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The regeneration in some caryophyllid corals from the Korytnica Clays (Middle Miocene; Holy Cross Mountains, Central Poland)

ABSTRACT: A common case of regeneration from very small fragments (composed even of those containing at least one entoseptum) is reported in some scleractinian corals coming from a specific, solitary-coral-dominated community of the near-to--shore facies of the Korytnica Clays (Middle Miocene, Badenian; Holy Cross Mountains, Central Poland). It concerns the specifically indeterminable caryophyllids, some individuals of which underwent regeneration twice. The **regeneration** itself (growth from tiny fragments of the primary individual) is discussed in its relation to the **reparation** (a repair of an injury within the animal's skeleton). The whole population of the regenerated caryophyllids, which dominated a local near--to-shore community within the Korytnica Basin, characterizes by the size distinctly smaller than that of normal individuals. This event is compared to that recognized in some populations of the present-day and ancient free-living bryozoans, those inhabiting the Korytnica Basin including. In both these groups (caryophyllid corals, and free-living bryozoans) the regeneration is discussed as an important mean for reproduction of the species, and as an immanent biological feature of some selected taxa.

INTRODUCTION

The aim of the present paper is to announce from the Korytnica Basin the occurrence of a rather unique material of the regenerated solitary corals which have not hitherto been reported from the fossil state. These are the caryophyllid corals, not having been yet determinable to a rank more precise than the family Caryophyllidae GRAY, 1847 [supposedly, the subfamily Caryophylliinae GRAY, 1847, and/or Parasmiliinae VAUGHAN & WELLS, 1943]. A disadventage in taxonomical recognition of these corals is not due to their regeneration, but due to an inadequate state of preservation of the calices grown from small fragments. Damages of fragile coralla, caused by washing and sifting procedure of the crude clay material, have resulted in a lost of morphological details typical of the common Miocene caryophyllid species known from many localities in the Austrian and Moravian parts of the Central Paratethys basins (*see* REUSS 1871, PROCHÁZKA 1893).

The presented material comes from a nearshore locality of the Middle Miocene (Badenian) sequence deposited within the Korytnica Basin on the southern slopes of the Holy Cross Mts, Central Poland. The caryophyllid-bearing locality belongs to the lower part of the Korytnica Clays, and the contained paleontological material dominated by solitary corals (caryophyllids, *Flabellum*, and *Stephanophyllia*), scaphopods (*Dentalium* and *Entalina*), and some gastropods (*Turritella*, *Nassa*, and *Natica*), corresponds well to the community *I* within the clay succession (*see* BAŁUK & RADWAŃSKI 1977a, Text-fig. 5 and p. 100).

THE INVESTIGATED MATERIAL

The investigated material of the regenerated caryophyllid corals from the Korytnica Clays consists of several tens of coralla, all of which are preserved more or less fragmentarily. The majority of the specimens, however, display their regenerated parts preserved without any damage (*see* Pls 1—3).

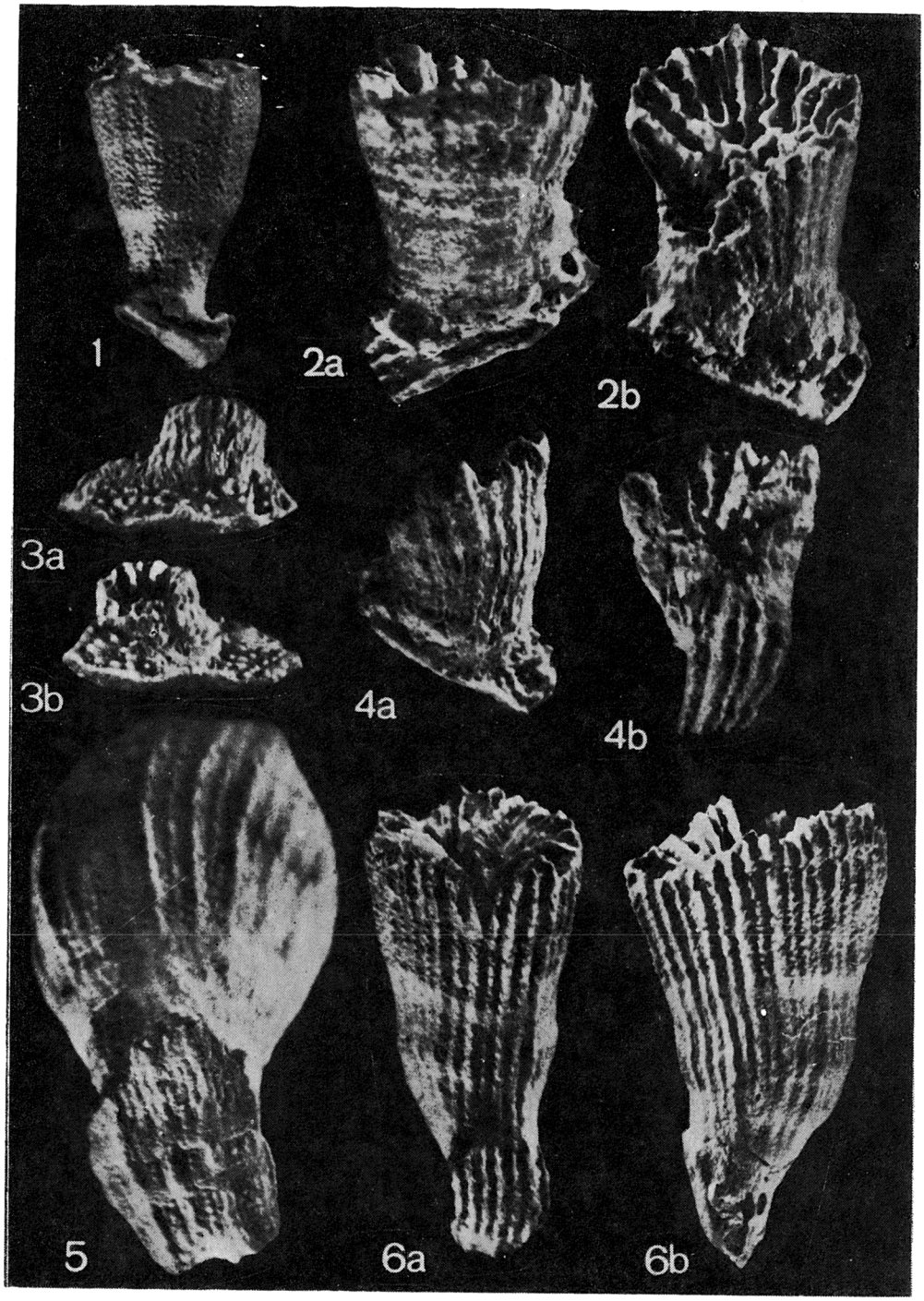
Within the caryophyllid-bearing locality which is dominated by solitary corals (caryophyllids, *Flabellum*, and *Stephanophyllia*), most of the caryophyllid specimens are regenerated. The event of regeneration of the caryophyllids within the obtained material is so common that it makes up a distinct feature of this specific community.

The regenerated caryophyllids, to judge by some, almost wholly preserved coralla, are evidently smaller when compared either with non-regenerated specimens from the same community, or with the Miocene species (*cf.* REUSS 1871, PROCHÁZKA 1893) to which they can be attributed or to which they are related more or less closely.

Before presentation of the collected material it is to state that a doubt may arise whether all the investigated specimens (Pls 1—3) are really regenerated. It might have been asked if they are the cases of corals attached, by the settlement of their larvae, to any available detrital fragments littering the seafloor, those of the same species including, and to extent the same as demonstrated impressively by GRIPP (1959, Pl. 1, Figs 1—18 and Pl. 2, Figs 1—15) for the present-day Mediterranean species, *Caryophyllia clavus* (SCACCHI). The latter question cannot be however answered positively due to the two reasons, as follows:

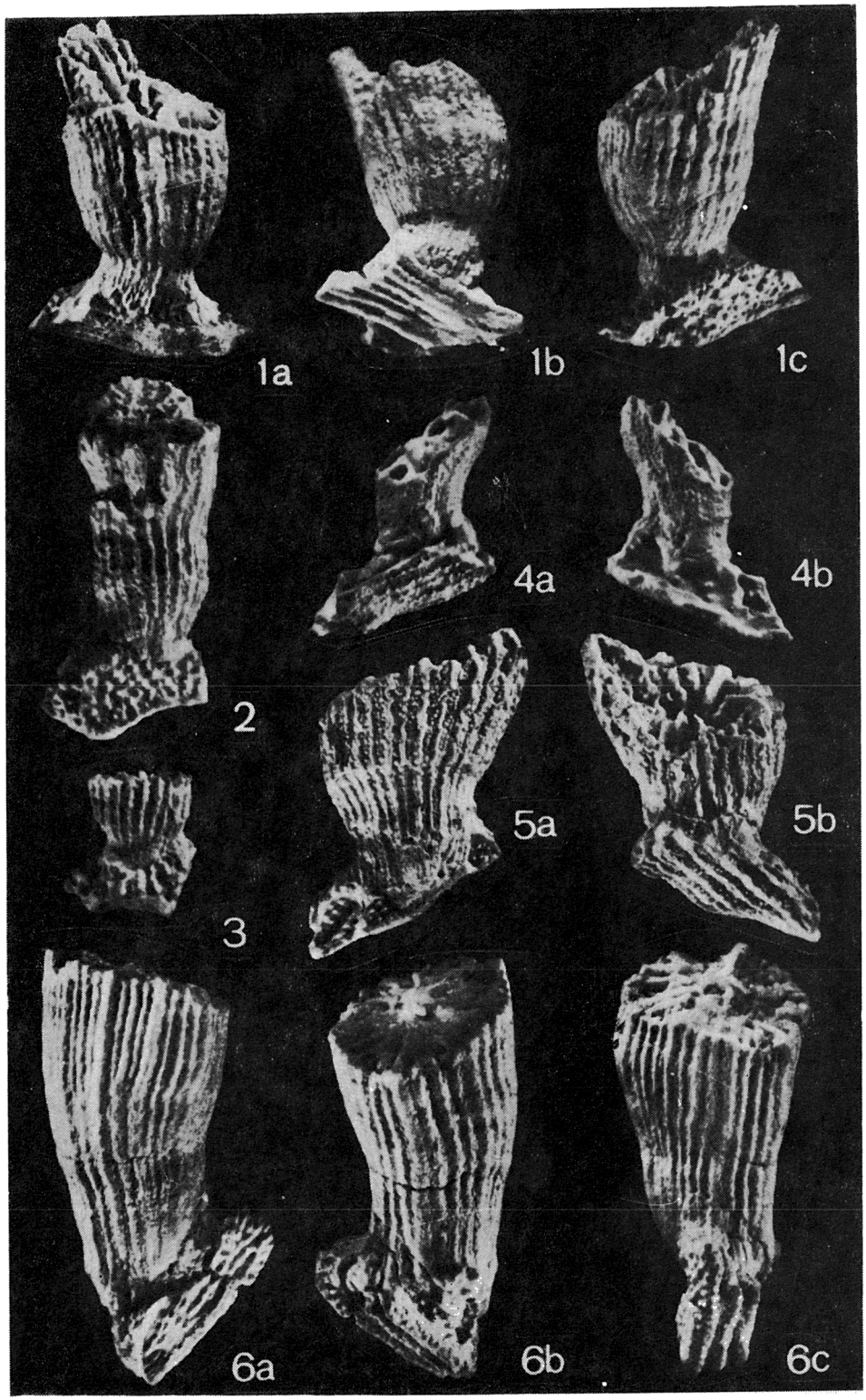
(i) In specimens which bear larger fragments of the original corallum, it is well visible that the morphological details (certainly indicative of a definite caryophyllid species) are identical both in the original part, and in the secondary corallum (*see* Pl. 1, Figs 5 and 6a; Pl. 2, Figs 5b and 6c; Pl. 3, Figs 1c and 2a);

(ii) In the same specimens which bear larger fragments of the original corallum, it is also discernible that the direction of growth in the two parts (original, and secondary) is the same, the regenerated part being always situated at the inner surface of the primary corallum (*see* Pl. 1, Figs 4b and 5; Pl. 2, Fig. 5b; Pl. 3, Fig. 1c).



Regenerated caryophyllid corals from the Korytnica Clays

All the specimens regenerated from single fragments; photographed in diverse views, to show the mutual relation between the primary fragment and the secondary corallum (detailed explanation in the text); taken × 7.5



Other examples of regenerated caryophyllid corals from the Korytnica Clays; taken × 7.5

The above data indicate that the investigated specimens of the caryophyllids have originated by a further growth of some fragments of the primary corals and they were able to reproduce the morphological features typical of a definite caryophyllid species. Of the fragmented pieces of a primary corallum, some at least were therefore able to survive and grow onwards to reproduce their specific features almost ideally, with the only exception of the size not attaining the value typical of the not-damaged specimens of the population and of the species.

REGENERATION *VERSUS* REPARATION

The **regeneration** is here understood as the process of a further growth by an animal's fragment which consequently attains, more or less ideally, the shapes and size typical of the adult specimens of the species. The regeneration may concern both the solitary animals, like the investigated scleractinian corals, and the colonial animals, exemplified for instance by the free-living bryozoans. The latter animals, the free-living bryozoans, the regeneration in which will be discussed hereafter, represent the most integrated forms in colony organization, and thus there recently appears a tendency to regard the whole colony as one animal (*see* COOK 1979, COOK & CHIMONIDES 1983). In consequence, the differences in organization of solitary and some colonial animals become less essential.

The event of a repair of the shell, as commonly known in some mollusks, especially scaphopods and gastropods, the Korytnica material including (*see* review *in:* RADWAŃSKI 1969, 1977; BAŁUK & RADWAŃSKI 1977a), and in some brachiopods (*see* review *in:* MAŁKOWSKI 1976), does not match the above definition and should be provided with another name. A new term, the **reparation,** is coined up herein, to cover all the cases of a repair of the shell, instead of the formerly used "regeneration of shells" or "regeneration of damages in shells".

PREVIOUS REPORTS ON REGENERATION IN CORALS

The reports on regeneration in scleractinian corals are very scant, and all concern the present-day specimens. Original descriptions are only two: the first one was given by VERRILL (1908), on a common regeneration of the caryophyllids (genus *Dasmosmilia*) in a material dredged off the Atlantic coast of the United States, and the second one was presented by BOSCHMA (1925) on a remarkably common regeneration in many fungiids collected at various localities of the western Pacific, and with a special attention to one species, *Halomitra philippinensis* STUDER, 1901, whose population in one of the investigated localities (at

Banda) was conspicuously dominated by regenerated specimens. These two reports have commented and/or supplemented in the two comprehensive casebook accounts by VAUGHAN & WELLS (1943, pp. 48—49), and by WELLS (1956, p. *F*350). No further reports have hitherto been available either to the present authors or to Dr. J. W. WELLS (*personal communications,* December 1977 and October 1984).

REGENERATED CARYOPHYLLIDS FROM THE KORYTNICA CLAYS

Most of the investigated caryophyllids have regenerated from single fragments of the primary animal (Pls 1—2 and Pl. 3 Fig. 3). A few specimens have however been found which regenerated from a group of fragments (Pl. 3, Figs 1—2), and in such specimens it happens that the regeneration might have occurred twice (Pl. 3, Fig. 2).

The single fragments of the primary corallum are always very small, usually more or less elongated lengthwise the primary individual (*see* Pl. 1, Figs 2—5; Pl. 2, Figs 1 and 4—6; Pl. 3, Fig. 3), but more rarely they are very short, almost isometric (*see* Pl. 1, Figs 1 and 6; Pl. 2, Figs 2—3). The number of septa in the primary fragments varies from over a dozen (Pl. 1, Fig. 5) to about five (for instance: 5 in the specimen presented in Pl. 1, Fig. 4a-4b; 6 in the specimens presented in Pl. 1, Fig. 6a-6b and Pl. 2, Fig. 5a-5b), attaining the minimum number of three (*e.g.* in the specimen presented in Pl. 2, Fig. 6a-6c). Taking into account the anatomical studies (VAUGHAN & WELLS 1943, WELLS 1956), it is concluded that the smallest fragment which could regenerate must had contained one entoseptum, supposedly does not matter of which cycle. In any case, these small fragments did not embrace two adjacent entosepta of the first cycle, as requested for the fungiids by VAUGHAN & WELLS (1943) and by WELLS (1956, p. *F*350), because then the regenerated fragment had to be about one-sixth of the primary-coral periphery.

PLATE 3

Regenerated caryophyllid corals from the Korytnica Clays

1a-1c — Specimen regenerated from a group of fragments of similar size; taken × 7.5

2a-2b — Double regenerated specimen: the first regeneration **(f)** from a group of fragments (arrowed; in *2a* arrowed is the largest fragment); the second regeneration **(s)** from a larger fragment (about one-third of the periphery), comparable to that in some once-regenerated specimens (cf. Fig. 3a-3b); taken × 7.5

3a-3b — Specimen regenerated from a larger, wedge-shaped fragment of the primary corallum; taken × 7.5


1a
1b
1c
S
3a
S
f
2a
3b
2b
f

As mentioned before, all the regenerated parts have grown at the inner surface of the primary corallum. Nevertheless, some differences are recognizable in the mutual orientation of the two parts, being variable from an almost tangential growth of the secondary corallum (Pl. 1, Figs 4 and 6), through an oblique in most cases, to a vertical one (Pl. 1, Fig. 3; Pl. 3, Figs 2 and 3). The latter case usually concerns the largest fragments, either wedge-shaped (Pl. 3, Fig. 3) or containing even about one-third of the primary specimen (Pl. 3, Fig. 2).

Regeneration from a group of fragments (Pl. 3, Figs 1—2) comprises the cases in which it took place from a few fragments amongst which one was distinctly larger (arrowed in Pl. 3, Fig. 2a), and it does also such ones when a few fragments are of similar size (Pl. 3, Fig. 1a-1c).

The double-regeneration is displayed by the specimens which regenerated from a group of fragments, and the regenerated corallum was subsequently injured again (Pl. 3, Fig. 2a-2b; arrowed are fragments preceding the first regeneration).

CAUSES OF FRAGMENTATION OF THE CORALS

In the two present-day environments from which the regenerated solitary corals have been reported, diverse explanations of their breakages are offered. In a deeper-water occurrence site of the caryophyllids, off the eastern coast of the United States (dredged material, 57 to 179 fathoms), the larger fishes and crabs were claimed to had been responsible for the breakages (VERRILL 1908). In a nearshore site in the Malay Archipelago (Banda, depth *ca.* 25 m), the majority of the regenerated specimens of *Halomitra philippinensis* STUDER comes from, the breakage was ascribed, partially at least, to the stones falling down from the rocky shore (BOSCHMA 1925, p. 241).

In the investigated locality at Korytnica, although situated very closely to the Middle Miocene (Badenian) shoreline featured by gently sloping rocks and clayey bottom (*see* BAŁUK & RADWAŃSKI 1977a, Text-figs 2 and 5), the littoral rubble is very scant and cannot be recognized as an agent of mechanical breakages. Biogenic activity is thus the more probable, similarly as it has been reported in the case of fragmentation of colonies of the free-living bryozoans (BAŁUK & RADWAŃSKI 1977b; *cf. also* 1984a, b).

When discussing the causes of colony fragmentation of the free-living bryozoans from the Korytnica Clays, the authors (BAŁUK & RADWAŃSKI 1977b) indicated that the activity of predators, either upon these bryozoans themselves or upon their commensals, was thought to had been responsible for the damages of the bryozoan colonies which subsequently regenerated. Particularly, an activity of holo-

thurians and hermit crabs has firstly been taken into account, since these very animals were living in the discussed bryozoan-bearing communities of the Korytnica Basin, and they are also known as predators of such bryozoans in the present-day environments (*see* review *in:* BAŁUK & RADWAŃSKI 1977b, pp. 150—151).

Concerning the investigated caryophyllid corals which were not too much larger than the free-living bryozoans, but which undoubtedly had more solid skeletons, the predation by holothurians does not seem to be suggestable. More probable are certainly the hermits and other crabs, the traces of whose activity are a common feature of many gastropod and scaphopod shells in the Korytnica Basin (*see* RADWAŃSKI 1969, 1977; BAŁUK & RADWAŃSKI 1977a, 1979).

Another group of animals which should be considered in respect of fragmentation of the caryophyllid corals in the Korytnica Basin are the fishes. These are commonly known as active bioeroders of corals in the present-day reef environments, and the best examples are presented by CLOUD (1959, pp. 398—399 and Pl. 131) from the Mariana Islands.

The bioerosion activity of such specialized groups as parrotfish (family Scaridae) and surgeonfish (Acanthuridae), which cause damage of the coral reefs in search of epi- and endolithic organisms, has recently been well documented from both the Indo-Pacific (CLOUD 1959) and Atlantic regions (GYGI 1975; BROMLEY 1975, 1978; FRYDL & STEARN 1978). The bioerosion in the modern reef environments is expressed not only by the total damage of coral skeletons, but also by production of gnawing marks (*see* RADWAŃSKI 1977, p. 252) on larger or more solid colonies, those of red-algal origin including (*see* CLOUD 1959, Pl. 130; GYGI 1975; BROMLEY 1975, 1978). Similar gnawing marks have also been reported from Recent blue-green-algal mats (stromatolites) in littoral environments devoid of coral reefs along the West Africa coast (Mauritania, the Gambia), and thus this bioerosion has been ascribed to the "ordinary" fish genera (SCHWARZ & *al.* 1975, MONTEILLET & PLAZIAT 1980). In all these present-day environments there have not however been noted any examples of the destruction of solitary corals comparable to those from the Korytnica Basin.

The fishes which lived in the Korytnica Basin have evidently no analogies to the modern highly specialized bioeroders of the coral reefs. Consequently, it is reasonable to ascribe the destructive activity to the common carnivorous fishes, such as e.g. *Ariosoma, Argyrosomus, Cepola,* which feed upon small invertebrates (crustaceans, mollusks, *etc.*), and whose activity in the Korytnica Basin is recently under investigation (RADWAŃSKA 1984).

The final conclusion upon the responsibility of crabs and fishes for the breakages of the caryophyllid corals in the Korytnica Basin is identical with that noted from a present-day community by VERRILL (1908).

BIOLOGICAL INTERPRETATION OF THE KORYTNICA SPECIMENS

The regenerated caryophyllid corals from the Korytnica Clays are interpreted as grown from small fragments originated due to a predatory attack, either of crabs or fishes, upon the primary specimens. Due to such an attack most of the primary specimens had been broken into isolated pieces (*see* Pls 1—2 and Pl. 3, Fig. 3), the minimum amount of which, to display ability to regenerate, was that having at least one entoseptum, does not matter of which cycle.

Some specimens, especially when their corallum was weakened by a predatory attack, might split lengthwise into larger, wedge-shaped pieces (*see* Pl. 3, Figs 2—3), comparable to those known in the present-day caryophyllids (*cf.* VERRILL 1908, VAUGHAN & WELLS 1943, WELLS 1956).

The regeneration from a group of fragments, does not matter if one was larger (*see* Pl. 3, Fig. 2) or all of similar size (*see* Pl. 3, Fig. 1), is thought to have occurred supposedly from one fragment which incorporated and fused the rest. In this case, the original animal was certainly beaten, but the polyp and corallum escaped from being torn into isolated pieces.

FINAL REMARKS

The recognized regeneration case has evidently a new bearing not only upon our knowledge of the paleobiology of caryophyllid corals, but also upon an understanding of the mode of reprodution of these corals. It has moreover a bearing upon indication of some general rules connected with the regeneration in the invertebrates, both ancient and modern.

The regeneration in the scleractinian corals, as far as the hitherto available reports concern, is confined to some groups, precisely to the caryophyllids and the fungiids. In these two groups it should therefore be regarded (*cf.* VAUGHAN & WELLS 1943, WELLS 1956) as an immanent feature of their biology.

Both in the investigated biotope of the Korytnica Basin, and in the two hitherto known present-day occurrence sites recognized by VERRILL (1908) and by BOSCHMA (1925), the community is dominated by the regenerated specimens. It is therefore concluded that regeneration, in caryophyllids always noted as from small or very small fragments (*see* VERRILL 1908), provides an important mean for reproduction of the species. It acts obviously to the same extent as it does in the free-living bryozoans (*see* MARCUS & MARCUS 1962; BOARDMAN & CHEETHAN 1973; BAŁUK & RADWAŃSKI 1977b, 1984a, b; COOK & CHIMONIDES

1983). In some present-day species of these bryozoans the cases are known of the occurrence of populations composed even entirely of regenerated colonies (COOK & CHIMONIDES 1983, p. 568). In the Korytnica Basin, the populations of one of the free-living species, *Cupuladria vindobonensis* BAŁUK & RADWAŃSKI, although unrecognizable as to their ideal contemporaneity, are highly dominated by the regenerated colonies (BAŁUK & RADWAŃSKI 1977b, 1984b). It is to note that such populations in the Korytnica Basin characterize by the presence of colonies of the size distinctly smaller than that of the colonies which did not undergo regeneration.

A smaller size of the animals which have grown due to regeneration, and which may dominate a given population (*cf.* BOSCHMA 1925, p. 241) is consequently thought to be a general biological rule, well demonstrated in the Korytnica environments both by the free-living bryozoans, and by the investigated caryophyllid corals. The frequency of the carnivorous animals does not seem to have a special control upon that rule, because in an extreme case one predatory individual may become responsible for the damage both of one "mother" specimen and of the whole population.

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