

Rhombifera Barrande, 1867, and the origin of the Blastoidea (Echinodermata, Blastozoa)

Rhombifera Barrande, 1867, y el origen de los Blastoidea (Echinodermata, Blastozoa)

Christopher R. C. PAUL , Bertrand LEFEBVRE , Martina NOHEJLOVÁ  & Samuel ZAMORA 

Abstract: *Rhombifera bohémica* Barrande is redescribed from Barrande's original material and new specimens from Spain and the Czech Republic. *Rhombifera* had a heteromorphic proximal stem, a theca with three basals, three infralaterals and five laterals, both greatly elongated, but a reduced oral area in which five, facet-bearing radials alternate with five interradial orals which form the oral frame. The CD oral plus two others share the hydropore and gonopore. *Rhombifera* is the only glyptocystitoid rhombiferan with a periproct surrounded by two plates, L4 and L5, and ambulacral facets on radial not oral plates. *Rhombifera* was derived from echinoencrinid glyptocystitoids, both sharing reduced oral areas with five, not six, radial plates and pectinirhombs with short oval slits. The oral areas of *Rhombifera* and *Lysocystites* are similar. In *Lysocystites* five facet-bearing 'ambulacral plates' alternate with five interradial orals forming the oral frame. Extra orals in the CD interambulacrum share the hydropore and gonopore. *Lysocystites*, coronates and blastoids all possess three basals, five 'radials', five deltoids and five homologues of blastoid lancet plates. We suggest that basals, laterals, radials and orals of glyptocystitoids are homologous with basals, radials, lancet plates and deltoids of blastoids, respectively. *Rhombifera* is a link between glyptocystitoid rhombiferans and blastoids.

Resumen: Se redescrive *Rhombifera bohémica* Barrande a partir de la colección original de Barrande y nuevos especímenes de España y República Checa. *Rhombifera* tenía un pedúnculo heteromórfico, y una teca con tres placas basales, tres infralaterales y cinco laterales. Las placas laterales e infralaterales son muy alargadas, pero la zona oral es muy reducida y en ella alternan las placas radiales, provistas de facetas braquiolares, con las cinco placas orales interradiales. El hidroporo y gonoporo se situaban en el interrudio CD entre placas orales adicionales. *Rhombifera* es el único rombífero gliptocistitido con el periprocto rodeado por dos placas laterales (L4 y L5) y facetas ambulacrales en las placas radiales, y no en las orales. *Rhombifera* derivó de los equinoencrinítidos gliptocistitoides, y ambos comparten la zona oral reducida con cinco placas radiales, y los pectinirrombos con hendiduras ovaladas cortas. Las zonas orales de *Rhombifera* y *Lisocystites* son similares. En *Lysocystites* hay cinco placas ambulacrales con facetas braquiolares que se alternan con cinco placas orales interradiales para formar la zona oral. El hidroporo y gonoporo se sitúan en placas orales adicionales en el interambulacro CD. *Lysocystites*, así como coronados y blastoideos, poseen tres placas basales, cinco "radiales", cinco deltoides y cinco placas homólogas a las placas lanceoladas de los blastoideos. Sugerimos que las placas basales, laterales, radiales y orales de los gliptocistitoides son homólogas respectivamente a las placas basales, radiales, lanceoladas y deltoides de los blastoideos. *Rhombifera* permite relacionar a los rombíferos gliptocistitoides con los blastoideos.

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Corresponding author:

Christopher R. C. Paul

glrcrc@bristol.ac.uk

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INTRODUCTION

The systematics of *Rhombifera* Barrande, 1867, puzzled palaeontologists for a long time, largely due to its preservation predominantly as incomplete internal moulds. Kesling (1962) gave a thorough history. *Rhombifera* was originally described in a volume on fossil pteropods, on the basis of a single species, *Rhombifera bohémica* Barrande, 1867, which becomes type species of the genus by monotypy. Barrande (1867, p. 175 *et seq.*; 1887, p. 175 *et*

seq.) redescribed the species as a fossil cystoid (echinoderm), in particular recognizing that it bore rhombs that are now referred to as pectinirhombs and are a key character of the superfamily Glyptocystitoida Bather, 1899. Barrande (1887, p. 80) also described a second species, which is a coronate blastoid *sensu lato*, as *Rhombifera? mira*. Jaekel (1899, p. 340) referred *Rhombifera* to his Dichoporita, which included the two rhombiferan superfamilies Glyptocystitoida

and Hemicosmitoidea Jaekel, 1918. Jaekel associated *Rhombifera* with a crinoid, *Tiaracrinus* Schultze, 1867, which has a superficially similar surface ornament, but lacks pectinirhombs. Bather (1900, p. 57) regarded *Rhombifera* as a cystoid, but classified it within the crinoid family Tiaracrinidae. Jaekel (1918, p. 99) again assigned *Rhombifera* to the Dichoporita, but also made *Rhombifera? mira* type species of a new genus *Stephanoblastus*, which he regarded as belonging to his new Order Coronata of the Blastoidea *sensu lato*. Bassler (1938, p. 15) assigned *Rhombifera* to the crinoids. Fay (1962) included *Rhombifera* in the Coronata, along with the genera *Mespilocystites* Barrande, 1887, *Paracystis* Sjöberg, 1915, *Stephanoblastus*, *Stephanocrinus* Conrad, 1842, and *Tormoblastus* Jaekel, 1927, but regarded the coronates as an order of the Crinoidea. Thus, the systematic position of *Rhombifera* remained uncertain before Kesling (1962) reinterpreted it on the basis of latexes of a critical specimen in the Barrande – de Verneuil collection in Paris. Kesling established that *Rhombifera* was undoubtedly a glyptocystitoid rhombiferan, but assigned it to a separate family, the Rhombiferidae, based on its unique morphology. Even so, several aspects of the morphology of *Rhombifera* remained unknown to Kesling, due to the rather poor preservation of specimens and their tendency to fall apart soon after death. In addition,

critical aspects of the morphology of the type species, *R. bohémica* were overlooked, such as its triangular cross-section. For 100 years *Rhombifera* was only known from the Upper Ordovician (Sandbian–Katian) of the Czech Republic and an unconfirmed listing from Portugal (Delgado, 1908). Then, Hélène Renard described a second species, *R. mattei* Renard, 1967, from the Montagne Noire, France. Renard's specimens were preserved in original calcite, rather than Barrande's natural moulds (Renard, 1967, 1968). She confirmed the presence of a stem and the basal circlet of plates, although not their number. According to Renard (1967, fig. 1), *R. mattei* differed from *R. bohémica* in having only three infralateral plates, and in having rhombs present on all five lateral plates (Fig. 1B, herein). Kesling (1962) had interpreted *R. bohémica* as having five infralateral and lateral plates and only three rhombs in each circlet (Fig. 1A). Yet Bather (1900, p. 57) had already claimed that *Rhombifera* had only three plates in the lower circlet (infralaterals). Renard was unable to identify the periproct in any specimens of *R. mattei*, so her interpretation of individual lateral plates is uncertain. More recently, *Rhombifera* has been discovered in the Katian of Spain (Gutiérrez-Marco et al., 1996; Villas et al., 2011; Colmenar et al., 2015), Sardinia (Sumrall et al., 2015) and Morocco (Zamora et al., 2022), although its presence in Portugal had long been known (Delgado, 1908) which we can confirm.

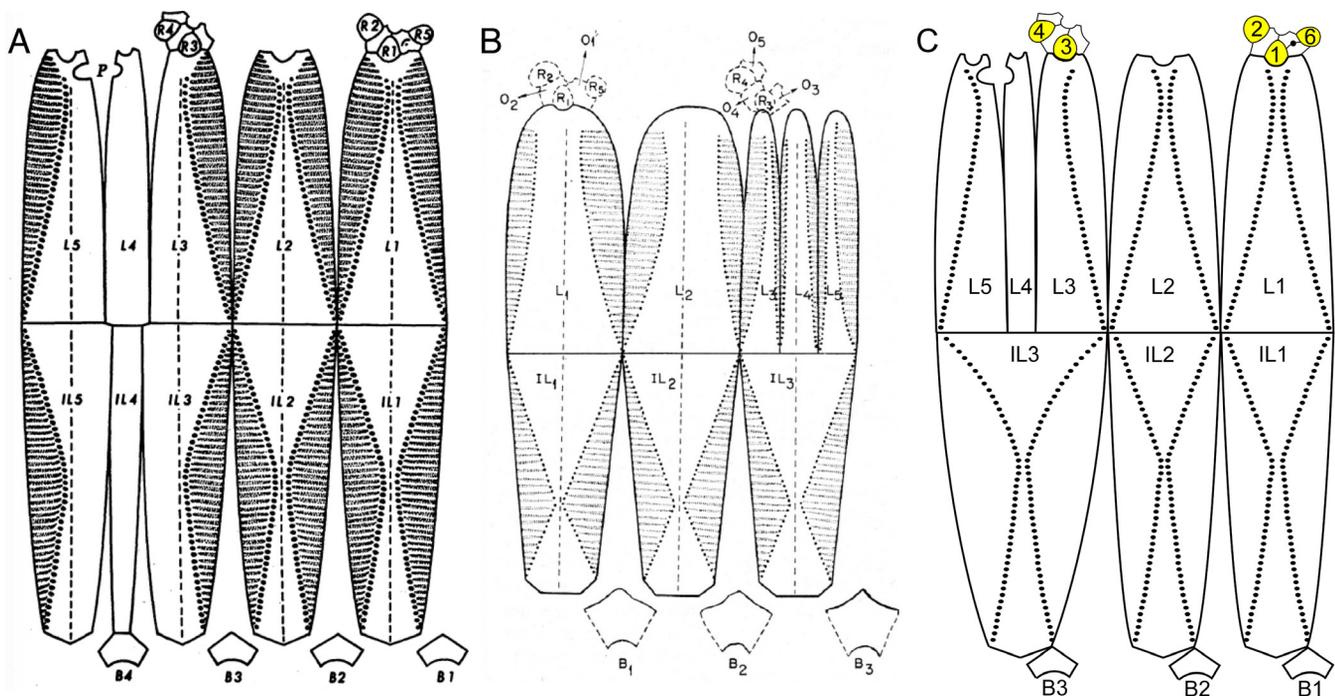


Figure 1. Interpretations of the plate arrangements in **A**, *Rhombifera bohémica* Barrande, 1867, after Kesling (1962, fig. 1); **B**, *Rhombifera mattei* Renard, 1967, after Renard (1967, fig. 1); **C**, *Rhombifera bohémica* adopted herein. Details of the oral (O1–O5) and radial (R1–R5) plates copied from Kesling (1962, fig. 1). Widths of IL plates not necessarily to scale. Note that Renard numbered the basal (B1–B3), infralateral (IL1–IL3) and lateral (L1–L5) plates from left to right, whereas the convention (observed by Kesling and ourselves) is to number them from right to left, which equals clockwise in oral view. Note, too, that infralateral plates are characterized by large, almost symmetrical rhombs, whereas the lateral plates have large, asymmetrical rhombs with the shorter part adoral. This enables isolated rhomb-bearing plates to be identified and orientated. Furthermore, in Renard's interpretation of *R. mattei* all infralateral and lateral plates have two half rhombs.

Current knowledge of its stratigraphic and geographic distribution is summarized in Figure 2. Most recently, Paul (2021) suggested that the genus *Rhombifera* shows characters intermediate between glyptocystitoid rhombiferans and blastoids *sensu lato*. Thus, a review of the morphology of the genus *Rhombifera* is timely, first to try to establish all its morphological features, then to confirm interpretations of its plate homologies or resolve any differences in interpretation, and finally to test suggestions of its evolutionary significance.

FOSSIL LOCALITIES, STRATIGRAPHY AND AGE

Specimens of *Rhombifera* we have examined include Barrande’s original type material as well as previously unstudied material of the type species, *R. bohémica*, from the Czech Republic preserved in the de Verneuil – Barrande collection, now in Lyon, France, as well as the original specimens seen by Kesling (1962) which are still in Paris. Prokop and Petr (1999, tab. 1) record *R. bohémica* from the Libeň, Letná, Vinice and Zahořany formations, of the Berounian local stage, which correlates with most of the Sandbian and the lower part of the Katian international stages (Gutiérrez-Marco et al., 2017, fig. 3; Kraft et al., 2023, fig. 4; Fig. 2 herein). New Spanish specimens of *R. bohémica* come from both Piedra del Tormo and Huerva Members of the Fombuena Formation of the Iberian Ranges, which is also of mid and late Berounian age (Villas et al., 2011, fig. 9; Colmenar et al., 2015, figs. 14, 19; Fig. 2 herein) as well as the Pizarras Intermedias Formation of Guadarranque – Villuercas, and the Cantera Shales of the Eastern Sierra Morena which are both of mid Berounian age.

Portuguese material came from the sierra Peneda de Goes, in the Amêndoa-Mação region (Delgado, 1908) and the Queixoperra Member of the Cabeço do Peão Formation from middle Berounian strata (Gutiérrez-Marco in Romão et al., 1995). In addition, Martin

(1990, p. 63) described and illustrated four specimens of ‘*Rhombifera* sp.’ from ‘the Upper Ordovician of Fluminimaggiore, Cagliari Province, Sardinia’. Sumrall et al. (2015, fig. 21) illustrated a partial theca of *Rhombifera*, which preserves parts of three infralateral plates, from the lower Katian, Portixeddu Formation of Sardinia, Italy (Loi et al., 2023, fig. 6). Zamora et al. (2022, fig. 8m) figured a single lateral plate (L3) from the Lower Ktaoua Formation near Tinerhir, Morocco. Álvaro et al. (2022, fig. 2) regarded the Lower Ktaoua Formation as of Berounian (early Sandbian to mid Katian) age (Fig. 2; see also Colmenar et al., 2022). Renard’s specimens of *R. mattei* all came from the ‘Calcaires à Cystoïdes’ at La Grange du Pin, Montagne Noire, France, which is now referred to the Gabian Formation, of late Katian (Kralodvorian Regional Stage) age (Colmenar et al., 2013, fig. 2; Lefebvre et al., 2023, fig. 9). Thus, it seems that *R. bohémica* ranges through the Sandbian to the mid Katian (Berounian), whereas *R. mattei* is slightly younger being confined to the late Katian (Kralodvorian).

MATERIALS AND METHODS

The specimens studied herein occur as internal and external moulds in fine-grained sedimentary rocks. Latex casts were made from key specimens and the casts whitened with ammonium chloride sublimated for photography. Latex casts were photographed with a Canon EOS 70 D digital camera. Measurements of pectinirhombs and other morphological features were made using a Kyowa binocular microscope with a graticule eyepiece or from photographs that included a mm scale. As we have seen no complete specimen, we have also reviewed the literature, principally for photographic illustrations to test our interpretation of the thecal plate arrangement of *Rhombifera*. Infralateral plates can be distinguished from laterals by their more symmetrical rhombs (contrast Figs. 3D,

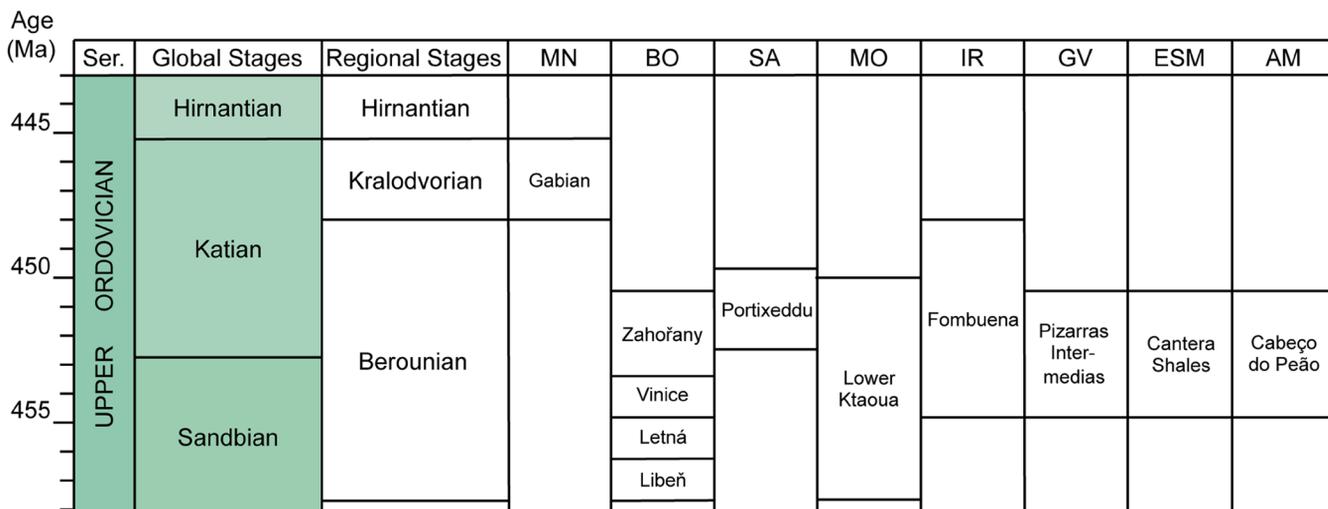


Figure 2. Stratigraphic correlation of formations in which *Rhombifera* occurs. MN, Montagne Noire, France; BO, Bohemia; SA, Sardinia; MO, Morocco; IR, Iberian Ranges, Spain; GV, Guadarranque – Villuercas, Spain; ESM, Eastern Sierra Morena, Spain; AM, Amêndoa – Mação, South of the Central Iberian Zone, Portugal; Ma, million years before present; Ser., series.

4A, 4B with Fig. 4D). With only three infralaterals and three rhombs, as first suggested by Renard (1967), all isolated infralaterals should have two half rhombs, one on each side. With more than three infralaterals, but three rhombs, at least some infralaterals of *R. bohémica* should bear only one half-rhomb on one side. So far, we have failed to find any infralaterals with one half-rhomb. Thus, we conclude that Renard was correct in her interpretation and that Kesling's (1962, fig. 1; 1968, fig. 82.1a, p. S178) restoration of the infralateral circling with five plates, as in all other glyptocystitoid rhombiferans, was understandable, but incorrect. *Rhombifera mattei* is distinguishable from *R. bohémica* in that it has rhombs on all five L:L sutures making a total of eight in all (Fig. 1B), whereas *R. bohémica* has only three rhombs in both circlings; a total of six (Fig. 1C).

Ray and interray designations follow Carpenter (1884, 1891). Plate circling terminology (basals, infralateral, laterals, radials and orals) follows Regnéll (1945). Terminology of pectinirhombs follows Paul (1968).

Repositories and institutional abbreviations

Material described herein is deposited in the Museo de Ciencias Naturales de la Universidad de Zaragoza (MPZ), the Natural History Museum, London (NHMUK), the palaeontological collections of Paris-Sorbonne University, Paris (SU.PAL), the National Museum, Prague (NMP) and Lyon 1 University, Villeurbanne (UCBL-EM), the Fernando Real Geology Museum, University of Trás-os-Montes e Alto Douro, Portugal (FRGM), and the Geological Museum of Lisbon (Laboratório Nacional de Energia e Geologia) (GML).

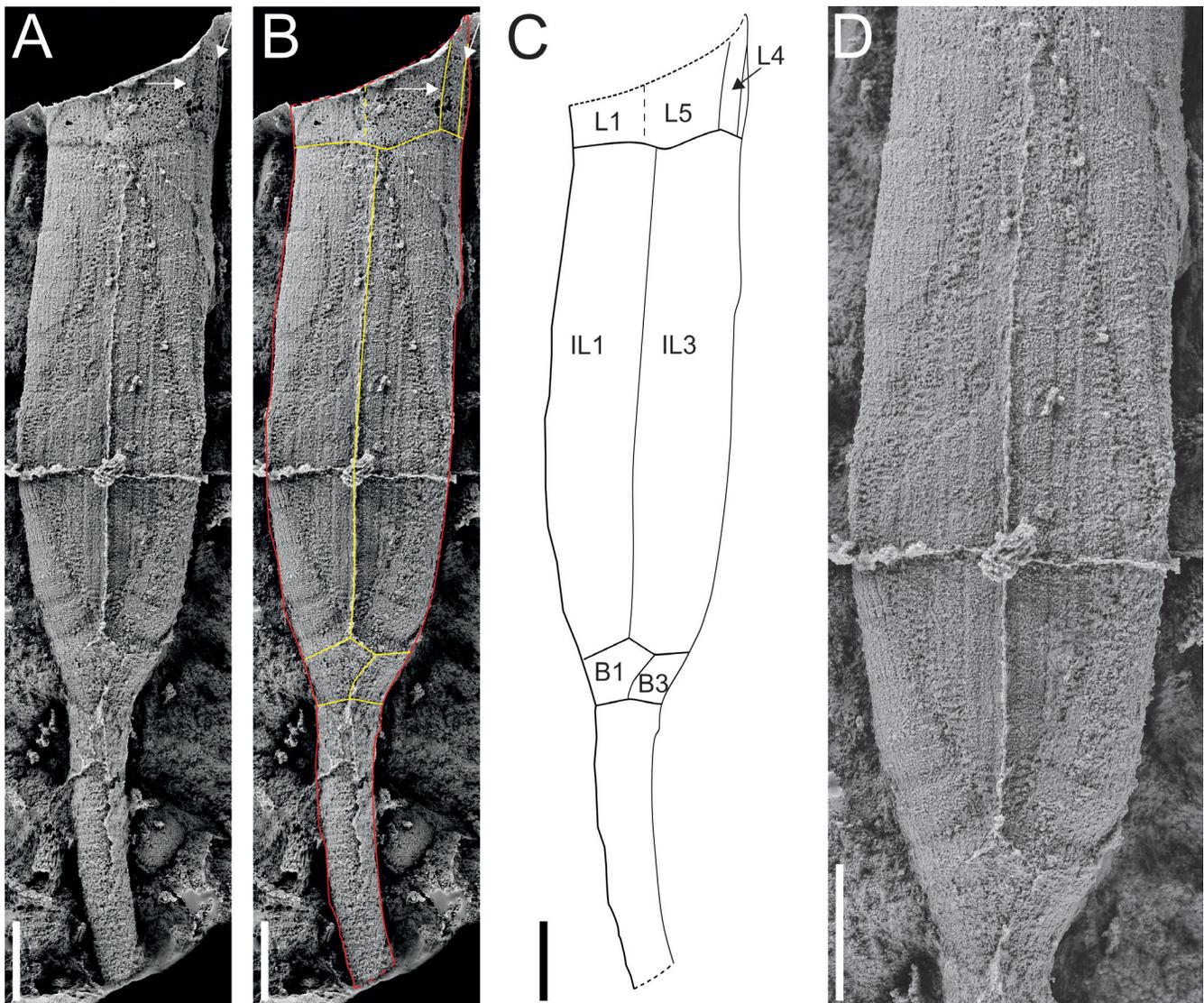


Figure 3. Interpretation of plate arrangement in *Rhombifera bohémica* Barrande, 1867 from latex cast of MPZ 2023/92, Huerva Member, Fombuena Formation, Santa Catalina (Fombuena), Spain. **A**, Lateral view of latex. Arrows point to two sutures on either side of narrow, rhombless plate L4; **B**, the same with thecal outline (red) and plates sutures (yellow) highlighted; **C**, interpretation of plate arrangement; B1, B3 basals, IL1, IL3 infralateral plates, L1, L4 and L5 lateral plates; **D**, enlargement of basal plates and IL1:IL3 pectinirhomb. Suture between L1 and L5 not clear. Latex whitened with ammonium chloride; scale bars = 5 mm.

SYSTEMATIC PALAEONTOLOGY

Class RHOMBIFERA Zittel, 1879

Order DICHOPORITA Jaekel, 1899. Emend. Paul, 1972

Superfamily GLYPTOCYSTITOIDA Bather, 1899

Diagnosis. (after Paul & Rozhnov, 2016, emended). Dichoporite rhombiferans with well-developed xenomorphic stem consisting of rapidly tapering proximal portion composed of alternating inner and outer annular columnals and distal portion composed of alternating longer and shorter cylindrical columnals; theca composed of three or four basals, three or five infralaterals, five laterals, four, five, six or ten radials, and seven orals.

Remarks. Glyptocystitoid rhombiferans typically bear pectinirhombs, composed of endothelial canals (dichopores) that open in slits and are developed across the sutures between two thecal plates. One or two genera, such as *Macrocystella* Callaway, 1877 and *Amecystis* Ulrich & Kirk, 1921, lack pectinirhombs, but retain the characteristic stem and fixed plate arrangement. *Cuniculocystis* Sprinkle & Wahlman, 1994, possesses modified epispines rather than pectinirhombs, and is also unique in having ten radial plates. Otherwise, glyptocystitoids vary little in their thecal plate arrangement. Nevertheless, this diagnosis is modified to accommodate *Rhombifera*, which is unique in having only three basals, not the usual four, and three infralaterals, not the usual five.

Family RHOMBIFERIDAE Kesling, 1962

Diagnosis. Glyptocystitoids with an elongate theca composed of three plates in the basal and infralateral circlets, plus five plates in the lateral and radial circlets and seven orals; the infralaterals and laterals are very large; the radials and orals small and alternate around the mouth. Radials bear facets for a single, erect food-gathering organ. Pectinirhombs confined to infralateral and lateral plates.

Remarks. This diagnosis differs considerably from those given previously due to the realization that *Rhombifera*, the only genus in the family Rhombiferidae, has a reduced number of basal and infralateral plates and erect food-gathering structures arising from radial not oral plates (Fig. 1C).

Genus *Rhombifera* Barrande, 1867

Type-species. *Rhombifera bohemia* Barrande, 1867, from the lower and middle Berounian (= Sandbian and lower Katian, Fig. 2; Gutiérrez-Marco et al., 2017) of the Czech Republic.

Diagnosis. As for the family, which is monotypic.

Occurrence. Sandbian to early Katian international stages, Czech Republic (Prokop & Petr, 1999), Sandbian to mid Katian, Morocco (Zamora et al., 2022), late Sandbian to mid Katian, Spain (Gutiérrez-Marco et

al., 1996; Villas et al., 2011; Colmenar et al., 2015) and Portugal (Delgado, 1908; Jacinto et al., 2014), early to mid Katian, Sardinia, Italy (Martin, 1990; Sumrall et al., 2015), and late Katian of France (Renard, 1967).

Rhombifera bohemia Barrande, 1867

Figures 1C, 3–8, 10C, 10D

- 1867 *Rhombifera Bohemica* Barrande, 1867, p. 175, pl. 11, figs. 1–13.
 1879 *Rhombifera* Barrande; Zittel, p. 424.
 1887 *Rhombifera Bohemica* Barrande; Barrande, p. 178, pl. 6, figs. 1–21.
 1899 *Rhombifera bohemia* Barrande; Jaekel, p. 342, pl. 10, fig. 8.
 1900 *Rhombifera* Barrande; Bather, p. 57.
 1908 *Rhombifera bohemia* Barrande; Delgado, p. 69, 83.
 1928 *Rhombifera bohemia* Barrande; Bouček, p. 8, 27.
 1937 *Rhombifera bohemia* Barrande; Bouček, p. 444.
 1943 *Rhombifera bohemia* Barrande; Bassler & Moodey, p. 667.
 1962 *Rhombifera bohemia* Barrande; Kesling, p. 281, pls. 1–2, text-figs. 1–2.
 1966 *Rhombifera bohemia* Barrande; Havlíček & Vaněk, p. 31, 53, 54, 56, 57.
 1968 *Rhombifera bohemia* Barrande; Renard, p. 81, pl. 14,
 1968 *Rhombifera bohemia* Barrande; Kesling, p. S178, fig. 82.1a–82.1c
 1976 *Rhombifera* sp.; Wolf, p. 102, pl. 3, fig. 9.
 1980 *Rhombifera bohemia* Barrande; Havlíček, p. 70.
 1982 *Rhombifera* sp.; Ballestra et al., p. 58.
 1990 *Rhombifera* sp.; Martin, p. 63, pl. 5, fig. 2, text-figs. 58–60.
 1992 *Rhombifera bohemia* Barrande; Gutiérrez-Marco et al., p. 80.
 1995 *Rhombifera bohemia* Barrande; Romão et al., p. 124.
 1996 *Rhombifera bohemia* Barrande; Gutiérrez-Marco et al., p. 111, pl. 2, figs. 1–5, 11 (non fig. 6).
 1996 *Rhombifera bohemia* Barrande; Liñán et al., 1996, fig. 10.
 2002 *Rhombifera bohemia* Barrande; Leone et al., p. 233.
 2011 *Rhombifera bohemia* Barrande; Villas et al., p. 12, pl. 3, fig. g.
 2014 *Rhombifera bohemia* Barrande; Zamora et al., p. 258, fig. 1a.
 2014 *Rhombifera bohemia* Barrande; Jacinto et al., p. 95, fig. 1B.
 2015 *Rhombifera bohemia* Barrande; Jacinto et al., p. 16–17, pl. 2, figs. A–G.
 2015^a *Rhombifera bohemia* Barrande; Jacinto et al., p. 164, tab. 1.
 2015 *Rhombifera bohemia* Barrande; Colmenar et al., p. 237, fig. 19A.
 ?2015 *Rhombifera* sp.; Sumrall et al., p. 178, fig. 2(i).
 2019 *Rhombifera bohemia* Barrande; Zamora et al., p. 22, fig. 10(A).
 2021 *Rhombifera* sp.; Paul, p. 53, figs. 6b, 19, 20A.
 2022 *Rhombifera* sp.; Zamora et al., p. 596, fig. 8l, 8m.

Lectotype. As far as we are aware, no type has previously been designated. We select as lectotype the original of Barrande, 1867, plate 11, figure 5, now in the National Museum, Prague (Reg. no. L13001), an external mould which preserves some plates of the infralateral, lateral, radial and oral circlets (Fig. 5). The

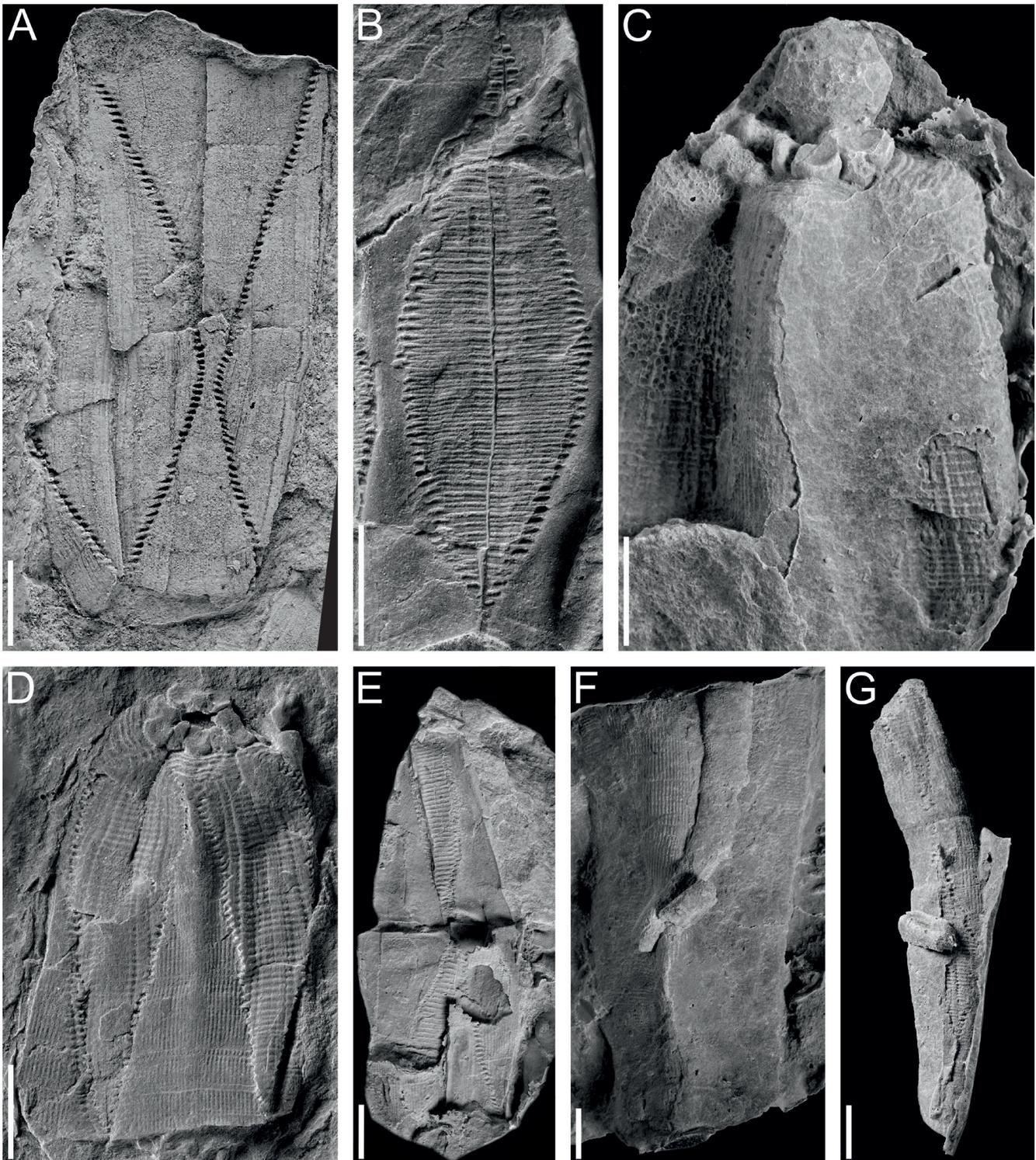


Figure 4. Latexes of *Rhombifera bohemica* Barrande, 1867, from the Czech Republic (A, B, D–F) and Spain (C, G). A, Paralectotype NMP L13000. External surface of large IL:IL pectinirhombs. Note short slits; B, SU.PAL.2017.054.15 Internal surface of IL:IL pectinirhomb. Note traces of dichopores between pectinirhomb slits; C, lateral view of MPZ 2023/91 showing large lateral plates plus some orals and radials (top). Note the lobate outline of the theca; D, 'Kesling's specimen' SU.PAL.2017.054.16 showing complete oral and radial circllet. Note the external ornament; E, UCBL-EM 12149. Another example showing both the IL and L circllets with two aligned rhombs; F, MPZ 2023/94, Huerva Member, Fombuena Formation, Santa Catalina (Fombuena), Spain. External surface of a large infrolateral plate showing fine vertical growth lines between the rhombs (centre top) and similar horizontal traces of the dichopores within the rhombs (top right); G, lateral view of specimen MPZ 2023/90 showing infrolateral and lateral circllets. Latexes whitened with ammonium chloride; scale bars = 5 mm.

specimen was illustrated again in Barrande (1887, pl. 6, fig. 21). Both illustrations are upside down in relation to modern standard orientation, with the infralateral plates above the laterals, and somewhat enhanced. Plate 11, fig. 5 shows the correct left-right orientation of the latex cast (see Fig. 5A), that is, it is a mirror image of the preserved external mould. Plate 6, figure 21 shows the correct orientation of the external mould. Remaining specimens illustrated by Barrande (1867) become paralectotypes.

Type locality. According to Barrande, 1867, explanation of plate 11, the lectotype and all other figured specimens came from Vráž, Czech Republic.

Type horizon. The type horizon could be in the Letná, Vinice or Zahořany formations (see Chlupáč 2002a, 2002b; personal communication Petr Budil and Vojtěch Turek). Early or mid Berounian regional stage, late Sandbian or early Katian International stages. In recent years all new material of *Rhombifera* has originated from the Letná Formation.

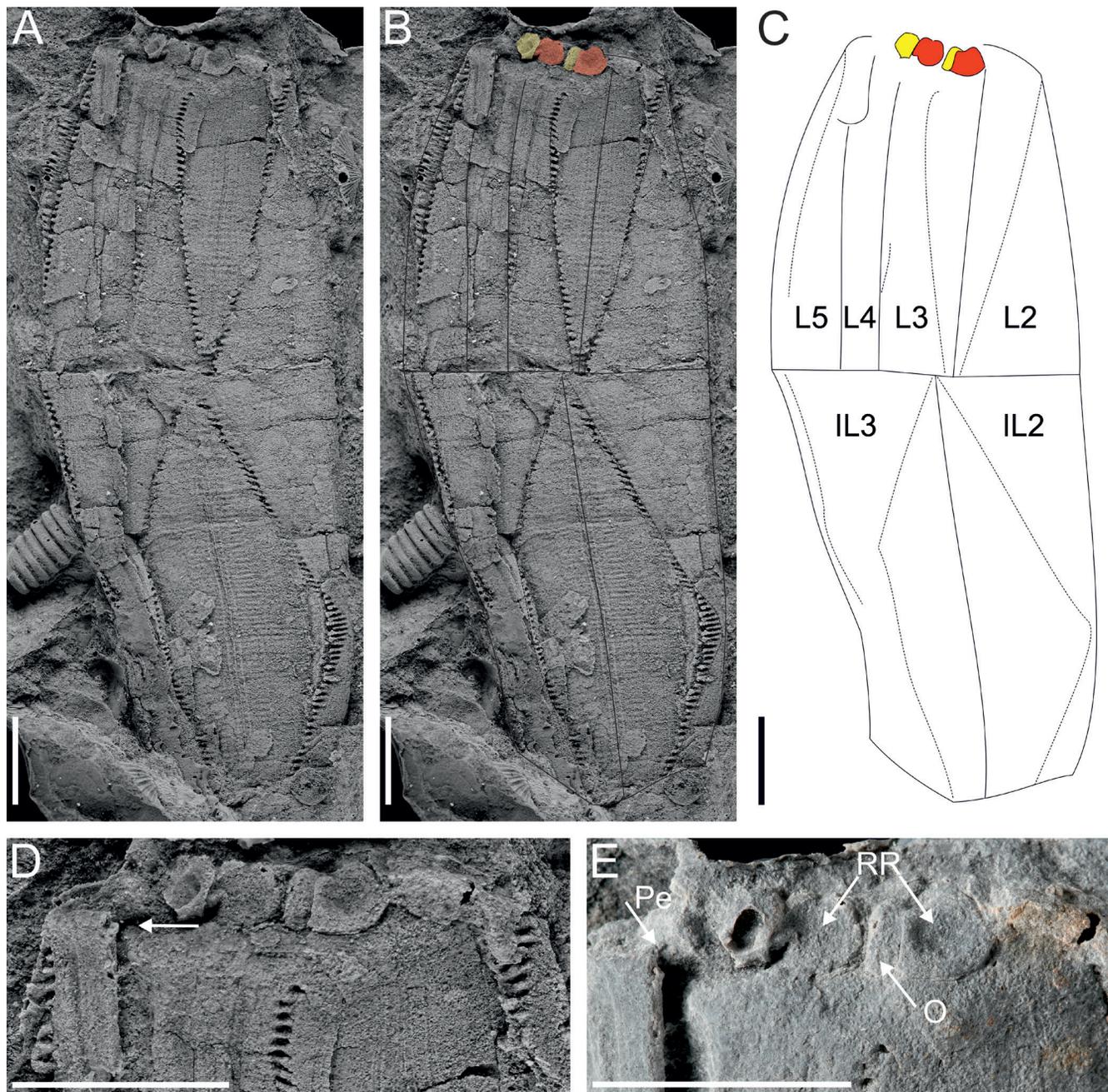


Figure 5. Latexes of the lectotype of *Rhombifera bohémica* Barrande, 1867, NMP L13001. **A**, Lateral view showing the infralateral plates (below), lateral plates (above) plus two orals and two radials (top). Note the very large IL:IL pectinirhomb (below) and asymmetrical L:L pectinirhomb above; **B**, the same with outlines of thecal plates indicated; **C**, interpretation of the visible thecal plating. Radial plates red, orals yellow; **D**, detail of the top of the theca showing notch for periproct in plate L5 (arrowed); **E**, slightly different view of top of theca with radial and oral plates indicated. Latexes whitened with ammonium chloride. **IL2**, **IL3** Infralateral plates, **L2–L5** Lateral plates, **O** oral plate, **Pe** notch for periproct, **RR** radial plates; scale bars = 5 mm.

Material. Latex casts of internal and external moulds of isolated plates and partial thecae in the Barrande – de Verneuil collections, Lyon and Paris, France (SU.PAL.2017.0.54.15–16, UCBL-EM.12146–12150), and the Barrande collection in the National Museum, Prague, Czech Republic; specimens in the Czech Geological Survey, Prague; partial thecae from the Fombuena and Cantera Shale formations, Fombuena (Zaragoza) and Viso del Marqués (Ciudad Real), respectively, Spain (MPZ); Cabeço do Peão Formation, Portugal; and from the Lower Ktaoua Formation, Tinerhir, Morocco (NHMUK EE14792)

Diagnosis. A species of *Rhombifera* with six pectinirhombs; three each in the infralateral and lateral plate circlets.

Description. *Rhombifera* had a long stem, an elongate theca (Fig. 3), triangular in cross-section aborally (Fig. 4A below), more quadrate adorally with distinct shoulders (Fig. 4C) and a small flattened oral prominence with five, rounded facets for unknown erect feeding structures (Fig. 4D).

The stem is circular; 17 mm of the proximal stem are preserved in specimen MPZ 2023/92 (Fig. 3A) where it

is slightly curved and tapers from 4.2 mm diameter at the base of the theca, to 3.0 mm where the latex ends. It is composed of thin, presumably annular columnals but no sign of a lumen remains. Externally the columnals have a weak central ridge encircling them and about 30 outer columnals remain on the latex.

The theca is very elongate, measuring 30.1 mm high by 3.9 mm maximum width in specimen MPZ 2023/90 which is incomplete orally (Figs. 4G, 6A, 6B). It was composed of five plate circlets, basals (abbreviation B, plural BB), infralaterals (IL, ILL), laterals (L, LL), radials (R, RR) and orals (O, OO), arranged as in Figure 1C. There were three relatively small basals, which taper into the stem in MPZ 2023/92 (Fig. 3A) and alternate with the three, elongate infralaterals above in MPZ 2023/90 (Fig. 6A, 6B). The infralaterals are the largest plates in the theca and bear large, nearly symmetrical pectinirhombs with 60 or more dichopores (Fig. 3D). The rhombs occupy the flat sides of the triangular lower theca (Fig. 4A, 4B), whereas the ILL plates bear ridges down their centres forming the angles of the triangle (Fig. 4F) Above the IL circlet is the L circlet composed of five large plates (Fig. 4E). The vertical sutures between the IL plates align with three of the sutures between the L plates (Figs. 1C, 4E, 6A, 6B). So, the L5:L1 suture is slightly offset to the left of the IL3:IL1 suture, L2:L3 is slightly offset to the right of IL2:IL3 and L1:L2 is slightly to the right of IL1:IL2. The slight offset of the almost aligned vertical sutures enables identification of individual plates of incomplete specimens that preserved parts of both plate circlets (Figs. 4E, 5A–5C). Lateral plates also bear large, asymmetrical pectinirhombs with up to 40 or more dichopores in the lower demirhomb but only three or four in the adoral demirhomb (Fig. 4D). Lateral plates are distinctly shouldered at the level of their rhomb axes (Fig. 4C) and the thecal outline becomes lobate. Pectinirhombs are confined to the infralateral and lateral circlets (Figs. 1C, 5A–5C) three rhombs in each circlet, and orientated so that if the thecal axis is vertical all the dichopores are horizontal (Fig. 4A, 4B, 4D). Pectinirhombs only cross sutures between plates of the same circlet and can be identified by the two plates on which they occur. So, *R. bohémica* has three IL:IL rhombs, IL1:IL2, IL2:IL3 and IL3:IL1, plus three L:L rhombs, L1:L2, L2:L3 and L5:L1 (Fig. 1C). They all have disjunct dichopores with short slits at either end (Figs. 4A, 5A). Externally, rhomb-bearing plates are ornamented with traces of the dichopores within the rhombs, as well as fine growth lines interrupted periodically by more prominent growth lines outside the rhombs, thus forming a reticulate ornament. (Figs. 4D, 5A, 6B). Lateral grooves at the most prominent growth lines continue between the prominent ridges on the shoulders of the lateral plates (Figs. 4C upper right, 4D, 7A). If annual, they suggest *Rhombifera* lived for about seven years. Internally, the plates are smooth except within the half-rhombs where traces of the dichopore walls show as fine raised ridges (Figs. 4B, 8B). The

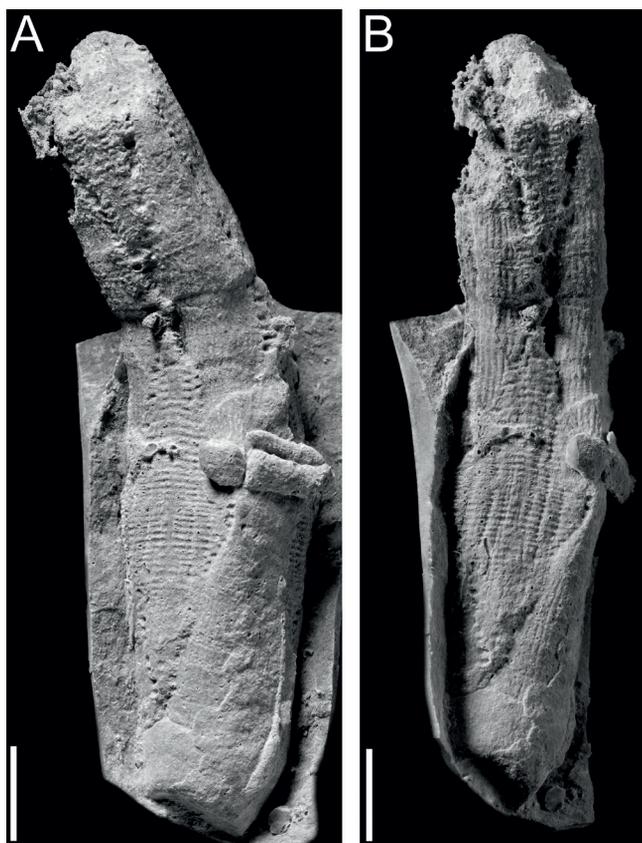


Figure 6. Latexes of Spanish *Rhombifera bohémica* Barrande, 1867, specimen MPZ 2023/90, Cantera Shales Formation, Viso del Marqués, Spain. **A**, lateral view showing complete infralateral rhomb (below left) with most of a lateral rhomb directly above it. Note the top of the basal plate below the lower rhomb; **B**, another lateral view showing the same two rhombs. Latexes whitened with ammonium chloride; scale bars = 5 mm.

dichopore slits are short (Figs. 5A, 5E, 8A), usually oval and typically two to three times as long (parallel to the dichopores) as wide. Slit spacing varies from one slit per 0.310 mm to 0.653 mm (N = 34, with a mean of 0.435 mm in examples from the Czech Republic, and from one slit per 0.389 mm to 0.619 mm with a mean of 0.484 mm (N = 10) in Portuguese examples (Tab. 1). The flat oral prominence is composed of thick alternating radial and oral plates (Fig. 4C top) surrounding the oval mouth (Fig. 7A, 7B). The mouth frame was formed by five, crudely T-shaped orals (for example, plate O4, Fig. 7C). These alternate with five, roughly equant radial plates (R1–R4 and R6, Fig. 7C), each of which bears a circular depression interpreted as the facet for attachment of unknown, erect, feeding structures (presumably biserial brachioles as in all other glyptocystitoid rhombiferans where the feeding structures are preserved). The facets are connected to the mouth by short food grooves (see plates R3 and R4, Fig. 7C). The CD interradius can be recognized by the presence of three oral plates (O1, O6, O7, Fig. 7C). A small roughly triangular depression across the O1:O7 suture is interpreted as the hydropore and a circular pit across the O6:O7 suture as the gonopore (Fig. 7C). The periproct is surrounded by only two lateral plates (L4 and L5) and lies near the oral prominence at the top of the lateral plate circllet in the BC interray (P Fig. 1C, Arrow Fig. 5D, Pe Fig. 5E).

Occurrence. Prokop and Petr (1999, tab. 1) record *R. bohémica* from the Libeň, Letná, Vinice and Zahořany formations, of the Berounian local stage, which correlates with most of the Sandbian and the early Katian international stages (Gutiérrez-Marco et al., 2017, fig. 3). New Spanish specimens of *R. bohémica* come from the Cantera Shales and Fombuena formations, which are also of Berounian age (Villas et al., 2011, fig. 9; Colmenar et al., 2015, figs. 14, 19).

Discussion. At first sight it appears that Barrande (1867, p. 176) was clear that what we now call the infralateral circllet was triangular in section and contained just three almost equal-sized plates. Unfortunately, this is not as certain as it seems because Barrande consistently illustrated examples upside down with respect to the standard modern orientation (Barrande, 1867, pl. 11, fig. 5; 1887, pl. 6, figs. 7, 8, 10, 21). Equally, in at least one case (Barrande, 1887, p. 175) he refers to an example as having a triangular base with a rhomb on each of its three sides (Barrande, 1887, pl. 6, figs. 4, 5). To us this specimen is more quadrate than triangular in cross section and clearly shows the oral surface. Nevertheless, some of his original illustrations do justify his statement (Barrande, 1867, p. 176) “that the general shape of the calyx of *Rhombifera* is that of an elongated truncated pyramid, with a triangular base. The 3 faces of this pyramid are equal they form between them equal dihedral angles, as indicated by the transverse section PI. 11, fig. 13”. Furthermore, Barrande (1867, pl. 11, figs. 1–3) showed opposite views of a crushed

infralateral circllet, with three rhombs and no space at all where additional plates without rhombs could exist. Barrande (1887, p. 174) made this same point about plate 6, figures 18 and 19, which though upside down also show opposite sides of the infralateral circllet with three rhombs and no space for additional plates. Bather (1900, p. 57) was equally clear that *Rhombifera* had a triangular theca. He wrote “Theca elongate, triangular in section; appears composed of two circllets – a lower, of three plates united by strong stereom folds, visible exteriorly only as terminal pores outlining “pore-rhombs”. One presumes Bather followed Barrande’s descriptions, but Barrande consistently got the orientation of the theca wrong, so why did Bather think

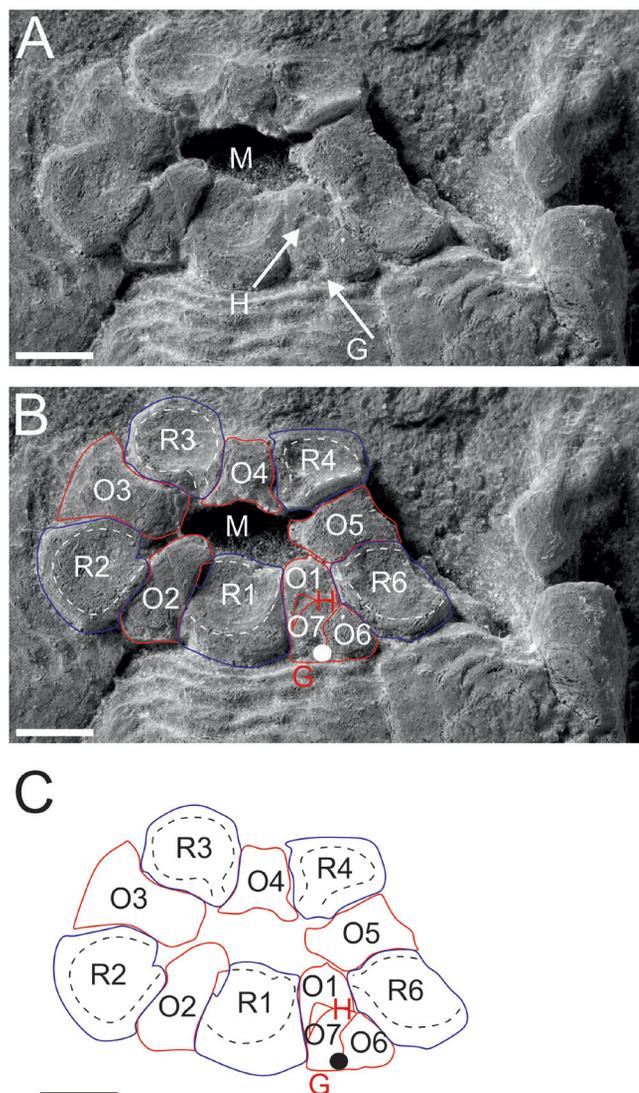


Figure 7. Detail of the oral area of *Rhombifera bohémica* Barrande, 1867, SU.PAL.2017.054.16. **A**, View of the oral prominence surrounding the mouth (M); **B**, the same with the interpretation of the five equant radial plates (R1–R5) with circular ambulacral facets alternating with the narrower oral plates (O1–O7). Note the three oral plates (lower right) with two associated pits interpreted as the gonopore (G) and hydropore (H); latex whitened with ammonium chloride; **C**, interpretation of the plating and orifices; scale bars = 1 mm.

Table 1. Slit-spacing in the pectinirhombs of *Rhombifera bohémica* Barrande, 1867.

Specimen	Rhomb	Position	Internal/external	No. slits	Spacing (mm)	Comment
NMP L13001	IL2:IL3	Axial in IL2	External	10	0.310	Lectotype
NMP L13001	IL2:IL3	Basal in IL2	External	10	0.395	Lectotype
NMP L13001	L2:L3	Aboral in L3	External	10	0.405	Lectotype
NMP L13001	L2:L3	Axial in L3	External	10	0.315	Lectotype
NMP L10799	IL:IL	Axis up	Internal	10	0.400	Paralectotype
NMP L10800	IL:IL	Base	Internal	10	0.400	Paralectotype
NMP L13000	IL:IL	Base	External	10	0.440	Paralectotype, same rhomb
NMP L13000	IL:IL	Axis up	External	10	0.445	Paralectotype, same rhomb
NMP L13000	IL:IL	Top	External	10	0.410	Paralectotype, different rhomb
NMP L13104	L1:L2	Top (Axial)	Internal	10	0.500	Paralectotype, c. 20 dichopores
NMP L13106	L1 or L2	Top (Axial)	Internal	10	0.440	Paralectotype c. 30 dichopores
NMP L13107	L:L	Aboral	Internal	10	0.410	Paralectotype c. 38 dichopores
NMP L13109	IL:IL	Above axis	Internal	10	0.400	Paralectotype
SU.PAL 2017.054.16	L1:L2	Aboral half	External	10	0.425	Figured, measured in L1
SU.PAL 2017.054.16	L1:L2	Top (Axial)	External	8	0.547	Figured, measured in L2
SU.PAL 2017.054.16	L1:L2	Aboral	External	9	0.506	Figured, measured in L1
SU.PAL 2017.054.17	IL:IL	Base	Internal	10	0.445	Figured, in same half-rhomb
SU.PAL 2017.054.17	IL:IL	Axial	Internal	10	0.335	Figured, in same half-rhomb
SU.PAL 2017.054.17	IL:IL	Top	Internal	7	0.653	Figured, in same half-rhomb
UCBL-EM 12146	IL:IL	Base	Internal	10	0.520	
UCBL-EM 12146	IL:IL	Axial	Internal	10	0.430	
UCBL-EM 12146	IL:IL	Top	Internal	10	0.470	
UCBL-EM 12147	IL:IL	Axial	Internal	10	0.330	
UCBL-EM 12147	IL:IL	Base or top	Internal	10	0.420	
UCBL-EM 12148a	L:L	Top (Axial)	Internal	10	0.350	
UCBL-EM 12148a	L:L	Nearly aboral	Internal	10	0.460	
UCBL-EM 12148b	IL:IL	Axial	Internal	10	0.380	
UCBL-EM 12148b	IL:IL	Base	Internal	10	0.480	
UCBL-EM 12149	L:L	Upper half	External	10	0.440	
UCBL-EM 12149	L:L	Aboral half	Internal	10	0.480	
UCBL-EM 12149	IL:IL	Axial	Internal	10	0.410	
UCBL-EM 12149	IL:IL	Top	Internal	10	0.400	
UCBL-EM 12150a	IL:IL	Above axis	External	10	0.420	
UCBL-EM 12150b	IL:IL	Above axis	Internal	7	0.612	
Mean spacing					0.4348 mm	
Standard deviation					0.0749 mm	
Coefficient of variation					17.235 %	
Portuguese examples						
FRGM CP089a	IL:IL	Axial	internal	10	0.4306	
FRGM CP089a	IL:IL	basal	internal	10	0.3889	
FRGM CP089a	IL:IL	Adoral	internal	10	0.4722	
FRGM CP089a	L:L	Aboral	External	10	0.5000	
FRGM CP089b	IL:IL	Axial	internal	10	0.4667	
FRGM CP089b	IL:IL	basal	internal	10	0.4000	
FRGM CP089b	IL:IL	Adoral	internal	10	0.4933	
GML DM1	IL:IL	Adoral	External	10	0.6190	
GML DM1	L:L	Aboral	External	10	0.4762	
GML DM1	IL:IL	Above axis	External	10	0.5952	
Mean spacing					0.4842 mm	
Standard deviation					0.0748 mm	
Coefficient of variation					15.457 %	

the lower circllet (*i.e.*, the infralaterals) had only three plates? Thus, Renard (1967, fig. 1) plate diagram illustrating *R. mattei* as having only three equal basal plates and three equal infralateral plates was not novel. Kesling (1962, p. 281 *et seq.*) introduced two alternative statements. First, he stated (p. 281) “Theca usually elongate, bipyramidal with the adoral and aboral halves shaped like high, square, truncated pyramids attached base-to-base.” (our emphasis). Secondly (p. 282) he added “Four ILL known from steinkerns described by Barrande (1867, p. 175–179; 1887, p. 175–178). Jaekel indicated a fifth IL in his reconstruction (1899, pl. 10, fig. 8), but he did not explain whether it was based on observed or hypothetical specimens.” The

only logical explanation for Kesling’s second statement is that he knew from the key specimen he described that there were five lateral plates with three rhombs and from Barrande’s original illustrations that the sutures between the two half-rhombs were aligned in the infralateral and lateral circllets. Thus, if the three lateral rhombs were L5:L1, L1:L2 and L2:L3 involving four lateral plates, L1, L2, L3 and L5, he assumed the infralateral circllet was identical with rhombs IL5:IL1, IL1:IL2 and IL2:IL3 (Fig. 1A). However, with only three infralateral plates, the sutures dividing the rhombs can still be aligned in both circllets if the infralateral rhombs are IL3:IL1, IL1:IL2 and IL2:IL3 (Fig. 1B). Indeed, Barrande’s cross section (1867, pl. 11, fig. 13) shows

precisely this arrangement, although without identifying either infralateral plates or rhombs. Thus, we conclude that both *R. bohémica* and *R. mattei* had three equal infralaterals and therefore three equal basals, two of which are clearly visible in MPZ 2023/92. Kesling's specimen (SU.PAL.2017.054.16.) confirms that there were also five laterals, five radials and seven orals. Thus, *Rhombifera* had a plate formula of 3BB, 3ILL, 5LL, 5RR and 7OO (Fig. 1C). No other glyptocystitoid rhombiferan has fewer than five infralateral plates.

ORIGIN OF RHOMBIFERA

Rhombifera is characterized by a theca composed of five plate circlets with a formula of 3BB, 3ILL, 5LL, 5RR and 7OO, as well as disjunct pectinirhombs with discrete dichopores that open in small oval pores. The presence of pectinirhombs suggests that the sister group must lie within the superfamily Glyptocystitoida Bather, 1899, but precludes the monotypic families Macrocystellidae Bather, 1899, and Cuniculocystidae Sprinkle & Wahlman, 1994, which lack pectinirhombs. The families Cheirocrinidae Jaekel, 1899, Pleurocystitidae Neumayr, 1889, and Glyptocystitidae Bather, 1899, are precluded because they retain the plesiomorphic six radial plates and have a large periproct surrounded by three to five thecal plates. The monotypic family Cystoblastidae Jaekel, 1899, is also precluded as it has only four lateral plates. This leaves the families Echinoencrinitidae Bather, 1899, and Callocystitidae Bernard, 1895, by default. The latter is characterized by advanced disjunct pectinirhombs with confluent dichopores and vestibule rims, whereas several echinoencrinitid genera, including the type genus *Echinoencrinites* von Meyer, 1826, have thecae with closed plate circlets, five radials and pectinirhombs with discrete dichopores opening in very short, oval slits. Furthermore, echinoencrinitids are characterized by reduced oral areas, as is *Rhombifera*, and typical pectinirhombs of *Echinoencrinites* open as small oval pores less than twice as long as wide. Altogether, *Echinoencrinites* appears to be the best candidate for sister group to *Rhombifera*. Kesling (1962, p. 285–286) came to the same conclusion for similar reasons. Nevertheless, *Rhombifera* is unique among all glyptocystitoids in having only three basals and three infralaterals, as well as a unique plate arrangement in which some plate sutures in the infralateral and lateral circlets are aligned in an interradian position, whereas normally the sutures alternate radial (IL) and interradian (LL). Furthermore, the small radial plates are centrally aligned in re-entrants to the lateral plates. *Rhombifera* also has a periproct surrounded by only two plates, L4 and L5. All these points are sufficient, in our opinion, to justify retention of the monotypic family Rhombiferidae Kesling, 1962.

Discussion. In comparison with more typical echinoencrinitids, the theca of *Rhombifera bohémica*

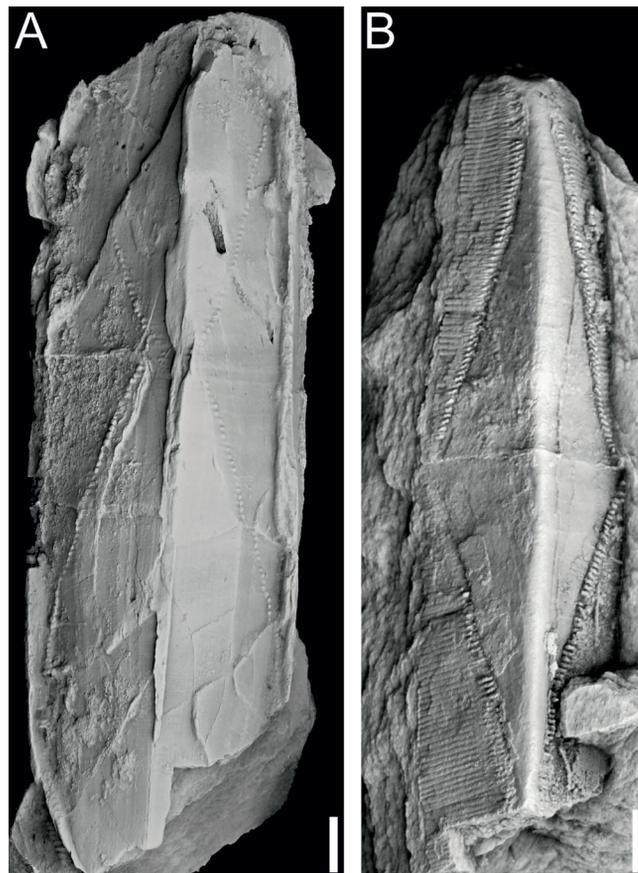


Figure 8. External (A) and internal (B) views of GML specimen showing the relatively smooth external surface and prominent pectinirhombs, Queixoperra Member of the Cabeço do Peão Formation, Peneda de Goes, Amêndoa-Mação, Portugal; scale bars = 5 mm.

Barrande, 1867, type species of *Rhombifera*, is very elongate. The three basals are small and lack any half pectinirhombs. From the position of the periproct it is clear that the undeveloped basal was B4 and the missing infralaterals were IL4 and IL5. The three remaining infralaterals are greatly expanded in an ad-aboral direction, accounting for over half the thecal height, and bear three large almost symmetrical pectinirhombs with 60 or more dichopores. The largest infralaterals reach nearly 50 mm height (Fig. 4F). The aboral portions of the laterals are similarly greatly enlarged but the adoral portions are not, giving rise to decidedly asymmetrical pectinirhombs with 40 or more dichopores in the aboral portion (below the axis) and five or fewer in the adoral portion. It is also doubtful that the dichopores adoral to the axis were fully functional in life. Some vertical sutures between the laterals align with those between the infralaterals. The periproct is high on the theca close to the oral ring. Two laterals, L4 and L5, form the periproct border, L5 contributing the larger portion. Only two periproct border plates is unknown in any other glyptocystitoid rhombiferan, although plate L5 is commonly the plate contributing the largest portion of the periproct border. Equally, the periproct is near the adoral margin of the lateral plates and therefore much higher in the theca relative to other glyptocystitoids. In

contrast to the infralaterals and laterals, the radials and orals are greatly reduced, alternate with each other and form a slightly raised oral ring around the mouth. The radial circlet was the last to form in ontogeny (Sumrall & Sprinkle, 1999), and is paedomorphic in that all the radials are small, pyriform plates isolated from each other by the orals. This is another unique character of *Rhombifera*, as is the fact that facets for ambulacral feeding structures (presumably brachioles) lie on the radial plates, which have short food grooves adorally. In addition, the adoral ends of the laterals bear curved indentations into which the isolated radials fit. Thus, the infralateral, lateral and radial circlets have plates that are all aligned in a radial position, rather than alternating with each other; another unique feature of *Rhombifera*. Seven inter-radial orals occur, three above the other, in the CD interambulacrum (Fig. 7C) and one each in the other four interambulacra.

To derive *Rhombifera* from a typical echinoencrinid, such as *Echinoencrinites*, requires expanding the relative length of the proximal stem; reducing the number of basals and infralaterals to three; greatly expanding the infralateral and lateral plates in an ab-adoral direction; confining the rhombs to the infralateral and lateral circlets and aligning rhombs in the two circlets one above the other; raising the periproct to become relatively closer to the oral prominence; intercalating the radial and oral plates; and developing the brachioles on the radial, not the oral, plates. In all these respects we think *Rhombifera* was a highly derived glyptocystitoid, although the oral prominence with its small, isolated radial plates is probably paedomorphic.

RELATIONSHIPS TO OTHER BLASTOZOANS

Paul (2021, p. 53) suggested that *Rhombifera* was the closest sister group to the blastoids *s.l.*, which include the eublastoids, coronates and the Silurian genus *Lysocystites* Miller, 1889. Bauer et al. (2022) criticised the cladistic analysis that accompanied this suggestion. In addition, a new interpretation of the thecal plate

arrangement in hemicosmitoid rhombiferans became known while the original paper was in press (Paul & Toom, 2021). The new interpretation suggested that hemicosmitoid and glyptocystitoid rhombiferans shared homologous thecal plates but arranged in three circlets in the former and four in the latter. This interpretation implies that the dichopores forming the rhombs in both groups could also be homologous. Briefly, if the cladistic analysis were done now, several hemicosmitoid and glyptocystitoid characters would be coded in significantly different ways. Furthermore, the preceding description of the anatomy of the genus *Rhombifera* itself enables us to code characters for *Rhombifera*, such as the three basal and three infralateral plates, that were unknown or unconfirmed when the original analysis was undertaken. Altogether, it is appropriate to repeat the analysis in the light of all these facts.

A phylogenetic analysis was undertaken by one of us (BL) using PAUP (version 4.0a build 169). Paul's (2021) original analysis included 14 taxa to which we have added *Echinoencrinites* von Meyer, 1826, and *Cystoblastus* Volborth, 1867 (Tab. 2). All parsimony-based analyses were far more informative than all maximum likelihood analyses, so only those results are presented here. All parsimony analyses produced the same consensus topology (Fig. 9), but varied in tree length, number of equally parsimonious trees and standard indices. Separate analyses were run for the original hypotheses of plate homology presented in Paul (2021, tab. 2) where homologues of glyptocystitoid infralaterals were considered present in all blastoids *s.l.* (hypothesis A) and the revised plate homologies presented here in which infralaterals are considered absent in all blastoids (hypothesis B; Tab. 3, Fig. 10). Heuristic searches produced six equally parsimonious trees under hypothesis A of length 78 and consistency index of 0.667. Identical searches under Hypothesis B produced nine equally parsimonious trees of length 75 and consistency index of 0.667. We conclude that hypothesis B is preferable to the original hypothesis.

Table 2. Key genera discussed in the text and used in the phylogenetic analyses.

Higher taxon	Family	Genus	Age	Key Reference
'Out group'	Eocrinidae	<i>Akadocrinus</i>	Middle Cambrian	Nohejlová and Fatka (2016)
	Cambrocrinidae	<i>Cambrocrinus</i>	Upper Cambrian	Dzik and Orłowski (1993); Zamora (2012)
	unassigned	<i>Ridersia</i>	Upper Cambrian	Zamora et al. (2017)
	unassigned	<i>Sanducystis</i>	Upper Cambrian	Zamora et al. (2017)
Glyptocystitoids	Macrocystellidae	<i>Macrocystella</i>	Tremadocian	Paul (1984); Nardin et al. (2009)
	Echinoencrinitidae	<i>Echinoencrinites</i>	Floian-Dapingian	Bockelie (1981); Paul and Rozhnov (2016)
	Rhombiferidae	<i>Rhombifera</i>	Sandbian-Katian	This paper; Kesling (1962)
	Callocystitidae	<i>Lepadocystis</i>	Katian	Sumrall and Carlson (2000); Sumrall and Waters (2012)
Hemicosmitoids	Cystoblastidae	<i>Cystoblastus</i>	Darriwillian-Sandbian	Paul and Toom (2021)
	Caryocrinidae	<i>Caryocrinites</i>	Katian-Silurian	Frest (1975); Sprinkle (1975); Lanc et al. (2015)
	Hemicosmitidae	<i>Hemicosmites</i>	Darriwillian	Bockelie (1979); Sumrall and Waters (2012)
	Thomacystidae	<i>Thomacystis</i>	Katian	Paul (1984)
Blastoids <i>sensu lato</i>	Lysocystitidae	<i>Lysocystites</i>	Silurian Wenlock	Sprinkle (1973)
Coronates	Stephanocrinidae	<i>Stephanocrinus</i>	Katian-Silurian	Brett et al. (1983)
Eublastoids	unassigned	<i>Macurdablustus</i>	Katian	Broadhead (1984); Bauer et al. (2019)
	Codasteridae	<i>Codaster</i>	L Carboniferous	Breimer and Macurda (1972); Macurda (1983)

DISCUSSION

Table 3 summarizes the new interpretations of plate homologies since Paul (2021). Paul (2021, tab. 2, p. 48) suggested that the basal, infralateral, lateral and radial plate circlets of glyptocystitoid rhombiferans were homologous with the basal, radial, deltoid and lancet plates of blastoids, respectively. The orals (or periorals) of glyptocystitoids were thought to be homologous with the first ambulacral side plates of blastoids (Tab. 3A). Now that we know *Rhombifera* had only three

infralateral plates, the possibility that the transition from *Rhombifera* to blastoids involved the complete loss of the infralateral circlet needs to be considered (Tab. 3B). The basal which is lost between *Echinoencrinites* and *Rhombifera* is B4, which occupies the AB and BC interrays. In *Lysocystites*, coronates and most eublastoids the small basal is in the AB interray. Similarly, the ILL plates lost between *Echinoencrinites* and *Rhombifera* are IL4 and IL5, but under the original hypothesis the number was restored to five in blastoids *s.l.* So, one advantage of the new hypothesis is that

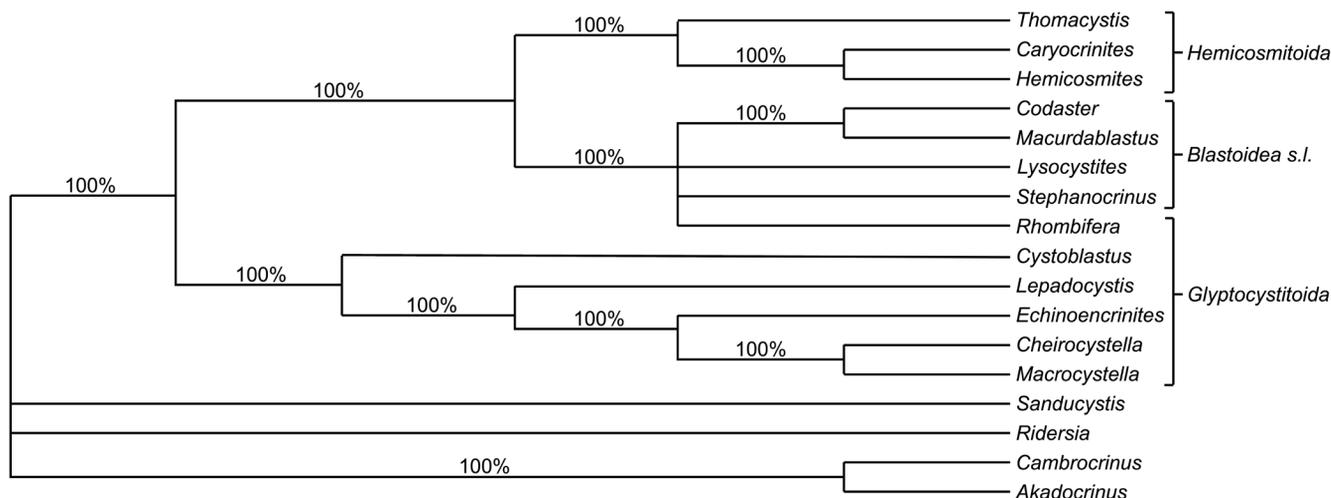


Figure 9. Cladogram derived from the two hypotheses that *Lysocystites*, coronates and eublastoids lack homologues of either the orals or the infralaterals of glyptocystitoids. See text for further explanation.

Table 3. Plate homologies in blastozoans with tetraserial ambulacra under the two hypotheses of plate homologies in blastoids *s.l.*

A Homologues with infralaterals present.

EAT	Circlets	Hemicosmitids	<i>Thomacystis</i> ¹	Glyptocystitoids	<i>Rhombifera</i> ²	<i>Lysocystites</i> ³	Coronates ⁴	Eublastoids
Axial		Brachioles	?	Brachioles	?	?	Brachioles	Brachioles
		Trunk plates	?	Floor plates	?	?	Brachiolar trunk	Side plates
Extraxial								
Perforate	5	?	Adorals (5)	Periorals (7)	Periorals (7)	?	?	?
	4	'Radials' (9)	----	Radials (4-6, 10)	R1-R4, R6	Ambulacrals (5)	Trunk mounting plates (5)	Lancets (5)
	3	L2-L5 + R1-R3, R5, R6	L2-L5 + R1, R3, R5, R6	L1-L5	L1-L5	Orals (5)	Deltoids (5)	Deltoids (5)
	2	IL1-IL5 + L1	IL1-IL5 + L1	IL1-IL5	IL1-IL3	Radials (5)	Radials (5)	Radials (5)
	1	Basals (4)	Basals (3)	B1-B4	B1-B3	Basals (3)	Basals (3)	Basals (3)
Imperforate		Stem	Stem	Stem	Stem	Stem	Stem	Stem

B Homologues with infralaterals absent.

EAT	Circlets	Hemicosmitids	<i>Thomacystis</i> ¹	Glyptocystitoids	<i>Rhombifera</i> ²	<i>Lysocystites</i> ³	Coronates ⁴	Eublastoids
Axial		Brachioles	?	Brachioles	?	?	Brachioles	Brachioles
		Trunk plates	?	Floor plates	?	?	Brachiolar trunk	Side plates
Extraxial								
Perforate	5	?	Adorals (5)	Periorals (7)	Periorals (7)	Orals (5)	Deltoids (5)	Deltoids (5)
	4	'Radials' (9)	---	Radials (4-6, 10)	R1-R4, R6	Ambulacrals (5)	Trunk mounting plates (5)	Lancets (5)
	3	L2-L5 + R1-R3, R5, R6	L2-L5 + R1, R3, R5, R6	L1-L5	L1-L5	Radials (5)	Radials (5)	Radials (5)
	2	IL1-IL5 + L1	IL1-IL5 + L1	IL1-IL5	IL1-IL3	Absent	Absent	Absent
	1	Basals (4)	Basals (3)	B1-B4	B1-B3	B1-B3	B1-B3	B1-B3
Imperforate		Stem	Stem	Stem	Stem	Stem	Stem	Stem

¹ Paul (1969), ² Herein, ³ Sprinkle (1973), ⁴ Brett, et al. (1983).

this loss of some IL plates followed by their restoration becomes unnecessary. In *Echinoencrinites* the lateral plates are interradial in position, whereas they are radial in position in *Rhombifera*. Under the original hypothesis they become interradial 'oral frame plates' in *Lysocystites*, coronates and eublastoids (Fig. 10). Thus, again the original hypothesis involves a reversal of position from interradial to radial and back again to interradial. This second evolutionary reversal is unnecessary under the new hypothesis. Another advantage of the new hypothesis is that in *Rhombifera* the radials are aligned with the laterals in small embayments that have the same topological relationship as the lancets do to the 'radials' of eublastoids. In *Rhombifera* the laterals are unusual in being positioned radially, so this requires a single change of the laterals from interradial in *Echinoencrinites* to radial in *Rhombifera*. There is no problem with the relationship of the basals to the plate circlet above. Blastoid basals remain basically interradial under this new hypothesis and alternate with the radially-positioned laterals (Fig. 10). The new hypothesis offers potential homologies between the individual basal plates of *Rhombifera* and those of blastoids *s.l.* If the infralateral circlet was lost entirely, the three basals would be forced to fit against the five lateral plates. The apex of B3 in *Rhombifera* is aligned with the junction between L3 and L4, which is in the AB interradius. Thus, under the new hypothesis, B3 of *Rhombifera* is homologous with the small basal, and B1 and B2 represent the two large basals, of blastoids *s.l.* (Fig. 10).

Equally, the new position of the laterals is consistent with the alternation of position seen in blastoids. Under the new hypothesis the radials of blastoids (=laterals of *Echinoencrinites*) alternate with the deltoids (=periorals of *Echinoencrinites*), as they do in *Rhombifera*. Thus, most of the changes required under the new hypothesis took place between *Echinoencrinites* and *Rhombifera*, including the reduction of the number of orals forming the mouth frame from six to five. The last can be explained equally well under both hypotheses. The new hypothesis means that the periorals now bear half the blastoid hydrospires, which is counter to the predictions of the Extraxial Axial Theory (EAT; Mooi & David, 1997), if orals are axial skeleton as suggested by Paul (2021, p. 46). Thus, although the new hypothesis explains several unique features of *Rhombifera*, it may create new difficulties in the homology of the deltoids of blastoids.

In glyptocystitoids with open plate circlets pectinirhombos never develop between plates of originally non-adjacent circlets, *i.e.*, across B:L, IL:R or L:O sutures. In eublastoids and coronates the pore structures are always across originally non-adjacent plates at the L:O sutures under hypothesis B. This raises two potential difficulties; the presence of pore structures across non-adjacent plates and the presence of pores in oral plates which were previously thought to be axial skeleton under the EAT. All hemicosmitoids have cryptorhombos

across plates of non-adjacent circlets. Plate L1 lies in the infralateral circlet so the B1:L1 cryptorhomb is 'non-adjacent'. Similarly, the IL1:R1, IL2:R2 and IL3:R3 cryptorhombos are 'non-adjacent'. So, presence of 'non-adjacent' pore structures is not confined to the eublastoids and coronates among the Dichoporita.

Paul (2021, p. 46) argued that in dichoporites with branched ambulacra the brachioles always arose from a pair of flooring or main trunk plates. He interpreted the flooring and main trunk plates as the first two modified brachiolar plates. The very first brachiole in each ambulacrum arose from a facet shared by an oral plate and another plate that Sumrall and Waters (2012, fig. 1) labelled 'L' plates. Extending this logic about flooring plates, Paul (2021) suggested that the oral and L plates were also modified first brachiolar plates and by extension axial skeleton under the EAT. Now, with pore structures developed in homologues of dichoporite orals, *i.e.*, the deltoids of blastoids and coronates, it seems much more likely that these plates are part of the perforate extraxial skeleton under the EAT. This is compatible with the fact that blastoids have from 1-7 posterior deltoids since extraxial skeletal plates may develop anywhere under the EAT. It also brings the deltoids into line with the orals of ambulacralian diploporites, which always bear diplopores, but never bear brachioles. So, we also amend the interpretation of dichoporite oral plates as being part of the perforate extraxial skeleton. This is in line with the fact that the posterior orals are usually associated with fundamental orifices, such as the hydropore and gonopore which are also characteristic of the perforate extraxial skeleton under the EAT.

Rhombifera has lost B4, IL4 and IL5 compared with *Echinoencrinites*. All the plates lost in *Rhombifera* are posterior and the periproct has moved up the theca to the top of the radial circlet. Thus, the movement of the periproct and hind gut may be associated with the plate loss. Blastoids appear to have inherited three more or less equal basals. Álvarez-Armada *et al.* (2023) described the gut of the blastoid *Hyperblastus reimani* (Kier, 1952), which scarcely extends below the level of the hydrospires. This observation is consistent with idea that in the transition from *Rhombifera* to blastoids *s.l.*, all the remaining infralateral plates were lost.

When one considers the position of the basals in blastoids, the small basal usually lies in the AB interradius. In *Echinoencrinites*, the single large basal, occupies the AB and BC interradial. Thus, positional arguments make it difficult to homologize the individual basal plates between typical blastoids *s.l.* and all glyptocystitoids other than *Rhombifera*. The single small basal of blastoids *s.l.* corresponds to half the single large basal of glyptocystitoids. However, if *Rhombifera* is an intermediate between glyptocystitoids and blastoids, it lost the single large basal before the blastoids evolved. With five 'radial' plates in the circlet above the three basals, it is a geometric necessity to have two large and one small

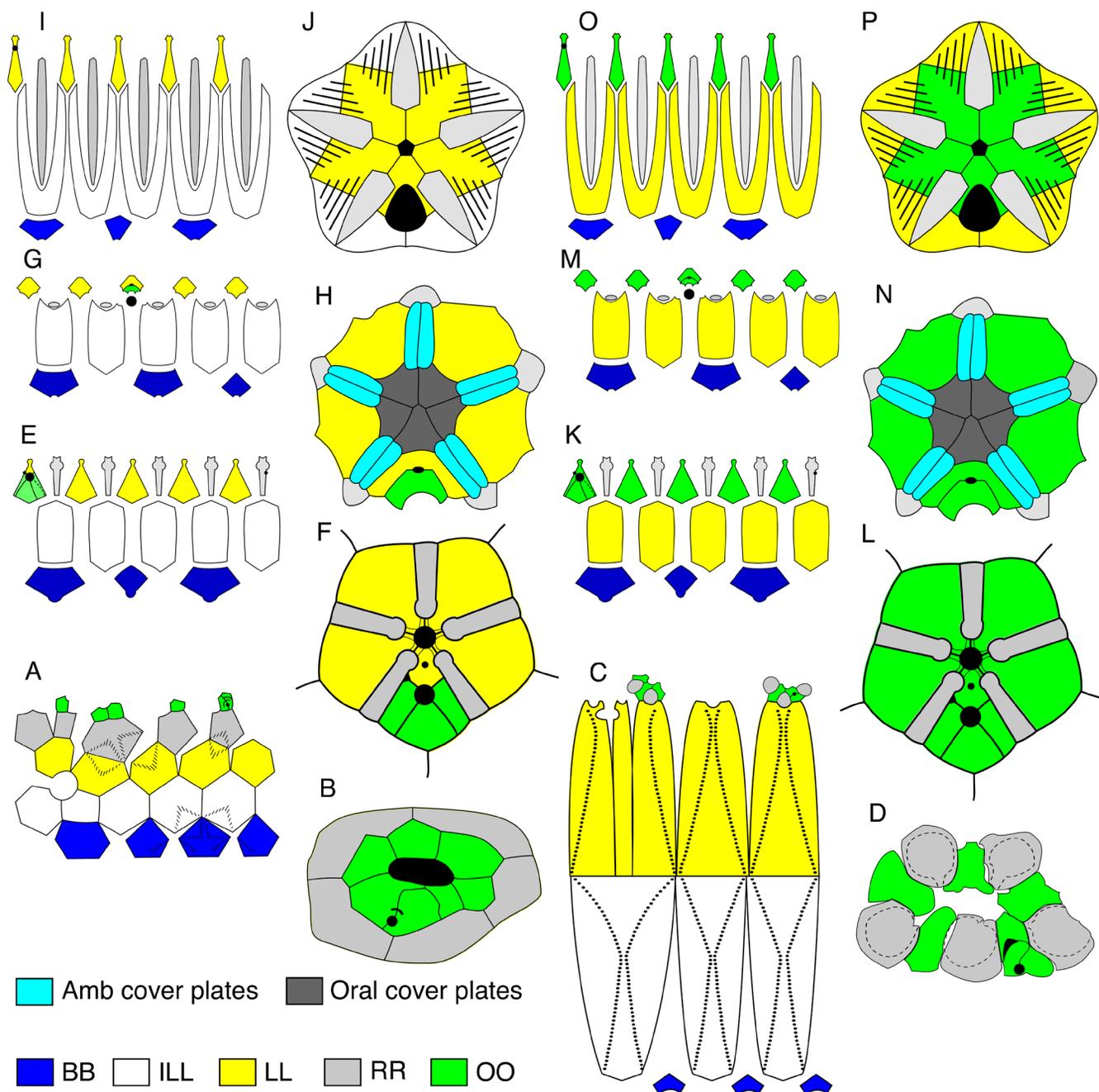


Figure 10. Plate diagrams illustrating the two hypotheses that *Lysocystites*, coronates and eublastoids lack homologues of either the orals (hypothesis A, E–J) or the infralaterals (hypothesis B, K–P) of glyptocystitoids. Evolution is thought to have gone from *Echinoencrinites* (A, B) to *Rhombifera* (C, D) and then to *Lysocystites* (E, F, K, L), coronates (G, H, M, N) and eublastoids (I, J, O, P). A–B, oral and lateral views of *Echinoencrinites* von Meyer, 1826; C–D, oral and lateral views of *Rhombifera* Barrande, 1867; E–F, K–L, oral and lateral views of *Lysocystites* Miller, 1889; G, H, M, N, oral and lateral views of *Stephanocrinus* Conrad, 1842; I and O, lateral views of a generalized eublastoid. J and P, oral views of the fissiculate eublastoid *Codaster* McCoy, 1849. Key, Amb ambulacral; BB basal plates, ILL infralateral plates, LL lateral plates, RR radial plates, OO oral plates. Primary orifices (mouth, anus, gonopore and hydropore) black. A redrawn from Kesling (1968, fig. 89.2b, p. S185); B redrawn from Bockelie (1981, fig. 2a, p. 80); E and K redrawn from Sprinkle (1973, figs. 34–35); F and L redrawn from Paul (2021, fig. 20B, p. 54; pp. 140–14); G and M redrawn from Paul (2021, fig. 12, p. 49); H and N redrawn from Brett et al. (1983, fig. 4A, p. 638).

basal plate in blastostoids (Paul, *in press*). In coronates, such as *Stephanocrinus*, and many blastostoids, the origins of the basal plates are equally spaced about the stem. In *Stephanocrinus* the origins form the corners of an equilateral triangle and the basal:basal sutures lie midway along the sides of the triangle.

There is nothing to suggest that the larger basal plates (zygous or paired basals) are two plates fused together. It seems likely therefore, that the occurrence of the so-called ‘azygous’ or small basal in the AB interradius of blastostoids is a consequence of the loss of the large glyptocystitoid basal (B4) in *Rhombifera*.

We conclude that the newly suggested homologies between the plate circlets of glyptocystitoids and blastoids *s.l.* (Tab. 3B) are an improvement on the original hypothesis. Basals are the same in both, those of *Rhombifera* and blastoids *s.l.* being B1, B2 and B3. Infralaterals of glyptocystitoids are entirely lost in blastoids *s.l.* Laterals of glyptocystitoids equate to radials of blastoids *s.l.* Radials R1-R4 and R6, of glyptocystitoids equate to the lancet plates of blastoids and trunk mounting plates of coronates. Finally, the orals of glyptocystitoids are homologous with blastoid deltoids and both are part of the perforate extraxial skeleton under the EAT.

CONCLUDING REMARKS

Detailed examination of available material of the blastozoan genus *Rhombifera* Barrande resulted in a refined definition of its morphology with significant consequences for its phylogenetic relationships. *Rhombifera* had three basals and three infralaterals, plus five, radially-positioned laterals and five, facet-bearing radials nested in the adoral edges of the laterals. These are unique characters among glyptocystitoid rhombiferans, but confirm the suggested relationship between glyptocystitoid rhombiferans and blastoids *s.l.* The newly confirmed characters suggested two alternative hypotheses about plate homologies which have been evaluated by cladistic analysis. Under either hypothesis, most of the significant morphological changes took place between *Rhombifera* and its ancestors rather than between *Rhombifera* and supposed descendants. The favoured new interpretation of plate homologies between glyptocystitoids and blastoids suggests that interradial orals (periorals of Paul, 1971, 1973) are part of the perforate extraxial skeleton of blastozoans. The interradial ‘deltoids’ of blastoids, five of which form the mouth frame and are therefore homologous with periorals, also bear the adoral halves of blastoid hydrospires. Previously (Paul, 2021, p. 46), it had been suggested that periorals of glyptocystitoids were the first ambulacral plates and therefore part of the axial skeleton.

Supplementary information. The nomenclatural acts contained in this paper have been registered with ZooBank, the online registration system for the ICZN: Nexus files are available as supplementary information.

Author contributions. CRCP conceived and coordinated the project; BL, MN and SZ provided the evidence to support it in the form of latexes of specimens preserved in museums in their respective countries, and relevant accompanying data. Photographs were taken by MN in Prague except those in Figures 3, and 8 where we used originals taken by SZ and J-C Gutiérrez-Marco, respectively. BL produced the stratigraphic summary (Fig. 2) and undertook the cladistic analysis. CRCP produced the other line diagrams. We all contributed to the text and approve the final version of the manuscript.

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Author details. Christopher R. C. Paul¹, Bertrand Lefebvre², Martina Nohejlová³, & Samuel Zamora^{4,5}. ¹School of Earth Sciences, University of Bristol, Life Sciences Building, 24 Tyndall Avenue, Bristol, BS8 1TQ Bristol, UK; glcrp@bristol.ac.uk; ²Université Claude Bernard Lyon 1, ENSL, CNRS, LGL-TPE, F-69622 Villeurbanne, France; bertrand.lefebvre@univ-lyon1.fr; ³Czech Geological Survey, Klárov 3, Praha 1, 118 21 Czech Republic; martina.nohejlova@geology.cz; ⁴Instituto Geológico y Minero de España (IGME-CSIC), Residencia CSIC, Campus Aula Dei, Av. Montañana 1005, 50059 Zaragoza, Spain; ⁵Grupo Aragosaurus-IUCA, Área de Paleontología, Facultad de Ciencias, Universidad de Zaragoza, 50009 Zaragoza; Spain, s.zamora@igme.es.

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