On the nature and development of graptoblasts

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Two specimens of graptoblasts, which provisionally may be assigned to '*Graptoblastoides*' sp. and '*Graptoblastus*' sp., are described from the early Llandovery of Anticosti Island (Québec, Canada). Previous reports of Silurian graptoblasts were restricted to a single specimen from Poland. One of the new specimens is morphologically distinct from all known graptoblasts – both chambers of the inner cavity contain numerous incomplete septae, here referred to as hemiseptae. SEM observations show distinct two-layered character of the transverse septum, whereas the hemiseptae show no trace of layering. Hemiseptae and the transverse septum are derivatives of the inner lining of the graptoblast. The 'genera' *Graptoblastus* Kozłowski, 1949 and *Graptoblastoides* Kozłowski, 1949 are interpreted as stages in graptoblast development, and are consequently replaced by the purely descriptive terms 'graptoblastus' and 'graptoblastoides'. The following stages of graptoblast development are recognized: (1) pre-graptoblastoides stage, (2) early graptoblastoides stage, (3) late graptoblastoides stage, (4) early graptoblastus stage, and (5) late graptoblastus stage. A graptoblast *s.s.* (i.e., devoid of a blastotheca) and its developmental stages strikingly resemble the earliest stages of the astogeny of the modern pterobranch *Rhabdopleura*. These observations support A.Urbanek's hypothesis that zooids became encysted within graptoblasts and rejuvenated by a process of metamorphosis.

Key words: Graptolites, graptoblasts, Crustoidea, ultrastructure, paleoecology, Silurian, Anticosti, Canada.

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Introduction

Graptoblasts are extremely rare Ordovician and Silurian organic microfossils; they were first described by Kozłowski (1949) on the basis of material from the famous exposure of late Tremadoc cherts near Wysoczki (Holy Cross Mountains, Poland). He considered them to be related in some way to the Pterobranchia or the Graptolithina, because their upper surface exhibits the typical fusellar pattern arranged along a distinctly zigzag line. Later, Kozłowski (1962) found these obscure fossils intimately associated with rhabdosomes of various crustoid graptolites. Nevertheless, Bulman (1970) treated graptoblasts as Graptolithina *incertae sedis* and found their relationship problematic because no Crustoidea had not been recorded from the Tremadoc. Finally, Kozłowski (1971) expressed the opinion that graptoblasts were produced by both crustoid and camaroid colonies, but this point of view was overlooked by later researchers. On the contrary, Mierzejewski (in Urbanek 1984) supposed that some encrusting Tremadoc graptolites, provided with a highly elaborated apertural apparatus and previously described by Kozłowski (1949) as camaroids, represent the order Crustoidea. These forms, similar in some aspects to the crustoid genus *Urbanekicrusta* Mierzejewski, 1985, may be responsible for the presence of graptoblasts in the Wysoczki material. Finally, Urbanek (1984: p. 323) stated that 'a tentative conclusion may be that graptoblasts are unique in Crustoidea'. However, the present writer has recently found a graptoblast-like dormant structures in autothecae of a camaroid graptolite from the Ordovician of Estonia (Mierzejewski 2000b).

The internal structure of graptoblasts was studied with an optical microscope by Kozłowski (1949, 1962). Further advances in graptoblast histology have been made with the transmission and scanning electron microscopes (Urbanek & Rickards 1974; Mierzejewski 1984a; Urbanek *et al.* 1986; Crowther *et al.* 1987).

The stratigraphic and palaeogeographic record of graptoblasts is scanty. Up to now, almost all the known specimens originate either from the late Tremadoc of Wysoczki or from Ordovician calcareous boulders of Baltic origin, gathered at various localities in central and northern Poland (Kozłowski 1949, 1962). In addition, the late Dr. Ralph Männil (personal information, 1985) found several specimens in Ordovician limestones of Estonia. More recently, Mitchell *et al.* (1993) described *in situ* colonies of crustoid graptolites with well-preserved graptoblasts from the Ordovician of Ohio (U.S.A.). The youngest record seems to be the specimen referred to as *'Graptoblastoides'* sp. and associated with the youngest known member of the Crustoidea, namely *Bulmanicrusta latialata* Kozłowski, 1962 from a Ludlow erratic boulder found in glacial deposits of Poland (Mierzejewski 1977). Fine structure of this graptoblast was studied by Urbanek *et al.* (1986).

Eisenack (1970) interpreted the enigmatic Ordovician organic microfossil *Xenotheka klinostoma* Eisenack, 1937 as a graptoblast, but recently Mierzejewski (2000a) has recognized it as the autotheca of a camaroid graptolite.

The purpose of this paper is to describe an intriguing find of early Llandovery graptoblasts from Anticosti Island (Québec, Canada). This is the first extra-European (and only the second world-wide) discovery of Silurian graptoblasts. Moreover, some biological aspects of these peculiar elements of graptolite colonies are discussed.

Material, techniques and terminology

The material used in this investigation comes from a sample of nodular limestone collected by Professor Lech Teller (Warsaw) during field work on Anticosti Island in 1981. The sample was gathered from the well known locality named A-5C, Beescie Formation, member 4, early Llandovery (see Barnes *et al.* 1981).

The material was extracted by dissolving the sample in formic acid, using standard techniques for graptolite work. The acid resistant residuum contained two graptoblasts, associated with a rich and varied assemblage of organic microfossils (scolecodonts, chitinozoans, and periderm fragments of an unidentified crustoid graptolite) and conodonts. The graptoblasts were cleaned of mineral impurities in hydrofluoric and nitric acids, dehydrated in graded ethanol solutions and propylene oxide, coated with gold--palladium, and studied with a Cambridge Stereoscan 180. The specimens have been deposited at the Institute of Palaeobiology, Polish Academy of Sciences, Warsaw (ZPAL).

The terminology adopted for the major features of graptoblasts is that of Urbanek *et al.* (1986). The new term **hemiseptum** (plural **hemiseptae**) is defined herein for the incomplete septae in the anterior and posterior chambers of the graptoblastus inner cavity.

There are some problems concerning taxonomy. Kozłowski (1949) introduced a classification of graptoblasts and erected two new 'genera', namely *Graptoblastoides* Kozłowski, 1949 and *Graptoblastus* Kozłowski, 1949, and twelve new 'species'. While these 'generic' and 'specific' names are in accordance with nomenclatural rules of ICZN, Kozłowski (1962) was of the opinion that his 'taxa' and classification should be regarded as a parataxonomic system, independent of graptolite systematics, because they were not intended to identify species in any biological sense. To avoid any taxonomic implications, the writer prefers to introduce two new purely descriptive terms, viz. a graptoblastus and a graptoblastoides, for two morphological stages of graptoblasts represented by the 'genera' *Graptoblastus* and *Graptoblastoides*.

Morphological observations

Graptoblastoides No. 1 (Fig. 1). — This complete graptoblastoides is wide, flat and almost square with a double cryptopyle, a well-developed talus and a short fragment of stolon. The blastotheca seems to have completely peeled away, but a characteristic fusellar pattern on the upper surface is still visible. In transmitted infrared light no traces of a transverse septum or hemiseptae (see below) have been observed. The specimen is 0.77 mm long and 0.83 mm wide; it closely resembles the form described by Kozłowski (1962: fig. 8) from an Ordovician glacial boulder.

Graptoblastus No. 1 (Figs. 2, 3). — The specimen is not preserved completely, because the lower wall (floor of some authors) is absent (Fig. 2A). This rather flat specimen is provided with a short fragment of stolon. It is 1.55 mm long and 0.81 mm wide. The blastotheca has peeled off, but impressions of its fusellar sutures are visible on the outer surface of the blastocrypt. The lack of this outer component of the graptoblast wall means that the fine structure of the blastocrypt can be observed (Fig. 3). It is almost identical to Ordovician forms described by earlier authors (Urbanek & Rickards 1974; Urbanek *et al.* 1986) and is built of a homogenous material perforated by a system of parallel canaliculi, perpendicular to the surface of the graptoblast. The inner surface of the blastocrypt is covered by a well-developed, slightly crushed inner lining (Fig. 2). The inner cavity is divided by the transverse septum into an anterior chamber, 0.68 mm long, and a posterior chamber, 0.72 mm long (Fig. 3). Both chambers are partially subdivided by short septae: hemiseptae. Hemiseptae are distributed along the lateral margins of chambers, quite regularly but not symmetrically. There are no evident differences in shape and dimensions of these element in either chamber. The distal ends of some hemiseptae in the anterior chamber are fused together, forming 'cells'. The anterior chamber is more distinctly subdivided than the posterior chamber. However, this is not caused by a stronger development of hemiseptae but is a consequence of the difference in chamber width – the posterior chamber being much wider than the anterior chamber.

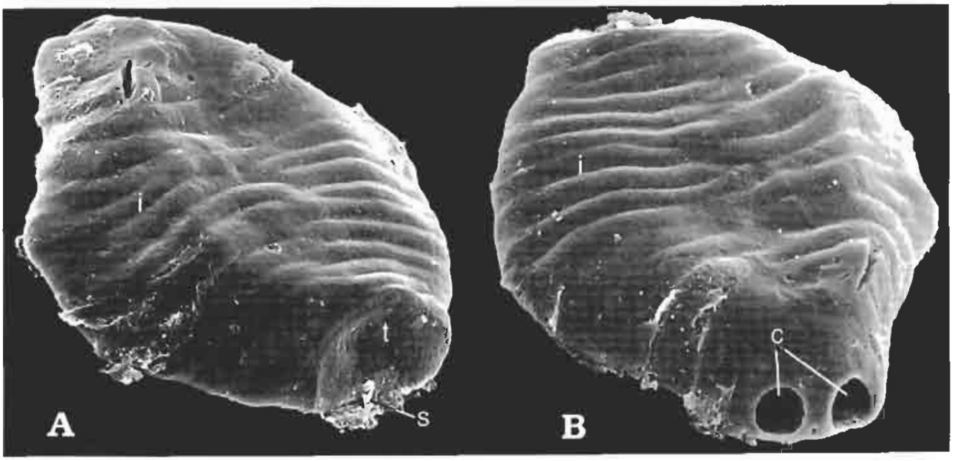

Fig. 1. Graptoblastoides No. 1. Anticosti Island, locality A-5C, Beescie Formation, member 4 (early Llandovery), ZPAL G/25/1. SEM micrographs. **A**. View showing the talus, × 40. **B**. View showing the cryptopyle, × 40. Abbreviations: **c**, cryptopyle; **i**, imprints of fuselli; **t**, talus; **s**, remnant of the stolon.

SEM micrographs show very clearly the two-layered character of the transverse septum (Fig. 2B). Both layers are of equal thickness and pass smoothly into the inner lining of the cavity. The hemiseptae and both layers of the transverse septum appear structureless. The bipartite character of the hemiseptum shown in Fig. 2B is an artifact caused by cracking. The inner lining shows traces of lamination. The cryptopyle is only partially preserved because its lower margin is truncated.

Developmental stages of graptoblasts

Until very recently, two morphological types of graptoblasts have been recognized differing in form of the inner cavities i.e. the graptoblastoides and the graptoblastus. The inner cavity of the graptoblastoides is devoid of any internal structures, whereas the cavity of the graptoblastus is subdivided into anterior and posterior chambers by a transverse septum. As a rule, the anterior chamber is smaller than, or at the very most equal to the posterior chamber. In contradistinction to all previously described graptoblasts, the specimen described above as the graptoblastus No. 1 has both chambers subdivided by several incipient hemiseptae. Thus, a morphological series of graptoblasts may be distinguished by the form of the inner cavity, i.e., (1) graptoblastoides, devoid of any internal structures (2) graptoblastus, provided with a transverse septum (3) graptoblastus, provided with both transverse septum and hemiseptae.

The occurrence of transverse septae and hemiseptae in the inner cavity of graptoblasts may be especially important from the biological point of view. It may be the key to a better understanding of these mysterious fossils. Previous authors did not discuss the significance of the division of the inner cavity when deliberating on the nature of graptoblasts. Only Urbanek (1984: p. 139) made a short remark that this phenomenon 'may be evidence of two stages in the morphogenetic changes during the latent period'.

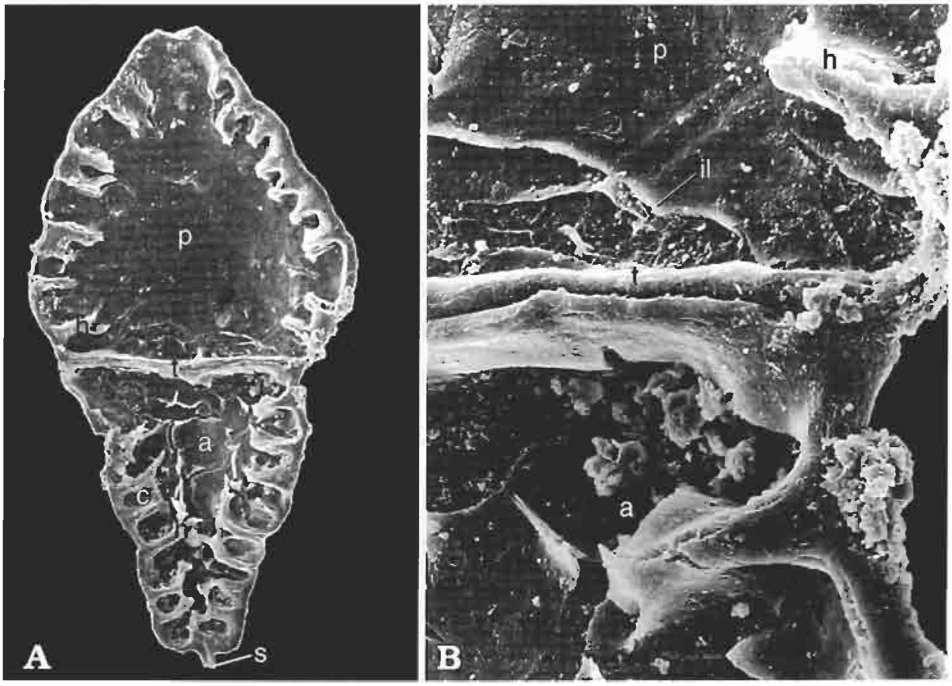

Fig. 2. Graptoblastus No. 1. Anticosti Island, locality A-5C, Beescie Formation, member 4 (early Llandovery), ZPAL G/25/2. SEM micrographs. **A**. View of graptoblast inner cavity showing the transverse septum and hemiseptae, × 55. **B**. Deatils of the transverse septum and hemiseptae, × 270. Abbreviations: **a**, anterior chamber; **bl**, blastocrypt; **c**, cell; **h**, hemiseptum; **il**, inner lining; **p**, posterior chamber; **s**, remnant of the stolon (filum); **t**, transverse septum.

Some peculiar morphological features of the graptoblastus under study may help to clarify the biological nature of graptoblasts. These features are as follows: (1) the two-layered structure of the transverse septum; (2) the continuity between the inner lining and layers of the transverse septum; (3) the presence of hemiseptae, developed equally in both chambers of the inner cavity; and (4) the formation of cells inside the anterior chamber.

The relationship between the transverse septum and other elements of the graptoblasts seem to be of a special interest. The previous authors have discussed the origin of this septum and its fine structure: a longitudinal section of the graptoblastus by Kozłowski (1949: fig. 64) suggests that it was formed by evagination of the blastocrypt; Urbanek (1984: fig. 1) was of the same opinion. The present observations, however, leave no place for such an interpretation. As shown in Fig. 6, each layer of the transverse septum is simply a continuation of the inner lining. This can be interpreted in the following manner. The inner lining was formed secondarily, somewhat later over the inner surface of the blastocrypt, growing gradually during as the graptoblast developed. At this time, it was secreted evenly, forming a thin, additional envelope for the soft tissues infilling the inner cavity. Next, during the process of terminal zooid metamorphosis, these soft tissues divided into two independent masses, anterior and posterior. Each mass continued to secrete an envelope secretion, thereby forming two hermetically sealed capsules separated by a transverse septum. Thus, the transverse septum is here considered to be a

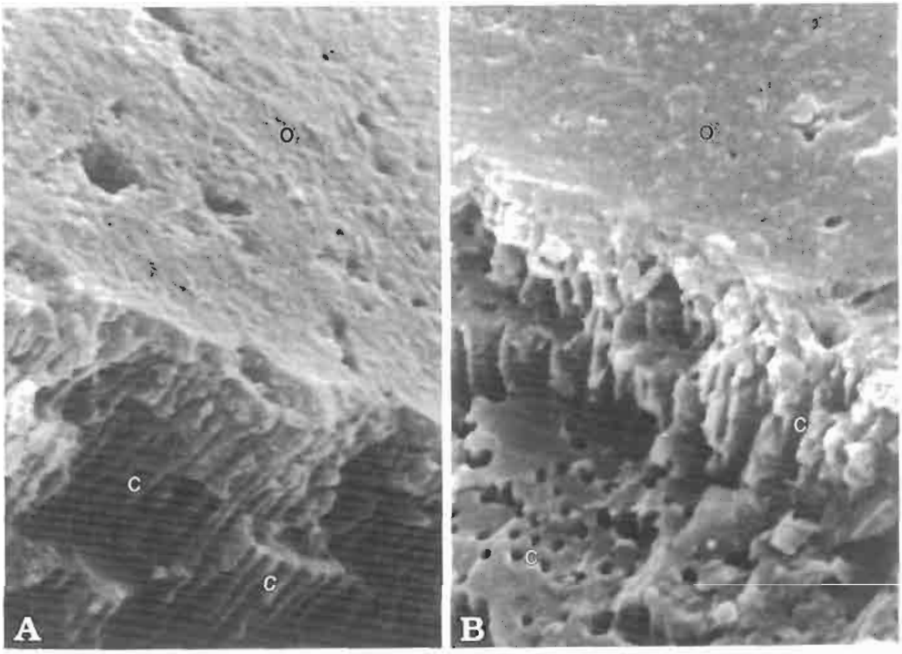

Fig. 3. Graptoblastus No. 1. Anticosti Island, locality A-5C, Beescie Formation, member 4 (early Llandovery), ZPAL G/25/2. SEM micrographs. **A**, **B**. Fine structure of the fractured blastocrypt, × 3000. Abbreviations: **c**, canaliculi of the blastocrypt; **o**, outer layer of the blastocrypt.

structure formed by the intimate contact of both capsules' walls. Further secretions made the walls (and consequently the transverse septum) distinctly thicker.

Until now, hemiseptae were unknown. It is clear that they are protrusions of the graptoblast inner lining, and were undoubtedly formed within invaginations of the epithelium which covered the two masses of soft tissue. Both masses of soft tissue in graptoblastus No. 1 must represent the same phase of organization and secretory activity because hemiseptae in the anterior and posterior chambers are very similar in form and length. Moreover, both layers of the transverse septum are of equal thickness.

At least three different interpretations of hemiseptae are possible: (a) hemiseptae were abnormalities in the growth sequence which occured only sporadically in graptoblasts; (b) hemiseptae were normal structures which appeared in the late stages of a grapotoblast's development; or (c) hemiseptae were restricted to specific graptoblasts of a type so far unknown.

On first consideration, all interpretations seem possible. However, there appears to be a morphological series leading from (1) a graptoblastoides form, in which the inner cavity is devoid of any internal structure, through (2) a graptoblastus form, in which the inner cavity is divided into two chambers, to (3) a graptoblastus form (represented by the specimen No. 2), in which the two chambers are partially divided by hemiseptae. In the writer's opinion, these three forms of graptoblast represent successive stages of ontogenetic development. If this interpretation is correct, it seems probable that graptoblast development followed these steps:

(1) Pre-graptoblastoides stage (Fig. 4A). This hypothetical stage was described by Urbanek (1984) as 'the young growth stage of a graptoblast'. It is distinguished by the presence of a diaphragm separating a terminal chamber from the rest of the stolotheca (housing a terminal zooid which would later become the proper graptoblast inhabitant). At this stage the wall is composed of only one layer, made of fuselli, forming the blastotheca.

(2) Early graptoblastoides stage (Fig. 4B). Now the wall comprises two layers, i.e., a fusellar blastotheca and a porous blastocrypt. The appearence of the blastocrypt marks the primary phase of zooid encystment and the formation of a true graptoblast.

(3) Late graptoblastoides stage (Fig. 4C). This is marked by the appearance of the third layer of the wall – a thin homogenous inner lining. The zooid encystment is completed.

(4) Early graptoblastus stage (Fig. 4D). The inner cavity of the graptoblast is divided transversely into two chambers (anterior and posterior). The two-layered structure of the transverse septum and its conformity with the inner lining are evidence that the zooid subdivided into two daughter masses, both of which continued to secrete their inner lining material, independently.

(5) Late graptoblastus stage (Fig. 4E). At this stage the anterior and posterior chambers are divided into a number of sacs by hemiseptae extending from the inner lining. The almost identical form of both chambers suggests that their inhabitants displayed similar biological activity.

In discussing the question of graptoblast development, it is worth comparing the fine structure of graptoblastoides specimens studied by earlier authors. Urbanek *et al.* (1986: p. 105) stated that: 'There are only traces of an inner lining in one of the Urbanek & Rickards (1974: pl. 16: 1) specimens, whereas the inner lining in the present specimens is very distinct'. This comparison clearly suggests that the former graptoblasts represent the early graptoblastoides stage of growth and the latter the late graptoblastoides stage.

According to Kozłowski (1962), the cryptopyle was formed in the graptoblast wall probably by resorption in the post-dormant period. According to Urbanek's (1984) interpretation of graptoblast function, the appearence of the cryptopyle should be regarded as the last stage of graptoblast development. The writer does not reject this point of view and is of opinion that the appearance of the cryptopyle was not correlated either with the formation of the inner lining or its derivatives (transverse septum, hemiseptae). It is quite clear that the formation of the cryptopyle was dependent upon two factors: (1) biological maturity and ability to germinate; and (2) favourable environmental conditions. It may be that when adverse conditions were long lasting, the graptoblast inhabitant became subject to biological processes connected with ageing. For example, degeneration leading to atrophy or to teratological changes and necrosis. Thus, one should not exclude the possibility that the appearance of the transverse septum and hemiseptae was due to ageing. This explanation might yet be the best solution to the mystery of the graptoblast inner cavity divisions, but further detailed study of this problem is required. According to Professor A. Urbanek (personal information 1999), the late graptoblastus stage may be compared to strobila, i.e., sessile polyp-like form which divides horizontally to produce jellyfish larvae.

It is worth mentioning here that Professor C.E. Mitchell as a referee was of the opinion that the different forms of graptoblasts documented here might just as readily be different types of encystment intended to survive different types or durations of unfavourable conditions.

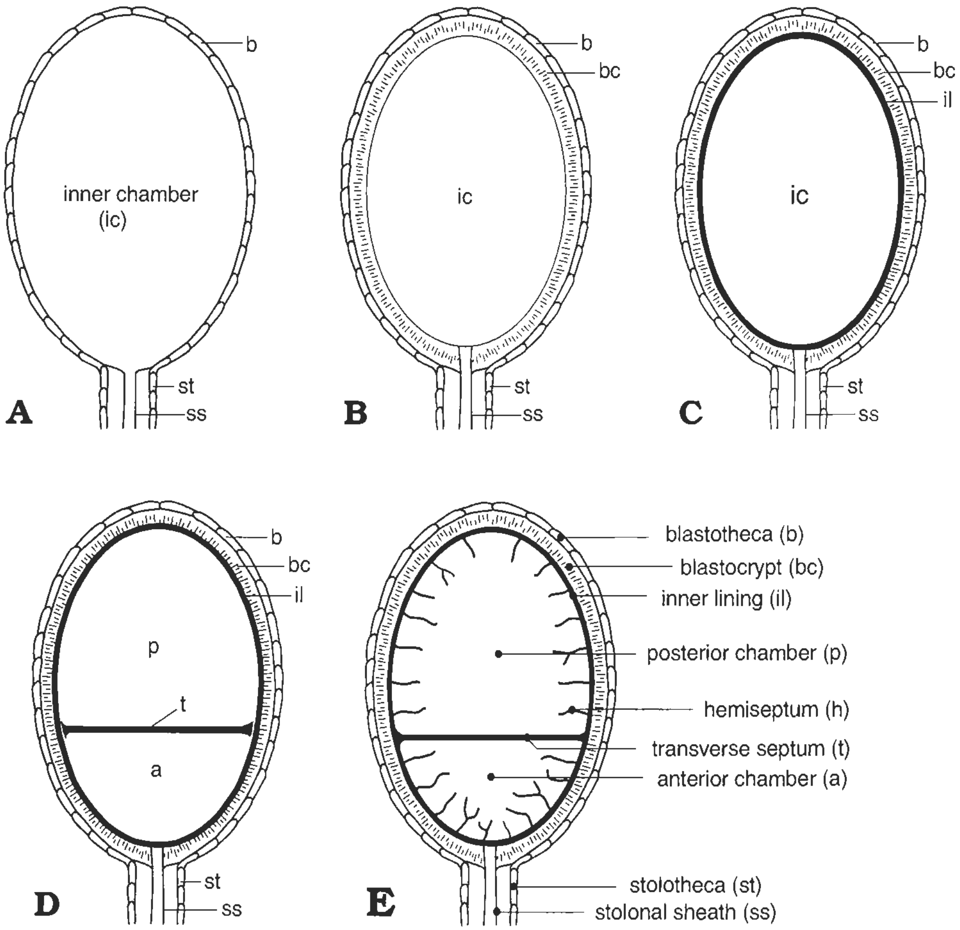

Fig. 4. Diagrams illustrating the developmental stages of the graptoblast. **A**. Pregraptoblastoides stage. **B**. Early graptoblastoides stage. **C**. Late graptoblastoides stage. **D**. Early graptoblastus stage. **E**. Late graptoblastus stage.

Nature of graptoblasts

Several opinions about the biological significance of graptoblasts have been published. Kozłowski (1949) supposed that they were related in some way to asexual reproduction. Later, he was of the opinion that graptoblasts have no analogue among recent animals, and threfore that their adequate interpretation is rather impossible (Kozłowski 1962). Finally, Kozłowski (1971) equated them tentatively with bryozoan statocysts. Urbanek & Rickards (1974: p. 186) suggested that the 'most plausible interpretation is that graptoblasts were formed as a result of degeneration of zooids on the growing tips of branches, followed by their encapsulation'. Later, Urbanek (1984) regarded graptoblasts as closed, resting terminal portions of the stolothecae, containing dormant buds, and he compared them to the hibernaculae of ctenostomate bryozoans. He pointed out that graptoblast zooids could never have functioned actively as feeding zooids. Lastly, Urbanek *et al.* (1986:

p. 101) defined the graptoblast as 'a widening of the sealed terminal portion of stolotheca resulting in an ovoid body composed of a blastotheca and a blastocrypt'. Urbanek's (1984) hypothesis was supported by observations of Mitchell *et al.* (1993).

The writer presents below some new thoughts about the biological nature of graptoblasts. He is of the opinion that the developmental stages described herein may be best interpreted by comparison with the initial stages of modern rhabdopleurid pterobranchs. It is noteworthy that these hemichordates constitute a group which in numerous respects closely resembles crustoids (Kozłowski 1962, 1966; Andres 1980; Urbanek & Mierzejewski 1984).

Schepotieff (1907) first described the initial part of recent *Rhabdopleura normani* Allman colonies. The larval development of *Rhabdopleura* has been studied in detail by Stebbing (1970) and Dilly (1973, 1985). According to their observations, the planuloid and ciliated larva settles and encapsulates itself completely within a sealed vesicle, called an 'embryonal vesicle' or 'dome'. The embryonal vesicle is provided with a lower, thin and flat attachment surface, named a 'floor', and an upper, thick and hemisphaerical wall. The entire structure differs from the rest of the coenecium in its lack of fusellar bands. The external surface is pitted with small, regularly or irregularly distributed holes of unknown origin, penetrating a short distance. After a short time, the encapsulated larva metamorphose and modifies its dome. It usually builds an incomplete transverse septum, dividing the dome near its widest point into two compartments. The function of the septum is not known. Judging from Dilly's (1985: pl. 2: a, c, e) micrographs, the septum seems to be bipartite and fluently expands on the inner surface of the dome forming an additional layer of the wall (inner lining). Finally, the larva, the graptoblast inhabitant, pierces a hole in the wall and escapes from the dome, in similar manner to the graptoblast inhabitant.

It is clear that the various structures of a rhabdopleurid embryonal vesicle all have their equivalents in the morphology of a graptoblast *sensu stricto*, i.e. graptoblast devoid of the blastotheca (= graptoblast proper of Urbanek & Rickards 1974; for further explanation of the term see Urbanek *et al.* 1986: p. 101). Moreover, graptoblast development is fully comparable with growth modifications of the prosicular stage in *Rhabopleura*. This suggests that the metamorphosed graptoblast zooids were very similar in morphology to larvae formed during sexual reproduction. The inevitable conclusion is that there were two types of free-moving larvae in the life cycle of crustoid graptolites connected with sexual or asexual reproduction.

It should be stated that the writer's observations and conclusions support Urbanek's (1984: p. 322) hypothesis that encapsulated graptoblast zooids rejuvenated during a process of metamorphosis. Urbanek supposed that the rejuvenated zooid produced small, probably planuloid and ciliated, reproductive bodies (propagules), which were ejected through the cryptopyle and responsible for the formation of new colonies. However, I prefer an alternative suggestion, previously rejected by Urbanek (1984), that the metamorphosed graptoblast inhabitant, once rejuvenated to a free-moving form and having built a structure similar to a rhabdopleurid embryonal vesicle, behaved consistently like a *Rhabdopleura* larva. In other words, it not only pierced the hole but also emerged through it. At this point, unlike the rhabdopleurid larva, it did not built an erect tube but swam away instead and settled to form a new colony. It is clear that for such an interpretation, the concept of hypothetical propagules is unnecessary.

Graptoblasts and paleoecology of the Crustoidea

As is well known, there is a very extensive literature on the palaeoecology of the Graptolithina. However, palaeoecologic knowledge of crustoid graptolites is still insufficient. The main reason for this situation is that they are extremely rare fossils and their known record is often limited to tiny fragments of isolated autothecae (Kozłowski 1962; Mierzejewski 1977, 1984b, 1985, 1988). Only in exceptional cases, one can find small fragments of colonies consisting of uniserial or biserial chains of autothecae. The nature of the fossil record is easily explaired, because most fossils were obtained by chemical methods. The morphology of crustoid autothecae suggests that they were attached to the substrate by their lower, structureless surfaces and formed incrusting colonies, resembling those of recent *Rhabdopleura* (Kozłowski 1962, 1966). Combining ecological information about mode of life and occurence of living rhabdopleurids with the striking similarity in morphology between the Crustoidea and the Rhabdopleurida, one may suppose that crustoid graptolites built colonies encrusting a firm substrate at moderate depth in relatively cold water. It is remarkable that chemically isolated crustoids were usually derived from marly limestones yielding tabulates, bryozoans, brachiopods, annelids, molluscs, pterobranchs and various benthic graptolites.

Unexpectedly, graptoblasts, in spite of their rarity, have begun to play an important role in discussions on palaeoecology of the Crustoidea. First, as noted above, Urbanek (1983) assumed that the presence of graptoblasts in crustoids was an adaptation allowing the species to survive adverse conditions when the rest of colony disintegrated. This point of view was fully supported by the important observations of Michell *et al.* (1993) on *in situ* colonies of *Bulmanicrusta*? sp. encrusting the surface of a hardground from the Upper Ordovician of Ohio, U.S.A. These authors were of the opinion that crustoids routinely produced graptoblasts, which presumably should be treated as a normal part of crustoid ecology. According to them, the Crustoidea 'were probably ecological opportunists of very low to low spatial persistence, and were adapted to inhabiting ephemeral or disturbing prone habitats in a shallow-water, low-latitude environment' (Mitchell *et al.* 1993: pp. 1014–1015). It is worth mentioning that Professor C.E. Mitchell in his review of this paper wrote as follows: 'The reproductive role of graptoblasts (...) seems to me entirely consistent with our view of these organisms as pioneering encrusters. The ability to produce mobile asexual larvae quickly following the return of favorable conditions would be of clear benefit to an opportunist colonizer of hard substrates.'

It is interesting to note here some entirely different observations made by myself (Mierzejewski unpublished). In 1985, I had the opportunity to study several *in situ* graptolite colonies encrusting surfaces of different calcareous fossils, namely nautiloids and echinoderms, originating from Ordovician deposits of Estonia. These forms, now housed at the Institute of Geology, Technical University of Tallinn (Estonia), were previously described by Öpik (1928, 1930) and Obut (1960, 1964) as dendroids and dithecoids. Kozłowski (1962 and personal communication 1975) regarded them as members of the Crustoidea; Bulman (1970) allocated them in the crustoid family Hormograptidae. When studying these graptolites, I found that the majority of colonies were provided with distinct terminal stolothecae, but there were no traces of graptoblasts. These colonies were very similar in shape to that of Mitchell *et al.* (1993). Therefore, one may suppose that graptoblasts may be not constant constituents of crustoid colonies, at least in the Hormograptidae. Moreover, the fact that two colonies of graptolites under discussion, assigned to *Hormograptus ramulus* (Öpik 1928), were found on the inner surface of a nautiloid shell shed new light on the crustoid mode of life. Thus, it is now clear that not all members of the Crustoidea were inhabitants of disturbance-prone environments, as it was suggested by Mitchell *et al.* (1993), because some of them inhabited cryptic environments, such as concave molluscs shells (as do Recent forms of *Rhabdopleura*, see Stebbing 1970). Presumably, there were any number of other suitable host shells for crustoids, e.g., empty skeletons of echinoderms, moults of arthropods, shells of brachiopods, and holes in rocks made by various borers. Such habitat was very favorable for colony survival and avoiding adverse conditions. It seems possible that crustoids inhabiting cryptic environments did not produce graptoblasts at all.

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O naturze i rozwoju graptoblastów

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Streszczenie

Z wapieni wczesnego landoweru wyspy Anticosti (Kanada, Quebec) opisano dwa graptoblasty. Jest to pierwsze znalezisko sylurskich graptoblastów na obszarze pozaeuropejskim. Reprezentują one oba dotychczas znane parataksonomiczne „rodzaje”, a mianowicie *Graptoblastus* Kozłowski, 1949 i *Graptoblastoides* Kozlowski, 1949.

Zbadany graptoblastus No. 1 ma we wnętrzu swoich obu komór nieznane dotąd niepełne przegrody, dla których wprowadzono nazwę hemiseptae. Wyrażono pogląd, że formy graptoblastoides i graptoblastus reprezentują kolejne stadia w rozwoju osobniczym graptoblastów. Zwrócono uwagę na uderzające podobieństwo graptoblastów do najwcześniejszych stadiów rozwojowych larwy współczesnej *Rhabdopleura* Allman, 1869 (Pterobranchia, Rhabdopleurida). Zdaniem autora, w graptoblastach zachodził proces metamorfozy pączka terminalnego do swobodnie poruszającej się larwy, wydostającej się na zewnątrz poprzez cryptopyle.