Helgoländer wiss. Meeresunters. 29, 404–413 (1977)

Monster zooids in *Cryptosula pallasiana* (Bryozoa, Cheilostomata Ascophora)

D. JEBRAM

Zoologisches Institut, Technische Universität Braunschweig; Braunschweig, Federal Republic of Germany

ABSTRACT: In the ascophoran bryozoan *Cryptosula pallasiana* (Moll) many examples of regenerative growth and of "abnormal" zooids have been observed. Most of the different forms of "monsters" are caused by fusion of zooids or zooid buds respectively. Zooids may often fuse laterally but in a few cases also distally. Some "monster zooids" have two polypides and "combined opercula" caused by various degrees of fusion of the apertures. Lack of sufficient space may lead to the formation of "dwarf zooids" or "remainder cystids".

INTRODUCTION

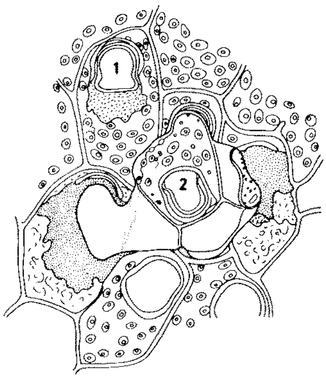
Single examples of bryozoan zooids exhibiting an "abnormal" anatomy have been described occasionally by several authors in the past. In 1971 the present author presented a comprehensive collection of new examples of "monster-zooids" produced by various recent species of the Cheilostomata in an informal report during the I. B. A. Symposium held in Durham, England (Jebram, unpublished). Recently Jebram & Voigt (1977) have published a representative amount of "abnormal" zooids from fossil and recent species of Cheilostomata Anasca and raised the question, whether real "monster-zooids" do commonly develop in species of the Cheilostomata Ascophora as well. Most of the literature concerning "abnormal" zooids of bryozoans has been summarized in the latter publication.

Cryptosula pallasiana (Moll) has been reared as a representative of the Cheilostomata Ascophora during several years (cf. Jebram, 1968). The decisive initial examples of "abnormal" zooids of *C. pallasiana* are found in the laboratory by intensive observations at cultivated colonies; later on this was confirmed by studies on specimens obtained from natural habitats, e.g. the littoral zones of Helgoland and Den Helder.

REGENERATIVE AND "ABNORMAL" GROWTH

Total regeneration

A dead zooid within a colony may be regenerated as a whole new zooid by one or more neighbouring zooids. In respect to the polarity axis three different possibilities for such a total regeneration have been observed in *Cryptosula pallasiana:* (a) The regenerating zooid grows from the proximal neighbour into the available space in the colony and with the same polarity axis as the surrounding zooids (Fig. 1, zooid 1). (b) The regenerating zooid may originate also from the distal neighbour and, therefore, has a polarity axis parallel to the neighbouring zooids but of opposite direction (Fig. 1, zooid 2; Fig. 2). (c) In a few cases the regenerating bud originated more or less laterally to the available space in the colony. Thus the polarity axis of



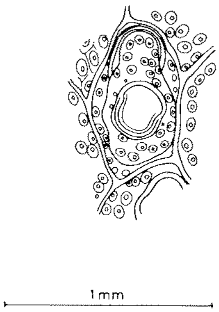
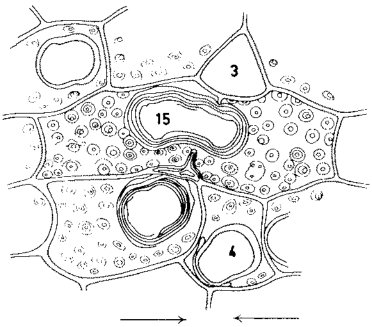


Fig. 1: *Cryptosula pallasiana.* Examples for total regeneration: *1* zooid regenerated in the same direction as the original one; *2* zooid regenerated with a polarity axis contrary to that of the original one and producing a secondary colony layer immuring the basal layer. (For simplification, the typical pseudopores have been drawn only in Figs. 1–4 and 14.)

Fig. 2: *Cryptosula pallasiana.* Totally regenerated zooid within the walls of the former zooid; the polarity axis of the regenerated zooid is contrary to the original one



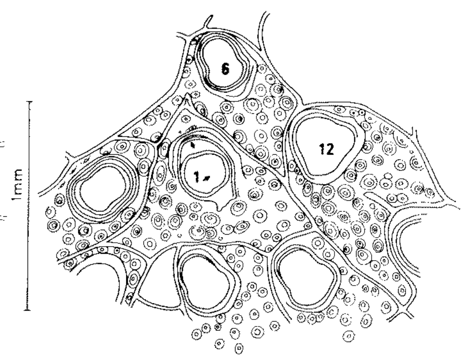


Fig. 3: *Cryptosula pallasiana.* A magnified part of the colony from Figure 6. *3* remainder cystid; *4* dwarf zooid with a normal aperture; *15* monster zooid with distally fused cystids and distally fused opercula; arrows indicate the direction of growth of the two meeting colony parts

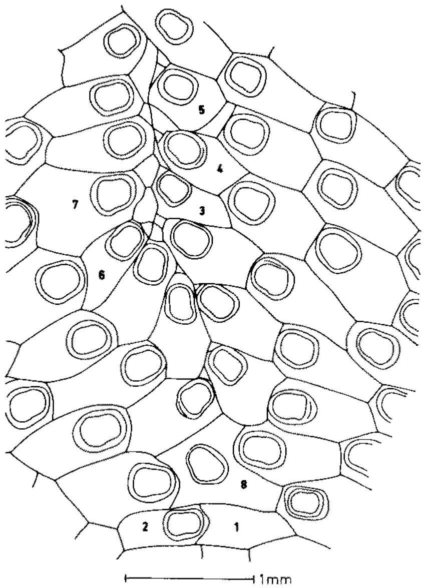
Fig. 4: *Cryptosula pallasiana.* A magnified part of the colony presented in Figure 6. *1* monster zooid built by cystid fusion, showing total regeneration with a right angle in relation to the former polypide axis; *6* zooid with fused cystids but a normal aperture; *12* zooid grown by fusion of two cystids and equipped with a broadened aperture

the regenerated zooid forms a distinct angle to the original axis. Figure 4 shows an example (zooid 1) in which in a fused cystid (see below) the primary polypide(s) directed from right to left-distal; total regeneration developed on the contrary from a proximal-left zooid toward right-distal into the empty old cystid walls; thus the new polarity axis forms a right angle to the original one as indicated by the distal margins of the apertures (and by arrows in the figured opercula).

Sometimes the total regenerating zooids lift themselves out of the space in the original zooid on the top of the primary colony layer and then give rise to a new secondary colony layer, which covers and immures the older one.

Dwarf zooids and remainder cystids

If the growing edges of two colonies or colony parts meet each other, further growth may become more or less suppressed at the meeting front. Because of the lack of space the developing buds are not able to attain the "normal" volume. While the larger ones of such buds have been found nevertheless to be able to produce an own



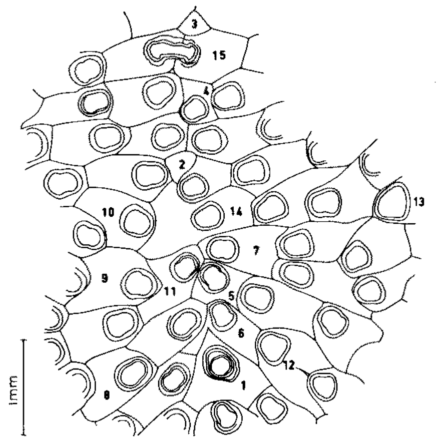


Fig. 5: *Cryptosula pallasiana.* At the line of contact between two lobes of the colony various abnormal forms were grown: *1* (and others) remainder cystid; *2–6* dwarf zooids with nearly normally sized opercula; *7* and *8* monsters with fused cystids and more or less normal apertures. (The pseudopores, typical for this species, are not drawn for simplification of the figure)

Fig. 6: *Cryptosula pallasiana.* Various abnormal animal forms in an area where two lobes of a colony meet: *1* fused cystids and total regeneration at a right angle; *2* and *3* remainder cystids; *4* and *5* dwarf zooids with normal apertures; *6–11* zooids built by fusions of cystids with more or less normal apertures; *12* and *13* broadened apertures in zooids with fused cystids; *14* large monster zooid grown by cystid fusion but with one normal aperture; *15* distally fused zooids with distally fused opercula. (The pseudopores, typical for this species, are not drawn for simplification of the figure)

polypide and to become "normal" in anatomy but "dwarf zooids" (Fig. 5, zooids 2–6; Fig. 6, zooids 4–5), the smaller ones continue the cystid bud stage and shall be called "remainder cystids" (Fig. 5, Bud 1 and many other ones, Fig. 6, buds 2–3).

Fused zooids and double "monsters"

In colonies of *Cryptosula pallasiana* it has been often observed that zooids or zooid buds may fuse and build up larger monster zooids. Cystid fusions have been found mainly where the growing edges of two colonies or lobes of a colony meet but also at various other places. Fusion may take place during regeneration of neighbouring cystids or buds which are damaged by larger animals, by movements of the substratum pieces, or by too strong brushing in the laboratory. In some cases no previous injury could be detected, but at this time it is not known for certain whether cystids may really spontanously fuse without preceding injuries.

In respect to the polarity axis two possibilities of fusions have been recognized: lateral and distal fusion of cystids. In fused zooids two polypides and "abnormal" opercula may occasionally develop.

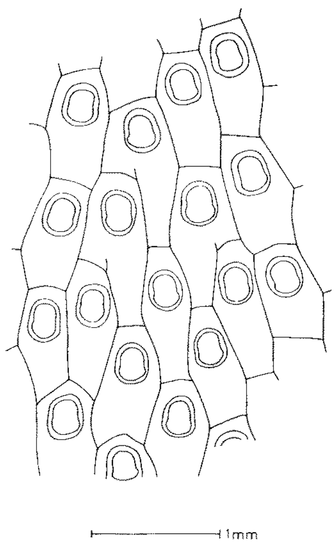


Fig. 7: *Cryptosula pallasiana.* Simple lateral fusion of cystids in zooids with normal apertures (frontal view)

Lateral cystid fusions

Lateral fusions of cystids have been found to be common in specimens of this species from natural habitats as well as in cultivated colonies.

In most cases concerning two partners the larger cystid dominates; it produces a polypide and fixes the polarity axis (indicated by the form and position of the

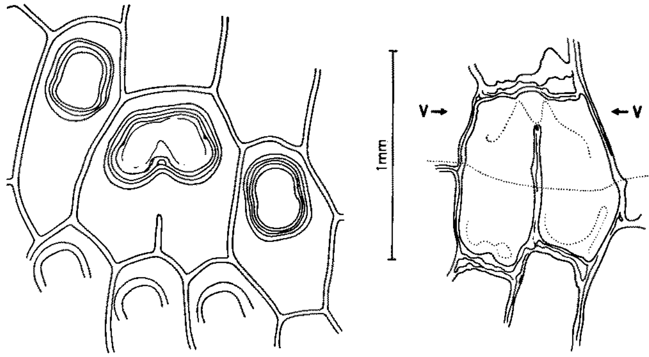


Fig. 8: *Cryptosula pallasiana.* Monster zooid with laterally fused cystids and opercula; at left frontal view, at right basal view; V, indication of the injuries which led to the fusion

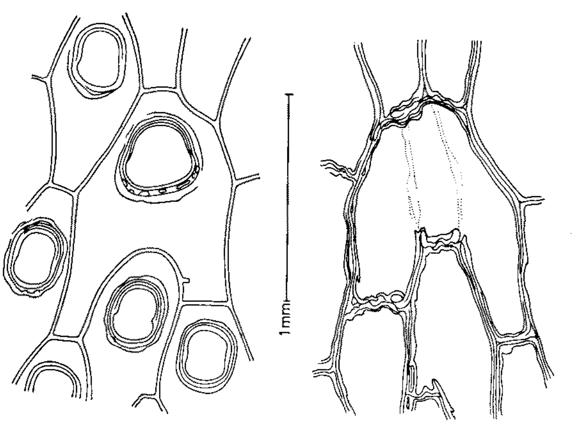


Fig. 9: *Cryptosula pallasiana.* Monster zooid (with normal aperture) formed by lateral fusion of 3 cystids; at left frontal view, at right basal view showing the damaged zooid walls

Fig. 10: *Cryptosula pallasiana.* Monster zooid (with broadened aperture) built by lateral fusion of 3 cystids; at left frontal view, at right basal view showing the damaged lateral walls

aperture), while the smaller cystid (bud) is subordinated to various degrees (Fig. 6, zooids 8 and 10; Fig. 7). Very rarely the position of the operculum indicates that the smaller partner is able to balance the potential of the larger one (Fig. 4, zooid 12) or to dominate (Fig. 6, zooid 9). The potential of both partners may balance each other (Fig. 8) in usual cases, if both are nearly the same size.

Sometimes three to five cystids or cystid buds may fuse (Figs. 9–14). Dominance and fixation of the polarity axis vary according to each special situation (compare chapter on "abnormal" opercula).

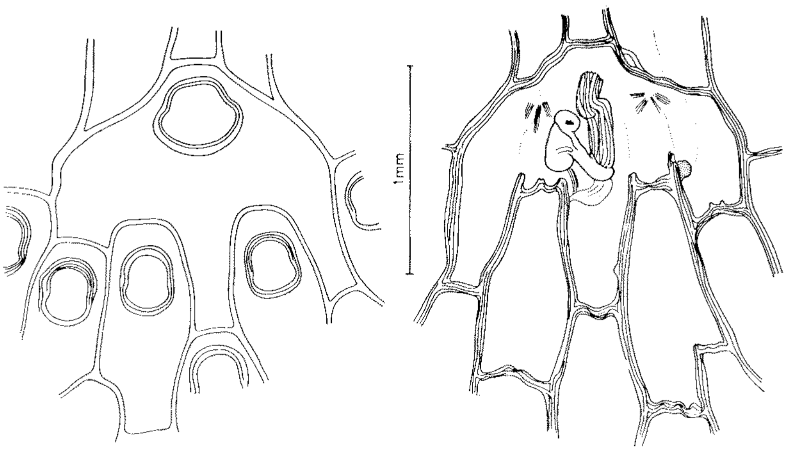


Fig. 11: *Cryptosula pallasiana*. Monster (with broadened aperture) produced by lateral fusions of 5 cystids; at left frontal view, at right basal view showing the polypide and the damaged zooid walls

Distal cystid fusions

Where the growing edges of the colony parts meet straight distally (with an angle of about 180°) zooids may fuse with their distal parts. Two examples have been observed in *Cryptosula pallasiana*. In Figure 6 (zooid 14), one partner dominates and only builds a polypide and an aperture. Another "monster" (zooid 15 in Figs. 3 and 6) demonstrates that the opercula as well as the cystids can fuse distally while each partner produces an own polypide. Even if expansions of these polypides could not be observed, they must have evaginated sometime through a slit of the composed aperture (towards the remainder-cystid 3): because of the coloured gut these polypides must have eaten protistans. The polypides in this "monster" appeared to have been replaced several times like in neighbour zooids.

Double polypides

In several "monsters" composed of two or more zooid buds, two polypides may develop (zooids 12 and 13 in Figs. 4 and 6; Figs. 8, 10, 13, 14); however, no more than two polypides per "monster" have been observed in this species. In

Cryptosula pallasiana fusions of the lophophores or of the guts have never been found until now. On the other hand in all cases of double polypides both fused their apertures and opercula in this species.

Frequently, both polypides in such a "monster" evaginated through their common aperture simultaneously (even in colonies from natural habitats). Perhaps this must happen every time, because a reduction of space in a common somatocoel by expansion of a compensation sac will press both polypides out of the cystid. There

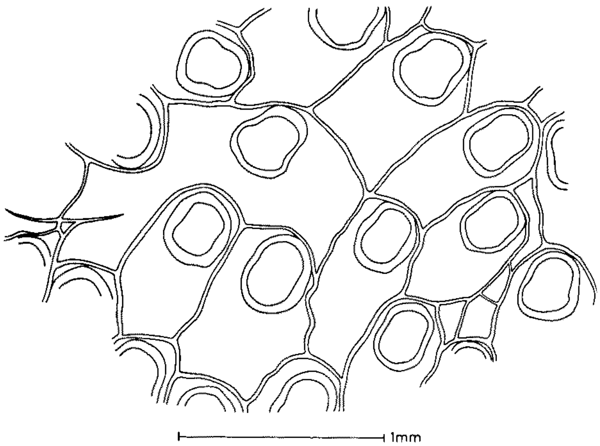


Fig. 12: *Cryptosula pallasiana*. Monster (with normal aperture) formed by more or less lateral fusions of various cystids or cystid buds (frontal view)

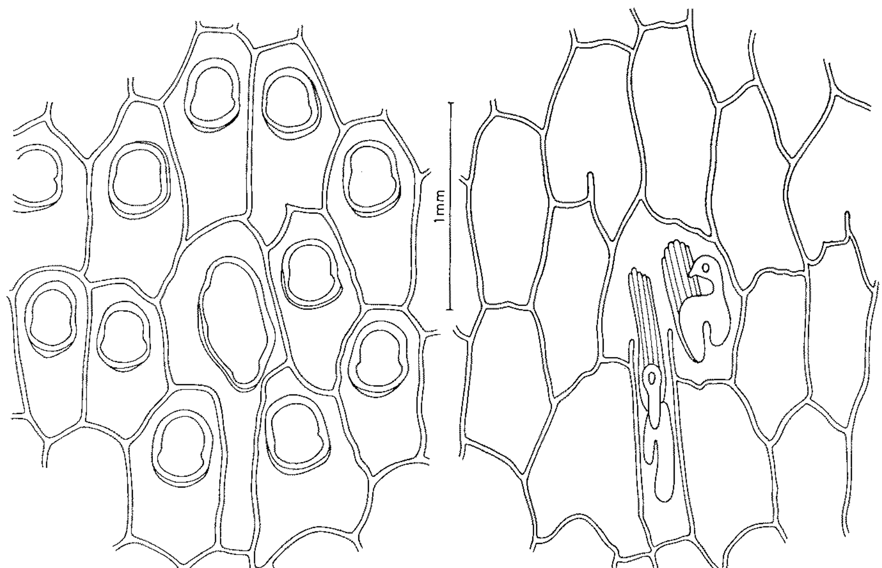


Fig. 13: *Cryptosula pallasiana*. Monster zooid with two polypides and an enlarged, strongly asymmetric operculum; at left frontal view, at right basal view

is no doubt that some double "monsters" were equipped with two compensation sacs (e.g. the fused zooids in Figs. 3 and 8), but it could not be ascertained whether in all cases of double polypides each partner had its own ascus (because no histological preparations have been made) or whether a composed compensation sac developed from the fused aperture.

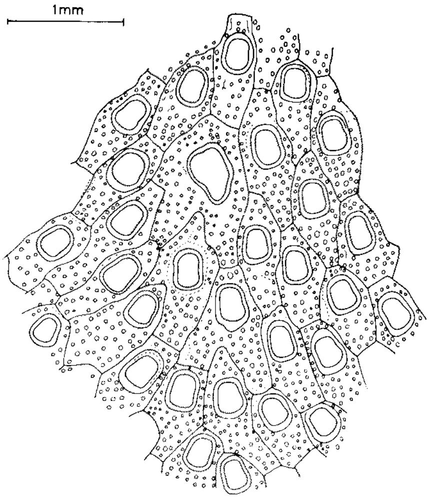


Fig. 14: *Cryptosula pallasiana.* Area where two colony lobes met leading to various forms of cystid fusions; in the center a monster with an enlarged, strongly asymmetric operculum (frontal view)

"Abnormal" opercula

Various forms of "abnormal" opercula could be observed in *Cryptosula pallasiana.* Opercula may become expanded laterally including all intermediate forms from "normal" to ones with a more than double the "normal" width (Figs. 4, 8, 10, 11). An extreme case of an "abnormal" operculum is the twinned operculum shown in Figure 3 which was caused by distal fusion of two apertures and unexpectedly seems to have allowed the polypides to evaginate through the larger lateral slit. The double operculum of the "monster" in Figure 8 makes it look as though there are tendencies to form intermediates between simple broadened opercula in laterally fused zooids towards distally fused opercula. If one of the polypide partners originates distinctly more distally than the other one the combined operculum forms obliquely. The most striking examples for this are shown in the Figures 13 and 14.

DISCUSSION

Totally regenerated zooids are common in most cheilostomatous bryozoans, including those with an opposing polarity axis. Total regeneration even in species of

Cheilostomata Ascophora have been detected very early as examples of "abnormal" zooid forms (e.g. Römer, 1906; Levinsen, 1907). The potential for the production of many subsequent colony layers above the older ones originating with totally regenerated zooids is well established in many species of Cheilostomata, in Anasca (e.g. *Electra crustulenta, Conopeum seurati, C. reticulum, C. commensale*) as well as in Ascophora (e.g. *Hippothoa hyalina,* many species of the Schizoporellidae and Celleporidae).

In the past only very few single examples of lateral fusions or incomplete separations of zooids have been reported (Marcus, 1926; Voigt, 1930; Silen, 1942; Illies, 1953; Larwood, 1962). In recent times numerous examples have been found, because cultivated colonies have been intensively observed in the laboratory (Jebram, 1968, 1973; Jebram & Voigt, 1977). This in turn has stimulated improved studies of specimens obtained from natural habitats. Since now many examples in recent and fossil species are known there is no doubt that lateral zooid-fusion is a common event in colonies of cheilostomatous bryozoans.

There appear to be three important differences in the potentials for the formation of "monsters" between Anasca and Ascophora: Firstly, serial zooid-fusions, which occur in anascan Cheilostomata and may be common in some species *(Membranipora membranacea:* Lutaud, 1961; *Conopeum seurati:* Jembran & Voigt, 1977), have never been observed in the ascophoran *Cryptosula pallasiana.* Secondly, likewise no "monster" of the ascophoran *C. pallasiana* has more than a single aperture (even if a combined one), while in Anasca up to 3 separate apertures per fused zooid were found in different species. Fusions of the apertures may appear in Ascophora as well as in Anasca. Thirdly, apart from the apertures no real fusions of the polypides themselves have developed in the ascophoran species studied, while in Anasca examples of various degrees of polypide fusions are described (cf. Jebram & Voigt, 1977) as well as reported from species of Bryozoa Phylactolaemata (Oda, 1954; Oda & Nakamura, 1973).

Acknowledgements. I wish to thank Prof. Dr. O. Kinne and Mr. A. Holtmann, Biologische Anstalt Helgoland, and Dr. C. Swennen, Nederlands Instituut voor Onderzoek der Zee, for hospitality in their institutes and for help during various research visits. My studies on cultivated bryozoans is supported by several grants from the Deutsche Forschungsgemeinschaft.

LITERATURE CITED

Illies, G., 1953. Variationsstatistische Untersuchungen an *Rhiniopora acus* (Bryd.) Bryoz. Cheil. aus der Oberkreide von Hemmoor/Niederelbe. Mitt. Geol. St. Inst. Hamb. **22**, 76–101.

Jebram, D., 1968. A cultivation method for saltwater Bryozoa and an example for experimental biology. Atti Soc. ital. Sci. nat. **108**, 119–128.

— 1973. Preliminary observations on the influences of food and other factors on the growth of Bryozoa with the description of a new apparatus for cultivation of sessile plankton feeders. Kieler Meeresforsch. **29**, 50–57.

— & Voigt, E., 1977. Monsterzooide und Doppelpolypide bei fossilen und rezenten *Cheilostomata Anasca* (Bryozoa). Abh. Verh. naturwiss. Ver. Hamburg **20** (in press).

Larwood, G. P., 1962. The morphology and systematics of some cretaceous cribrimorph Polyzoa (Pelmatoporinae). Bull. Br. Mus. nat. Hist. (Geol.) **6**, 1–285.

Levinsen, G. M. R., 1907. Sur la régénération totale des Bryozoaires. K. danske Vidensk. Selsk. Forh. **1907**, 151–159.

Lutaud, G., 1961. Contribution a l'étude du bourgeonnement et de la croissance des colonies chez *Membranipora membranacea* (Linné), Bryozoaire Chilostome. Thèse Fac. Sci. Univ. Paris 151 pp.

Marcus, E., 1926. Beobachtungen und Versuche an lebenden Meeresbryozoen. Zool. Jb. (System. Geogr. Biol. Tiere) **52**, 1–102.

Oda, S., 1954. On the monsters of polypides in freshwater Bryozoa. Collecting Breed. Tokyo **16**, 13–18.

— & Nakamura, R. M., 1973. The occurrence of double polypides in freshwater Bryozoa. In: Living and fossil Bryozoa. Ed. by G. P. Larwood. Acad. Press, London, 523–528.

Römer, O., 1906. Untersuchungen über Knospung, Degeneration und Regeneration von einigen marinen ectoprocten Bryozoen. Z. wiss. Zool. **84**, 446–478.

Silén, L., 1942. On the formation of the interzooidal communications of the Bryozoa. Zool. Bidr. Uppsala **22**, 433–488.

Voigt, E., 1930. Morphologische und stratigraphische Untersuchungen über die Bryozoenfauna der Oberen Kreide. I. Teil. Die cheilostomen Bryozoen der jüngeren Oberkreide in Nordwestdeutschland, im Baltikum und in Holland. Leopoldina **6** (Walther-Festschrift), 379–579.

— 1975. Heteromorphy in cretaceous Bryozoa. Doc. Lab. Géol. Fac. Sci., Lyon, H. S. **3** (1), 77–95.

Author's address: Dr. D. Jebram
Zoologisches Institut
Technische Universität Braunschweig
Pockelstraße 10a
D - 3300 Braunschweig
FRG