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The colony regeneration and life habitat of free-living bryozoans, *Cupuladria canariensis* (Busk) and *C. haidingeri* (Reuss), from the Korytnica Clays (Middle Miocene; Holy Cross Mountains, Poland)

ABSTRACT: The colony regeneration of free-living cheilostome bryozoans from the Korytnica Clays (Middle Miocene, Holy Cross Mountains, Central Poland) is revealed by two cupuladriid species, *Cupuladria canariensis* (Busk) and *C. haidingeri* (Reuss), the first of which is extant. In these species, the regeneration is for the first time recorded from ancient environments, the phenomenon itself being formerly known in the present-day forms. The regeneration in colonies from the Korytnica Clays often happened from very tiny fragments, some of which were composed of only one zooid that survived the breakage of the primary colony and remained alive. Contrary to previous views, the investigated specimens were well adopted to the clay-bottom environment if the water-circulation conditions were favorable for their life requirements (bottom currents in action, no settling of clay particles from turbid waters). It is also shown that these cupuladriid species are indicative of tropical and/or subtropical conditions prevailing in the Korytnica basin.

INTRODUCTION

The free-living cheilostome bryozoan species *Cupuladria canariensis* (Busk, 1859) is one of a few whose biology and ecology is recognized the best. It has long been the subject of special interest, both in respect to its life habit much deviated from normal bryozoans, and to its ability to regenerate the colonies from small fragments. Various aspects of its ecology were discussed in a very concise and comprehensive study by Lagaaij (1963), and emphatically entitled by him as *"Cupuladria canariensis* (Busk) — portrait of a bryozoan". This study showed

the ecological requirements of present-day forms, and made serious implications on the paleoecology of the ancient forms of this species which evolved in the earliest Miocene. As it clearly appears from his study, Lagaaij (1963, p. 172) was undoubtedly right when stated that "one ecologically well-known species is worth more than a hundred *tabulae rasae*". To contribute on the knowledge of the Miocene representatives of such a very species is the aim of this paper.

Nevertheless, it happened soon afterwards the Lagaaij's study appeared that the species has been revised by Miss P. L. Cook (1965a, b), who demonstrated that a part of the material discussed by Lagaaij really belongs to the species *Cupuladria biporosa* Canu & Bassler, 1923, the remainder being left in *C. canariensis* (Busk, 1859). As these two species are closely related, some older references on the occurrrence, or new reports on the ecology, if concerned one of these species, may furthermore be regarded as referable to the both.

Further investigations by Cadée (1975) demonstrated that the species *Cupuladria monotrema* (Busk, 1884), previously regarded by Cook (1965b) as possibly conspecific with *C. biporosa*, is really a different species. On the other hand, within the material referred to as *C. canariensis* by former authors, Cadée (1975) distinguished a separate species, *C. surinamensis* Cadée. Consequently, it is apparent that the *Cupuladria canariensis* group *sensu* Cook (1965a) now comprises at least four species: *C. canariensis* (Busk, 1859); *C. biprosa* Canu & Bassler, 1923; *C. monotrema* (Busk, 1884); and *C. surinamensis* Cadée, 1975.

Of these four species, only *Cupuladria canariensis* (Busk) is known to be relatively common in some Miocene deposits of both Europe and North America (*cf.* Lagaaij 1963, Buge & Debourle 1971, Buge 1973). The second species, .*C. biporosa* Canu & Bassler, appears in the American Miocene (*cf.* Cook 1965b, p. 204 & 209; Buge & Debourle 1971), but it has never been reported from the Miocene of Europe. The last two species, *C. monotrema* (Busk) and *C. surinamensis* Cadée, are Recent, and no evident ancient representatives of theirs have hitherto been found.

When starting to discuss the other Miocene cupuladriid species of Europe, an attention has to be paid to the genus *Discoporella* d'Orbigny, 1852, whose extant species, *Discoporella umbellata* (Defrance, 1823), is also reported from Europe (*cf.* Buge & Debourle 1971, Buge 1973). This species formerly has often been confused by some authors with *Cupuladria canariensis* what makes much trouble (*cf.* Cook 1965b, p. 200) with older synonymies. The latter species, the same as the other ones belonging to genus *Discoporella* are easily recognizable from *Cupuladria* in living material. In the fossil deposits however, when their state of preservation is inadequate, they become hardly distinguishable from *Cupuladria canariensis*. In connection with this, a problem of the species *Cupuladria haidingeri* (Reuss, 1847) appears: this species is commonly reported from the Neogene (both Miocene, and Pliocene), but only of Europe (*cf.* Lagaaij 1952, 1953; Cook 1965b, p. 210 & 213; Buge & Debourle 1971; Buge 1972, 1973), and it has never been stated in present-day materials. It is therefore thought to be either an extinct, endemic European species, or it really is, in some cases at least (*cf.* Cook 1965b, p. 200), a preservation state of the ancient colonies of *Discoporella umbellata* (Defrance).

As seen from the above review, some broader taxonomic terms are handy for the following discussion. Such terms in use are two, as follows:

cupuladriid bryozoans — representatives of the family Cupuladriidae Lagaaij, 1952, which according to Cook (1965a) comprises only two genera, *Cupuladria* Canu & Bassler, 1919, and *Discoporella* d'Orbigny, 1852;

lunulitiform bryozoans — the same as used by Cook (1965a), namely the family Cupuladriidae, and a morphologically similar, but certainly not closely related (*cf.* Cook 1965a; Hakansson 1973, 1976) extinct genus *Lunulites* Lamarck, 1816. Other genera, called by some authors (*e.g.* Greeley 1967, 1970; Cadée 1975) as also lunulitiform, are excluded from that group in the present paper.

The investigated material comprises two of the above discussed cupuladriid species, viz. *Cupuladria canariensis* (Busk) and *C. haidingeri* (Reuss), the taxonomy of which is regarded as identical with that used by the former students of the Miocene cupuladriids of Europe (*cf.* Lagaaij 1953, Buge 1973). The relation of the so-understood paleontological species to the present-day forms of *Cupuladria canariensis* (Busk) and *Discoporella umbellata* (Defrance) is out of the scope of the present paper.
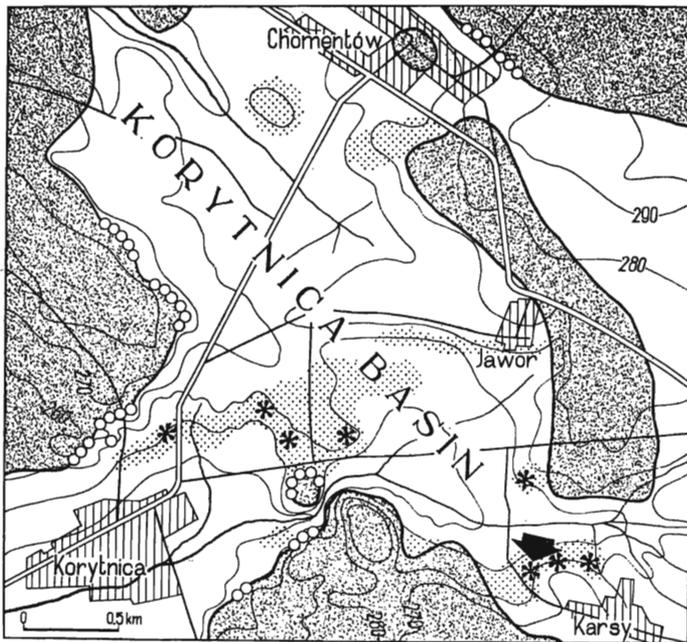

Fig. 1. Paleoenvironmental sketch of the Korytnica basin (*cf.* Bałuk & Radwański 1977, Text-fig. 2)

Indicated are: marine area of the Korytnica basin during the Middle Miocene (Badenian) transgression (*blank*) and present-day outcrops of the Korytnica Clays (*stippled*); preserved fragments of littoral structures (*circled*); land or island areas along the seashore (*hachured*)

Asterisked are the sampling areas that yielded the investigated cheilostome bryozoans, *Cupuladria canariensis* (Busk) and *C. haidingeri* (Reuss); the sampling localities represent the uppermost part of the Korytnica Clays sequence (*cf.* Bałuk & Radwański 1977, Text-figs 4—6)

Arrowed is the sampling area of *Cupuladria canariensis* (Busk) reported by Cook (1965b, p. 199; *cf.* also Bałuk & Radwański 1977, Text-fig. 2); this sampling area is also the holothurian-bearing site (*cf.* Walkiewicz 1977, Text-fig. 1)

The investigated material comes from the world-famous Middle Miocene (Badenian) Korytnica Clays developed on the southern slopes of the Holy Cross Mountains, Central Poland. The species *Cupuladria*

canariensis was first recorded from these clays, at the exposure of Karsy (*cf.* Text-fig. 1), by Cook (1965b, p. 199 — collection of R. Lagaaij), whereas *C. haidingeri* (Reuss) was formerly unknown.

The abundance of various fossils that occur in the Korytnica Clays allows to recognize the facies conditions under which the diversified organic communities lived (Bałuk & Radwański 1977). It is thereby possible to discuss some aspects of the ecology of the two title species, *Cupuladria canariensis* (Busk) and *C. haidingeri* (Reuss), and to make comparisons with the life requirements of the extant stock of *Cupuladria canariensis*.

THE INVESTIGATED MATERIAL

The investigated material of the regenerated cupuladriid bryozoans, collected in the uppermost part of the Korytnica Clays consists of over twenty entire colonies and numerous fragments of various size. As these colonies are very fragile and unresistant both to sedimentary and burial conditions, preserved entirely is certainly only a part of the total population. All the best preserved specimens (Pls 1—4) were found in the clay material filling the gastropod shells, the place being a common "preservation trap" for smaller-sized invertebrates in the Korytnica basin (*cf.* Bałuk & Radwański 1977).

The smallest regenerated colonies of *Cupuladria canariensis* (Busk) attain a diameter of 2.0 mm (*cf.* Pl. 1, Fig. 1), 2.1 mm (*cf.* Pl. 1, Fig. 2), 2.5 mm (*cf.* Pl. 1, Fig. 3), 2.3 mm (*cf.* Pl. 2, Fig. 1), or 2.6 mm (*cf.* Pl. 2, Fig. 2). The largest regenerated colonies of this species attain 5.1 mm (*cf.* Pl. 3, Fig. 1) and 5.8 mm (*cf.* Pl. 3, Fig. 2), respectively. The maximum size of the regenerated colonies is generally smaller than that of the undamaged ones, as evidenced by a fragment measuring 5.8 mm in length (*cf.* Pl. 2, Fig. 5) which is derived from a colony whose diameter may be estimated as about 12.0 mm. The latter value is well comparable to that of the present-day forms (*cf.* Lagaaij 1963).

The smallest regenerated colonies of *Cupuladria haidingeri* (Reuss) are 1.6 mm (*cf.* Pl. 4, Fig. 1) and 2.3 mm (*cf.* Pl. 4, Fig. 2) in their diameter, whilst the largest one (*cf.* Pl. 4, Fig. 4) attains 3.4 mm. The latter figure is also much smaller than that of the undamaged colonies whose maximum size, estimated from a fragment 4.3 mm in diameter (*cf.* Pl. 4, Fig. 7), may be evaluated as about 11.0 mm.

The larger undamaged (not regenerated) colonies in the samples from the Korytnica Clays are represented only by fragments. Such colonies were certainly too large to be commonly entrapped in the gastropod shells lying empty on the seafloor, and being embedded in the clay itself, they underwent damage by compaction.

MODE OF LIFE OF THE COLONIES

The opinions on the mode of life of the cupuladriid bryozoans, exemplified by *Cupuladria canariensis* (Busk) as the best known present-day species, have long been much controversial. Various schools of interpretations were kept, ranging from their either restling or "straddling" by hypothetical rootlets on the seafloor, to almost free swimming (even planktic, as reported by Silén 1942, p. 13; *cf.* also Cook 1965b, p. 194; Greeley 1967) or attaching to algal fronds (*cf.* Lagaaij 1963, pp. 184—187). Discussing all these former views, Lagaaij (1963) first concluded on a truly benthic mode of life of *Cupuladria canariensis*. The present-day forms of this species live on a stable, small-particle bottom at depths sufficient not to be washed up and stranded ashore, i.e. below wave base (*cf.* also Stach 1936, Silén 1942).

The larvae of the *Cupuladria* species settle upon and attach to small objects on the seafloor, such as sand grains or shell debris. The growing colonies gradually stretch out of the margins of these objects, and become free living, the sedimentary particle having been incorporated into the enlarging colony (*cf.* Silén 1942; Lagaaij 1963; Greeley 1967; Driscoll & al. 1971; Håkansson 1973; Tavener-Smith 1973, Text-figs 1a and 2d).

As observed in living specimens of such cupuladriid species as *Discoporella umbellata* (Defrance) by Marcus & Marcus (1962), *Cupuladria doma* (d'Orbigny) and *Discoporella umbellata* by Cook (1963) who reared these species in seawater aquaria, as well as in the case of the latter species and of *Cupuladria biporosa* Canu & Bassler examined by Greeley (1967) not only in an aquarium, but for the first time also in a natural environment in the Gulf of Mexico, the adult colonies rest on the bottom in an apex-up position. They are supported by the stiff, marginal vibracular setae which, being in constant motion, sweep the surface of the colonies.

The same mode of life is to be inferred to the ancient stock of *Cupuladria canariensis* (Busk), and to *C. haidingeri* (Reuss) which inhabitated the Korytnica basin. None of the collected specimens display any attachment scars (*cf.* Pls 1—4), and therefore all are regarded as living completely free; being semi-vagile on the seafloor in a way comparable to that presented in aquaria by Greeley (1967, Pls 1—2).

A similar mode of life has recently been postulated by Håkansson (1976) also for some *Lunulites* from the Upper Cretaceous, whilst for some others from the Eocene demonstrated by Greeley (1970) from the growth of commensal corals; such a mode of life (*cf.* also Rider & Cowen 1977) may therefore be regarded as typical of all the lunulitiform bryozoans.
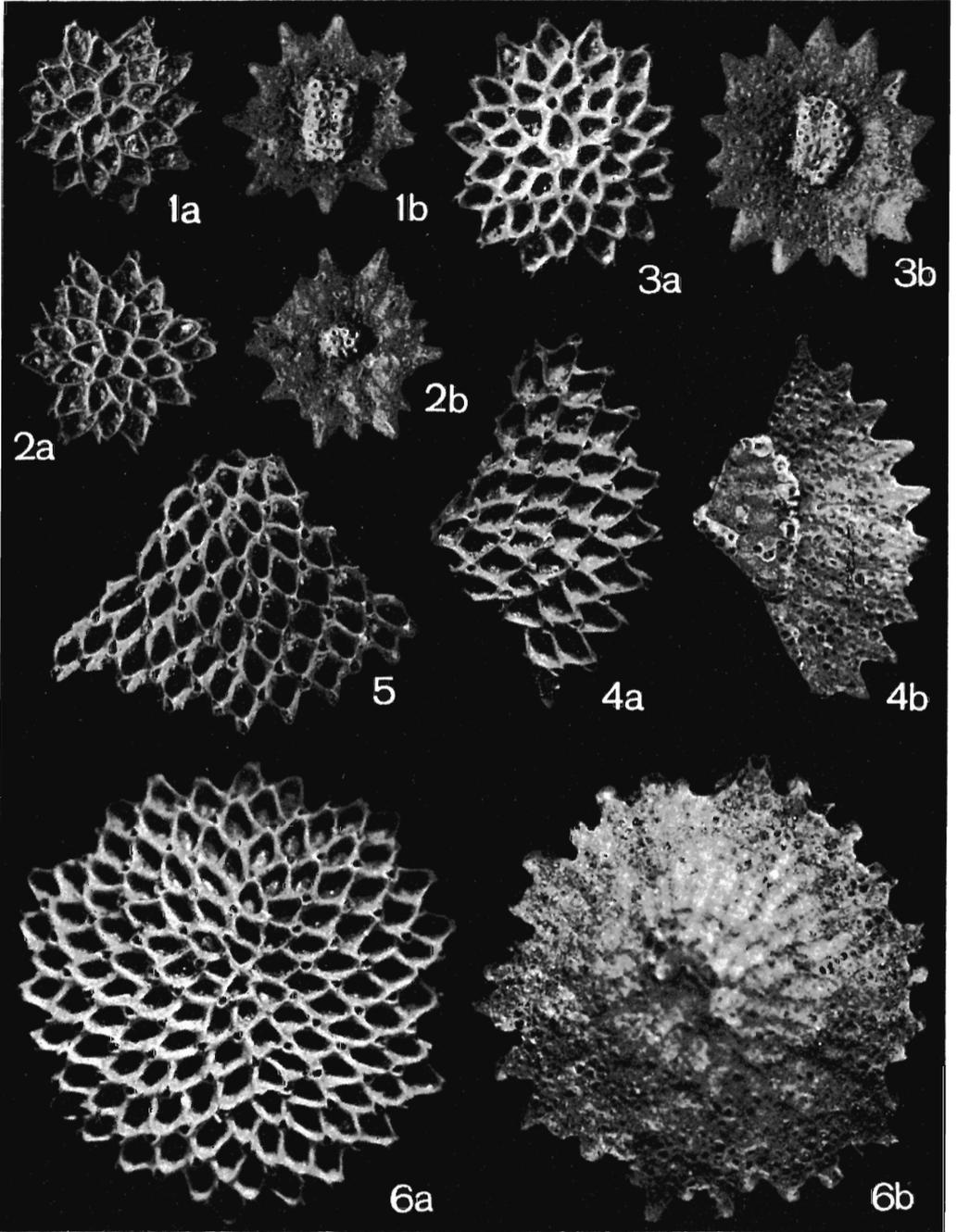
REGENERATED COLONIES

The regeneration in the investigated cupuladriids is displayed by various, usually small fragments of primary colonies, around which a radial outgrowth, disconnected with the former array of zooecia, took place. The zooecia of the first rim of the regenerated part of the colony are distinctly smaller than those of the primary colonies, and they gradually become larger and larger attaining finally, if the regenerated colony in its size much exceeds the incorporated fragment, such dimensions as typical of the primary colony. The latter feature is best visible in the largest regenerated colonies (*cf.* Pl. 2, Fig. 4; Pl. 3, Figs 1—2).

In most cases, the fragments or primary colonies, due to their larger zooecia and their different arrangement, are well detectable on the frontal (upper) side of the investigated specimens. When analysing the basal (lower) side of the regenerated colonies, it is visible that in *Cupuladria canariensis* (Busk) a broken fragment of the primary colony is well pronounced and distinctly stretches out of the basal wall (*cf.* Pls 1—3), while in *C. haidingeri* (Reuss) it is not so (*cf.* Pl. 4; e.g. Figs 3 and 5—6).

In some specimens of *Cupuladria canariensis* (Busk), the larger size of only one zooecium, and arrangement of the first rim of regenerated zooecia, show that it belonged to the only zooid that survived the breakage of the primary colony and remained alive (Pl. 1, Figs 2—3). One specimen (Pl. 1, Fig. 1) displays, at its center, a body composed of two zooecia with three vibracula derived from the primary colony.

A single zooid that becomes the nucleus of the regenerated colony is to some extent similar to that described by Marcus & Marcus (1962) who called it the *pseudoancestrula* (*cf.* also Cook 1965a, p. 158). Recent investigations show however (Håkansson 1973; Boardman & Cheetham 1973, p. 173) that *Cupuladria*, during the initial partitioning of its larval coelom produces three primary zooids (*ancestrular triplet* of Håkansson 1973), none of which should be referred to as an ancestrula. Previously, the presence of the latter was believed, or suggested, but never observed, by Silén (1942), Lagaaij (1963), and other students (Cook 1965a, b, Driscoll & al. 1971, Tavener-Smith 1973, Cadée 1975).

Cupuladria canariensis (Busk) from the Korytnica Clays

1—3 small, regenerated colonies, *4—5* fragments of regenerated colonies, *6* indistinctly
regenerated colony; further explanations in the text

a frontal view, *b* basal view; all figures × 15, taken by L. Łuszczewska, M. Sc.
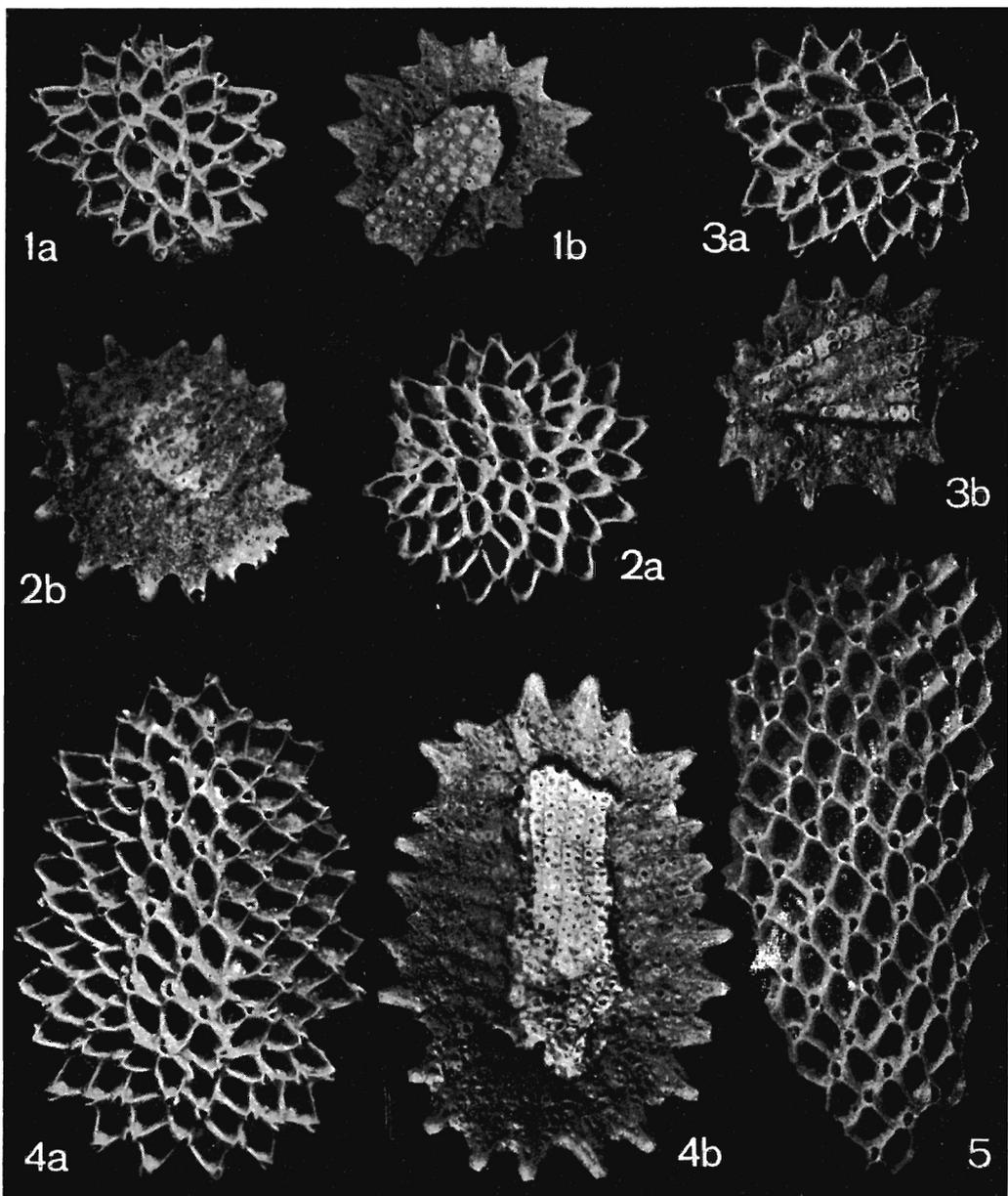
Cupuladria canariensis (Busk) from the Korytnica Clays

1—4 regenerated colonies of various size and shape, 5 fragment of a large, unbroken colony;
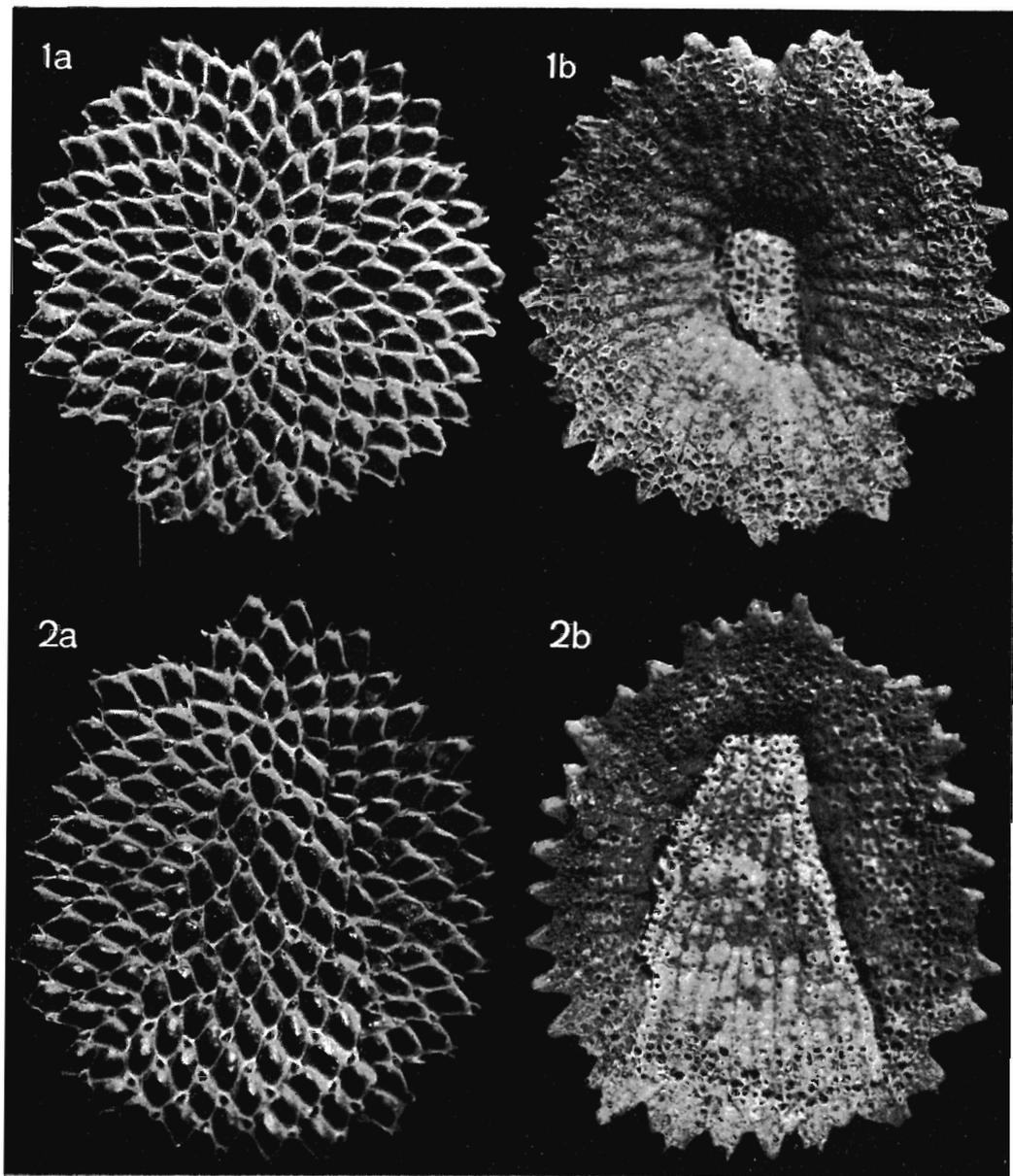further explanations in the text
a frontal view, *b* basal view; all figures × 15, taken by L. Łuszczewska, M. Sc.

Cupuladria canariensis (Busk) from the Korytnica Clays

1—2 large, regenerated colonies; further explanations in the text
a frontal view, b basal view; all figures × 15, taken by L. Łuszczewska, M. Sc.

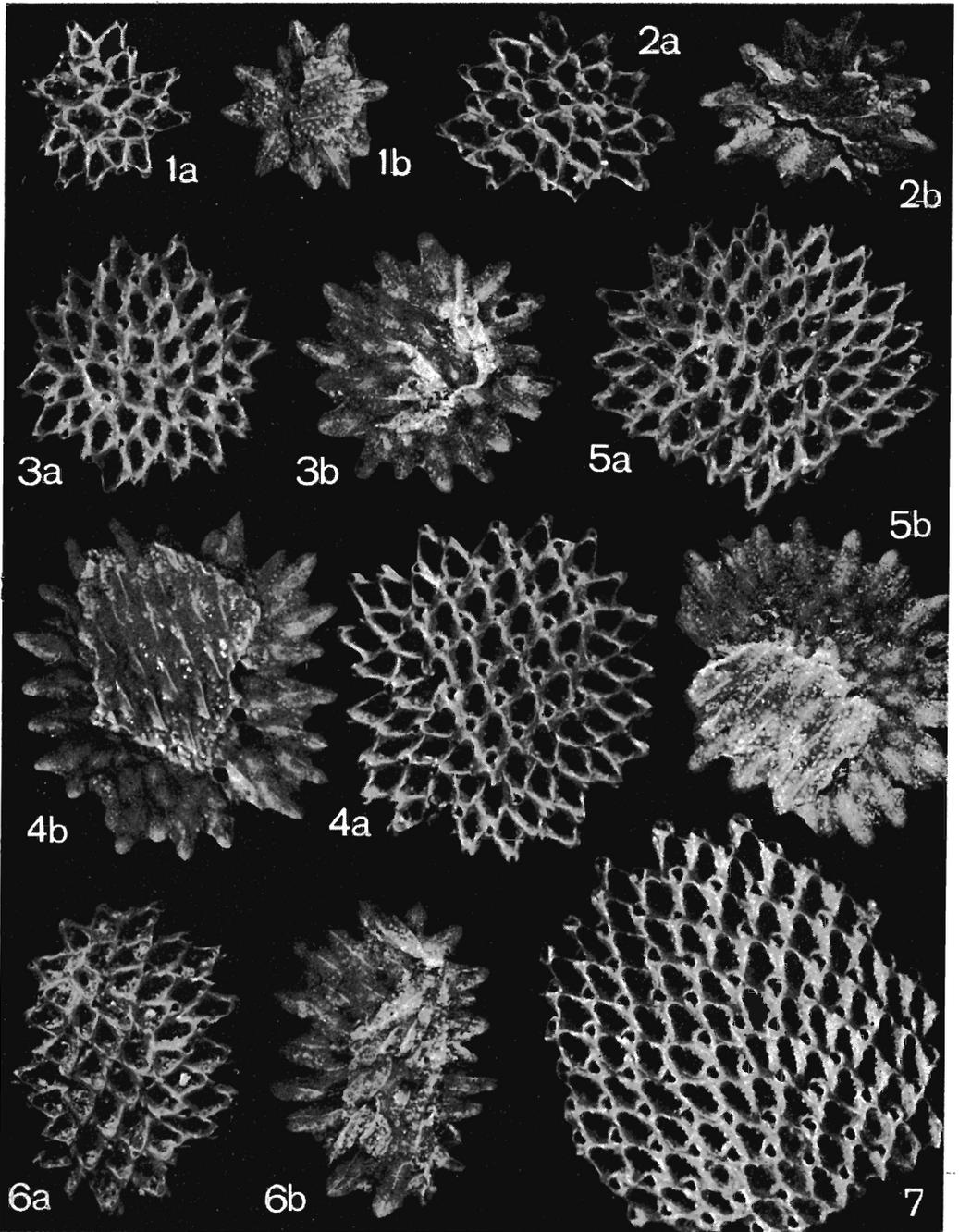*Cupuladria haidingeri* (Reuss) from the Korytnica Clays

1—6 regenerated colonies of various size and shape, 7 fragment of a large, unbroken colony;
further explanations in the text
a frontal view, *b* basal view; all figures × 15, taken by L. Łuszczewska, M. Sc.

In some other specimens of *Cupuladria canariensis* (Busk), the regeneration is not very distinct (*cf.* Pl. 1, Fig. 6), and it looks as if being developed on a large sector that contains the apical part of the primary colony (see Pl. 1, Fig. 6b — a part upper right of the center, whitish in its tint, and embracing about one third of the colony). The pattern of zooecia, when looking at the frontal side of this colony, is disturbed (*cf.* Pl. 1, Fig. 6a), but it is difficult to say whether this results from the regeneration of the missing two thirds of the colony, or it is only the healing of the fractures which have not led to a total fragmentation of the primary colony.

The final shape of the regenerated cupuladriid colonies, if the primary colony fragments were comparatively small, become more or less circular, typical of the undamaged colonies (*e.g.* Pl. 1, Figs 1—3; Pl. 2, Fig. 2; Pl. 3, Fig. 1; Pl. 4, Figs 3—4). If the broken fragments were much deviated from an isometric outline, the regenerated colonies became elongated (*e.g.* Pl. 2, Fig. 4; Pl. 3, Fig. 2; Pl. 4, Fig. 6), or irregular (*e.g.* Pl. 2, Fig. 3; Pl. 4, Fig. 2).

As pointed out before, all the regenerated colonies in the investigated material are much smaller than those which have grown undamaged. In *Cupuladria canariensis* (Busk), the largest regenerated colony is slightly over twice smaller than that one which is assumed not to have been broken during its astogeny (*cf.* Pl. 3, Fig. 2 with Pl. 2, Fig. 5). In *Cupuladria haidingeri* (Reuss), the largest colony which was regenerated is over three times smaller than that one which has not been damaged (*cf.* Pl. 4, Fig. 4 with Pl. 4, Fig. 7).

The regeneration in lunulitiform bryozoans was first recognized, in their ancient forms, by Dartevelle (1933, 1935) in *Lunulites quadrilatera* Canu & Bassler from the Eocene of Belgium. In this very genus, it was also reported from other fossil occurrences: Greeley (1970) presented regeneration in *Lunulites jacksonensis* (Canu & Bassler) and *L. bouei* Lea from the Eocene of the Gulf Costal Plain, United States, and Buge & Moniz (1974) in *Lunulites barbosae* Buge & Muniz from the Paleocene of Brasil.

It also was Dartevelle (1935) who first reported on the regeneration in the cupuladriid bryozoans, and it was the present-day material: *Cupuladria canariensis* (Busk) from Madeira, and another specimen kept in the Busk collection, British Museum (Natural History), and taken off Râs-el-Amouch at the Algerian coast, western Mediterranean (*cf.* Dartevelle 1935, Pl. 19, Figs 1—2; reillustration *in:* Lagaaij 1963, Pl. 25, Fig. 5); similar regeneration was also displayed by "*Cupuladria lowei* (Busk)" [correctly: *Discoporella umbellata* (Defrance) — vide Marcus & Marcus (1962, p. 294), and Cook (1965a, pp. 158 and 177—178)] from Madeira.

Subsequently, Silén (1942) stated a common regeneration in various species of *Cupuladria*, and exemplified this (Silén 1942, Pl. 3, Figs 10—12) in the species *C. guineensis* (Busk) from the west coast of Sumatra. On the other hand, Marcus & Marcus (1962; Pl. 1, Fig. 3; *cf.* Cook 1965b, p. 203) exemplified it by a specimen of *Cupuladria biporosa* from Brasil. Cook (1965a) reported on the regeneration in *C. elongata* Sakakura, and in her new species, *C. indica* Cook.

Fossil examples of the regenerated cupuladriids have not hitherto been evidently reported[1], and the here illustrated material (Pls 1—4) gives the first contribution in this matter.

CAUSES OF FRAGMENTATION OF THE COLONIES

The fragmentation of the cupuladriids during their life, evidenced both in the investigated ancient material, as well as in the present-day forms, is so common that it is regarded (Marcus & Marcus 1962; Boardman & Cheetham 1973, p. 173) as proving an important means of colony reproduction. Nevertheless, the causes of fragmentation of their undoubtedly very brittle and fragile colonies, are not definitely clarified. As it appears from the references, the predatory activity of various benthic animals should mostly be taken into account when discussing these very causes (cf. Lagaaij 1963, Cadée 1975).

The fragmentation of zoaria of *Cupuladria canariensis* (Busk) by predatory animals has been first recognized by Lagaaij (1963) who noted the presence of fragments, and even of entire colonies, in the stomach of a holothurian. Formerly, Silén (1942, p. 13) reported on the colonies found in the stomach of the sea-urchin *Meoma ventricosa* from the Caribbean. In consequence, Lagaaij (1963) postulates that fragmentation of the *Cupuladria* colonies results mostly from the destructive activity of the animals, and it is not due to mechanical breakage in a highly agitated environment which earlier was commonly suggested (Dartevelle 1933, 1935; Stach 1936). Subsequently, Greeley (1967) reported also on a slight damage of *Cupuladria biporosa* Canu & Bassler and *Discoporella umbellata* (Defrance) by small hermit crabs which search for the commensal coelenterates growing on the basal side of the bryozoan colonies.

In the Korytnica basin, of the discussed animals both holothurians and hermit crabs may be regarded as the most responsible for the damage of the cupuladriid colonies. The holothurian sclerites are especially common in samples taken in the area from which a part of these bryozoans come (cf. Walkiewicz 1977, Text-fig. 1), whilst they are very scarce or missing in other sites. The serious damages caused by hermit crabs are recognizable almost everywhere in the basin, and they are pronounced mostly in gastropods and some scaphopods (cf.

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[1] A report by Dartevelle (1933, 1935), based on his interpretation of former data by Canu & Bassler (1920), on the regeneration in a Miocene species from the United States, is probably a mistake (cf. text by Canu & Bassler, 1920, 1923; and a note by Cook 1965b, p. 217).

Not evident is also a report by Cook (1965b, p. 223) on a *Cupuladria* from the supposed uppermost Oligocene of Germany, and illustrated over a century ago by Münster in the Goldfuss' *Petrefacta Germaniae* of 1829 (cf. also Buge & Debourle 1971, p. 42).

On the other hand, regenerated is certainly another fragment presented by Canu & Bassler (1923, Pl. 15, fig. 4) from the Miocene of the United States; the illustration however does not allow to recognize to which cupuladriid species it belongs [attention to this example was kindly paid by Dr. E. Håkansson].

Radwański 1969, 1977; Bałuk & Radwański 1977). Many other vagile animals may however be also regarded as potential, either accidental or predacious, destroyers of the investigated cupuladriids (*cf.* Lagaaij 1963; and observations in aquaria by Greeley, 1967).

In conclusion, it seems that the activity of predators, either upon the cupuladriids themselves, or upon their commensals is the most probable cause of the colony fragmentation in the Korytnica basin.

LIFE HABITAT

The present-day representatives of *Cupuladria canariensis* (Busk) preferentially choose small-particle bottom, composed either of small--sized quartz or carbonate sand, to which they are confined in life by the requirements of their larvae to settle upon such very particles (Lagaaij 1963). A similar, sandy bottom material with larger amounts of calcareous skeletal grains was noted in the life environment of various cupuladriids on the Guyana shelf (Cadée 1975). The same was also the case reported by Greeley (1967) in a life spot of *Cupuladria biporosa* Canu & Bassler and *Discoporella umbellata* (Defrance) in the Gulf of Mexico.

The species *Cupuladria canariensis* can tolerate only a small amount of clay sedimentation, and owing to the possession of vibracular setae the animals stir the nearby water to prevent the clay deposition upon them (Lagaaij 1963). The species, as reported by Lagaaij (1963, p. 181), never occurs on a bottom consisting entirely of clay.

The environmental conditions offered by the Korytnica Clays may seem, at the first insight if only the name is kept in mind, to be quite opposite to the latter one. The recognition of these conditions in the sedimentary basin allows however to find out how the cupuladriid bryozoans could there live.

The Korytnica Clays are colored yellow, evidencing a well ventillated environment, and the abundant shell detritus of various size replaced here the small clastic particles favourable for the settlement of cupuladriid larvae. The analysis of ecological successions in the macrobenthic communities (Hoffman 1977) shows that the clay material was transported primarily by bottom currents, and hence the sedimentation from suspension was subordinate. Such conditions might have been strictly comparable to those of clean, sandy bottoms required by present-day *Cupuladria canariensis* and other cupuladriids.

It is noteworthy that the environmental conditions under which the whole sequence of the Korytnica Clays was deposited, was rather unconvenient for the other bryozoans which are extremely scarce here. The free-living species, *Cupuladria canariensis* and *C. haidingeri*, become

therefore a distinct exception comparable to those from the Miocene of northern France (cf. Buge 1972) and of the North Sea Basin (cf. Lagaaij 1953, Buge 1973). In any way, however, the total frequency of the cupuladriid bryozoans in all these three Miocene sites is remarkedly low if compared with the present-day habitats in which such populations as yielding 15500 specimens per sq m were noted on the Guyana shelf (Cadée 1975; here other references on the density value).

The depth of the Korytnica basin during sedimentation of the clays, as it is apparent from the succession of organic communities (cf. Radwański 1969, 1974; Hoffman 1977; Bałuk & Radwański 1977) was ranging in meters from about 60—40 to a few. To the latter figure it was successively closing throughout the whole basin during its gradual filling with the sediments. All the collected specimens of *Cupuladria canariensis* and *C. haidingeri* come from the uppermost part of the clay sequence (cf. Text-fig. 1) that originated on the bottom densely covered by sea grasses (cf. Hoffman 1977; Bałuk & Radwański 1977, Text-fig. 6), at the depth of a few meters. This value is much lower than the minimum depth for the present-day cupuladriids that usually live below wave base (cf. data given by Silén 1942, Lagaaij 1963, Cheetham & Sandberg 1964; and by Cadée, 1975, who reports on the absence of the cupuladriids at depth of less than 20 m). However, in a protected area, and such one was the Korytnica basin (cf. Text-fig. 1; and Bałuk & Radwański 1977, Text-fig. 1), this minimum depth might have been much smaller, the same as it was postulated by Buge (1973) for some parts of the Miocene North Sea Basin.

CLIMATIC REQUIREMENTS

The species *Cupuladria canariensis* (Busk) appears a good climatic indicator. Its present-day distribution is limited by the 14°C surface isocrymes (Lagaaij 1963) what makes that in Europe it occurs only in southern Portugal, just at the Strait of Gibraltar, through which the species enters also the African coast of the western Mediterranean. Its distribution is here limited to the extent of the Atlantic water, and its further easternward expansion being stopped by the increasing salinity in the Mediterranean (cf. Lagaaij 1963).

The species *Cupuladria canariensis* (Busk) may therefore be regarded as tropical and/or subtropical (cf. also Lagaaij 1952, 1953; Cheetham & Sandberg 1964; Cook 1965b; Buge 1972, 1973). Similar climatic conditions are also required by *Discoporella umbellata* (Defrance), as indicated by Lagaaij (1953), Cook (1965a) and Cadée (1975). To the authors' knowledge, these are the only two bryozoan species

from the Miocene assemblages of Europe (*cf.* also Buge 1972, 1973) whose climatic requirements are higher than those of the present-day southernmost European species.

The species *Cupuladria canariensis* (Busk) is consequently to be included into the list of the tropical and/or subtropical elements in the European Miocene. The previous reports in this list (*cf.* Bałuk & Radwański 1967, 1977; Bałuk 1975; Radwański 1975) comprise some benthic uni- and bivalved gastropods *(Parastrophia, Berthelinia),* chitons *(Craspedochiton, Cryptoplax),* cirripedes *(Creusia),* as well as nectic fish, mostly sharks *(Hemipristis)* and rays *(Aëtobatis).*

DISTRIBUTION IN THE MIOCENE

It is peculiar that the species *Cupuladria canariensis* (Busk), although being free living, displays a very limited occurrence in the Miocene deposits of Europe. In most of the occurrence sites it is very rare, and only some localities in the Atlantic gulfs of northern France (*cf.* Buge 1972), and in the North Sea Basin (*cf.* Lagaaij 1953, Buge 1973, Cadée 1977) are an outstanding exception.

In the two last-named Miocene areas, Atlantic gulfs and the North Sea Basin, *Cupuladria canariensis* (Busk) is usually associated with *C. haidingeri* (Reuss) and *Discoporella umbellata* (Defrance), the assemblage of which even dominates the whole bryozoan spectrum (*cf.* Buge 1972, Table 3; 1973, Table 1). In this respect, these occurrence sites are comparable to those of the Recent Guyana shelf where the cupuladriid bryozoans make their own, and densely populated communities (*cf.* Cadée 1975).

Within the Miocene deposits of the Paratethys basins in Central Europe, *Cupuladria canariensis* is recorded (*cf.* Lagaaij 1963, Fig. 15a) only from a few localities in the Vienna Basin (*cf.* also Manzoni 1877, Canu & Bassler 1925), Kostej in the Transylvanian Basin (Cook 1965b), and from two localities in the Fore-Carpathian Depression in southern Poland, viz. Benczyn at the Carpathian margin (*cf.* Małecki 1951, Lagaaij 1963), and the here reported Korytnica. It is noteworthy that in the Fore-Carpathian Miocene the discussed free-living cheilostomes appear only within the clay facies of limited distribution (Korytnica, Benczyn), but of a similar lithology and sedimentary environment.

Outside the above presented regions, *Cupuladria canariensis* in the Miocene deposits of Europe is known from the Aquitanian Gulf, and from various parts of the Mediterranean (*cf.* Lagaaij 1963, Fig. 15a). Moreover, it is commonly reported from the Miocene of Nigeria and Cameroun, Venezuela and Costa Rica, Caribbean islands (Jamaica, San Domingo, Trinidad), and from the U.S. coast of the Gulf of Mexico (*cf.* Lagaaij 1963, Fig. 4).

ZOOGEOGRAPHIC SIGNIFICANCE

Recent distribution of the species *Cupuladria canariensis* (Busk) is limited to the Atlantic province, ranging from Africa (south-western Mediterranean including) to the Caribbean and Gulf of Mexico (Silén 1942, Lagaaij 1963, Cheetham & Sandberg 1964, Cook 1965a, b, Cadée 1975), being however occasionally extended to the Eastern Pacific, from Gulf of California to Ecuador and Galapagos (Cheetham & Sandberg 1964). The Indo-Pacific province is characterized by the presence of two other species, *Cupuladria guineensis* (Busk, 1854), and *C. indica* Cook, 1965, ranging from the eastern African coast through Japan and Australia (Silén 1942, Cook 1965a, b), and the former of which from that region is also known from the Tertiary and Quaternary deposits (Cook 1965a; *cf.* also Buge & Debourle 1971).

When analysing the Miocene communities of Central and Southern Europe, it was stated (Radwański 1974, 1975; *cf.* also Bałuk & Radwański 1977) that they contain many elements typical of the Recent Indo-Pacific province. It was consequently postulated, that the Miocene areas of Europe were highly influenced by, or they directly belonged to the north-western outskirts of the Miocene Indo-Pacific province. At the Miocene decline, the damming of the routes of oceanic connections through Turkey and the Persian Gulf resulted from the coeval crustal upheavals, and this was responsible both for a cessation of warm water inputs, and of faunal spreads (Radwański 1975, p. 399).

On the other hand, the Miocene basins of western Europe (Atlantic gulfs of Portugal and France, North Sea Basin) which were strongly separated from the Mediterranean (Tethys and Paratethys) basins (*cf.* Bałuk & Radwański 1977, Fig. 1; Radwański 1977, Fig. 1) have certainly been better influenced by waters of tropical Atlantic, as it is also apparent from an older faunal analysis presented by Gripp (1961; *cf.* Radwański 1975, p. 400). If so, the common presence of *Cupuladria canariensis* (Busk) in the Miocene deposits of western Europe may prove such very connections, and indicate that this cheilostome species should be regarded as a tropical Atlantic rather than Indo-Pacific element in the organic communities of the European Miocene.

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REFERENCES

BAŁUK, W. 1975. Lower Tortonian gastropods from Korytnica, Poland; Part 1. *Palaeontol. Polon.*, **32**, 1—186. Warszawa—Kraków.
   — & RADWAŃSKI, A. 1967. Miocene cirripeds domiciled in corals. *Acta Palaeontol. Polon.*, **12** (4), 457—521. Warszawa.

— & — 1977. Organic communities and facies development of the Korytnica basin (Middle Miocene; Holy Cross Mountains, Central Poland). *Acta Geol. Polon.*, **27** (2) *[this issue]*. Warszawa.

BOARDMAN, R. S. & CHEETHAM, A. H. 1973. Degrees of colony dominance in stenolaemate and gymnolaemate Bryozoa. *In:* R. S. BOARDMAN, A. H. CHEETHAM & W. A. OLIVER, Jr. *(Eds)*, Animal colonies development and function through time, pp. 121—220. *Dowden, Hutchinson & Ross;* Stroudsburg, Pennsylvania.

BUGE, E. 1972. Bryozoaires. *In:* P. BASSOMPIERRE & al., Le gisement redonien de Fécamp (Seine-Maritime). *Bull. Bur. Rech. Géol. Min. (Sér. 2)*, No. **1**, 29—47. Orléans.

— 1973. Les Bryozoaires Miocènes du Nord-Ouest de l'Allemagne. *Paläontol. Zt.*, **47** (1/2), 32—53. Stuttgart.

— & DEBOURLE, A. 1971. Présence dans le Bartonien d'Aquitaine occidentale de *Cupuladria boulangeri* n. sp. (Bryozoaire Cheilostome). *Bull. Centre Rech. Pau-SNPA*, **5** (1), 35—47. Pau.

— & MUNIZ, G. 1974. *Lunulites (Heteractis) barbosae*, nouvelle espèce de Bryozoaire lunulitiforme (Bryozoa, Cheilostomata) du Paléocène du nord-est du Brésil. *Annales de Paléontol. (Invertébrés)*, **60** (2), 191—202. Paris.

CADÉE, G. C. 1975. Lunulitiform Bryozoa from the Guyana shelf. *Netherlands Journal of Sea Research*, **9** (3/4), 320—343. Leiden.

— 1977. Bryozoa from the Late Miocene mica clay of Morsum Kliff, Sylt, Western Germany. *Meded. Werkgr. Tert. Kwart. Geol.*, **14** (2), 43—50. Leiden.

CANU, F. & BASSLER, R. S. 1920. North American Early Tertiary Bryozoa. *Smithsonian Inst. U. S. Natl. Mus. Bull.*, **106**, 1—879. Washington.

— & — 1923. North American Later Tertiary and Quaternary Bryozoa. *Smithsonian Inst. U. S. Natl. Mus. Bull.*, **125**, 1—302. Washington.

— & — 1925. Contribution à l'étude des Bryozoaires d'Autriche et de Hongrie. *Bull. Soc. Géol. France, Sér. 4*, **24**, 672—690. Paris.

CHEETHAM, A. H. & SANDBERG, P. A. 1964. Quaternary Bryozoa from Louisiana mudlumps. *J. Paleontol.*, **38** (6), 1013—1046. Menasha.

COOK, P. L. 1963. Observations on live lunulitiform zoaria of Polyzoa. *Cahiers Biol. Mar.*, **4** (4), 407—413. Roscoff.

— 1965a. Notes on the Cupuladriidae (Polyzoa, Anasca). *Bull. Brit. Mus. (Nat. Hist.), Zoology*, **13** (5), 153—187. London.

— 1965b. Polyzoa from West Africa. The Cupuladriidae (Cheilostomata, Anasca). *Bull. Brit. Mus. (Nat. Hist.), Zoology*, **13** (6), 191—227. London.

DARTEVELLE, E. 1933. Contribution à l'étude des Bryozoaires fossiles de l'Éocène de la Belgique. *Ann. Soc. Royale Zool. Belg.*, **63**, 55—116. Bruxelles.

— 1935. Zoarial regeneration of free Polyzoa. *Ann. Mag. Nat. Hist., Ser. 10*, **15** (89), 559—561. London.

DRISCOLL, E. G., GIBSON, J. W. & MITCHELL, S. W. 1971. Larval selection of substrate by the Bryozoa *Discoporella* and *Cupuladria*. *Hydrobiologia*, **37** (2), 347—359. The Hague.

GREELEY, R. 1967. Natural orientation of lunulitiform bryozoans. *Geol. Soc. Amer. Bull.*, **78** (9), 1179—1182. Boulder, Colorado.

— 1970. Life-orientation relationships of some Eocene bryozoan-coral associations. *J. Paleontol.*, **44** (2), 343—345. Menasha.

GRIPP, K. 1961. Klima und Tierwenderung. Versuch einer Charakterisierung der Mollusken-Faunen im marinen Tertiär West Europas. *Meyniana*, **10**, 113——117. Kiel.

HÅKANSSON, E. 1973. Mode of growth of the Cupuladriidae (Bryozoa, Cheilo-
    stomata). *In:* G. P. LARWOOD *(Ed.),* Living and Fossil Bryozoa, pp. 287—
    —298. *Academic Press,* London — New York.
— 1976. Population structure of colonial organisms. A palaeoecological study
    of some free-living Cretaceous bryozoans. *Docum. Lab. Géol. Fac. Sci.
    Lyon,* H. S., 3 (2), 385—399. Lyon.
HOFFMAN, A. 1977. Synecology of macrobenthic assemblages of the Korytnica
    Clays (Middle Miocene; Holy Cross Mountains, Poland). *Acta Geol. Polon.,*
    27 (2) *[this issue].* Warszawa.
LAGAAIJ, R. 1952. The Pliocene Bryozoa of the Low Countries and their bearing
    on the marine stratigraphy of the North Sea region. *Mededel. Geol.
    Stichting, Ser. C,* 5, 1—233. Maastricht.
— 1953. The vertical distribution of the lunulitiform Bryozoa in the Tertiary
    of the Netherlands. *Mededel. Geol. Stichting, n. ser.,* 7, 13—19. Maastricht.
— 1963. *Cupuladria canariensis* (Busk) — portrait of a bryozoan. *Palaeontology,*
    6 (1), 172—217. London.
MAŁECKI, J. 1951. Contribution à la connaissance des Bryozoaires du Miocène
    de Benczyn. *Roczn. PTG (Ann. Soc. Géol. Pologne),* 19, 487—491. Kraków.
MANZONI, A. 1877. I Briozoi fossili del Miocene d'Austria ed Ungheria. *Denkschr.
    Akad. Wiss. Wien.,* 37 (2), 49—78. Wien.
MARCUS, E. & MARCUS, E. 1962. On some lunulitiform Bryozoa. *Bol. Fac. Fil.
    Cien. Letr. Univ. Sao Paulo, Zoologia,* 24, 281—324. Sao Paulo.
RADWAŃSKI, A. 1969. Lower Tortonian transgression onto the southern slopes
    of the Holy Cross Mts. *Acta Geol. Polon.,* 19 (1), 1—164. Warszawa.
— 1974. Palaeoecological observations on Miocene communities of Poland.
    Bull. Geol. Soc. Denmark, 23 (3/4), 336—340. København.
— 1975. Climatic changes recorded by marine macrofauna. *Proc. 6th Congr.
    Mediterran. Neogene Stratigr.,* 1, 397—400. Bratislava.
— 1977. Present-day types of traces in the Neogene sequence; their problems
    of nomenclature and preservation. *In:* T. P. CRIMES & J. C. HARPER
    (Eds), Trace Fossils 2 *(Geol. J. Spec. Issues,* 9). Liverpool.
RIDER, J. & COWEN, R. 1977. Adaptive architectural trends in encrusting
    ectoprocts. *Lethaia,* 10 (1), 29—41. Oslo.
SILÉN, L. 1942. On spiral growth of the zoaria of certain Bryozoa. *Arkiv Zool.,*
    34A (2), 1—22. Stockholm.
STACH, L. W. 1936. Correlation of zoarial form with habitat. *J. Geol.,* 44 (1),
    60—65. Chicago.
TAVENER-SMITH, R. 1973. Some aspects of skeletal organization in Bryozoa.
    In: G. P. LARWOOD *(Ed.),* Living and Fossil Bryozoa, pp. 349—359. *Aca-
    demic Press,* London — New York.
WALKIEWICZ, A. 1977. Holothurian sclerites from the Korytnica Clays (Middle
    Miocene; Holy Cross Mountains, Poland). *Acta Geol. Polon.,* 27 (2) *[this
    issue].* Warszawa.