Dispatches

Animal Evolution: Last Word on Sponges-First?

D. Timothy J. Littlewood
Department of Life Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, UK
Correspondence: t.littlewood@nhm.ac.uk
http://dx.doi.org/10.1016/j.cub.2017.02.042

A major problem in understanding animal evolution is where early branching phyla, especially sponges and comb jellies (sea gooseberries), sit in the tree of life. A new study seeks to overcome this problem by sampling more species and data cleansing.

The sheer numbers and diversity of life forms alive today provides a daunting challenge in uncovering their evolutionary relationships. A popular visual metaphor to portray organismal interrelationships is a tree diagram, with branches growing and splitting and each terminal leaf representing a taxon, whether extant or extinct. Famously, the only illustration in Darwin's *On the Origin of Species* was just such a tree. Described as one of the most important organizing principles in biology, the tree is more than just a metaphor; it is a framework we can use to infer evolutionary events, patterns and processes. There is a lot at stake in reconstructing evolutionary trees (phylogenies) accurately. Adequate taxon representation is important and with sufficient density to ensure the diversity of the higher taxon (e.g. family, phylum) under scrutiny is reflected. Likewise, sufficient informative characters need to be included, as insufficient phylogenetic signal shortens internal branches of the tree and weakens nodal support. When molecular characters (i.e. nucleotide or amino acid sequences) are used, multiple genes are preferred in order to better estimate a species tree and not just the evolutionary history of the genes themselves. A tree with no clear bifurcating pattern has little utility as a platform for inference. In contrast, competing phylogenies, with markedly different, yet well supported, topologies from identical data sets, can lead to considerable debate, especially when they challenge widely-accepted interpretations. Untangling the origins and early branching patterns of animal evolution has been particularly problematic. Now, with improved taxon and sequence sampling, a study in this issue of *Current Biology* by Simion *e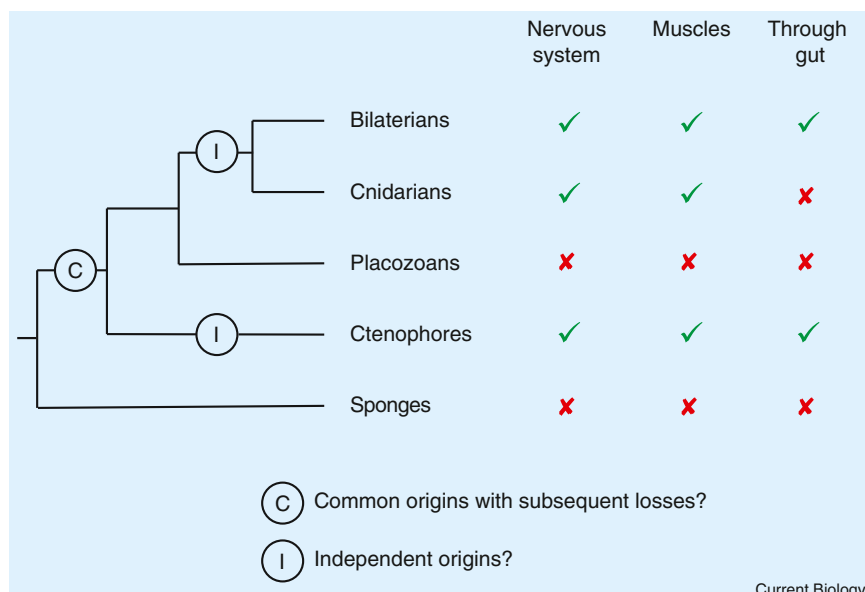t al.* [1] has added stability at the base of the animal tree with a singular familiar solution borne from multiple checks and balances focused on quality data and error avoidance.

At the heart of the problem is the position of four phyla — the Porifera (sponges), Ctenophora (comb jellies, or sea gooseberries), Cnidaria (corals, jellyfish, sea anemones and allies) and Placozoa (*Trichoplax*) — relative to all other, bilaterally symmetrical animals (Bilateria). This positioning has profound implications for our understanding of how animals evolved [2]. Sponges have long been considered the sister group to all other animals (Figure 1). With their simple organization, lacking a nervous system and musculature, they might appear like an attractive intermediate in the transition from single- to multi-cellularity at the origin of the animals. Sponges have rudimentary epithelial cells, but they are poorly differentiated and their function appears unlikely to seal tissue layers physiologically [3]. In contrast ctenophores and cnidarians are demonstrably more complex with sophisticated neural systems, muscles and epithelial tissues — all features aligning with the conventional view that they must have arisen after the origin of sponges. Placozoans, with a single genus and possibly just one species, are frustratingly simple with neither neurons nor muscles and even fewer cell types than sponges, providing little indication as to whether their simplicity reflects an alliance with sponges, an early evolutionary divergence or a secondary morphological simplification. Settling the relationships between these phyla and the bilaterians has consequences for understanding the evolution of the nervous systems, gastrulation, musculature and epithelia. Did animals start with a simple organisation and become more complex or did animal evolution follow a more complicated trajectory?

A spotlight has fallen on the ctenophores since they turned out as the sister group to all other animal phyla in another analysis [4]. If this scenario holds, muscles and a nervous system would have appeared in the earliest lineage of animals, and were subsequently lost and gained. Critics have suggested that this controversial placement is anomalous and likely due to systematic error [5,6], whereas its supporters have presented iterative improvements with ctenophores remaining at the base of the metazoans [7,8]. All agree that cnidarians are the sister to the bilaterians, and that the placozoans are sister to both these groups, but disagreement, discord and dissent is rife in deciding which phylum is sister to all other animals. Better data and refined analyses are required.

The new demonstrably improved phylogenomic solution of Simion *et al.* [1] comes from a metazoan-wide assembly of 1,719 genes with enhanced taxonomic sampling (61 species) of early divergent, non-bilaterian phyla, including six sponges, five ctenophores and eight cnidarians. Rather than relying on an uninterrupted bioinformatics pipeline, where computationally demanding routines can be scaled with the data, the authors applied stringent manual control of intermediate results to source and remove errors. Iterative detection and removal of error may hold the key to improving phylogenomics. An entirely new protocol for data matrix assembly included: rounds of careful orthology assessment, removal of ancient gene duplications, identifying and removing genes that might unduly affect branch lengths, reducing the source of

	Nervous system	Muscles	Through gut
Bilaterians	✓	✓	✓
Cnidarians	✓	✓	✗
Placozoans	✗	✗	✗
Ctenophores	✓	✓	✓
Sponges	✗	✗	✗

C — Common origins with subsequent losses?

I — Independent origins?

Current Biology

Figure 1. Sponges return as the sister to all other animals.
The origin of muscles, neurons and through-guts (each lacking in sponges) is not obvious and may be a single common origin (C) or multiple independent origins (I). Simple placozoans keep things complicated.

contaminants, as well as excluding taxa with too much missing data. Improving the data and its handling is key. Simply adding more data is not the solution for better phylogenomics [9].

Molecular phylogeny methods are based on assumptions about how the evolutionary process works. Explicit models allow parameters to be estimated, but an overly complex model can become computationally intractable so they are necessarily simplified. In the analysis of large data sets, for instance from transcriptomes and genomes, systematic errors arise due to heterogeneity of nucleotide compositions, rate variation across lineages and also within-site rate variation; errors are exacerbated when the amount of data increases further. In contrast, random sampling (or stochastic) errors occur when limited data lead to inaccurate model parameter estimates. Sampling errors are overcome with increasing the amount of data, but reducing systematic errors and increasing robustness to substitution model violations are of greater value [10].

Especially problematic are lineages in which genes evolve quickly or heterogenously over time, leading to long branches in the phylogenetic tree.

Without appropriate data modelling and choice, long branches attract each other. Long branch attraction occurs because the genes of long-branching lineages share nucleotide or amino acid positions by chance, and not due to common ancestry, because of accelerated substitution rates. Simple models necessary to analyse large data sets are prone to long branch attraction artefacts. Ctenophores and sponges both exhibit long branches reflecting a relatively fast pace of molecular evolution, and the selection of outgroups used to root the tree is known to influence the placement of at least ctenophores [6]. Employing a site-heterogeneous model (e.g. CAT, capable of modelling multiple categories of site substitution) may handle long branch attraction artefacts better than site-homogeneous substitution models [11], although not everyone agrees [12]. Until now, well-supported conflicting solutions described as 'unambiguous' have left a knotty problem at the base of the animal tree.

Simion et al. [1] have untangled the early branches of the animal tree of life with demonstrable improvements to sampling and data handling. Levels of congruence between the tree and the data are higher than in analyses that used alignments developed through manual

curation or automatic assembly alone. Missing data amount to just 39% and the resulting dataset is discernibly better than other recent compilations, suggesting the resolution of ctenophores as the sister to all other animals is indeed a likely artefact of long branch attraction. This high level of data acquisition and scrutiny sets new standards for phylogenomics, particularly in addressing problems beset by long branch attraction. Perhaps the most important result of their analysis is that the pendulum has returned and sponges regain their position as sister to all other metazoans. With ctenophores arising immediately thereafter we are way off a scenario of increasing complexity towards the bilaterians. Morphological, developmental and genomic studies have more to add. Cell organisation in the osculum of sponges, the opening through which water is expelled, suggests early evolutionary steps towards sensory and coordination systems found in more complex animal groups [13].

Meanwhile, the placozoans remain enigmatically modest in structure and form. Their placement arising after the sponges and ctenophores suggests secondary simplification from a more complex ancestor, or that ctenophores and Cnidaria+Bilateria have independently acquired a nervous system, synapses, and muscles. Ctenophores have recently been shown to have a through-gut [14] as had the ancestor to bilaterians, but cnidarians have blind-ending guts [2]. Detecting common or independent origins of these major evolutionary innovations may help interpret the tree further. If, for instance, knockouts of ctenophore genes orthologous to bilaterian synaptic genes might lead to phenotypes consistent with synaptic deficiencies, neurons can be argued to have descended from a common ancestor [15]. Future gene knockout experiments may arbitrate between independent and common origins of other key traits at the base of the tree.

One certainty emerges – upon further examination nothing is truly simple. But consensus may be achievable. Charles Darwin's famous sketch of a phylogeny in one of his notebooks with the words "I think" acts as a reminder that phylogenies are hypotheses. As such, they can always

be tested. Currently, our best estimate with the best data, and arguably the best tools, tells us sponges are the sister group to all other metazoans — we think.

REFERENCES

1. Simion, P., Philippe, H., Baurain, D., Jager, M., Richter, D.J., Di Franco, A., Roure, B., Satoh, N., Quéinnec, E., Ereskovsky, A., et al. (2017). A large and consistent phylogenomic dataset supports sponges as the sister group to all other animals. Curr. Biol. 27, 958–967.

2. Telford, M.J., Budd, G.E., and Philippe, H. (2015). Phylogenomic insights into animal evolution. Curr. Biol. 25, R876–R887.

3. Leys, S.P., Nichols, S.A., and Adams, E.D. (2009). Epithelia and integration in sponges. Integr. Comp. Biol. 49, 167–177.

4. Dunn, C.W., Hejnol, A., Matus, D.Q., Pang, K., Browne, W.E., Smith, S.A., Seaver, E., Rouse, G.W., Obst, M., Edgecombe, G.D., et al. (2008). Broad phylogenomic sampling improves resolution of the animal tree of life. Nature 452, 745–749.

5. Philippe, H., Derelle, R., Lopez, P., Pick, K., Borchiellini, C., Boury-Esnault, N., Vacelet, J., Renard, E., Houliston, E., Quéinnec, E., et al. (2009). Phylogenomics revives traditional views on deep animal relationships. Curr. Biol. 19, 706–712.

6. Pisani, D., Pett, W., Dohrmann, M., Feuda, R., Rota-Stabelli, O., Philippe, H., Lartillot, N., and Wörheide, G. (2015). Genomic data do not support comb jellies as the sister group to all other animals. Proc. Natl. Acad. Sci. USA 112, 15402–15407.

7. Borowiec, M.L., Lee, E.K., Chiu, J.C., and Plachetzki, D.C. (2015). Extracting phylogenetic signal and accounting for bias in whole-genome data sets supports the Ctenophora as sister to remaining Metazoa. BMC Genom. 16, 987.

8. Whelan, N.V., Kocot, K.M., Moroz, L.L., and Halanych, K.M. (2015). Error, signal, and the placement of Ctenophora sister to all other animals. Proc. Natl. Acad. Sci. USA 112, 5773–5778.

9. Philippe, H., Brinkmann, H., Lavrov, D.V., Littlewood, D.T., Manuel, M., Worheide, G., and Baurain, D. (2011). Resolving difficult phylogenetic questions: why more sequences are not enough. PLoS Biol. 9, e1000602.

10. Yang, Z., and Rannala, B. (2012). Molecular phylogenetics: principles and practice. Nat. Rev. Genet. 13, 303–314.

11. Lartillot, N., and Philippe, H. (2008). Improvement of molecular phylogenetic inference and the phylogeny of Bilateria. Phil. Trans. R. Soc. B 363, 1463–1472.

12. Whelan, N.V., and Halanych, K.M. (2017). Who let the CAT out of the bag? Accurately dealing with substitutional heterogeneity in phylogenomic analyses. Syst. Biol. http://dx.doi.org/10.1093/sysbio/syw084.

13. Ludeman, D.A., Farrar, N., Riesgo, A., Paps, J., and Leys, S.P. (2014). Evolutionary origins of sensation in metazoans: functional evidence for a new sensory organ in sponges. BMC Evol. Biol. 14, 3.

14. Presnell, J.S., Vandepas, L.E., Warren, K.J., Swalla, B.J., Amemiya, C.T., and Browne, W.E. (2016). The presence of a functionally tripartite through-gut in Ctenophora has implications for metazoan character trait evolution. Curr. Biol. 26, 2814–2820.

15. Ryan, J.F. (2016). Did the ctenophore nervous system evolve independently? Zoology 117, 225–226.

Sensorimotor Neuroscience: Motor Precision Meets Vision

Kit D. Longden, Stephen J. Huston, and Michael B. Reiser*
Janelia Research Campus19700, Helix Drive, Ashburn, VA 20147, USA
*Correspondence: reiserm@janelia.hhmi.org
http://dx.doi.org/10.1016/j.cub.2017.02.047

Visual motion sensing neurons in the fly also encode a range of behavior-related signals. These nonvisual inputs appear to be used to correct some of the challenges of visually guided locomotion.

The ability to pivot on the spot and change your direction is a useful skill, and not just for a politician. To do so our motor systems edit our visual responses, augmenting and adjusting our reality. This motor creation of sensory news happens in many and sophisticated ways, some of which are well known, and some have only recently been discovered [1,2]. At the most basic level, we structure our movements to suit our visual systems — witness a dancer 'spotting' a pirouette to minimize the time spent experiencing visual blur [3]. At the neural level, motor control centers conveniently silence our visual perception during rapid eye-movements — saccades — when the world is also blurred, such that we never see the blur [4]. Recent data from mice and flies indicate that visual processing is also widely affected by locomotion, such that neurons serving many visual circuits encode not only visual motion, but also self-motion velocity, even in the dark [2,5].

Two new studies [6,7] indicate that flies pack all this motor modulation of visual processing into one visual pathway. For those of us studying sensory systems, this is something of a revelation — the motor activity occurs in benchmark cells for understanding efficient coding of sensory information [8]. For those with a motor bent, the discoveries echo many of the principles operating in state-dependent reflexes and their disengagement in voluntary actions, in cells with proposed roles in visual course control and object detection [9,10]. To dig into these stories, we need to meet the protagonists, the fly's horizontal system (HS) and vertical system (VS) cells.

The fly's HS and VS cells are found in a visual brain area, the lobula plate (Figure 1A). They are exquisitely accessible for physiological recordings, and many decades of study have led to a