 Acta Palaeontologica Polonica 50 (4): 721–724, 2005

The world's oldest crustoid graptolites from the upper Tremadocian of Poland

PIOTR MIERZEJEWSKI, CYPRIAN KULICKI, and ADAM URBANEK

The Crustoidea are an order of sessile basic graptolites that are morphologically intermediate between the extant genus *Rhabdopleura* (Rhabdopleuroidea) and the extinct sessile order—the Dendroidea (Kozłowski 1962, 1966; Bulman 1970; Urbanek 1986). So far these rather poorly known graptolites of significant phylogenetic importance have been reported from the upper Arenigian or lower Llanvirnian (Kozłowski 1962) to the upper Ludlow (Mierzejewski 1977). Isolated fragments of the graptolite stolon system were chemically extracted from upper Tremadocian chert nodules from Wysoczki (Holy Cross Mountains, central Poland) and examined with SEM. Because of the characteristic trifurcation and fine annulation of the stolons they are recognized as remnants of the crustoid graptolites. This discovery extends the stratigraphic distribution of the crustoid graptolites and explains the enigmatic presence of graptoblasts in the upper Tremadocian beds of Wysoczki.

Introduction

The upper Tremadocian chalcedony beds exposed in the outcrop at Wysoczki (Holy Cross Mountains, Poland) exhibit a unique association of non-calcareous fossils, namely blue-green algae, acritarchs, sponge spicules, inarticulate brachiopods, trilobites, graptolites, and conodonts (for references see Szaniawski 1980). This locality has been world famous since Kozłowski's (1938, 1949) fundamental investigations on the graptolite hemichordates. Kozłowski recognized some fifty new species of benthic graptolites, representing the order Dendroidea and three new orders, i.e., the Stolonoidea, Camaroidea, and Tuboidea, as well as some other hemichordate-like groups (Acanthastida, Graptoblasti, and Graptovermida). The fossils from Wysoczki are of fragmental nature, however, they exhibit an excellent state of macro- and microscopic preservation (see for example Kozłowski 1949; Starmach 1963; Urbanek and Mierzejewski 1986). The stratigraphic setting of the chalcedony beds at Wysoczki has been discussed by Bednarczyk (1971) and Szaniawski (1980).

In 1974, Professor Roman Kozłowski put at Piotr Mierzejewski's disposal several samples of chalcedonies collected in the early 1950s by him and Adam Urbanek (at that time both from the University of Warsaw) from the locality at Wysoczki. The fossils were extracted from these samples by standard chemical procedures using hydrofluoric acid and manual sorting of residues under the microscope. The acid resistant residuum contained several well-preserved bundles of the hemichordate stolon system, associated with a rich and varied assemblage of benthic graptolite remains. The dried material was platinum-coated and examined with a Philips scanning electron microscope XL 20. The described material is deposited in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw (abbreviated ZPAL).

General remarks

The presence of well-developed stolon system in both extant pterobranchs and extinct sessile graptolites was of essential importance for Kozłowski's (1938, 1947, 1949, 1966) conception of a close phylogenetic relationship between these two groups (for the biological significance, morphology, histology, homology, and evolution of the hemichordate stolon system see: Urbanek 1986 and Urbanek and Dilly 2000). This system is a complicated structure composed of numerous branched tubular elements called the stolons. In some orders, the stolons are connected with various vesicular structures, as capsules of the dormant buds in the Rhabdopleuroidea, and graptoblasts and cysts in the Crustoidea. In the majority of sessile graptolites, elements of the stolon system are heavily sclerotized and capable of preservation as resistant to diagenetic agents. The stolon and stolonal derivatives differ both structurally and chemically from the periderm made of fusellar and cortical tissue (Bulman 1944; Urbanek and Towe 1974; Crowther 1981; Briggs et al. 1995). According to Mierzejewski (1984, 1986), fossil remnants of hemichordate stolon system are fairly numerous organic microfossils to be found in marine deposits, however, they were usually misinterpreted as remains of the "chitinous hydroids", problematica or *incertae sedis* forms (e.g., Kozłowski 1959; Skevington 1965). Investigations on these microfossils are of great importance for phylogenetical studies because the graptolite stolons display a wide array of structural differentiation. However, the present state of knowledge is far from satisfactory.

Urbanek and Dilly (2000: 222) pointed out that primitive graptolites of the order Crustoidea "offer exceptional opportunities to study the anatomy of their heavily sclerotized stolon system, which becomes exposed due to the destruction of the membranous lower walls of their encrusting colonies." As it was

http://app.pan.pl/acta50/app50-721.pdf

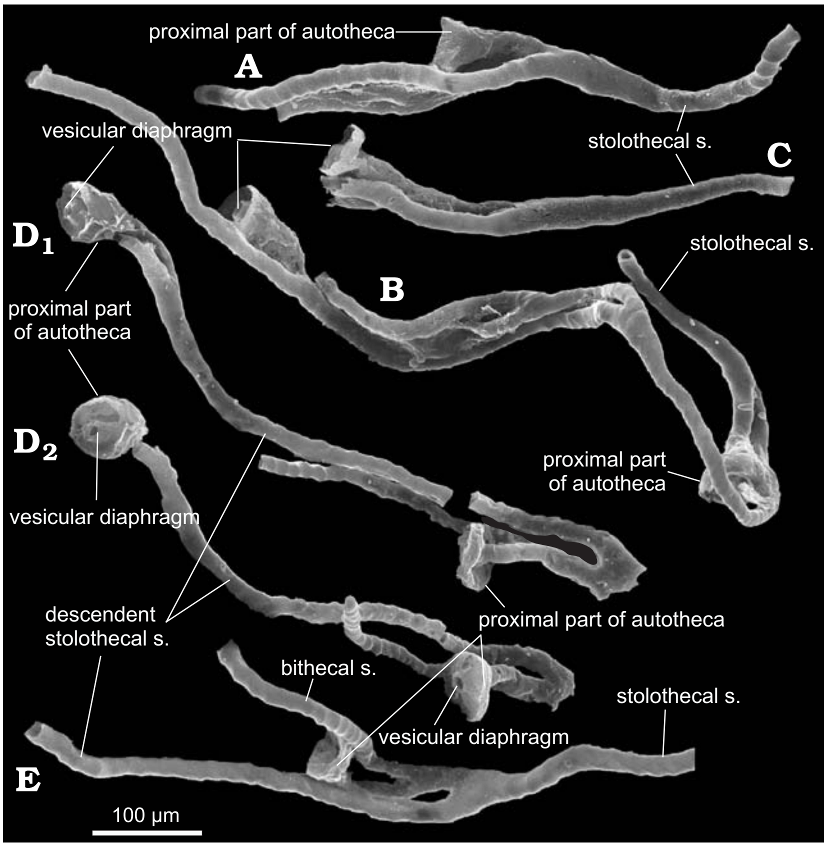

Fig. 1. Fragments of the stolon system of the Crustoidea. Wysoczki outcrop (Holy Cross Mts., Poland), upper Tremadocian. SEM micrographs. **A**, **B**, **D**. Specimens with two nodes (ZPAL G.36/1–3). **C**, **E**. Specimens with one node (ZPAL G.36/4–5). s., stolon.

shown by Kozłowski (1962), the crustoid stolons, marked with characteristic fine transverse annulations, branched regularly producing three stolons, i.e., a triad of the thecal stolons (autothecal, bithecal, and stolothecal stolons as a rule), similarly as in the order Dendroidea, accordingly to Kozłowski's "Wiman's rule". The beaded stolons, i.e., provided with fine transverse annulations, were considered a characteristic feature of the Crustoidea by Kozłowski (1962). However, some portions of the crustoid stolons are more or less smooth (Urbanek and Mierzejewski 1984). Single fragments of crustoid stolothecae containing the stolon do not differ from the stolonal tubes of *Rhabdopleura* (Kozłowski 1962, 1966): they are coalescent with the lower wall of the stolonal tubes.

Description

The material under study consists of six bundles of the graptolite stolon system displaying well-developed nodes at the point of origin of the stolonal triads (Fig. 1). Two larger specimens (0.9 and 1.1 mm) are provided with two nodes (Fig. 1A, B, D) and three smaller fragments (0.6–0.8 mm long) with one node (Fig. 1C, E). The stolons are strongly sclerotized, 0.015–0.02 mm wide, with a wall about 0.003 mm thick, made of crassal fabric showing no internal structure (Fig. 2G), and provided with characteristic fine transverse annulations (Figs. 1, 2). The stolons swell at the nodes of trifurcation (Fig. 2H). As observed under a light microscope, they appear to be made of jet black, opaque, and matt material.

The stolon branching in triads in these specimens is not so regular or symmetric as in the Dendroidea (see Bulman 1944: fig. 7; Kozłowski 1949: fig. 2; Urbanek 1986: figs. 2C, 3A) or in the "classic" Crustoidea as described by Kozłowski (1962: figs. 1–5; see also Bulman 1970: fig. 32,1; Mierzejewski 1984: fig. 1), but distinctly irregular or asymmetric. This irregular triad branching may be even interpreted as two diad buddings produced in a rapid succession (Figs. 1E, 2H). By comparison with Kozłowski's (1962) observations, the descendant stolons in the triads may be identified as autothecal, bithecal, and stolothecal stolons (Figs. 1, 2). As a rule, the first "diad" of the triad forms as a result of bifurcation of the parental stolothecal stolon into the very long descendant stolothecal stolon and an extremely short stolon called by us the prezooidal stolon (new term). Next, the prezooidal stolon bifurcate into the second "diad": the autothecal (sometimes with distinct vesicular diaphragm) and bithecal stolons. Such a situation is illustrated also by Kozłowski (1962: figs. 24B, 25B) in some specimens of the crustoid graptolites *Wimanicrusta urbaneki* Kozłowski, 1962 and *W. cristaelinguata* Kozłowski, 1962.

The autothecal stolons are much shorter than bithecal ones and perforate centrally rather delicate cup-like structures, interpreted as the most proximal parts of the autothecae (Fig. 2A, B, D, F, H). Sporadically, one can recognize indistinct traces of fusellar increments in these structures.

Sometimes, one can observe irregular shreds of pellicle-like structure connecting stolons which may be interpreted as remnants of the basal structureless membrane (Fig. 2C).

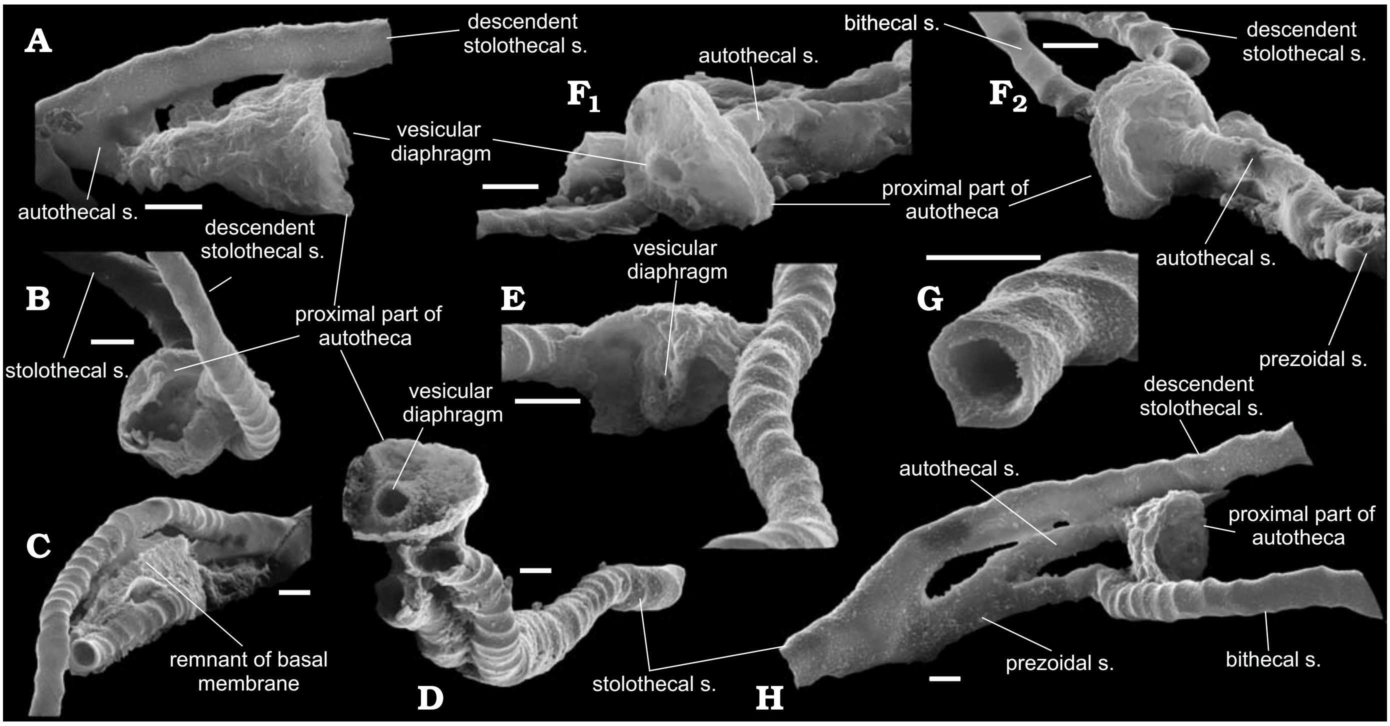

Fig. 2. Micromorphology of the stolon system of the Crustoidea. Wysoczki outcrop (Holy Cross Mts., Poland), upper Tremadocian. SEM micrographs. **A**, **B**, **F**. Proximal part of autotheca (ZPAL G.36/1–3). **C**. Triad with ?remnants of basal membrane (ZPAL G.36/5). **D**. Triad of stolons (ZPAL G.36/4). **E**. Vesicular diaphragm near the base of autotheca (ZPAL G. 36/6). **G**. Fractured stolon showing no internal structure (ZPAL G.36/5). **H**. Distinctly asymmetric triad (ZPAL G.36/3). s., stolon. Scale bars 20 µm.

Discussion

The fragments of the stolon system from Wysoczki reveal features diagnostic for the Crustoidea, namely: (i), budding in triads; (ii), transverse annulations of stolons; and (iii) penetration of the autothecal stolon into the proximal part of the autotheca. Therefore, we interpret these fossils as remains of the crustoid graptolites. The crustoid stolons as described by Kozłowski (1962) differ distinctly from all known stolons of other sessile hemichordates.

The Crustoidea, are extremely rare fossils. Their stratigraphic and paleogeographic record is scanty and limited to tiny fragments of rhabdosomes (usually isolated and undeterminable remnants of autothecae and crushed stolon system) found in Ordovician and Silurian deposits. In exceptional cases, one can find crustoid colonies encrusting calcareous fossils (Kozłowski 1962; Mierzejewski 2000) or hardgrounds (Mitchell et al. 1993).

The significance of our finding is twofold. First, it extends the stratigraphic range of the order Crustoidea. Secondly, it clear up the puzzle of the presence of graptoblasts in the Lower Ordovician deposits.

So far, *Lapworthicrusta aenigmatica* Kozłowski, 1962 was regarded as the earliest known crustoid graptolite: it comes from a Baltic glacial boulder of the upper Arenigian or Llanvirnian age (Kozłowski 1962). Much more precisely dated remains of the Crustoidea were noted by the late Dr. Ralph Mannil (personal information in 1977) and Mierzejewski (1977) from the *Eoplacognathus pseudoplanus* Zone (= Aluojan Baltic substage, Llanvirnian) of Estonia and Baltic drift material, respectively. Moreover, Mierzejewski (unpublished data) found *Wimanicrusta* aff. *urbaneki* in Arenigian of the Isle of Öland, Sweden.

The Graptoblasti were described by Kozłowski (1949) from Wysoczki as the intriguing hemichordate-like group, comprising two genera and thirteen species (for their taxonomic status see: Kozłowski 1962; Mierzejewski 2000), and related in some way to the pterobranchs or the graptolites because their upper surface exhibits the typical fusellar pattern arranged along a distinctly zigzag line. Later, Kozłowski (1962) recognized graptoblasts as a constituent of crustoid colonies and suggested their connection with dormancy and asexual reproduction (see also: Kozłowski 1971; Urbanek 1983, 1986; Urbanek et al. 1986; Mitchell et. al. 1993; Mierzejewski 2000). Bulman (1970) treated the Graptoblasti as Graptolithina *incertae sedis* and found their relationship problematic because Kozłowski's (1949) findings of graptoblasts from Wysoczki were not associated with the Crustoidea and no crustoid graptolites had not been recorded from the Tremadocian. Mierzejewski (1977) has reported the youngest known crustoids from the Upper Silurian (Ludlow), which are associated with the youngest known graoptoblasts as well. If the specimens described here from the upper Tremadocian chalcedones of Wysoczki are indeed the remains of crustoid stolons, then the lower limits of the stratigraphic distribution of graptoblasts and crustoid remains are also coincident. Thus, the first appearance of crustoids may be in the upper Tremadocian *Drepanoistodus deltifer* conodont Zone (Szaniawski 1980). According to the late Dr. Ralph Mannil's observations (1977, and personal information in 1984), there is also coincidence in the lower limit of stratigraphic distribution of the crustoids and graptoblasts in the Lower Ordovician deposits of Estonia, namely in the Aluoja substage of Kunda Regional Stage.

Acknowledgements.—We thank our peer-revievers Dr. Michael J. Melchin (St. Francis Xavier University, Antigonish, Canada) and Dr. Charles E. Mitchell (University at Buffalo, Buffalo, USA) for reading and improving our manuscript as well as for their valuable remarks. Our work was financially supported by the Committee for Scientic Research (KBN), Poland, grant number KBN 3 P04C 03522 to Adam Urbanek. Scanning electron micrographs were made at the Institute of Paleobiology.

References

Bednarczyk, W. 1971. Stratigraphy and palaeogeography of the Lower Ordovician in the Holy Cross Mts. *Acta Geologica Polonica* 21: 574–616.

Briggs, D.E.G., Kear, A.J., Baas, M., de Leeuw, J.W., and Rigby, S. 1995. Decay and composition of the hemichordate *Rhabdopleura*: implications for the taphonomy of graptolites. *Lethaia* 28: 15–23.

Bulman, O.M.B. 1944. A monograph of the Caradoc (Balclatchie) graptolites from the limestones in Laggan Burn, Ayrshire. *Palaeontographical Society Monographs* 1: 1–42.

Bulman, O.M.B. 1970. Graptolithina, with sections on Enteropneusta and Pterobranchia. *In*: C. Teichert (ed.) *Treatise on Invertebrate Paleontology, Part V* (2nd edition) 32 + 162 pp. Geological Society of America and University of Kansas Press, Lawrence, Kansas.

Crowther, P.R. 1981. The fine structure of graptolite periderm. *Special Papers in Palaeontology* 26: 1–119.

Kozłowski, R. 1938. Informations préliminaires sur les Graptolithes du Tremadoc de la Pologne et sur leur portée théorique. *Annales Musei Zoologici Polonici* 13: 183–196.

Kozłowski, R. 1947. Les affinitiés de Graptolithes. *Biological Reviews* 92: 93–108.

Kozłowski, R. 1949. Les Graptolithes et quelques nouveaux groupes d'animaux du Tremadoc de la Pologne. *Palaeontologia Polonica* 3: 1–71.

Kozłowski, R. 1959. Les hydroides Ordoviciens à squelette chitineux. *Acta Palaeontologica Polonica* 4: 209–271

Kozłowski, R. 1962. Crustoidea – nouveau groupe de Graptolites. *Acta Palaeontologica Polonica* 7: 3–52.

Kozłowski, R. 1966. On the structure and relationships of graptolites. *Journal of Paleontology* 40: 489–501.

Kozłowski, R. 1971. Early development stages and the mode of life of graptolites. *Acta Palaeontologica Polonica* 16: 313–343.

Mierzejewski, P. 1977. The first discovery of Crustoidea (Graptolithina) and Rhabdopleurida (Pterobranchia) in the Silurian. *Bulletin de l'Académie Polonaise des Sciences. Série des Sciences de la Terre* 25: 103–107.

Mierzejewski, P. 1984. *Xenocyathus* Eisenack, 1982—a crustoid graptolite. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1984: 300–302.

Mierzejewski, P. 1986. Ultrastructure, taxonomy and affinities of some Ordovician and Silurian organic microfossils. *Palaeontologia Polonica* 46: 349–366.

Mierzejewski, P. 2000. On the nature and development of graptoblasts. *Acta Palaeontologica Polonica* 45: 227–238.

Mierzejewski, P., Urbanek, A., and Kulicki, C. (in press). Discovery of the oldest remains of crustoid graptolites and its phylogenetic significance. *North American Paleontology Convention 2005. Abstracts*. Halifax, Nova Scotia.

Mitchell, C.E., Wilson, M.A., and John, M.S. 1993. In situ crustoid graptolite colonies from an Upper Ordovician hardground, Southwestern Ohio. *Journal of Paleontology* 67: 1011–1016.

Skevington, D. 1965. Chitinous hydroids from the Ontikan limestones (Ordovician) of Öland, Sweden. *Geologiska Foreningens i Stockholm Forhandlingar* 87: 152–162.

Starmach, K. 1963. Blue-green algae from the Tremadocian of Holy Cross Mountains (Poland). *Acta Palaeontologica Polonica* 8: 451–460.

Szaniawski, H. 1980. Conodonts from the Tremadocian chalcedony beds, Holy Cross Mountains (Poland). *Acta Palaeontologica Polonica* 25: 101–121.

Urbanek, A. 1984. The significance of graptoblasts in the life cycle of crustoid graptolites. *Acta Palaeontologica Polonica* 28 (for 1983): 313–326.

Urbanek, A. 1986. The enigma of graptolite ancestry: Lesson from a phylogenetic debate. *Oxford Monographs on Geology and Geophysics* 5: 184–226.

Urbanek, A. and Dilly, P.N. 2000. The stolon system in *Rhabdopleura compacta* (Hemichordata) and its phylogenetic implications. *Acta Palaeontologica Polonica* 45: 201–226.

Urbanek, A. and Mierzejewski, P. 1984. The ultrastructure of the Crustoidea and the evolution of graptolite skeletal tissue. *Lethaia* 17: 73–91.

Urbanek, A. and Mierzejewski, P. 1986. A possible new pattern of cortical deposit in Tremadocian dendroid graptolitem from chert nodules. *In*: C.P Highes and R.B. Rickards (eds.), Palaeoecology and Biostratigraphy of Graptolites. *Geological Society Special Publication* 20: 13–19.

Urbanek, A., Mierzejewski, P., and Rickards, R.B. 1986. New observations on the fine structure of graptoblasts. *Lethaia* 19: 97–107.

Urbanek, A. and Towe, K.M. 1974. Ultrastructural studies on graptolites, 1: The periderm and its derivatives in the Dendroidea and *Mastigograptus*. *Smithsonian Contributions to Paleobiology* 22: 1–48.

Piotr Mierzejewski [mierzejewski@graptolite.net], Instytut Paleobiologii, Polska Akademia Nauk, ul. Twarda 51/55, Pl-00-818 Warszawa, Poland. Present address: ul. Filtrowa 83/49, Pl-02-032 Warszawa, Poland;
Cyprian Kulicki [kulicki@twarda.pan.pl] and Adam Urbanek [urbanek@twarda.pan.pl], Instytut Paleobiologii, Polska Akademia Nauk, ul. Twarda 51/55, Pl-00-818 Warszawa, Poland.