INTRODUCTION

It is common knowledge that marine bryozoans feature bilateral symmetry. However, since they are sedentary colonial organisms, they may show relatively conspicuous occurrences of symmetry breaking in the outer structure of colonies and in their constituent zooids. As noted by V.N. Beklemishev (1964), this secondary lack of symmetry, or disymmetry, does not cause any inconvenience to the sedentary animals, and a great number of them retain strict bilateral symmetry, whereas a disymmetry is observed in them variously and individually. Analysis of available data show that this disymmetry of zooids and colonies, which occurs in various unrelated groups of ancient and modern marine bryozoans, can be classed into two modifications—left (sinistral) and right (dextral) forms of each of these structures—and thus can be attributed to the phenomenon of enantiomorphism.

In the Great Soviet Encyclopedia the term “enantiomorphism” means a phenomenon of oppositely arranged forms and is derived from the Latinized Greek ἀνάντιος (opposite) and morphe (form). In the glossaries of terms available in different editions of Treatise on Invertebrate Paleontology dealing with bryozoans, both the original (Bassler, 1953) and revised (Boardman, et al., 1983), this term is absent. However the glossaries of terms of the two monographs dealing exclusively with the bryozoans of the order Ctenostomata (Pohowsky, 1978; Hayward, 1985) explain that zooids and colonies are enantiomorphic, if they are mirror images of one another, i.e., are represented by sinistral and dextral forms.

It is believed that in colonial organisms enantiomorphism is not as common as in solitary organisms. It is possibly the reason why the papers of Russian authors on fossil and modern bryozoans, with the only exception (Viskova and Pakhnevich, 2010), contain no information on enantiomorphism in these colonial animals. Review of the foreign literature on bryozoans (obviously, not exhaustive) has shown that only in some papers was given a special attention to the enantiomorphism of zooids and colonies (Pohowsky, 1978; Hayward, 1985). In other publications it is indirectly confirmed by the detailed description of the developmental features of dextral and sinistral colonies or the asymmetry or polarity of zooids (Lagaaij, 1963; Cheetham, 1968; McKinney, 1980; McKinney and Burdick, 2004; Taylor, 1978; McKinney and Wass, 1981; Cook, 1981; Chimonides and Cook, 1994; Grischenko et al., 1999; etc.). The analysis of publications and available material on fossil and modern bryozoans has allowed the generalization of all these data and discrimination of distinct types of enantiomorphic zooids and enantiomorphic colonies in both ancient and recent representatives of the classes Stenolaemata and Eurystomata.
PHENOMENON OF ENANTIOMORPHISM IN MARINE BRYOZOANS

chemical means. The substrate surface (shells of various mollusks) retains the traces of stolons and zooids that bud off from them and the apertures corresponding to the openings of autozooids through which the lophophores protruded for carrying out all vital functions. Pohowsky (1978) was the first to describe the enantiomorphic zooids of boring bryozoans, both ancient and recent. These zooids are identified by the position of their apertures relative to the stolon: on the right side or along it zooids are dextral; on left side they are sinistral. According to Pohowsky’s (1978) data, the presence of dextral and sinistral zooids is characteristic of the colonies of boring bryozoans of such genera as Terebripora d’Orbigny, 1847 (Eocene–Recent) and Immerngentia Silén, 1946 (Miocene–Recent) and this character is included in the diagnoses of these genera. These zooids may be sporadic in some colonies and numerous in others. For example, in T. ramosa d’Orbigny, 1847 (Pliocene–Recent, United States, Chile) or I. patagoniana Pohowsky, 1978 (Recent, Argentina), the majority of zooids are either dextral or sinistral. In addition, the above-mentioned species and such boring bryozoans as Ropalanoria? arachne (Fischer, 1866) (Callovian–Oxfordian, France), Marcusopora ripleysensis Pohowsky, 1978 (Maastrichtian, United States), and T. falunica Fisher, 1866 (Recent, Brazil) may also contain reversed zooids.

As emphasized by Pohowsky, in boring bryozoans of the genus Cookobryozoon Pohowsky, 1978 (Miocene of California, Pliocene of Australia), with a single species C. lagaaiji Pohowsky, 1978, enantiomorphism may to a large extent show itself in the normal and reversed orientation of zooids, in addition, the reversed zooids may constitute most of the colony. The principal stolon diverging distally from the proximal end of the ancestrula always buds exclusively reversed zooids. The latter may be sinistral, if all their apertures are located on the left side of this stolon, and dextral, if all of them are on its right side (Fig. 1a) 1. The zooids that have the normal orientation and apertures on or along the right side of the stolon are treated as dextral. Enantiomorphic zooids of this species are also easily recognizable in the remote marginal regions of the colony. In other boring bryozoans the dextral and sinistral zooids, which are more or less easily recognizable at the early stages of the colony development, are frequently barely recognizable at a distance from the ancestrula. It is possible that in colonies of C. lagaaiji the development of enantiomorphic zooids of two types and domination of reversed zooids gave them certain advantages over the other boring bryozoans. Emphasizing the extensive overgrowth of colonies of C. lagaaiji in all directions around the ancestrula, Pohowsky believed that this overgrowth proceeded very rapidly and without too much hindrance and that the stolons located near the ancestrula were longer than the subsequent stolons and grew freely. Here it is worth noting that Pohowsky used the term enantiomorphic not only for the zooids but also for the colonies of C. lagaaiji, since the stolon growing from the ancestrula always buds reversed zooids with apertures on the left side (colonies are sinistral) or on the right side (colonies are dextral), and the same position of apertures occurs on other stolons (Pohowsky, 1978, p. 93).

Infrequent reversed zooids were also observed in the species Orbignyopora opulenta Viskova et Pakhnevich, 2010. This boring bryozoan from the Middle Callovian of the Moscow region was discovered in the superficial almost transparent layer inside of an oyster shell (Viskova and Pakhnevich, 2010). In the colony there were two types of autozooids—short and long—that budded off from the principal and lateral stolons and were arranged bilaterally along stolons and characterized by the predominantly normal orientation (Fig. 1b). However some short zooids, which budded on lateral stolons, occasionally exhibited enantiomorphism. It was displayed by the development of reversed zooids with an aperture on the proximal end in addition to the normal zooids.

American researcher Cheetham (Cheetham, 1968; Bordman and Cheetham, 1969) very graphically demonstrates the left and right handedness of zooids using cheilostome bryozoans of the family Poricellariidae (Maastrichtian–Recent) as an example; however, he treated this phenomenon as the asymmetry of zooids. The dendroid articulate colonies of these bryozoans consist of segments in which zooids open only on one side and are arranged in four longitudinal rows (Fig. 1c). Two of these rows of zooids are frontal (one left, another right) with the midline separating them, and the other two rows of zooids are lateral (one left, another right). In all rows the openings (opesia) of zooids are inclined to the median line of the frontal side of the segment. This author emphasizes that the left frontal and left lateral rows of zooids are mirror reflections of the right frontal and right lateral rows of zooids, respectively (Cheetham, 1968, p. 187). But this pattern of the arrangement of zooids in colonies of the Poricellariidae and their morphology suggest that these zooids are enantiomorphic. It is noteworthy that this was noted by Pohowsky (1978, p. 40). According to Cheetham’s investigations (1968) during the Late Cretaceous—Recent the Poricellariidae changed the budding pattern and morphology of zooids (their width, length, and the slope angle of opesia; the number, measurements, and orientation of adventitious avicularia; etc.). In addition in the zooids of lateral rows the changes were faster than in the zooids of frontal rows. As noted by Cheetham, the zooids of Poricellariidae that were monomorphic in the Cretaceous become dimorphic in the Oligocene. Dimorphic zooids are also characteristic of the present-day representatives of this family. It is interesting to note that the

1 In this and other figures given in the paper the size (scale representation) of some individual figures slightly differ from that of the same figures in the original papers but this does not affect the perception.