

Viewpoints

Bryophytes are not early diverging land plants

Summary

Phylogenetic trees have permeated biology. However, an understanding of how to interpret phylogenies has lagged behind, notably in publications outside of evolutionary biology. Here I argue that some language commonly used in plant systematics has contributed to the confusion by describing phylogenetic trees using intuitive but misleading terms reminiscent of Aristotle's *Scala Naturae*. These terms (perhaps inadvertently) misrepresent evolution, not as a process acting on all living species, but rather as a progression of successively diverging lineages leading to a group that represents a subjectively defined endpoint. My goal here is to show how thinking of the tree of life in terms of early-diverging lineages and higher groups can distort evolutionary literacy, confound interdisciplinary communication, and potentially bias research agendas. I focus on the relationship between bryophytes and angiosperms as a case study, but the theme applies to all branches of the tree of life. Fortunately, evolutionary biologists have developed an easily understood alternative framework – tree thinking – which I highlight as a means to promote a clear understanding of phylogenies across sub-disciplines of biology, and between practicing biologists and students, or members the public which funds much of our work.

A case study on the (mis)use of early diverging lineages – the problem

A phylogenetic tree appears to be a relatively simple diagram (Fig. 1a). The tree consists of branches, or lineages, whose tips can be species, individuals within a species, alleles, or gene copies. For extant species, the tip of each branch represents the present, and the tree describes the genealogical relationships among the species. The branches are connected at nodes, which represent the most recent common ancestor of two branches. Going further back in time, pairs of branches successively connect to their common ancestor, until all descendants in the tree are connected at the root, the oldest part of the tree. The relationship between any two tips is shown by the node, or common ancestor, that connects them; two tips that share a more recent common ancestor than two other tips are by definition more closely related. Thus, the arrangement of the tips in the present is immaterial, provided that the connections of the nodes depict the correct most recent common ancestors (e.g. in

Fig. 1(a), D and E can switch places without changing the tree; similarly A could be listed to the right of the rest of the branches, provided A still connects with the others at node 4). The information in the phylogeny is contained only in the branching order along the axis from the root to the tips.

The interpretation of phylogenies simple enough to teach in Introductory Biology classes, and many widely-used textbooks now cover the subject well. To facilitate learning this skill, many instructors use letters to designate tips, as in Fig. 1(a). In this example, it's straightforward to see that D and E share a common ancestor at node 1, and they are the most closely related tips. Slightly less obvious is that A is no more closely related to B than it is to E, because both of these species pairs share the same common ancestor at node 4. The letters are a useful pedagogical tool because we have no preconceived notions about their relationships, or their perceived evolutionary distance from a node in the past. However, labeling the tips with known species can sometimes make these relationships harder to grasp precisely because we, perhaps unconsciously, bring additional information about those species beyond what is specifically contained in the branching pattern in the tree.

To see how our understanding of organisms can color our interpretation of phylogeny, consider how the bryophytes *Marchantia polymorpha* and *Physcomitrella patens*, now genomic model systems (Bowman *et al.*, 2017; Lang *et al.*, 2018), are presented in research outside of evolutionary biology. The genomics revolution brought renewed interest in diverse model systems, and it is now routine to see comparisons of gene function between bryophytes and angiosperms. Indeed, the relative simplicity of bryophyte development, the gametophyte-dominant life cycle, and their ability to undergo efficient gene targeting make these species models of choice for studying many cellular and developmental phenomena.

The simple morphology and gametophyte-dominant life cycle of *M. polymorpha* and *P. patens*, however, misleads some to conclude that these species are themselves primitive, and therefore represent the ancestral condition in plants (for other examples, see Crisp & Cook, 2005). For it to be true, however, bryophytes must have stopped evolving 400 or so million years ago when their ancestor split from the ancestor of the vascular plants. The thousands of different species of bryophytes indicate that this cannot be the case (Laenen *et al.*, 2014). Indeed, in the time since the common ancestor of land plants, the lineages leading to *P. patens* and *M. polymorpha* axiomatically must have evolved for exactly as many years as the lineage leading to *Arabidopsis thaliana* (or any other vascular plant for that matter). Bryophytes almost certainly have evolved for more generations, given that most bryophytes reproduce annually, whereas, many vascular plants, including the ancestors of modern seed plants, probably took several years to mature.

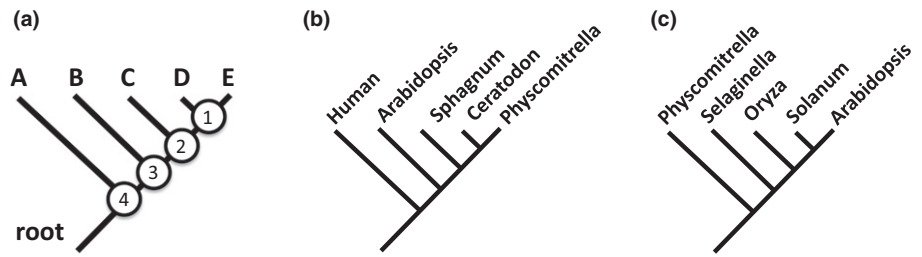


Fig. 1 Phylogenies illustrating the evolutionary relationships among: (a) five hypothetical species, A–E, with most recent common ancestors, 1–4, shown on the nodes; (b) animals, angiosperms, and three moss genera; (c) five land plant genera.

During the time since mosses and vascular plants last shared a common ancestor, each lineage has acquired many derived traits but retained some ancestral ones. While aspects of the bryophyte life-cycle are primitive – and therefore shared with the last common ancestor of bryophytes and vascular plants, a *bona fide* early land plant – the majority of traits have changed during that time. For example, the small sporophyte of *P. patens*, is in fact, a derived trait, having evolved from a larger sporophyte within the past 5 million years (McDaniel *et al.*, 2010).

Yet, it has become popular to label bryophytes as ‘ancient’, ‘basal’, or ‘early diverging’ lineages and imply that they have some special significance by virtue of this fact. The underlying logic seems to be that since they diverged long ago from the lineage that ultimately gave rise to the most diverse and familiar group of plants, the conspicuous and economically important angiosperms, the bryophytes must have a unique role to play in inferring evolutionary directionality – that bryophytes must be somehow evolutionarily closer to the ancestor of land plants (Crisp & Cook, 2005). However, there is a flaw in this logic: think of a speciation event that produces two descendent species. Which species is the early diverging one? Neither, of course, they diverged from one another at the same time. *All phylogenies are a series of such bifurcations*. It is only if one lineage subsequently radiates into a large number of species that we are likely to think of one (the diversified lineage) as the main branch, and the other as the ‘ancient’ lineage, the ‘basal’ branch.

For example, in Fig. 1(a), some may think of species A and B as basal lineages. In Fig. 1(b), though, humans and *A. thaliana* somewhat uncomfortably occupy those lineages, ‘basal’ to three moss genera. Phylogenetically this is correct (mosses share a more recent common ancestor with *A. thaliana* than with humans), but no one would present such a tree because it seems to misrepresent evolution. But does it? The reality is that although the phylogeny in Fig. 1(c) is more familiar to us, with its implication of evolutionary progress toward the ‘main lineage’ of ‘higher’ plants, the tree depicted in Fig. 1(b) is perfectly valid. By implying that any one lineage represents a more derived, or higher form of plant evolution, we are simply applying a subjective judgment that this lineage is more important, a claim that cannot be defended on evolutionary principles (for examples from entomology, see Krell & Cranston, 2004).

Thinking of some lineages as ‘intermediates’ is similarly fraught. Bryophytes are sometimes referred to as intermediates between algae and vascular plants, or ferns are thought to be intermediate between bryophytes and seed plants. To see why it is problematic to refer to a lineage as intermediate, consider the phylogeny in Fig. 1(b) – is *Arabidopsis* intermediate between humans and mosses? While *Arabidopsis* may possess some traits that are indeed intermediate

between mosses and humans, this observation is specific to those traits, not the lineages as a whole. *Arabidopsis* is certainly not in transition to become more moss-like. Of course, many more traits are likely to appear to be transitional in comparisons among more closely related groups. These traits, however, are not evolving toward the state in the so-called ‘higher’ lineage, but rather they are diverging from their common ancestor; each lineage is on its own independent evolutionary trajectory. For example, while the liverwort sporophyte is an intermediate size between the sporophytes of algae and vascular plants, the emerging consensus that the bryophytes are monophyletic (Puttick *et al.*, 2018; de Sousa *et al.*, 2019) indicates that the liverwort sporophyte may have undergone a reduction in size since the common ancestor of extant land plants.

The idea of lower, intermediate, and higher organisms is a modern manifestation of Aristotle’s *Scala Naturae*, with stones at the base and angels at the top (Fig. 2). Obviously, we no longer include inanimate objects nor celestial creatures in our phylogenies, but the terms that describe a ladder-like hierarchy of life have proven more difficult to remove from our interpretations of phylogenetic trees. The terms basal lineage and early diverging lineage, like higher and lower, have absolutely no phylogenetic or topological meaning, except to reinforce our subjective notions of which is the main branch of the tree of life.

Let us pause and consider why we think of the angiosperms as the main branch of plants. The implication is often that because the flowering plants have the most species, they must be the most evolutionarily successful lineage. But diversification is a peculiar measure of success: diversification simply means that reproductive isolation evolved quickly enough to produce new species faster than extinction removed them. This criterion is not universally applied across the tree of life, either, or else rodents would be considered more successful than primates. Perhaps angiosperms are more exquisitely adapted to their surroundings than are the bryophytes, but it is practically impossible to provide quantifiable evidence to support this claim. Other measures of evolutionary success – geographic spread, number of individuals, and so on – are similarly selectively applied across the tree of life and, therefore, similarly fail to provide an objective measure of success. The only defensible position is that all extant organisms are evolutionary successes, because they have continued to reproduce themselves.

I should interject here that the traits that we use to identify the major lineages of land plants – carpels in angiosperms, microphylls in the lycophytes, seta in the bryophytes – of course appeared in the fossil record at different times, some far more recently than others. Because taxonomic names are based on the possession of a particular character, the taxon Magnoliophyta is younger than the Lycophyta;

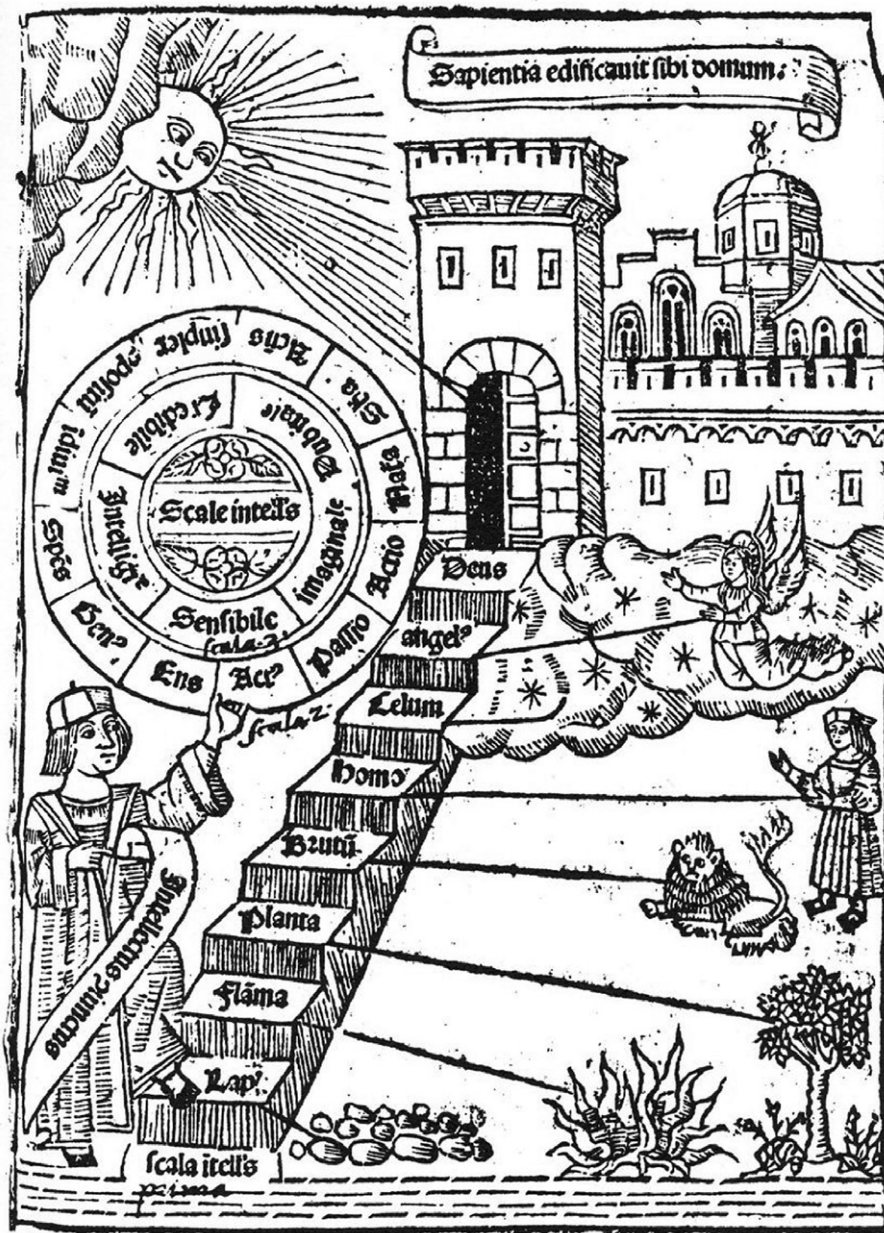


Fig. 2 The mediaeval *Scala Naturae* as a staircase to the kingdom of heaven (from Ramon Lull, *Ladder of Ascent and Descent of the Mind*, 1305).

that is, the defining character of angiosperms arose more recently than the defining character of lycophytes. Nevertheless, even though a character that we find taxonomically useful evolved at a particular point in time, the term lineage implies *continuity* rather than *category*. The evolutionary essence of a lineage (as opposed to a taxonomic unit) is not defined by the traits that we use to identify a taxon. Instead, a lineage is an amalgam of many ancestral and derived traits, that vast majority of which are invisible to us.

Clearly we need diagnostic traits to identify taxa. When we define a lineage by such traits, however, we risk engaging in taxonomic essentialism, the tendency to understand that lineage as discrete, fixed, and uniform, and the nature of these defining characters informs our view of the entire lineage (cf. racial essentialism, Bastian & Haslam, 2006; Williams & Eberhardt, 2008). Linking the evolutionary character of a lineage to a

subjective subset of traits is a vestige of pre-evolutionary thinking that is reinforced by terms like basal and early diverging.

Why bother fixing this?

We as biologists (mostly) take terms like early-diverging or basal lineage as simple shorthand for describing the phylogenetic position of a group with respect to a highly diverse or familiar group. It can seem cumbersome to describe the relationships or use potentially unfamiliar taxonomic names. So why should we exert the effort? Although interpreting phylogenetic trees is now second nature within the evolutionary biology community, this skill may be less familiar for people outside of the discipline, including our colleagues in other areas of biology, our students, and the public that funds much of our work. When we teach using terms like 'basal

grade' or 'early diverging lineage', our students are more likely to misunderstand the basics of interpreting phylogenies. They are more likely to think, for example, that mosses are more closely related to ferns than gymnosperms, or that *Amborella* is more closely related to waterlilies than roses.

Grouping organisms based on shared ancestral traits is a fundamental error in one of the core concepts of modern biology (for effective teaching tools to avoid this error, see Omland *et al.*, 2008; Meisel, 2010; Halverson, 2011; Baum & Smith, 2013; Smith, 2016; Gibson & Cooper, 2017). Why are we still using terms that conform to our students' cognitive biases, allowing them to make such errors, rather than using terms that promote evolutionary thinking? Unwittingly we have tapped into a pre-existing narrative that twists our hard-won phylogeny into Aristotle's ladder of life, with stones at the base and angels at the top. We have allowed students to think of extant species as living fossils, ancestors to other extant species.

One of the most spectacular examples of thinking of extant species as living fossils comes from *The atlas of creation* (Yahya, 2006), a coffee-table book that infamously was mailed to university scientists in 2007. The book is filled with hundreds of glossy photographs of truly stunning fossils that the author attempts to marshal for an argument against evolution – I encourage you to give it a look. Each page shows a well-preserved organism from millions of years ago alongside a photograph of a modern representative that looks remarkably like the fossil. The caption of each pair of photographs raises the same question: how can evolution (i.e. descent with modification) be true when the modern organism looks just like its fossilized ancestor?

The answer, as we well know, is that the physical appearance, and in fact any subset of characteristics, tells only part of the story. Such characters do not represent the essence of the lineage. Although parts of the gross morphology remain remarkably consistent, the physiology, biochemistry, and life history of an organism, the parts that do not fossilize in sediment, are likely to have all changed in a multitude of ways. We can learn a great deal about these traits by studying the genomes of the modern descendants of fossilized organisms, even though these traits are not preserved in sedimentary rock. We may even learn that the genetic basis of an apparently ancient, conserved form has changed dramatically over the eons (Sommer, 2008). But when we use the term 'early diverging lineage' for an extant organism that looks like a fossil or reconstructed ancestor, we are making an argument very similar to *The atlas of creation*. The rich history that we can infer using genomic or experimental tools is undermined by language that inadvertently communicates that some species are 'living fossils,' which, by implication, have remained frozen since they diverged from a subjectively labeled 'main branch' of evolution.

What do we say instead?

One comment I hear over and over is: 'OK, so "basal lineage" is bad, but you need to tell me a simple word that I can use in its place.' At first blush, this question seems quite reasonable. However, upon closer inspection, it misses a fundamental point. To illustrate this, consider the Copernican revolution that replaced geocentrism with

heliocentrism. Before the observations and math describing gravity and elliptical orbits around the sun, Aristotle and others had conceived of the firmament as composed of celestial bodies in concentric aethers revolving around the earth. Absorbing the heliocentric view was no doubt challenging. You can imagine a similar comment to what I described: OK, so you say that 'aether' is not correct, but what is a word that I can use in its place?

It is not so much that the words aether and basal are bad, it is more that they represent relationships that we now know do not exist. These words are embedded in falsified concepts of nature (Geocentrism, Scala Naturae), and there is no one-to-one match with the current concept. Just as the terms used to describe a geocentric solar system do not map onto a heliocentric view, the terms derived from the Scala Naturae (Fig. 2) do not map onto the tree-thinking perspective of modern evolutionary biology.

We can more accurately describe the lineages in a phylogenetic tree using the language of family relations, like sister groups and their common ancestors (Omland *et al.*, 2008; Baum & Smith, 2013). Species that share a recent common ancestor are like siblings. Species that share a deeper common ancestor (like a grandparent) are like cousins. Our cousins are not early diverging lineages, they are just more distantly related to us. Thinking in terms of a family tree makes it clear that we cannot read an evolutionary progression from left to right across the tips of a tree (Omland *et al.*, 2008). For example, in Fig. 1(b), saying that 'animals are sister to plants', or 'tracheophytes are sister to bryophytes' is a less biased way to describe these relationships.

We should also consider whether the best substitute for 'basal lineage' is nothing at all – is the phylogenetic position of the study organism even worth mentioning in the first place? Certainly for comparative analyses, where the goal is to reconstruct ancestral states, it is necessary to explain the phylogenetic relationships of the relevant species. But does it make sense to emphasize the interesting phylogenetic position of a particular group if the point of a study is to understand variation within that group? In many manuscripts, the phylogenetic position of a study organism is only tangentially related to the subject of the study. In fact, situating the study organism in the tree of life may distract us from the natural history of the organism, which is often key for understanding the research problem. For example, is the phylogenetic position of mosses relevant if we are interested in variation in drought tolerance among a few closely related species? It could be, but most often it will be the organisms themselves, not the interesting phylogenetic position, that makes for exciting research.

I started off this Viewpoint talking about two model organisms, *P. patens* and *M. polymorpha*, that have been mischaracterized as basal plants. The great value of studying conserved features among distantly related model organisms is that it allows us to peer deep into history, not because any extant plants represent ancestors, but because they share ancient common ancestors. I want to finish by suggesting that these plants can help us understand important processes which may not lie so deeply buried in history. The biological variation within bryophytes has intrinsic value, not because of its phylogenetically interesting position sister to the vascular plants, but rather because they are themselves important for understanding the world around us. Exploring the variation in

understudied groups opens whole new research avenues that complements what we learn from major model systems.

However, it is hard not to suspect that the use of terms like ‘basal lineage’ may bias how we as scientists evaluate such a research agenda. This is not to suggest that resources are directed away from ‘basal’ organisms, but rather that the terms we use for a group may influence the kinds of research questions that we prioritize for that group. For example, would it seem strange to study adaptive radiation in a so-called ancient, basal clade, or stasis in a so-called derived clade? I do not know of psychological studies that address these specific terms, but studies of unconscious bias certainly indicate that the terms that we use to describe a group shape our perceptions of that group.


Tree thinking is a relatively simple conceptual framework that avoids the bias inherent in the ladder-like view of nature, and may promote more effective exchanges between evolutionary biologists and researchers from many other disciplines of biology. It will be easier to fully realize the synergistic potential of interdisciplinary collaboration if we abandon language left over from the days of pre-evolutionary taxonomy (e.g. basal lineage, early diverging group, and living fossils) that conform to unconscious biases and misconceptions regarding the process of evolution (e.g. notions of evolutionary success). The linear march through the phyla presented in textbooks is indeed a convenient order for teaching students about the evolution of taxonomically or functionally important organismal features. However, if we retain an attitude of taxonomic essentialism, in which lineages are defined by those traits, the stories that we tell students may inadvertently suggest that some taxonomic groups have ‘progressed’ evolutionarily, while others have ceased to evolve following their origin.

Interdisciplinary communication is challenging, but we can make it easier and more productive by using terms that help our colleagues understand our field rather than sow confusion. The payoff from using the language of familial relationships – clearer interdisciplinary communication using terms that are congruent with our modern understanding of evolution – is well worth the small amount of extra effort it takes to recognize that all extant branches of the tree of life are still evolving.

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