

**Аннотации научных работ, представленных  
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Монография

**Ostrovsky A.N.** 2013. Evolution of the sexual reproduction in marine invertebrates: example of gymnolaemate Bryozoa. Springer Verlag: Dordrecht, Heidelberg, NewYork, London. 356 pp.

Монография посвящена комплексному сравнительному анализу репродуктивных паттернов и стратегий представителей отряда мшанок Cheilostomata в целях реконструкции основных этапов и тенденций в эволюции полового размножения данной группы Bryozoa. Используя морских мшанок в качестве примера, анализируются пути эволюции водных беспозвоночных в целом.

Three major aspects of this book are (1) it contains the most detailed analysis of the sexual reproduction (oogenesis, fertilization and embryonic incubation) in a particular phylum of the aquatic invertebrates (Bryozoa) ever made; this analysis is based on an exhaustive review of the literature on that topic published over the last 260 years, as well as extensive original histological, anatomical and morphological data obtained during studies of both extant and extinct species; (2) this broad analysis has made it possible to reconstruct the major patterns, stages and trends in the evolution of sexual reproduction in various bryozoan clades, showing numerous examples of parallelisms during transitions from broadcasting to embryonic incubation, from planktotrophic to non-feeding larvae and from lecithotrophy to placentation; corresponding shifts in oogenesis, fertilization and embryonic development are discussed in detail; and (3) the key evolutionary novelties acquired by Bryozoa are compared with similar innovations that have evolved in other groups of marine invertebrates, showing the general trends in the evolution of their sexual reproduction. Ecological background of these innovations is considered too.

Статьи

**Ostrovsky A.N.**, Lidgard S., Gordon D.P., Schwaha T., Genikhovich G., Ereskovsky A.V. 2015. Matrotrophy and placentation in invertebrates: a new paradigm. *Biological Reviews*. DOI: 10.1111/brv.12189 (on-line).

Крупнейшая к настоящему времени сводка, посвященная феномену матротрофии и плацентарным аналогам у беспозвоночных. Анализ показал, что эти феномены встречаются у представителей 22 из 34 типов животных, меняя устоявшуюся парадигму о том, что плаценты распространены, в основном, среди беспозвоночных.

Matrotrophy, the continuous extra-vitelline supply of nutrients from the parent to the progeny during gestation, is one of the masterpieces of nature, contributing to offspring fitness and often correlated with evolutionary diversification. The most elaborate form of matrotrophy—placentotrophy—is well known for its broad occurrence among vertebrates, but the comparative distribution and structural diversity of matrotrophic expression among invertebrates is wanting. In the first comprehensive analysis of matrotrophy across the animal kingdom, we report that regardless of the degree of expression, it is established or inferred in at least 21 of 34 animal phyla, significantly exceeding previous accounts and changing the old paradigm that these phenomena are infrequent among invertebrates. In 10 phyla, matrotrophy is represented by only one or a few species, whereas in 11 it is either not uncommon or widespread and even pervasive.

Among invertebrate phyla, Platyhelminthes, Arthropoda and Bryozoa dominate, with 162, 83 and 53 partly or wholly matrotrophic families, respectively. In comparison, Chordata has more than 220 families that include or consist entirely of matrotrophic species. We analysed the distribution of reproductive patterns among and within invertebrate phyla using recently published molecular phylogenies: matrotrophy has seemingly evolved at least 140 times in all major superclades: Parazoa and Eumetazoa, Radiata and Bilateria, Protostomia and Deuterostomia, Lophotrochozoa and Ecdysozoa.

Dick M.H., Komatsu T., Takashima T., **Ostrovsky A.N.** 2014. A mid-Cretaceous (Albian–Cenomanian) shell-rubble bryozoan fauna from the Goshoura Group, Kyushu, Japan. *Journal of Systematic Palaeontology* 12(4): 401-425.

В статье анализируется строение скелетов древнейших хейлостомных мшанок из меловых отложений Японии. Пять из шести описанных видов относятся к подотряду Malacostegina - примитивной группе аскофорных хейлостомат, характеризующихся отсутствием какой-бы то ни было фронтальной скелетной стенки, и представляя, таким образом, самую раннюю стадию в эволюции отряда Cheilostomata. Обсуждается значение таких признаков как криптоциста, муральные шипы и кенозооиды для систематики и эволюции рассматриваемого отряда.

Early Cretaceous bryozoans are key to understanding the evolutionary radiation of order Cheilostomata, the dominant modern group. Prior to the current study, there were few records of any Cretaceous cheilostomes from eastern Asia, and no pre-Cenomanian records. We found bryozoan fossils to be common in brackish-water to marine deposits representing estuary–tidal-flat and shoreface–inner-shelf habitats in the late Albian–early Cenomanian Goshoura Group, Goshoura Island, Kyushu, Japan. We erect the new genus *Haplostoechios* for two new *Conopeum*-like malacostegans (*H. hayamiae* and *H. clusum*), and describe another new malacostegan as *Charixa goshouraensis*. Additionally, we briefly describe three species detected from a single specimen each: the malacostegan *Incertae sedis* sp. 1 and neocheilostomes *Incertae sedis* sp. 2 and sp. 3. The Goshoura fauna is dominated by cheilostomes rather than cyclostomes, with malacostegans marginally outnumbering neocheilostomes. Bryozoans were a common component of the shell-rubble community, encrusting shells of one brachiopod and a broad variety of molluscan species, including 15 bivalves, two gastropods, an ammonite, a nautiloid and wood fragments containing *Teredolites*.

**Ostrovsky A.N.** 2013. From incipient to substantial: evolution of placentotrophy in a phylum of aquatic colonial invertebrates. *Evolution* 67(5): 1368-1382.

В статье рассмотрены основные этапы эволюции плацентотрофии у представителей отряда мшанок Cheilostomata. Показано, что возникновение этого эволюционного новшества осуществлялось поэтапно через стадию «зачаточной матротрофии», независимо в пределах различных семейств хейлостомат. Переход к плацентарному питанию эмбриона сопровождался скоррелированными изменениями в характере оогенеза, выразившимися в переходе от макролецитальных к олиголецитальным ооцитам.

Matrotrophy has long been known in invertebrates, but it is still poorly understood and has never been reviewed. A striking example of matrotrophy (namely, placentotrophy) is provided by the Bryozoa, a medium-sized phylum of the aquatic colonial filter feeders. Here I report on an

extensive anatomical study of placental analogues in 21 species of the bryozoan order Cheilostomata, offering the first review on matrotrophy among aquatic invertebrates. The first anatomical description of incipient placentotrophy in invertebrates is presented together with the evidence for multiple independent origins of placental analogues in this order. The combinations of contrasting oocytic types (macrolecithal or microlecithal) and various degrees of placental development and embryonic enlargement during incubation, found in different bryozoan species, are suggestive of a transitional series from the incipient to the substantial placentotrophy accompanied by an inverse change in oogenesis, a situation reminiscent of some vertebrates. It seems that matrotrophy could trigger the evolution of sexual zooidal polymorphism in some clades.

Lidgard S., Carter M.C., Dick M.H., Gordon D.P., **Ostrovsky A.N.** 2012. Division of labor and recurrent evolution of polymorphisms in a group of colonial animals. *Evolutionary Ecology* 26(2): 233-257.

В статье рассматриваются важнейшие эволюционные приобретения, позволившие хейлостомным мшанкам стать одной из лидирующих эпибентосных групп в современных донных биоценозах: полиморфизм, сложные фронтальные щиты и выводковые камеры, в том числе – с плацентарными аналогами.

Rendering developmental and ecological processes into macroevolutionary events and trends has proved to be a difficult undertaking, not least because processes and outcomes occur at different scales. Here we attempt to integrate comparative analyses that bear on this problem, drawing from a system that has seldom been used in this way: the co-occurrence of alternate phenotypes within genetic individuals, and repeated evolution of distinct categories of these phenotypes. In cheilostome bryozoans, zooid polymorphs (avicularia) and some skeletal structures (several frontal shield types and brood chambers) that evolved from polymorphs have arisen convergently at different times in evolutionary history, apparently reflecting evolvability inherent in modular organization of their colonial bodies. We suggest that division of labor evident in the morphology and functional capacity of polymorphs and other structural modules likely evolved, at least in part, in response to the persistent, diffuse selective influence of predation by small motile invertebrate epibionts.

Moosbrugger M., Schwaha T., Walzl M.G., Obst M., **Ostrovsky A.N.** 2012. The placental analogue and the pattern of sexual reproduction in the cheilostome bryozoan *Bicellariella ciliata* (Gymnolaemata). *Frontiers in Zoology* 9: 29. doi:10.1186/1742-9994-9-29

В статье рассматриваются особенности оогенеза и плацентарного питания у хейлостомной мшанки *Bicellariella ciliata* (Gymnolaemata). Описываются анатомия и ультраструктура овария, плацентарного аналога и эмбриона.

Matrotrophy or extraembryonic nutrition – transfer of nutrients from mother to embryo during gestation – is well known and thoroughly studied among vertebrates, but still poorly understood in invertebrates. The current paper focuses on the anatomy and ultrastructure of the oogenesis and placentotrophy as well as formation of the brood chamber (ovicell) in the cheilostome bryozoan *Bicellariella ciliata* (Linnaeus, 1758). Our research aimed to combine these aspects of the sexual reproduction into an integral picture, highlighting the role of the primitive placenta-like system in the evolution of bryozoan reproductive patterns.

**Ostrovsky A.N., Porter J.S.** 2011. Pattern of occurrence of supraneural coelomopores and intertentacular organs in gymnolaemate bryozoans and its evolutionary implications. *Zoomorphology* 130:1-15.

В статье рассмотрена эволюция женской гонопоры (интертентакулярного органа (ИТО) и супраневральной целомопоры) в свете двух альтернативных гипотез. Первая гипотеза предполагает, что ИТО возник за счет укорачивания и слияния двух щупалец с терминальными порами. Альтернативная гипотеза предполагает, что ИТО возник из целомопоры за счет базальных участков двух дисто-медиальных щупалец. Поддерживается вторая гипотеза, в соответствии с которой ранние гимнолемные мшанки с унисериальным ростом и первым паттерном полового размножения обладали целомопорой.

The evolution of bryozoan female gonopores (the supraneural coelomopore (SNP) and the intertentacular organ (ITO)) is considered in the light of two alternative hypotheses. In the first hypothesis it is proposed that the ITO originated from the shortening and fusion of two tentacles possessing terminal pore(s), with further transformation into a simple pore. In the alternative hypothesis it is suggested that the ITO evolved from a coelomopore with a contribution from the basal parts of two disto-medial tentacles in an ancestor. Favouring the second hypothesis, in this paper we present a hypothetical scenario, according to which the earliest gymnolaemate bryozoans with uniserial growth and a broadcasting reproductive pattern possessed the supraneural coelomopore (SNP). This could serve both as a female gonopore and as a conduit for sperm entry. Evolution of large colonies of closely packed zooids led to development of the tube-like intertentacular organ (ITO) that is formed by epithelial proliferation of the basal parts of two dorso-medial tentacles.

**O'Dea A., Ostrovsky A.N., Rodríguez F.** 2010. Embryonic brooding and clonal propagation in tropical eastern Pacific cupuladriid bryozoans. *Journal of the Marine Biological Association of the United Kingdom* 90: 291-299.

В статье представлены оригинальные данные об особенностях репродуктивной биологии хейлостомных мшанок из семейства Cupuladriidae и рассматривается их связь с бесполом размножением.

Colonial invertebrates often mix sexual and asexual methods of propagation, and a comprehensive understanding of both is required for life history study. The asexual cloning of new colonies in cupuladriid bryozoans is much better studied than the formation of new colonies by sexual reproduction. As such, the relative investments of sexual and asexual modes of propagation remain uncertain. This preliminary study explores patterns of embryonic brooding as a measure of investment into sexual reproduction. We conduct a survey of quantity and arrangement of embryos in tropical eastern Pacific cupuladriid colonies and compare this to the frequency of cloning. Species populations show considerable variation in embryonic brooding. Patterns of brooding, both across and within species strongly support the hypothesis that as cloning increases, investment into sexual reproduction decreases. We find preliminary evidence that individual cupuladriid colonies that propagate sexually may senesce like solitary organisms, while species that regularly clone only appear to experience senescence at the level of the zooid.

Yagunova E.B., Ostrovsky A.N. 2010. The influence of substrate type on sexual reproduction of the bryozoan *Cribrilina annulata* (Gymnolaemata, Cheilostomata). A case study from Arctic seas. *Marine Biology Research* 6(3): 263-270.

В статье рассматривается зависимость полового размножения хейлостомных мшанок вида *Cribrilina annulata* от условий существования, а именно – типа субстрата.

This study compared the fecundity of the colonies of the cheilostome bryozoan *Cribrilina annulata* (Fabricius, 1870) collected from two differing substrates \_ shingles and the algae *Odonthalia dentata* (Linnaeus) Lyngbye, 1819 \_ in the White and the Barents Seas. Almost all colonies growing on algae had brood chambers (ovicells), and their numbers per colony were high. In contrast, colonies with ovicells were rare on shingles, having fewer brood chambers. Colonies growing on *O. dentata* started reproduction at a smaller size (having fewer zooids per colony) than those on the shingles. These data contradict the generally accepted opinion that stable substrates are favourable for bryozoan sexual reproduction. We also found that ancestrulae are larger in the colonies growing on shingles, which suggests that the larval pool might be subdivided into two 'subpopulations'. Conditions for such subdivision are discussed.

Ostrovsky A.N., Nielsen C., Vávra N., Yagunova E.B. 2009. Diversity of the brooding structures in calloporid bryozoans (Gymnolaemata: Cheilostomata): comparative anatomy and evolutionary trends. *Zoomorphology* 128(1): 13-35.

В статье представлены оригинальные данные о строении выводковых структур у хейлостомных мшанок из семейства Calloporidae и рассматриваются возможные пути их эволюции.

Comparative anatomical studies of 12 species from 10 genera (*Callopora*, *Tegella*, *Amphiblestrum*, *Parellisina*, *Corbulella*, *Crassimarginatella*, *Valdemunitella*, *Bryocalyx*, *Concertina*, *Cauloramphus*) belonging to one of the largest and most diverse bryozoan taxa, the Calloporidae, and one species from the genus *Akatopora* belonging to the related taxon Antroporidae, were undertaken to elucidate the morphological diversity of brooding structures and to recognize main trends in their evolution. Most of the species studied possess ovicells (specialized brooding receptacles) formed by the distal and maternal (egg-producing) autozooids. The distal zooid can be an autozooid, a vicarious avicularium or a kenozooid. The calciWed protective hood (ooecium) is an outgrowth from the distal zooid. Hyperstomial or prominent ovicells are most common. They were found in species of the genera *Callopora*, *Tegella*, *Amphiblestrum*, *Parellisina*, *Corbulella*, *Bryocalyx* and *Concertina*. Subimmersed ovicells were found in *Valdemunitella*, and immersed ovicells in *Crassimarginatella* and *Akatopora*. *Cauloramphus* has an internal brooding sac and a vestigial kenozooidal ooecium, budded by the maternal zooid.

Ostrovsky A.N., Gordon D.P., Lidgard S. 2009. Independent evolution of matrotrophy in the major classes of Bryozoa: transitions among reproductive patterns and their ecological background. *Marine Ecology Progress Series* 378: 113-124.

В статье рассматривается распространение плацентарных аналогов среди хейлостомных мшанок и анализируются пути эволюции их репродуктивных паттернов в связи с



появлением плацент.

Bryozoa are unique among invertebrates in possessing placenta-like analogues and exhibiting extraembryonic nutrition in all high-level (class) taxa. Extant representatives of the classes Stenolaemata and Phylactolaemata are evidently all placental. Within the Gymnolaemata, placental-like systems have been known since the 1910s in a few species, but are herein reported to be widespread within this class. Placental forms include both viviparous species, in which embryonic development occurs within the maternal body cavity, and brooding species, in which development proceeds outside the body cavity. We have also identified an unknown reproductive pattern involving macrolecithal oogenesis and placental nutrition from a new, taxonomically extensive anatomical study of 120 species in 92 genera and 48 families of the gymnolaemate order Cheilostomata. Results support the hypothesis of evolution of oogenesis and placentation among Cheilostomata from oligolecithal to macrolecithal oogenesis, followed by brooding, through incipient matrotrophy combining macrolecithal oogenesis and placentation, to oligolecithal oogenesis with subsequent placental brooding. The distribution of reproductive patterns within the phylum suggests that variations of placentation evolved in all 3 bryozoan classes, and possibly several times within both gymnolaemate orders. We infer that extraembryonic nutrition may be advantageous to species through enhanced developmental plasticity, and, in fast-growing ephemeral colonies, simultaneous volumetric growth and embryonic development may facilitate earlier larval release and occupation of vacant space.

**Ostrovsky A.N., O'Dea A., Rodríguez F.** 2009. Comparative anatomy of internal incubational sacs in cupuladriid bryozoans and the evolution of brooding in free-living cheilostomes. *Journal of Morphology* 270: 1413-1430.

В статье представлены оригинальные данные о строении внутренних выводковых структур у хейлостоминых мшанок из семейства Cupuladriidae и рассматриваются возможные пути и причины их возникновения.

Numerous gross morphological attributes are shared among unrelated free-living bryozoans revealing convergent evolution associated with functional demands of living on soft sediments. Here, we show that the reproductive structures across free-living groups evolved convergently. The most prominent convergent traits are the collective reduction of external brood chambers (ovicells) and the acquisition of internal brooding. Anatomical studies of four species from the cheilostome genera Cupuladria and Discoporella (Cupuladriidae) show that these species incubate their embryos in internal brooding sacs located in the coelom of the maternal nonpolymorphic autozooids. This sac consists of a main chamber and a narrow neck communicating to the vestibulum. The distal wall of the vestibulum possesses a cuticular thickening, which may further isolate the brood cavity. The presence of this character in all four species strongly supports grouping Cupuladria and Discoporella in one taxon. Further evidence suggests that the Cupuladriidae may be nested within the Calloporidae. Based on the structure of brooding organs, two scenarios are proposed to explain the evolution of the internal brooding in cupuladriids. The evolution of brood chambers and their origin in other free-living cheilostomes is discussed. Unlike the vast majority of Neocheilostomina, almost all free-living cheilostomes possess nonprominent chambers for embryonic incubation, either endozooidal and immersed ovicells or internal brooding sacs, supporting the idea that internal embryonic incubation is derived. We speculate that prominent skeletal brood chambers are disadvantageous to a free-living mode of life that demands easy movement through sediment in instable sea-floor settings.