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Phoronida—A small clade with a big role in understanding the evolution of lophophorates

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Abstract

Phoronids, together with brachiopods and bryozoans, form the animal clade Lophophorata. Modern lophophorates are quite diverse—some can biomineralize while others are soft-bodied, they could be either solitary or colonial, and they develop through various eccentric larval stages that undergo different types of metamorphoses. The diversity of this clade is further enriched by numerous extinct fossil lineages with their own distinct body plans and life histories. In this review, I discuss how data on phoronid development, genetics, and morphology can inform our understanding of lophophorate evolution. The actinotrocha larvae of phoronids is a well documented example of intercalation of the new larval body plan, which can be used to study how new life stages emerge in animals with biphasic life cycle. The genomic and embryonic data from phoronids, in concert with studies of the fossil lophophorates, allow the more precise reconstruction of the evolution of lophophorate biomineralization. Finally, the regenerative and asexual abilities of phoronids can shed new light on the evolution of coloniality in lophophorates. As evident from those examples, Phoronida occupies a central role in the discussion of the evolution of lophophorate body plans and life histories.

KEYWORDS

biomineralization, biphasic lifecycle, regeneration, Spiralia, tommotiida

1 | INTRODUCTION

Phoronida is a clade of exclusively marine, sessile worms, that occur worldwide and, in some environments, can form relatively abundant and numerous aggregations (Figure 1a; e.g., Emig, 1982; Temereva & Neklyudov, 2018). In terms of species number, they are among the least speciose of the high-rank animal clades—for instance, World Register of Marine Species recognizes only 13 valid species of phoronids (WoRMS, 2022). However, the exact number of phoronid species still remains controversial among taxonomists, as some of them probably represent complexes and new species of phoronids are still reported, based on both morphological and molecular data (Collin et al., 2019; Hirose et al., 2014; Osipova & Temereva, 2021; Santagata & Cohen, 2009; Temereva & Chichvarkhin, 2017; Temereva & Neklyudov, 2018; Temereva et al., 2016).

The poor taxonomical diversity of phoronids is also reflected in their comparatively limited morphological

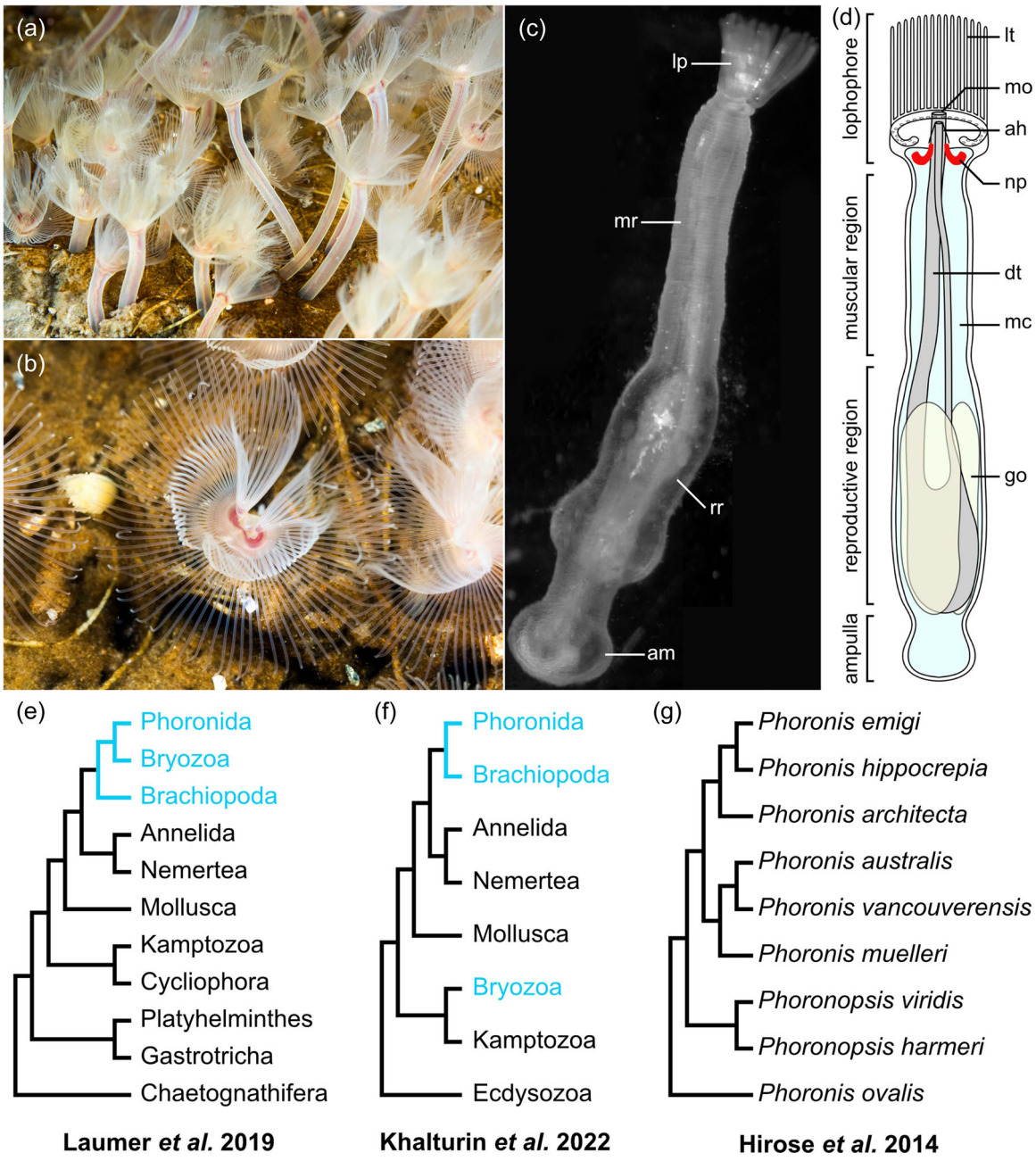

FIGURE 1 General morphology and phylogeny of phoronids. (a). An aggregation of *Phoronopsis harmeri* (Pixell, 1912) from Amur Bay, Sea of Japan. (b) Details of the lophophore of the same species. (c) Juvenile of *Phoronopsis viridis* (Hilton, 1930) from Coos Bay (United States), showing the division of the body into four major regions. (d) General morphology of the adult phoronid. (e, f) Topology of the spiralian phylogeny based on phylogenomic analysis by Laumer et al. (2019) (e) and Khalturin et al. (2022) (f). Note that three lophophorate lineages form a clade in (e), but are polyphyletic in (f) (in blue). (g) Internal phylogeny of phoronids based on the analysis of combined *COI* + *18S* + *28S* sequences by Hirose et al. (2014). Photographs on panels (a), (b), and (c) courtesy of Elena Temereva. *ah*, anal hill; *am*, posterior ampulla; *dt*, digestive tract; *go*, gonads; *lp*, lophophore; *lt*, tentacle of the lophophore; *mc*, metacoel; *mo*, mouth opening; *mr*, muscular region of the trunk; *np*, metanephridium; *rr*, reproductive region of the trunk. [Color figure can be viewed at wileyonlinelibrary.com]

diversity (e.g., Hermann, 1997). Although the arrangement of particular organs and systems can differ between species, they all follow quite a uniform overall body plan. The adult phoronid body is divided into a cylindrical trunk, which on one end is adorned with a crown of ciliated tentacles—the so-called lophophore (Figure 1b) used for food capture and respiration—and on the opposite side, it bulges into the posterior anchoring ampulla (Figure 1c,d). The U-shaped gut extends from the mouth—which opens in between tentacles of the

lophophore, loops through the trunk, and ends just outside of the lophophore on the inconspicuous anal hill located on the dorsal side of the animal (Figure 1d). Therefore, the lophophore can be divided into the oral and anal sides. The shape and arrangement of the lophophore are one of the most variable and taxonomically important features of the phoronid body plan (e.g., Emig, 1982; Temereva & Kuzmina, 2022; Temereva et al., 2016; Temereva, 2019a, 2020). In some of the species, the bases of tentacles form almost an oval field, while in others the lophophore is horseshoe-shaped, extending into branches that bend towards the anal side (Figure 1b). Those anally-bent branches can form several spiral or helicoidal coils in the species with the most complex lophophore morphology. It is worth noting that species with the spirally coiled lophophore develop through the juvenile stages with consecutive oval and horseshoe-shaped lophophores (Temereva, 2020).

Phoronids are coelomate animals and their coelom is divided into three compartments—the vestigial protocoel that occupies a small flap of tissue covering the mouth opening (the so-called epistome), mesocoel that forms the coelomic cavity of the lophophoral tentacles, and the metacoel that represents major coelomic cavity occupying most of the trunk (Emig, 1973b, 1982; Hermann, 1997; Temereva & Kuzmina, 2022; Temereva & Malakhov, 2011, 2015). However, it remains debatable whether protocoel is a coelomic cavity at all (Bartolomaeus, 2001). The blood vessels of the metacoel are lined with podocyte-like cells (Storch & Herrmann, 1978) while near the base of the lophophore, this cavity connects to the outside by a pair of ciliated metanephridia that develops from the larval protonephridia (Figure 1d; Bartolomaeus, 1989; Gąsiorowski et al., 2021; Temereva & Malakhov, 2006).

Historically, based on the presence of the lophophore and tripartite coelom, phoronids were unified with Brachiopods and Bryozoans into the clade Lophophorata (Emig, 1977b, 1982, 1984; Hyman, 1959; Temereva & Kuzmina, 2022). Several of the characteristics of the putative lophophorates are superficially somehow intermediate between proto- and deuterostomes and because of that in the age of morphology-based phylogenies, lophophorates were often considered as an evolutionary link between those two major bilaterian groups (e.g., Ax, 1989; Backeljau et al., 1993; Emig, 1982, 1984; Nielsen et al., 1996). However, with the advent of molecular phylogenetics, it turned out that all three of those clades are nested deeply within Protostomia, forming a clade Lophotrochozoa together with e.g. Annelids and Mollusks (Field et al., 1988; Halanych et al., 1995; Halanych, 1996).

The exact relationship between phoronids and other lophophorates remains controversial up to this day (Figure 1e,f). The early molecular phylogenies were placing phoronids as a shell-less in-group of Brachiopoda—e.g. Cohen proposed that Phoronida should be treated as a subphylum Phoroniformea within brachiopods (Cohen & Weydmann, 2005; Cohen, 2000, 2013; Santagata & Cohen, 2009). However, later transcriptome-based analyses were rather favoring a sister relation of phoronids and bryozoans (Figure 1e; Laumer et al., 2015, 2019; Marlétaz et al., 2019; Nesnidal et al., 2013; Zverkov et al., 2019), with which they seem to share some potential morphological and genetic synapomorphies (Temereva, 2017b, 2019b; Wernström et al., 2022), while brachiopods were retrieved as the more distant branch within monophyletic Lophophorata. Recently, the increased sampling of the bryozoan transcriptomes once again challenged the monophyly of Lophophorates resulting in the topologies in which phoronids and brachiopods form sister groups, while bryozoans, together with kamptozoans, form clade Polyzoa only distantly related to the other lophophorates (Figure 1f; Drábková et al., 2022; Khalturin et al., 2022). As for today, the close relatedness of phoronids and brachiopods seems well-established (Drábková et al., 2022; Dunn et al., 2008; Khalturin et al., 2022; Kocot et al., 2017; Laumer et al., 2015, 2019; Luo et al., 2018; Marlétaz et al., 2019; Zverkov et al., 2019), however, their relation to bryozoans remains disputable. Therefore, the immediate sister group of phoronids is still effectively unknown.

In contrast to the extensive research on the position of phoronids within animal phylogeny, the studies on their internal phylogeny remain sparse and limited to single-gene-based phylogenies (Hirose et al., 2014; Santagata & Cohen, 2009). An important, recurring similarity between otherwise conflicting topologies of the internal phoronid phylogenies, is that *Phoronis ovalis* Wright, 1856, a semi-colonial phoronid with a simple, oval lophophore and minute body size, represents a sister group to all the remaining phoronid species (Figure 1g).

Despite being a small and morphologically relatively uniform clade, phoronids recently have been experiencing increased attention in the field of evolutionary developmental biology. During the last decade, the embryological and genetic data from phoronids have been used in the investigation of the evolution of numerous developmental, physiological, and morphological traits such as cleavage pattern (Pennerstorfer & Scholtz, 2012; Santagata, 2015), mesoderm formation (Andrikou et al., 2019; Andrikou & Hejnol, 2021), biomineralization (Luo et al., 2018; Wernström et al., 2022), ion channels (Martí-Solans et al., 2023), neuropeptides (Thiel et al., 2021), spiralian larval types (Gąsiorowski & Hejnol, 2020; Temereva, 2017a) and ciliary bands (Wu et al., 2020), as well as bilaterian

excretory organs (Gąsiorowski et al., 2021), nerve cords (Temereva, 2012; Temereva & Wanninger, 2012), and heads (Gąsiorowski & Hejnol, 2020; Luo et al., 2018). In the following sections, by reviewing historical and recent findings on the evolution of phoronid larvae, biomineralization, and regeneration, I will demonstrate why phoronids are important for understanding the evolution of lophophorate body plans and specify which of the questions about their evolution have already been confidently resolved and which still await investigation with the modern biological approaches.

2 | ACQUISITION OF THE NEW LARVAL BODY PLAN AND EVOLUTION OF PHORONID LIFE CYCLE

As with many sessile marine invertebrates, phoronids develop through a distinctive larval stage that allows the dispersal and colonization of new habitats. With a single exception of *Phoronis ovalis*, all known phoronid species possess a characteristic feeding larva, the so-called actinotrocha (Figure 2). Due to the distinctive and very complex morphology, the actinotrocha larvae were, upon their discovery in 1846 (Müller, 1846), considered adult planktonic animals from the family Actinotrochidae (hence *Actinotrocha* is also a younger synonym of *Phoronis*; WoRMS, 2022) and only in 1866, they were recognized as the larval phoronids (Kovalevsky, 1866). Although often neglected in the planktonic samples, actinotrochas can reach high densities in the water column (comparable to those of the vertebrate or echinoderm larvae) and may play important roles in the planktonic food webs (Collin et al., 2019; McGuinness et al., 2022; Omelyanenko & Kulikova, 2011).

An extensive body of literature provides details on the morphological development of actinotrocha and its organ systems in various species of phoronids. In general, the first larval stage (sometimes referred to as preactinotrocha) is a small planktotrophic organism (Figure 2a) composed of a prominent oral hood and an inconspicuous trunk, the latter harboring a short, straight gut that opens through the anus surrounded by the locomotory, ciliated telotroch (e.g., Andrikou et al., 2019; Emig, 1977a, 1982; Rattenbury, 1954; Santagata, 2002, 2015; Silén, 1954; Temereva & Malakhov, 2007, 2012). Over time, a wreath of ciliated feeding tentacles develops below the oral hood, leading to the formation of the typical actinotrochal body plan (Figure 2b). As the larval development progress, the trunk expands and new internal structures form, such as excretory organs (Bartolomaeus, 1989; Emig, 1982; Gąsiorowski et al., 2021; Hay-Schmidt, 1987; Temereva & Malakhov, 2006), compartments of the digestive system (Emig, 1977a; Temereva, 2010), coelomic cavities (Bartolomaeus, 2001; Emig, 1977a), and blood system (Bartolomaeus, 2001; Temereva & Malakhov, 2000, 2012), leading to the establishment of the late larva which may spend weeks in the plankton before metamorphosis. An initially small ectodermal pocket, the so-called metasomal sac, can be found on the ventral side of mid-stage actinotrocha (Figure 2b), and in advanced larvae, it reaches a considerable length, filling most of the larval internals (Emig, 1982; Gąsiorowski & Hejnol, 2020; Silén, 1954; Temereva & Malakhov, 2015; Temereva & Tsitrin, 2013; Temereva, 2010). This structure plays a crucial role during a rapid metamorphosis of the larva (Figure 2c)—during settlement, the internal pressure of the contracting larval muscles everts the metasomal sac, which becomes the rudiment of the adult trunk (Emig, 1982; Santagata, 2002; Silén, 1954; Temereva, 2010; Temereva & Malakhov, 2015; Temereva & Tsitrin, 2013). The gut, which is attached to the wall of the metasomal sac, is dragged into the newly everted trunk, leading to the formation of the U-shaped intestine typical of adult phoronids (Temereva, 2010; Temereva & Malakhov, 2015; Temereva & Tsitrin, 2013). Hence, the antero-posterior axis of the larvae is not identical to the oral-aboral axis of the adult worm. Instead, the oral-anal axis of the adult phoronid corresponds to the dorsal side of the larva, while the entire trunk represents a ventral outgrowth of the larval body (Figure 2c). The dramatic rearrangement of the body axes is accompanied by substantial losses of the larval tissues (Santagata, 2002; Temereva & Malakhov, 2015). For instance, most of the oral hood and trunk epidermis is lost during metamorphosis. Although in some species the larval tentacles are also shed at this stage, in others, they form the primary tentacles of the juvenile and hence correspond to the adult lophophore (Santagata, 2002, 2015; Temereva & Malakhov, 2015; Temereva & Tsitrin, 2013).

Recently, considerable progress has also been made in the understanding of the molecular underpinnings of actinotrochal development. It has been shown that while patterning of the germ-layers (especially mesoderm) and developing excretory organs is shared between phoronids and brachiopods (Andrikou et al., 2019; Andrikou & Hejnol, 2021; Gąsiorowski et al., 2021), both groups differ substantially when it comes to the expression of the Hox genes during their embryonic and larval development (Gąsiorowski & Hejnol, 2020). In brachiopods, the Hox genes are already expressed in the early embryonic stages and most of them show continuous expression from embryos, throughout larval development, up to the postmetamorphic juveniles in the similar domains that span most of the larval and adult bodies (Gąsiorowski & Hejnol, 2019; Schiemann et al., 2017). In contrast, Hox

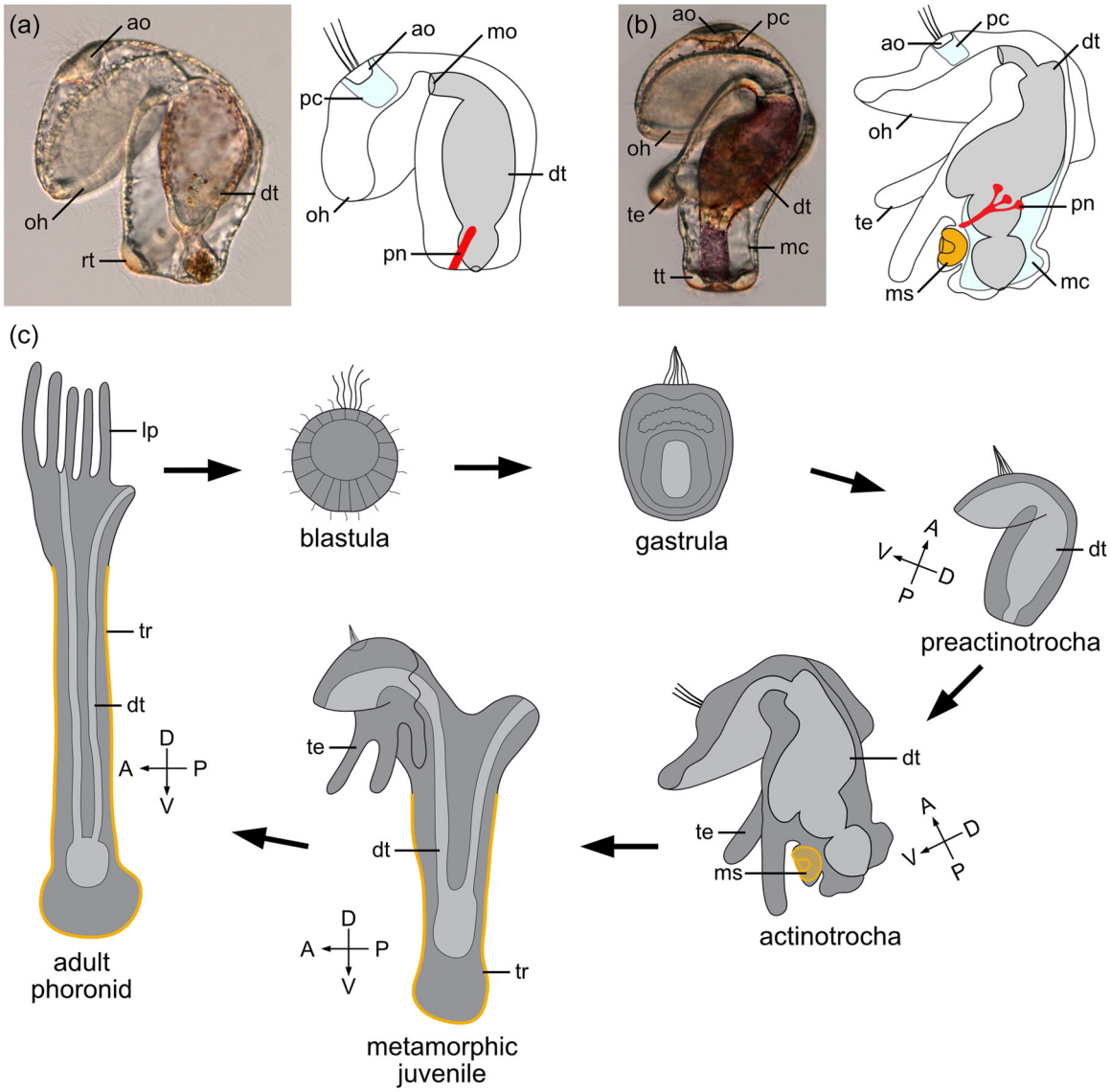

FIGURE 2 Phoronid development. Morphology of preactinotrocha (a) and midstage actinotrocha (b) of *Phoronopsis viridis*, from Coos Bay (United States). (c) Life cycle of a phoronid. The trunk of the adult animal develops from the ventrally located metasomal sac (both in orange). As a result, the longitudinal axis of the adult corresponds to the dorso-ventral axis of the larva. Photographs on panels (a) and (b) courtesy of Elena Temereva. *ao*, apical organ; *dt*, digestive tract; *lp*, lophophore; *mc*, metacoel; *mo*, mouth opening; *ms*, metasomal sac; *oh*, oral hood; *pc*, protocoel; *pn*, larval protonephridium; *rt*, rudiment of the larval tentacle; *te*, larval tentacle; *tr*, trunk; *tt*, telotroch; A, anterior; D, dorsal; P, posterior; V, ventral. [Color figure can be viewed at wileyonlinelibrary.com]

genes are not expressed in the phoronid embryo and their expression is activated only when most of the actinotrocha is already formed (Figure 3a,b; Gąsiorowski & Hejnol, 2020). Additionally, the Hox genes are predominantly expressed in the developing metasomal sac and some other posterior larval structures, while most of the actinotrochal body represents a Hox-free territory (Figure 3b). Interestingly, despite lack of temporally or spatially staggered expression, the Hox genes of phoronids form a well-organized cluster in their genome (Figure 3c; Luo et al., 2018). On the other hand, several transcription factors with a conserved head-patterning function are expressed throughout the body of the developing actinotrocha—in the oral hood, apical organ, protocoel, digestive system, and developing larval tentacles (Figure 3a,b; Andrikou et al., 2019; Gąsiorowski & Hejnol, 2020).

The lophophore is likely a homolog of the bilaterian head (Gąsiorowski & Hejnol, 2020; Luo et al., 2018) and, therefore, the larval tentacles of the actinotrocha can be used as a landmark of the head region in the larval body plan. In many Bilaterians, the Hox genes are not expressed in the head and are only involved in the patterning of the trunk region, which is considered an

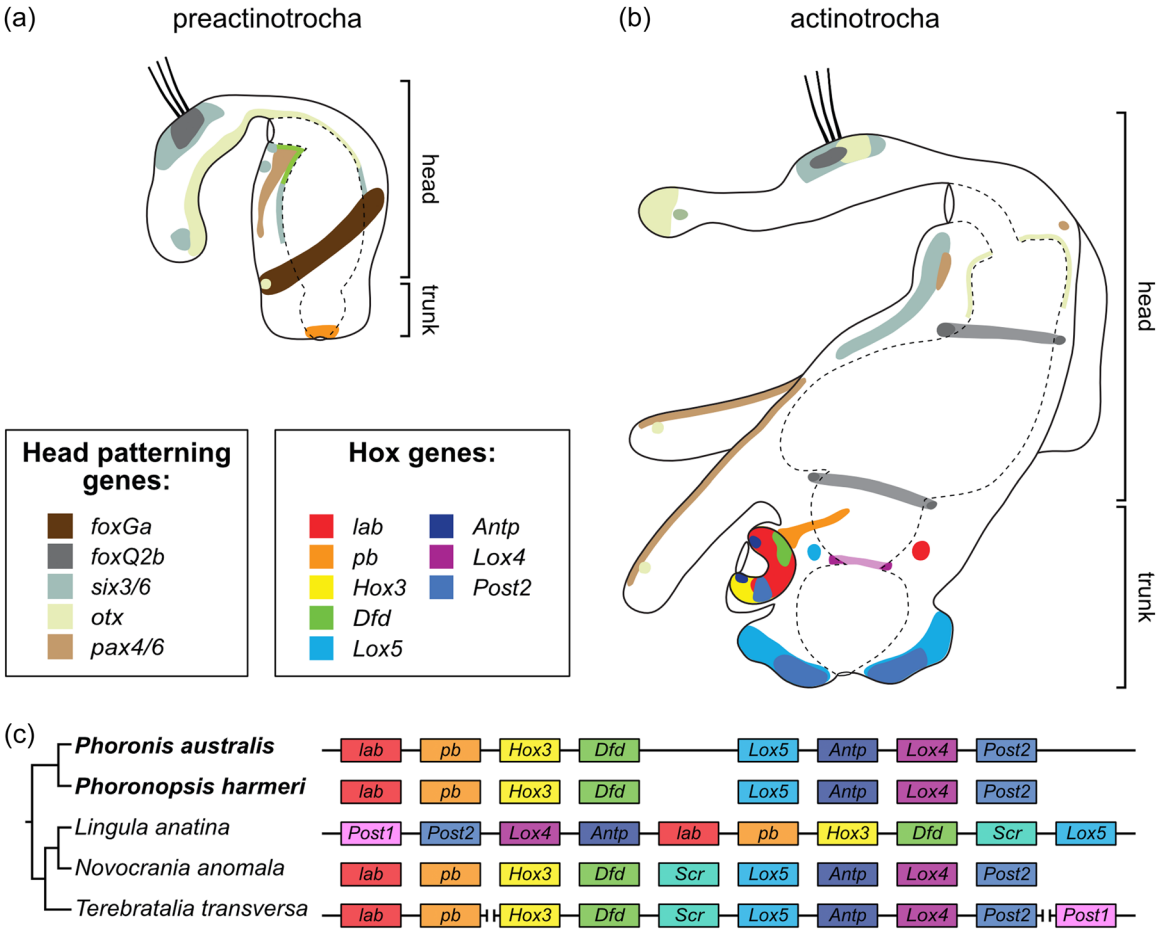

FIGURE 3 Expression of the head patterning and Hox genes in preactintrocha (a) and actinotrocha (b) of *Phoronopsis harmeri*, based on Gąsiorowski and Hejnol (2020). Note that actinotrocha represents a larva mostly composed of prospective head tissues. (c) Hox gene complement and genomic arrangement in phoronids (in bold) and brachiopods, based on Gąsiorowski and Hejnol (2020); Luo et al. (2018); and Schiemann et al. (2017). Note, that phoronids lost genes *Scr* and *Post1*, which are expressed in the shell- and chaetae-forming cells of brachiopods. For *P. harmeri* and *Novocrania anomala* only the Hox complement is available (data on cluster organization are missing). The vertical bars indicate the boundaries of the particular scaffolds of the split Hox cluster in *Terebratalia transversa*. [Color figure can be viewed at wileyonlinelibrary.com]

ancestral bilaterian feature (e.g., Gąsiorowski & Hejnol, 2020; Gonzalez et al., 2017; Hiebert & Maslakova, 2015; Luo et al., 2018; Martín-Zamora et al., 2023; Steinmetz et al., 2010). Taking those two circumstances into account, it seems that most of the actinotrochal body should be considered as an elaboration of the head-derived structures (Figure 3). This puts actinotrocha into the category of the so-called head larvae, which have been also reported in some hemichordates, arthropods, and annelids (Gonzalez et al., 2017; Martín-Zamora et al., 2023; Strathmann, 2020). Those larvae are supposedly secondary in nature and evolved multiple times in different bilaterian groups (Martín-Zamora et al., 2023; Strathmann, 2020) either by precocious development of the head structures or by delayed development of the trunk region (Gąsiorowski & Hejnol, 2020; Gonzalez et al., 2017; Martín-Zamora et al., 2023). The fact that *Phoronis ovalis*, the sister species to all the remaining phoronids (Figure 1g), develops without the actinotrocha stage (Silén, 1954), indicates that the actinotrocha is a later evolutionary innovation that was intercalated into the phoronid life cycle after the body plan of adult phoronids was already established (Gąsiorowski & Hejnol, 2020).

Even though the interpretation of actinotrocha as a secondary head larva is well-established, there is still a missing piece in the puzzle of the phoronid larval evolution—the nature of the bizarre larval stage present in *P. ovalis*. This larva has been described by Silén in 1954 as a turbellarian-like, actively creeping, lecithotrophic worm, that lives freely for about a week before settling and undergoing an obscure metamorphosis (Silén, 1954). Up to this date, the internal morphology of this larva and the details of its metamorphosis have not been studied. It

remains unknown whether it represents an extreme modification of the actinotrocha (e.g., as a consequence of a non-feeding lifestyle), an ancient larval type preserved in *P. ovalis*, or a new larval type that evolved independently in the lineage of *P. ovalis*.

3 | EVOLUTION OF BIOMINERALIZATION AND CHAETAE IN LOPHOPHORATA—A PHORONID PERSPECTIVE

Many representatives of the clade Lophotrochozoa exhibit some degree of biomineralization—e.g., brachiopods and most of the mollusks possess hard external shells, while sessile annelids and bryozoans often dwell in mineralized tubes or cells. Moreover, several extinct lophotrochozoans also show the presence of biomineralized skeletons with various degrees of structural integration—e.g., Machaeridia (considered as extinct stem-group annelids), *Cotyledion* (a stem-group Kamptozoan), tommotiids (a probably paraphyletic assemblage of stem and crown group lophophorates) and hyoliths (an extinct clade with possible affinity to lophophorates) were all equipped with either sclerites that build the external armor or bona fide shells (e.g., Guo et al., 2022; Li et al., 2019; Moysiuk et al., 2017; Parry et al., 2014, 2019; Skovsted et al., 2008, 2011; Sun et al., 2018; Taylor et al., 2010; Vinther et al., 2008; Zhang et al., 2013). Based on the phylogenetic distribution of biomineralizing capacities and the existence of extinct biomineralized close relatives of contemporary soft-bodied taxa, some authors suggested that biomineralization was already present in the common lophotrochozoan ancestor (e.g., Conway Morris & Peel, 1995; Li et al., 2019; Taylor et al., 2010; Zhang et al., 2013). This idea recently got support from developmental and gene-expression studies that showed the presence of an ancestral biomineralizing toolkit, shared by mollusks and brachiopods (Jackson et al., 2015; Luo et al., 2015; Wernström et al., 2022).

Adult phoronids are exclusively sessile, and although they do not form external hard skeletons, they often dwell in multilayered organic tubes secreted by the trunk epidermis (Emig, 1982; Fernandez et al., 1991; Pourreau, 1979; Temereva et al., 2001, 2020). In many species, the tubes can be secondarily incrusted with sediment particles—e.g., sand grains or detritus (Emig, 1982; Temereva et al., 2020). If indeed the last common ancestor of Lophotrochozoa had some sort of external hard skeleton, it would imply that phoronids secondarily lost the ability for biomineralization. Based on the extensive fossil record of stem-group lophophorates and comparative genetic data we can now more confidently reconstruct events leading to this alleged reduction.

For obvious reasons, the fossil record is biased toward organisms with hard structures, and therefore the fossil record of phoronids is very poor when compared to that of brachiopods or bryozoans (Taylor et al., 2010). There are some fossilized structures interpreted as preserved borrowings of phoronid-like animals (Emig, 2010; Taylor et al., 2010), however, they seem to be identical to the borrowings of modern-day phoronids (Emig, 2010) and do not tell us anything about the steps leading to the establishment of the phoronid body plan. Instead, the crucial fossil groups that can be used to infer the evolution of phoronid lineage are tommoitiids.

Tommotiida was originally described based on isolated phosphate microfossils from early Cambrian, which can be found worldwide and sometimes in large quantities (e.g., Bengston, 1970; Guo et al., 2022; Holmer et al., 2008; Skovsted et al., 2008, 2011; Taylor et al., 2010). Initially, they were interpreted as possibly related to machaeridians (Bengston, 1970) or halkieriids (Ushatinskaya, 2002), however, with the more detailed studies of *Micrina* and *Mickwitzia*, which show properties intermediate between typical tommotiids and brachiopods (Balthasar, 2004; Holmer et al., 2008; Skovsted & Holmer, 2003), they were reinterpreted as closely related to lophophorates. Most of the tommotiids are known from isolated sclerites and the in vivo arrangement of those elements or the morphology of the animals that bear them remained mysterious for decades. The discovery of articulated fossils of *Eccentrotheca* (Skovsted et al., 2008, 2011) and reanalysis of *Micrina* (Holmer et al., 2008) indicated that although the sclerites of particular tommotiids can look superficially similar, their arrangement can be quite different—in *Eccentroteca* multiple sclerites build an external conical tube (Figure 4), while in *Micrina* there are only two sclerites that form a bivalved, shell-like structure. This led to the assumption that despite similarities in the microstructure, tommotiids do not form a monophyletic group but instead, they represent a paraphyletic assemblage of stem and crown group lophophorates—one group of tommotiids, the so-called camenellids, represent sister-group to crown-group lophophorates, *Eccentroteca* is a stem group phoronid, while tannuolinids (including *Micrina*), are more closely related to the brachiopod lineage (Skovsted et al., 2008, 2011; Taylor et al., 2010). The close affinity of *Eccentroteca* and phoronids was proposed on the basis of the common presence of an organic, tube-like structure that in *Eccentroteca* was additionally reinforced with the mineralized sclerites.

The recent discovery of juvenile camenellids (Steiner et al., 2021) and adult animals with the preserved soft

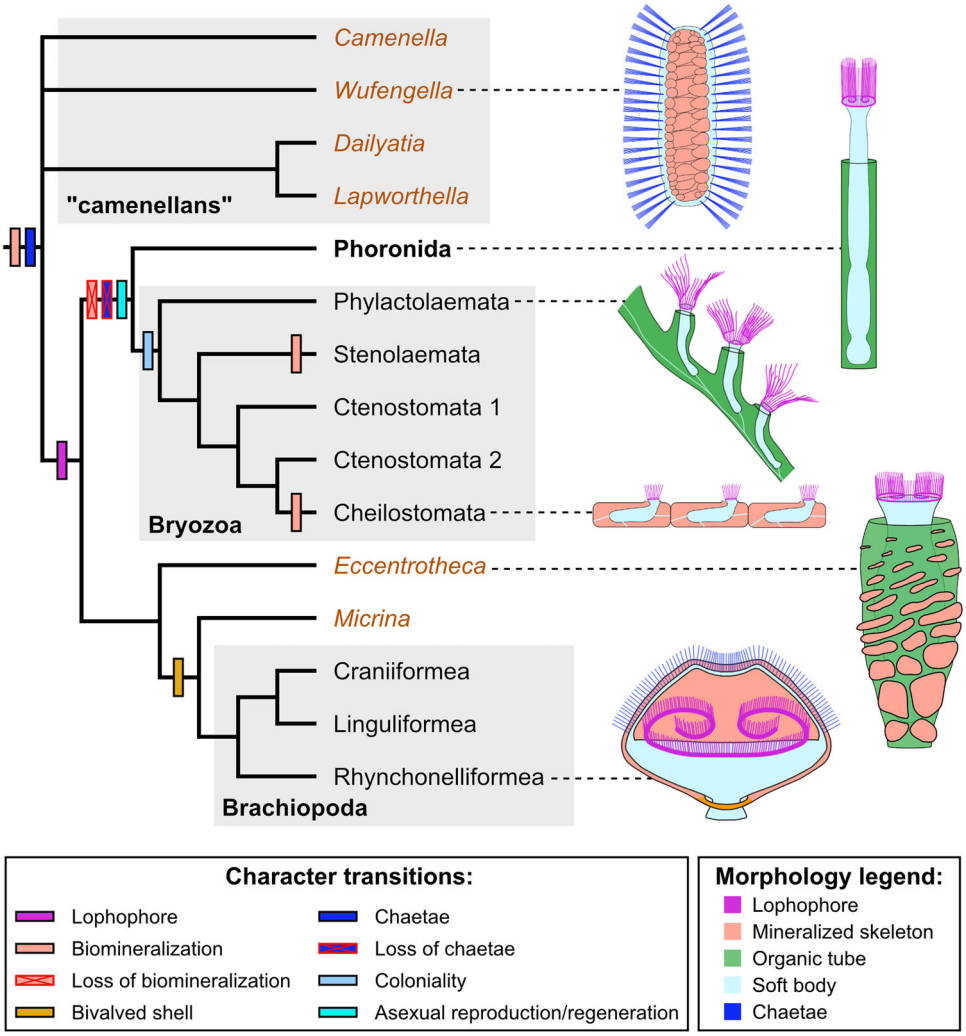

FIGURE 4 Scenario for the evolution of discussed characters in lophophorates. The topology of the tree is based on the phylogenetic analyses of Guo et al. (2022) for the affinity of particular tommotiids (names in brown) and Waeschenbach et al. (2012) for the internal phylogeny of bryozoans. [Color figure can be viewed at wileyonlinelibrary.com]

body and articulated scleritome (Guo et al., 2022) showed that this group of tommotiids was characterized by yet another body plan (Figure 4)—a bilateral worm, without a lophophore but with dorsal complex armor and with lateral multiple bundles of stiff chaetae. The new, more comprehensive phylogenetic analysis that took into account those newly discovered camenellid fossils, suggested that *Eccentrotheca* is not a sister taxon of phoronids but instead, it belongs to the brachiopod lineage of tommotiids (Figure 4; Guo et al., 2022). The same analysis showed that phoronids are more closely related to bryozoan than to any other known group of fossil tommotiids—a topology reminiscent of most of the modern molecular phylogenies (Laumer et al., 2015, 2019; Marlétaz et al., 2019; Nesnidal et al., 2013; Zverkov et al., 2019).

Interestingly, even though many of the modern bryozoans possess inorganic zoecia, the internal phylogeny of this clade suggests that they represent secondarily biomineralized lineages (Figure 4), while ancestrally the bryozoans were soft-bodied (e.g., Fuchs et al., 2009; Saadi et al., 2022; Schwaha et al., 2020; Taylor et al., 2010; Taylor & Waeschenbach, 2015; Waeschenbach et al., 2012). In this case, the common ancestor of phoronids and bryozoans lost the ability to biomineralize (which would explain the lack of phoronid- or bryozoan-affiliated tommotiids) and only later the stenolaemate and cheilostome bryozoans re-evolved inorganic skeletons (Figure 4; Wernström et al., 2022). Recent re-description of the early Cambrian *Glossolites magnus* suggested that this animal, lacking biomineralization and dwelling in the inorganic tube, might represent a stem species of the Phoronida+ Bryozoa branch, (Sun et al., 2022), reinforcing the idea that the ancestor of that clade had only organic skeleton (however, the affinity of *Glossolites* was not tested within

the phylogenetic framework and remains problematic). Such a scenario is additionally supported by the genomic comparative data. Investigation of the phoronid Hox genes complement showed that phoronids, which in general have quite a conserved Hox cluster, lack gene *Scr* (Figure 3c; Gąsiorowski & Hejnol, 2020; Luo et al., 2018) that in brachiopods is associated with the developing shell-forming structures (Gąsiorowski & Hejnol, 2019; Schiemann et al., 2017). Moreover, it has been recently shown that phoronids and bryozoan show similar patterns of loss of other biomineralization-related structural genes (Wernström et al., 2022).

A similar case can also be made for the evolution of chaetae in Lophotrochozoa. Contemporaryly, only annelids and brachiopods have chaetae, that share morphological and molecular similarities (Gąsiorowski & Hejnol, 2019; Gustus & Cloney, 1972; Lüter, 2001; Schiemann et al., 2017). However, in the fossil record, similar structures are also present in mollusks (Thomas et al., 2020) and tommotiids (Balthasar, 2004; Guo et al., 2022; Holmer et al., 2008; Williams & Holmer, 2002), indicating that chaetae belong to the lophotrochozoan ground pattern. This implies that the common ancestor of phoronids and bryozoans might have also lost chaetae (Figure 4). Concordantly, the Hox gene *Post1*, which is expressed in the chaetal sacs of both brachiopods and annelids (Fröbius et al., 2008; Gąsiorowski & Hejnol, 2019; Kulakova et al., 2002, 2007; Schiemann et al., 2017), is missing from the genome of phoronids (Figure 3c; Gąsiorowski & Hejnol, 2020; Luo et al., 2018) and likely also of bryozoans (as indicated by the degenerate polymerase chain reaction primers search by Passamaneck & Halanych, 2004). Yet, the systematic survey of the conserved genes involved in chaetogenesis has not been performed in lophotrochozoans, so the case of chaetal evolution remains somewhat more speculative.

The topic of skeletal and chaetal evolution in Lophophorata is a perfect showcase of how a multidisciplinary approach combining fossil, morphological, genomic, and developmental data can provide a comprehensive picture of the evolution of morphological characters. Although the scenario described above is elegant and seemingly resolved, there are still some open questions related to that topic, which require further studies. First of all, some of the newest molecular phylogenies did not support the sister position of bryozoans and phoronids (Figure 1f; Drábková et al., 2022; Khalturin et al., 2022), which might indicate a convergent loss of biomineralization and chaetae (and associated genes) in both lineages. Second, following the current understanding of the evolution of morphological traits, it can be hypothesized that the organic tubes of phoronids and nonmineralized bryozoans should be homologous to each other but also, at least at some level, to the organic part of the brachiopod shell. So far, however, there is no evidence (neither structural nor genetic) for such a homology. Finally, even though the most recent common ancestor of Bryozoa and Phoronida did not have any sclerites, there should be some biomineralized extinct forms representing the stem group of the (Phoronida+Bryozoa) clade. Is it possible that some of the already known tommotiids occupy such a position but due to their isolated nature it remained unnoticed? Or maybe new fossil forms of animals intermediate between phoronids and bryozoans will be unearthed, shedding more light on the history of biomineralization and chaetogenesis in Lophophorates.

4 | PHORONIDS AS A POTENTIAL MODEL CLADE TO STUDY THE EVOLUTION OF REGENERATION, ASEXUAL REPRODUCTION, AND COLONIALITY IN METAZOA

Another apparent similarity between phoronids and bryozoans is related to their ability to regenerate and reproduce asexually. In Bryozoa, asexual reproduction (budding) is a basis for coloniality, characteristic (and ancestral) for most members of the clade, while regeneration is used to replace polypids (lophophore and digestive system), which accumulate metabolic waste products during the bryozoan life cycle (Schwaha et al., 2020). Phoronids, on the other hand, are predominantly solitary animals, however, they can form aggregations of multiple individuals, that—at least in some species—probably originate through asexual reproduction by the mean of architomy (Marsden, 1957; Silén, 1954, 1955). Moreover, it has been reported that when stressed or injured, phoronids can shed their lophophore and regenerate a new organ within weeks (Marsden, 1957; Silén, 1955).

The morphological details of phoronid regeneration have been described in several species based primarily on the microscopical observation of regenerating animals and histological sections of the regenerates (e.g., Emig, 1972a, 1972b, 1973a, 1973b; Marsden, 1957; Silén, 1955 and references therein). Immediately after amputation, the wound is covered by mesodermally derived scar tissue, which later becomes overgrown by the epidermal cells (Emig, 1972a, 1973a). Afterward, the mass of undifferentiated cells, a blastema, forms below the epidermis, followed by the reestablishment of the missing body elements (Emig, 1972a, 1973a). It seems that the regeneration mostly relies on the dedifferentiation of the preexisting

tissues (Emig, 1973a), similar to what has been described in e.g., annelids (Kostyuchenko & Kozin, 2021).

Interestingly, it seems that different species of phoronids have different capacities for regeneration. All of the tested species are capable of lophophore regeneration (Emig, 1972a, 1972b, 1973a, 1973b; Marsden, 1957), however, in some of them, posterior regeneration is only possible if the tissue of the posterior reproductive trunk region is part of the regenerate (Marsden, 1957). Most of the phoronids are not capable to regenerate the trunk from the isolated tentacular region (Marsden, 1957; Silén, 1955), yet, in *Phoronis ovalis*, it was reported, that the autonomously shed lophophores can serve as a propagative stage: they are able to resettle on the substrate and regenerate a fully functional individual, that feeds, builds a tube and bores into a mollusk shell (Silén, 1955).

Regeneration experiments on phoronids are relatively easy to perform, however, there is virtually no data on that process originating after 1970s. Studies of the regeneration with modern tools, such as antibody staining, labeling of mitotically active cells, in situ RNA hybridization or comparative transcriptomics, are needed to better understand tissue dynamics during the process and to confirm some of the observations made by the pioneers of the field in mid 20th century.

Although most phoronids are solitary organisms, some species can form gregarious aggregations of multiple individuals (Figure 1a), while others, e.g., *P. ovalis*, are forming pseudocolonies, where a single branching tube is occupied by multiple animals originating through an asexual reproduction (Silén, 1954). Even though such pseudocolonies show a low level of zooidal integration, it seems that a potential to form (pseudo) colonies is a feature inherited from the common ancestor of Bryozoa and Phoronida. Mapping of the characters on the phylogenetic tree (Figure 4) shows that the common ancestor of both clades was capable of asexual reproduction and lophophore regeneration and it probably formed simple pseudocolonies (characters retained in *P. ovalis*), while later the bryozoan lineage evolved strict coloniality and asexual reproduction by budding. An interesting approach to investigate the evolution of coloniality in lophophorates has been recently applied by Santagata (2021), who looked for the positively selected genes shared by bryozoans, colonial kamptozoans, and associative *Phoronis ijimai* Oka, 1897. The analyses demonstrated that there are some genes selected for in all colonial lophophorates, however, it remained inconclusive on whether this is due to the common colonial ancestry or independent acquisition of colonial lifestyle in each lineage. An important caveat of this study is the lack of data from *P. ovalis*, which is the most colonial among known phoronid species, and which occupies a crucial phylogenetic position in the phoronid phylogeny (Figure 1g; Hirose et al., 2014; Santagata & Cohen, 2009). If the hypothesis put forward in this review is true, then it would also be interesting to test whether there is an enrichment of commonly positively selected coloniality genes shared between *P. ovalis* (its transcriptome has been recently sequenced and published by Saadi et al., 2022) and bryozoans that are not shared with kamptozoans, which likely evolved coloniality independently.

The ease of the phoronid manipulation, their great regenerative capacities, and the limited number of species with quite diverse regenerative and asexual capacities make them an interesting model clade for studies on the evolutionary interplay between regeneration and coloniality. Moreover, the presence of both strictly solitary (brachiopods) and colonial (bryozoans) close relatives gives a unique opportunity to study developmental and genetic mechanisms leading to the emergence of a colonial lifestyle in a comparative framework. Especially future studies on enigmatic *Phoronis ovalis* might play a profound role in understanding how the solitary and probably non-regenerating ancestor of lophophorates gave rise to the clade of animals capable of regeneration, asexual reproduction, and formation of clonal colonies.

5 | CONCLUSIONS

Although lophophorates, including phoronids, lost their status as a clade occupying a central role in animal phylogeny, they are still important for the discussion on the evolvability of development and morphology. On one hand, lophophorates show some strikingly conservative characters—such as lophophore or tripartite coelom present in all members of the clade—on the other, they exhibit wide variation in multiple other features—biomineralized versus soft bodies, presence or absence of chaetae, coloniality versus individuality, new versus ancestral larval types, etc. Data from Phoronida are crucial for understanding the evolution of those diverging characters within lophophorates, but can also be used for a general discussion on how and why morphological characters evolve at all. Taking into account the available tools and resources (sequenced genome and transcriptomes of several species, very well-studied morphology and development, established protocols for spawning and gene expression studies, ease of tissue-specific transcriptomics) phoronids have the great potential for playing an important role in the endeavor of studying the evolution of the animal body plans in the nearest future.

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DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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