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REVIEW

Recent progress in reconstructing lophotrochozoan (spiralian) phylogeny

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Abstract

Lophotrochozoa (also called Spiralia), the sister taxon of Ecdysozoa, includes animal taxa with disparate body plans such as the segmented annelids, the shell bearing molluscs and brachiopods, the colonial bryozoans, the endoparasitic acanthocephalans and the acoelomate platyhelminths. Phylogenetic relationships within Lophotrochozoa have been notoriously difficult to resolve leading to the point that they are often represented as polytomy. Recent studies focussing on phylogenomics, *Hox* genes and fossils provided new insights into the evolutionary history of this difficult group. New evidence supporting the inclusion of chaetognaths within gnathiferans, the phylogenetic position of Orthonectida and Dicyemida, as well as the general phylogeny of lophotrochozoans is reviewed. Several taxa formerly erected based on morphological synapomorphies (e.g. Lophophorata, Tetraneuralia, Parenchymia) seem (finally) to get additional support from phylogenomic analyses.

Keywords Lophotrochozoa · Chaetognatha · Phylogenomics · Rare genomic changes · Annelida

Molecular systematics revolutionized and revitalized the field of animal phylogenetics. The landmark publications of Halanych et al. (1995) and Aguinaldo et al. (1997) shaped our new view of animal phylogeny by establishing a system where the vast majority of bilaterian diversity is grouped into Deuterostomia, Ecdysozoa and Lophotrochozoa (Halanych 2004). These results were initially derived from the analysis of a single gene (18S ribosomal RNA), but have been also supported by phylogenomic analyses using datasets with hundreds of genes and extended taxon sampling (Telford et al. 2015; Halanych 2016). During the last decade, next-generation sequencing data—especially Illumina short reads—became available for reasonable prices, allowing to conduct transcriptomic and genomic analyses of non-model organisms for pure phylogenetic interest (McCormack et al. 2013). Availability of such data allowed phylogenomic analyses of many lophotrochozoan taxa, providing well-supported frameworks of their phylogeny e.g. for the species-rich taxa Annelida (Struck et al. 2011; Weigert et al. 2014; Andrade et al. 2015; Laumer et al. 2015a; Struck et al. 2015; Struck 2019), Platyhelminthes (Egger et al. 2015; Laumer et al. 2015b) or Mollusca (Kocot et al. 2011; Smith et al. 2011). However, the phylogeny within Lophotrochozoa is still strongly debated. One of the few phylogenetic hypotheses which unambiguously received support from molecular and morphological analyses is the grouping of Gnathostomulida, Micrognathozoa and Rotifera (Fig. 1b) (including Monogononta, Bdelloidea, Acanthocephala and *Seison*, see for example in Wey-Fabrizius et al. (2014)) in the taxon Gnathifera (Ahlrichs 1995; Sørensen 2003). Some authors suggested that lophotrochozoans with a simple organization should be unified in a taxon Platyzoa (Cavalier-Smith 1998), comprising Gnathifera, Platyhelminthes and Gastrotricha. Platyzoan monophyly was supported by some phylogenomic analyses (Hejnol et al. 2009), but rejected by others (Struck et al. 2014). Two reviews published in 2014/2015 focussing on the current state of animal phylogeny discussed the knowledge of lophotrochozoan phylogeny and basically summarized lophotrochozoan relationships as a polytomy (see Fig. 2a), indicating the lack of congruence on this issue (Dunn et al. 2014; Telford et al. 2015). Since then, several studies covering lophotrochozoan phylogeny have been published which are briefly summarized and discussed.

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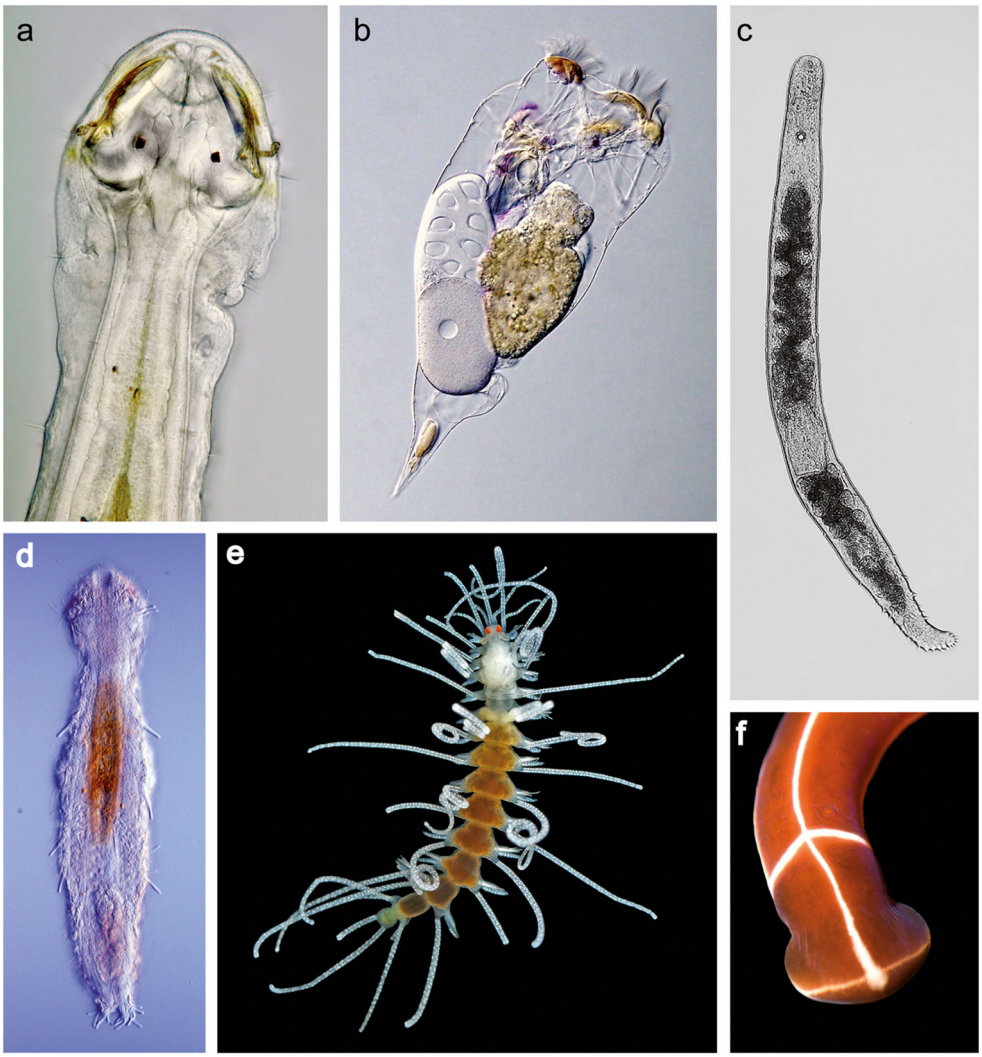

Fig. 1 Representatives of major lophotrochozoan taxa representing diverse body plans. **a** *Spadella cephaloptera* (Chaetognatha), picture provided by Rafael Martin-Ledo. **b** *Synchaeta littoralis* (Rotifera), picture provided by Rafael Martin-Ledo. **c** Otoplanidae sp. (Platyhelminthes), picture provided by Ole Riemann. **d** *Dactylopodola baltica* (Gastrotricha), picture provided by Alexander Kieneke. **e** *Amblyosyllis clarae* (Annelida), reprinted with permission from Aguado et al. (2019). **f** *Tubulanus superbus* (Nemertea), reprinted and modified with permission from Beckers et al. (2013)

Naming issues

Naming the sister taxon of Ecdysozoa led to a severe discussion of how to choose names and which names to apply. This group is either named Lophotrochozoa or Spiralia and basically every argument has already been made about which name to prefer (Laumer et al. 2015a; Telford 2019). The biggest problem is that both names are at the same time also used to describe subordinated taxa within each other. For example, some authors use Spiralia for a subclade within Lophotrochozoa, while others define Lophotrochozoa as subclade within Spiralia (Halanych 2016). To avoid confusion, I will use Lophotrochozoa as name for the sister taxon of Ecdysozoa, but will treat Spiralia synonymously to Lophotrochozoa.

The phylogenetic position of chaetognaths

The enigmatic chaetognaths (Fig. 1a) have been puzzling for scientists since their description. Around 130 species have been described of this small predators, most of whom are planktonic (Gasmi et al. 2014). In many classic systematic zoology textbooks, chaetognaths had been classified as part of or related to deuterostomes based on their embryology; however, molecular phylogenetic analyses and characters of the nervous system supported an affiliation with protostomes (Harzsch and Müller 2007; Perez et al. 2014). Nielsen (2001) suggested in the second edition of his book on animal evolution that chaetognaths are part of Gnathifera. The presence of chitinous jaws was interpreted as uniting synapomorphic character for this grouping. However, in

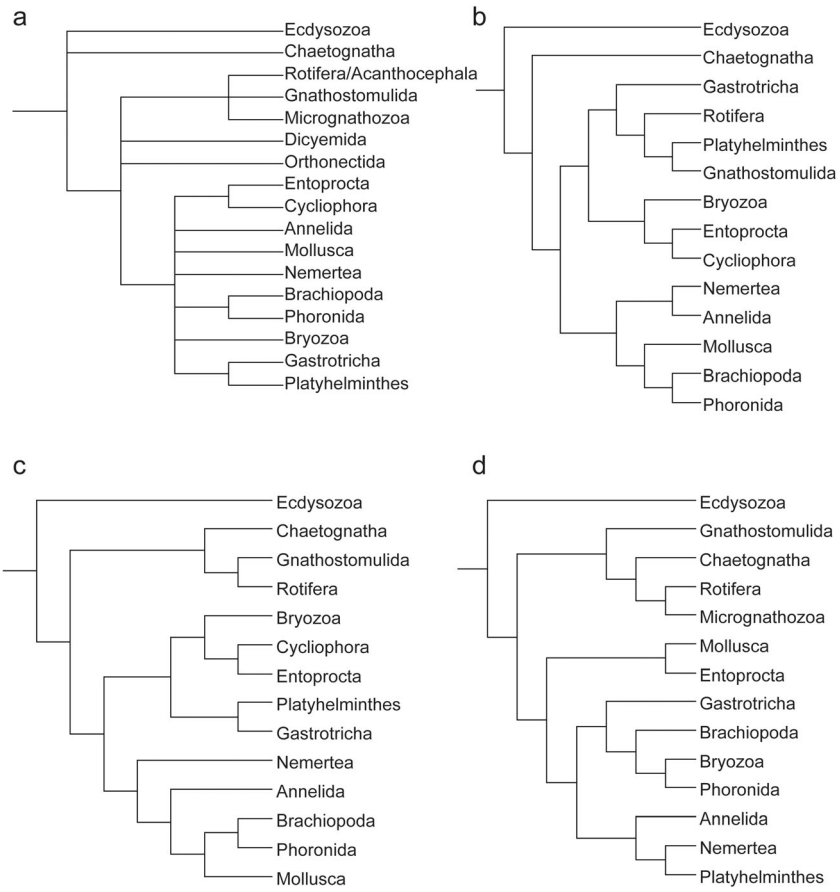

Fig. 2 Hypotheses of lophotrochozoan relationships. **a** State-of-the-art review from Telford et al. (2015) summarizing the knowledge at that point. **b** Phylogenomic analysis of Lophotrochozoa based on 638 orthologs by Kocot et al. (2017). **c** Phylogenomic analysis of Lophotrochozoa based on 1/6 of 638 orthologs selected to minimize the patristic distance across taxa by Kocot et al. (2017). **d** Phylogenomic analysis of 267 orthologs with amino acids recoded according 6 Dayhoff groups to reduce saturation by Marlétaz et al. (2019)

the third edition of his book, Nielsen (2012) revoked this idea. The hypothesis of placing chaetognaths with Gnathifera found now strong support stemming from three different lines of evidence: *Hox* genes, phylogenomics and the fossil record.

Hox genes are a family of transcription factors which are involved (among other processes) in the patterning of the antero-posterior axis of bilaterian animals (Carroll 1995). These genes are remarkably conserved across distantly related taxa and are often organized in a genomic cluster, resulting from gene duplication events (Ferrier and Holland 2001). As a result of gene duplication or gene loss, *Hox* gene content varies across bilaterians (Balavoine et al. 2002). Fröbius and Funch (2017) analyzed the *Hox* gene content and expression of a monogonontan rotifer (*Brachionus manjavacas*). A comparison across Bilateria in general revealed the presence of a specific sequence motif in the flanking region of the homeodomain of the *lox5* gene restricted to the analyzed rotifers and chaetognaths. Moreover, phylogenetic analyses supported that Rotifera and Chaetognatha share the presence of a *Hox* gene (*MedPost*) which has not been found in any other analyzed Metazoa so far. Based on these characters, an inclusion of chaetognaths within Gnathifera is advocated by Fröbius and Funch (2017).

Marlétaz et al. (2019) inferred the phylogenetic position of chaetognaths by expanding the available transcriptomic data. Phylogenomic analyses of ten chaetognath species and selected bilaterian taxa representing their phylogenetic diversity recovered a clade uniting Chaetognatha and Gnathifera (Fig. 2d). The monophyly of this group was consistently supported across analyzing schemes differing in taxon sampling or reconstruction methodology. Chaetognaths appear as sister group to Rotifera + Micrognathozoa, while gnathostomulids represent the sister taxon of remaining Gnathifera. However, the branch support values for resolving the phylogeny within Gnathifera are rather weak. Nevertheless, a sister group relationship of Rotifera and Micrognathozoa has been also supported by morphological characters (Sørensen 2003). Some more support for grouping chaetognaths with Gnathifera came from phylogenomic analyses by Kocot et al. (2017). These authors performed a wide range of analyses for a diverse lophotrochozoan taxon sampling using subsets of orthologs selected by different criteria. Subsets of orthologs minimizing branch lengths differences between taxa or saturation of selected orthologs found chaetognaths as sister taxon of Gnathifera (Fig. 2c), whereas other analyses grouped them outside of Lophotrochozoa (Fig. 2b). Similarly, a phylogenomic study by Laumer et al. (2019) focussing on metazoan phylogeny found in some of the analysed subsets support for placing chaetognaths within Gnathifera.

Finally, Vinther and Parry (2019) re-analyzed a Burgess Shale fossil described by Charles D. Walcott (1911) named

Amiskwia sagittiformis. This species has been originally placed within chaetognaths (which were regarded as an annelid subtaxon in the classification Walcott used), but subsequent authors affiliated it with Nemertea (Owre and Bayer 1962) or regarded the systematic position as unresolvable due to the absence of critical characters in the fossil record (Morris 1977). However, Vinther and Parry (2019) suggested the presence of a bilateral pharyngeal jaw apparatus in *Amiskwia*, which is homologized with the jaws of Gnathifera. Other characters found in the fossil indicate a close relationship with chaetognaths, such as the presence of lateral fins and a horizontal caudal fin. This view has been challenged by Caron and Cheung (2019) who argue that *Amiskwia* represents a stem-lineage gnathiferan. Nevertheless, the palaeontological evidence suggests that *Amiskwia* is either a stem-lineage chaetognath with gnathiferan jaws, or represents a stem-lineage gnathiferan with chaetognath-like appearance and life-style.

These different studies represent the best we can hope to place a rogue taxon such as Chaetognatha, which shows a derived morphology (even though it might be closer to the gnathiferan ground pattern than other groups of this taxon) and also very long branches in molecular systematic studies. Here, carefully conducted phylogenomic studies can be reconciled with analyses of so-called rare genomic changes markers and the fossil record, altogether converging to place them with Gnathifera (Fig. 3).

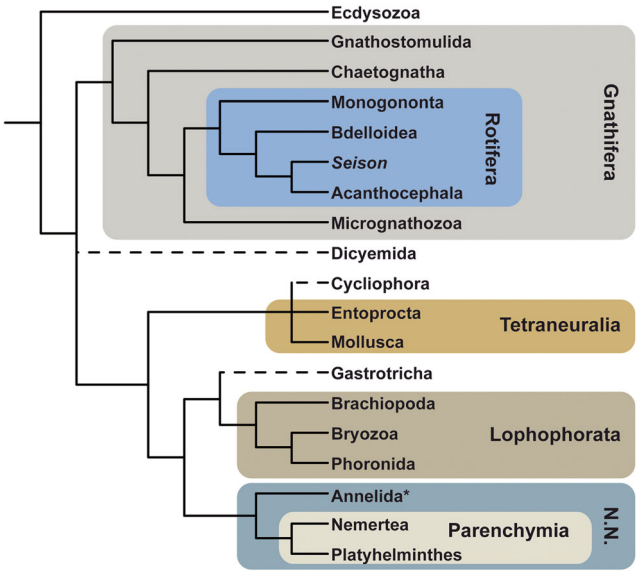

Fig. 3 A hypothesis of lophotrochozoan phylogeny as discussed in this review. This topology shows a summary of different phylogenomic studies (Weigert et al. 2014; Wey-Fabrizius et al. 2014; Schiffer et al. 2018; Marlétaz et al. 2019). *Please note that several taxa formerly regarded to be placed outside Annelida (Echiura, Myzostomida, Orthonectida, Pogonophora, Sipuncula and Vestimentifera) are now firmly placed as annelid ingroups. Annelida relationships are (mostly) well resolved, see discussion in the text and Struck (2019) for review

The phylogenetic position of the former "Mesozoa": Orthonectida and Dicyemida

The latest edition of the classic zoology textbook *Invertebrates* (Brusca et al. 2016) has a special chapter called "Four enigmatic protostome phyla" comprising Dicyemida (Rhombozoa), Orthonectida, Chaetognatha and Gastrotricha, because all of them have been notoriously difficult to place in a phylogenetic system. Orthonectida and Dicyemida comprise minute parasitic invertebrates with complex life cycles using other invertebrates as host. Whereas Dicyemida are highly specialized and only found in nephridia of cephalopods, Orthonectida are reported from acoelomorphs, platyhelminths, annelids, molluscs, nemerteans, echinoderms and chordates (Nakano and Miyazawa 2019). Both taxa were thought to lack any body cavities or discrete organ systems such as a gut or the nervous system. Due to their morphological simplicity, they had been initially seen as a possible link between Metazoa and their unicellular relatives, which is the reason why they had been united in the taxon Mesozoa (Stunkard 1954). Detailed research on the morphology revealed that life-history stages of dicyemids, which were usually seen as comparable semaphoronts of adult orthonectids, only superficially resemble each other. Consequently, it was proposed to treat them as different and possibly unrelated taxa (Kozloff 1969). Moreover, immunohistochemistry staining revealed the presence of a small but distinct serotinergic nervous system in female orthonectids (Slyusarev and Starunov 2016). First, molecular phylogenetic studies using 18S rRNA gene sequence data also indicated the polyphyly of mesozoans, but the presence of long branches in all analyzed species did not allow a well-supported placement within the animal tree of life (Pawlowski et al. 1996).

A first low-coverage genome of an orthonectid became available and phylogenomic analyses of hundreds of genes using different models of sequence evolution placed them highly derived within Lophotrochozoa (Mikhailov et al. 2016). Subsequent analyses including reconstruction of mitochondrial genomes and transcriptomic data found orthonectids to cluster within Annelida, whereas dicyemids remain difficult to place with any lophotrochozoan taxon with certainty (Lu et al. 2017; Schiffer et al. 2018; Bondarenko et al. 2019). Nevertheless, the inclusion of dicyemids into lophotrochozoans is further substantiated due to a specific *Hox* gene sequence motif in the flanking region of the homeodomain of *lox5* (Kobayashi et al. 1999). The inclusion of orthonectids within annelids is another example of secondarily highly simplified invertebrates originating from a segmented annelid ancestor, as already shown for several taxa formerly known as archiannelids (Laumer et al. 2015a; Struck et al. 2015).

Phylogenetic relationships of Lophotrochozoa

Progress has been made to find the phylogenetic position of several "problematic" (difficult to place) or "minor" (species poor) lophotrochozoan taxa, of which many of them have been formerly treated as separate phyla. Several of these former phyla have now been placed with strong support as annelid ingroups. Within Annelida the species-rich Errantia (e.g. nereidids, syllids, phyllodocids) and Sedentaria (e.g. orbiniids, sabellids, clitellates) are sister taxa forming the Pleistoannelida. The remaining annelid taxa form a paraphyletic grade, with Oweniidae and Magelonidae representing the sister taxon of all other annelids (Struck 2019). Orthonectida are placed within Annelida, but it remains unclear which annelids are closely related to them. Other taxa which have been formerly regarded as higher ranked taxa outside annelids are placed with higher certainty. The unsegmented Echiura are placed within Sedentaria as sister to Capitellidae (Bleidorn et al. 2003). The also unsegmented Sipuncula are the sister group of amphinomids and together with them they form the sister taxon of Pleistoannelida (Weigert et al. 2014). The enigmatic Myzostomida are more difficult to place, but mitochondrial gene order clearly supports a pleistoannelid affinity (Weigert et al. 2016). Species classified as Pogonophora or Vestimentifera are now united within Siboglinidae (Pleijel et al. 2009), which are part of the Sedentaria (Struck et al. 2011). However, the general backbone of lophotrochozoan phylogeny still remains discussed. Currently, the following higher ranked taxa are part of the Lophotrochozoa (in alphabetical order): Annelida (including Echiura, Myzostomida, Orthonectida, Pogonophora, Sipuncula and Vestimentifera), Brachiopoda, Bryozoa, Chaetognatha, Cycliophora, Dicyemida, Entoprocta, Gastrotricha, Gnathostomulida, Micrognathozoa, Mollusca, Nemertea, Phoronida, Platyhelminthes and Rotifera (including Acanthocephala, Bdelloidea, Monogononta and *Seison*). Three phylogenetic trees recovered in two recent and comprehensive phylogenomic analyses addressing lophotrochozoan phylogeny (Kocot et al. 2017; Marlétaz et al. 2019) are shown in Fig. 1 b–d and not a single sister group relationship of any of these taxa is unequivocally supported. Differences between the analyses are due to taxon sampling, strategies of compiling orthologs for the final super matrix, coding of characters, as well as the model of sequence evolution which has been applied. Under the presence of strong phylogenetic signal, differences in these strategies should not have a major impact on the recovered phylogeny. For example, Cunha and Giribet (2019) received basically the same topology of gastropod relationships independent of the analysis strategy of their phylogenomic data set. In the case of lophotrochozoan relationships, the chosen strategy of analysis has a strong influence on the resulting topology. Especially the coding strategy for the super matrix seems to be sensitive regarding phylogenetic inference. Lophotrochozoan lineages likely diverged in the Cambrian (485–541 mya) or even before (dos Reis et al. 2015) and phylogenetic relationships of this age are usually inferred using amino acid sequences of protein coding genes. One problem for inferring such old relationships is the saturation of the data, which means that phylogenetic signal is blurred by convergent substitutions of amino acids (Philippe and Laurent 1998). Recoding strategies have been introduced to increase the ratio of phylogenetic signal to non-phylogenetic signal. Recoding according the six main Dayhoff categories of chemically related amino acids (Dayhoff and Schwartz 1978; Susko and Roger 2007) became a widely used strategy to reduce saturation bias in protein coding data. The idea behind this strategy is that amino acid changes within these groups are more common (and therefore more saturated), whereas changes between groups occur less frequent and therefore carry more phylogenetic information (or less saturation) (Embley et al. 2003). Such a recoding obviously results into loss of information; however, simulation studies have shown that this might be negligible in comparison with the improvement in topology estimation (Susko and Roger 2007, but see Hernandez and Ryan (2019) for a different view on this topic). Following this strategy, Marlétaz et al. (2019) found support for grouping most lophotrochozoans into four clades: Gnathifera (already discussed above), Lophophorata, Tetraneuralia and an unnamed clade comprising Annelida, Nemertea and Platyhelminthes (see also Fig. 3). Moreover, these clades found also strong support when analyzing (without recoding) a subset of the initial taxon sampling only keeping taxa with the slowest evolutionary rates and steady deviating amino acid composition (Marlétaz et al. 2019).

Lophophorata (or Tentaculata) comprise brachiopods, phoronids and bryozoans, and this group has been already proposed by several morphologists (Hatschek 1888; Hyman 1959; Emig 1977). Uniting synapomorphy is the presence of a horseshoe-shaped lophophore situated around the mouth with a single row of tentacles in all three taxa (Emig 1984). However, monophyly of this group was doubted by other morphologists (Lüter 2000; Nielsen 2012), as well as by several molecular phylogenetic studies (Dunn et al. 2008; Helmkampf et al. 2008; Paps et al. 2009). Claus Nielsen even wrote "I hope that the name Lophophorata will disappear from the zoological vocabulary" (Nielsen 2012), a wish that does not seem to come true. Opponents to the Lophophorata concept mostly advocated to place bryozoans with other lophotrochozoans e.g. with entoprocts and cycliophorans into the taxon Polyzoa (Cavalier-Smith 1998; Hejnol et al. 2009). On the other hand, phoronids and brachiopods were often united into the taxon Brachiozoa (Cavalier-Smith 1998; Helmkampf et al. 2008; Hausdorf et al. 2010). The phylogenomic analyses by Marlétaz et al. (2019) supports

the monophyly of Lophophorata, a result which has been also confirmed by the phylogenomic study of Laumer et al. (2019); Hernandez and Ryan (2019). This is in congruence with recent analyses on the homology of the innervation pattern of the lophophore in lophophorate taxa, which was additionally interpreted as strong support for this group (Temereva and Tsitrin 2015; Temereva 2017a; Temereva 2017b). Interestingly, monophyletic Brachiozoa were not supported and, instead, phoronids seem to be the sister taxon of bryozoans and not brachiopods (Fig. 2d).

A sistergroup relationship of molluscs and entoprocts has been already proposed based on several morphological synapomorphies. The presence of a tetraneural nervous system with a pair of ventral (pedal) longitudinal nerve cords and a pair of lateral (visceral) longitudinal nerve cords was used to derive the name Tetraneuralia (Wanninger 2009). Further support came from fine structure of the of the larval foot sole in entoproct creeping larvae and neomeniomorph molluscs (Haszprunar and Wanninger 2008). Finally, the presence of a body cavity with a lacunal system for the transport of hemolymph is interpreted as tetraneuralian autapomorphy, which also led to the introduction of the alternative name Lacunifera (Ax 2000). Besides the phylogenomic study by Marlétaz et al. (2019), basically no other molecular phylogenetic study (but see below) recovered Tetraneuralia. However, the arrangement of mitochondrial gene order of entoprocts and molluscs shows highly conserved regions of up to 17 successive genes (of 37 genes in the mitochondrial genome), including tRNA genes which are usually prone to be highly rearranged (Yokobori et al. 2008). The usefulness of mitochondrial gene order as further supporting character for the monophyly of Tetraneuralia should be systematically explored in the future. Several phylogenomic analyses indicated a close relationship of entoprocts and cycliophorans (Hejnol et al. 2009; Nesnidal et al. 2013; Struck et al. 2014; Kocot et al. 2017). However, Cycliophora had not been included in the study of Marlétaz et al. (2019). Interestingly, in a phylogenomic study focussing on the phylogeny of molluscs, an analysis with an expanded outgroup taxon sampling found weak support for the inclusion of cycliophorans into Tetraneuralia (Kocot et al. 2011). Moreover, Funch (1996) already noted similarities (a ciliated foot, frontal organ, a pair of protonephridia with multiciliated terminal cells) between the cycliophoran chordoid larvae and entoproct larvae and suggested a close relationship between these two taxa.

Due to their simplified morphology (e.g. acoelomate, simple blind-ending gut without anus), platyhelminths (Fig. 1c) have long been regarded as early branching Bilateria, closely resembling the urbilaterian ground pattern (Willmer 1990; Ax 1995). However, molecular phylogenetic analyses, development via spiral cleavage and their *Hox* gene complement clearly support a lophotrochozoan origin of this taxon (Balavoine 1997; de Rosa et al. 1999; Dunn et al. 2008). Their position within Lophotrochozoa is highly disputed, but several phylogenomic analyses recovered a taxon named Rouphozoa where they are united with Gastrotricha (Fig. 1d), forming the sister group of the remaining non-gnathiferan lophotrochozoans (sometimes called Lophotrochozoa sensu stricto) (Struck et al. 2014; Laumer et al. 2015a). Rouphozoa found some additional support from analyzing the complement of short RNAs such as microRNAs and piRNAs (Fromm et al. 2019).

The newly recovered clade uniting Platyhelminthes, Annelida (Fig. 1e) and Nemertea (Fig. 1f) has not been proposed before and so far this hypothesis has not been named. A sister group relationship of Nemertea and Platyhelminthes was supported by cladistic analysis of morphological character matrices. The absence of a hyposphere in larvae of both taxa is inferred as synapomorphic character supporting the so-called Parenchymia (Nielsen et al. 1996; Sørensen et al. 2000). The similarity between nemertean pilidium larvae and platyhelminth Götte and Müller's larval types has been noted by many authors, but homology was often rejected because of phylogenetic considerations (Rawlinson 2010). Even though this larvae occur in derived groups within Platyhelminthes (Polycladida) and Nemertea (Pilidiophora), homology of ciliary bands of these larvae with the prototroch of trochophora larvae had been suggested (Nielsen 2018). Interestingly, in the development of a basally branching nemertean, a vestigial prototroch has been found, suggesting a trochophora-like larvae as plesiomorphic for Nemertea (Maslakova et al. 2004). In the case of Platyhelminthes, trochophora-like larvae are only found in Polycladida, while all other free-living taxa show direct development. Given the phylogenetic position of Polycladida, a loss of a planktotrophic larvae has to be assumed to have appeared independently in Catenulida, Macrostomorpha, Lecithoepitheliata and Euneoophora (Egger et al. 2015).

The sister taxon of annelids remained ambiguous since the rejection of the Articulata hypothesis. Several molecular phylogenetic analyses supported a taxon Trochozoa, including Mollusca, Annelida, Nemertea, Brachiopoda and Phoronida, and different combinations of these taxa represented the sister taxon of annelids (Dunn et al. 2014; Kocot 2016). However, Trochozoa is now rendered as polyphyletic, with molluscs as member of Tetraneuralia and brachiopods and Phoronida as members of the Lophophorata (Marlétaz et al. 2019). Instead, Parenchymia is favoured as annelid sister group. It is intriguing that annelids, platyhelminths and nemerteans all include species with high regenerative abilities (Bely et al. 2014; Zattara et al. 2019). Whereas the molecular basis for the process of regeneration is well studied especially for tricladid Platyhelminthes (Rink 2013), only the role of a few selected candidate genes has been investigated for some annelids (Özpolat and Bely 2016) and no data is available for Nemertea. Platyhelminth regeneration relies on neoblasts, a

population of somatic stem cells, which are present across the mesenchyme (Baguna 2012; Gehrke and Srivastava 2016). A similar stem cell replacement system is also known to be present in acoelomorphs, which together with xenoturbellids (likely) represent the sister taxon of all other bilaterians (Nephrozoa) (Egger et al. 2009). Originally, the term neoblast was used to describe specialized cells observed during the regeneration in the clitellate annelid *Lumbriculus* (Randolph 1891). Activity of neoblasts during regeneration has also been described for some nemerteans (Coe 1929). Annelid and platyhelminth neoblasts were regarded as morphologically and functionally distinct. Whereas neoblasts of platyhelminths are small undifferentiated cells found in large numbers throughout the body, annelid neoblasts have been initially reported as large cells found in small numbers along the ventral nerve cord (Myohara 2012). Also, in platyhelminths, neoblasts are the only proliferating cells during regeneration; whereas in annelids, proliferation and dedifferentiation of other cells contribute to the regeneration process (Myohara 2012; Zattara et al. 2016). Moreover, for most (if not all) non-clitellate annelids with high regeneration capacity, typical neoblasts have not been described (Herlant-Meewis 1964). However, when analyzing the posterior regeneration of the capitellid annelid *Capitella teleta*, cells that do not fit the description of the typical clitellate neoblasts migrate into the regenerating tissue and exhibit stem cell character (as evidenced by the expression of the stem cell marker gene *vasa*) (de Jong and Seaver 2018). Similarly, Probst (1931) already mentioned that actively proliferating cells involved in the regeneration of the posterior end in the orbiniid annelid *Phylo foetida* are only gradually different from the neoblasts described from clitellates. In summary, the presence of neoblasts in annelids and nemerteans needs to be investigated in more detail (and in more taxa) (Zattara 2015). The possible homology of this cell type and details of their function during regeneration processes should be comparatively analyzed for annelids, nemerteans and platyhelminths, as this might reveal further support for the close relationship of these three taxa. It should be noted that gastrotrichs also show the ability to regenerate, but so far neoblast-like cells have not been described from this taxon (Manylov 1995). Similarly, whole body regeneration is also described for ectoprocts, entoprocts and phoronids (Bely 2010) and the cellular basis of this process needs to be investigated in these taxa as well.

Outlook

Progress has been made in understanding lophotrochozoan relationships. However, differences remain between different phylogenomic analyses and the choice of methodology has a strong impact on the outcome. Whereas some taxa are still underrepresented, it has become clear that solely generating more data might not solve the dispute about different phylogenetic hypotheses (Philippe et al. 2011; Philippe and Roure 2011). One reason is that large-scale phylogenomic analyses often are biased by systematic errors e.g. violation of assumptions made by the selected substitution model for tree inference (Bleidorn 2017). Under such a scenario, the inclusion of more data only leads to better supported but erroneous trees, due the non-stochastic distribution of the error (Jeffroy et al. 2006). Logically, the development of more realistic ("better") substitution models is often suggested to escape this problem. Moreover, methods which compare the fit of the used model to the underlying data should be used to evaluate phylogenetic hypotheses derived from the same dataset, but with different models (Brown 2014). However, it seems also to be important to better integrate other types of data, such as morphology, fossils or rare genomic changes, into the analysis. A main problem remains of how to use this additional data to make phylogenetic decisions. In this short review, possible synapomorphies were hand-picked to discuss them in the light of the newest phylogenomic inferences. Other ways of including them in a real analyses would be certainly preferable, but it remains difficult to combine hundreds of thousands of molecular characters with few morphological characters. Similarly, inclusion of fossil taxa remains methodologically challenging, but also promising for the solution of difficult phylogenetic questions (Edgecombe 2017). Nevertheless, finding consilience of different approaches has to be explored as a way to decide between competing phylogenetic hypotheses in the phylogenomic era.

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