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Boring ctenostomate bryozoans from the Korytnica Clays (Middle Miocene; Holy Cross Mountains, Central Poland)

ABSTRACT: An assemblage of boring ctenostomate bryozoans that comprises well developed and well preserved colonies of *Spathipora* sp., *Terebripora* sp., and *Penetrantia* sp. is recognized in circum-apertural parts of some gastropod shells contained within the Middle Miocene (Badenian) Korytnica Clays exposed on the southern slopes of the Holy Cross Mountains, Central Poland. Taphonomical features of the bryozoan-infected shells evidence the settlement of the bryozoans after the death of the gastropod. The choice of some special gastropod shells by the bryozoans suggests furthermore that taken by the bryozoans became the shells inhabited by the hermit crabs to whom the bryozoans were the commensals. This biologic relationship is discussed in comparison with the other commensals to the hermit crabs that have dwelled in the Korytnica basin.

INTRODUCTION

The aim of the present contribution is to discuss the taphonomical and ecological significance of the boring ctenostomate bryozoans living within the gastropod shells embedded in the Middle Miocene (Badenian) Korytnica Clays developed on the southern slopes of the Holy Cross Mountains, Central Poland. A general setting of the basin and environmental conditions prevailing during sedimentation of the Korytnica Clays are given by the present authors in separate reports (Bałuk & Radwański 1977a, 1979).

Within the much fossiliferous, mostly gastropod-bearing Korytnica Clays the bryozoans are rather very rare components of the organic assemblages (*cf.* Bałuk & Radwański 1977a, p. 97; 1977b). The boring bryozoans fall into the category of shell endozoans, which comprises the shell destroying sponges, polychaetes, and pelecypods (*cf.* Bałuk & Radwański 1977a, 1979; Kern 1979). The presence of the boring ctenostomate bryozoans has been announced formerly, and exemplified by borings of *Spathipora* sp. (*see* Bałuk & Radwański 1977a, p. 107 and Pl. 6, Fig. 4).

GENERAL STATUS OF BORING CTENOSTOMATE BRYOZOANS

The boring ctenostomate bryozoans have long been known in literature and their taxa have either been regarded as denoting the body animals, or as the borings (*cf.* Soule & Soule 1969, Pohowsky 1978). Some present-day species have been first described from the borings, and their soft parts recognized afterwards. Consequently, there still exists a great confusion which taxa are established for the animal species, and which denote only the type of the borings regardless their assignation to a definite species (*see* Boekschoten 1970, Pohowsky 1978). The same situation appears for the fossil forms, some of which have remained long under discussion on their nature and taxonomy in the limits either of body or trace fossils (*cf.* Boekschoten 1966, 1967, 1970; Bromley 1970; Häntzschel 1975; Warme 1975; full references *in* Pohowsky 1978).

The recent investigations of boring ctenostomate bryozoans show that the borings, when treated with polyester resin, deliver the casts fully corresponding in their shape to that of the animal body; it has therefore been suggested that the so-investigated borings should be regarded as a normal paleontological material of the body-fossils type (Pohowsky 1974, 1978). However, if one can regard the ancient borings (or their resin casts) as the body fossils, from a formal point of view and their relation to calcareous substrate they remain in the ichnological category of borings. Moreover, as they are produced by the animal to embed the whole body into the calcareous substrate for protection, they should not be named as the etchings (*cf.* Radwański 1977, p. 249)[1].

THE STUDY OF THE KORYTNICA MATERIAL

The colonies of the boring ctenostomate bryozoans recognized in the Korytnica gastropods have been studied only under the binocular glasses as the attempts to clean the clay from the zooids and obtain the resin casts remained unsuccessful. As these very methods are nowadays decisive in recognition of particular taxa (*cf.* Soule & Soule 1976, Pohowsky 1978), especially at their specific rank, the present authors had to make only the generic determination. The investigated colonies have therefore been assigned generally to the genera *Spathipora* Fischer, 1866, *Terebripora* d'Orbigny, 1842, and *Penetrantia* Silén, 1946.

At the present state of knowledge it is also difficult to make any comparisons with the contemporaneous forms of other European regions. Except of the Loire basin in France therefrom collected specimens are discussed by Pohowsky (1978), the Neogene deposits of other basins have yielded rather very poor materials. The

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[1] The true etchings composed of a series of shallow pits are displayed only by some cheilostomate bryozoans, as evidenced primarily by the genus *Electra*; the discussion upon these etchings is omitted here (*cf.* Boekschoten 1966, 1967; Bromley 1970; Bromley & Surlyk 1973; Warme 1975; Radwański 1977, p. 249).

three genera recognized in the Korytnica shells are briefly reported from the Pliocene of Belgium (Boekschoten 1966, 1967) and Italy (Pohowsky 1978; *cf. also* Robba & Ostinelli 1976); *Spathipora* sp. is also known from the Upper Miocene of the Island of Sylt (Cadée 1977).

From the Paratethys basins the only reports on *Spathipora* sp. and *Terebripora* sp. are coming from Lapugy in the Transylvanian basin (Pohowsky 1978, pp. 108 and 118; Pl. 15, Figs 5—7), and on *Penetrantia* sp. both from Lapugy, and from Grund in the Vienna basin (Pohowsky 1978, p. 89).

DISTRIBUTION ON THE GASTROPOD SHELLS

The three recognized boring ctenostomate bryozoans display the same distribution on diverse gastropod shells from the Korytnica Clays. Generally, infected by the bryozoans are parts around the shell aperture, with a tendency to spread towards the shell apex, and to avoid the siphonal groove. The most frequently therefore are taken the upper parts of the both lips, and the region around, which in the following discussion are shortly called as the circum-apertural region of the shell. Rarely, the boring bryozoans have also infected the opposite (abapertural) part of the shells. On the other hand, the inner wall of the shell at the aperture has often been occupied by the invading colonies.

The colonies of particular genera of the boring bryozoans occur on the gastropod shells (*see* Pls 1—8) either separately, as demonstrated by *Spathipora* sp. (*cf.* Text-fig. 1 and Pls 1—3), *Terebripora* sp. (*cf.* Pls 4—6), and *Penetrantia* sp. (*cf.* Pl. 8), or jointly one with the other (*cf.* Pl. 7).

Within the infecting colonies, generally there is no orientation of the stolons and zoecia in regard to a definite part of the gastropod shell, although in well preserved and not very dense colonies, the stolons are usually (with exceptions, *see* Pl. 1) spreading out of the aperture. This is certainly the case of newly domiciling colonies, while in old colonies (or a few ones living simultaneously, or in successive generations) within the meshwork of the borings, such an orientation vanishes. If the extent of the whole colony is clearly recognizable, as in the case of *Spathipora* sp., its ancestrular region and adjacent proximal parts of the colony (*see* Text-fig. 1) may also be situated at the abapertural side of the shell (*Ancilla glandiformis*, in this case), whereas the distal parts with endings of the stolons disperse in almost all directions (*cf.* Text-fig. 1 and Pl. 2).

The state of preservation of particular colonies is diverse. Besides the very well preserved colonies (*see e.g.* Pls 1—2; Pl. 4; Pl. 6, Fig. 1; and Pl. 8, Fig. 1), there are also colonies slightly (*see e.g.* Pl. 3, Fig. 2; Pl. 5, Fig. 1; and Pl. 6, Fig. 2) and more or less deeply abraded (*see e.g.* Pl. 5, Fig. 2, and Pl. 8, Fig. 2). The abrasion partly at least resulted from the biogenic activity of different biota which had subsequently settled upon the bryozoan-infected shell. This might have realized either just on the sea bottom, as exemplified by borings of the sponges (*see* Pl. 6, Fig. 1), or within the sediment when the shells became buried, as indicated by etchings produced presumably by the seagrass roots (*see* Pl. 5, Fig. 2; *cf.* Radwański 1977, p. 250, *and* Bałuk & Radwański 1977a, p. 101). Some damages of the bryozoan-infected shells (Pl. 5, Fig. 1; and Pl. 8, Fig. 2) are ascribed to the activity of hermit crabs that inhabited these very shells (*see below*).

Of the damages produced by the boring sponges *Cliona*, some are evidently subsequent to the activity of boring bryozoans (as indicated above; *cf.* Pl. 6. Fig. 1), but the others are unclear as to such a relation (*cf.* Pl. 6, Fig. 2). Anyway, as compared with the destruction by these boring sponges of the other shell material within the Korytnica basin, it is assumed that the destruction happened after the death of gastropods when their empty shells were resting on the sea bottom (*cf.* Bałuk & Radwański 1977a).

As there are no obvious examples of gastropod reaction to the boring bryozoans, or overgrowth of their borings by the gastropod shell, it seems reasonable to conclude that the ctenostomate bryozoans were infecting the gastropod shells after the death of their hosts.

The list of the gastropod taxa infected by the boring ctenostomate bryozoans (Table 1) comprises 16 species, the selection of which is considered in the following chapter.

ECOLOGICAL INTERPRETATION

The distribution in diverse gastropod shells, and frequency of particular genera (*cf.* Table 1) show that the boring ctenostomate bryozoans were infecting preferably the shells of *Ancilla glandiformis* (Lamarck). This species, although rather common within the Korytnica Clays, does not dominate the gastropod assemblages which are featured by the abundance of two species of *Clavatula*, one species of *Turritella*, one of *Murex*, and four or five species of *Natica*. It is therefore apparent that the boring bryozoans do not take the most common species. The same is stated for the other infected shells which belong to rather rare species within the Clays.

Of the shells infected (*cf.* Table 1), one may indicate a few general features which are typical of their gastropod species: most of these shells are more or less oblong either completely smooth (*Ancilla, Natica, Lyria, Conus, Cassis*), or almost plain (*Ranella marginata, Sveltia, Euthria*) while the remainder are moderately sculptured and devoid of any more projecting ornamentation details (*Triton, Fusus, Ocenebra*); the more pronouncedly sculptured shells are an exception (*Ranella nodosa, Xenophora*). Moreover, most of the infected shells are heavier from one side, usually from

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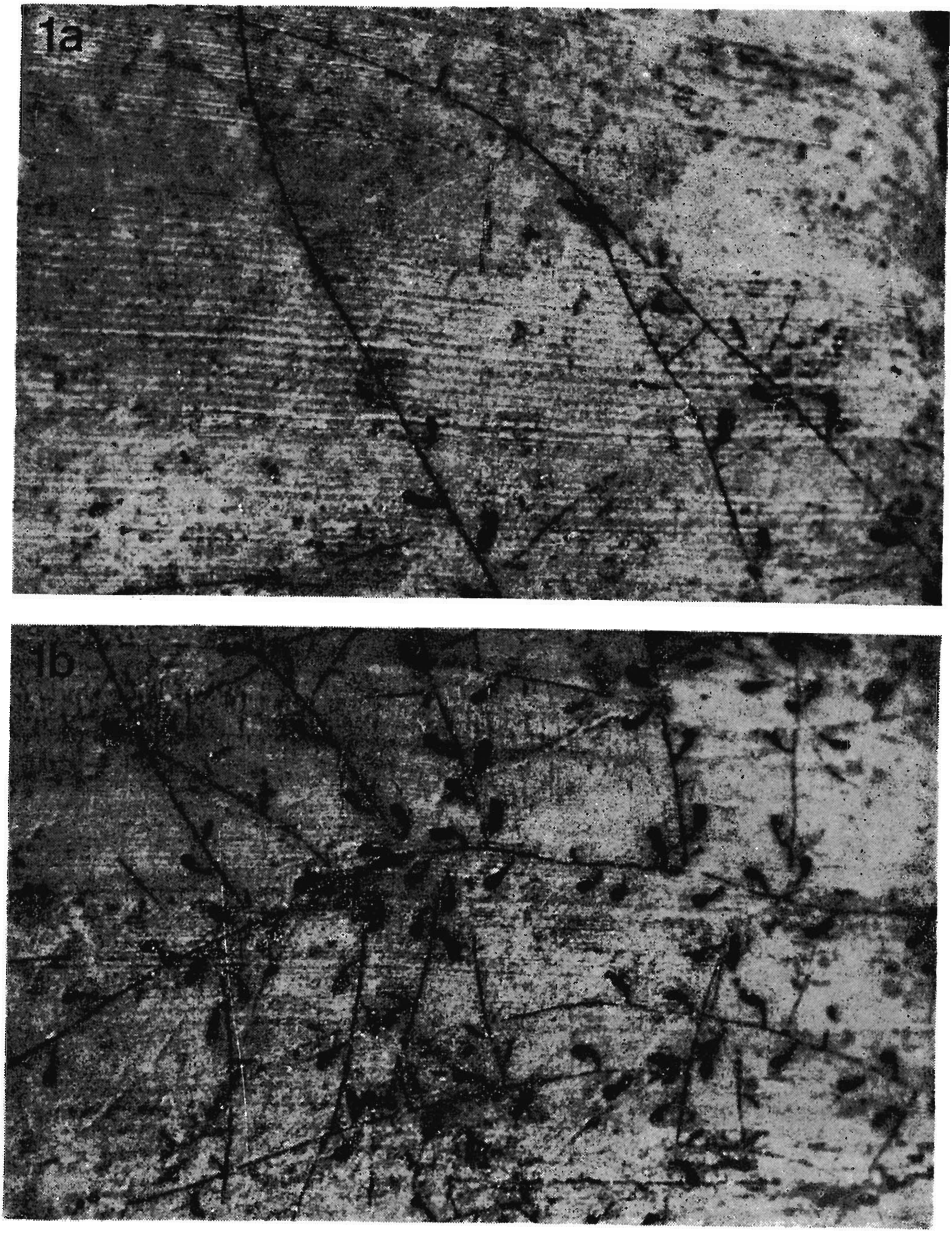
PLATE 1

Central part of the colony of *Spathipora* sp. on the apertural side of *Triton nodiferum* Lamarck; direction of the colony growth is from the apex towards the aperture (up in the photo) where a fragment of *Terebripora* sp. colony is also visible; ×20



Close-up views of the well preserved colony of *Spathipora* sp. developed on the abapertural side of *Ancilla glandiformis* (Lamarck) and presented in Text-fig. 1: **1a** — distal part of the colony, **1b** — near-center part of the colony; ×20 adapertural, apical one; on the other hand they are rather thick-walled, and bear relatively large aperture. The boring bryozoans have not infected the shells provided with more pronounced nodes, or with prickles, the same as the shells more elongated and/or bearing longer siphonal groove, globular in shape, as well as thin-walled, and having small, narrow, or slit-like aperture. Taking into account the number of

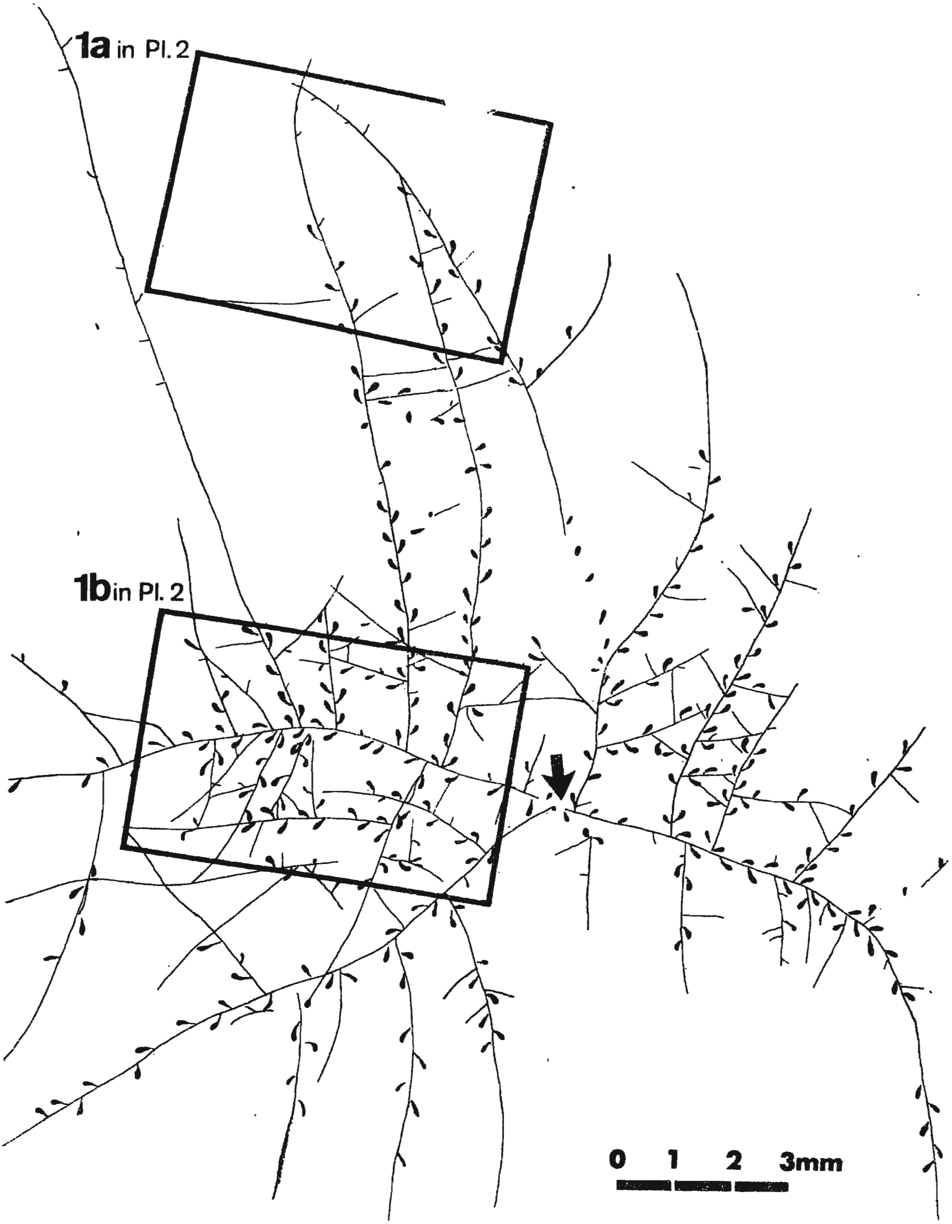


Fig. 1. The whole colony of *Spathipora* sp. developed on the abapertural side of *Ancilla glandiformis* (Lamarck); arrowed is the ancestrular region of the colony; rectangled are fragments presented in Pl. 2

Table 1

List of gastropod species whose shells are infected by boring ctenostomate bryozoans, arranged according to the frequency of the bryozoans: S — *Spathipora*, T — *Terebripora*, P — *Penetrantia*

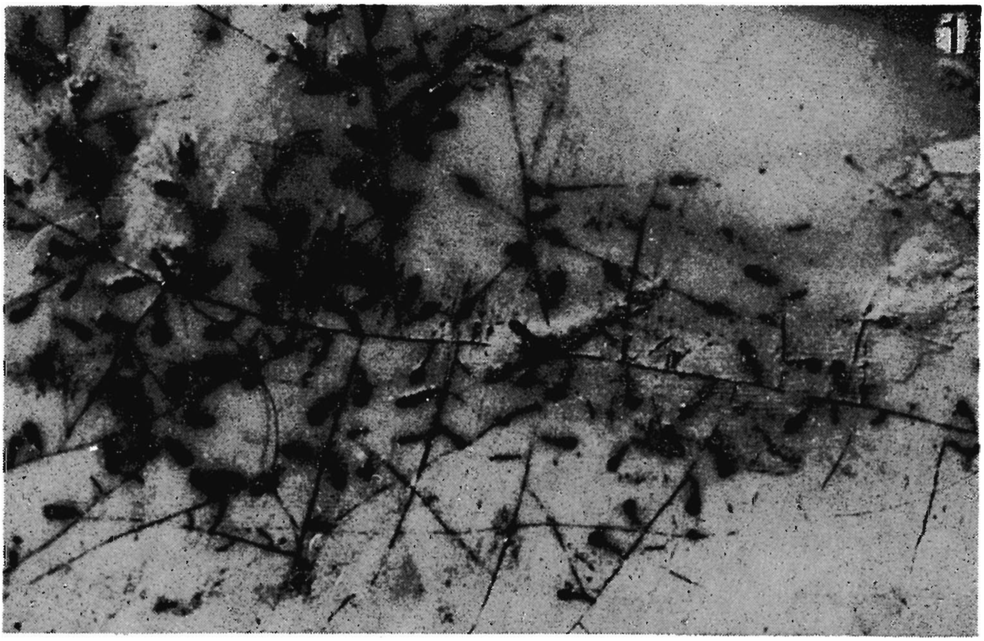
The gastropods are determined after Friedberg (1911—1928)

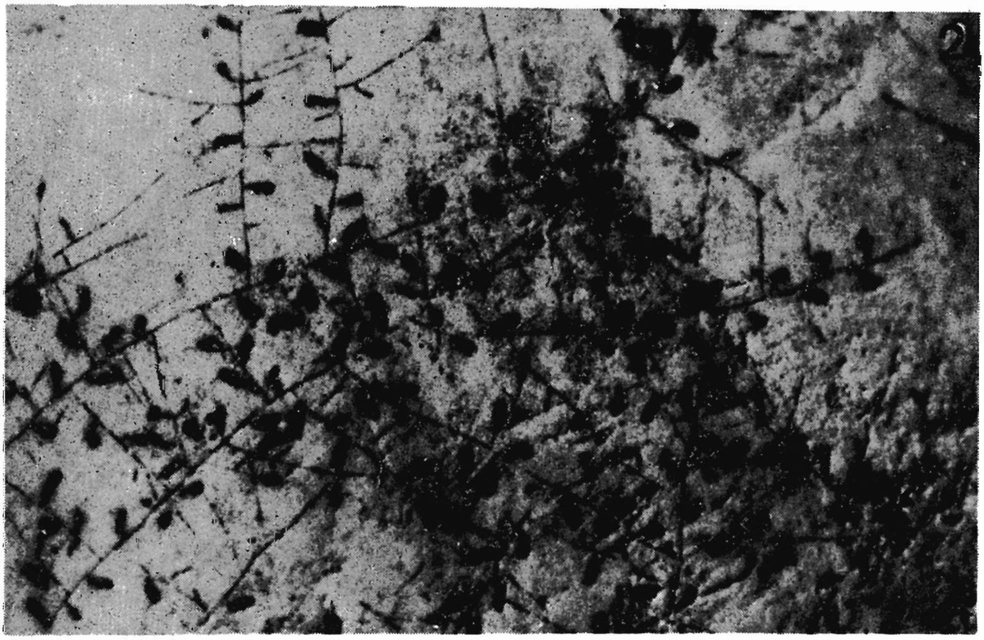
Species	Number of shells infected	Boring bryozoans	*Helicotaphrichnus commensalis*	
			in specimens with boring bryozoans	noted by Kern (1979) in other specimens
Ancilla glandiformis (Lamarck, 1810)	commonly	S T P	+	+
Ranella marginata (Martini, 1777)	30	S T P*	+	+
Sveltia inermis (Pusch, 1837)	6	S T P	+	+
Fusus hoessi Partsch, 1856	6	T P	+	+
Natica redempta Michelotti, 1847	5	S T P		
Euthria puschi (Andrzejowski, 1830)	3	S T		+
Triton affine Deshayes, 1832	3	T P		+
Triton nodiferum Lamarck, 1822	2	S T P		+
Lyria taurinia Bonelli, 1826	2	S P		
Conus sp.	1	S T P		
Ranella nodosa Borson, 1825	1	S		
Crepidula crepidula (Linnaeus, 1766)	1**	S		
Xenophora deshayesi (Michelotti, 1847)	1	T		
Ocenebra erinacea (Linnaeus, 1777)	1	T		+
Cassis miolaevigata (Sacco, 1890)	1	T		
Euthria intermedia (Michelotti, 1847)	1	P	+	+

P* — dominated by *Penetrantia* sp.
** — *Crepidula* living in empty shell of *Fusus* (see the text)

the inspected shells which reaches some 30,000, and number of the species which are more common in the Korytnica Clays (being about one hundred), the discussed relation does not seem accidental. Following investigations of the biologic relationships between the species of the Korytnica communities (*cf.* Bałuk & Radwański 1977a), the present authors have thought that this relation may be easily understood when assuming that the infected shells were occupied by hermit crabs. This explains the choice of the shells with relatively large apertures to contain the crab, devoid any projecting ornaments that could disturb the dragging of the shell, rather heavier and well balanced, solid and thick-walled to save this secondary occupant.

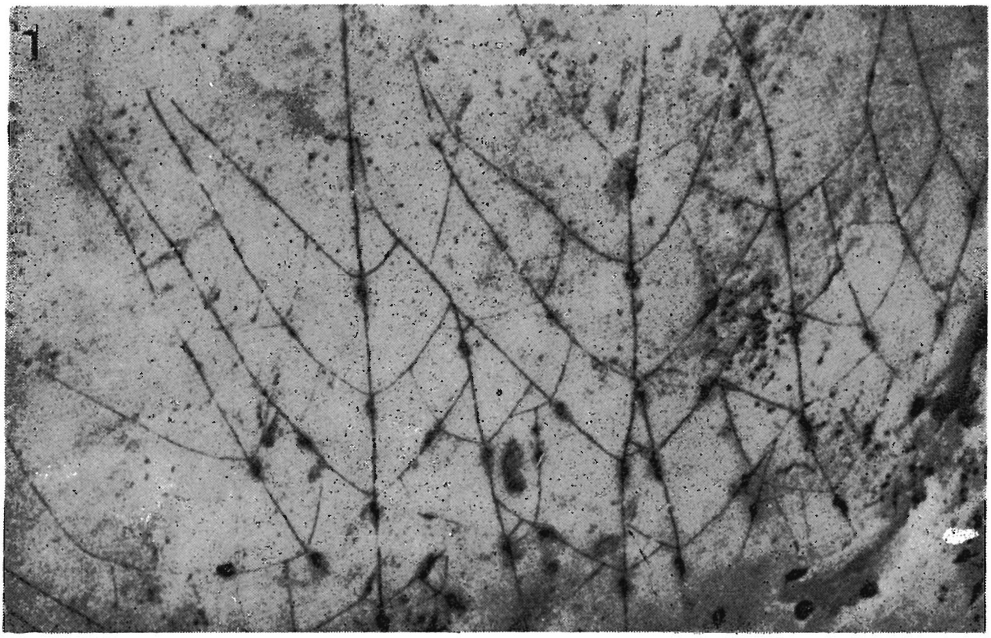
The positive arguments for the suggested relationship cannot be obviously presented. All arguments remain therefore indirect, the first one coming from the occurence of *Helicotaphrichnus commensalis*, a tube produced in gastropod shells and attributed, similarly as in the present-day environments, to the spionid polychaetes that are commensal to the hermit crabs inhabiting such shells (*see* Kern 1979, Kern & *al.* 1974). Within the Korytnica gastropod shells, those yielding *Helicotaphrichnus commensalis* are primarily the oblong shells (*cf.* Kern 1979), smooth or almost plain, with other characteristics similar to these infected by boring bryozoans, and with *Ancilla glandiformis* being taken the most commonly, although some exceptions,

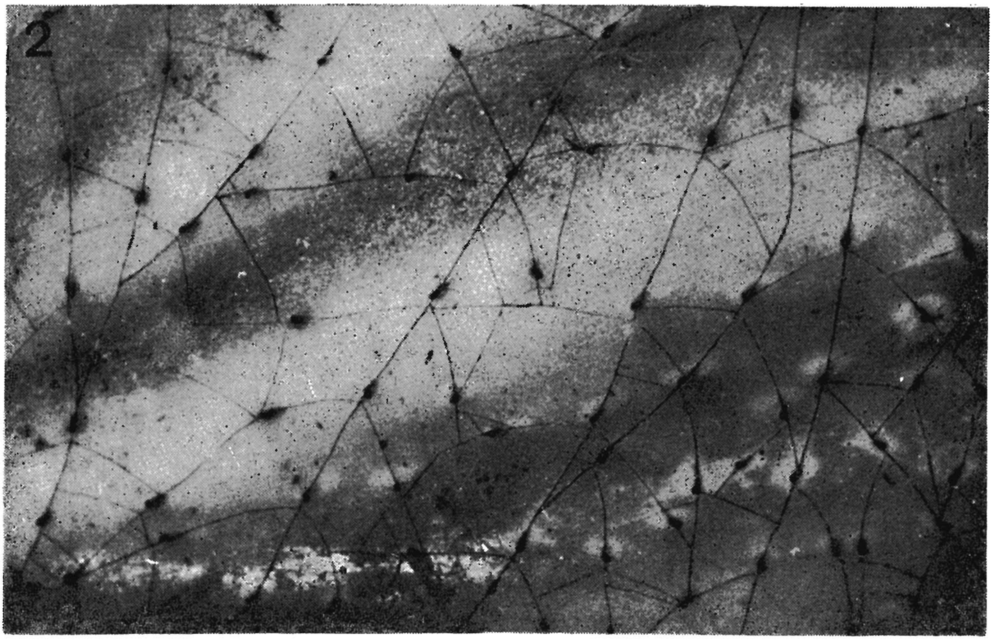




1 — Well preserved fragment of the central part of *Spathipora* sp. colony developed on the inner lip of *Ancilla glandiformis* (Lamarck); ×20

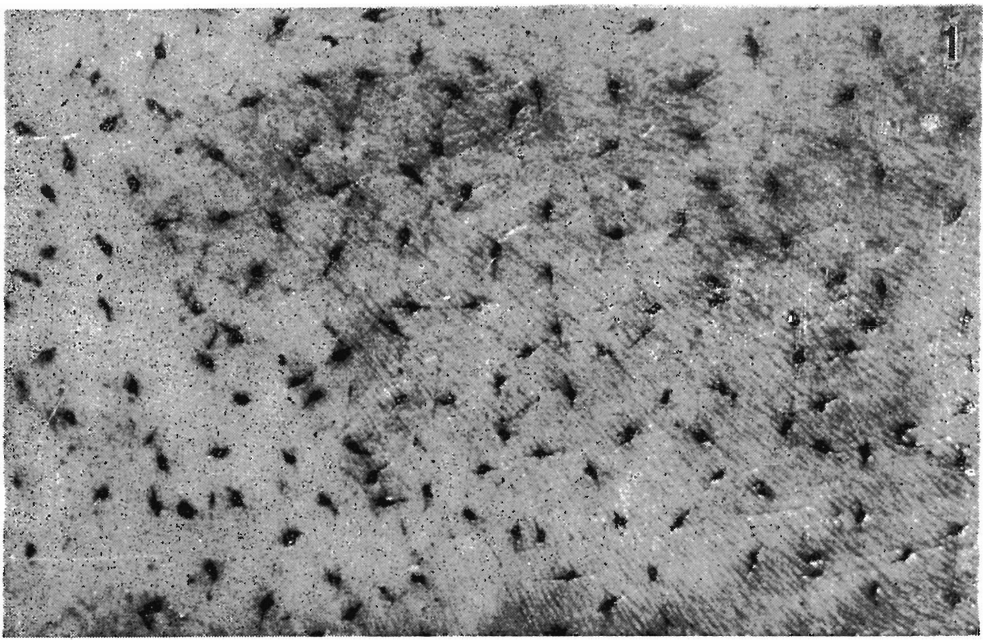
2 — Partly abraded fragment of *Spathipora* sp. colony developed on the apical part of *Ancilla glandiformis* (Lamarck); this is another fragment of the colony illustrated formerly (Bałuk & Radwański 1977a, Pl. 6, Fig. 4); ×20

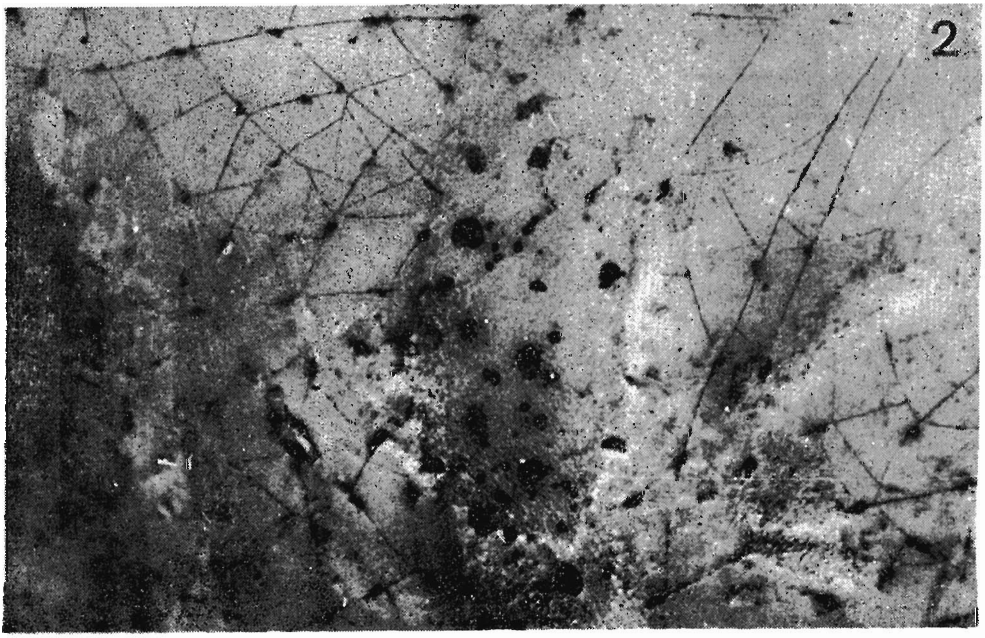




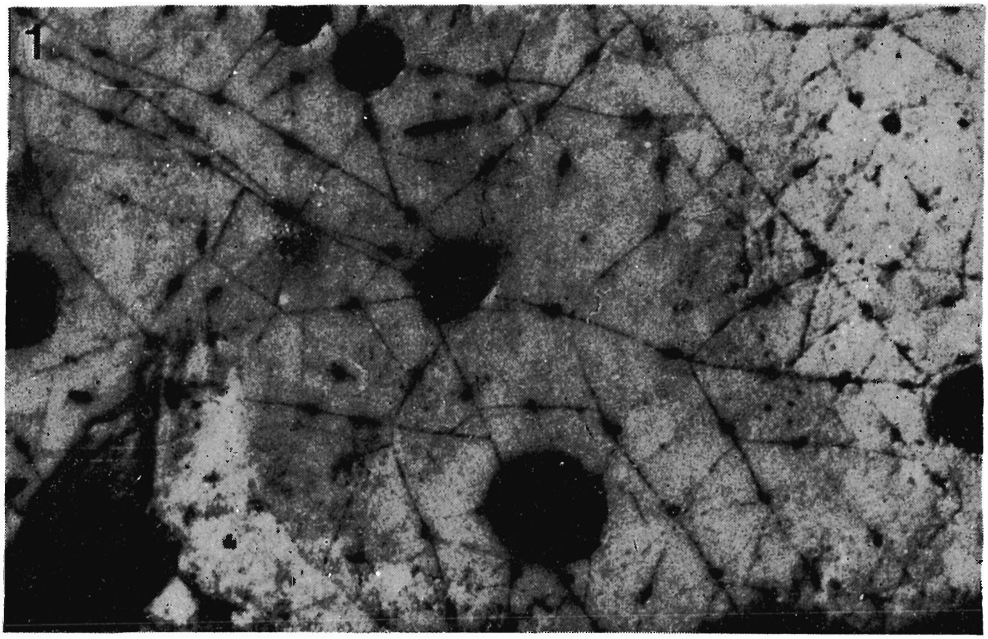
1 — Well preserved fragment of the distal part of *Terebripora* sp. colony developed on the abapertural side of *Ancilla glandiformis* (Lamarck), near the apex (*cf.* Pl. 5, Fig. 2); the endings of the stolons are visible; ×20

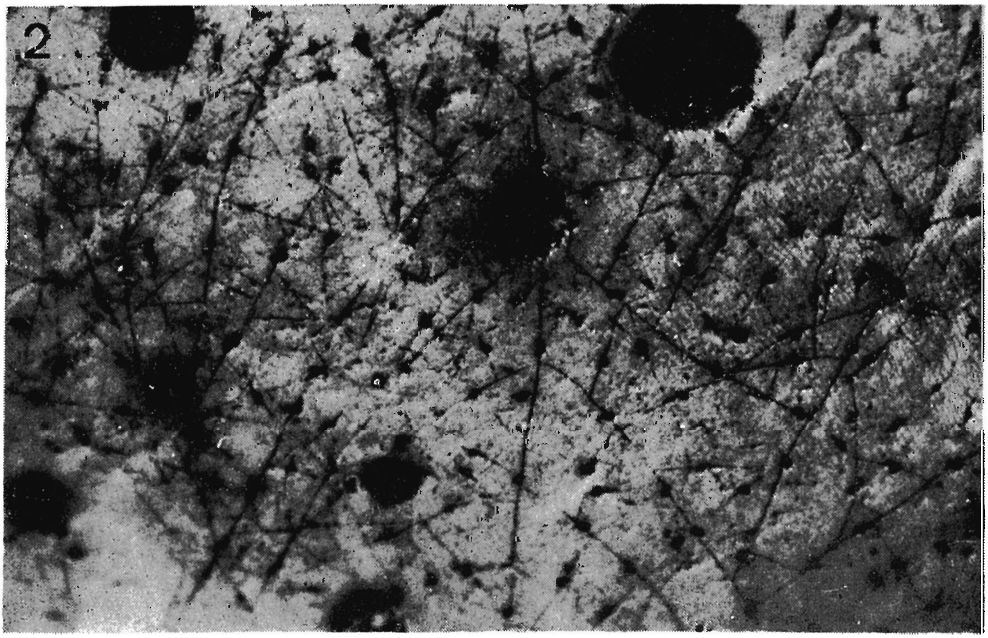
2 — Well preserved fragment of the near-distal part of *Terebripora* sp. colony, developed on the apertural side of *Ancilla glandiformis* (Lamarck), near the apex; × 20





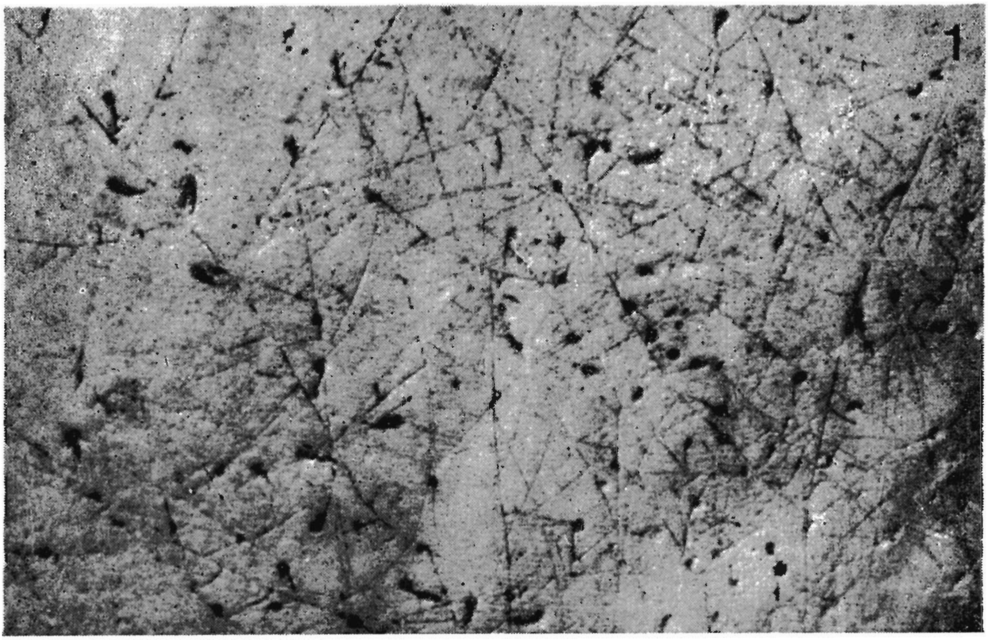
1 — Slightly abraded fragment of the central part of *Terebripora* sp. colony developed on the apertural side of *Ancilla glandiformis* (Lamarck); this is the region of the shell which displays the features of wearing marks resulted from dragging of the shell by a hermit crab; ×20
2 — Fragment of the distal part of *Terebripora* sp. colony, partly destroyed by the etchings produced presumably by the seagrass roots when the shell became buried in the sediment; the colony was developed on the abapertural side of *Ancilla glandiformis* (Lamarck), and this is the same colony as that presented in Pl. 4, Fig. 1; ×20

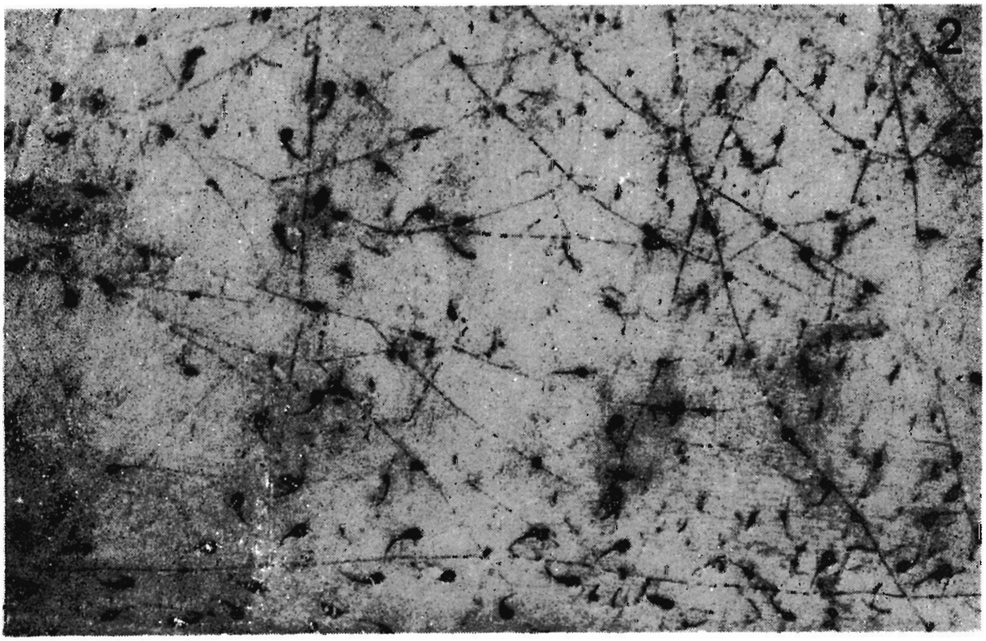




1 — Well preserved fragment of the central part of *Terebripora* sp. colony developed on the inner surface of the shell whorl of *Xenophora deshayesi* (Michelotti), bored by the sponge *Cliona vastifica* Hancock; the *Cliona* borings are younger and cut the stolons; ×20

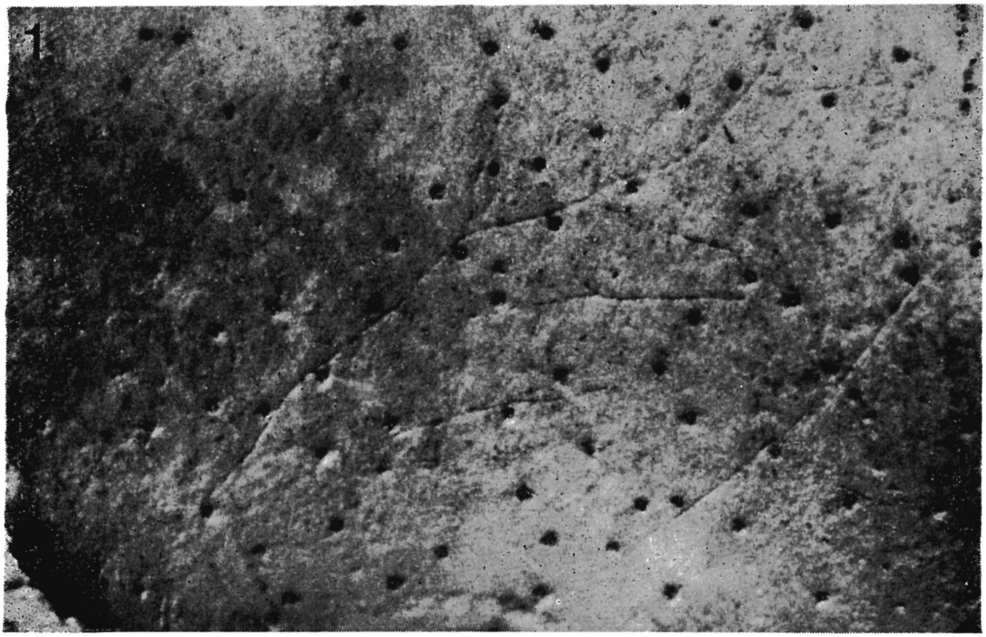
2 — Slightly abraded fragment of the central part of *Terebripora* sp. colony developed on the apertural side of *Ancilla glandiformis* (Lamarck) bored by *Cliona celata* Grant; ×20

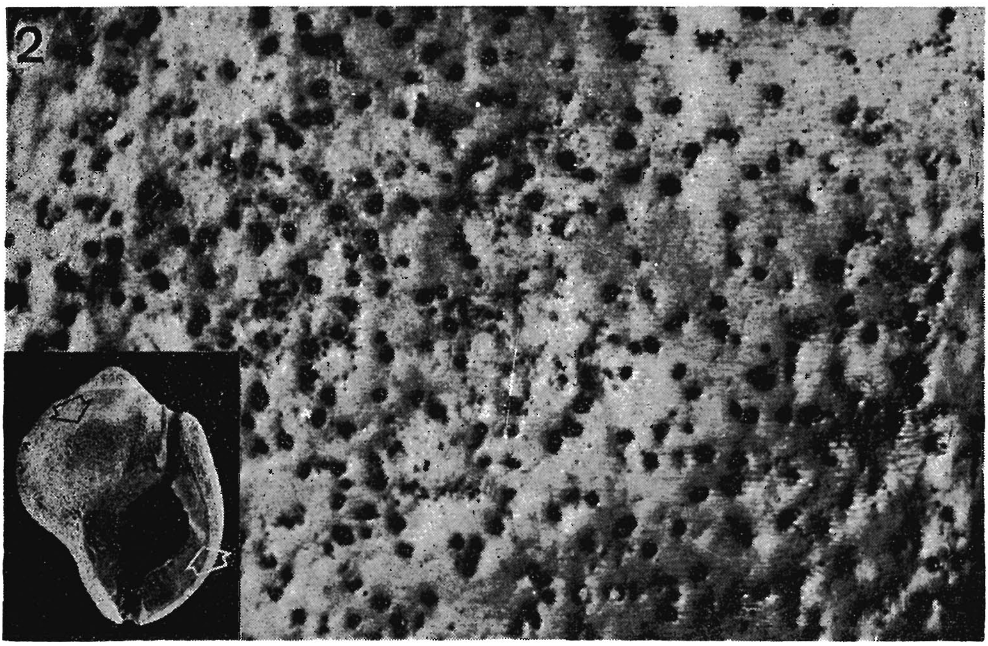




1 — Slightly abraded colonies of *Spathipora* sp. and *Terebripora* sp. developed on the apertural side of *Ancilla glandiformis* (Lamarck); ×20

2 — Well preserved colonies of *Spathipora* sp. and *Terebripora* sp. developed on the inner lip of *Natica redempta* Michelotti; ×20





1 — Well preserved central part of the colony of *Penetrantia* sp., with visible stolons, and developed on the inner lip of *Sveltia inermis* (Pusch); ×20

2 — Abraded central part of *Penetrantia* sp. colony developed on the adapertural side (*black arrowed* in the insert) of *Ranella marginata* (Martini), ×20; the insert shows the shell of *Ranella marginata* in its actual size with visible wearing marks (*black arrowed*) and an incision on the outer lip (*white arrowed*), both resulting from the activity of a hermit crab especially with *Clavatula*, have also been stated (*cf.* Kern 1979, Table 1 and Text-fig. 3).

The relation of the time of settling of the spionid polychaete and of the boring bryozoan on a given gastropod shell cannot be clearly recognized. There appear some specimens in which the bryozoan stolons penetrate the wall of the boring *Helicotaphrichnus commensalis* which indicates the spreading of the bryozoan colony to that place (but not its settlement) after the death of the polychaete. On the other hand, however, there are also present the shells infected by bryozoans whose colonies have been damaged when the shell was dragged on the sea bottom by the hermit crab (*cf.* Pl. 5, Fig. 1 and Pl. 8, Fig. 2). The latter damages are well demonstrated in shells of *Ranella marginata* (Martini) which were preferably infected by *Penetrantia* sp. (*see* Table 1). The wearing marks on these shells appear on their left adapertural, apical side which becomes worn almost flat (*black arrowed* in the insert in Pl. 8, Fig. 2), likewise in other known examples (*cf.* Ehrenberg 1931; Boekschoten 1966, 1967; Radwański 1977, p. 252). In the same shells there sometimes also occurs a distinct incision or a notch on the outer lip (*white arrowed* in the insert in Pl. 8, Fig. 2) which presumably results from the rubbing by the crab's claw, likewise in some other comparable examples (*cf.* Boekschoten 1966). Consequently, only a general conclusion may be drawn that the spionid polychaete and the boring bryozoans were spreading into and over the gastropod shell more or less simultaneously, and when that shell had already been occupied by the hermit crab. It is therefore thought that the spionid polychaete and one or a few different boring bryozoans were the commensals to the hermit crabs within the Korytnica environment, to the same extent as diverse epi- and endobionts are in present-day environments. To exemplify the latter commensals, such commonly known forms may be indicated as *Hydractinia* and some sea anemones (*cf.* Ehrenberg 1931, Papp 1947), acrothoracican barnacles *Trypetesa* boring in gastropod columellas (*cf.* Tomlinson 1953, 1955, 1969; Boekschoten 1966), and some cheilostomate bryozoans (*cf.* Cook 1964).

In the Korytnica environment, the discussed two commensals being the suspension-feeders were gaining and benefiting from a water flow induced by the hermit crab moving over the sea bottom. This water flow was certainly more efficiently requested by the larger commensal, the spionid polychaete, which has been settling just at the crab, whereas the tiny bryozoans could spread, as indicated above, over the whole circum-apertural region of the gastropod shell, and even more outwardly where the water motion was becoming relatively weaker.

The discussed two commensals, as apparent from their distribution in diverse gastropod shells (*comp.* Table 1, *and* Kern 1979, Table 1), were often infecting the same gastropods although their simultaneous occurrence on a given shell is relatively rare, and it realizes only in the species the most commonly invaded, i.e. *Ancilla glandiformis* (Lamarck) and *Ranella marginata* (Martini). It may therefore be interpreted that the commensals could take different shells and even different crabs in particular situations, changing their partners from place to place, and rarely meeting each other in one shell. A similar relation is noted in present-day biotopes of *Polydora commensalis* Andrews, the spionid polychaete to which *Helicotaphrichnus commensalis* is partly at least attributed (Kern & *al.* 1974), and which changes both the shell and the hermit crab from one locality to another (Blake 1969).

If this was the general rule, some exceptions should also be taken into account. One concerns the shell of *Crepidula crepidula* (Linnaeus) infected by *Spathipora* sp., as this gastropod lives inside empty shells of diverse gastropods (*see* Bałuk & Radwański 1977a). In this case, either *Spathipora* was a non-commensal settler, or it domiciled in the slipper-limpet shell when the *Fusus* shell (*cf.* Table 1) was inhabited by a hermit crab who, regardless the being of the slipper limpet alive or dead, had to carry this obstacle still adhered to the internal wall of its own house.

The other exception is with two instances of the shells deeply incised by some crabs, the cuttings of which destroy the colonies of boring bryozoans. The activity of the crabs is here clearly younger than the settlement of boring bryozoans, but it should not be ascribed to the hermit crabs. Formerly, the present authors (Radwański 1977, Bałuk & Radwański 1977a) have regarded such deep incisions as made by the hermit crabs, the same as diverse smaller cuttings. This conclusion has been recently objected by Förster (1979) who indicated that presumably the more responsible for such deep damages were the crabs of the genus *Calappa* which is remarkedly common in the Korytnica Clays, and which in present-day environments opens the gastropod shells searching just for the hermits (*cf. also* Shoup 1968, Bishop 1975). It is therefore possible that such very relation has also realized in the Korytnica environment. If so, it may be thought that the presence of the hermit crabs in gastropod shells was not only necessary to the ctenostomate bryozoans for their settlement, but sometimes it became dangerous for their further existence.

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