Glyptocystitida Bather, 1899

Family Pleurocystitidae Neumayr, 1889

Subfamily Henicocystinae Jell, 1983

Emended diagnosis.—Pleurocystitids with trapezoidal to subpyriform thecal outline with no posterior lobe and flattened thecal flanges; periproct large with no anal lobe; one relatively compressed pectinirhomb at L3/L4; two uniserial feeding appendages (emended from Jell 1983: 212).

Remarks.—Jell (1983) considered the family Pleurocystitidae as an order (Pleurocystitida) within the rhombiferans and erected the new family Henicocystidae to classify the atypical genus *Henicocystis* Jell, 1983. Pleurocystitids are here ranked as a family; we propose to lower the henicocystids into a subfamily rank. The Henicocystinae differs from the other subfamilies by having apparent uniserial feeding appendages and a single rhomb located at the L3/L4 suture. The re-examination of the specimens of *Regulaecystis* Dehm, 1932 and the fragments of feeding appendage preserved in *Coopericystis* Parsley, 1970 (USNM 114198a) suggest uniserial plating, which justify their assignment to the Henicocystinae.

In blastozoans, "each ambulacral complex […] is spatially subdivided into the ambulacral zone extending directly along the thecal surface and the brachioles" (Rozhnov 2002: S604). The feeding appendages of the Henicocystinae possess all characteristics of brachioles (food-gathering, free and erect unbranched exothecal structures), except for the biserial plating. The ambulacral zone is strongly reduced and shows an atomous branching pattern (sensu Nardin et al. 2010). Modifications of the typical biserial brachiolar plating to biserial opposite and apparent uniserial plating are relatively common within the blastozoans, such as in some eocrinoids (e.g., *Haimacystis*, rhipidocystids; Sprinkle 1973; Sumrall et al. 2001; Rozhnov 2002), paracrinoids (Regnéll 1945; Parsley and Mintz 1975), and some diploporans (e.g., asteroblastids; Rozhnov 2002). Typical brachioles show bi-

serial alternate plating (Sprinkle 1973). The secondary uni-serial plating of the brachioles of the Henicocystinae might have resulted from an abnormal or displaced growth pattern leading to a pseudo-uniserial plating or to a biserial opposite plating altered during the fossilisation process. Those hypotheses have been suggested for the rhipidocystid eocrinoids and the paracrinoids; Sprinkle 1973; Sumrall et al. 2001; Rozhnov 2002; Guensburg et al. 2010).

Stratigraphic and geographic range.—Members of the Henicocystinae are known from the Middle Ordovician (*Coopericystis*, *Regulaecystis*) to the Middle Devonian (*Coopericystis*, *Henicocystis,* Pleurocystitidae gen. et sp. indet. A, B, C and *Regulaecystis*) of North America, Europe, and Australia.

Genus *Regulaecystis* Dehm, 1932

Type species: *Regulaecystis pleurocystoides* Dehm, 1932, Bundenbach (Germany), Hunsrückschiefer (Emsian).

Species included: *Regulaecystis pleurocystoides* Dehm, 1932 (type species); *R. testudineus* sp. nov.

Emended diagnosis.—Theca subtrapezoidal in outline lacking posterior lobes; abanal face ornamented with a reticulate network; large angular periproct; single conjunct pectinirhomb relatively compressed (L3/L4); uniserial feeding appendages (emended from Paul 1974: 349).

Description.—*Regulaecystis* is distinguished by an angular outline. Six plates form the periproctal frame. The single pectinirhomb is asymmetrical and compressed with few slits (5–20). B1 is relatively small. The circlets of the thecal plates are organised in large arcs across the abanal face. The ornamentation of the theca is composed of granules and radiating narrow ridges. Robust brachiolar plates with an apparent uniserial arrangement are often ornamented with one thick granule on the opposite of the food groove.

Discussion.—*Regulaecystis* clearly differs from *Amecystis* Ulrich and Kirk, 1921, *Deltacystis* Sprinkle, 1974, *Plethoschisma* Sprinkle, 1974, *Pleurocystites* Billings, 1854, *Praepleurocystis* Paul, 1967 and *Pygecystis* Paul, 1984 on the number of pectinirhombs. Within the forms with a single pectinirhomb, *Regulaecystis* contrasts with *Turgidacystis* Parsley and Sumrall, 2007 by having uniserial brachioles, angular thecal outline, different thecal plating, and wider pectinirhomb with more slits. It possesses neither the typical features of *Coopericystis*: more roundish thecal outline, strong peripheral ornamentation, and more symmetrical pectinirhomb with less slits (USNM 114198a), nor those of *Henicocystis*: subquadratic thecal outline and compressed symmetrical pectinirhomb with less slits (Jell 1983). Paul (1974, 1984) proposed the genus *Coopericystis* as synonym of the genus *Regulaecystis*, based on the close resemblance in the thecal outline and the presence of a single pectinirhomb at the suture between L3 and L4. However, the morphology of the new specimens and the re-examination of the deposited specimens of *R. pleurocystoides* suggest that this synonymy should be rejected. *Coopericystis* retains the typical features of the Henicocystinae, but shows specifically a

subpyriform theca with a roundish posterior outline (vs. a straight angular outline for *Regulaecystis*), a localised raised area on the dorsal face surrounded by lateral ridges, and different plating in the basal and infralateral circlets. The generic attribution of *R. devonica* Paul, 1974 from the early Middle Devonian of Devon (Great Britain) was already questioned by Sumrall and Sprinkle (1995). The re-examination of this form suggests an assignment to *Coopericystis*, regarding the subpyriform thecal outline, the crossing position of B1 and the similar ornamentation (notably the sinuous margins of the raised area; see Paul 1974: pl. 1), and the thecal plating as shown in *C. pyriformis* Parsley, 1970. The main difference between those two species is concentrated on the shape of the pectinirhomb and the size of the laterals.

Stratigraphic and geographic range.—Emsian (Early Devonian) and Eifelian (Middle Devonian) of Germany.

Regulaecystis testudineus sp. nov.

Figs. 2, 3.

1997 Crinoide sp. indet B.; Hauser 1997: 15, 179–180, pl. 75: 4, 5.
2001 Crinoide sp. indet B. = ?Cystoidea; Hauser 2001: 151.
2010 Cystoidee sp. indet. aff. *Caryocrinites* sp.; Hauser 2010: 19, figs. 47a, b.
2010 *Caryocrinus* [sic] *ornatus*-Formenkreis.; Hauser 2010: 19, figs. 47a, b.
2010 Cystoidea sp. indet. aff. *Caryocrinites ornatus* Say, 1825 Formenkreis; Hauser 2010: 41, pl. 8: 8–10.

Etymology: From Latin *testudineus*, turtle-like; after the shape of the theca in lifetime posture.

Type material: Holotype GIK-2276, incomplete theca showing most of the abanal face connected to the proximal stem (Figs. 2E, 3B); Paratype GIK-2277, incomplete theca showing most of the plating of the thecal faces, the oral area and the insertion of the two brachioles (Figs. 2A, 3A); Paratype GIK-2278, partial theca showing details of the abanal face ornamentation and of the stem insertion (Figs. 2D, 3C).

Type locality: Locality 3, "Schurf 3" (S Brühlborn), Prüm Syncline, Eifel (Rhenish Massif, Germany).

Type horizon: *Tortodus kockelianus* Conodont Zone, Eifelian, Middle Devonian.

Remarks.—The privately published monographs of Hauser (1997, 2001, 2010) figuring specimens now identified as *Regulaecystis testudineus* sp. nov. contained misinterpretations. Striking in this context are his interpretations of the figured cystoids as "cupressocrinid or stylocrinid like crinoids" (1997: 179–180) and as *Caryocrinus* [sic!] *ornatus* (2010: 19). These monographs are given no further consideration herein.

Additional material.—One incomplete theca connected with an incomplete proximal stem, one incomplete theca showing the oral region, both housed in private collection (non-figured), eight isolated plates and twelve stems (GIK-2279–2280).

Diagnosis.—A species of *Regulaecystis* with a strongly inflated theca and a rhombic pectinirhomb at L3/L4 suture; plate ornament as granules and prominent radiating ridges; B1 restricted to the anal face; flanges of proximal columnals ornamented with granules.
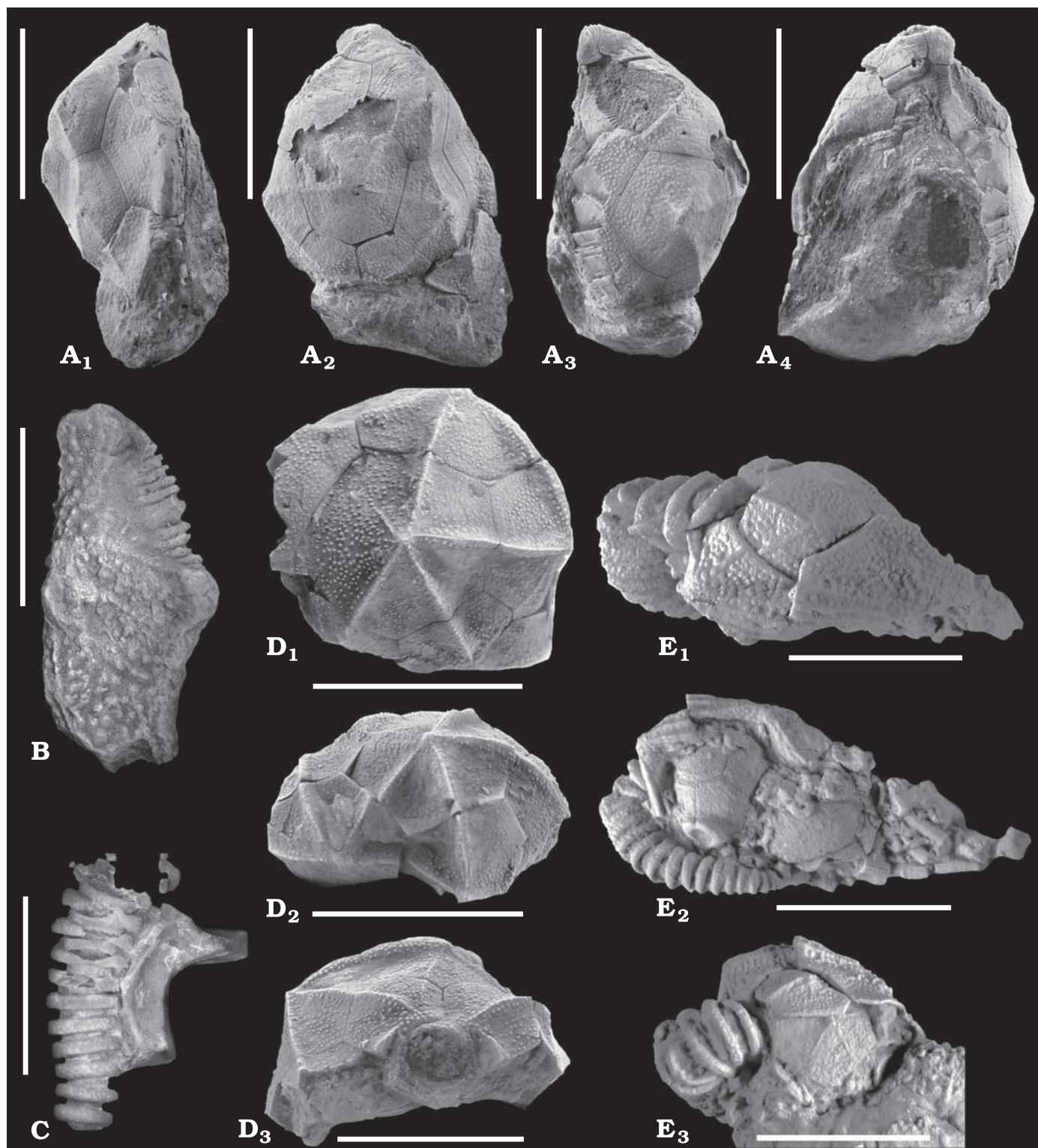
Fig. 2. Pleurocystitid blastozoan *Regulaecystis testudineus* sp. nov., Nims Member of the Junkerberg Formation (Eifelian, Middle Devonian), Prüm Syncline (Rhenish Massif, Germany). **A**. Paratype GIK-2277, lateral view showing the flattened thecal flange and the rounded shape of the theca (A_1), dorsal view showing the arched organisation of the plates (A_2), lateral view showing the single pectinirhomb located at L3/L4 suture (A_3), ventral view showing the organisation of the oral area (A_4). **B**. Isolated plate GIK-2280, showing the slits of the pectinirhomb. **C**. Pluricolumnals adjacent to a reversed basal plate GIK-2279, showing the typical alternation of external and internal columnal in the proximal stem of the glyptocystitids. **D**. Paratype GIK-2278, dorsal view of the theca showing the reticulate ornamentation (D_1), lateral view showing the intercalation of the circlets of plates (D_2), aboral view showing the stem insertion and the organisation of the basals (D_3). **E**. Holotype GIK-2276, lateral view showing the flattening of the theca, and the strong ornamentation (E_1), ventral view showing the ornamentation at the margin of the theca and the elongate proximal portion and the thin ornamented distal portion of the stem (E_2), and oblique dorsal view on the stem insertion and basal plates (E_3). Scale bars 10 mm.
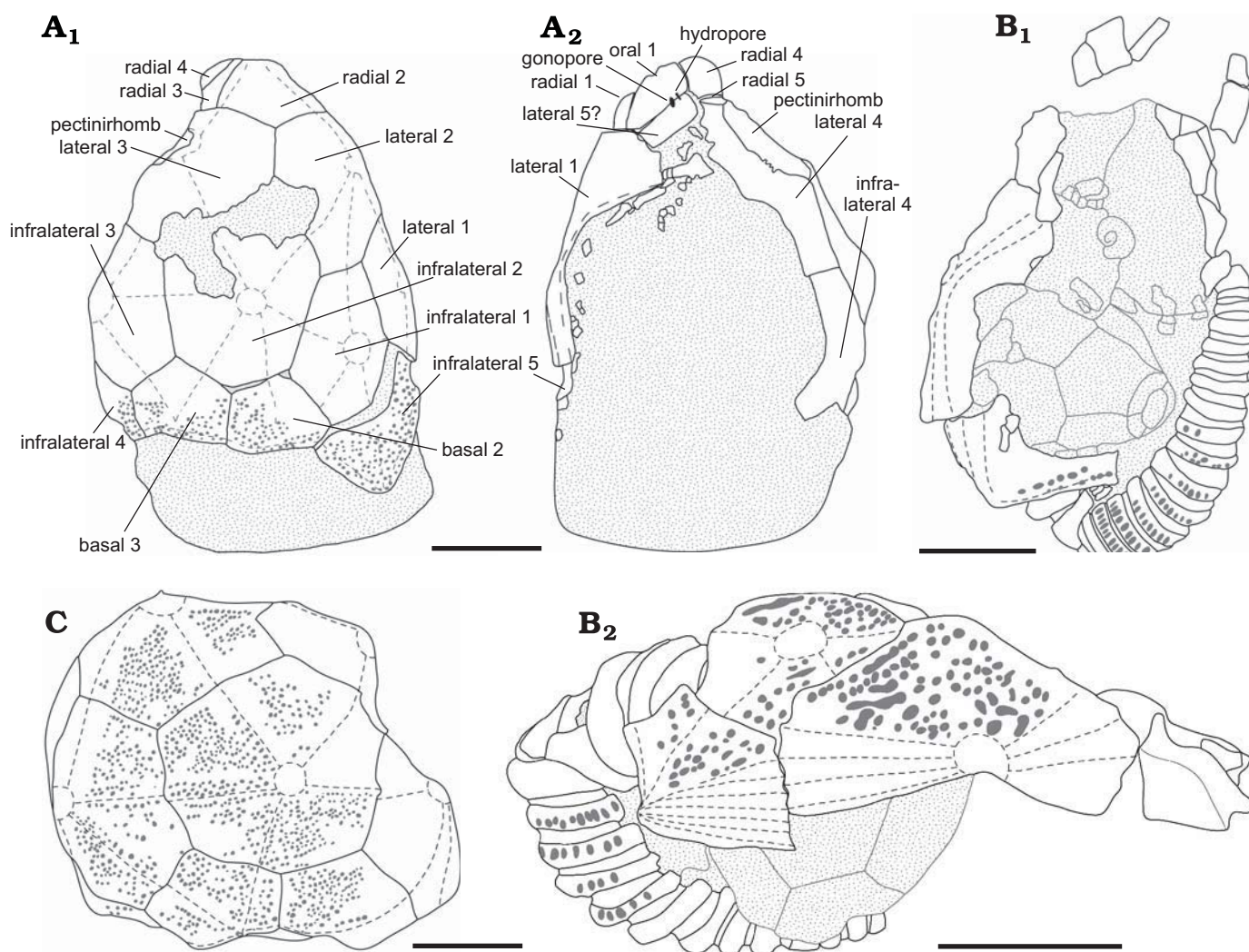
Fig. 3. Interpretative camera lucida drawings of the pleurocystitid blastozoan *Regulaecystis testudineus* sp. nov., Nims Member of the Junkerberg Formation (Eifelian, Middle Devonian), Prüm Syncline (Rhenish Massif, Germany). **A**. Paratype GIK-2277, abanal face showing the plate names (A$_1$) and anal face showing the shape of the periproct and the organisation of the primary opening area (A$_2$). **B**. Holotype GIK-2276, anal face showing the insertion of the ornamented stem (B$_1$) and lateral view showing the strengthening of the thecal margins due to strong ornamentation in thick ridges and thick granules (B$_2$). **C**. Abanal face of the paratype GIK-2278 showing the dense granulation. Cup and isolated plates of *Stylocrinus tabulatus* (Goldfuss, 1839) are preserved in the anal face. Plate names abbreviations follow Kesling (1967). Scale bars 5 mm.

Description.—Approximate thecal size is up to 22 mm in length and up to 18 mm in width, based on the combination of two specimens (GIK-2276, GIK-2277). Thecal outline is broadly trapezoidal characterised by a shoulder-angle circa 45° (sensu Bather 1913) without aboral thecal lobes (Fig. 2E$_2$). The abanal face of the theca is strongly inflated leading to a probable subvertical orientation of the single pectinirhomb (Fig. 2A$_3$, D$_1$, E$_1$). Thecal margins are slightly curved due to the flattened fluted fringe (Fig. 2A$_1$, A$_2$, E$_2$). Periproct is large, aborally rectangular without anal lobe.

The abanal and anal faces are composed of 16 and 12 plates, respectively. Periproct is surrounded by six plates (B1, B4, IL4, IL5, L1, L4), and the stem insertion, by five plates (four basals and IL5). Thecal plates are up to 0.55 mm thick in their edge and to 0.75 mm when ridged (GIK-2278, GIK-2280–2281).

Basals are unequal and localised in the stem insertion area. B2 and B3 are pentagonal with a wide base on the abanal face (Figs. 2D$_1$, 3C). B1 is small quadrangular in shape, and mostly restricted to the anal face (Fig. 2D$_3$). B4 seems to be fused with IL4, forming the posterior left corner of the anal face (Fig. 3A$_1$). Infralateral circlet is composed of five large plates disposed in a broad arc across the abanal face. IL1, IL2 and IL3 are confined on the abanal face (Fig. 3A$_1$). IL2 is large, hexagonal, and located along the thecal midline. IL1 and IL3 are smaller, pentagonal and deformed due to the curvature of the abanal face (Fig. 2D$_2$). The medium-sized IL4 and IL5 straddle the posterior thecal edges, forming the left and the right corner of the abanal face, respectively (Fig. 3A$_1$, B$_1$). Laterals are unequal in size and shape. Four laterals are placed in a broad arc across the abanal face. L2 and L3 are medium-sized and hexagonal.

The large and elongate L1 and L4 form the thecal margins. They are characterised by a flattened fringe bearing beaded ridges continuously with the subjacent infralaterals (Fig. 2A, B, F, H). L5 is relatively small, possibly located above the L1–L4 junction. Radial plates are not aligned in a circlet. R2 and R3 are large, pentagonal and restricted on the abanal face. R1 and R4 form the right and left oral edge of the theca, respectively. R5 is small and localised transversally between L4 and R4 (Fig. 2A$_3$). Oral plates are no completely preserved on the available specimens. On the abanal face, O1 bears the slit-like hydropore and the elliptical gonopore with the partially preserved elongate plates interpreted as L5 (Figs. 2A$_4$, 3A$_2$). O1 is pentagonal, transversally elongate surrounding the peristomial opening.

Ornamentation is highly variable. Theca is at least granulated with prominent umbones and sometimes bears sharp radial ridges. When present on the abanal face, ridges radiate from the umbones to join the middle of the plate edges. They define rhomb-like areas continuously from the basal to the lateral circlets and within each circlet. GIK-2277 and GIK-2278 have granules and few narrow radial ridges formed by the incomplete coalescence of the granules (Fig. 2D$_1$). The rest of the non-weathered material exhibits relatively thick granules with sharp primary ridges (GIK-2276; Figs. 2E$_1$, 3B$_2$). Thecal margins are relatively flat and strengthened by multiple beaded ridges.

A single conjunct pectinirhomb with confluent dichopores (sensu Paul 1968) occurs between L3 and L4. The pectinirhomb contains an estimated maximum of 20 slits (Fig. 2A$_4$, B). It is sunk within prominent vestibule rims (L/W ratio about 1.25), leading to the absence of an umbo on L3. Silts are partially lost on the L3 half-rhomb, probably covered by stereom (Fig. 3A$_1$).

Uniserial brachiolar plates are stout and triangular in transversal section. They internally show one relatively deep central groove and two small lateral facets, interpreted as serving for the articulation of the cover plates.

Periproctal membrane is poorly preserved, probably composed of numerous smooth polygonal platelets, up to 0.7 mm across (Fig. 3A$_2$). Anal pyramid is unknown.

No stem is completely preserved. The short proximal part is plated by circa 20 thin holomeric pairs of inner and outer columnals (Fig. 2C, E$_2$). The maximal length of the preserved stems is about 18 mm (GIK-2276). It tapers from 4.2 to 2.1mm in diameter (GIK-2276) or from 5.4 to 3.5 mm for the longest preserved isolated stem (GIK-2281). The flanges of the outer columnals are up to 0.7 mm thick and ornamented by beaded longitudinal ridges or isolated granules (Fig. 2E$_3$). The distal part seems to be composed of narrow barrel-shaped and ornamented holomeric plates (Fig. 2E$_2$).

Discussion.—Despite their incomplete preservation, the combination of the features of the different specimens allows the reconstruction of the complete morphology. Within the genus *Regulaecystis*, *R. pleurocystoides* from the Lower Devonian Hunsrückschiefer is similar to *R. testudineus* sp. nov. in its an-

gular thecal outline. However, it clearly differs by having a more flattened theca, a longer and unornamented proximal stem and a simple network of three primary ridges, two across the infralateral circlet and one on L2 (SMF-HS-424, MB-E-1853). The flattening is partly due to the mode of preservation in the compressed mudstone of the Hunsrückschiefer. Nevertheless, the consistency of the thecal framework could suggest that the theca was strongly flattened before the fossilisation process.

Regulaecystis testudineus resembles *R. inconstans* Paul, 1984 from the late Ordovician of Wales and England. Both species show a trapezoidal thecal outline, relatively thick thecal plates, and a complex granulate and reticulate ornamentation on the abanal thecal face and granules on the proximal outer columnals. However, they distinctly differ on the position of B1 (crossing to the thecal faces in *R. inconstans*), the inflation of the theca, the relative dimensions and the number of the elements in the proximal stem, and on the pectinirhomb, which is highly compressed and symmetrical with few slits in *R. inconstans* (GSM-ZI-9227).

The isolated elements attributed to Pleurocystitidae gen. et sp. indet A and B Prokop and Petr, 2004, from the Loděnice Formation (Pragian, Early Devonian) of the Barrandian area (Bohemian Massif, Czech Republic) show morphological features similar to *R. testudineus*. They differ on the size of the pectinirhomb, the size of the plates and the strength of the ornamentation.

Stratigraphic and geographic range.—Nims Member of the Junkerberg Formation, Eifelian (Middle Devonian; *Tortodus kockelianus* Conodont Zone) from the Prüm Syncline, Eifel (Rhenish Massif, Germany).

Pleurocystitidae gen. et sp. indet. C
Fig. 4.

1932 *Regulaecystis pleurocystoides*; Dehm 1632: 90.

Material.—Two specimens (SMF-HS-420, SMF-HS-422) showing the anal and abanal faces, respectively, from Hunsrückschiefer (lower Emsian, Early Devonian) of Bundenbach (Rhenish Massif, Germany).

Description.—Theca is flattened and strongly pear-shaped in outline. Posterior area is circular with thecal lobes, surrounded by a raised flattened flange. Anterior area is elongate and trapezoidal. Abanal face is partly preserved in SMF-HS-422 (Fig. 4A). Basals are pentagonal. B2 and B3 are joining in the thecal midline and surround the stem insertion. B4 is more elongate and form the left posterior thecal edge. B1 is smaller, crossing the thecal periphery at the right thecal angle. Five infralaterals are organised in a broad arch transversally to the abanal face and bear the raised flat rim. IL4 and IL5 compose the right and the left thecal periphery, respectively. IL1 and IL2 are large and hexagonal. Only two laterals (L2 and L3) are partially preserved on SMF-HS-422. Ornamentation is reduced to few prominent ridges, stretching from the stem insertion to IL5, IL1 and IL3, and from IL2 to the two preserved laterals. The circular periproct area is at
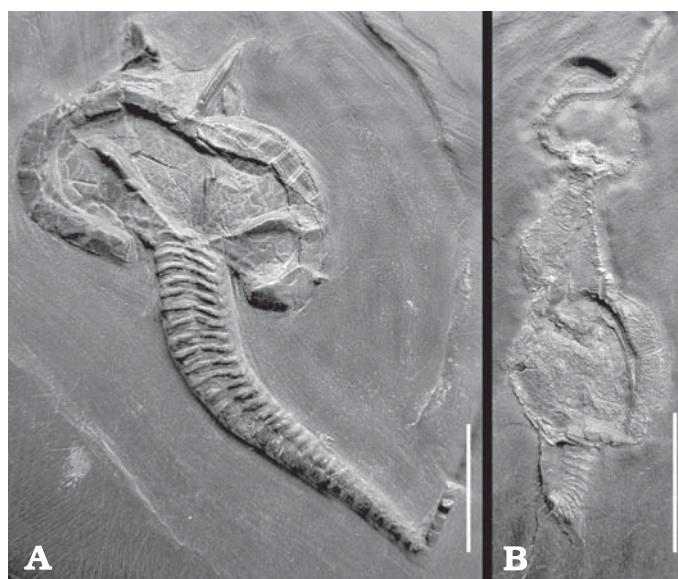
Fig. 4. Pleurocystitida gen. et sp. indet. C from Hunsrückschiefer (Emsian, Lower Devonian), Bundenbach (Rhenish Massif, Germany). **A**. SMF-HS-422, abanal face. **B**. SMF-HS-420, anal face. Scale bars 10 mm.

least surrounded by B1, B4, IL4, and L4, and covered by a tegmen of smooth polygonal platelets (Fig. 4B). Anal pyramid is apparently located in the left posterior corner of the periproctal area. Oral area is narrow with apparent regular plating, bearing laterally the two brachioles. Preserved stems show a relatively long proximal part composed of 23 pairs of unornamented outer and inner columnals. Distal stem, partly preserved in SMF-HS-422, is composed of narrow barrel-shaped plates.

Discussion.—The re-examination of the material from the Hunsrückschiefer, deposited in the SMF-HS, led to the rediscovery of those two specimens initially attributed to *Regulaecystis pleurocystoides* by Dehm (1932). Despite the distortion due to their preservation, the specimens show morphological features strongly varying from the typical characteristics of *R. pleurocystoides*. They differ by having roundish thecal outline with posterior lobes, raised flat peripheral rim, no swelling at the sutures IL4–L4, and IL5–L1 on the anal face (MB-E-1855), and abanal ornamentation reduced to few longitudinal ridges. The raised thecal flanges could be interpreted as the external imprint of the periproctal margin. However, they arise on the infralateral circlet, whereas the periproct should be extended up to the laterals. The lack of clear preservation of pectinirhomb excludes undoubted systematic assignment. The size of the periproct area and the roundish outline with posterior lobes notably prevent their attribution to the Deltacystinae and to the Henicocystinae, respectively. Thecal plating and periproctal features suggest their attribution to the Pleurocystitinae. Pleurocystitidae gen. et sp. indet. C could be regarded as comparable to the genus *Turgidacystis*, considering the outline and the plating of the theca, the lateral insertion of the brachioles.

Phylogenetic context and evolution

Procedure and characters.—Pleurocystitid rhombiferans retain the major apomorphies of the glyptocystitid rhombiferans, having a theca composed of five plate circles, a bipartite stem and pectinirhombs as respiratory structures (when present). They are differentiated by a strong thecal flattening leading to a reduced number of ambulacral rays and to a large polyplated periproct area, and fewer rhombs (Parsley 1970; Sumrall and Wray 2007). Pleurocystitids range from the Early Ordovician to the Middle Devonian.

The Devonian pleurocystitids were historically less studied than the Ordovician genera, probably because of their scarcity (Parsley 1970). They exhibit a relatively high morphological variability, expressed in the plating of the brachioles, the shape of the single pectinirhomb and of the periproct area, and the plating, the flattening and the outline of the theca. *Regulaecystis* is interpreted as having (pseudo-) uniserial brachioles, inflated theca with reduced peripheral flat flange and angular trapezoidal outline, and rhombic pectinirhomb located at L3/L4 suture (Fig. 2). *Coopericystis* is only known from the abanal thecal face. The original description and the re-examination of specimen no. USNM 114198 suggest that this genus could also possess uniserial brachioles, roundish posterior thecal outline and highly compressed single pectinirhomb. The Pleurocystitidae gen. et sp. indet. C (SMF-HS-420), rediscovered in the collections of the SMF-HS exhibits atypical features, such as pear-shaped thecal outline and raised peripheral flat rim; those features being not compatible with the diagnoses of the pleurocystitid genera. *Henicocystis* is characterised by subquadratic outline, compressed single pectinirhomb and uniserial brachioles. The more problematic morphology of *Hillocystis* Jell, 1983 (elongate spindle-shaped theca, elongate elliptical periproct, no pectinirhomb, and one uniserial brachiole) resulted in the establishment of a family distinct from the pleurocystitids and in the incomprehension of the phylogenetic context (Jell 1983).

Morphological details on the other pleurocystitids genera (*Amecystis*, *Deltacystis*, *Plethoschisma*, *Pleurocystites*, *Praepleurocystis*, *Pygecystis*, and *Turgidacystis*) were taken from specimen observations and from recent literature (Paul 1967, 1984; Parsley 1970, 1982; Broadhead 1974, 1978; Sprinkle 1974; Broadhead and Strimple 1975; Sumrall and Sprinkle 1995; Brower 1999; Parsley and Sumrall 2007).

The investigation of the phylogeny of the 11 recumbent rhombiferan genera should clarify the relationship of the revised non-American Devonian genera and to point out the evolutionary trends among these unusual forms. The Pleurocystitidae gen. et indet. C was excluded from this analysis, because of the lack of most of clear diagnostic features (Fig. 4). This analysis is partly based on previous published studies on the pleurocystitids (Sumrall and Sprinkle 1995; Parsley and Sumrall 2007). Three outgroup taxa were used to

polarise character states and to root trees (*Cuniculocystis* Sprinkle and Wahlman, 1994, *Macrocystella* Callaway, 1877 and *Cheirocystella* Paul, 1972). The 23 characters of those previous studies (for complete details see Sumrall and Sprinkle 1995: 775–776) have been updated for *Coopericystis* and *Regulaecystis*, and scored for the Australian genera (*Henicocystis* and *Hillocystis*). Characters 7, 14, and 18 have been slightly modified according to the taxa examined in the present analysis (see Appendix 1). The revision of the Devonian genera suggests a larger variability than previously expected in the thecal proportions, leading to the addition of the state "theca as wide as long [1]" in the character 14. The consideration of *Hillocystis* induces the modification of the state "two ambulacral rays [1]" into "reduced number of rays [1]" of the character 18 to avoid the autapomorphy of having a single ray. The character matrix has been completed by 3 new characters (see Appendix 1). Character 24 concerns the size of the periproct relative to the size of the theca. Character 25 refers to the plating of the brachioles (biserial [0] vs. apparently uniserial [1]). Character 26 qualifies the slope of the lateral thecal margins, being shallow [0] or flat [1]. Phylogenetic analysis was performed, using parsimony and a branch-and-bound algorithm to guaranty the computation of the complete set of most parsimonious trees in PAUP 4.0 (Swofford 2003). All characters were equally weighted and unordered. A bootstrap analysis of 1000 pseudoreplicates was performed on the character matrix and the Bremer support indices have been calculated to evaluate the robustness of the clades (Felsenstein 1985; Bremer 1994).

Results.—The analysis retrieves four most parsimonious trees (TL = 45, CI = 0.6889, RI = 0.7778, HI = 0.3111), of which the strict consensus with the main apomorphies is shown in Fig. 5. Pleurocystitidae is unambiguously supported in all four cladograms, and with the support indices (Bremer Index of 6). Ingroup is distinguished by a flattened theca with a modified plating (elongate L1, reduced to absent L5, and 5 radial plates), a medium-sized pyriform periproct, and a reduced number of ambulacral rays; each bearing one brachiole.

The internal relationships of Pleurocystitidae are stable across all four shortest cladograms, except for the branching of *Amecystis*. The clade of the Deltacystinae (*Deltacystis* and *Plethoschisma*), which forms the sister group to all other genera, is based upon the peristome on the abanal face, a relatively small elliptical periproct surrounded by four plates, a strongly modified B1, and depressed pectinirhombs at L3/L4 and B2/IL2 sutures. The remaining cladogram is characterised by a highly constrained thecal plating (B1 crossing the ambitus, small L5, and a thecal margin formed by at least L1 and IL5), a large periproct area, surrounded by at least eight plates, and a vestibule rim around the pectinirhomb when present. *Amecystis* branches isolated within this †crown group (term sensu Monks 2002). Its peculiar morphology shows ancestral characteristics, such as a pyriform thecal outline and a theca longer than wide, as well as derived features, such as the absence of rhomb, a strongly flattened

theca, a large periproct, and the possession of thecal lobes. The union of *Pleurocystites*, *Praepleurocystis*, and *Pygecystis* (called here the *Pleurocystites*-group) is characterised by an additional pectinirhomb at the L1/L2 suture and the possibility to develop a periproctal lobe. The second clade of the †crown group unifies the genera occurring in the Devonian strata (*Hillocystis*, *Turgidacystis*, and the trichotomy of *Coopericystis*, *Henicocystis*, and *Regulaecystis*). This last trichotomy is based on the presence of uniserial brachioles, a theca with angular outline and a peripheral flat rim, B1 strongly reduced, and a single pectinirhomb at the L3/L4 suture. Despite its location within the second clade of the †crown group, *Turgidacystis* seems to retain several plesiomorphies of the *Pleurocystites*-group, such as a sloping thecal edge and a medium-sized periproct surrounded by six plates. *Hillocystis* is placed as sister group to this clade, sharing the uniserial brachiolar plating with the trichotomy but differing by the regular organisation and size of the smooth thecal plates.

Discussion.—This analysis is mostly congruent with the results of Parsley and Sumrall (2007), also when performed with only the initial 23 characters used in the original study (not shown here). Differences mainly concern the ambiguous position of *Amecystis*, the consideration of the Australian genera (*Henicocystis* and *Hillocystis*) and the branching of *Coopericystis*, *Regulaecystis*, and *Turgidacystis*.

The subfamily Deltacystinae is unambiguously supported by this analysis and the position of this clade on the cladogram confirms that *Deltacystis* and *Plethoschisma* show most of the plesiomorphies and could be interpreted as transitional forms from the roundish glyptocystitids to the derived pleurocystitids (see Sprinkle 1974; Sumrall and Sprinkle 1995).

The addition of the specific characters and the re-examination of specimens of *Coopericystis*, *Henicocystis*, and *Regulaecystis* lead to their union as a monophyletic group and justify the establishment of the distinct subfamily (Henicocystinae [Jell 1983]). Jell (1983) placed *Hillocystis* in a different family (Hillocystidae) and order (Hillocystida) within the rhombiferans. However the branching of *Hillocystis* within the Henicocystinae group would suggest that this genus should be placed in the Pleurocystitidae, in the independent subfamily Hillocystinae (Jell 1983). *Turgidacystis* appears here to be more closely related to the Henicocystinae than to the Pleurocystitinae, possibly due to the ornamentation (not included in the character set), the shape and inflation of the theca, the presence of a single pectinirhomb, and the periproctal shape (Fig. 5). The taxonomic attribution of *Turgidacystis* into the Pleurocystitinae is justified by the thecal plating, the biserial brachioles, and the characteristics of the pectinirhomb (Parsley and Sumrall 2007). This would suggest that the inflation of the theca could have evolved at least twice within the Pleurocystitidae, as in *Pleurocystites beckeri* Foerste, 1924, *Turgidacystis*, *Praepleurocystis*, and the Henicocystinae, as suggested by Fadiga and Sumrall (2011) for the Pleurocystitinae.
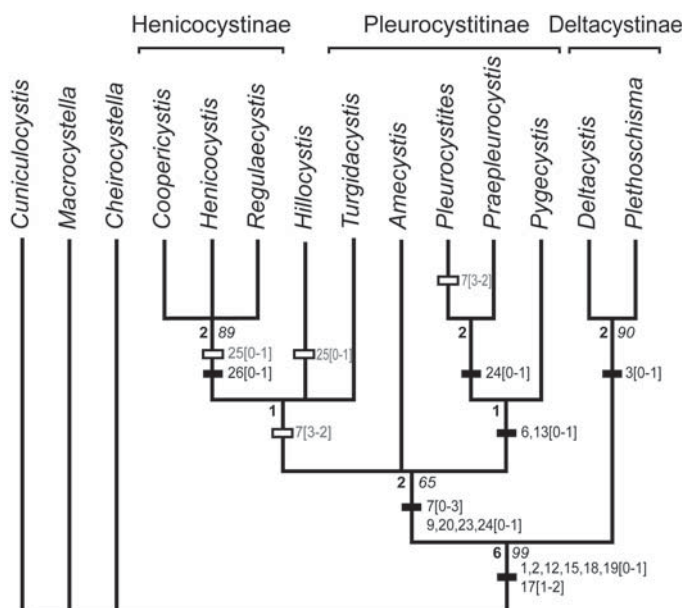
Fig. 5. Strict consensus tree of the four shortest trees (45 steps) derived from PAUP and based on character data set in Appendix 2. The numbers adjacent to the nodes denote the respective support values: bold numbers being Bremer indices, italic numbers being bootstrap values > 50%. Major apomorphies have been reported on branches of the supported clades (see text and Appendix 1).

The status of *Amecystis* is partly beyond the scope of this analysis. Nonetheless this particular Pleurocystitinae genus shares morphological features with the two †crown groups. The atypical combination of characters may suggest that this genus represents an independent lineage in comparison to the two monophyletic groups. The reduction in the number of functional pectinirhombs may have not been a unique event in the Pleurocystitidae, but could have occurred several times as proposed by Parsley (1970) and Broadhead and Strimple (1975).

Four main evolutionary trends can be suggested: (i) the expansion of the periproct and the resulting modification of the thecal plating, with the reduction of the size of L5 (as proposed by Sprinkle, 1974); (ii) the general decrease in the number of pectinirhombs and a reduction of their size; (iii) the increase in the thecal area either by the elongation of the theca (*Pleurocystites*-group) or by its enlargement (Henicocystinae); and (iv) the strengthening of abanal face by the densification of the network of the ornamental ridges (*Pleurocystites*-group) and by the expansion of a raised ornamented central area linked with a gradual thecal swelling (Henicocystinae, *Praepleurocystis*, and *Turgidacystis*). No clear trend can be observed in a potential co-evolution between the reduction of the number of pectinirhombs and the increase of the size of the periproct (Broadhead and Strimple 1975). However, a relation between the thecal flattening and the increase of the size of the periproct might be envisaged. Forms with an inflated theca possess an angular periproct with a size between 30% and 60% of the anal face, while forms with a flattened theca have a large subpyriform periproct.

Palaeoecology

Regulaecystis testudineus nov. sp. appears to have a restricted stratigraphic occurrence to the Nims Member of the Junkerberg Formation (Eifelian, Middle Devonian), despite extensive fieldwork in the strata of the consecutive members. This sudden appearance in the fossil record is not unusual among the other Devonian pleurocystitid species, which are mostly restricted in one member (e.g., *Turgidacystis graffami* Parsley and Sumrall, 2007, from the Cravatt Member of the Bois d'Arc Formation, Parsley and Sumrall [2007]; *Henicocystis darraghi* Jell, 1983 from the Flowerdale Member of the Humevale Formation, Jell [1983]), at the contrary of most of the Ordovician species (e.g., *Amecystis laevis* [Raymond, 1921], known from the Late Ordovician of Ontario, Quebec, Michigan, Minnesota, and Kentucky (Broadhead 1974, 1978, Broadhead and Strimple 1975); *Pleurocystites squamosus* Billings, 1854 from several late Middle and Late Ordovician localities in Quebec, Ontario, Illinois, Kentucky, Michigan, and New York (Hussey 1928; Sinclair 1954; Parsley 1970, 1982; Paul 1984). A strong stenotypy in the Devonian pleurocystitids might be inferred. Pleurocystitids are usually interpreted to live as vagrant epibenthic echinoderms, laying with their anal face on muddy substrate (e.g., *Amecystis, Plethoschisma, Pleurocystites*; Paul 1967; Sprinkle 1974; Broadhead and Strimple 1975; Sumrall 2000).

The apparent robustness and flexibility of the proximal stem, and the presence of thicker granules on the abanal side of the columnals in *R. testudineus* could suggest that this form may have been able to slowly crawl over the substrate in producing sluggish wagging or sinusoidal movements (as proposed by Brower [1999] for *Pleurocystites*).

Specimens of *R. testudineus* collected in the localities 1 and 2 show fine ornamentation and a strongly inflated abanal thecal face; whereas those collected in the locality 3 seem to be more flattened with a coarser ornamentation. Localities 1 and 2 are characterised by quiet shallow water environment with a component-dominated firm substrate. Locality 3 depicts a moderately to highly agitated shallow water environment with a muddy soft substrate. Therefore, the thecal inflation shown by the specimens from the localities 1 and 2 might be either interpreted as strong intraspecific variability (less likely) or as an adaptation to epibenthic lifestyle on a relatively firm substrate, which necessitates a less-expressed snowshoe strategy in comparison to the flattened forms living on strictly soft substrates (e.g., *R. testudineus* from the locality 3, *R. pleurocystoides* from Hunsrückschiefer). This hypothesis is sustained by the fact that most of the Ordovician species with an inflated theca occur only in marl or shale strata characterised by abundant fine- to medium-grained components (e.g., *Praepleurocystis watkinski* (Strimple 1948), from the Poleville Member of the Bromide Formation in Oklahoma (Parsley 1982); *Pleurocystites beckeri* Foerste, 1924, from the lower and middle Maquoketa Formation in Iowa).

The degree of ornamentation expansion could be related to the hydrodynamism. The raised prosopon of the abanal surface (thick granules and high radiating ridges), as shown by the specimens from the locality 3, could have acted as spoilers to reduce lift due to high water agitation and therefore may have helped to maintain the organism on the bottom, as proposed for *P. watkinski* by Parsley (1982).

The presence of a single pectinirhomb argues for the use of a complementary respiratory mechanism. Paul (1967), Parsley (1970), Sprinkle (1974), Broadhead and Strimple (1975), Brower (1999), and Parsley and Sumrall (2007) proposed that the large flexible periproct could have been associated with respiratory exchanges occurring in gut through the cloacal pumping. This interpretation seems to be reasonable in the case of *R. testudineus* because the presence of a bowed ornamented periproctal periphery could have slightly heightened the flexible periproct membrane and eased its movements, as it has been interpreted for *Turgidacystis* by Parsley and Sumrall (2007). The absence of fully preserved brachioles precludes any interpretation on their feeding mode.

R. testudineus occurs at the maximum of diversity of the suspension feeding invertebrates from the Middle Devonian of the Eifel, with apparently a high ecological pressure (competition for space and resources; Bohatý 2009a). The atypical mode of life of this rhombiferan glyptocystitid could have partly filled in free ecological niche of the vagile bottom dwellers (representing less than 10% of the fauna preserved in these strata).

Acknowledgements

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Appendix 1

List of phylogenetic characters, modified and emended from Sumrall and Sprinkle (1995: 778, appendix).

1. Thecal cross section round (0); or flattened (1)
2. Numerous brachioles per ambulacral ray (0); or one brachiole per ambulacral ray (1)
3. Peristome centred on summit edge (0); or on the dorsal surface (1)
4. Pectinirhomb at B2/IL2: absent (0); or present (1)
5. Pectinirhomb at L3/L4: absent (0); or present (1)
6. Pectinirhomb at L1/L2: absent (0); or present (1)
7. Plating of the periproctal rim composed of IL4, IL5, L4, (L1) (0); or IL4, IL5, L4, L5, (L1) (1); or B1, B4, IL4, IL5, L4, L1 (L5) (2); or B1, B4, IL1, IL3, IL4, IL5, L1, L4, (R5) (3)
8. B1 confined on anal face (0); or crossing ambitus (1)
9. Peripheral margin formed from at least IL1 and L2 (0); or from at least IL5 and L1 (1)
10. Hollow ridges: absent (0); or present (1)
11. Periproct: without periproctal lobe (0); or with periproctal lobe (1)
12. L1 not elongate (0); or elongate (1)
13. Relative size of R2 and R3: similar (0); or R2 larger than R3 (1)

14. Proportion of the theca: longer than wide (0), or as long as wide (1); or wider than long (2)
15. Position of L5 between L1 and L4 (0); or above L1 and L4 (1)
16. Pectinirhomb at IL3/L4: absent (0); or present (1)
17. Number of radials: ten (0); or six (1); or five (2)
18. Number of ambulacral rays: 5 (0); or lower than 5 (1)
19. Hydropore crossing orals (0); or crossing L5 (1)
20. L5 large (similar in size to the other laterals) (0); or smaller than the other laterals (1)
21. B1 relatively large (similar in size to the other basals) (0); or smaller than the other basals (1)
22. Posterior lobes of the theca: absent (0); or present (1)
23. Vestibule rim on pectinirhomb: absent (0); or present (1)
24. Size of the periproct: small (0–30%) (0); or medium-sized (30–60%) (1); or large (60–100%) (2)
25. Brachiolar plating: biserial (0); or apparently uniserial (1)
26. Thecal periphery: slope (0); flat rim (1)

Appendix 2

Data set for pleurocystitid rhombiferans, modified and emended from Parsley and Sumrall (2007: 1493, appendix 2). Hyphen indicates a gap, question mark indicates missing character.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Cuniculocystis	0	0	0	0	0	0	0	–	–	0	0	0	–	0	0	0	0	0	0	0	0	–	–	0	0	–
Macrocystella	0	0	0	0	0	0	1	–	–	0	0	0	0	0	0	0	1	0	0	0	0	–	–	0	0	–
Cheirocystella	0	0	0	1	0	0	1	–	–	1	0	0	0	0	0	1	1	0	?	0	0	–	0	0	0	–
Amecystis	1	1	0	0	0	0	3	1	1	1	0	1	(0,1)	0	1	0	2	1	1	1	0	1	–	2	0	0
Coopericystis	1	1	0	0	1	0	?	0	1	1	?	1	0	0	?	0	?	1	?	?	1	0	1	?	1	1
Deltacystis	1	1	1	0	0	0	0	0	0	1	0	?	0	2	?	0	2	1	1	0	1	1	–	0	0	0
Henicocystis	1	1	0	0	1	0	2	0	1	1	0	1	0	1	?	0	2	1	?	1	1	0	1	2	1	1
Hillocystis	1	1	?	0	0	0	2	1	1	1	0	1	0	0	0	0	?	1	?	1	0	0	–	2	1	0
Plethoschisma	1	1	1	1	0	0	0	0	0	1	0	1	0	2	1	1	2	1	?	0	1	0	0	0	0	0
Pleurocystites	1	1	0	(0,1)	1	1	2	1	1	1	(0,1)	1	1	0	1	0	2	1	1	1	0	1	1	1	0	0
Praepleurocystis	1	1	0	1	1	1	3	1	1	1	0	1	1	0	1	0	2	1	1	1	0	0	1	1	0	0
Pygecystis	1	1	0	(0,1)	1	1	3	1	1	1	1	1	1	0	1	0	2	1	1	1	0	1	1	2	0	0