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# Changing Patterns in the Development of Zooidal Buds in the Evolution of the Bryozoan Order Cheilostomata and the Appearance of Multiserial Forms

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**Abstract**—The transition from uniserial to multiserial forms in the evolution of the bryozoan order Cheilostomata resulted from the change from a proxipetal sequence of development of buds in zooids to a distopetal. Possible morphogenetic mechanisms of this transformation are discussed.

## INTRODUCTION

The sequence of the development of buds in zooids is one of the major factors defining the structure of a bryozoan colony (Nikulina, 2001). Studies of extant bryozoans of the order Cheilostomata show that there are two patterns in the development of buds in zooids, i.e., the proxipetal and distopetal sequences. In species with proxipetal budding, each zooid first forms a distal bud, and the lateral buds, which occur more proximally, develop later. The chains of zooids grow rapidly in length and then branch through the development of the lateral buds. New chains grow in the space between those that appeared earlier and also branch. The resulting colonies are composed of separated rows of zooids (Fig. 1a). These forms are traditionally called uniserial. The distopetal pattern shows the reverse sequence of bud development, i.e., from the proximal end of a zooid to the distal. Because the lateral buds appear first, the development of unbranched chains of zooids is impossible. This results in the formation of rounded multiserial colonies with a compact arrangement of hexagonally packed zooids (Fig. 1b).

These two colonial types (uniserial and multiserial) did not appear at the same time in the history of Cheilostomata. Many studies on the evolution of Cheilostomata indicate that the earliest (Jurassic) Cheilostomata had uniserial encrusting colonies (Pohowsky, 1973; Taylor, 1981, 1994). Multiserial colonies first appeared in the Early Cretaceous and were composed of compactly arranged zooids (Cheetham, 1954; Dzik, 1975). Many workers agree that the evolution of Cheilostomata shows a trend toward the transition from uniserial to multiserial colonies (Lidgard, 1985; Lidgard and Jackson, 1989). The ecological and morphophysiological aspects of this change in the organization of a colony were repeatedly discussed in the literature (Boardman and Cheetham, 1973; Lidgard, 1985; Lidgard and Jackson, 1989; Lidgard *et al.*, 1993). However, the morphogenetic basis of this

change remains poorly understood. Data on the development of extant bryozoans (Nikulina, 2001) allow the hypothesis that the transition from the uniserial to multiserial colonies in the evolution of Cheilostomata resulted from the replacement of the proxipetal pattern by the distopetal.

One way to check this hypothesis is to study the morphogenesis of fossil bryozoans. Although their growth cannot be observed directly, the succession of bud development may be revealed based on the analysis of colonial morphology; isolated rows of zooids, characteristic of proxipetal budding, never develop through distopetal budding, except for cases when lateral buds are formed irregularly (Nikulina, 2001). In addition, if the margin of the colony is not destroyed, the succession of bud appearance may sometimes be reconstructed by comparing the phases in bud development.

Thus, the review of the paleontological data allows the study of budding succession, i.e., the factor that largely controls the organization of the colony.

## RESULTS AND DISCUSSION

### *Succession of the Zooid Budding in the Evolution of the Cheilostome Bryozoans*

Two stages may be recognized in the historical development of the cheilostome bryozoans. The first stage, embracing the Late Jurassic and Early Cretaceous, shows numerous morphologically similar species. During the second stage commencing in the Late Cretaceous, the order radiated and the morphology of the colonies became much more diversified.

**Jurassic and Early Cretaceous taxa.** Until now, only a few early Cheilostomata have been discovered. Colonies of the two species of the single Jurassic genus *Pyriporopsis* Pohowsky were uniserial (Pohowsky, 1973; Taylor, 1981, 1986a, 1994). Early Cretaceous bryozoans showed similar morphology, e.g., numerous species of *Pyripora* d'Orbigny, *Herpetora* Lang, *Charixa*

Lang, and *Spinicharixa* Taylor (Thomas and Larwood, 1956; Taylor, 1986b). These colonies show distinct zooidal chains that indicate that the buds in zooids developed proxipetally. This conclusion is also supported by the comparison of these taxa with extant bryozoans of similar structure: *Electra crusulenta* (Pallas), *Electra pilosa* (L.), and *Conopeum seurati* (Canu) (Fig. 2a, 2b), in which the succession of the bud development was previously studied (Nikulina, 1999a, 2001).

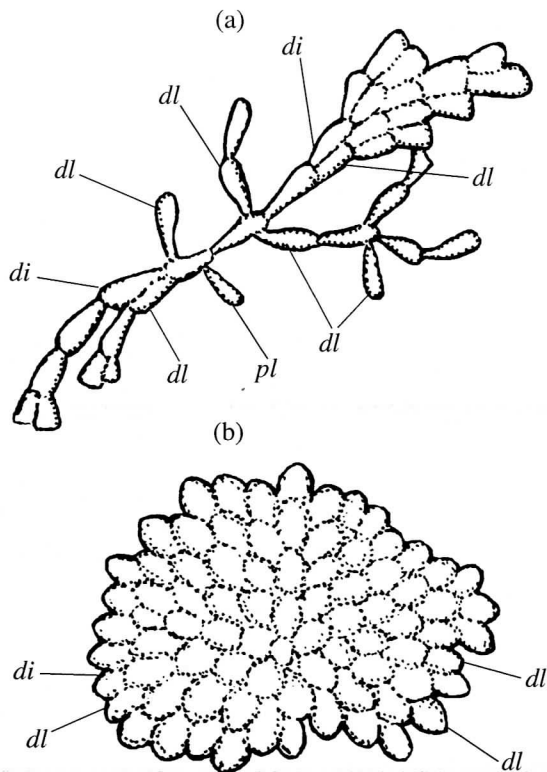
The species of the genera *Charixa* and *Spinicharixa*, apart from the unbranched chains characteristic of proxipetal budding, have separate multiserial regions of the colony with regularly arranged zooids (Taylor, 1986b, text-fig. 1–27). Such a combination of parts with different organization is characteristic of many Cretaceous bryozoans, although it also occurs in some extant Cheilostomata. In the colonies of *Electra crustulenta* (Pallas), the bryozoan species with proxipetal budding, multiserial regions develop where the growth points of distolateral buds are displaced distally (Fig. 1a). This results in the nearly simultaneous development of closely spaced distal and distolateral buds growing in the same direction (Nikulina, 1999a, 2001). In this case, the rows of zooids grow in parallel forming a compact multiserial region of the colony.

The first representative of Cheilostomata with possible distopetal budding *Wawalia crenulata* Dzik was found in the Lower Cretaceous (Valanginian) of Poland (Dzik, 1975). The rounded shape of the colony and the pattern of the compact arrangement of zooids around the ancestrula are also observed in extant species with the distopetal type of budding (Fig. 1b), e.g., in *Cribrilina annulata* (Fabricius) and others (Nikulina, 2001).

Another bryozoan with a similar colony type, *Wilbertopora mutabilis* Cheetham, was found in the Albian and Cenomanian of Texas (Cheetham, 1954; Dzik, 1975; Boardman and Cheetham, 1969, 1973). This species includes two varieties. The first variety has rounded colonies similar to those formed by distopetal budding in extant species. The second variety apparently developed similarly to the extant species *E. crustulenta*, from isolated chains to multiserial regions by the simultaneous development of the distal and distolateral buds. If these varieties are not separate species, this irregular pattern could be a product of the irregular development of the lateral buds (Nikulina, 2001).

In the remaining five Early Cretaceous species (not assigned taxonomically) (see Larwood, 1975), the succession of budding cannot be revealed because they are not pictured, and the descriptions are very brief. The lack of information on the development of these rare bryozoans does not preclude the conclusion that the majority of species occurring in the Early Cretaceous had a proxipetal succession of budding. This feature is also observed in all known Jurassic Cheilostomata.

**Late Cretaceous and Cenozoic Taxa.** Species with distinct distopetal budding, rare in the Early Cretaceous, became widespread in the Late Cretaceous.

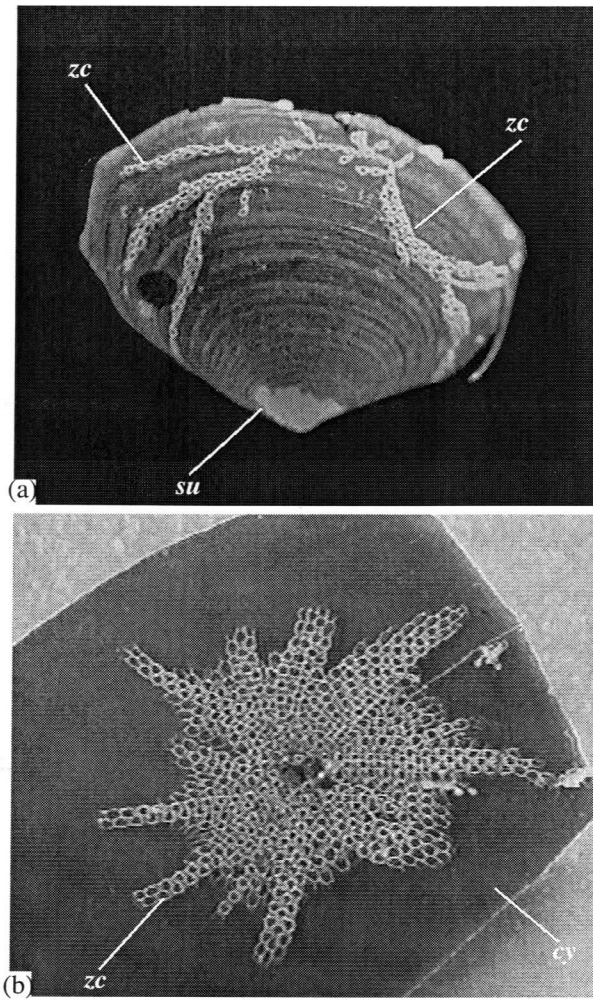


**Fig. 1.** Scheme showing the differences in organization of colonies with proxipetal and distopetal sequences of budding: (a) colony of *Electra crustulenta* (Pallas) with the proxipetal sequence in bud development in zooids and (b) colony of *Cribrilina annulata* (Fabricius) with the distopetal sequence in bud development in zooids. Explanations: *di*—distal buds, *dl*—distolateral buds, *pl*—proxilateral buds.

I studied bryozoans from Turonian and Coniacian from a few localities in the Donets Basin [coll. Paleontological Institute, Russian Academy of Sciences (PIN), no. 2922], which included many Cheilostomata species, and at least half of these have a typical multiserial pattern characteristic of distopetal budding: *Crassimarginatella* Canu, *Aplousina* Canu et Bassler, *Aechmella* Canu et Bassler, etc. Some colonies show an ancestrula with zooids of early generations (Figs. 3a, 3b). Their arrangement is similar to that of the majority of extant bryozoans with distopetal budding (species of *Callopora* Gray, *Cribrilina* Levinsen, *Escharella* Gray, etc.).

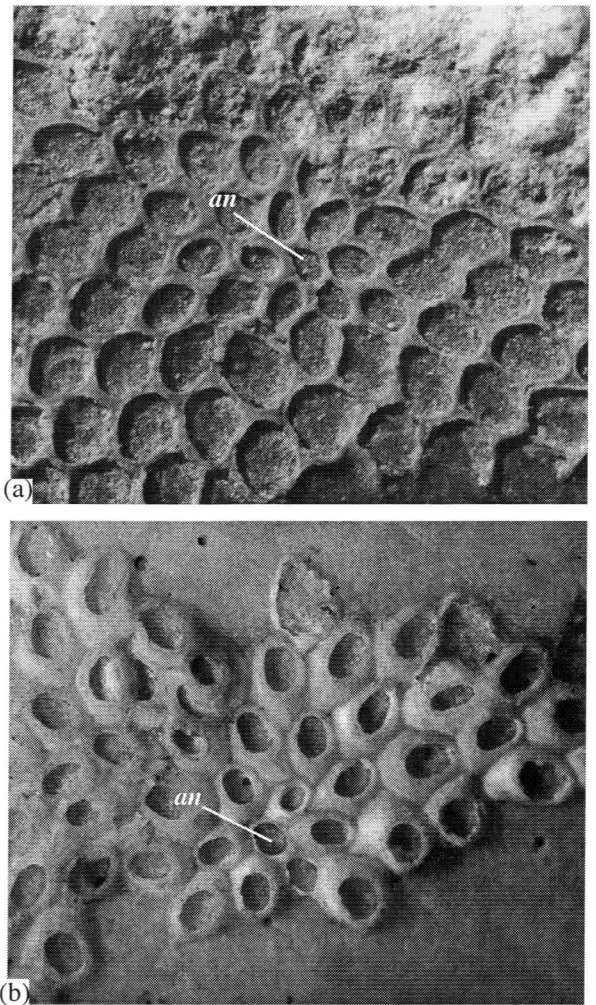
The remaining species have a mixed organization of colonies. For instance, colonies of *Onychocella* Jullien, *Marginaria* Römer, and *Stichomicropora* Voigt have multiserial regions alongside solitary chains of zooids or their isolated groups. This may be interpreted as a result of proxipetal budding or of the irregular development of the lateral buds during distopetal budding (Nikulina, 2001). The type of budding in these taxa has not been revealed.

Similar colonies with a combined structure (Fig. 4a) were also found in the collection from the Maastrichtian of Kazakhstan (PIN, coll. no. 3086) and the Neth-



**Fig. 2.** Colonies of species with the proxipetal sequence in bud development in zooids: (a) *Electra crustulenta* var. *arctica* Borg, specimen no. 4146/3001,  $\times 5.4$ , White Sea, Recent, (b) *Electra pilosa* (L.), specimen no. 4146/3002,  $\times 4.3$ , White Sea, Recent. Explanations: *zc*—zooidal chains; *su*—substrate.

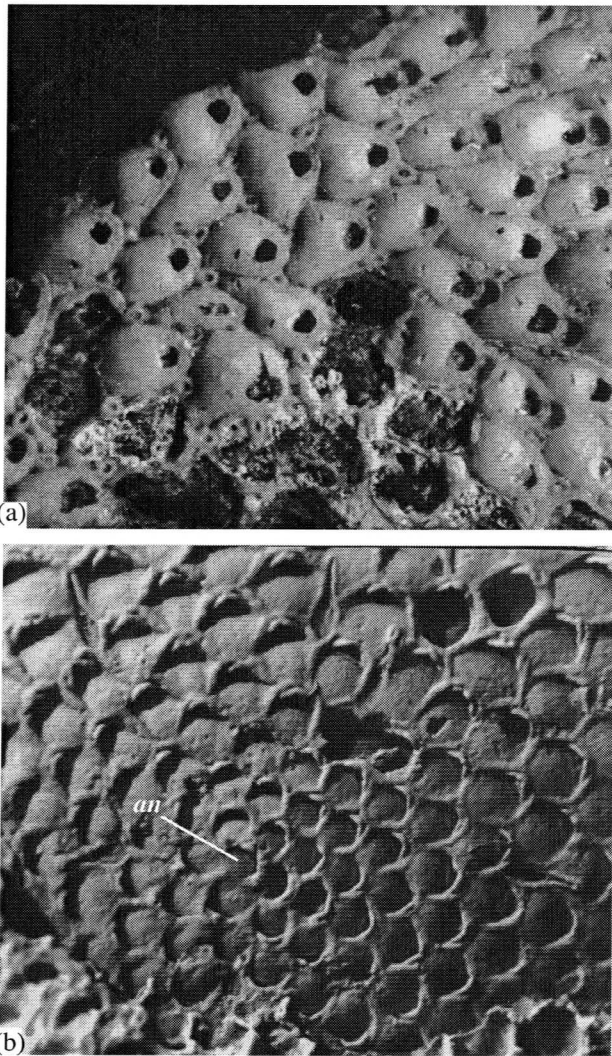
erlands (PIN, coll. no. 4859) containing over 30 Cheilostomata species, but it is visibly dominated by bryozoans with a multiserial pattern typical of distopetal budding. For instance, the colony of *Aechmella stenostoma* Voigt (Fig. 4b) shows an ancestrula and five periancestrular zooids. A similar pattern of zooids of the early generation is observed in some extant bryozoans with distopetal budding, e.g., the family Smittinidae Levinsen. In the species *Porina foveolata* (v. Hagenow), *P. quinquepunctata* (v. Hagenow), *Taeniopora arachnoidea* (Goldfuss), *Ubagsia reticulata* (Ubags), *Escharifora* sp., *Acoscinopleura* sp., *Beisselina* sp., etc., the budding is also distopetal. Only a single species in the collection studied, *Herpetopora laxata* (d'Orbigny) from the Lower Maastrichtian of South Emba, was found with certainty to have proxipetal budding.



**Fig. 3.** Colonies of species with the distopetal sequence in bud development in zooids: (a) *Aplousina* sp. specimen no. 2922/3013,  $\times 18$ , Ukraine, Zimogor'e, Turonian-Coniacian, and (b) *Crassimarginatella* sp. specimen no. 2922/3007,  $\times 24$ , Donetsk Basin, Slavyansk, Turonian-Coniacian. Explanations: *an*—ancestrula.

The dominance of distopetal budding, established in the Late Cretaceous (apparently in the Maastrichtian), persisted throughout the Cenozoic to the Present Day. Of several hundred genera known from this interval, only a few have proxipetal budding. These are the species of the genera *Electra* Lamouroux, *Conopeum* Gray, *Hippothoa* Lamouroux, *Scruparia* Oken, *Eucratea* Lamouroux, and some others (Nikulina, 1999b).

Thus, the analysis of fossil material allows for the conclusion that proxipetal budding appeared geochronologically earlier. The colony structure indicating proxipetal budding was present, not only in the earliest known, Late Jurassic, Cheilostomata, but also in Middle and Late Jurassic Ctenostomata, their probable ancestral group (Banta, 1975; Taylor, 1990); this also lends support to the theory of the primitive nature of proxipetal budding. Distopetal budding appeared later,

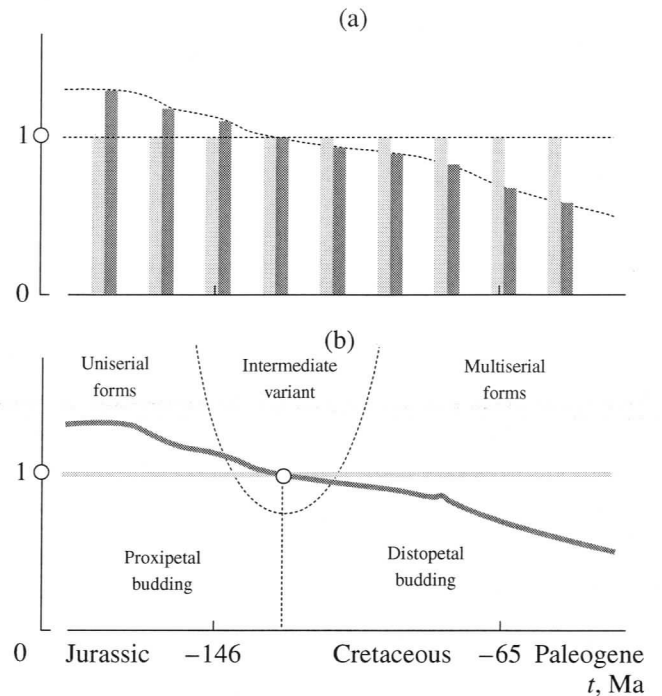


**Fig. 4.** Late Cretaceous Cheilostoma with different colonial organization: (a) *Hopliataechmella smitti* (Hennig) with uncertain colonial structure, specimen no. 3068/3002,  $\times 26$ , South Emba, Maastrichtian, and (b) colony of *Aechella stenostona* Voigt with typical distopetal budding, specimen no. 3068/3001,  $\times 16$ , South Emba, Maastrichtian. Explanations: *an*—ancestrula.

in the early Cretaceous, and became dominant from the end of the Cretaceous. Apparently, this type of budding evolved from the proxipetal budding that was ancestral in Cheilostomata. Furthermore, data on the development of Recent bryozoa (Nikulina, 1999a, 1999b, 2001) allows morphogenetical interpretations of this transformation.

*Heterochrony in the Development of Zooids and the Evolution of the Planar Organization of a Colony*

The previous study of extant bryozoans with proxipetal and distopetal budding showed a different time of emergence of the distal and lateral buds in both cases. This difference suggests that the transition from the



**Fig. 5.** Scheme of the temporal change in the appearance of zooidal buds in the evolution of Cheilostomata. A scale of geological time is along the horizontal axis, relative time is along the vertical axis, a relative time unit is an interval from the beginning of bud development (0) until the formation of the distal wall of the zooid with a bud of the succeeding generation (1). (a) Evolutionary succession of the zooidal ontogenies. Gray lines show the interval until the emergence of the distal bud in zooid; black lines show the interval until the emergence of the lateral buds. (b) Evolution of the succession of the buds development in zooid (transition from proxipetal to distapetal budding) and organization of a colony (from uniserial to multiseriate). The gray line indicates the time of emergence of the distal bud; the black line shows the time of emergence of the lateral buds.

first pattern to the second occurred because of a shift in the bud emergence to the earlier morphogenetic stages of the maternal zooid (Fig. 5). It is a well-known fact that the growth of the bryozoan bud occurs from the proximal part to the distal. The differentiation of its wall occurs in the same direction as the new parts of the developing zooid appear, i.e., a well-pronounced proxidistal gradient in development is observed. The distal wall, which is formed later than the others, has a bud of the next generation, which soon begins to grow. After this, in the case of proxipetal budding, the buds emerge on the lateral walls. If the gradual shift of bud emergence to earlier developmental stages in a zooid is assumed, the emergence of the lateral buds prior to the distal ones would be a logical outcome of this process (Fig. 5a). In these cases, the time of bud emergence coincides with the sequence of differentiation of corresponding parts of the zooid as it grows. This type of development is typical of distopetal budding. It is noteworthy that in the ancestrules (the first zooids in a col-

ony to appear after the metamorphosis of a larva), all the parts develop synchronously, and, in this case, the succession of budding is not distorted by the proxidistal gradient of the development characteristic of autozooids. In the ancestrules of most species, including those with distopetal budding, buds develop proxipetally.

The above hypothetical evolutionary transition from proxipetal to distopetal budding suggests gradual quantitative changes in the morphogenesis of the zooid. This suggests transitional forms, in which the buds of a zooid (distal and lateral) developed synchronously (Fig. 5b). Among the extant bryozoans, the synchronous appearance of the buds (alongside the typical proxipetal budding at earlier stages of colony development) may be observed in *E. crustulenta*. Such taxa show a combination of uniserial and multiserial organization. A similar mixed colonial morphology was widespread among the Cretaceous Cheilostomata (Fig. 4a). Apparently, these bryozoans are a supposed transitional type.

The evolutionary change that led to the multiserial pattern is a heterochrony that did not require essential morphogenetical changes. Therefore, the transition from proxipetal to distal budding could be rapid and occurred repeatedly in the phylogeny of bryozoans. The earliest occurrence of Cheilostomata is from the Oxfordian or Kimmeridgian (Taylor, 1994), while the first bryozoan with probable distopetal budding appeared already in the Valangianian. However, in the entire order, the transition from one type of budding to another extended from the early Cretaceous (when the first bryozoans with distopetal budding appeared) to the Maastrichtian (when they became dominant). This can probably be explained by the fact that the heterochrony described affected a few phylogenetic lineages within the Cheilostomata. This is supported by the fact that at the same time with bryozoans with distopetal budding (which probably occurred very early in the evolution of Cheilostomata), throughout the Cretaceous, transitional forms of bryozoans existed in various taxonomic groups.

### CONCLUSION

Analysis of the fossil material, supported by the data on the morphogenesis of extant bryozoans, suggests that the evolution of the Cheilostomata showed a gradual transition from proxipetal to distopetal budding occurring in most groups within the order. To understand the causes of these morphogenetic changes, further investigation is needed. Existing data on the ecology of this group (Lidgard and Jackson, 1989) may partly explain the ecological aspect of this heterochrony. A gradual shift of bud emergence toward the earlier stages of the development of the maternal zooid leads to the reduction of the interval before the next generation appears, and, consequently, to an increase in the colony's growth rate. Growth rate is essential in competition between encrusting organisms (Lidgard,

Jackson, 1989; Lidgard *et al.*, 1993). Therefore, it is possible that the direction of the heterochrony described resulted from selective pressure towards an increase in the colony's growth rate.

However, because of the change from the proxipetal to distopetal budding, the development and structure of the colonies changed, and the colonies became compact and rounded, growing along the circumference, and formed by hexagonally packed zooids. The appearance of such colony structure led to the appearance of the various multiserial forms that dominate modern marine bryozoan communities, and have done so since the Late Cretaceous.

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