The Late Cambrian eocrinoid *Cambrocrinus*

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Morphology of the stem in Cambrocrinus *regularis* Orłowski 1968 from the early Late Cambrian of the Holy Cross Mts, with only one type of columnals in its proximal conical part but with well developed marginal fulcra connecting them alternately in pairs, places it in between the Middle Cambrian Acadocrinus and Late Cambrian Ridersia. In the presence of thecal ribbing with ribs radiating toward plate comers, which is definitely not homologous to the ribbing of Ridersia, Macrocystella, and later cystoids, it departs from the main eocrinoid lineage leading to the rhombiferans. A new family Cambrocrinidae is therefore proposed to include Cambrocrinus and Eocystites.

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Introduction

Echinoderms are known to occur at two levels in the Cambrian of the Holy Cross Mountains. The older assemblage of ctenocystoids, initially erroneously identified as archaeocyathans (Orlowski 1959, 1964; see Palmer in Sprinkle 1973: p. 111) and still awaiting redescription, occurs in the Paradoxides *insularis* Zone of the Jugoszow Sandstone Member (Orłowski 1975) in the eastern part of the area. The present paper is devoted to the population of the eocrinoid Carnbrocrinus described by Orłowski (1968) from the early Late Cambrian *Olenus* Zone of the Wisniowka Sandstone Formation at Wąworków. Additional material, collected since the time of original description, provides more data on the morphologic variability of this early pelrnatozoan. Cambrocrinus definitely deserves more attention than given to it previously because of its important position in the phylogeny of the Cystoidea, suggested by Sprinkle (1973) and Paul (1988).

Geological age

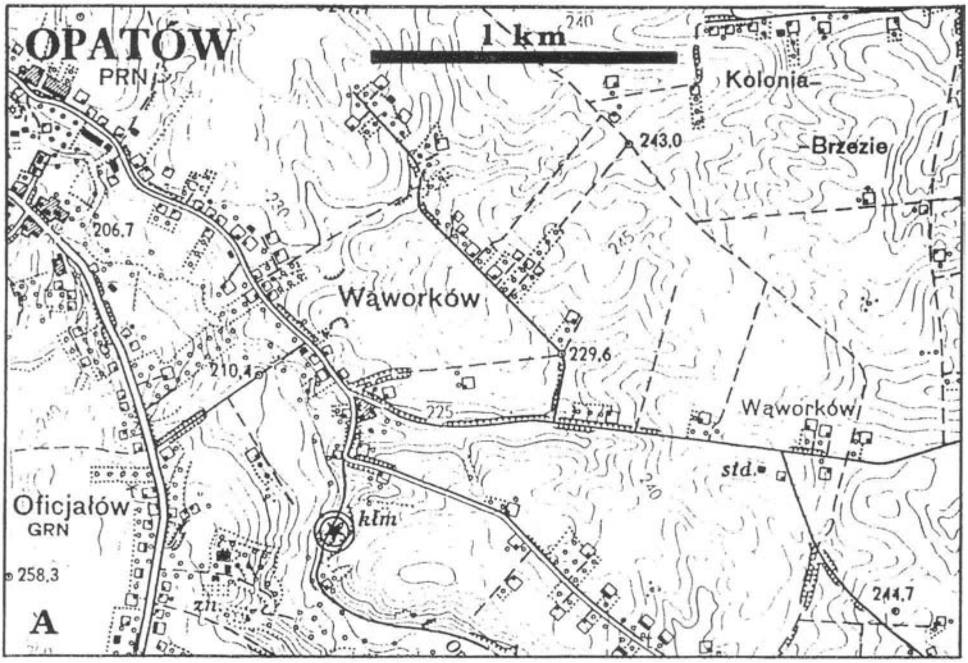
The fossil assemblage containing *Cambrocrinus* remains occurs in the section of the Wisniowka Sandstone Formation (Orlowski 1975, 1992) at Waworkow near Opatow, in the eastern part of the Holy Cross Mountains (Fig. 1). Together with the eocrinoids and brachiopods, trilobites *Olenus rarus* Orłowski 1968, *Protopeltura olenusorum* Orłowski 1968, and *Protopeltura* sp. have been identified in these strata. They indicate the early Late Cambrian age of the fauna, corresponding to the transition between the Baltic *Agnostus obesus* and *Parabolina spinulosa* Zones (Orlowski 1975, 1992).

Description

Thecal plates. — Among 56 articulated thecae that have been found in Waworkow (Fig. 2) only three specimens are complete enough to enable reliable orientation and identification of plates. The boundaries between plates are not visible but it is quite clear from isolated plates dispersed at the rock bedding surface that they invariably possess strong ribs radiating from the plate center to its corners (Fig. 4). The plate boundaries can thus be inferred from the course of the ribs, as already done by Orłowski (1968). Unlike typical cystoids, with ribs radiating to the centres of plate edges being then arranged in triangles, the ribs in *Cambrocrinus* form a rhombic pattern at the surface of the theca. The distribution of the thecal plates varies among specimens and is not quite regular, except for the two basalmost rings. However, even if splitting of some plates may happen, particular rings are easily identifiable in most of the thecae. Although they arc hardly homologous to those in the cystoids or crinoids with more stable plate arrangement, to make description easier we named the seven usually identifiable rings of plates as infrabasal (IB), basal (B) infralateral (IL), lateral (L), supralateral (SL), infraoral (IO), and oral (O) (Fig. 3).

The specimen WGUW W-1103, in which the basal part is missing, shows the best preserved adoral part of the theca. A complete set of the lateral, supralateral and infraoral rings can be identified in it. They are composed of six, seven, and seven plates, respectively, of various sizes and shapes (Figs 2C, 3C). In the lateral ring two plates (L1, L2) are heptagonal, two (L4, L5) hexagonal, and the remaining two pentagonal. In the ring of supralateral plates one (SL6) is heptagonal, five are hexagonal, and only a single (SL7) is pentagonal. The infraoral ring consists of a single heptagonal plate (IO4), five hexagonal, and a single one pentagonal (103). The two largest oral plates are those located in the wider interambulacrum, thus

Fig. 1. ❑A. Location of the exposure of the Wisniowka Sandstone Formation at Waworkow near Opatow, eastern Holy Cross Mts, indicated with asterisk. OB. View from the south on the Waworkow quarry. OC. The fossiliferous bed, about 1 m thick. Pictures taken in 1965.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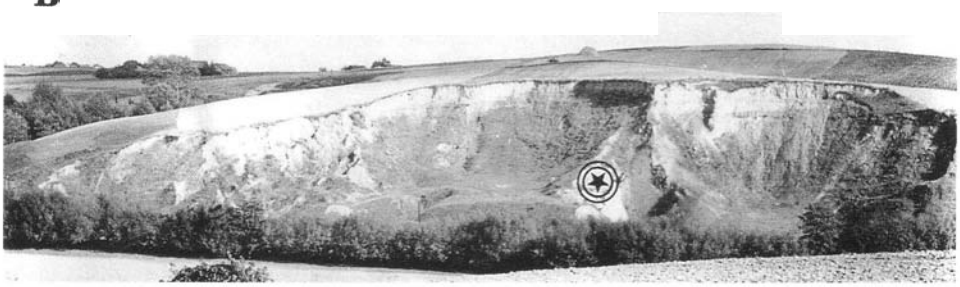

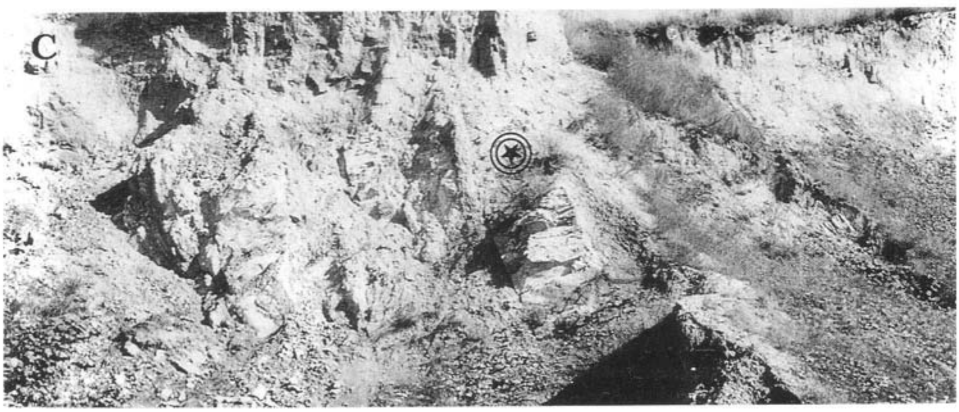
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in the CD interray. They enclose a poorly preserved conical elevation (possibly representing the anal pyramid). Both of the ambulacral grooves bordering the area are located at sutures between oral plates. The remaining three grooves are probably located at a single oral plate each. Although boundaries of particular oral plates can hardly be determined with any confidence, the position of mouth and distribution of ambulacral grooves at the oral surface of the theca is easily identifiable. The grooves bifurcate at their ends, which is clearly visible in the D ray and suggested by widening at the tips of the remaining ones.

More completely preserved specimen WGUW W-974 shows also an elevation in the place where the anal pyramid could be expected to be located. The precise number of plates in particular rings cannot be here identified with confidence (Figs 2D–E, 3A). In the infraoral ring the plate IO5 is heptagonal and three other plates have been identified, all hexagonal in shape. In the supralateral ring the plate SL4 is pentagonal, two other hexagonal plates can also be recognized but shapes, sizes and number of the others remain unknown. The lateral ring consists of certainly heptagonal L4 and possibly L6, L2, the remaining plates being too poorly preserved to be properly identified. In the infralateral ring the plate IL3 is heptagonal, IL5 hexagonal, shapes of the remaining plates can be only very tentatively restored. The basal plates seem to be all hexagonal but only in three of them is this well documented. Infrabasals are pentagonal, relatively high in shape. The identification of a plate below B5 is not certain as it is not clear whether an elevation present there represents a rib or rather a boundary between displaced infrabasal plates. The most remarkable feature of the specimen is the split in two plates [labelled as upper (u) and lower (l)] in locations IL2 and L5 that thus form incipient additional rings.

The specimen UWWG W-1110 is the most complete, even with nucleus of the theca interior preserved, but some areas on its surface are damaged (Figs 2A–B, 3B). Only plating of the AB interray is fully preserved. In the infraoral ring only a single hexagonal plate has been identified (IO1?), similarly in the supralateral one, with heptagonal SL1 plate. The most interesting is the presence of smaller plates surrounding the damaged area in the C ray. Plates L5 and IL5 are large, heptagonal, as are also plates L2 and IL1, although incompletely preserved. The area in between these plates, however, was filled with at least ten much smaller, irregularly distributed plates. This also affected the morphology of the basal ring, in which the plates B5 and B1 are smaller and of irregular shape.

The internal mould of the theca W-1110 shows the internal surfaces of the plates, which are almost smooth, with indistinct elevations in place of ridges. The boundaries of the plates can be recognized only in places where they were displaced in result of postmortem deformation. The oral plates were probably much thicker than the remaining ones but their internal morphology cannot be restored because the sandstone matrix is too coarse.

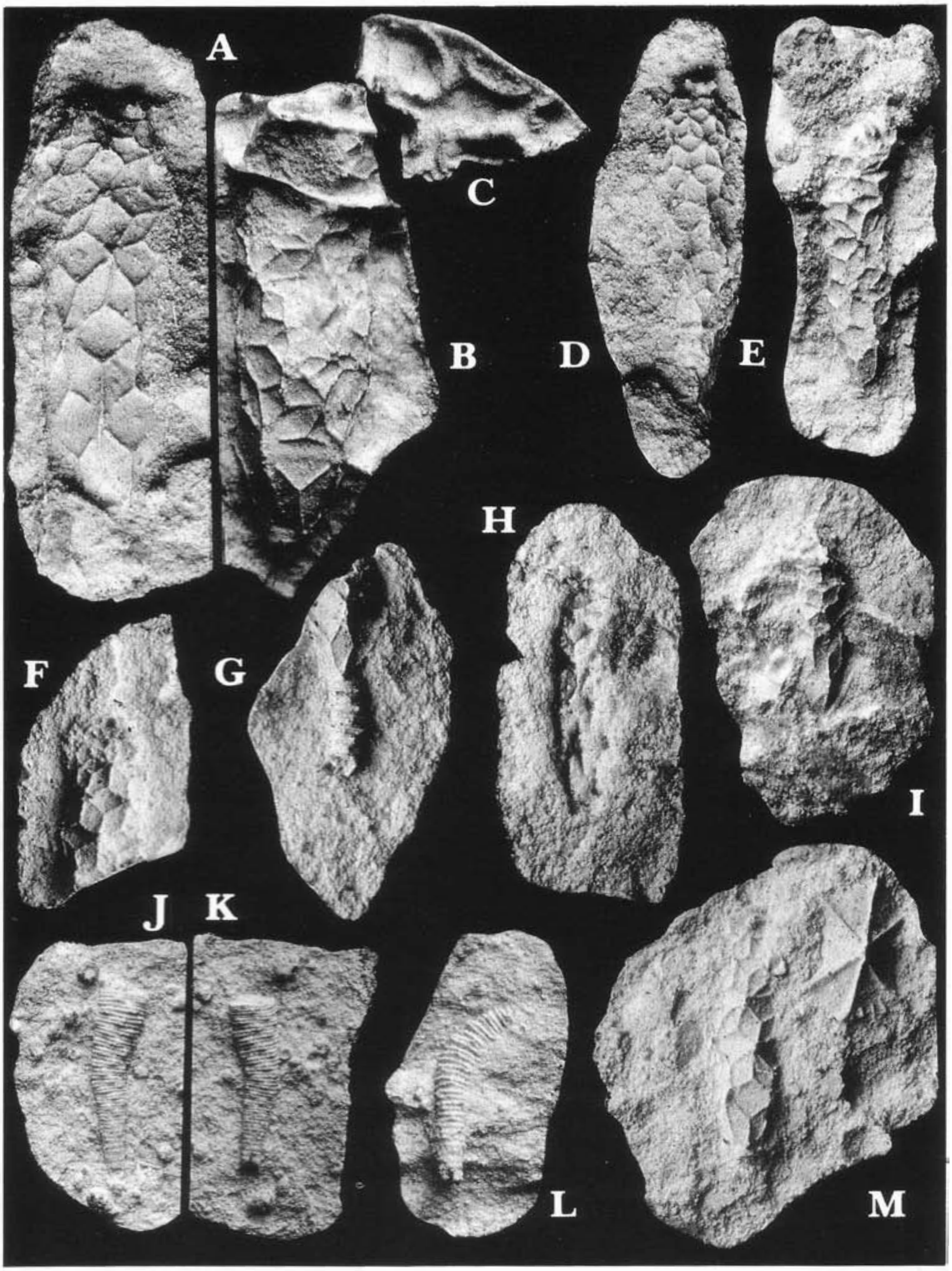

Fig. 2. *Cambrocrinus regularis* Orłowski 1968, Late Cambrian Wisniowka Sandstone Formation, Wąworków near Opatow, Holy Cross Mts, Poland, latex casts from moulds in coarse sandstone; all x 3. A–B. Specimen UWWG W-1110, part and counterpart. C. Oral area of the specimen UWWG W-1103. D–E. Theca UWWG W-974, part and counterpart. F–G. Basal part of theca UWWR W-1111 with proximal part of the stem. H. Juvenile specimen UWWG W-1010. I. Juvenile specimen UWWG W-1110. J–K. Proximal portion of the stem UWWR W-976, part and counterpart. L. Stem UWWR W-1104. M. Juvenile theca UWWG W-972 in association with isolated plate of a large specimen.

Large areas of thecae are preserved also in specimens W-1213, 1027, 1193, 1205, 1225, 1216, 1221, and 975. Smaller groups of articulated thecae are also present in the collection. Interestingly, in juvenile specimens W-1213, 1216, and 1221 all the preserved plates are hexagonal, as is also the case with the large specimen W-975. Although no more than a one third of the whole thecal surface is preserved in any of them, this may indicate much more regular arrangement of plates than in the three best preserved specimens described above.

The other extreme is represented by isolated plates W-982, 1127, and 1188, which are octagonal. Their mother thecae must have thus bear several smaller penta- or even tetragonal platelets, even more than in the specimens W-1110.

The number of plates, generally variable in Cambrocrinus, seems to be smaller in juvenile thecae but the two lowermost rings are invariably of almost the same morphology, with prominent longitudinal elevation at the center of the basal plates. This part of the theca shows the most strict pentaradial symmetry. As long as invariably seven oral plates are associated in Cambrocrinus with five basals, any theca must contain at least two sets of penta- and heptagonal plates. Although it cannot be proven with poorly preserved available material, the upper rings in the theca evidently changed number of their plates in the course of ontogeny. The pattern of insertion is not clear but bifurcations of ribs common among isolated plates express accommodation to changing arrangement of plates, with new insertions modifying shapes of neighboring plates (Fig. 4). As it could be expected, the plates smaller in size are tetra- and pentagonal in shape. These are mostly small intercalatory plates inserted at later stages of ontogeny. Generally, the number of ribs is positively correlated with the plate size, as shown by measurements of 85 isolated plates (Fig. 4). However, octagonal plates are not larger but more elongated than heptagonal ones. Evidently, these are mostly infralateral plates with shapes modified by late intercalations of small plates.

Stem. — Sprinkle (1973: p. 111), commenting on casts taken from the original specimens by Georges Ubaghs, suggested that wedge-shaped colurnnals are present in the proximal parts of Cambrocrinus stem. This is not the case, as shown by the well preserved specimen UWWG W-976 (Fig. 2J–K). Less complete proximal parts of the stem, 18 in number, show the same surface morphology.

Isolated columnals, although common on the rock bedding surface, are preserved in too coarse matrix to provide reliable evidence on the morphology of the articulating surfaces. This can be only inferred from the surface morphology of articulated stems. Colurnnals in the most proximal part of the stem are very low, with peripherally located fulcra connecting them in pairs. There is no evidence of more than one kind of columnal and the arrangement of fulcra is also different from that in *Macrocystella* as described by Paul (1968). The fulcra are arranged spirally at the stem surface. Repeatable morphologic series of five columnals can be distin-

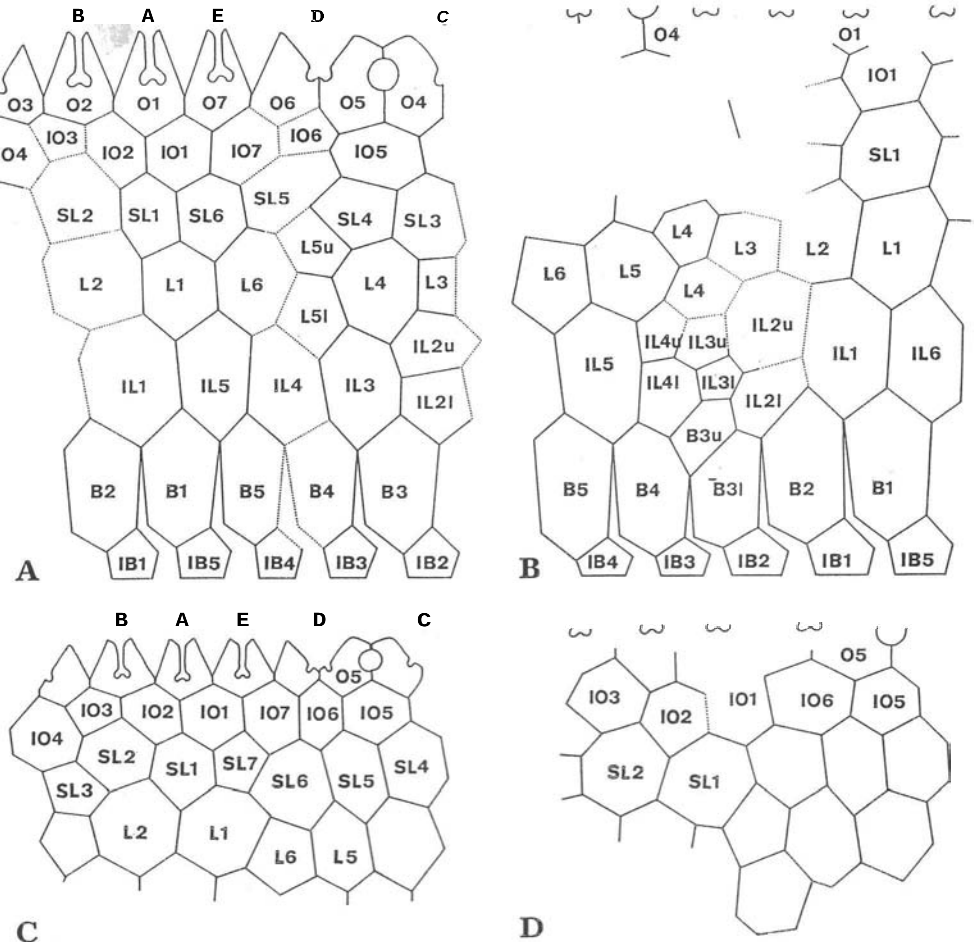

Fig. **3.** Plate diagrams of thecae of *Cambrocrinus regularis* Orłowski 1968 from the Late Cambrian Wisniowka Sandstone Formation, Waworkow near Opatow, Holy Cross Mts, Poland; proposed terminology of the plates and ambulacral radii indicated with symbols. A. Specimen UWWG W-974. B. Specimen UWWG W-1110. C. Specimen UWWG W-1103. D. Specimen UWWG W-1120.

guished. This means that the number of fulcra varies from columnal to columnal (presumably from 2 to 4), and that their distribution is not radially symmetrical.

With the stem diameter decreasing distally the fulcra gradually disappear and colurnnals become smooth and cylindrical in shape. All the available stem fragments are relatively short so the length of the stem, as well as its attachment organ (if present) remain unknown.

Position of anal pyramid.— The area in the C ray of the specimen W-1110, with smaller plates forming a field surrounded by larger plates, is suggestive of a presence of laterally located periproct. It is located in exactly the same place in *Macrocystella* and *Mimocystites* (see Ubaghs

1967; Paul 1968). The elevation between the ambulacral grooves in CD interray would then correspond to the hydropore and/or gonopore.

Although this cannot be completely excluded there are several arguments against such an interpretation. In the specimen W-1103, where the whole lateral ring is well preserved no irregularities in the distribution of plates are visible, which means that a periproct, if present, could be located only even lower, between the infralateral and basal rings. Similarly, in the specimens W-974, although the C ray plates are not easily traceable, there is no sign of any irregularity in plating, which might suggest the presence of anything similar to the finely plated field in the specimen W-1110. It seems thus much more likely that this was a teratological feature of that particular specimen and the conical elevation at the oral surface of the theca represents the anal pyramid. This is the primitive location of the anal pyramid, which characterizes older eocrinoids and also Ridersia from the Late Cambrian of Queensland (Jell et al. 1985). This is thus the interpretation followed here.

Relationships

The most exceptional feature of Cambrocrinus is the ornamentation of its thecal plates. Although superficially similar to ridged plates of other early pelmatozoans they basically differ in merging not at the middle of the plate sides but at the corners. The only other known eocrinoid with plates bearing radial ribs that are directed toward plate angles is Middle Cambrian Eocystites *primaevus* Billings 1868 from New Brunswick, Canada, which is known only from isolated plates (Ubaghs 1967: p. 493; Sprinkle 1973: p. 122). Similar plates have been also described from the Jince Formation of Bohemia (Fatka & Kordule 1984: Pl. 11: 2–3). Such morphology must have developed from smoothly convex plates of Acadocrinus type independently of ridges in Ridersia and Macrocystella. Thus, this feature does not allow us to identify more precisely the relations of Cambrocrinus.

The proposed position of the anal pyramid makes Cambrocrinus similar to Ridersia but this is just a primitive pelmatozoan feature inherited by both these forms from their common ancestor, probably close to *Acadocrinus*.

The organization of the stem seems to be much more significant (Paul 1988). Its subdivision into two part and the development of fulcral articulation of colurnnals in its proximal part place Cambrocrinus above the level of the morphologic organization of Acadocrinus, in which columnals are still somewhat irregular (wedge shaped) and without any articulation structures (see Ubaghs 1967; Fatka & Kordule 1991). The stem morphology of Ridersia is different from that of Cambrocrinus in showing alternation of wider and narrower columnals (Jell et al. 1985), which extends to its distal parts. In Macrocystella, more derived in having large lateral periproct, the distinction between proximal and distal parts of the stem is more prominent. This stem type, which is quite unlikely to develop

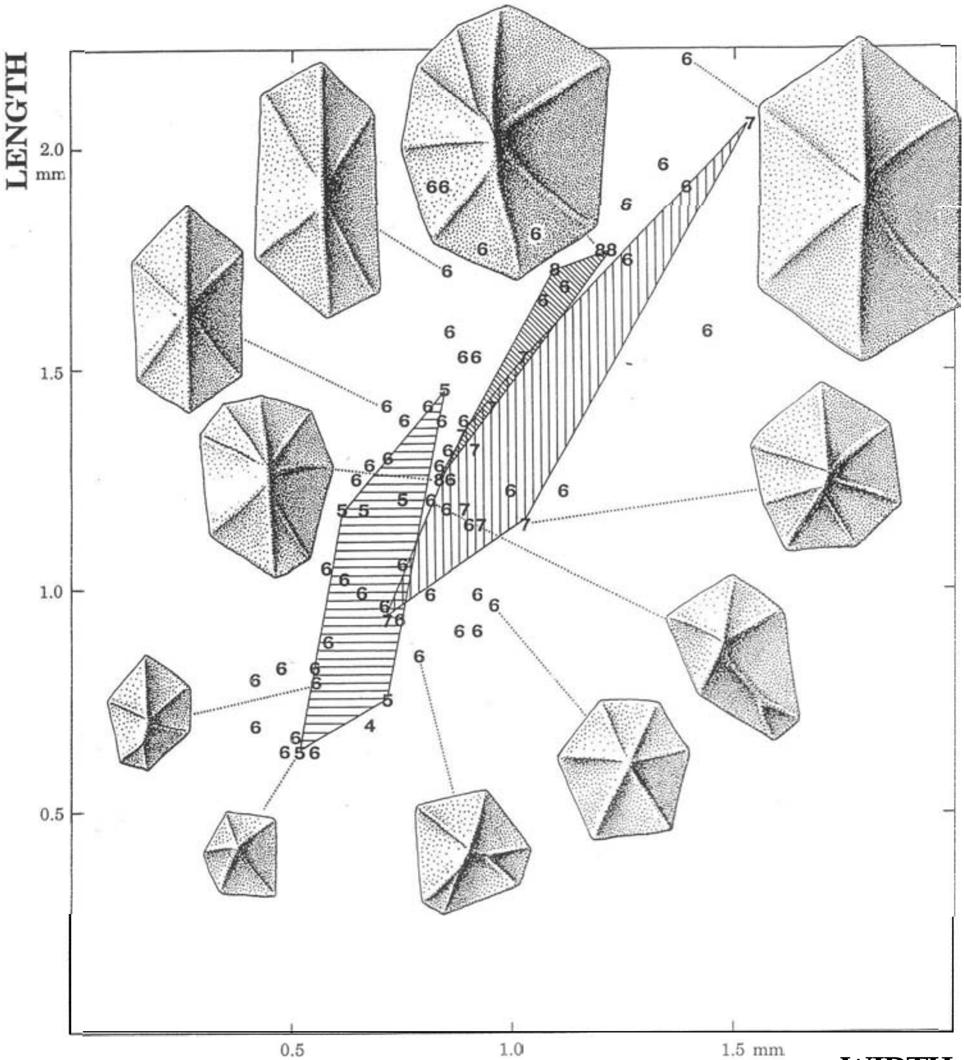

Fig. 4. Scattergram of length versus width of isolated plates of *Cambrocrinus regularis* Orłowski 1968 from the Late Cambrian Wiśniówka Sandstone Formation, Waworków near Opatów, Holy Cross Mts, Poland; number of ribs indicated, fields of non-hexagonal shadowed. Note that insertion of new plates (inferred from bifurcation of the ribs). occurred at various stages of ontogeny.

independently in other lineages, was inherited from Macrocystella by its successors, the glyptocystitid rhombiferan cystoids.

Macrocystella shows clear rhombiferan traits with incipient rhombs well visible on the internal side of the thecal plates (Ubaghs 1967). At the plate surface they correspond to series of elevated ridges (Paul 1968). *Cambrocrinus*, with its completely smooth inner surface of the plates and strong ribs in the place of rhombs, hardly has anything to do with the lineage leading to *Macrocystella*. *Ridersia* is slightly more similar (see Jell

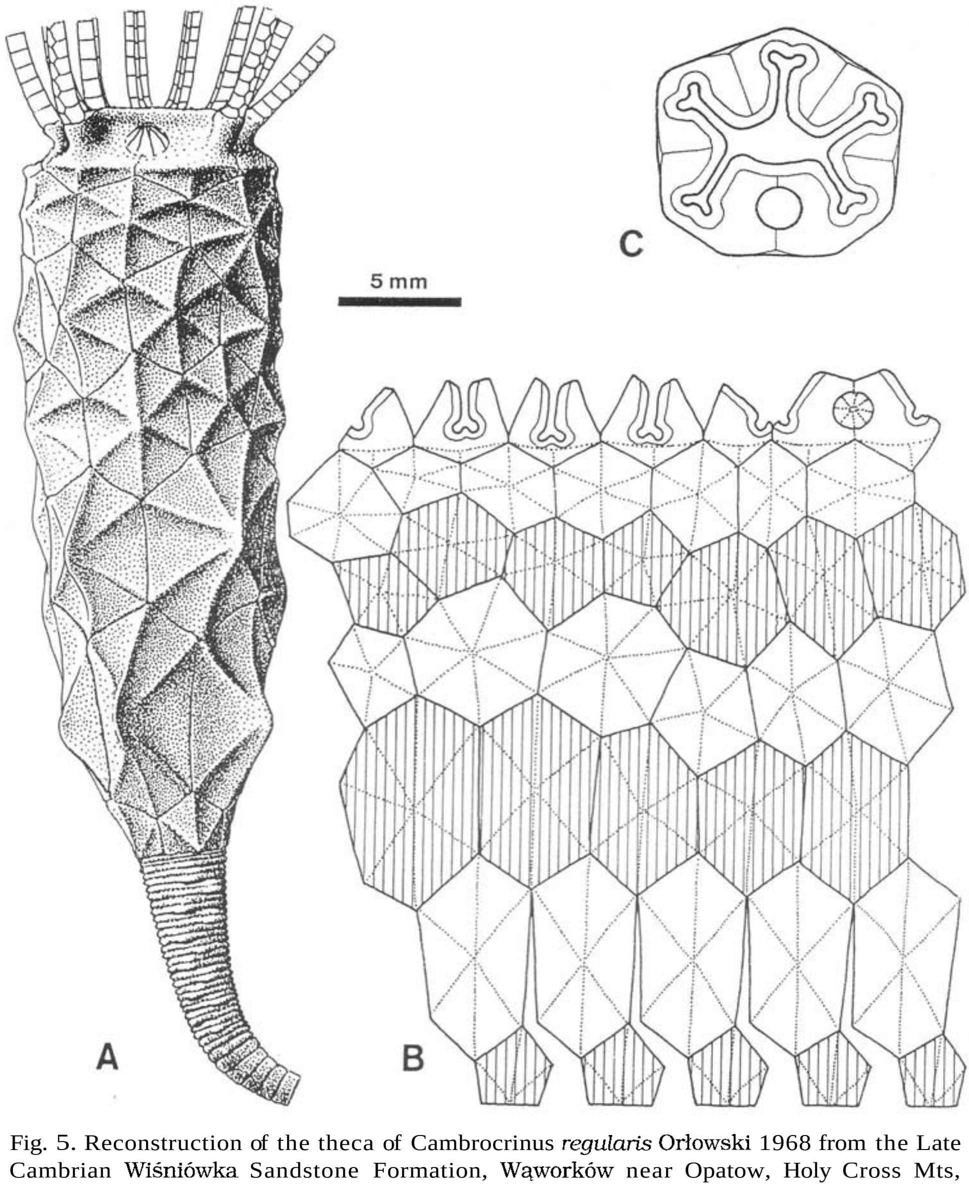

Fig. 5. Reconstruction of the theca of Cambrocrinus *regularis* Orłowski 1968 from the Late Cambrian Wiśniówka Sandstone Formation, Wąworków near Opatow, Holy Cross Mts, Poland. A. View at D–C interradius. B. Composite plate diagram based mainly on the specimen UWWG W-1103 (see Figs 2C and 3C). C. Diagram of the oral surface of the same specimen.

et al. 1985) but ribs at the surface of its plates are homologous rather to those in the rhombiferan cystoids than *Cambrocrinus.* The theca of *Ridersia* is ornamented with tubercles similar to those in *Bockia* (see Bockelie 1981), which makes it even more unlike the Polish eocrinoid. Thus *Carnbrocrinus* represents clearly a separate branch of the eocrinoids, not leading to any of the Ordovician branches of the group, and deserving taxonomic separation at least at the family level.

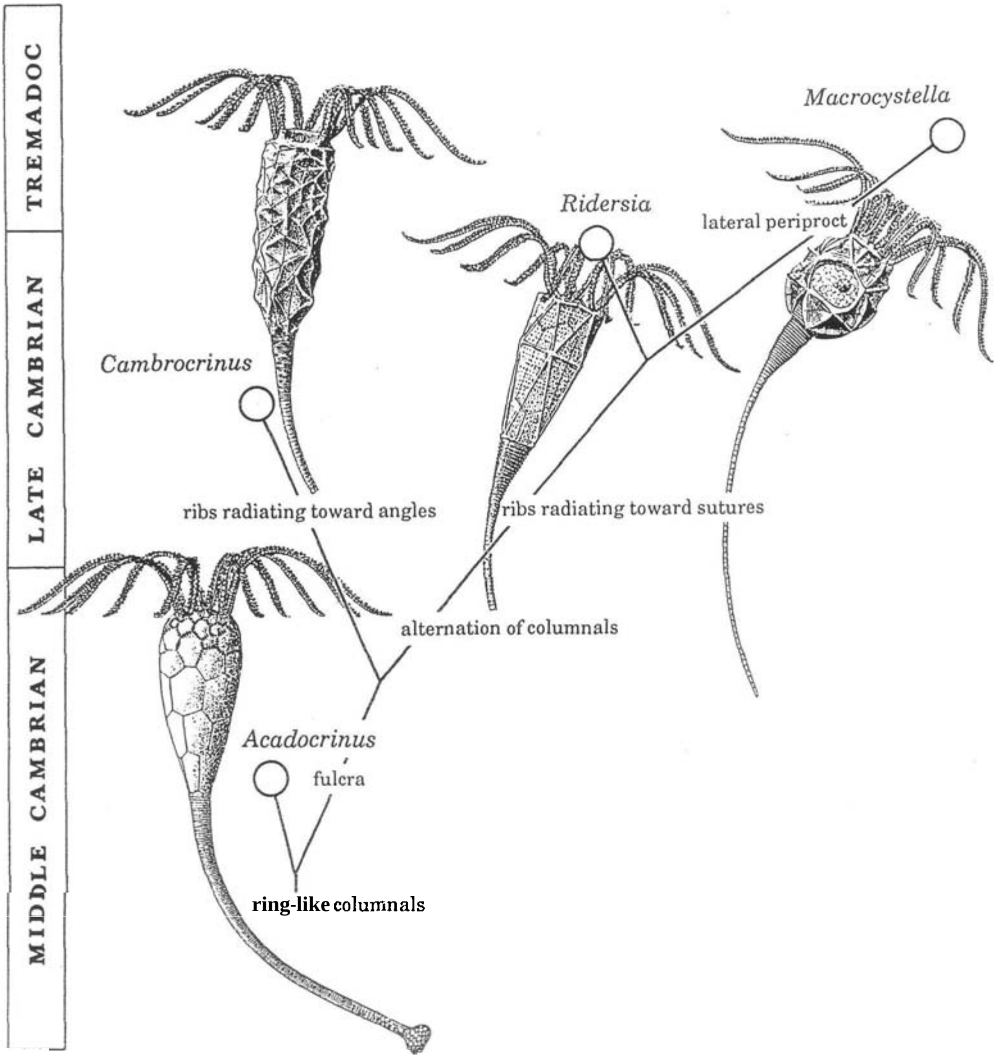

Fig. 6. Proposed relationships of *Cambrocrinus*. Data from Paul (1968), Jell et *al.* (1985), and Fatka & Kordule (1991).

Despite the apparent variability in details, the number of rings and the number of plates within particular rings of the *Cambrocrinus* theca were evidently under genetic control. This means that there was a more or less stable relationship between size of a morphogenetic field of particular plate and the surface of the theca. With the size of the plates increasing in the course of evolution from *Gogia* to Macrocystellamore and more precise and regular organization in the distribution of plates resulted. *Cambrocrinus* was intermediate in this respect. *Akadocrinus*, preceding it stratigraphically and morphologically also seems to vary in plate morphology (Sprinkle 1973: p. 106). The differences in number of plates and the presence of epispires, usually interpreted as specific characters (see Prokop & Fatka 1985; Fatka & Kordule 1991), may express rather population and ontogenetic variation within a single species of *Akadocrinus* of the Jince Formation, as is the case with *Cambrocrinus* plating. *Macrocystella*, being more advanced than *Canbrocrinus* in the reduction of plate number, hardly shows any variation in this respect (see Paul 1968) and this refers also to later rhombiferans.

Taxonomy

Class Cystoidea

Order Eocrinida Jaekel 1918

Remarks. Paul (1988) included *Cambrocrinus* in his informal branch of the glyptocystitid rhombiferans, basing this assignment on the morphology of its stem. We concur with him regarding the interpretation of the phylogenetic position of *Carnbrocrinus*. However, it does not seem likely that this echinoderm was really close to the lineage of *Macrocystella* because this is contradicted by the distribution of ribs on the plates. The very derived position of the anus in *Macrocystella* together with the presence of incipient rhombs provides a convenient point of separation of the whole group of the rhombiferan cystoids, allowing its precise demarcation. Definitely several large groups of post-Cambrian non-crinoid pelmatozoans derived from the eocrinoids and, as pointed out by Paul (1988) there is hardly any reason to continue to classify them at the class rank. It does not seem reasonable, however, to abandon the taxon completely. Its position as an order, containing the most primitive stem-bearing pelmatozoans with epispires or imporous plates, within the class Cystoidea would be convenient.

Carnbrocrinidae fam. n.

Diagnosis.— Theca without epispires composed of plates with sharp ridges radiating from the center to the corners. Anal pyramid at the oral surface of the theca. Stem composed of circular colurnnals, subdivided in two parts: the proximal widely conical one composed of thin columnals with fulcra and the distal one with smooth cylindrical columnals.

Genera included: Cambrocrinus Orłowski 1968, Eocystites Billings 1868.

Cambrocrinus Orłowski 1968

Type species: Cambrocrinus regularis Orłowski 1968.

Diagnosis.— As for the type species.

Species included: Monotypic.

Cambrocrinus regularis Orłowski 1968

Figs 2–5.

Carnbrocrinus *regularis* sp. n.; Orłowski 1968: p. 265, Pl. 3:1–13.

Holotype: UWWG W-970; Orłowski 1968: Pl. 3: 5.

Type horizon and locality: Early Late Cambrian Wisniowka Sandstone Formation, Wąworków near Opatów, Holy Cross Mountains, Poland.

Emended diagnosis.—Elongated subcylindrical theca composed of seven circles of plates, mostly hexagonal in shape. The flattened oral area bears five ambulacral grooves, each terminating in a pair of brachiolar bases, and small anal pyramid. Stem strongly tapering proximally, composed there of thin columnals connected by fulcra marginally, distally narrow, with smooth cylindrical columnals.

Acknowledgements

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Streszczenie

Szkarlupnie znane są z dwu obfitych stanowisk w kambrze Gor Świętokrzyskich. Starszy zespol ze środkowokambryjskich piaskowcow z Jugoszowa, niegdys pomylkowo zinterpretowany jako reprezentujqcy archeocjaty, wciąż oczekuje szczegolowej rewizji taksonomicznej. Przedmiotem tego artykułu jest zas populacja Cambrocrinus regularis Orłowski 1968 z Wąworkowa, występująca w obrębie formacji późnokambryjskich piaskowcow z Wiśniówki.

Zgromadzona przez drugiego autora kolekcja skarnienialosci *Cambrocrinus* liczy 56 mniej lub bardziej kompletnych kielichów, 85 pojedynczych plytek oraz 18 fragmentow łodyg. Chod gruboziarniste piaskowce, w których występują ośródki kielichów Cambrocrinus, nie przechowały szczegółow ich morfologii, material jest dostatecznie obfity by umożliwić identyfikację nie tylko struktury kielicha ale i zakresu jego wewnqtrzpopulacyjnej zmiennosci.

Kielich dojrzalego C. regularis skladal się z siedmiu kręgów liczących zazwyczaj po pięć do siedmiu plytek. Odmienność liczby plytek w gomych i dolnych kręgach wymuszała odejscie od standardowego sześciokątnego kształtu części z nich. Innym czynnikiem zwiększającym rónorodność kształtów było wklinowywanie dodatkowych plytek w strukturę kielicha powodujqce przybieranie siedmio- lub nawet ośmioboczności przez ·ich sąsiadów. Rozkład częstości poszczegolnych typów plytek i ich wydłużenia oraz polozenie miejsc rozwidlania się żeber na powierzchni plytek wskazują na wyraźne zwiększanie się ich liczby w trakcie wzrostu. Stan zachowania powierzchni gębowej najkompletniejszych kielichów pozwala jedynie na stwierdzenie, że odchodzilo od niej pied par brachiol. Nie jest natomiast pewne, czy wzgorek znajdujqcy się pomiędzy szerzej rozstawionymi bruzdami ambulakralnymi byl piramidą analną. Bardzo mało prawdopodobne jest jednak występowanie bocznego periproktu w kielichu C. *regularis* bowiem nie ma nan miejsca w żadnym z bardziej kompletnych okazow. Zasadne jest wiec przypuszczenie, ie Cambrocrinus zachowal pierwotną dla lodygowych szkarlupni organizację ciała, z odbytem położonym w bliskosci otworu gębowego.

Najbardziej niezwykłą cechq C. regularis jest uklad żeber, ktore dochodzą do naroży plytek miast srodka ich bokow, jak u prawie wszystkich pozostalych pierwotnych szkarlupni. Cambrocrinus jest wiec przedstawicielem osobnej gałęzi ewolucyjnej eokrynoidow, wywodzącej się zapewne od srodkowokambryjskiego Acadocrinus o prawie gładkich plytkach kielicha. Progresywną cechą Cambrocrinus, różniącą go od Acadocrinus a zbliżającą do ordowickich cystoidow Rhombifera, jest wyodrebnienie stożkowatej przykielichowej części lodygi. Można wiec domniemywać, że gałąź ewolucyjna Cambrocrinus odszczepila się od linii wiodącej od Acadocrinus ku późnokambryjskiemu australijskiemu eokrynoidowi Ridersia po wykształceniu złożonej lodygi ale przed wyposażeniem kielicha w żebra przechodzące posrodku szwow między plytkami.