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AN INTERPRETATION OF *RHOMBIFERA BOHEMICA* BARRANDE, 1867, AN UNUSUAL HYDROPHORIDEAN CYSTOID

BY

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CONTENTS

INTRODUCTION

THE ORDOVICIAN SPECIES from Bohemia described by Barrande in 1867 as *Rhombifera bohemica* has been considered, at various times, to be a conularid, a cystoid, and a crinoid. The uncertainty about its taxonomic position can be attributed both to its unusual shape and to the preservation of specimens.

Without doubt, *Rhombifera* was one of the most bizarre cystoids ever to evolve. It presented the ultimate in unstable construction. Each side of the long quadrate spindle had at least one full-length suture, the equator was formed of five horizontal sutures nearly in a plane, and, on three of the sides, the thin thecal walls were perforated by closely spaced pores of two extremely large rhombs, one above the other. Little wonder, then, that no complete specimen has yet been discovered. In some, the adoral and aboral halves broke apart along the equatorial sutures. In most, the separated half collapsed, displaying scarcely more rigidity than an open cardboard prism. With any subsequent distortion, the thecal walls tore along the lines formed by the pores of the rhombs. As if these factors were not enough to obliterate the original form, nearly all specimens are preserved as internal molds, only a few retaining vestiges of the thin walls.

On March 27, 1962, Professor G. Ubaghs of the Laboratoire de Paléontologie Animale, Université de Liège, graciously sent me three latex casts of *Rhombifera bohemica* which he made some years ago of specimens in the Barrande-de Verneuil collection in the Geological Department of the University of Paris. Because the status of *Rhombifera* must be decided for the forthcoming Volume S of the *Treatise on Invertebrate Paleontology,* which

concerns the hydrophorideans, carpoids, eocrinoids, paracrinoids, edrioasteroids, edrioblastoids, and blastoids, I was particularly delighted by Professor Ubagh's perspicacity in recognizing the significance of the specimens, his care and technique in preparing the excellent casts, and his generosity in offering them to me for study.

Two of the casts were made of a specimen with exceptional preservation. The fossil consisted of the external mold of the adoral half of a collapsed theca, into which fitted part of the steinkern. One latex cast was made with the part of the steinkern removed; it shows the form of the external surface of the thecal half on one side. The other latex cast, poured with the piece of steinkern in place, reveals the form of the inner surface of the opposite side. Both casts show the ring of small plates around the peristome. Thus, although the specimen was incomplete and crushed, the two casts demonstrate the features of both sides and their relationships. From the study of the casts, which are illustrated in Plate I, the adoral half of *Rhombifera bohemica* can be reconstructed with considerable assurance.

The third cast is a mold of the steinkern of one side of the aboral half of another specimen. The illustrations published by Barrande in 1867 and 1887 and by Jaekel in 1899 also add to the knowledge of this part of the theca. The observations of form and structure in the aboral half must be accommodated and harmonized with those in the adoral half. Some guidance is available from the rare specimens having conjoined parts of both halves, as illustrated by Barrande.

The reconstruction presented here is a consistent attempt to interpret and incorporate all information known on *Rhombifera bohemica* at this time. Probably, when better specimens are found, some modifications will be required. For the present, however, it can be shown that the rhomb-shaped structures are true pore rhombs, thus proving that the genus *Rhombifera* Barrande, 1867, is a hydrophoridean cystoid of the order Rhombifera Zittel, 1879. Hence, through coincidence, the genus is in the order of the same name.

Again, my thanks to Professor Ubaghs for permission to study these enlightening casts.

PREVIOUS WORK

In 1867 (pp. 175–79, Pl. 11, Figs. 1–13), Barrande described and illustrated *Rhombifera* at the end of a volume on pteropods in the appendix entitled "Fossiles divers." By monotypy, *R. bohemica* became the type species. Barrande expressed some doubt about the taxonomic affinities of *Rhombifera* and compared it with echinoderms as well as pteropods.

Twenty years later (1887, pp. 175–78, Pl. 6, Figs. 1–21), Barrande again considered *Rhombifera bohemica*. He began his discussion (p. 175) with:

> 1867. Nous avons associé provisoirement à la classe des Ptéropodes les fossiles auxquels nous conservons le nom de *Rhombifera*. Cette association était une erreur grave.

After this apology for his earlier classification, Barrande explained his reasons for assigning the genus to the cystoids. He directed attention to the three pore rhombs in each of the oral and aboral halves. Because most of his specimens retained no vestiges of the thecal walls, he expressed some doubt about the suture lines. He oriented the specimens in an inverted position, since he was convinced that the peristomial region represented the junction of stem and theca. Although one of his specimens was shown (1887, Pl. 6, Figs. 4–5) to have a quadrate shape in oral view, Barrande thought this was a product of distortion and described the theca as triangular pyramids.

Jaekel (1899, pp. 340–42, Pl. 10, Fig. 8) offered some observations on *Rhombifera bohemica* and presented reconstructions of the theca and a cross section in the oral half. He correctly determined that the theca was four-sided, although his reconstruction incorrectly showed parts of pore rhombs extending around a corner onto another face of the theca. Jaekel studied molds of specimens in arriving at his interpretation. He stated (1899, p. 341):

> Dadurch, dass mir Herr Prof. Ant. Fritsch in Prag freundlichst gestattete, Abgüsse der Steinkern und Hohldrucke zu machen, die Barrande von der Theca dieser Gattung vorlagen, glaube ich ein klareres Bild von der Gesammtform derselben erlangt zu haben.

It is noteworthy that Jaekel placed *Rhombifera* in the Dichoporita, his category corresponding to the order Rhombifera of the hydrophoridean cystoids. He said (1899, p. 340) that he originally intended to name the family including *Rhombifera* and *Tiaracrinus* Schultze the Rhombiferidae, but decided to name it Tetracystidae instead because of possible confusion with his use of Rhombiferae for all rhombiferan cystoids. As a result of this decision, Jaekel's family Tetracystidae is not based on any genus, and must be rejected.

Bather (1900, p. 57) classified *Rhombifera* as a cystoid in the family Tiaracrinidae. His description strongly influenced the understanding of the genus up to the present time:

> Theca elongate, triangular in section; appears composed of two circlets—a lower, of three plates united by strong stereom-folds, visible exteriorly only as terminal pores outlining "pore-rhombs"; an upper, of six (?) plates, of which three pairs are united by pore-rhombs, similar to those of the lower circlet, and vertically above, not alternating with them. Oral region unknown. Aboral region passes gradually, by smaller plates, into a cylindrical stem.

Bather followed Barrande's interpretation regarding shape in cross section and oral-aboral orientation.

In 1918 (p. 99), Jaekel again put *Rhombifera* in his subclass Dichoporita (= Rhombifera) and created a special order, Tetracystida, to accomodate it. To the order, he also assigned *Tiaracrinus* Schultze, with question. He diagnosed the Tetracystida as stemmed dichoporites (rhombiferans) with four-sided thecae, a few large, regular plates and pore rhombs, and a reduced number of brachioles concentrated around the mouth.

In 1938 (p. 15), Bassler assigned *Rhombifera* to the crinoids. He was aware that the species described by Barande (1887, p. 80) as *Rhombifera? mira* was, in 1900, referred by Bather (p. 145) to the genus *Stephanocrinus,* and, in 1918, selected by Jaekel (p. 110) as the type species of his new genus *Stephanoblastus*. Jaekel (1918, p. 110) assigned both *Stephanoblastus* and *Stephanocrinus* Conrad to the family Stephanoblastidae of his order Coronata in the blastoids. Bassler (1938, pp. 15, 174, 175) placed the two genera in the family Stephanocrinidae in the Inadunata Larviformia. Since he did not explain his reasons for the classification, it is not possible to say whether or not Bassler was strongly impressed by the fact that the type species of *Stephanoblastus* and *Rhombifera* were both originally described in the same genus. There seems no other logical reason, however, for classifying *Rhombifera* as a crinoid.

It seems significant that Moore and Laudon (1943) did not include *Rhombifera* in their comprehensive study of Paleozoic crinoids. In the same year, however, Bassler and Moodey (1943, p. 667) followed Bassler's earlier classification, and placed *Rhombifera* in the family "Stephanocrinidae (Inadunata-Larviformia)."

The latest disposition of *Rhombifera* is by Fay, who in March, 1962, proposed that the Coronata should be made a new order of Crinoidea. To the Coronata, Fay relegated *Mespilocystites* Barrande, 1887, *Paracystis* Sjöberg, 1915, *Rhombifera* Barrande, 1867, *Stephanoblastus* Jaekel, 1918, *Stephanocrinus* Conrad, 1842, and *Tormoblastus* Jaekel, 1927. He discussed the morphology of only one species, *Stephanocrinus angulatus* Conrad, and apparently presumed that all other echinoderms assigned to the genera in his list were similarly constructed. He stated (1962, p. 206) that the common characters of the genera he included in the Coronata were:

> All have three basal plates, with the azygous one in the right anterior interradial position, five radials and five interradials that extend into coronal processes, and an anal opening on the adoral side of the coronal process at the junction of two adjacent radial limbs with the anal interradial. High ridges, in the form of pore-rhombs, extend at right angles to the sutures on the sides of the calyx, giving the appearance of a pore-rhomb cystoid. These ridges are superficial and are not extended in depth.

Of these characters, the only two that I can verify for *Rhombifera* are the

presence of five radials and ridges at right angles to the sutures. As demonstrated below, the rhombic areas constitute true pore rhombs, the theca does not include five plates that qualify as true interradials, and no coronal processes are developed.

DESCRIPTION

Class CYSTOIDEA Buch
Subclass HYDROPHORIDEA Zittel
Order RHOMBIFERA Zittel, 1879
Superfamily Glyptocystitida Bather, 1900

Rhombiferidae, fam. nov.

Type genus.—*Rhombifera* Barrande, 1867.

Description.—Rhombiferan cystoids with the theca elongate and consisting of five *OO,* five *RR,* five *LL,* at least four *ILL* (presumably five), and presumably four *BB.* Rhombs developed only between *ILL* and between *LL. RR* reduced to small plates, alternating with *OO* and with them forming a slightly elevated ring around the peristome. Brachioles erect, attached to facets on the *RR.*

Remarks.—The necessity for creating this new family is explained below under "Interpretation." At present, only the type genus is known. Its age is Upper Ordovician.

Genus *Rhombifera* Barrande, 1867
Type species.—*Rhombifera bohemica* Barrande, by monotypy.
Rhombifera bohemica Barrande, 1867

(Figs. 1–2; Pl. I, Figs. 1–2; Pl. II, Figs. 1–7)

The following description is based on the three latex casts sent by Professor Ubaghs and on published descriptions and illustrations.

Shape.—Theca unusually elongate, bipyramidal with the adoral and aboral halves shaped like high, square, truncated pyramids attached base-to-base. Each face of the two pyramids somewhat convex. Ring of *OO* and *RR* slightly elevated at the peristome. Periproct directed upward, with its aboral side extended outward and its adoral side inward.

The shape of the adoral half of the theca can be deciphered from the two casts illustrated in Plate I. The association with the aboral half was shown by Barrande in 1867 (Pl. 11, Fig. 5; see Pl. II, Fig. 4 in this paper) and in 1887 (Pl. 6, Fig. 21; see Pl. II, Fig. 5 in this paper). Internal molds of several aboral halves were shown by Barrande in other illustrations.

Thecal plates.—*BB* unknown. However, the aboral edges of IL_1 and

IL_2 diverge as an obtuse angle (Pl. II, Fig. 2), indicating that the plate below was probably a B_2 with its apex at the juncture of the two *ILL*. The markings on a steinkern illustrated by Barrande (1887, Pl. 6, Fig. 15) support this interpretation. Presumably, the *BB* were the least modified of all thecal plates (Fig. 1).

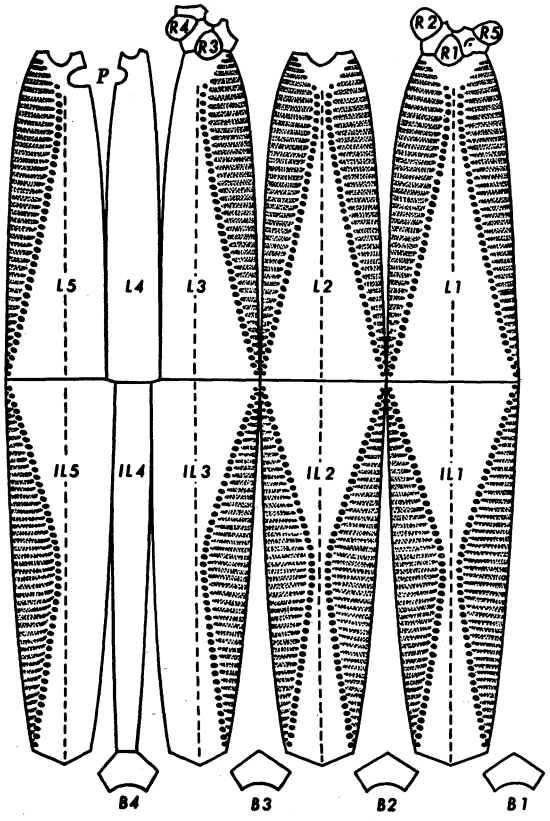

FIG. 1. *Rhombifera bohemica* Barrande. Reconstructed plate diagram, x 2. Dashed lines represent angulations or bends of the theca. Spacing of pores not exact.

Four *ILL* known from steinkerns described by Barrande (1867, pp. 175–79; 1887, pp. 175–78). 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 four known plates bear three full rhombs, IL_1/IL_2, IL_2/IL_3, and IL_1/IL_5. Each plate shaped like a high trapezoid, except for the aboral side, which is obtusely acuminate instead of straight; plate provided with a longitudinal angulation or bend, which forms an edge of the bipyramidal theca. IL_1 and IL_2 identical, each bilater-

ally symmetrical, with the longitudinal bend through the middle and a half-rhomb along each side (Fig. 1; Pl. II, Fig. 2). IL_3 a mirror image of IL_5; in IL_3 the longitudinal bend to the left of center and the half-rhomb along the right side, whereas in IL_5 the bend offset to the right and the half-rhomb along the left side (Fig. 1). I suppose that IL_4 is a narrow plate between IL_3 and IL_5, lacking both angulation and pore rhombs, as reconstructed by Jaekel.

Five *LL*, forming a high truncated pyramid that is bilaterally symmetrical except for the periproct, with the plane of symmetry between L_1 and L_2 and through the middle of L_4. Each of the four corners or angles of the *LL* pyramid beveled at the top to form shoulders (Pl. I, Figs. 1–2), so that the *LL* fit against the ring of *RR* and *OO* (Fig. 2). Unlike the arrangement in any other hydrophoridean, the *LL* set immediately above the corresponding *ILL* instead of alternating with them (Fig. 1). L_1 and L_2 identical, each bilaterally symmetrical, with the longitudinal bend through the middle and a half-demirhomb on each side. L_3 a mirror image of L_5, except

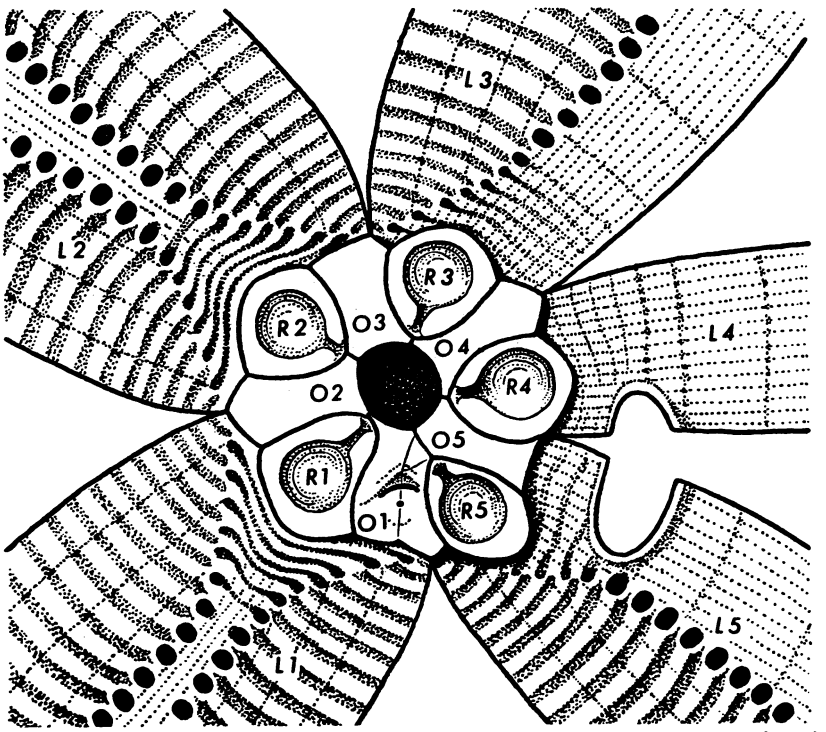

FIG. 2. *Rhombifera bohemica* Barrande. Reconstructed plate diagram of peristome region, x 8. Spacing of pores not exact.

for the indentation in L_5 to accommodate most of the periproct; in L_3 the longitudinal bend left of center and the half-demirhomb along the right side, but in L_5 the longitudinal bend right of center and the half-demirhomb along the left side (Fig. 1; Pl. I, Figs. 1–2; Pl. II, Figs. 1, 3). L_4 narrow, without longitudinal bend or pore rhombs (Pl. I, Fig. 2), with an indentation near the adoral end to accommodate part of the periproct (Fig. 2; Pl. II, Fig. 3). Thus, the demirhombs of the *LL* are set immediately above and in line with the full rhombs of the *ILL*, so that the *LL* and *ILL* circlets are nearly symmetrical with respect to the equatorial plane of the theca (Fig. 1).

RR small, suboval, inserted between *OO* to form a ring around the mouth. Each *R* apparently separated from the mouth by small lateral projections of the adjacent two *OO* (Fig. 2; Pl. II, Fig. 1). Each *R* provided with a subcircular concavity, apparently a facet for attachment of an erect brachiole, with a short V-shaped groove leading to the mouth (Fig. 2; Pl. II, Fig. 1). Probably, a few small ambulacral covering plates roofed over each of the five grooves and adjoined the peristomial covering plates, so that the food grooves were like those of other rhombiferans.

OO small, radially elongate, their adoral margins with lateral projections extending to those of adjacent *OO*, the rest of their extent alternating with the *RR* to form a slightly raised peristomial ring (Fig. 2; Pl. II, Fig. 1). Hence, *OO* forming a circlet only in their adoral parts. O_1 apparently tripartite as in many other rhombiferans, bearing a distinct hydropore surmounted adorally by a chevron-shaped ridge (Fig. 2; Pl. II, Fig. 1). Probably, the small indentation below the hydropore is the gonopore, although it is not distinct (Pl. II, Fig. 1). Aborally, O_1 bordered by L_1 and L_5, O_2 by L_1 and L_2, and O_3 by L_2 and L_3; from the disposition of other *LL* and *OO* indicated in one of the latex casts (Pl. I, Fig. 2), one may judge that O_4 probably is bordered by L_3 and L_4 and that O_5 is bordered by L_5 only.

Ornamentation.—The exterior of *BB* and *ILL* unknown. *LL* longitudinally striate with closely spaced striae (4.8 per mm). Growth lines extend horizontally across the striate area of each plate and vertically through the areas within the demirhombs, revealing rather clearly the successive outlines of the plate (Pl. I, Fig. 1). Areas within demirhombs corrugated, with ridges from one side to the other connecting corresponding pores (Pl. I, Fig. 1). Shoulders of each *L* bearing deep grooves more or less concentric to the ring of *RR* and *OO*; each deep groove terminating in a pit, with the pits in curved lines leading to the pores of the demirhomb (Fig. 2). Most of the deep grooves on the shoulders seem to be growth lines, but a few of

them do not appear to be continuous with any lines in the adjacent demirhomb areas (Pl. I, Fig. 1).

Except for the concavities presumed to be brachiole facets in the *RR*, all *RR* and *OO* smooth.

Pore rhombs.—Six large rhombs. Three full rhombs along vertical sutures between *ILL*: IL_1/IL_5, IL_1/IL_2, and IL_2/IL_3. These rhombs known only from steinkerns, which, however, show the spacing of the pores, the relative thinness of the intrarhomb areas, and the structure on the inner surface of the rhomb-bearing plates.

Three demirhombs along vertical sutures between *LL*: L_1/L_5, L_1/L_2, and L_2/L_3 (Pl. II, Figs. 4–6). These set immediately above the full rhombs between corresponding *ILL* (Pl. II, Figs. 4–5). Exterior of intrarhomb area (Pl. I, Fig. 1) corrugated with ridges between corresponding pores on the two facing plates (Fig. 2). Intrarhomb area about half as thick as remainder of plate, very similar to the area in *Lepadocystis moorei* (Meek), another Upper Ordovician rhombiferan (Kesling and Mintz, 1961, p. 133, Pl. 5, Fig. 1). Interior surface of demirhomb (Pl. I, Fig. 2) like that of full rhomb below (Pl. II, Fig. 2): ridges linking pairs of pores, with each ridge bearing a thin groove along its middle, the ridges separated by rather broad, flat-bottomed grooves (Pl. I, Fig. 2).

Spacing of pores nearly the same in both *ILL* and *LL* pore rhombs: about 0.35 mm between centers. In an IL_1/IL_2 rhomb (Pl. II, Fig. 2) 60 pores occur in the 20.7 mm length of the rhomb. In an L_1/L_2 demirhomb (Pl. I, Fig. 1) 47 pores occur in the 16.5 mm length. At its greatest width, each of the *ILL* full rhombs (Pl. II, Fig. 2) and each of the *LL* demirhombs (Pl. I,Fig. 1) nearly as broad as the thecal face.

INTERPRETATION

The presence of thecal pores (Pl. I, Fig. 1) identifies *Rhombifera* as a hydrophoridean cystoid. These pores are arranged in rhombs, with unit pores extending across sutures (Pl. I, Fig. 2), so that the genus *Rhombifera* belongs in the order Rhombifera Zittel, 1879.

The thecal plates include five *LL*, five *RR*, and five *OO*. Four *ILL* are known; and should the IL_4 lie immediately below L_4, as the other *ILL* plates lie below the corresponding *LL*, then *Rhombifera* has five *ILL*. This was the arrangement indicated in Jaekel's reconstruction (1899, Pl. 10, Fig. 8), although the specific source of his information was not given. As for the *BB*, no plates in this series have been found. However, the aboral edges of L_1 and L_2 diverge (Pl. II, Fig. 2), so that the apex of a basal plate must have fitted in the indentation. By analogy with other rhombiferans,

this plate should have been B_2. One of the illustrations of Barrande (1887, Pl. 6, Fig. 11) shows a steinkern with a marking that may well represent the oral edge of a basal; it is copied here as Plate II, Figure 5. Briefly, there is no reason to doubt that *Rhombifera bohemica* had the basic twenty-four plates characteristic of the superfamily Glyptocystitida Bather, 1900.

Within the Glyptocystitida, *Rhombifera* can be readily excluded from the families Pleurocystitidae Jaekel, 1899, Cheirocrinidae Jaekel, 1899, and Glyptocystitidae Bather, 1900, by the small size of its periproct (Pl. I, Fig. 1; Pl. II, Figs. 1, 3). It can be distinguished from the family Cystoblastidae Jaekel, 1899, which has a bud-shaped theca, long demirhombs between *RR* and *LL*, and petal-like recumbent ambulacra. *Rhombifera* can also be readily separated from the family Callocystitidae Bernard, 1893, characterized by long ambulacra which are recumbent and extend far down over the theca. It finds its closest affinities, perhaps, in the family Echinoencrinitidae Bather, 1900, but it clearly lacks the large *RR*, ovate to subglobular theca, and produced periproct typical of that family. Hence, even apart from its unique shape and alignment of *ILL* and *LL*, *Rhombifera* cannot fit into any of the extending families in the superfamily Glyptocystitida. The only recourse is to make it the type of a new family, the Rhombiferidae.

The Rhombiferidae is characterized, as stated above, by reduction of the *RR* to small plates inserted in a peristomial ring, pore rhombs present only between *ILL* and between *LL*, brachioles erect and clustered around the peristome, and elongate theca. Unless, and until, additional species of *Rhombifera* or other related undescribed cystoids are discovered, this will serve as a basis on which the Rhombiferidae can be compared with other families. Inasmuch as *Rhombifera* is the only genus known, the line between familial and generic characters must be drawn upon arbitrary grounds. Nevertheless, it may be presumed that the familial description should refer only to features that are diagnostic in other families in the superfamily or which appear to be limited to the Rhombiferidae.

Under generic characters should be included the unique vertical alignment of *ILL* and *LL* and the bipyramidal shape of the theca. One may presume that, as in other cystoids, such features as ornamentation of theca, proportions of plates, and spacing of pores should be relegated to the specific level.

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PLATES

EXPLANATION OF PLATE I

(Both figures x 4)

Rhombifera bohemica Barrande

FIGS. 1–2. Stereograms of two latex casts made of the same specimen. Figure 1, a cast showing the exterior surface, made from the external mold; view centered on L_1. Figure 2, a cast showing the inner surface of the opposite side, made from the external mold with part of the steinkern in place; view centered on L_3; the dent in the adoral part of L_1 is a defect in the cast. In both figures, the ring formed around the mouth by *OO* and *RR* is distinctly shown at the top, and the periproct at the upper right. Original specimen in the Barrande-de Verneuil collection in the Geological Department of the University of Paris. Casts prepared by Professor G. Ubaghs.

PLATE I

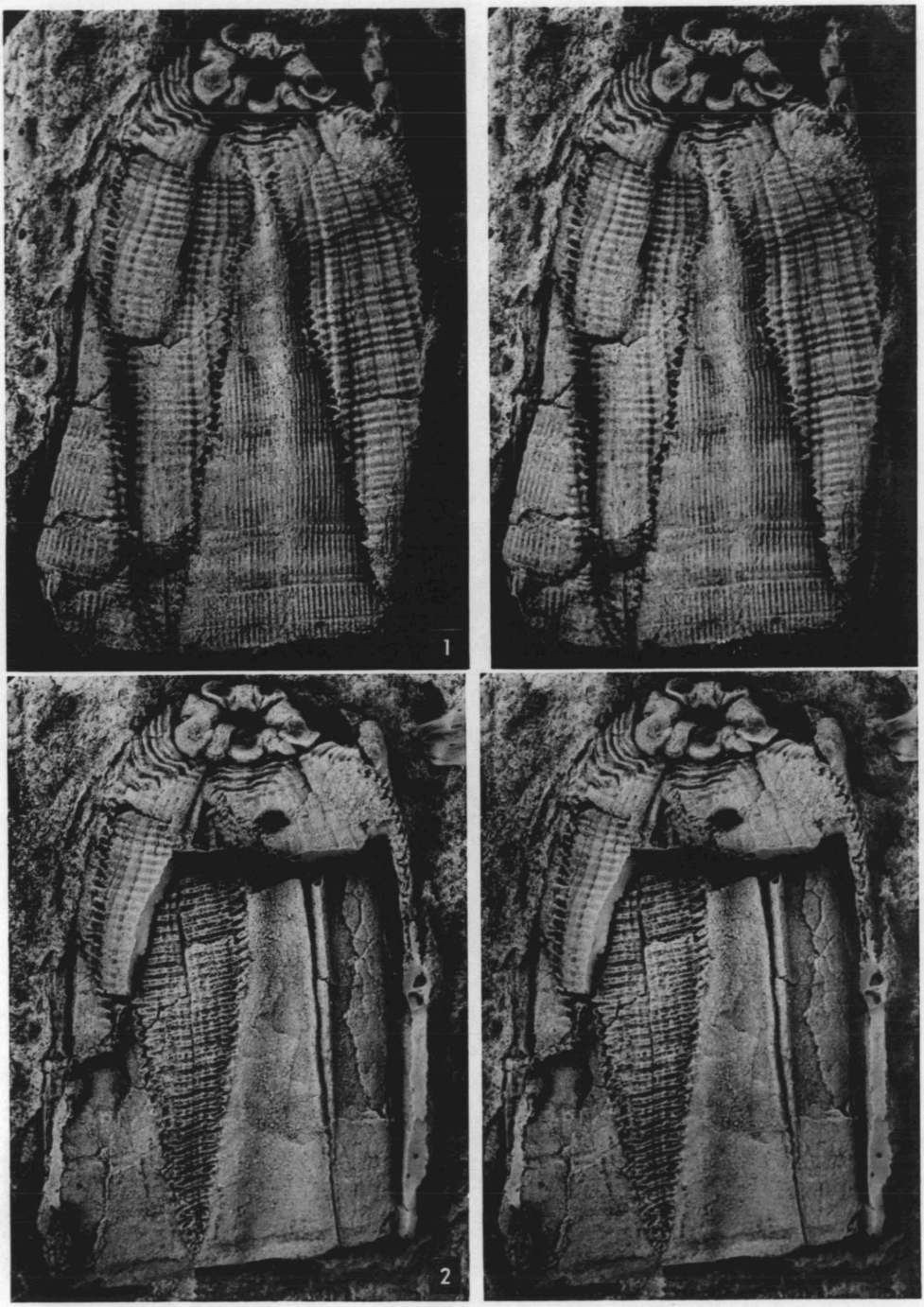
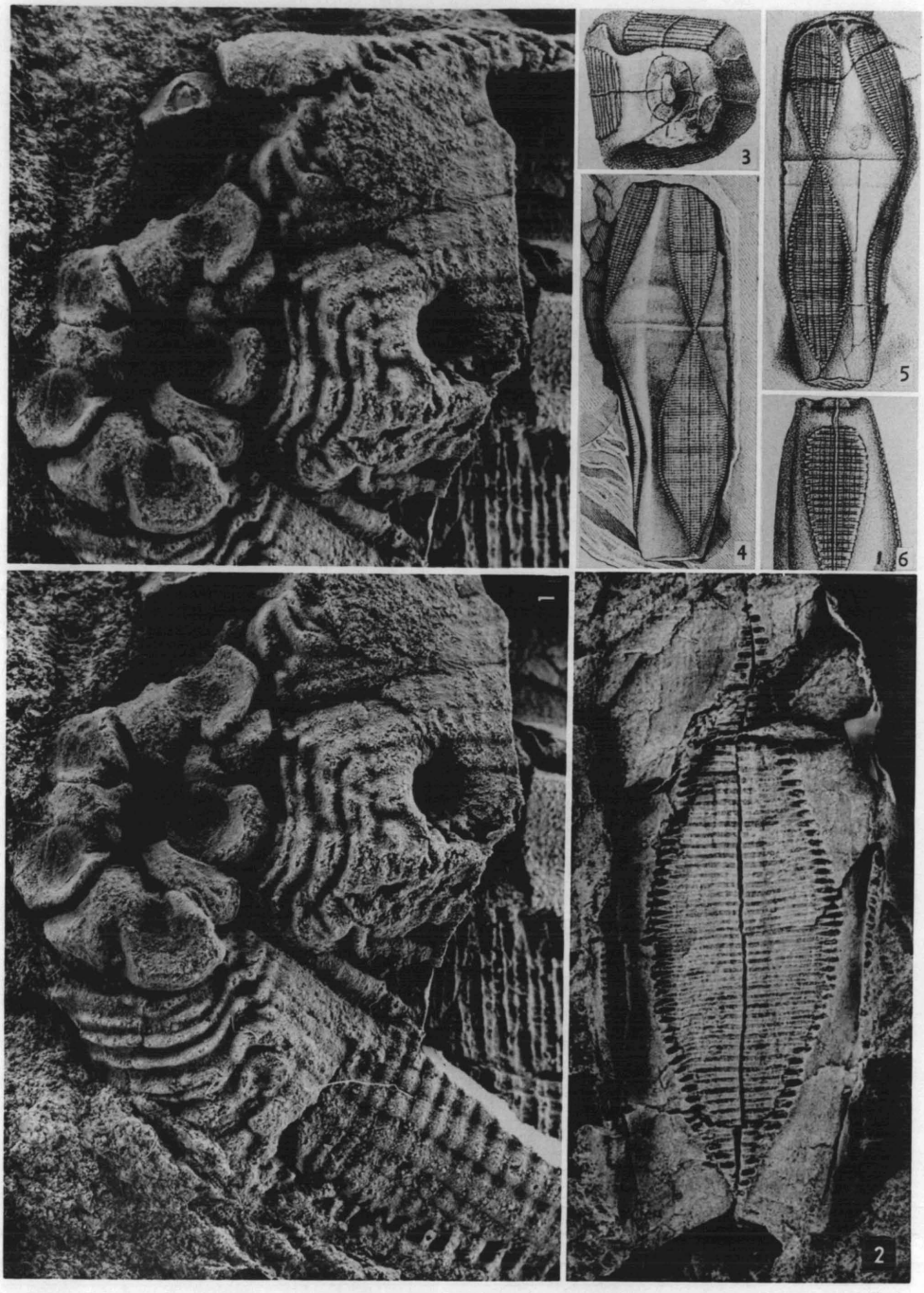


PLATE II



EXPLANATION OF PLATE II

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FIG. 1. Stereogram of latex cast shown in Pl. I, Fig. 2, oriented to show the *RR* and *OO* plates, x 7½.

FIG. 2. Latex cast of parts of IL_1 and IL_2 showing the internal surface of the plates, made from an incomplete steinkern, x 4. Original specimen in the Barrande-de Verneuil collection in the Geological Department of the University of Paris. Cast prepared by Professor G. Ubaghs.

FIG. 3. Oral view of a steinkern, showing the shape of the theca, the arrangement of plates and pore rhombs, and the periproct, x 2. Copied from Barrande, 1887, Pl. 6, Fig. 5.

FIG. 4. Lateral view of steinkern, showing the association of *ILL* and *LL*, x 1. Copied (inverted) from Barrande, 1867, Pl. 11, Fig. 5.

FIG. 5. Lateral view of steinkern, x 1. Copied (inverted) from Barrande, 1887, Pl. 6, Fig. 21.

FIG. 6. Lateral view of part of steinkern, showing demirhomb L_2/L_3, plate L_4 at the left, and the periproct at the upper left corner, x 2. Copied (inverted) from Barrande, 1887, Pl. 6, Fig. 11.