Homology of the lophophore and its evolution within lophophorates

Elena N. Temereva[1,2*], Tatyana V. Kuzmina[1]

[1] *Invertebrate Zoology Department, Lomonosov Moscow State University, Leninskie Gory 1-12, 119234 Moscow, Russia.*
[2] *Faculty of Biology and Biotechnology, National Research University Higher School of Economics, 101000 Moscow, Russia.*
* *Corresponding author: temereva@mail.ru*
Elena Temereva: ORCID 0000-0001-7791-0553
Tatyana Kuzmina: ORCID 0000-0001-7978-7608

ABSTRACT: The lophophore is a tentaculated organ — a specificity of Lophophorata. Since molecular phylogeny has yielded contradictory data on the monophyly of lophophorates, results of comparative morphology are used here to shed light on the question about the homology of the lophophore in different groups of lophophorates. We compare the morphology of the lophophore and the organization of its coelomic, nervous, and muscular systems in three different phyla of lophophorates: phoronids, bryozoans, and brachiopods. The morphology of the lophophore and the structure of all lophophoral organ systems are examined in respect to the standard criteria of homology. The comparative analysis supports the homology of the lophophore and suggests the monophyly of the lophophorates. We present a hypothetical scenario of lophophore evolution based on our analyses. Accordingly, the ancestral lophophore of lophophorates had a horseshoe-shaped brachial axis and was innervated by supraenteric and subenteric nerve centers, which were connected by circumenteric connectives and a circumoral nerve. This ancestral lophophore then evolved in three different phyla by two pathways: (i) by complication and (ii) by simplification.

Гомология лофофора и его эволюция у лофофорат

Е.Н. Темерева[1,2,*], Т.В. Кузьмина[1]

[1] *Кафедра зоологии беспозвоночных, Московский государственный университет им. М.В. Ломоносова, Ленинские горы 1-12, Москва, 119234 Россия.*
[2] *Факультет биологии и биотехнологии Национального исследовательского университета Высшая школа экономики, 101000 Москва, Россия.*
* *Corresponding author: temereva@mail.ru*

РЕЗЮМЕ: Лофофор представляет собой щупальцевый орган, который характерен для представителей группы Lophophorata. Поскольку молекулярная филогения не дает однозначного ответа о монофилии лофофорат, в данной работе мы используем результаты сравнительной морфологии, чтобы пролить свет на вопрос о гомологии

лофофора в разных группах лофофорат. Мы сравниваем морфологию лофофора и организацию его целомической, нервной и мышечной систем у трех различных типов лофофорат: форонид, мшанок и брахиопод. Морфология лофофора и строение всех систем органов лофофора рассмотрены в соответствии со стандартными критериями гомологии. Сравнительный анализ подтверждает гомологию лофофора и предполагает монофилию лофофорат. В данной работе предложена гипотеза эволюции лофофора: у предка лофофорат лофофор имел подковообразную брахиальную ось и иннервировался надглоточным и подглоточным нервными центрами, которые соединялись окологлоточными коннективами и околоротовым нервом. В трех типах лофофорных животных предковая форма лофофора эволюционировала двумя путями: в сторону упрощения и в сторону усложнения.

Introduction

Lophophorata is a group of invertebrates that has traditionally been regarded as a phylum (Emig, 1982) or superphylum (Ruppert *et al*., 2004). According to traditional view (Hyman, 1959), lophophorates are the closest relatives to deuterostomians: individuals from both groups exhibit radial non-determined cleavage of the egg, an enterocoelic origin of coelomic mesoderm, and three compartments of the coelomic system — protocoel, mesocoel, and metacoel. Data from molecular phylogeny have cast doubt on this traditional view by showing relationships between lophophorates and typical trochozoans — annelids and mollusks (Halanych *et al*., 1995). Accordingly, a new clade — the Lophotrochozoa — has been established. In order to substantiate these new results and determine differences between lophophorates and deuterostomians, new studies of lophophorates morphology and development were conducted. They reveal that lophophorates (phoronids and bryozoans, in particular) do not have three coelomic compartments (Bartolomaeus, 2001; Gruhl *et al*., 2005, 2009; Schwaha *et al*., 2011, Schwaha, 2018); the organization of the larval nervous system in phoronids has more in common with that in trochozoans (Santagata, Zimmer, 2002); and egg cleavage is similar to the spiralian pattern (Pennestorfer, Scholtz, 2012).

At the same time, new morphological and embryological data revealed similarities in development and anatomy of different lophophorates and deuterostomians. Thus, the presence of two patterns of coelom organization — bipartite and tripartite — has been discovered in phoronids (Temereva, 2015) and brachiopods (Temereva *et al*., 2015). Comparative analysis demonstrated the plesiomorphy of the tripartite pattern of the coelom organization in the lophophorates (Temereva, Malakhov, 2011a; Ratnovskaya, Kuzmina, 2022). The pattern of egg cleavage depends on the type of development and can exhibit spiralian features in those phoronids whose development occurs completely in water (Temereva, Malakhov, 2012). Deuterostome- and trochozoan-like features are present in the organization of the apical organ of phoronid larvae (Temereva, Wanninger, 2012) and in the larval nervous system (Santagata, Zimmer, 2002; Temereva, Tsitrin, 2014). Thus, lophophorates combine protostome- and deuterostome-like features. This combination provides hypothesis that lophophorates inherited these features from the last common bilaterian ancestor and retained them. Such features, however, are combined with the specificities of the body plan.

Another important issue concerning lophophorates is their monophyly or paraphyly. According to traditional view, lophophorates is a monophyletic group that includes three phyla: Phoronida, Bryozoa, and Brachiopoda. The presence of the lophophore is regarded as a synapomorphy of lophophorates. The lophophore is "a tentaculated extension of the mesosome that

embraces the mouth but not the anus and has a coelomic lumen" (Hyman, 1959). According to some authors (Nielsen, 1977; Ruppert, Barnes, 1994), entoprocts, which also have the specific tentacle apparatus, are regarded as lophophorates or closest relatives thereof. Nonetheless, the organization of the tentacle apparatus of entoprocts greatly differs from that of the lophophore and does not correspond to the definition of the lophophore because the anus is surrounded by tentacles. Moreover, the innervation of tentacle apparatus in entoprocts is completely different from that of the lophophore in all lophophorates (Borisanova et al., 2019). The differences concern the organization of the main nervous elements and the innervation of the tentacles.

The relationships within lophophorates are not definitively established. Traditionally, phoronids and bryozoans are grouped together based on the similarity of their body plan: in both groups, the ventral side is very long, whereas the dorsal side is short (Beklemishev, 1964). In contrast, brachiopod's body plan is traditionally regarded as resulting from folding of the brachiopod ancestor on the ventral side (Nielsen, 1991). Thus, in brachiopods, the dorsal side is very long, whereas the ventral side is short. The origin of the brachiopod body plan is regularly discussed in the literature and the "brachiopod fold hypothesis" has supporters (Nielsen, 1991; Kuzmina et al., 2019; Plandin, Temereva, 2022) and detractors (Altenburger et al., 2013, 2017).

In the late 1990s, a new phylogeny of Bilateria was suggested (Halanych et al., 1995; Aquinaldo et al., 1997). According to new data, lophophorates are regarded as trochozoan animals, and the present study demonstrates the paraphyly of the lophophorates for the first time: the specific position of bryozoans in respect to the remaining lophophorates has been suggested by Halanych et al. (1995). The specific position of bryozoans on the phylogenetic tree of Bilateria will be outlined in several future papers. At the same time, the location of bryozoans with regard to other Lophotrochozoa has been extremely variable (Temereva, 2014). Many papers support the close relation of bryozoans and entoprocts (Hausdorf et al., 2007). Moreover, bryozoans, entoprocts, and cycliophorans have been united into the clade Polyzoa

(Hejnol et al., 2009). Over the past twenty years the monophyly of lophophorates has been rejected due to data provided by molecular phylogeny. Nonetheless, some molecular data do support the monophyly of the lophophorates (Jang, Hwang, 2009; Nesnidal et al., 2013). This contradiction revealed that molecular phylogeny is unable to present a convincing reconstruction and needs help from comparative morphology. This prompted the present study of lophophore morphology.

Terminology

The lophophore is "a tentaculated extension of the mesosome that embraces the mouth but not the anus and has a coelomic lumen" (Hyman, 1959).

Brachial axis is a row of tentacles (Rudwick, 1970, see fig. 1 in Kuzmina et al., 2021). The mouth is located in the middle of the brachial axis. New tentacles form at the ends of the brachial axis (Rudwick, 1970; Kuzmina, Malakhov, 2007).

Brachial (food) groove is located between the brachial fold and tentacles and serves as a canal for transporting the filtered food particles to the mouth (Rudwick, 1970; Williams et al., 1997).

Brachial fold (lip) or epistome is an extension of the body wall that stretches along the brachial axis above the mouth and food groove (Rudwick, 1970).

Oral tentacles are located behind the mouth. In phoronids and bryozoans, a brachial axis contains a single row of uniform tentacles. In most brachiopods, the oral tentacles form a single row, the rest of the brachial axis contains a double row of tentacles: inner ridged (adlabial) tentacles are located closer to the brachial fold; outer grooved (ablabial) tentacles are located farther away from the brachial fold (Rudwick, 1970; James et al., 1992; Williams et al., 1997; Kuzmina, Malakhov, 2007). All tentacles have four ciliary zones: a frontal, two lateral, and an abfrontal. The frontal ciliary zone faces the brachial fold; the lateral ciliary zones are heavily ciliated and located on the lateral sides of the tentacles. The abfrontal ciliary zone is sparsely ciliated and is opposite to the frontal ciliary zone (see fig. 12 in Kuzmina, Malakhov, 2007).

Tentacular lamina is supporting structure that is formed by the fused tentacle bases.

Lophophore arms (brachia) represent parts of the brachial axis that do not adhere to the body wall, but are freely raised (Rudwick, 1970; Kuzmina, Malakhov, 2007).

Brachidium is the calcareous skeleton of the raised lophophore of some brachiopods that supports most of the brachial axis (Williams *et al*., 1997).

Coelomic canal of lophophore extends along the brachial axis and gives off branches into each tentacle. In brachiopods, this canal corresponds to the small coelomic canal (see fig. 1 in Kuzmina *et al*., 2021).

Large (great) canal is a coelomic canal of the lophophore of most brachiopods and perform a hydroskeletal function (Williams *et al*., 1997).

Brachial pouch is an additional coelomic canal in the lateral arms of the lophophore of some brachiopods (plectolophous lophophore of terebratulids) (Williams *et al*., 1997).

Homology: In this paper we use the term "homology" in its native meaning: "homology is similarity due to shared ancestry between a pair of structures in different taxa". We have used four criteria of homology: position (in respect to the mouth and tentacles), structure (certain lophophoral and tentacular coeloms, nerves, and musculature), intermediate (presence of transitional forms of brachial axis), and criterion of special quality (in respect to peritoneal nerves of the tentacles).

Phoronida

Lophophore morphology

In phoronids, the mouth and anus are located close to each other on the anterior end of the body. The short dorsal side is located between mouth and anus. Because of specificity of the body plan, phoronids have an oral side and anal side (Emig, 1982). The brachial axis bears a single row of tentacles; it extends along the oral side, passes to the lateral sides, turns again to the mouth, and terminates on the dorsal side behind the mouth. The brachial axis has different shapes and defines the type of lophophore. The current opinion is that lophophore shape depends on body size: small phoronids have a simple lophophore morphology, whereas large phoronids have a more complexly shaped lophophore

(Emig, 1982). Several main types of the lophophore morphology have been described in phoronids (Emig, 1982; Temereva, Malakhov, 2009a). The simplest is oval-shaped and bears 20–24 tentacles. This type is known in *Phoronis ovalis*, which is the smallest phoronid species. The typical phoronid lophophore is horseshoe-shaped type, bears 100–120 tentacles, and occurs in many phoronid species. The spiral lophophore can form several coils (from 0.5 to 3) and bears 100–1500 tentacles. The helicoidal lophophore has the most complex morphology: it forms several coils, one above the other. The helicoidal lophophore is known in a single species — *Phoronopsis californica*.

It is generally accepted that the phoronid lophophore has evolved from the simplest oval-shaped type to more complex types (Emig, 1976). According to an alternative opinion (Temereva, 2019a), however, it has evolved via two different pathways: from the ancestral horseshoe-shaped type to (i) the oval type via simplification and to (ii) the spiral type via complication.

Lophophore coelom

The lophophore contains the lophophoral coelom, i.e. mesocoel, which has a voluminous basis and projections into the tentacles (Hyman, 1959). The lophophoral coelom basis contains afferent and efferent lophophoral blood vessels. The coelom morphology repeats the shape of the lophophore and ends blindly at the tips of the brachial axis. It is separated from the trunk coelom, i.e. metacoel, by a thick diaphragm. Some phoronids exhibit a protocoel, which occupies the epistome (Herrmann, 1976, 1979; Temereva, Malakhov, 2011b; Temereva, 2015).

Lophophore musculature

Although there are certain differences in different phoronid species, the general pattern of musculature organization can be defined (Temereva, 2019a, b). The ground plan includes (i) a circular muscle, (ii) longitudinal muscles of the tentacular lamina, (iii) groups of paired distal muscles of the tentacular lamina, and (iv) frontal and abfrontal muscles of the tentacles. The circular muscle extends along the outer side of the lophophore base and connects with the longitudinal muscles of the tentacular lamina. The groups of paired distal muscles of

the tentacular lamina are associated with the longitudinal muscles and are located at the base of each tentacle. Each tentacle contains frontal and abfrontal tentacle muscles, which are anchored to the paired distal muscles of the tentacular lamina.

Lophophore nervous system and tentacle innervation

The phoronid central nervous system includes three main elements: the dorsal nerve plexus, the tentacle nerve ring, and the minor nerve ring. The dorsal nerve plexus is usually called "dorsal ganglion", but this nerve element does not have a structure typical for a ganglion, and it is organized as stratified neuroepithelium (Temereva, Malakhov, 2009b). The dorsal nerve plexus is located on the dorsal side of the body, between the mouth and anus, and gives rise to the tentacle nerve ring, which extends along the outer side of the lophophore base. The dorsal nerve plexus gives rise to the minor (inner) nerve ring, which extends along the inner side of the lophophore base.

The tentacle nerve ring and the minor nerve ring contribute to the innervation of tentacles. Each tentacle is innervated by six groups of nerves, which extend intraepithelially: one frontal, two laterofrontal, two lateroabfrontal, and one abfrontal. The tentacle nerve ring gives rise to the abfrontal and lateroabfrontal tentacle nerves. The minor nerve ring gives rise to the frontal tentacle nerves and intertentacular nerves, which bifurcate and give rise to the laterofrontal tentacle nerves extending to adjacent tentacles. In phoronids with a lophophore of complex morphology, the laterofrontal tentacle nerves originate from intertentacular groups of perikarya, which do not connect to the minor nerve ring (Temereva, 2020a). In addition to intraepithelial tentacle nerves, there are peritoneal nerves extending between the extracellular matrix and coelomic lining.

Bryozoa (=Ectoprocta)

Lophophore morphology

Ectoprocts have a body plan similar to that of phoronids: their mouth and anus are located close each other, and the body has oral and anal sides. Because of the miniaturization, the ectoprocts have a simpler lophophore structure than phoronids. There are two groups of ectoprocts: Phylactolaemata and Myolaemata, the latter consisting of two recent classes Cyclostomata and Gymnolaemata (the latter encompassing Ctenostomata and Cheilostomata) (Schwaha *et al.*, 2020). Phylactolaemates are freshwater ectoprocts that lack the myoepithelial pharynx characterizing myolaemates and typically have a large and morphologically complex lophophore. This lophophore is called "horseshoe-shaped", but it differs from the phoronid type. In phylactolaemates, a horseshoe-shaped lophophore forms two large arms (horns), which are directed to the anal side and are clearly separated from the lophophore base. This lophophore is known in *Cristatella mucedo* and *Plumatella repens* and bears 30–70 tentacles. A distinct feature of phylactolaemates is the presence of an intertentacular membrane at the lophophore base. In some phylactolaemates and most myolaemates, the lophophore is bell- or circle-shaped. The bell-shaped variant has a large base and bears 24–38 tentacles, the circle-shaped one is very small and bears 6–12 tentacles.

Lophophore coelom

Bryozoans exhibit two types of organization of the lophophore coelom. In all phylactolaemates, there is an oral coelomic canal ("ring" canal) and anal forked canal. The oral "ring" canal does not form a true ring; it extends under the oral tentacles and supplies only a few of them: from four to eight tentacles. The forked canal is located on the anal side of the lophophore and supplies only four to six anal tentacles. The forked canal is lined by a peritoneum, which is heavily ciliated and is traditionally regarded as a vestigial metanephridium (Gruhl *et al.*, 2009; Schwaha *et al.*, 2011, 2020; Schwaha, 2018). The excretion from the forked canal occurs via terminal pores located on the tips of tentacles. Coelomic canals of the lateral tentacles of the lophophore and the lophophore arms connect to the metacoel: there are no borders between metacoel and tentacles. Thus, lateral tentacles are filled with the metacoel. Phylactolaemates have an epistome, which contains a coelomic cavity.

In all myolaemates, the lophophore coelom is represented only by a ring canal, which is located at the lophophore base, repeating the

shape of the lophophore; it gives rise to the coelomic canals of all tentacles (Shunatova, Tamberg, 2019). The coelomic ring is open at the anal side and therefore does not form a true ring. In gymnolaemates, the anal ends of the ring canal bears paired openings to the remaining body cavity (e.g. Mukai *et al.*, 1997; Schwaha *et al.*, 2011). In cyclostomes, such openings are absent.

Lophophore musculature

The lophophore musculature includes the muscles of tentacles and muscles of the lophophore base (Gawin *et al.*, 2017; Schwaha, Wanninger, 2018). In all bryozoans, each tentacle contains frontal and abfrontal bands of longitudinal muscles. In most bryozoans (except phylactolaemates), the tentacle muscles do not connect with the musculature of the lophophore base (Schwaha *et al.*, 2011, 2018; Schwaha, Wanninger, 2018).

The musculature of the lophophore base is associated with the digestive tract. The phylactolaemates feature a circular musculature of the pharynx, which gives rise to the two of three roots that form the frontal longitudinal muscle of most oral tentacles. One pair of muscle bands extend along the base of each lophophore arm; these bands are the part of the retractor muscle (Gavin *et al.*, 2017). Muscle bands of the lophophore arm give rise to short stubs that extend toward the tentacles and connect the frontal longitudinal muscle of tentacles. In addition to a circular musculature of the pharynx and lophophoral base muscles, phylactolaemates have prominent muscles of the ring canal and epistome.

In myolaemates, musculature of the lophophore base can be categorized into (i) longitudinal muscles of the lophophoral base, (ii) circular lophophoral base muscles of gymnolaemates, (iii) buccal dilatators, and (iv) proximal lophophoral base muscle of cyclostomates (Schwaha *et al.*, 2020; Schwaha, 2021). Cyclostomates feature frontal and abfrontal longitudinal muscles of the lophophoral base, whereas only abfrontal muscles are present in gymnolaemates. In many gymnolaemates, abfrontal muscles of the lophophoral base are associated with the v-shaped muscles. The circular lophophoral base muscles are represented by a complete muscular ring located above the mouth, or by short intertentacular muscle fibers. Cyclostomates lack

prominent circular lophophoral base muscles, but have a circular musculature of the pharynx. Buccal dilators extend between circular and longitudinal muscles of the lophophoral base. The proximal lophophoral base muscles have been described in cyclostomates and extend along the buccal dilators.

Lophophore nervous system and tentacle innervation

The central nervous system includes the cerebral ganglion and the circumoral nerve ring. The cerebral ganglion is located in the center of the lophophore, between mouth and anus. In bryozoans from different groups (Phylactolaemata, Myolaemata: Cyclostomata, Gymnolaemata), it contains an inner cavity and is formed by a neuroepithelium, which is submerged under the body wall. Cells of the cerebral ganglion are connected to each other via cell junctions and bear microvilli and a cilium. Only in cheilostome bryozoans the cerebral ganglion lacks the inner cavity and neuroepithelium. The cerebral ganglion gives rise to the circumoral nerve ring, which extends around the mouth and includes basal projections of large serotonin-immunoreactive perikarya. These perikarya are located around the mouth between the tentacle bases. The arrangement of serotonin-immunoreactive perikarya exhibits the standard pattern: three oral perikarya, which are separated from other perikarya via "serotonergic gaps" — two places between tentacles that lack such perikarya (Schwaha, Wanninger, 2015). In phylactolaemates, the lophophoral concavity lacks serotonin-immunoreactive perikarya.

Some ctenostomate and cyclostomate bryozoans have an outer nerve ring (Temereva, Kosevich, 2016, 2018). It usually consists of several thin neurites that emanate from the cerebral ganglion and extend along the outer side of the lophophore base. In most of studied bryozoans, the outer nerve ring does not connect to other nerves and does not contribute to tentacle innervation. In *Flustrellidra hispida*, however, which has large bell-shaped lophophore, the outer nerve ring gives rise to the abfrontal neurites, which contribute to the tentacle abfrontal nerves (Temereva *et al.*, 2022).

Phylactolaemates and cyclostomates have six longitudinal tentacle nerves: one mediofron-

tal, one pair of laterofrontal, one abfrontal, and one pair of the laterofrontal nerves (Shunkina *et al*., 2015; Schwaha, 2021). Gymnolaemates in general have four tentacular nerves: one mediofrontal, one abfrontal, and one pair of laterofrontal (Weber *et al*., 2014; Schwaha, Wood, 2011). Tentacle nerves originate from the circumoral nerve ring and from intertentacular nerves. In phylactolaemates all tentacle nerves emanate from the intertentacular nerves, whereas in myolaemates, mediofrontal nerves extend from the circumoral nerve ring, but other tentacle nerves originate from the intertentacular nerves. At the same time, in *E. pilosa*, in contrast, the abfrontal nerve also originates from the circumoral nerve ring (Lutaud, 1973), and in *Crisia eburnea* the abfrontal nerve appears as a branch of the lateroabfrontal nerve (Temereva, Kosevich, 2018).

In addition to six or four intraepithelial nerves, many ectoprocts have two peritoneal tentacular nerves (Mukai *et al*., 1997; Weber *et al*., 2014; Temereva, Kosevich, 2016). According to some data (Weber *et al*., 2014), these neurites show no immunoreactivity against acetylated alpha tubulin and thereby cannot be regarded as nerve elements.

Brachiopoda

Lophophore morphology

The body of brachiopods is enclosed by a shell consisting of a pair of valves: dorsal and ventral. The body wall forms a mantle that extends along the inner surfaces of the valves and surrounds the mantle cavity. Brachiopods are subdivided into three subphyla: Linguliformea, Craniiformea, and Rhynchonelliformea, which differ from each other by the structure and chemical compsition of the shell, soft body anatomy, and ontogenesis (Williams *et al*., 1996). Rhynchonelliformea includes three recent orders: Rhynchonellida, Thecideida, and Terebratulida.

The lophophore of all brachiopods is located in the mantle cavity and is therefore protected by the shell. In brachiopods, the length of brachial axis depends on body size: an increase in body size is associated with an elongation of the brachial axis (Rudwick, 1970; Williams *et al*., 1997). In large brachiopods, the brachial axis curves in different ways to fit in the mantle

cavity. Nine types of lophophores have been identified in recent species and 15 types in extinct species (Kuzmina *et al*., 2021).

In the taxolophe, trocholophe, schizolophe and ptycholophe, the brachial axis completely adheres to the anterior body wall and dorsal mantle. The taxolophous lophophore has the simplest organization. The brachial axis forms a crescent, and new tentacles are formed at its distal ends, dorsal to the mouth. These lophophore types are present only in the ontogeny of most brachiopods and may be bypassed in the ontogeny of some rhynchonelliforms (Emig, 1992). The trocholophous lophophore has a ring-like brachial axis (fig. 1 in Atkins, 1959a). The brachial axes of the trocholophe and taxolophe are simple: they consists of a single row of ridged tentacles (Atkins 1958, 1959a,b,c, 1961a; Atkins, Rudwick, 1962; Temereva, 2020b; Kuzmina *et al*., 2021). These tentacles remain behind the mouth in more complex type of lophophore and were named oral tentacles (Temereva, 2020b). On cross section, the oral tentacles are round; the lateral ciliary zones are located at equal distance between frontal and abfrontal sides of the tentacles. The schizolophous lophophore has a horseshoe form and consists of two short loops that are also attached to the dorsal mantle (fig. 9 in Atkins, 1958). The brachial axis of the schizolophe and more complex lophophore types consists of alternating inner and outer tentacles. The inner tentacles have a frontal ciliary ridge, the abfrontal zone is narrow, the lateral ciliary zones are located closer to the abfrontal surface of the tentacle (Kuzmina, Temereva, 2022). The outer tentacles have the frontal groove and a wide abfrontal ciliary zone; the lateral ciliary zones are located closer to the frontal surface of the tentacle. The trocholophe and schizolophe are initial stages in lophophore ontogenesis in all brachiopods and also occur in some adult forms (Emig, 1992) that are apparently paedomorphic (for example, see Zezina, 2015). In ptycholophous lophophores, the brachial axis remains attached to the dorsal mantle, but its brachial axis grows and forms several large loops (fig. 6 in Atkins, 1960). The ptycholophe occurs in two orders of recent rhynchonelliforms: thecedeids (Lüter *et al*., 2003; Logan, 2004) and terebratulids (Megatheridae) (Atkins, 1960). This type of lophophore was recon-

structed in a completely extinct class of rhynchonelliform brachiopods — Strophomenata (Kuzmina *et al*., 2021).

In the spirolophe, zygolophe, plectolophe, modified zygolophe, and modified spirolophe, the brachial axis detaches from the anterior body wall and is freely located in the mantle cavity arms (or brachia). In ontogenesis, the spirolophous lophophore is formed when the distal end of the brachial axis of each short loop of a shizolophe was raised into the space of the mantle cavity and formed two spiral arms (fig. 11a in Kuzmina *et al*., 2021). This is the most widespread type of lophophore in recent and extinct brachiopods and occurs in representatives of three subphyla (Carlson, 2016; Kuzmina *et al*., 2021). The zygolophous lophophore has two lateral arms that expose to the mantle cavity (for example, see Atkins, 1959a,b,c, 1961a). The brachial axis of each lateral arm forms a loop and returns to the mouth. Each zygolophe arm therefore consists of two brachial axes (fig. 4 in Atkins, 1961a). The zygolophe is usually the transitional form of the plectolophous lophophore and also occurs in several species of terebratulids (Emig, 1992). In the plectolophe, a spiral third median arm is formed. The plectolophe therefore consists of three arms, one median and two lateral, each of which contains two brachial axis (fig. 11d in Kuzmina *et al*., 2021). The plectolophe is the most complicated type of lophophore in extant brachiopods and occurs solely in terebratulids. The brachial axis of all the lophophore types listed above is directed anteriorly from the mouth. In recent discinids of linguliform brachiopods, the brachial axis is directed posteriorly (Kuzmina, Temereva, 2019). The modified zygolophe consists of two posteriorly directed lateral arms; like the common zygolophe, each of its lateral arms consists of two brachial axes (fig. 2 in Kuzmina, Temereva, 2019). The modified spirolophe develops from the modified zygolophe by the addition of two spiral arms located in the anterior part of the mantle cavity (fig. 1a in Zezina, 2015).

There are two different opinions about lophophore evolution in brachiopods. The hypotheses based on the ontogeny of extant species consider the schizolophe as ancestral for all other types (Emig, 1992; Williams *et al*., 1997). Recent findings from the Chengjiang Lager-

stätte, however, reveal that most brachiopods in the Early Cambrian possessed the simple spirolophous lophophore. Each arm of the simple spirolophe consists of one brachial axis that formed one or two spire whorls (e.g., Zhang *et al*., 2011a, b, 2020). This led to the supposition that the simple spirolophe is plesiomorphic in brachiopods (Carlson, 2007, 2016; Pakhnevich, 2017; Kuzmina *et al*., 2021). Since the spirolophe occurs in different groups of recent brachiopods, the simple spirolophe can give rise to the spirolophous lophophore in other brachiopods. Nonetheless, in ontogenesis the ptycholophe, zygolophe and plectolophe are formed from the schizolophous stage, and the modified zygolophe and modified spirolophe are formed from the taxolophous stage, but not from the simple spirolophe (Kuzmina, Temereva, 2019). The assumption was that these lophophore types evolved by paedomorphosis (Kuzmina *et al*., 2021).

Coelomic system of the lophophore

The first stages of lophophore ontogenesis, i.e. the taxolophe and trocholophe, contain only one small coelomic canal, which extends along the brachial axis and sends blind branches (tentacle canals) into each tentacle (Atkins, 1961b). The structure of the lophophore coelomic system in the trocholophe of adult brachiopods, i.e. *Gwynia* (see Swedmark, 1967) and *Goniobrochus* (see Emig, 1992), is unknown. The other lophophore types of recent brachiopods feature the additional large coelomic canals, which also extend along the brachial axis (Williams *et al*., 1997). The left and right small coelomic canals are connected to each other through the periesophageal coelom, which surrounds the esophagus (Kuzmina, Malakhov, 2011; Plandin, Temereva, 2021; Ratnovskaya, Kuzmina, 2022). In contrast, the left and right large canals are isolated from each other in the region near the mouth (fig. 3 in Kuzmina, Temereva, 2019). The small and large coelomic canals end blindly on the tips of the brachial axis. The small lophophoral canal contains a blood vessel and performs the circulatory function. The large canals function as a hydroskeleton.

In the zygolophe, plectolophe, modified zygolophe, and modified spirolophe, each lateral arm consists of two brachial axes, therefore each lateral arm must contain two small and

two large coelomic canals. In the modified zygolophe and spirolophe of discinids, two large coelomic canals in each lateral arm are located in a common extracellular matrix (Kuzmina, Temereva, 2019), whereas in the zygolophe and plectolophe of terebratulids, the two lateral coelomic canals of each lateral arm are fused (Atkins, 1959a,b,c, 1961a; Ratnovskaya, Kuzmina, 2022). Moreover, each lateral arm of the plectolophe has an additional coelomic canal, the brachial pouch, which is a protrusion of the perivisceral coelom (Atkins, 1959a,b, 1961a,b; Ratnovskaya, Kuzmina, 2022). Accordingly, in the zygolophe and plectolophe the lateral arms contain the most complicated coelomic system. In the zygolophe and plectolophe of terebratulids, the median arm also contains two brachial axes, but the two large canals are separated from each other (Atkins, 1959a,b,c, 1961a; Ratnovskaya, Kuzmina, 2022).

In linguliforms, the protocoel extends into the brachial fold, i.e. epistome (Temereva, 2017).

Lophophore musculature

In brachiopods, the lophophoral muscles adjoin the myoepithelial cells of the coelomic canals (fig. 1 in Kuzmina et al., 2018; Kuzmina, Temereva, 2022). The lophophore muscles of linguliform and craniiform brachiopods are better developed than that in rhynchonelliforms.

All brachiopods have a brachial longitudinal muscle that extends along the small coelomic canal (Pross, 1980; Robinson, 2014; Kuzmina et al., 2018). In linguliforms and craniiforms, this muscle is much expanded, and in discinids it entirely occupies the lumen of the small canal (Kuzmina, Temereva, 2019). In rhynchonelliforms, the brachial muscle is relatively small. The brachial muscles of brachiopods are lophophore retractors (Robinson, 2014). The small canals also contain the transverse muscle that forms the wall of the lophophoral blood vessel (Kuzmina et al., 2018). The periesophageal coelom that connects with small coelomic canals forms muscles surrounding the esophagus (Kuzmina et al., 2018; Plandin, Temereva, 2021). In addition, brachiopods have a group of longitudinal and transverse muscles of the large coelomic canal. The contraction of these muscles regulates the hydrostatic pressure of the coelomic fluid of the large coelomic canals (Kuzmina et al., 2018).

Brachiopod tentacles contain the frontal and abfrontal longitudinal muscles (Reed, Cloney, 1977; Kuzmina, Temereva, 2022). Only craniiforms lack the abfrontal tentacle muscles (Kuzmina, Temereva, 2022). In the most species, the frontal tentacle muscle is well-developed and forms the tentacle blood vessel, whereas the abfrontal muscle is very small. This organization may be a plesiomorphic feature of all brachiopods. The tentacle muscles are not connected with the brachial muscle (Kuzmina et al., 2018).

Lophophore nervous system and tentacle innervation

The brachiopod central nervous system includes two main elements: supraenteric and subenteric ganglia. These nervous centers are located in the thickened epithelium and cannot be called "true ganglia" (Kuzmina, Temereva, 2021). The two ganglia are connected by the circumenteric connectives (Bemmelen, 1883; Temereva, 2020b, 2022; Temereva, Kuzmina, 2021).

Only rhynchonelliform brachiopods possess a supraenteric ganglion that is located above the mouth and gives rise to the main nerves of the lophophore (Bemmelen, 1883; Williams et al., 1997; Temereva, Kuzmina, 2021). In adult craniiforms, dorsal thin neurites are located above the mouth and connect the left and right main brachial nerves; the circumenteric connectives emanate laterally from the subenteric ganglion and connect with the main brachial nerves, forming a ring around the esophagus (Temereva, 2022). The same structure of the main nervous system is known in adult lingulids (Linguliformea) (Blochmann, 1900). However, juveniles of *Novocrania anomala* (Craniiformea) with a trocholophe have a prominent supraenteric ganglion that consists of two lobes and the commissure between them. In ontogenesis (in juveniles with schizolophe), the commissure between the two lobes of the ganglion extend and become the main brachial nerve in adults (Temereva, 2020b, 2022). Juvenile *Glottidia pyramidata* (Linguliformea) with trocholophous lophophore swim in the water and have the prominent apical ganglion located in the medial tentacle (Hay-Schmidt, 1992; Santagata, 2011).

The subenteric ganglion of all brachiopods is located under the mouth and innervates the

mantle and muscles (Hancock, 1857; Bemmelen, 1883; Blochmann, 1892, 1900). In rhynchonelliforms (Temereva, Kuzmina, 2021), the subenteric ganglion also gives rise to the lower brachial nerves. In linguliforms (Blochmann, 1900) and craniiforms (Temereva, 2020b, 2022), the lower nerves connect with the circumenteric connectives. In juvenile *G. pyramidata*, the dorsal nerve connects the apical and subenteric ganglia, giving rise to the abfrontal nerves of the tentacles (Santagata, 2011), and is possibly homologous to the circumenteric connectives of other brachiopods.

Brachiopods have four brachial nerves that run along the brachial axis of the lophophore: main, lower, accessory, and second accessory nerves (fig. 12 in Temereva, Kuzmina, 2021). The main brachial nerves are always located in the epithelium at the base of the brachial folds. In rhynchonelliforms, the main nerves originate from the supraenteric ganglion (Bemmelen, 1883; Temereva. Kuzmina, 2017, 2021), whereas in adult craniiforms and linguliforms the main nerves originate from the nerves located above the mouth (Blochmann, 1900; Temereva, 2020b). In the ontogenesis of craniiforms, the main nerve originates from the commissure of the juvenile supraenteric ganglion (Temereva, 2020b). In linguliforms, the development of the main nerve is unknown. In all investigated brachiopods, main nerves give rise to the series of cross nerves that extend in the connective tissue and join with the accessory nerve in linguliforms (Temereva, Tzitrin, 2015) and craniiforms (Temereva, 2022), and with the second accessory nerve in rhynchonelliforms (Temereva, Kuzmina, 2017, 2021).

The lower brachial nerves are located in the epithelium and extend along the outer side of each brachial arm near the tentacle base. In rhynchonelliforms, the lower nerves start from the subenteric ganglion (Temereva, Kuzmina, 2017, 2021); in craniiforms and linguliforms, they start from the circumenteric connectives (Blochmann, 1900; Temereva, 2020b, 2022). In all brachiopods, lower nerves give rise to abfrontal nerves and latero-abfrontal nerves (the latter only in rhynchonelliforms) of outer tentacles (Temereva, Tzitrin, 2015; Temereva, Kuzmina, 2017, 2021; Temereva, 2020b, 2022). In the ontogenesis of craniiforms, the lower nerves appear in juveniles at the stage of the

schizolophous lophophore with double tentacle row, whereas the trocholophous lophophore lacks lower nerves and abfrontal nerves of oral tentacles (Temereva, 2020b). Swimming juveniles of linguliforms with a trocholophe exhibit the dorsal nerve ring that gives rise to abfrontal nerves of oral tentacles (Santagata, 2011); that nerve ring apparently corresponds to the circumenteric connectives of adults.

The accessory nerve is located in the epithelium of the brachial groove of all investigated brachiopods (exception: terebratulids) (Temereva, Tzitrin, 2015; Temereva, Kuzmina, 2017, 2021; Temereva, 2020b, 2022). The accessory nerves apparently correspond to the inner ventral nerve ring in swimming juveniles of linguliforms (Santagata, 2011). In juvenile and adult linguliforms, the accessory nerve gives rise to the frontal and lateral nerves of tentacles (Santagata, 2011; Temereva, Tzitrin, 2015). In juvenile and adult craniiforms, this nerve gives rise only to the frontal nerves of tentacles (Temereva, 2020b, 2022). In rhynchonellids, the accessory nerve does not connect to any other nerves (Temereva, Kuzmina, 2017).

The second accessory nerve is located in the epithelium between the bases of the tentacles and occurs in all brachiopod groups (exception: linguliforms) (Temereva, Tzitrin, 2015; Temereva, Kuzmina, 2017, 2021; Temereva, 2020b, 2022). The second accessory nerve gives rise to the lateral nerves of the inner and outer tentacles, the abfrontal nerves of the inner tentacles; in terebratulids, it also gives rise the frontal nerves of the outer tentacles. In the ontogenesis of craniiforms, the second accessory nerves appear in the schizolophous lophophore (Temereva, 2020b). Linguliforms have a row of separated groups of perikarya, i.e. intertentacular perykaria, at the base of the tentacles and give rises the abfrontal nerves of the inner tentacles (Temereva, Tzitrin, 2015); they apparently correspond to the second accessory nerve of other brachiopods (Temereva, Kuzmina, 2021).

Linguliform and craniiform brachiopods have nerves that extend in the epithelium on the outer part of lophophore and connect the main and lower nerves. They are represented by nerves of the lophophore base in craniiforms and by circular neurite bundles in linguliforms (Temereva, Tzitrin, 2015) and are apparently homolo-

gous to each other (Temereva, 2022). The craniiforms have additional main and additional lower nerves (Temereva, 2022). Such a complex lophophore innervation apparently correlates with the exceptional mobility of lophophore muscles in this brachiopod group.

Brachiopods have five tentacle nerves. Frontal nerves are located in the epithelium of the frontal ciliary zone. Lateral nerves are located in the epithelium that forms lateral ciliary zones. In inner tentacles, the lateral nerves are located near the abfrontal sides of the tentacles, and in some papers, they were referred to as latero-abfrontal nerves (Temereva, Tzitrin, 2015). In outer tentacles, the lateral nerves are located near the frontal side of the tentacles, and some papers refer to them as latero-frontal nerves (Temereva, Kuzmina, 2017). Abfrontal nerves are located in the epithelium of the abfrontal side of the tentacles. There are latero-abfrontal nerves in the epithelium of the outer tentacles in craniiform and rhynchonelliform brachiopods. These nerves are located in the epithelium of the abfrontal ciliary zone between the lateral and abfrontal nerves. The presence of the latero-abfrontal nerves in the outer tentacles reflects their wide abfrontal ciliary zone.

Comparative analysis

Homology of the morphology of the lophophore types

The lophophore types are distinguished by the form of the brachial axis. In all lophophorates, two main groups of lophophores can be distinguished: adhered and elevated.

In adhered lophophores, the brachial axis is fully adhered to the body wall.

1. The lophophore with a crescent-shaped brachial axis consists of about 3–8 tentacles, corresponds to the taxolophe of brachiopods, and is the first ontogenetic stage in the most lophophorates (Kuzmina *et al.*, 2021).

2. The lophophore with a circle brachial axis is the trocholophe of brachiopods, which contains about 12–30 tentacles (Yatsu, 1902; Atkins, 1960; Rowell, 1960; Kuzmina *et al.*, 2021). This type is apparently corresponds to the oval-shaped lophophore of *Ph. ovalis,* which consists of 20–24 tentacles, and with the circle-shaped or bell-shaped lophophore of some phylactolae-

mates and most of myolaemates, which bears 6–38 tentacles (Fig. 1a,d,e,h).

3. The schizolophous lophophore has a horseshoe-shaped brachial axis and consists of two loops. This type occurs in adults of some brachiopods and phoronids and is an ontogenetic stage of most lophophorates (Fig. 1b,c,g).

4. The spiral and helicoidal lophophores occur only in some phoronids. In these cases, the brachial axes forms two very long loops, each comprising a spiral, i.e. each spiral part consists of two brachial axes and the ends of brachial axis are located above the mouth. The brachial axis is completely adhered to the body wall (Fig. 1i).

5. The ptycholophous lophophore, in which the brachial axis is very bent and forms several loops, occurs only in brachiopods.

In elevated lophophores, the brachial axis detaches from the body wall and forms lophophoral arms.

1. The spirolophe occurs only in brachiopods. In this type, the ends of the brachial axis are located distally, far from the mouth (Fig. 1j–k).

2. The zygolophe consists of two arms, each containing two brachial axes. This type occurs in some terebratulids and may be compared with the horseshoe-shaped lophophore of phylactolaemates, in which two arms consisting of two brachial axes are separated from the body wall (Fig. 1f).

3. The plectolophe, modified zygolophe, and modified spirolophe occur only in brachiopods (see description above).

Because the attached horseshoe-shaped or schizolophous lophophore is present in all three phyla of the lophophorates, it was probably characteristic of the lophophorate ancestor (Fig. 1). The high diversity of lophophore types in brachiopods can be explained by the presence of the shell, the appearance of double rows of tentacles, and the position of the ends of the brachial axis, which are not connected with the oral region. In phoronids and bryozoans, in contrast, the ends of the brachial axis are always located near the mouth, and lophophore growth involves a lengthening of the loop, which consists of two brachial axes.

Homology of the lophophoral coelom

The coelomic system of the lophopore in different lophophorates consists of mesocoel.
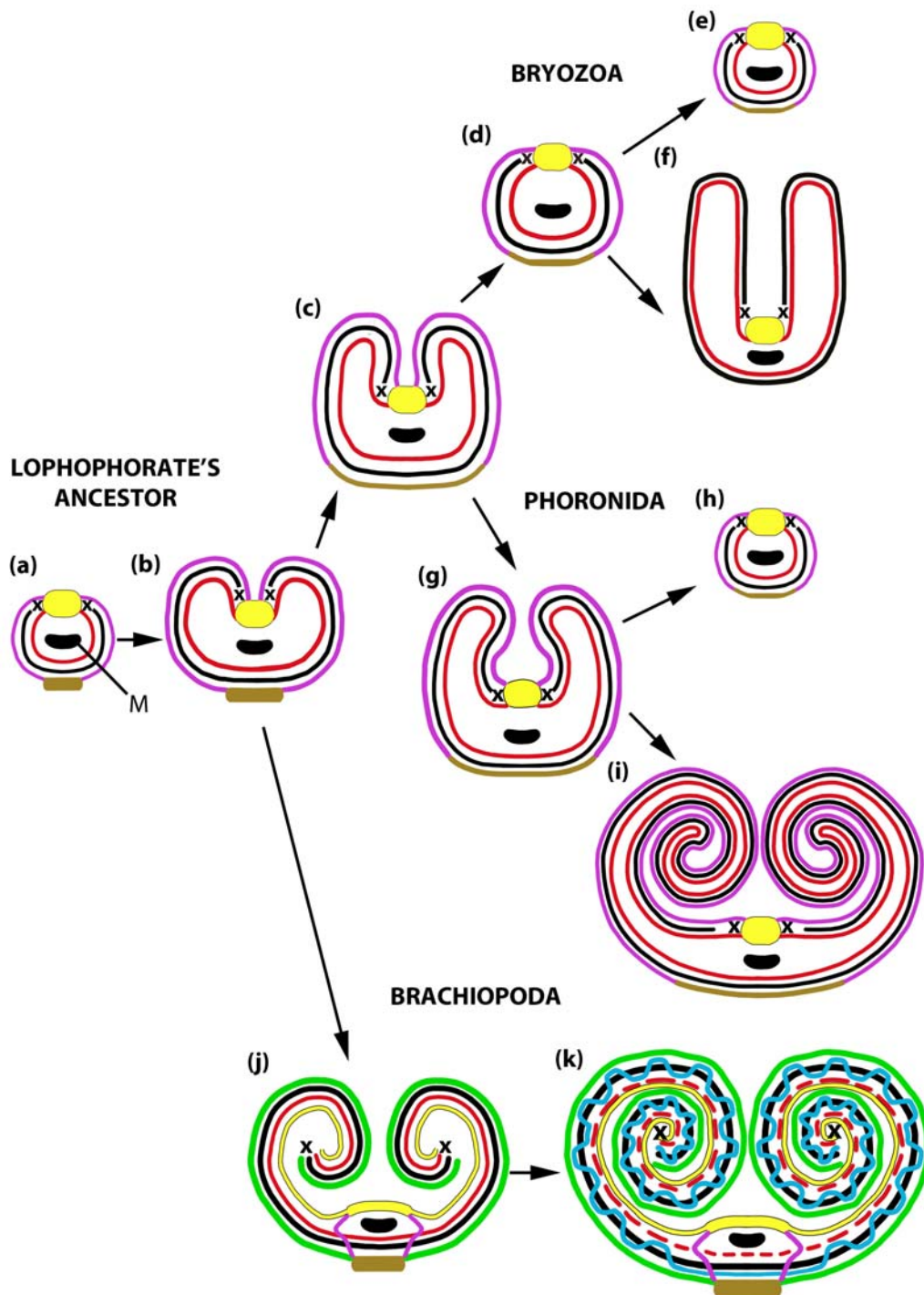
Fig. 1. Evolution of the lophophore in lophophorates. a — circle-shaped lophophore presented in ontogenesis of lophophorate ancestor; b — horseshoe-shaped lophophore of lophophorate ancestor; c — horseshoe-shaped lophophore of phoronid and bryozoan ancestor; d — bell-shaped lophophore of bryozoan ancestor; e — circle-shaped lophophore of myolaemates; f — elevated horseshoe-shaped lophophore of phylactolaemates; g — adhered horseshoe-shaped lophophore of phoronid ancestor; h — circle-shaped lophophore of *Phoronis ovalis*; i — spiral (or helicoidal) lophophore of phoronids; j — simple spirolophe of brachiopod ancestor; k — spirolophe of brachiopods (evolution of different forms of brachiopod lophophore is not specified). Color code: black — brachial axis; brown — subenteric ganglion; yellow — supraenteric ganglion (=the cerebral ganglion of bryozoans and the dorsal nerve plexus of phoronids) and main nerves of brachiopods; purple — circumenteric connectives (=outer nerve of bryozoans and tentacle nerve ring of phoronids); red — circumoral nerve ring (=minor nerve ring of phoronids and accessory nerves of brachiopods); green — lower nerves of brachiopods; blue — second accessory nerves of brachiopods. Abbreviations: M — mouth; X — end of brachial axis.

Рис. 1. Эволюция лофофора у лофофорат. a — лофофор в форме круга в онтогенезе предка лофофорат; b — подковообразный лофофор предка лофофорат; c — подковообразный лофофор предка форонид и мшанок; d — лофофор в форме колокола предка мшанок; e — лофофор миолемат в форме простого круга; f — приподнятый подковообразный лофофор филактолемат; g — приросший подковообразный лофофор предка форонид; h — лофофор *Phoronis ovalis* в форме круга; i — спиральный (или геликоидальный) лофофор форонид; j — простой спиролофный лофофор предка брахиопод; k — спиролофный лофофор брахиопод (эволюция разных форм лофофора у брахиопод не уточняется). Цветами обозначены: черный — брахиальная ось; коричневый — надглоточный ганглий; желтый — подглоточный ганглий (=церебральный ганглий мшанок и дорсальное нервное сплетение форонид) и главные нервы брахиопод; фиолетовый — окологлоточные коннективы (=наружный нерв мшанок и щупальцевое нервное кольцо форонид); красный — околоротовое нервное кольцо (=малое нервное кольцо форонид и добавочные нервы брахиопод); зеленый — нижние нервы брахиопод; синий — вторичные добавочные нервы брахиопод.
Обозначения: M — рот; X — конец брахиальной оси.

The protocoel occurs in phoronids, brachiopods, and phylactolaemates in the epistome. The mesocoel is represented by the lophophoral coelom in phoronids, the ring canal in bryozoans, and by small canals with periesophageal coelom and large canals in brachiopods. The mesocoel is isolated from the metacoel, i.e. the perivisceral or trunk coelom. The mesocoel extends along the brachial axis and is always interrupted at the ends of the brachial axis, i.e. the mesocoel never forms the closed ring. The lophophoral coelom, oral ring canal, and small canals with periesophageal coelom give rise to the tentacle coelomic canals that end blindly at their tips. In brachiopods, the mesocoel consists of the small and large coelomic canals, making it more complicated than in the remaining lophophorates. The presence of the large coelomic canals is an apormorphic feature of brachiopods. They perform the function of a hydrostatic skeleton, which is necessary for elongation of the brachial axis (Rudwick, 1970; Kuzmina *et al.*, 2021).

In some brachiopods and bryozoans, the metacoel also participates in the coelomic system of the lophophore. In the brachiopod order Terebratulida, the metacoel gives rise to the brachial pouches that extend along the lateral arms of plectolophe; they contain the digestive diverticula (Ratnovskayia, Kuzmina, 2022). In phylactolaemates, the forked canals with canals of the anal tentacles and the coelomic canals of the lateral tentacles are parts of the metacoel.

Thus, all lophophorates have a protocoel and mesocoel in the lophophore, making it a plesiomorphic feature of lophophorates. The presence of the metacoel in the lophophore in some brachiopods and bryozoans is an independently developed secondary state.

In phylactolaemates, the tentacles of the lophophore are supplied by coelomic cavities from three different structures: ring canal, forked canal, and visceral coelom (metacoel). Such an unusual connection of different tentacles with different coeloms leads to the suggestion of a specific evolution of the phylactolaemate lophophore in comparison with other bryozoans. This specificity leads to an unusual organization of the lophophore nervous system (Schwaha, Wanninger, 2015) and musculature in phylactolaemates.

Homology of the musculature

According to their location in respect to the mouth, anus, and tentacles, similar muscles can be recognized in the lophophore of different groups of lophophorates. Thus, the circular lophophoral muscle of phoronids corresponds to the circular muscle of the lophophore base in gymnolaemates, to the circular musculature of the pharynx in cyclostomates and phylactolaemates, and to the brachial muscle of brachiopods. The longitudinal muscles of the tentacular lamina in phoronids correspond to the abfrontal longitudinal muscles of the lophophoral base in myolaemates. Compared with other lophophorates, phylactolaemates exhibit a specific organization of the lophophore musculature. This specificity is expressed in the presence of muscles retractors of the lophophore arms, which connect with the frontal longitudinal muscles of tentacles. Only in the oral area is the musculature organized similarly to the lophophoral musculature of phoronids, brachiopods and the remaining bryozoans. Brachiopods have fewer lophophoral muscles than phoronids and bryozoans. This is presumably due to the reduction of tentacular lamina in the brachiopod lophophore. Abfrontal and frontal muscles of the tentacles are possibly homologous in all lophophorates.

Thus, the lophophorate ancestor might have had a circular lophophoral muscle that extends along the brachial axis and gives rise to the musculature of the tentacle lamina, which connects to the tentacle muscles. In brachiopods, the connection between the tentacle muscle and circular (brachial) muscle disappeared due to reduction of a tentacle lamina.

Homology of the nervous system

Based on the morphological results, the lophophore has several main nerves that are homologous among different lophophorates. The dorsal nerve plexus of phoronids is homologous to the cerebral ganglion of bryozoans and to the supraenteric ganglion and main brachial nerve of brachiopods (Kuzmina, Temereva, 2021). The minor nerve ring of phoronids is homologous to the accessory brachial nerve of brachiopods and to the circumoral nerve of bryozoans (Temereva, 2020b). The tentacular nerve ring of phoronids is possibly homologous to the outer nerve of ctenostome bryozoans and to the circumenteric connectives of brachiopods. In brachiopods, the lower and second accessory nerves do not have homologues because they arose independently.

The tentacles of all lophophorates are innervated by intraepithelial and peritoneal nerves. Typically, there are three groups of intraepithelial nerves: frontal, lateral, and abfrontal nerves. The frontal nerves of phoronids, bryozoans, and brachiopods are possibly homologous to each other and originate from the minor nerve ring, circumoral nerve, and the accessory nerve, respectively. Lateral nerves of brachiopods are associated with the lateral ciliated zones and probably correspond to the laterofrontal nerves of phoronids and bryozoans. The abfrontal nerves of phoronids and the bryozoan *F. hispida* are apparently also homologous and originate from the tentacle nerve ring and outer nerve ring, respectively. Only in brachiopod juveniles do the abfrontal tentacle nerves originate from the circumenteric connective (=the dorsal nerve) of swimming juvenile *G. pyramidata* (see Santagata, 2011). In the adult brachiopod lophophore, the lower nerve gives rise to the abfrontal tentacle nerves. Moreover, in brachiopods the second accessory nerve appears in craniiforms and rhynchonelliforms, while the accessory nerve is gradually reduced and disappears entirely in terebratulids (Temereva, Kuzmina, 2021). The presence of the second accessory nerve is an apomorphic feature of brachiopods that occurs due to the appearance of the double row of tentacles (Temereva, 2020b; Temereva, Kuzmina, 2021). In craniiforms and rhynchonelliforms, the second accessory nerve takes on the role of the accessory nerve and gives rise to the lateral nerves, and, in terebratulids, to the frontal nerves of tentacles as well.

The peritoneal nerves have been discovered in all lophophorates. These are neurites of large diameter; they have an electron-lucent cytoplasm and contain numerous longitudinal microtubules. Peritoneal nerves usually extend along the lateral sides of the tentacles. Only in some brachiopods do the peritoneal neurites exhibit acetylated alpha-tubulin-like immunoreactivity. The presence of such specific nerves may be regarded as a criterion of special quality in the frame of lophophore homology.

The assumption is therefore that the lophophorate ancestor had supraenteric and subenter-

ic ganglia, which were connected by circumenteric connectives and by a circumoral lophophoral nerve (Fig. 1). The connectives gave rise to the abfrontal tentacle nerves; the circumoral nerves gave rise to the frontal and lateral tentacle nerves.

Evolution of the lophophore

The transformation of the lophophore nervous system correlates with the evolution of the lophophore. According to the most common view, this evolution in different lophophorates occurred from a simple to a complex-shaped type (Emig, 1976; Kuzmina, Temereva, 2019). There is, however, an alternative opinion concerning the evolution of the lophophore in phoronids and brachiopods. Thus, new data on the lophophore muscle organization suggest two evolutionary pathways of the phoronid lophophore: through the simplification from the horseshoe-shaped to the oval-shaped; and through the complication from the simple horseshoe-shaped type to the spiral and helicoidal type (Temereva, 2019a). The same pathway has been suggested for brachiopods based on the deep analysis of paleontological and morphological data: the simple spirolophe was regarded as a plesiomorphic feature, which gave rise to more complex types and more simple forms by paedomorphosis (Kuzmina *et al*., 2021). Concerning the evolution of the bryozoan lophophore, two different ideas have also been advanced: the evolution from simple to complex (Schwaha, Wanninger, 2015) or from complex to simple (Temereva, Kosevich, 2016). Both notions are discussed in the literature (Schwaha, 2020; Isaeva *et al*., 2021; Temereva *et al*., 2022).

According to the morphological data, the lophophorate ancestor probably had an adhered horseshoe-shaped or schizolophous lophophore. In ontogenesis, the ancestor had passed the stages of a taxolophous and circle-shaped lophophore (Zhang *et al*., 2004). The brachial axis of the ancestral lophophore probably had a single row of tentacles, a protocoel in the epistome, and the ring coelomic canal (mesocoel), the latter giving rise to the tentacle canals. The ring coelomic canal contained the circular lophophoral muscle, and the tentacle canals contained the frontal and abfrontal muscles. This lophophore was innervated by a supraenteric and subenteric ganglion, which were connected by circumenteric connectives and a circumoral nerve. The connectives gave rise to the abfrontal tentacle nerves, and the circumoral nerve gave rise to the frontal and lateral tentacle nerves (Fig. 1). In the phoronid and bryozoan ancestor, the subenteric ganglion was reduced; the connectives lengthened and surrounded the outer surface of the tentacles. The ends of the brachial axis were retained on the oral region, and the outer lophophoral nerve (=circumenteric connectives) was connected with the cerebral ganglion (=supraenteric ganglion). In this case, the further growth of the lophophore was possible only by the elongation of the loop, while the ends of the brachial axis were located above the mouth.

The bryozoan ancestor presumably had a bell-shaped lophophore, such as in *F. hispida* (Temereva *et al*., 2022). This type showed two evolutionary pathways: (i) miniaturization in all myolaemates and (ii) complication in phylactolaemates. The elevated horseshoe-shaped lophophore of phylactolaemates developed by lengthening of the brachial axis. The formation of a large horseshoe-shaped lophophore *de novo* led to modifications of the lophophore organ systems in phylactolaemates (see above).

The phoronid ancestor presumably had the horseshoe-shaped lophophore, which was adhered to the body wall (Temereva, 2019). *Ph. ovalis*, with its circle-shaped lophophore, is possibly a paedomorphic species. The spiral and helicoidal lophophores of phoronids were developed by lengthening of the brachial axis (Fig. 1).

During the evolution of the brachiopod lophophore, the brachial axis lengthened due to an increase in the distance between its ends and the oral region. This led to the simple spirolophous lophophore (Fig. 1). In this case, the supraenteric ganglion formed the brachial main nerve, the circumenteric connectives were retained but shortened, the accessory nerve (=circumoral nerve) elongated, and the lower nerve arose. The appearance of a double row of tentacles in brachiopods led to the formation of the second accessory nerve and gradual reduction of the accessory nerve. The elongation of the brachial axis in brachiopods also led to the formation of the large coelomic canals, which create the hydrostatic pressure. In rhynchonelliforms, cal-

careous skeletal structures support the lophophore and its long brachial axis. As noted above, the brachiopod lophophore is the most diverse among the lophophorates. The evolution of different forms of brachiopod lophophore was recently described (Kuzmina *et al*., 2021).

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