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THE SIGNIFICANCE OF GRAPTOBLASTS IN THE LIFE CYCLE OF CRUSTOID GRAPTOLITES

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Graptoblasts are small ovoid bodies with a flat lower, and a convex upper, wall, the latter provided with a costulation having a fusellar aspect. First found as isolated bodies associated with graptolite remains, graptoblasts were later recognized as a constituent of crustoid colonies (Kozłowski 1949, 1962). Their biological role remains largely enigmatic. The view that graptoblasts were formed within the authothecae is rejected and a conclusion is advanced that graptoblasts were closed, resting terminal portions of the stolothecae, housing encysted dormant zooids. They may be compared with the resting terminal zooids in *Rhabdopleura* and with the hibernacula of ctenostome bryozoans. Grapto-blasts provided an adaptation allowing the species to survive the periods of adverse conditions when the rest of the colony disintegrated. One could hypo-thesize that after germination the graptoblasts produced small propagules ejected through a narrow cryptopyle and forming new colonies after they settled on the substrate.

K e y   w o r d s : Graptoblasts, Graptolithina, Crustoidea, dormancy, germination, propagules, life cycle.

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ESSENTIAL DATA ON GRAPTOBLASTS

Graptoblasts are small, ovoid or vesicular bodies, with flat lower and convex upper walls, made of organic material and described by Kozłowski (1949) as a provisional group of fossils in some way related to graptolites or pterobranchs (fig. 1). This preliminary conclusion was convincingly confirmed in his later studies (Kozłowski 1962). He established that graptoblasts found *in situ* are intimately associated with the colonies of the Crustoidea. These observations which solved in general the problem of the morphological nature of graptoblasts have recently been completed by a rather detailed analysis of their micromorphology and ultrastructure (Urbanek and Rickards 1974; Urbanek, Mierzejewski and Rickards, in press). Yet, in spite of a considerable growth of know-

ledge of the structural details, the biological role of graptoblasts remains enigmatic. It is intuitively restricted to their fairly vague relation with some mode of asexual reproduction (Kozłowski 1949, 1962, 1971).

The description of the graptoblast morphology and fine structure may be found elsewhere (see papers cited above) while, for the purpose of the present study, it is enough to emphasize the double nature of their wall. It consists of a fairly thin outer layer revealing all features of a fusellar tissue and a thick, inner opaque or electron dense layer made of a peculiar material which abounds in numerous canaliculi (Urbanek and Rickards 1974). Recent observations indicate that these two components are present both in the upper wall, where they are quite thick, and in the lower wall in a much more attenuated form.

Each graptoblast, when completely preserved, is therefore provided with a double encasement: the outer layer produced by the entirety of the fuselli and named *blastotheca*, and the inner lining built solely of
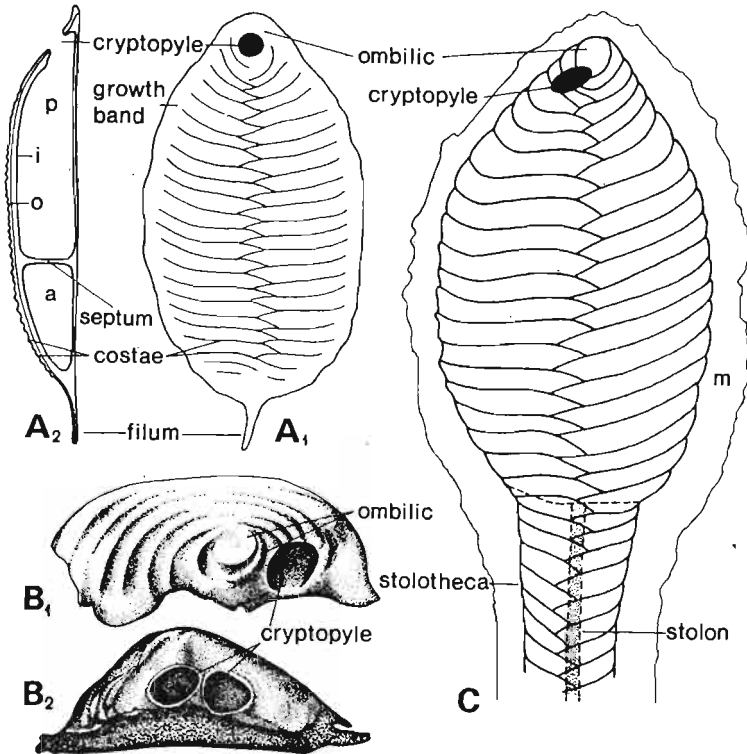

Fig. 1. Main features of morphology of the graptoblasts; A_1—A_2 top view and longitudinal section of *Graptoblastus* Kozłowski; B_1—B_2 single and paired cryptopyle (monorhinal and diplorhinal conditions), C — relation of a graptoblast to the parental stolotheca within a crustoid colony. The subdivision of the inner cavity into two chambers (a, p) as shown on A_2 occurs only in some graptoblasts ("genus" *Graptoblastus*) but is absent in others ("genus" *Graptoblastoides*). (From Kozłowski, modified) i — inner component of the wall, (= blastocrypt), l — lower surface, m — marginal (basal) membrane, o — outer component of the wall, (= blastotheca).

electron dense fabric with numerous canals and termed *blastocrypt* (Urbanek, Mierzejewski and Rickards, in .press, comp. fig. 2 B—D, herein). The fusellar component is frequently peeled off leaving only some imprints of fuselli and a zig-zag suture on the upper surface of the blastocrypt ("costulation").
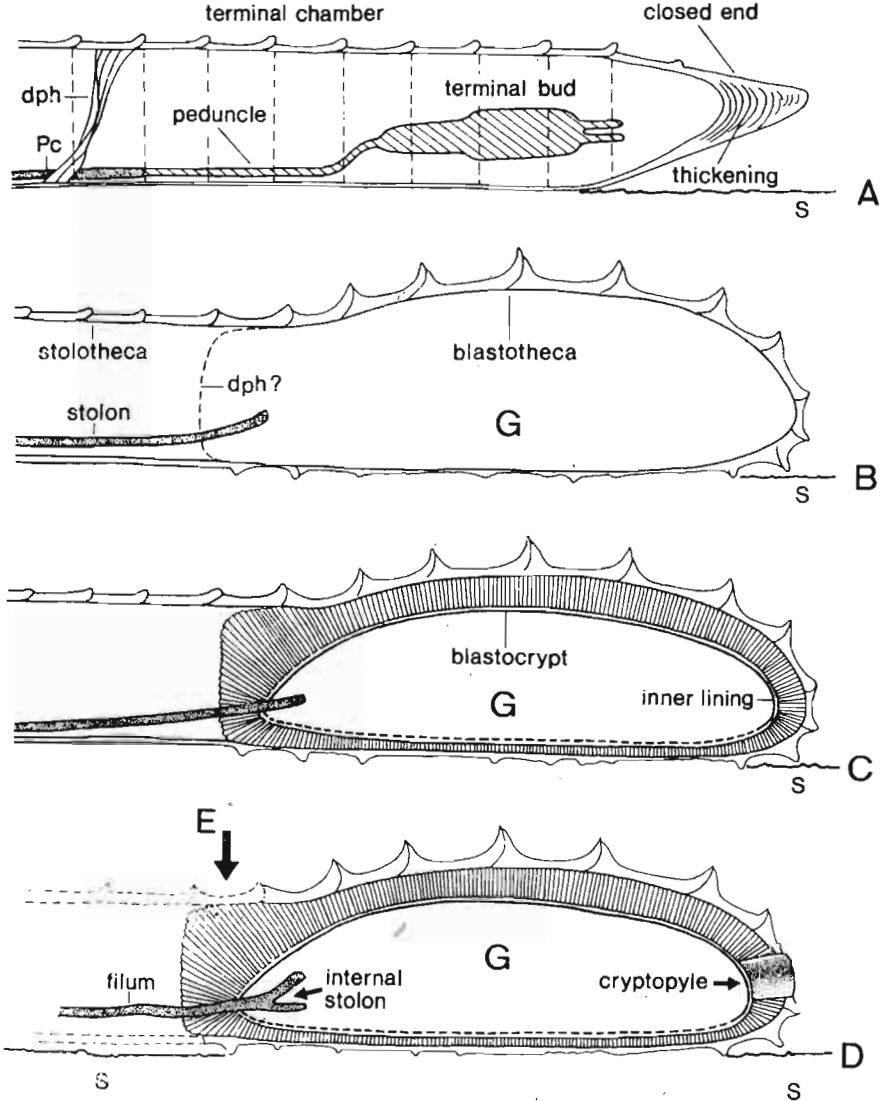

Fig. 2. Homology of the terminal chamber of a resting creeping tube in *Rhabdopleura* (A) with the young growth stage of a graptoblast (B) as well as further developmental stages of the latter showing the formation of the blastocrypt (C) and cryptopyle (D). Note the destruction of the stolotheca in D due to the environmental factors (E). Legend: dph = diaphragm separating terminal chamber from the rest of the tube, presence of such diaphragm in B is questionable, the transverse septum being probably provided only later by the blastocrypt as shown in C, G = graptoblast, pc = pectocaulus, a stolon provided with peridermal sheath, s = substrate. Further explanations in text.

Both components of the graptoblast, though intimately fused, were secreted separately, the blastocrypt being secondarily formed within the blastotheca (fig. 2, C). The latter component is anatomically an equivalent of a graptolite theca but differs from the standard theca to some degree. It is sealed during the resting period, then develops a peculiar single or paired opening (crystopyle) formed most probably due to resorption (fig. 2 D). Kozłowski (1962) provided evidence of a direct relation between the parental stolotheca and the daughter graptoblast in the crustoid colonies, the blastotheca being a direct continuation of the stolothecal wall. The stolon extends into the graptoblast, and a short fragment of it is preserved in the majority of the cases as a rudimentary appendix, the filum (Kozłowski, 1949, 1962). New observation show that the stolon penetrates well into the graptoblast cavity, and may split into branches (fig. 2, D). This suggests that a single graptoblast could house more than one zooid: a paired cryptopyle (diplorhinal condition fig. 1 B_1) might indicate the presence of at least two zooids, while a single cryptopyle (monorhinal condition fig. 1 B_2) may imply a sole inhabitant.

MORPHOLOGICAL HOMOLOGIES AND FUNCTIONAL SIMILARITIES

After the reconsideration of Kozłowski's (1962) data and specimens I have found his statement that the graptoblast is "formed inside" or "occurs within" some autothecae of crustoids inadequate. The fusellar layer of the graptoblast, (the blastotheca) is a direct continuation of its parental stolotheca and its growth bands are without interruption passing into the fusellar system of the upper wall of the graptoblast (fig. 1 C, fig. 2 B). At the same time Kozłowski regarded those fuselli as the upper wall of the autotheca, containing the given graptoblast. Such autothecae are, hovewer, devoid of an aperture and an apertural apparatus, and the graptoblast fills completely their inner cavity. In fact, such "autothecae" were no more than completely closed fusellar encasements of graptoblasts, which never functioned actively. Zooids encysted in the graptoblasts were the only inhabitants of such thecae which never contained any additional autothecal zooids. In other words, there are no reasons to classify these modified thecae as autothecae, except that they developed as a direct extension of the parental stolotheca. Much more convincing and coherent seems the approach suggested in this paper and regarding the graptoblasts as sealed, resting terminal portions of the stolothecae. (fig. 2 B). This provides a certain analogy with the closed, characteristically pointed terminal portions of the creeping zooidal tubes (= stolothecae) in *Rhabdopleura*, as described by Schepotieff (1907: pl. 22, figs. 10—13), formed most probably during an arrest of the growth of the colony (fig. 2 A. herein).

Similarly, certain stolothecae in crustoid colonies were subject to an arrest of their growth and produced instead of a subsequent triade, only a single closed theca, the graptoblast. Its fusellar covering, the blastotheca, was later underlain by a secondary inner layer forming the blastocrypt, a morphological effect of encystation of some sort, combined most probably with a resting period (fig. 2 B—C).

While the actively growing creeping tubes in *Rhabdopleura* have their ends open (Lankester 1884), there is no clear evidence that the formation of their closed terminal portions is related to the arrest of growth of the colony. Such an explanation follows, however, from Schepotieff's (1906, 1907) observations that the sealed and pointed portions of the tubes are usually preceeded by a number of closed chambers containing buds at early growth stages (Schepotieff 1907: pl. 22, fig. 13) or even provided a termination of branches made exclusively of chambers with cysts (*ibidem*: pl. 22, fig. 11). A complete colony may exhibit a number of growing tips most of which concurrently ceased to grow and are closed (Schepotieff, 1906: pl. 25, fig. 1). Substantial part of Schepotieff's material was collected in the autumn off Bergen (Norway) which also seems relevant to the explanation suggested. The sealing and heavy thickening of graptoblasts provides a striking analogy with the resting zooecia or *hibernacula* of some ctenostome bryozoans (fig. 3). These closed, thick-walled dormant zooecia are considered to be a common adaptation to promote survival during the periods of unfavourable or wholly adverse conditions.

Two kinds of hibernacula (fig. 3) have been recognized in some ctenostome bryozoans, e.g. in the well-known species *Victorella pavida* (Kent) and *Paludicella articulata* (Ehrenberg). Some hibernacula are fixed to the substrate and formed directly on the creeping stolons. They are highly modified, nodular thick-walled zooecia, rather variable in size and form. The other kind of hibernacula appears on branches above the substrate and represents arrested buds of a polypide, coated with a thickened cuticle having a spindle-like or rounded shape (Braem 1911, 1914, 1951, Wiebach 1958, Carrada and Sacchi 1964, Ryland 1970). Graptoblasts, in their adaptive aspect, are more similar to the first type of hibernacula, while both the graptoblasts and the incrusting hibernacula bear resemblance to the sessile statoblasts (sessoblasts, S statoblasts) of phylactolaemate bryozoans. Statoblasts are also dormant bodies attached to the substrate and providing a means of persistent occupation of a given location (Lacourt 1964). There is, however, a basic morphological difference between the hibernacula and the graptoblasts on the one hand and the statoblasts on the other. While the hibernaculum and the graptoblast are zooids arrested on a certain growth stage, capable of dormancy, and provided with a thickened periderm (zooecium, theca) — the statoblast, like the gemmules of sponges, is essentially only an aggregate of undiffe-
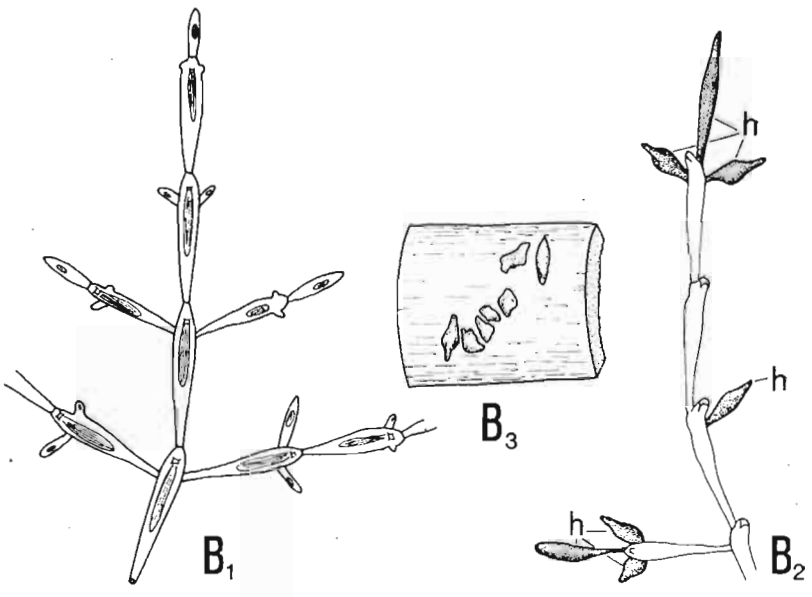
daughter zooecium

primary
zooecium

stolon

A_1

A_2

h

h

A_3

h

B_1

B_3

B_2

h

h

h
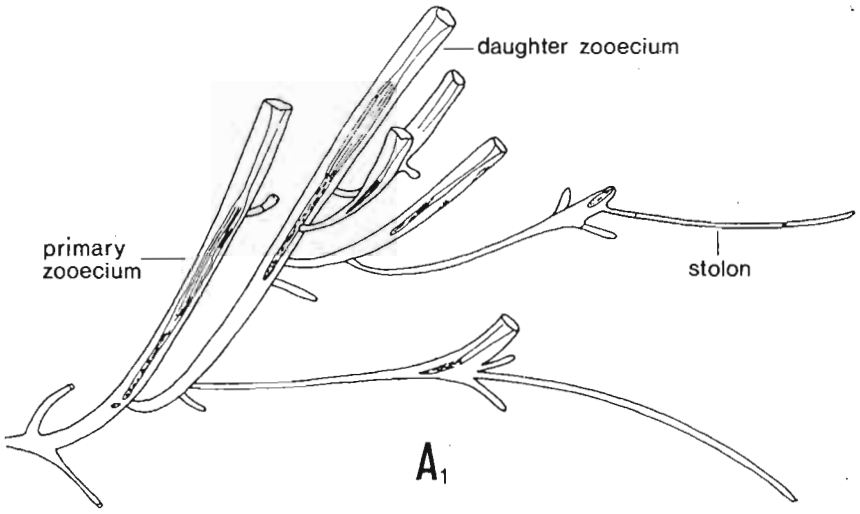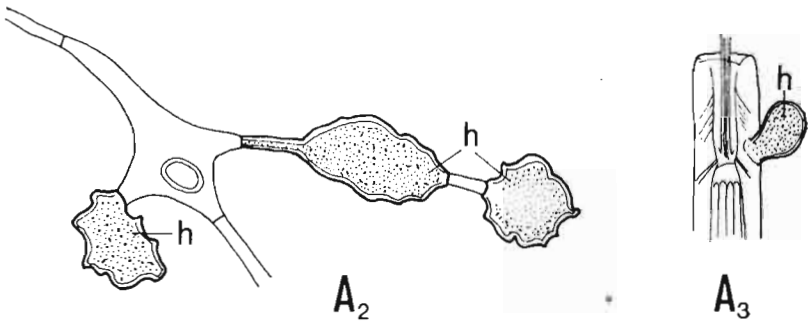
rentiated cells, coated with an encasement. It follows, therefore, that the graptoblast could be compared morphologically only with the hibernaculum of gymnolaemates both being equivalent structures. Its resemblance to the sessile statoblasts of phylactolaemates, noticed already by Kozłowski (1949, 1971) is merely of a functional nature.

From the same reasons the comparison of the cysts in *Rhabdopleura* with the hibernacula of *Paludicella* suggested by Lankester (1884) and supported by Schepotieff (1907) and van der Horst (1936) seems misleading.

Schepotieff (1907) rightly criticised the comparison of the cysts in *Rhabdopleura* with the statoblasts but erroneously ascribed this view to Lankester (1884) who quite clearly rejected this idea "because the true statoblasts of Phylactolaema have a totally different origin and position — are in fact formed within body cavity and have no relation to ordinary buds" (*ibidem*: 639). On the contrary, graptoblasts as dormant thecae and hibernacula as dormant zooecia present not only a strong functional analogy but also an example of essential homology.

HIBERNATION AND ITS ADAPTIVE ROLE

Proceeding from this analogy, the first period of the graptoblast life cycle, following the formation of the blastocrypt, may be explained most probably as hibernation, or a resting period (fig. 2 C). During this period the zooids were probably subject to a certain reorganization or metamorphosis — an idea put forward by Kozłowski (1949). The formation of a transverse septum and the subdivision of the inner cavity into an anterior and a posterior chamber in *Graptoblastus* may be evidence of two stages in the morphogenetic changes during the latent period. An elaborated system of canaliculi within the blastocrypt provided the necessary pathways for the respiration of the dormant tissues of the zooids, which later became reactivated or germinated.

Encapsulation supplied a protective covering, which transformed the graptoblasts into dormant bodies, resistant to adverse environmental conditions and capable of surviving even the destruction of the colony. While the delicate zooids were dying off and the fragile thecae of the

Fig. 3. Some examples of the hibernacula in recent ctenostomate bryozoans resembling the graptoblasts of crustoid graptolites. A_1—A_3 *Victorella pavida* (Kent) showing a young colony which in the early period of the summer season is composed of fully grown tubular zooecia, buds and stolons (A_1), whilst A_2—A_3 illustrate hibernacula (h) formed in the late summer season either on stolons creeping over the substrate (A_2) or on erect portions of the zooecia (A_3); B_1—B_3 *Paludicella articulata* (Ehrenberg) creeping branches of the colony in an early (B_1) and late (B_2) summer season, the latter with numerous hibernacula (h) and empty zooecia, whilst B_3 shows a group of overwintering hibernacula fixed to a stem of the reed (*Phargmites*) after the degeneration of the rest of the colony (after Braem, modified).

rhabdosome desintegrated, the thick-walled and resistant graptoblasts were in most cases preserved *in situ*. One could, however, imagine them being sometimes detached by water motions and dispersed by currents in viable condition, around the vicinity (see fig. 4 A—B and legend to these figures). Only in this limited sense every graptoblast may be compared with a single statoblast of phylactolaemate bryozoans, especially with
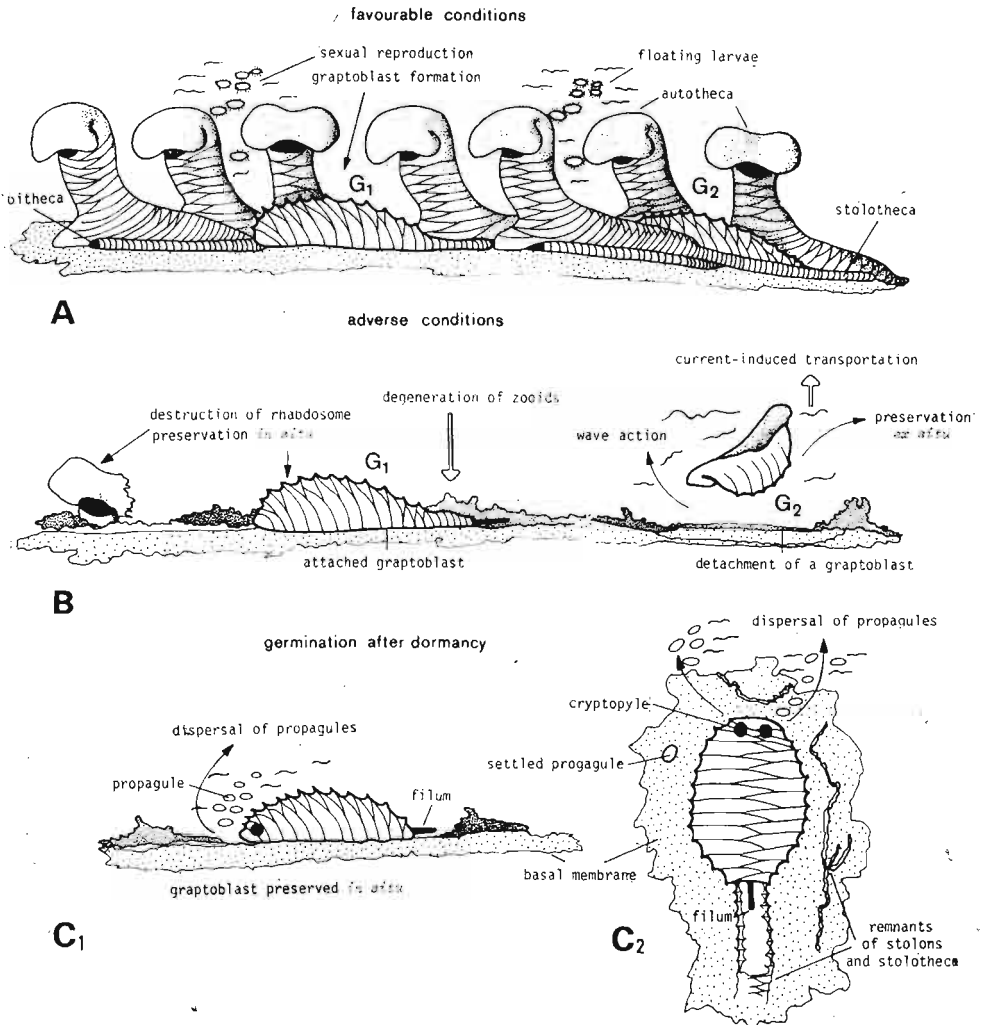

Fig. 4. A hypothetical life cycle of a crustoid graptolite started in favourable conditions from ordinary astogeny (A) involving the proliferation of zooids by budding, the formation of graptoblasts (G_1, G_2) and including seasonally a sexual process with larvae produced from fertilized eggs of the autozooids. The colonies passed periodically through adverse conditions (B) when zooids disintegrated whilst heavily coated graptoblasts survived *in situ* (G_1) or *ex situ* (G_2). After dormancy they were capable of germination as marked by the formation of a cryptopyle. The germinated graptoblast is shown *in situ* attached to a preserved portion of the basal membrane and seen laterally (C_1) and in the top view releasing hypothetical propagules. Further explanations in the text.

their sessile form (S statoblast) as suggested by Kozłowski (1949), otherwise they are entirely different. The elaboration of graptoblasts as dormant bodies may suggest that crustoids periodically faced unfavourable conditions and that probably their colonies were dying down seasonally, leaving heavily coated graptoblasts *in situ* as a means of survival and continuous occupation of a given location. On the other hand, viable graptoblasts placed *ex situ* by wave action served to disseminate the species over larger areas. Similarly those bryozoan hibernacula which are formed on the branches of a zooarium may accidentally fall down to be later dragged along the ground by the currents. This is not the case with sessile hibernacula, as they usually remain attached to the substrate. The detachment of viable graptoblasts was probably not very common either, since it involves the preservation of a complete lower wall usually firmly adpressed to the substrate.

The invention of the graptoblast gave crustoids a clear adaptive advantage: the species could survive through the wholly adverse periods, lethal to all the active zooids as well as to the larvae, and to reestablish active forms of life as a result of germination (fig. 4 B—C_1—C_2). Ordinary cysts, also present in the Crustoidea, were bags of yolk-filled cells evidently unable to germinate. Whilst cysts served for the maintenance of the zooids in a viable condition when food was less abundant, it appears that the major rôle of the graptoblasts was to restore the colony after the drastic changes of the environment. This division of function explains the otherwise seemingly redundant presence in the crustoid colonies of two types of hibernating bodies: dormant buds (cysts, "Winterknospen") and graptoblasts. *Rhabdopleura compacta* represents a less specialized stage and some dormant buds are capable in extreme conditions of developing into new zooids after all the old zooids in the colony died out. Usually they serve, however, only as a foodstore for the colony (Stebbing 1970).

While bryozoans developed either dormant zooecia (hibernacula of some ctenostomes) or dormant buds capable of dispersal (statoblasts of phylactolaemates), crustoids succeeded, through the invention of a graptoblast in combining both into a single adaptation. They were resting zooids capable to produce after the dormancy period a number of daughter reproductive bodies.

POSTDORMANT PERIOD, GERMINATION AND DISSEMINATION OF PROPAGULES

Germination after a dormant period was followed by the formation of a single or paired cryptopyle (fig. 2 D), probably, owing to resorption (Kozłowski 1962). Prior to perforation the blastotheca was comptely

sealed and terminated on its posterior end with an ombilic, forming a protuberance comparable with the pointed end of a closed terminal portion of the creeping tube in *Rhabdopleura*, while the thick blastocrypt produced an entire inner lining. A thickened peridermal "cork" at the end of the resting tube in *Rhabdopleura* might exhibit an incipient stage of a similar process of encystation (fig. 2 A). The cryptopyle which reestablished communication with the outer environment is indicative of the onset of active life, but its small diameter as compared with the width of the graptoblast (fig. 1 B_1—B_2) indicates that after germinating zooids were either extremely slender or even reduced. The hibernacula, or resting zooecia of some ctenostome bryozoans when dormant have their peristomial tubes reduced and later reconstituted, after they have returned to active life (Braem 1951, Carrada and Sacchi 1964). A similar course of events and ample budding should have followed the dormant period in the life cycle of graptoblasts. There is no indication, however, that rejuvenated zooids emerged from the germinating graptoblast and formed an erect thecal tube (neck and aperture!) or that they produced any daughter thecae. The only reasonable solution is that, as a result of germination the graptoblast zooids were transformed into specialized gemmiparous individuals producing propagation bodies, fairly small (judging from the diameter of the cryptopyle) probably free-swimming and revealing no protective covering (at least no traces of it have been found in the fossil material). One could visualize such hypothetical "propagules" as small, planuloid, probably ciliated buds which were released into the water through the cryptopyle, settled after a short period of free existence and initiated the formation of new colonies by budding of daughter zooids (fig. 4 C_1—C_2). These events closed the possible life cycle of crustoid graptolites (fig. 4 A—C).

While the hypothetical crustoid propagule may be considered a simplified equivalent of an individual statoblast, the germinated graptoblast may be compared with a whole series or a cluster of statoblasts, which developed on a common cord (stolon, funiculus) owing to the gemmation of the germinated zooid. And not just that. One should also imagine such cluster first encapsulated and later opened to enable the detached individual propagules (= statoblasts) to be disseminated.

The nature of the processes involved in the production of hypothetical propagation bodies are obscure and difficult to define on the basis of the preserved fossil remains. Asexual formation by budding seems perhaps most probable, although the presence inside the graptoblast of more than one zooid does not exclude a sexual process either. However a paired cryptopyle has two openings of equal diameter which may be indicative of the same sex of both zooids or at least the lack of sexual dimorphism between these specialized zooids — a remarkable difference from the rest of the individuals of the colony.

TAXONOMIC UNIQUENESS OF ADAPTIVE SOLUTIONS AND SOME AFTERTHOUGHTS

The systematic assignement of graptoblasts presents a problem which so far has not been solved satisfactorily. Kozłowski (1962) found them being a component of crustoid colonies, however his earlier findings of graptoblasts in the famous Wysoczki fauna from the Upper Tremadocian cherts (Holy Cross Mts, Central Poland) were not associated with the crustoid remains. Consequently, he has advanced a hypothesis that some Camaroidea were also capable of producing graptoblasts, especially such species which have broad autothecae with a flat upper surface. The Camaroidea, however, as emphasized by Kozłowski, never display on their upper surfaces fusellar sutures distinct enough to be comparable with graptoblasts. Dr P. Mierzejewski (Warsaw, personal inf.) believes that some of the graptolites with a highly elaborated apertural apparatus identified by Kozłowski (1949) preliminarily as camaroids, are in fact crustoids and may be responsible for the presence of the associated graptoblasts in the Wysoczki fauna. Moreover, there is a coincidence in the upper limit of stratigraphic distribution of the graptoblasts and the crustoid graptolites, both exhibiting their last occurrence in Upper Silurian (Ludlow) as shown by Mierzejewski (1977). Thus a tentative conclusion may be that graptoblasts are unique in Crustoidea.

Judging, however, from Kozłowski's (1949) observations camaroids themselves were capable of sealing their apertures by a thin film of peridermal material (occlusion of the autothecae). In those species where a tubular collum (neck) is absent this material was deposited directly over the aperture providing a kind of cork. When the collum was present, a diaphragm, was formed inside it and at its base. The sealing of the autothecae is accompanied by a secondary thickening of the thecal walls, thus providing a means of isolation from the outer environment. Occlusion of the autothecae in some dendroids, while by no means rare, seems to be related rather to degeneration or necrosis of zooids than to the dormancy. In the camaroid colonies occluded autothecae are common and, as observed by Kozłowski (*ibidem*: 173) exhibit a simple case of encystment, following an active period in the life of the autozooid. While representing a largely similar solution of the problem posed by the environment (dormancy!), such primitive encysted zooids are far away from highly specialized dormant bodies realized by crustoids in the form of graptoblasts. It follows from thin sections examined by Kozłowski than occluded autothecae are filled with a delicate membranous, spongy tissue surronding the denser contours of spherical or elliptical vesicles interpreted by him as traces of eggs. After the occlusion the autozooids were probably subjected to degeneration, making place for eggs. If these assumptions were correct, one could conclude that the occluded autothecae of camaroids correspond to the ovicells (Kozłowski 1971) rather than to the hibernating zooecia of bryozoans.

The invention of specialized dormant bodies practically by a single group of sessile graptolites poses a number of questions. Hibernacula which present a similar solution of an adaptive problem are absent from purely marine bryozoans and occur only in the species invading the

brackish or fresh-water environments. They provide an adaptation which enables the survival during periodic deterioration of the milieu due to drastic changes of salinity or temperature. Were crustoids facing similar severe environmental problems? Why were Crustoidea the only group that succeeded in the formation of graptoblasts while other sessile graptolites, which displayed a very similar adaptive type and apparently lived in similar habitats, remained conservative or exhibited like Camaroidea, rather limited achievements? These and a number of other questions must be left unanswered because of the very nature of fossil material and the kind of explanation which could be offered by palaeontologist or evolutionary biologist.

The interpretation of biological significance of graptoblasts, as suggested above is related to a common category of explanations used in phylogenetic studies and termed rather ironically "the adaptive stories" (Allen *et al.* 1977). They are accused to present a kind of *ex post* rationalization of evolutionary events rather than true explanations, their limited heuristic value being recognized by the critics of the contemporary Darwinism (eg Sahlins, 1976) as well as by the adherents of the natural selection theory (eg. Gould 1978). The "adaptive stories" show *a priori* every change as adaptive due to the mere nature of the evolutionary process contrólled by selection and consider each step of phylogeny as a logical necessity leading to an evolutionary improvement and an increase of fitness. Yet, they never offer any explanation why, in a given case, a certain solution was chosen instead of an alternative pathway, as it evidently has been the case in some other lineages. The reason for this limitation may partly be connected with a considerable share of random factors in the evolutionary changes and therefore a very restricted predictability of phylogenetic events. Following the tradition of the adaptive stories which remain a *malum necessarium* of evolutionary biology one could assume that the production of dormant zooids was first attained as a local adaptation of some marginal crustoid populations facing extreme environmental conditions, e.g. in benthic habitats heavily affected by an intense volcanic activity connected with the Late Cambrian orogenic movements. Such habitats were periodically subject to deterioration of conditions, and an ability to persist through such periods and to occupy steadily the location, granted those populations both survival and escape from competition with other benthic organisms unable to co-occur in such habitats. This local novelty was later improved and once its general adaptive significance was recognized in different biota with fluctuating conditions it became fixed as a norm for the entire group. In any case it seems fairly safe to generalize that the invention of graptoblasts was in some way related to periodic deteriorations of the environment in which the extinct crustoids lived — "the rest is silence".

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ZNACZENIE GRAPTOBLASTÓW W CYKLU ŻYCIOWYM GRAPTOLITÓW Z RZĘDU CRUSTOIDEA

Streszczenie

Graptoblastami nazwał R. Kozłowski (1949) małe, owalne ciałka zbudowane z materiału organicznego i opatrzone wypukłą górną oraz płaską dolną ścianą. Ta pierwsza ma żeberkowanie przypominające fuzellusy graptolitów lub pióroskrzelnych. Po raz pierwszy graptoblasty opisano jako oddzielne skamieniałości towarzyszące szczątkom graptolitów tremadockich, zaś następnie wykazano, że stanowią one część kolonii graptolitów z rzędu Crustoidea (Kozłowski 1962). Znaczenie biologiczne graptoblastów jest w znacznym stopniu zagadkowe. Zakwestionowano pogląd, że graptoblasty powstawały wewnątrz autoteki, natomiast wysunięto interpretację, że stanowiły one spoczynkową terminalną część stoloteki, zawierającą incystowane, przetrwalnikowe zooidy. Graptoblasty można homologizować ze spoczynkowymi terminalnymi zooidami w płożących się rurkach *Rhabdopleura* oraz z hibernaculami tj przetrwalnikowymi zooeciami mszywiołów Ctenostomata. Natomiast ich podobieństwo do statoblastów Phylactolaemata jest tylko częściowe i czysto funkcjonalne.

Graptoblasty stanowiły przystosowanie umożliwiające przeżycie okresów niekorzystnych, powodujących degenerację reszty kolonii. Wysunięto hipotezę, że po okresie hibernacji graptoblasty podlegały aktywacji i tworzyły cryptopyle umożliwiające wyrzucanie pływek (rozmnóżek), tworzących po osadzeniu się na podłożu nowe kolonie. W rezultacie graptoblasty umożliwiały stałe utrzymywanie się gatunków Crustoidea w danym siedlisku, mimo głębokich zmian warunków środowiskowych.