Haeckel's Biogenetic Law and the Land Plant Phylotypic Stage

KARL J. NIKLAS, EDWARD D. COBB, AND ULRICH KUTSCHERA

Haeckel's 150-year-old biogenetic law has been refuted by embryological studies of metazoans (predominantly vertebrates). However, modern empirically viable variants exist, such as the concept of the phylotypic stage that emerged predominantly from the study of metazoans. We briefly review the history of the biogenetic law and the evidence for the metazoan phylotypic stage, we explore whether a phylotypic stage exists for the land plants by comparing the embryogenesis of diploid sporophytes across nonvascular and vascular lineages, and we examine whether homologies exist for haploid gametophytes. If homology is defined as "the same structure(s) achieved by the same developmental patterning(s)," we fail to find a single phylotypic stage for land plant sporophytes or gametophytes based on morphological criteria. We speculate that land plant embryogenesis has undergone three major evolutionary transformations (heralding the appearance of bryophytes, pteridophytes, and seed plants) that correspond with evolutionary transformations in the preceding ancestral phylotypic stage.
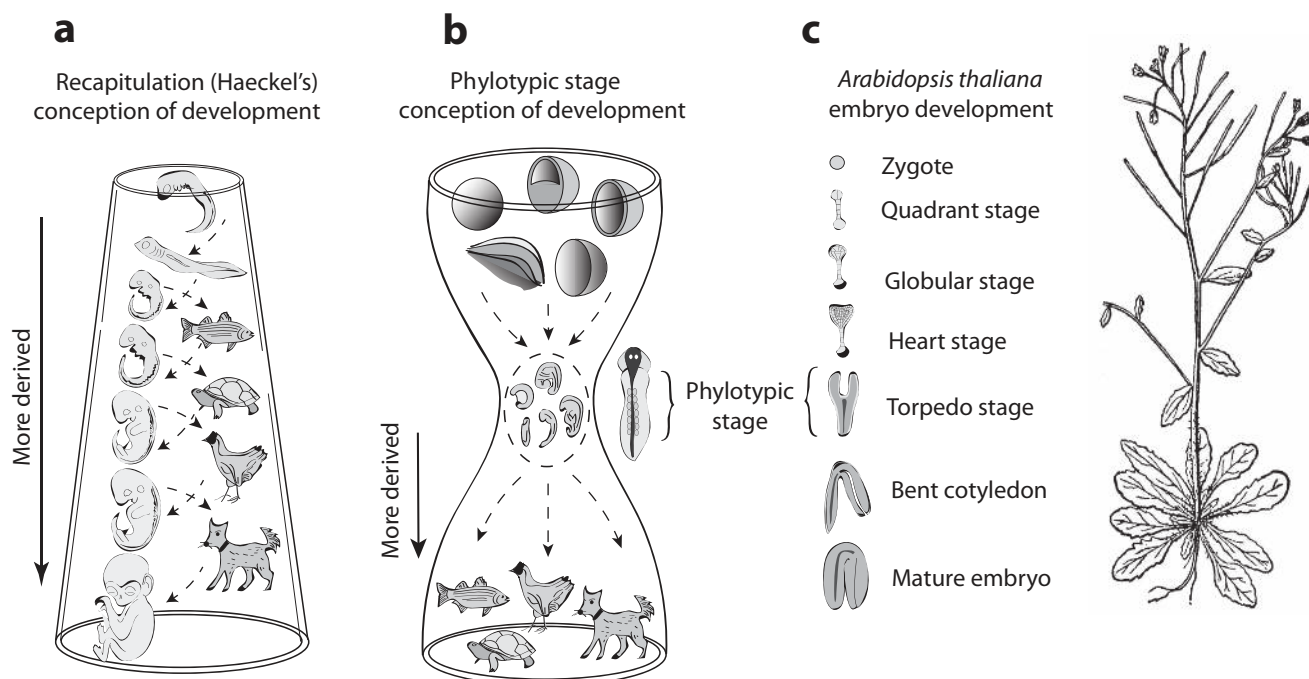
Keywords: developmental biology, embryology, plant evolution, recapitulation

Ernst Heinrich Philipp August Haeckel (1834–1919) is widely considered to be the author of the biogenetic law (Richards 2002, Hoßfeld and Olsson 2003, Levit et al. 2015), which is summed up by the well-known phrase "ontogeny recapitulates phylogeny" (figure 1a). Although it has been long discredited, empirically viable modern versions of Haeckel's biogenetic law exist. Among these is the concept of a phylotypic stage in vertebrate embryogenesis—that is, the stage when all of the major body parts appear in their final positions as undifferentiated organ primordia (Ballard 1981, Raff 1996, Prud'homme and Gompel 2010, Svorková 2012). This stage in metazoan embryogenesis is also reached at approximately the same body size, possibly because the majority of vertebrates are oviparous or ovoviparous and because egg size varies comparatively little across animal phyla (O'Farrell 2015). More recent molecular studies of such phylogenetically diverse organisms as *Caenorhabdites*, *Drosophila*, and the zebrafish (*Danio rerio*) have identified the equivalent of a *transcriptome phylotypic stage*—that is, the point in embryo development at which the transcriptome is dominated by highly conserved genes involved in the patterning of the metazoan body plan (Richardson 2012). Indeed, there is mounting evidence to support the claim that the basic metazoan body plan is predicated on a developmental program that is highly conserved across diverse metazoan phyla. For example, a gradient in a signaling molecule of the transforming growth factor (TGF)-β type appears to guide the dorsiventral polarity of the metazoan embryo, whereas the local expression of

different homeotic-type transcription factors subdivide the anteroposterior embryo axis (Shen 2007).

Evidence also supports the notion that the phylotypic stage is resistant to evolutionary modification, as was suggested by Raff (1996). For example, within the *Drosophila melanogaster* species subgroup, spatial and temporal differences in embryological gene expression domains as well as the loss and gain of expression domains occur before or after, but not during, the phylotypic stage (Rebeiz et al. 2011), which is consistent with the notion that the pre- and postphylotypic stages within this *Drosophila* species subgroup have undergone evolutionary modification but that the phylotypic stage itself has not. These and other embryological phenomena support three conclusions: (1) The metazoan phylotypic stage is resistant to evolutionary modification, (2) the differences among species within a lineage or clade reflect evolutionary modifications of developmental events preceding or following the phylotypic stage, and (3) the differences among lineages reflect modifications of the phylotypic stage itself. In this respect, Haeckel's ontogeny recapitulates phylogeny (figure 1a) has been replaced by the view that early metazoan embryogenesis is divergent even among related species but converges onto a shared pattern (the phylotypic stage) only to subsequently diverge once again (figure 1b). This bottleneck in embryological patterning provides evidence for the evolution of an early and successful strategy for achieving the basic metazoan body plan.

The existence of a phylotypic stage in metazoan embryogenesis (and a recent report of one for the fungi; see Cheng

---

Advance Access publication 19 February 2016

a Recapitulation (Haeckel's) conception of development

b Phylotypic stage conception of development

c *Arabidopsis thaliana* embryo development

Zygote
Quadrant stage
Globular stage
Heart stage
Torpedo stage
Bent cotyledon
Mature embryo

*Figure 1. Schematics of the biological theory of recapitulation as advocated by Haeckel (a), the more modern conception of the metazoan phylotypic stage (b), and the various designated stages in the embryogenesis of the **Arabidopsis** sporophyte (c). (a) Haeckel conceived of embryogenesis as the terminal addition of developmental novelties to the ontogeny of previous life forms that could be arranged in a linear ancestor–descendant sequence (from top to bottom). (b) The hourglass-like metazoan phylotypic stage is that stage in embryogenesis when the body plan and organ primordia become distinguishable. (c) On the basis of transcriptome analyses of the **Arabidopsis** sporophyte embryogenesis, Quint and colleagues (2011) reported that the torpedo stage is the phylotypic stage for the land plants (see text for details). Mature sporophyte of **Arabidopsis** shown to the right.*

et al. 2015) raises two important but challenging questions: Does a morphological or transcriptome phylotypic stage exist for the monophyletic land plants, and, if so, does homology at the genomic level (as revealed by comparative transcriptomics) translate into the morphological level (as revealed by comparative embryogenesis)? The first of these questions emerges from the report that a transcriptome hourglass-like pattern exists during the embryogenesis of the model plant *Arabidopsis thaliana*, a late divergent eudicot. By mapping the appearance of developmentally important genes onto the phylogeny of plants (i.e., by constructing a phylostratigraphic map), Quint and colleagues (2012) estimated the ages of genes and their sequence divergences for *A. thaliana*, for its sister species *A. lyrata*, and for other related taxa and subsequently mapped these two evolutionary indices onto the transcriptome profiles of seven stages in the embryogenesis of the *A. thaliana* sporophyte (figure 1c). The result is an hourglass-like pattern in which gene age and sequence divergence are initially very large, subsequently converge at the torpedo embryonic stage, and diverge once again. Quint and colleagues (2012) interpreted this pattern to indicate that the torpedo stage is the phylotypic stage of the land plants (see also Drost et al. 2015). It is worth noting that the *torpedo stage* is that stage

when the embryonic suspensor degenerates and the shoot and root apical meristems are formed (Maheshwari 1950). In the absence of similar molecular studies, we speculate that if a single transcriptome phylotypic stage exists for the land plants or just for the angiosperms, one or both of these two embryological events might serve as morphological markers for its identification.

Although the study of Quint and colleagues (2012) is so far unique, it raises the intriguing possibility that a single phylotypic transcriptome stage exists for the monophyletic land plants. It is nevertheless mute regarding the second question concerning the translation of homology at one level of biological organization to another level of organization. The concept of homology is most certainly complex and continues to be debated (Müller 2003, Wagner 2014, Roux et al. 2015). The computational challenges of translating transcriptome data into morphogenesis are equally intellectually daunting. However, in the context of the phylotypic stage, particularly in the absence of phylogenetically extensive transcriptomic analyses of land plant embryogenesis, a reasonable definition for *homology* is "the same structure(s) achieved by the same developmental phenotypic patterning(s)." When this definition is embedded in the context of embryology, organs are homologous if they

develop from the same embryonic tissues. Armed with this definition, our goal is (a) to provide a brief review of the conceptual history of biological recapitulation to make its biological assumptions and assertions clear and (b) to examine whether a phylotypic stage exists for all, most, or some land plant lineages. The first of these two goals is important because the assumptions and assertions of Haeckel's biogenetic law and the concept of the phylotypic stage are historically interconnected. The second goal is important because the metazoan life cycle has one multicellular life form and typically involves a determinate ontogeny (i.e., body size and the number of body parts do not increase throughout the life time of the animal). In contrast, the land plant life cycle involves the ontogeny of two multicellular life forms, a diploid sporophyte and a haploid gametophyte (Hofmeister 1851), one of which is indeterminate (i.e., body size and the number of body parts increase throughout the life time of the plant). Furthermore, sporophyte embryogenesis most likely evolved from the co-option of genomic toolkits participating in the ontogeny of the gametophyte because all available evidence indicates that the ancestors of the land plants lacked a diploid multicellular life form in their life cycle (Niklas and Kutschera 2009, 2010). Logically, therefore, if a phylotypic stage cannot be ascertained for the land plants using the sporophyte as a template, it might be found in the ontogeny of the land plant gametophyte that in turn traces its genetic toolkits back to the charophycean-like ancestors of the land plants.

Haeckel's Biogeneic Law and the metazoan phylotypic stage

Like Darwin (1851, 1859), Haeckel used comparative developmental studies of postgastrulation embryogenesis to establish the classification of metazoans, because, at the time, this approach shed what was considered to be the best light on character homologies and therefore could be used to establish phylogenetic relationships (Haeckel 1866, 1874; see Gould 1977, Olsson et al. 2010). Indeed, Haeckel's biogenetic law, which emerged from blending Darwinism with Lamarck's hereditary theory of acquired traits, is based on two assertions: (1) Evolutionary novelties appear first in the adult form, and (2) phylogeny is the result of the successive tacking of novel adult character states onto a preexisting embryological series of forms.

However, comparative developmental studies that began during the late nineteenth century demonstrated the importance of pregastrulation embryogenesis and its potential for explaining evolutionary change. Ultimately, this focus led to the concept of a phylogenetic stage, which can be traced to a paper written by Friedrich Seidel (1897–1992) on the relationship between ontogeny and phylogeny for a symposium at a meeting of the German Zoological Society celebrating the 100th anniversary of the publication of *On the Origin of Species* (Darwin 1859). In this paper, Seidel provided examples of different morphological pathways during the pre- and early-gastrulation stages of cnidarians,

annelids, mollusks, echinoderms, and vertebrates (Seidel 1960). At the end of each diagram, Seidel used the term *körpergrundgestalt* (loosely translated as "body shape" or "body plan") to designate the stage at which each of the different developmental pathways converged across otherwise divergent embryological sequences. In taxa with life cycles containing two multicellular life forms (e.g., those with larva and adult), Seidel designated two *körpergrundgestalts*, one for each of the two life forms. Subsequently, Alfred Kühn (1885–1968) developed the notion that there could be different early developmental pathways within different metazoan phyla that nevertheless converged on the same homologous embryonic stage. In a study on the different developmental pathways preceding the polyp stage in hydrozoans, Kühn (1914) used for the first time the term *körpergrundgestalt* to designate the embryological homologue across all metazoan phyla. *Körpergrundgestalt* was subsequently translated into English as "phylotypic stage" by Sander (1983).

The phylotypic stage and the land plant sporophyte
Haeckel's biogenetic law and the concept of the phylotypic stage are conceptually as well as historically interconnected because they both assume that the developmental programs of otherwise diverse organisms can be aligned on the basis of well-defined morphological or transcriptome homologies that reflect ancestral–descendant relationships. As has been noted, the evidence for a metazoan phylotypic stage is impressive. In contrast, the evidence for a land plant phylotypic stage is based on molecular data and limited to one late divergent eudicot taxon (Quint et al. 2011; see also Doust et al. 2015). Currently, comparable data for other land plant lineages are lacking, which raises the following question: Can a morphological phylotypic stage be discerned for the land plants on the basis of an alignment of embryological phenotypes?

The answer appears to be *no*. Embryological comparisons of the sporophytes of the different land plant lineages reveal significant differences between the developmental patternings observed for the nonvascular lineages (mosses, liverworts, and hornworts), the seedless vascular plant lineages (horsetails, ferns, and lycopods), and the seed plants (gymnosperms and angiosperms; reviewed by Niklas 2008). Crudely put, the fundamental difference between nonvascular and vascular plant embryogenesis is polarity: The sporophyte of nonvascular plants "grows exogenously out of the gametophyte," whereas the sporophyte of vascular plants, with few exceptions, "grows endoscopically into the gametophyte" (figures 2–4).

Specifically, with few exceptions, the first division of the land plant zygote is transverse with respect to the axis of the egg-bearing structure (the archegonium) to produce two cells, one above the other (the epibasal and the hypobasal cells; see figure 2). Among the nonvascular plants, the hypobasal cell develops into the foot and lower portions of the stalk-like seta, and the epibasal cell develops into the
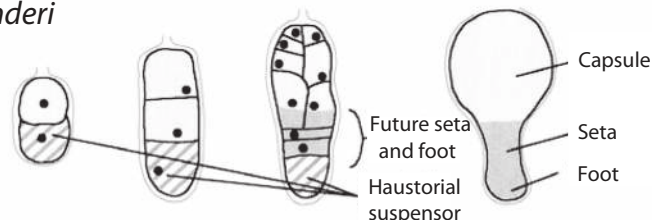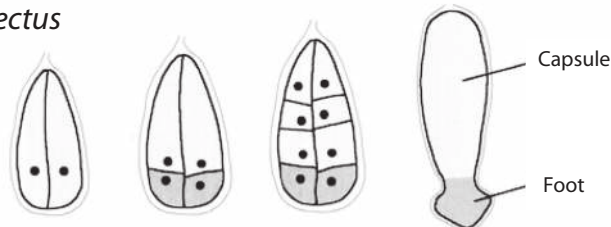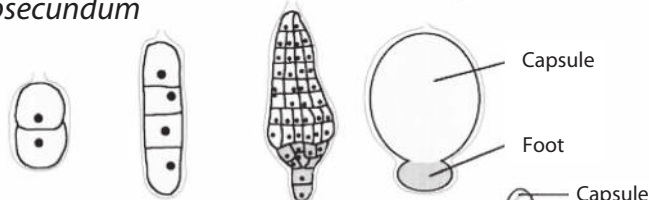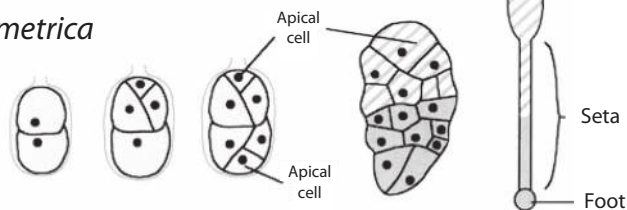
Figure 2. Exoscopic sporophyte embryo development of representative nonvascular land plants, beginning with the first division of the zygote (on left) to the mature sporophyte (far right). The orientation of the archegonial neck (top) and venter (bottom) is indicated by a thin line in each zygotic stage. The outlined areas with black dots denote cells; the outlined areas without dots denote multicellular portions of the embryo or mature sporophyte. The differently shaded areas are used to indicate shared cell lineages. The representative taxa are as follows: **Marchantia polymorpha** *(thalloid liverwort; Marchantiophyta, Marchantiaceae);* **Pellia epiphylla** *(leafy liverwort; Marchantiophyta, Metzgerineae);* **Porella bolanderi** *(leafy liverwort; Marchantiophyta, Jungermannineae);* **Anthoceros erectus** *(hornwort; Anthocerophyta, Anthocerotaceae);* **Sphagnum subsecundum** *(moss; Bryophyta, Sphagnaceae); and* **Funaria hygrometrica** *(moss; Bryophyta, Bryidae). Adapted with permission from Niklas (2008).*

sporangium and the upper part of the seta. In contrast, with very few exceptions (e.g., some ferns and *Equisetum*) in early-divergent lineages (see Rai and Graham 2010), the embryo of vascular plants develops in the reverse orientation and involves the formation of a structure called the *suspensor* (figure 3). Suspensors are produced by the hypobasal cell in some bryophytes (e.g., *Porella*; see Parihar 1962). However, these are unicellular and lie beneath the cells that ultimately give rise to the foot. In contrast, among vascular plants, the epibasal cell gives rise to the suspensor, which may enlarge and become multicellular.

These differences in polarity might suggest that two sporophyte phylotypic stages exist, one for the nonvascular plants and another for the vascular plants. However, even this is unrealistic because different embryological patternings exist even among the seed plants. For example, across the lineages represented by the cycad *Zamia*, *Ginkgo*, and the gymnosperms *Ephedra* and *Pinus*, early embryogenesis involves free nuclear divisions that produce a multinucleated coenocyte (figure 4), whereas with comparatively few exceptions (e.g., *Paeonia*), the angiosperm sporophyte embryo is cellular *ab initio* (Maheshwari 1950, Esau 1967). Another difference involves the establishment of the root–shoot polarity in the embryo. For example, in some ferns (e.g., *Gymnogramme sulphurea*; see figure 3), the cell quadrate in early embryogenesis is located relative to the anterior–posterior axis of the gametophyte and relative to the inner–outer axis of the egg-bearing archegonium. During embryogenesis, the shoot apex arises from the inner and left-most quadrant, the root apex arises from the quadrant opposite the shoot apex (the upper and right-most quadrant), and the first leaf and a structure known as the foot arise from the other two quadrants. This arrangement recalls that seen in the angiosperms (i.e., the shoot pole arising in opposition to the root pole). However, with four cells and two polarities, the fern embryo differs from that of the angiosperm embryo, which begins with a transverse (micropylar–chalazal) division, to produce an embryo with two leaves in early-divergent angiosperms (Bower 1908; Bierhorst 1971).

Equisetum arvense

Ophioglossid ferns

Ophioglossum vulgatum

Botrychium virginianum

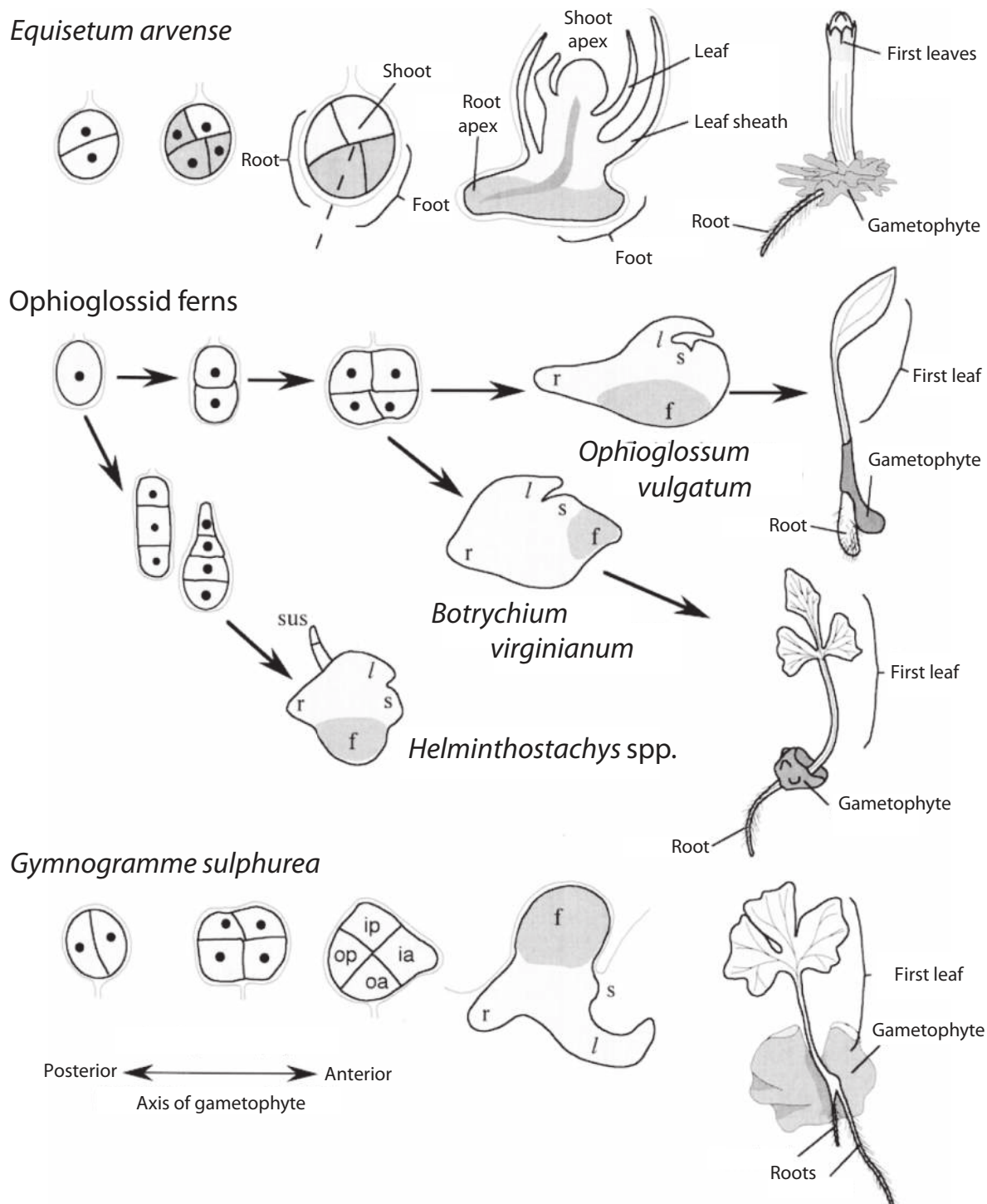*Helminthostachys* spp.

Gymnogramme sulphurea

Figure 3. The stages in sporophyte embryogenesis of representative seedless vascular plants, beginning with the first division of the zygote (left) and concluding with the juvenile sporophyte (far right). The orientation of the archegonial neck and venter is indicated by a thin line in each zygotic stage. The outlined areas with black dots denote cells; the outlined areas without dots denote multicellular portions of the embryo or young sporophyte. The differently shaded areas are used to indicate shared cell lineages. The representative taxa are as follows: **Equisetum arvense** *(horsetail; Equisetaceae; exoscopic development); three eusporangiate ophioglossoid ferns, specically* **Ophioglossum vulgatum** *and* **Botrychium virginianum** *(exoscopic development) and* **Helminthostachys spp.** *(Ophioglossales; endoscopic development); and the leptosporangiate fern* **Gymnogramme sulphurea** *(Filicales; (endoscopic development). Abbreviations: f, foot; ip, inner posterior cell; ia, inner anterior cell; l, first embryonic leaf; op, outer posterior cell; oa, outer anterior cell; r, embryonic root; s, site of future shoot apex. Adapted with permission from Niklas (2008).*

Zamia pumila
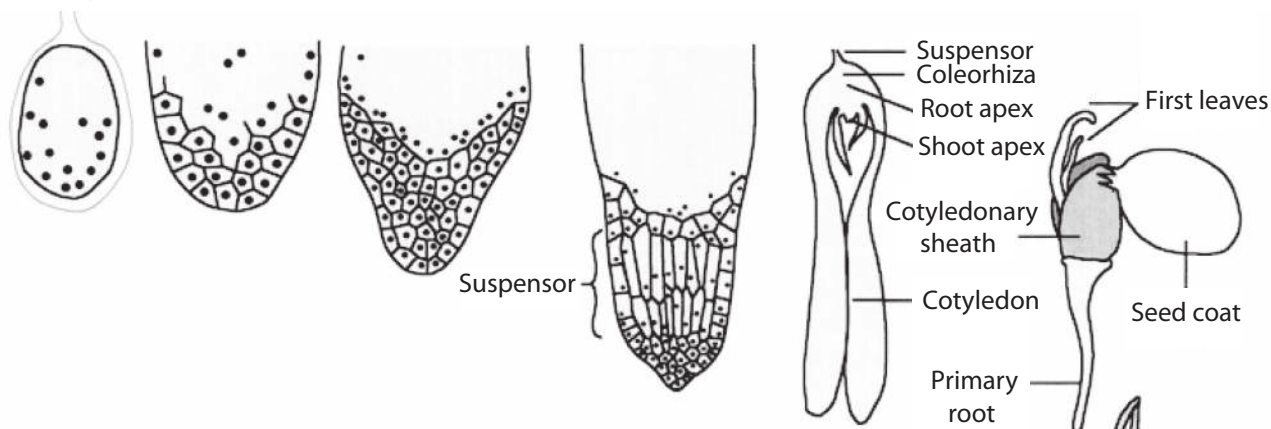
Ginkgo biloba
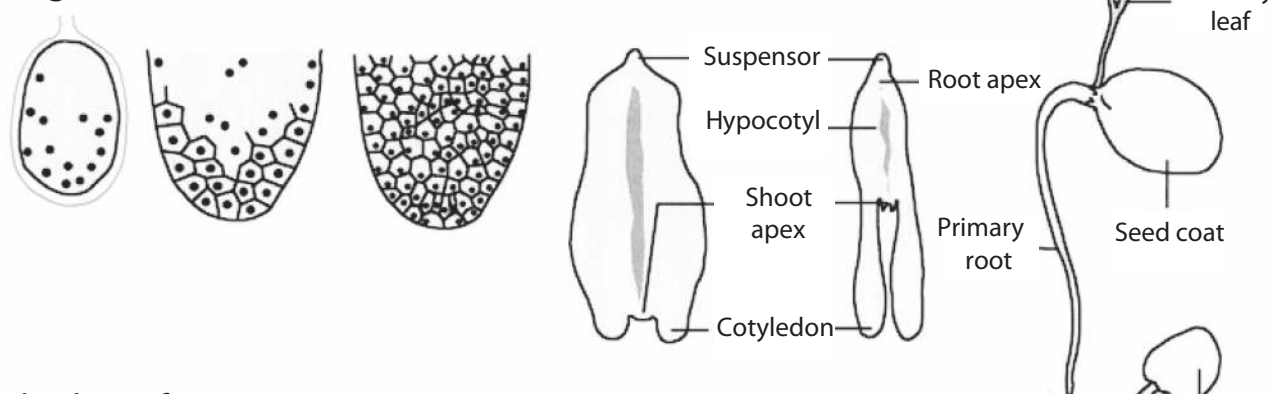
Ephedra trifurca
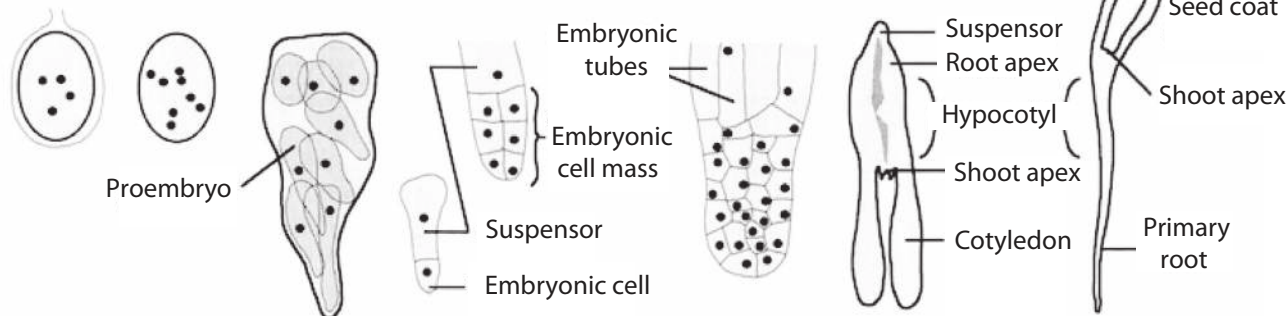
Figure 4. The embryo development of representative gymnosperms, beginning with the first division of the zygote (on left) to the seedling (far right). The orientation of the archegonial neck (top) and venter (bottom) is indicated by a thin line in each zygotic stage. The orientation of the seeding is such that the root axis is pointing in the direction of the micropyle. The outlined areas with black dots denote cells; the outlined areas without dots denote multicellular portions of the embryo or seedling. The differently shaded areas are used to indicate shared cell lineages. Representative taxa are as follows: **Zamia pumila** *(cycad; Cycadales);* **Ginkgo biloba** *(Ginkgophyta, Ginkgoaceae); and* **Ephedra trifurca** *(Gnetales, Gnetaceae). Adapted with permission from Niklas (2008).*

The phylotypic stage and the land plant gametophyte

Does the land plant gametophyte hold the key to identifying the land plant phylotypic stage? This question emerges because (a) all of the available evidence indicates that the charophycean algae and the land plants shared a last common ancestor and (b) the charophycean algae lack a diploid multicellular life form in their life cycle and therefore lack an analog to the land plant sporophyte (Niklas and Kutschera 2009, 2010, Wickett et al. 2015, Niklas 2016). It is reasonable, therefore, to suppose that the gene regulatory networks that gave form to the first land plant sporophytes were co-opted from those that gave form to the ancestral gametophyte

generation. Therefore, the land plant phylotypic stage might be revealed by the patternings observed during land plant gametogenesis (possibly even in the development of the multicellular charophycean life form, which is the analog of the land plant gametophyte).

Unfortunately, few if any meaningful development comparisons can be drawn between the development of the charophycean gametophyte and the gametogenesis of even the nonvascular land plants. The charophycean algae lack a parenchymatous tissue construction (they consist of unbranched or branched filaments that grow by apical or intercalary cell divisions). Although the early development of moss gametophytes and some liverwort gametophytes results in unbranched filaments (called *protonema*), subsequent growth typically produces a parenchymatous tissue construction. In turn, whereas gametogenesis across the nonvascular plant lineages and the nonseed plant lineages is *ab initio* cellular, the early development of seed plant gametophytes is acellular (coencytic).

The existence of a single phylotypic stage based on morphological criteria is equally questionable even within what is undoubtedly the most intensely studied land plant clade, the angiosperms. Across the flowering plants, free nuclear divisions give rise to a coenocyte that subsequently develops into the multicellular egg-bearing megagametophyte (Maheshwari 1950), a developmental patterning that is reminiscent of the early development of gymnosperm sporophytes (figure 4; Schnarf 1933). However, the diversity by which multicellularity is achieved in the flowering plant megagametophyte rivals that observed during nonvascular plant gametogenesis (Maheshwari 1950, Parihar 1962). For example, on the basis of molecular phylogenies (e.g., Soltis and Soltis 2004, Soltis et al. 2011), the ancestral condition for angiosperm megagametogenesis is monosporic (i.e., only one of the four haploid megaspore nuclei gives rise to the egg-bearing gametophyte), and in the majority of cases, the mature gametophyte consists of four cells and four nuclei. However, this differs significantly from the megagametophyte of *Amborella trichopoda* (Friedman 2006), which is currently considered to be at the very base of the entire flowering plant clade (e.g., Soltis and Soltis 2004, Soltis et al. 2011). Unlike all other angiosperms, the *Amborella* megagametophyte consists of eight cells and nine nuclei. This configuration results when one of the three cells located at the micropylar end of the megagametophyte divides to give rise to the egg cell and what can be considered a third synergid cell (figure 5a).

A parallel exists between the formation of the egg in the *Amborella* megagametophyte and the formation of the egg in some gymnosperm gametophytes, such as those of *Zamia* (figure 5b). In *Zamia*-type megagametogenesis, the cell that will form the egg-bearing archegonium divides transversely to give rise to a basal central cell and a smaller apical cell that subsequently divides to form a two-celled neck (Schnarf 1933, Bierhorst 1971). The central cell then divides transversely to produce a ventral canal cell located above the egg cell (or a binucleate cell, one of whose nuclei functions as an egg nucleus). In this respect, the cell that gives rise to the egg cell and the third synergid in the *Amborella* megagametophyte is an analog of the *Zamia*-type central cell (figure 5b). Beyond this tenuous comparison, few if any meaningful analogies can be drawn among the developmental patternings of megagametogenesis observed for extant seed plants. Therefore, if a transcriptome phylotypic stage exists for all land plants, or even for just the seed plants, it fails to correlate with a morphological phylotypic stage.

Conclusions

Our review of land plant embryogenesis and gametogenesis was stimulated by a seminal transcriptome study reporting the existence of a phylotypic stage for the flowering plant sporophyte (Quint et al. 2012). A review of the literature shows that the concept of the phylotypic stage historically traces its roots to the theory of embryological recapitulation and Haeckel's biogenetic law. However, unlike the long-since discredited theories of Haeckel, the existence of a single phylotypic stage for metazoans has received strong empirical support based on extensive comparative morphological and molecular studies across a broad spectrum of animal phyla.

In contrast, the existence of a phylotypic stage for the land pants is currently based on the study of a single—albeit important—model taxon within a late divergent angiosperm lineage, the eudicots. In the absence of comparable molecular (transcriptome) studies, we turned to morphological criteria to determine whether a single land plant phylotypic stage can be identified. Using this approach, our review of land plant embryogenesis failed to identify a single phylotypic stage across all land plant sporophytes. Likewise, on the basis of the assumption that the genomic toolkits dictating sporophyte embryogenesis had to be co-opted from those responsible of gametogenesis, our review failed to elucidate a phylotypic stage for the land plant egg-bearing megagametophyte. Specifically, the sporophytes of extant nonvascular plants are multicellular *ab initio*, develop exogenously, and lack a rootshoot organization, whereas the sporophytes of the majority of seed plants are initially coenocytic, develop endogenously, and have a rootshoot organization. Comparable dissimilarities are observed over the course of megagametogenesis; for example, the egg cells of gymnosperm megagametophytes develop after cellularization, whereas the egg cells of angiosperm megagametophytes are determined before or during the cellularization process. The only reasonably well-defined and ubiquitous developmental event in land plant embryogenesis and megagametogenesis is the establishment of some form of apicalbasal polarity by means of one or more loci of meristematic activity, such as during the torpedo stage of *Arabidopsis* (figure 1b). It is possible, therefore, that the formation of apical meristems (or more generally the establishment of an apicalbasal polarity) provides a morphological criterion by which the land plant phylotypic stage can be identified.
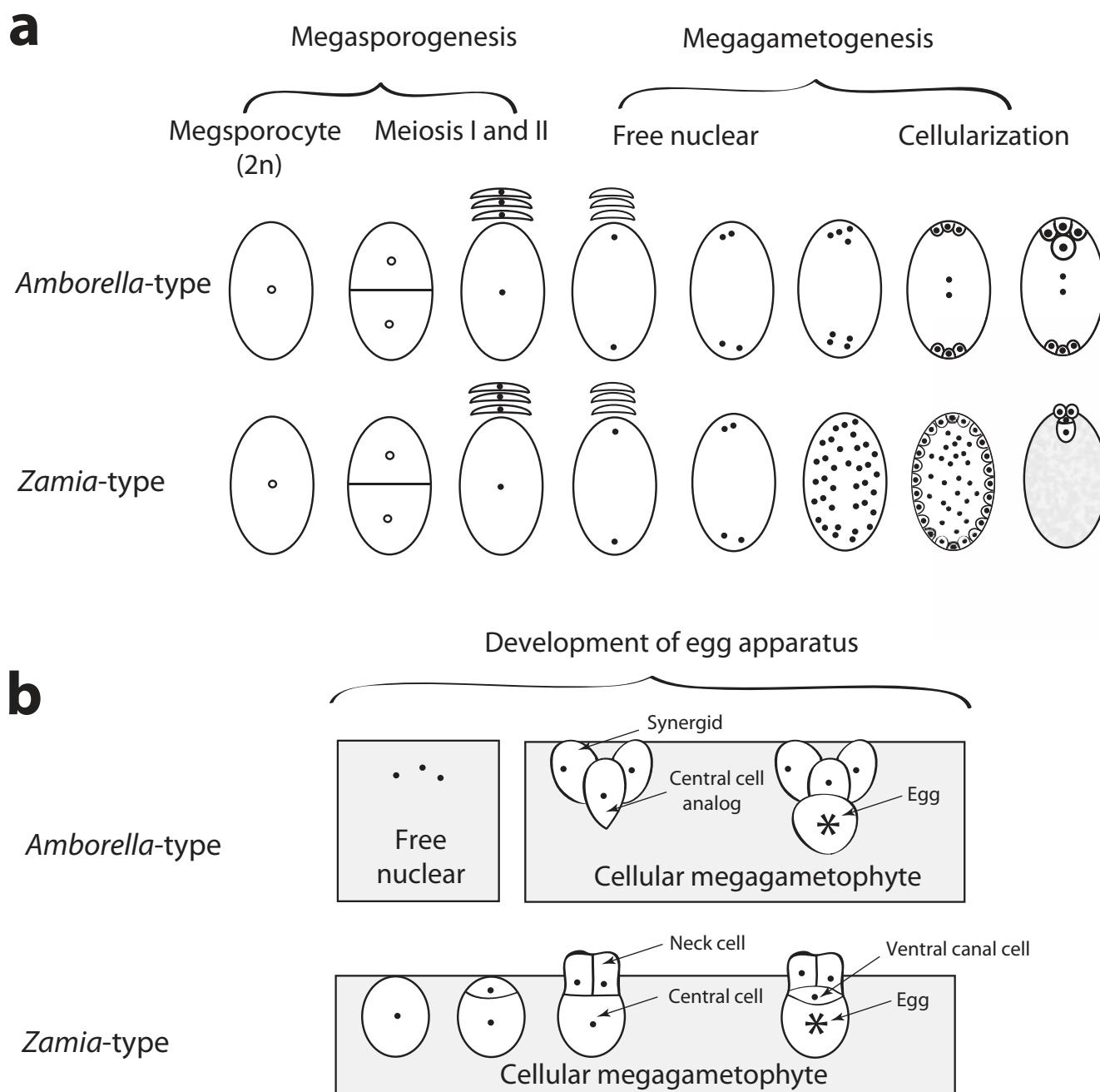
Figure 5. A schematic comparison of megasporogenesis and megagametogenesis (a) and the formation of the egg cell (b) in the Amborella-*type and* Zamia-*type of megagametogenesis. Diploid nuclei and nuclei in meiosis I are denoted by the open circles. Haploid nuclei are denoted by the small black dots. Note that the egg-cell nucleus is formed after the gametophyte has cellularized.*

In the absence of extensive comparative transcriptomic analyses of model plant systems other than *Arabidopsis* (e.g., *Physcomitrilla* and *Selaginella*), we draw attention to the possibility that the land plant phylotypic stage may have undergone three major evolutionary transformations, one attending the evolutionary appearance of the nonvascular land plants, another with the appearance of the pteridophytes, and a third with the evolution of the seed plants (figure 6). This speculation is consistent with the notion that the phylotypic stage is itself resistant to extensive evolutionary modification and that differences among closely related species are the result of modifications preceding or following the phylotypic stage. This hypothesis can be tested by comparing transcriptomes within each of the three land plant groups and by comparing transcriptomes among the three groups. If our hypothesis is correct,
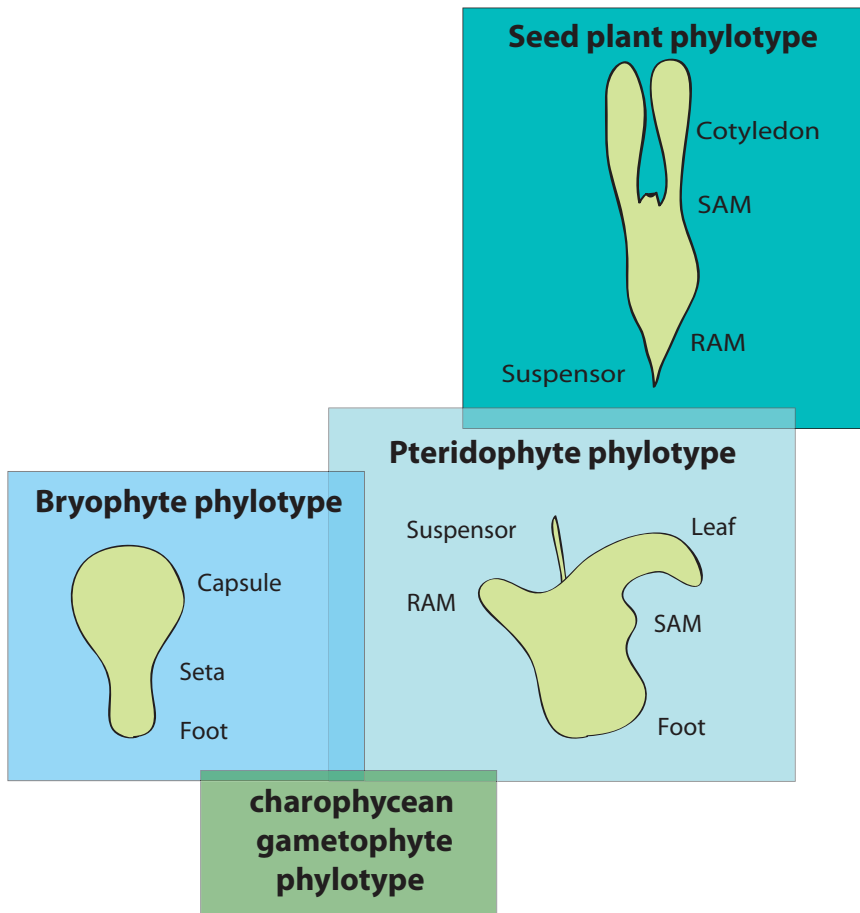
Figure 6. Schematics of the hypothetical relationships among the three embryological patterning (and their respective phylotypic stages) observed for extant bryophytes (mosses, liverworts, and hornworts), the pteridophytes (ferns, horsetails, and lycopods), and the seed plants (gymnosperms and angiosperms), as well as their relationship to a charophycean algal complex (and the phylotypic stage of its haploid gametophytic life form; note that the charophycean algae lack a multicellular analogue of the sporophyte). The hypothesis diagrammed here postulates three major evolutionary transformations: one leading from a charophycean phylotypic stage to a bryophytic phylotypic stage, another that resulted in the pteridophytic phylotypic stage, and a third obtaining the seed plant phylotypic stage. Abbreviations: RAM, root apical meristem; SAM, shoot apical meristem.

within-group comparisons will reveal a conserved transcriptome that corresponds to the molecular phylotypic stage for each group, whereas among-group comparisons will reveal differences.

Acknowledgments

References cited

Ballard WW. 1981. Morphogenetic movements and fate maps of vertebrates. American Naturalist 21: 391–399.

Bierhorst DW. 1971. Morphology of Vascular Plants. Macmillan.

Bower FO. 1908. The Origin of a Land Flora. Macmillan.

Cheng XJ, Hui JHL, Lee YY, Law PTW, Kwan HS. 2015. A "developmental hourglass" in fungi. Molecular Biology and Evolution 32: 1556–1566.

Darwin C. 1851. A Monograph on the Fossil Lepadidae, or Pedunculated Cirripedes of Great Britain, vol 1. Palaeontological Society.

———. 1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. John Murray.

Drost HG, Gabel A, Grosse I, Quint M. 2015. Evidence for active maintenance of phylotranscriptomic hourglass patterns in animal and plant embryogenesis. Molecular Biological Evolution 32: 1221–1231.

Esau K. 1967. Plant Anatomy, 3rd ed. John Wiley.

Friedman WE. 2006. Embryological evidence for developmental lability during early angiosperm evolution. Nature 441: 337–340.

Gould SJ. 1977. Ontogeny and Phylogeny. Harvard University Press.

Haeckel EA. 1866. Generelle Morphologie der Organismen: Allgemeine Grundzüge der Organischen Formen-Wissenschaft, Mechanisch Begründet Durch die von Charles Darwin Reformirte Descendenz-Theorie. Georg Reimer.

Haeckel EA. 1874. Die Gastraea-Theorie, die phylogenetische klassification des tierreiches und homologie der Keimblätter. Jenaische Zeitschrift für Naturwissenschaft 8: 1–55.

Hoßfeld U, Olsson L. 2003. The road from Haeckel: The Jena tradition in evolutionary morphology and the origins of "evo-devo". Biology and Philosophy 18: 285–307.

Hofmeister W. 1851. Vergleichende Untersuchungen der Keimung, Entfaltung und Fruchtbildung Hoeherer Kryptogamen (Moose, Farne, Equisetaceen, Rhizokarpeen und Lykopodiaceen) und der Samenbildung der Coniferen. Verlag Wilhelm Hofmeister.

Kühn A. 1914. Entwicklungsgeschichte und verwandtschaftsbeziehungen der Hydrozoen I: Die Hydroiden, Ergebnisse. Fortschritte der Zoologie 4: 1–284.

Levit GS, Hoßfield U, Olsson L. 2015. The integration of Darwinism and evolutionary morphology: Alexej Nikolajevich Sewertzoff (1866-1936) and the developmental basis of evolutionary change. Journal of Experimental Zoology B Molecular Developmental Evolution 15: 343–354.

Maheshwari P. 1950. An Introduction to the Embryology of Angiosperms. McGraw-Hill.

Müller GB. 2003. Homology: The evolution of morphological organization. Pages 51–70 in Müller GB, Newman SA, eds. Origination of Organismal Form: Beyond the Gene in Developmental and Evolutionary Biology. MIT Press.

Niklas KJ. 2008. Embryo morphology and seedling evolution. Pages 103–129 in Leck MA, Parker VT, Simpson RL, eds. Seedling Ecology and Evolution. Cambridge University Press.

———. 2016. Plant Evolution. University of Chicago Press.

Niklas KJ, Kutschera U. 2009. The evolutionary development of plant body plants. Functional Plant Biology 36: 682–695.

Niklas KJ, Kutschera U. 2010. The evolution of the land plant life cycle. New Phytologist 185: 27–41.

O'Farrell PH. 2015. Growing an embryo from a single cell: A hurdle in animal life. Pages 1–24 in Heald R, Hariharan IK, Wake DB, eds. Size Control in Biology: From Organelles to Organisms. Cold Spring Harbor Laboratory Press, Cold Spring Harbor.

Olsson L, Levit GS, Hossfeld U. 2010. Evolutionary developmental biology: Its concepts and history with a focus on Russian and German contributions. Naturwissenschaften 97: 951–969.

Parihar NS. 1962. An Introduction to Embryophyta, vol. 1: Bryophyta. Central Book Deport.

Prud'homme B, Gompel N. 2010. Evolutionary biology: Genomic hourglass. Nature 468: 768–769.

Raff RA. 1996. The Shape of Life: Genes, Development, and the Evolution of Animal Form. University of Chicago Press.

Rai HS, Graham SW. 2010. Utility of a large, multigene plastic data set in inferring higher-order relationships in ferns and relatives (monilophytes). American Journal of Botany 97: 1444–1456.

Rebeiz M, Jikomes N, Kassner VA, Carroll SB. 2011. Evolutionary origin of a novel gene expression pattern through co-option of the latent activities of existing regulatory sequences. Proceedings of the National Academy of Science 108: 10036–10043.

Richards RJ. 2002. The Romantic Conception of Life: Science and Philosophy in the Age of Goethe. University of Chicago Press.

Richardson MK. 2012. A phylotypic stage for all animals? Development and Cell 22: 903–904.

Roux J, Rosikiewicz M, Robinson-Rechavi M. 2015. What to compare and how: Comparative transcriptomics for evo-devo. Journal of Experimental Zoology B: Molecular and Developmental Evolution 324: 372–382.

Sander K. 1983. The evolution of patterning mechanisms: Gleanings from insect embryogenesis and spermatogenesis. Pages 137–159 in Goodwin BC, Holder N, and Wylie CC, eds. Development and Evolution. Cambridge University Press.

Schnarf K. 1933. Embryologie der Gymnospermen. Von Gebrüder Borntraeger.

Seidel F. 1960. Körpergrundgestalt und Keimstructur-eine Eröterung über die Grundgestalt der vergleichenden und experimentellen Embryologie unter deren Gültigkeit bei phylogenetischen Überlegungen. Zoologischer Anzeiger 164: 245–305.

Shen MM. 2007. Nodal signaling: Developmental roles and regulation. Development 134: 1023–1034.

Soltis DE, et al. 2011. Angiosperm phylogeny: 17 genes, 640 taxa. American Journal of Botany 98: 704–730.

Soltis PS, Soltis DE. 2004. The origin and diversification of angiosperms. American Journal of Botany 91: 1614–1626.

Svorková J. 2012. The phylotypic stage as a boundary of modular memory: Non-mechanistic perspective. Theory in Biosciences 131: 31–42.

Quint M, Drost H-G, Gabel A, Ullrich KK, Bönn M, Grosse I. 2012. A transcriptomic hourglass in plant embryogenesis. Nature 490: 98–101.

Wagner GP. 2014. Homology, Genes, and Evolutionary Innovation. Princeton University Press.

Wickett NJ, et al. 2015. Phylotranscriptomic analysis of the origin and early diversification of land plants. Proceedings of the National Academy of Sciences 111: E4859–E4868. (4 March 2016; www.pnas.org/cgi/doi/10.1073/pnas.1323926111).

Karl J. Niklas (kjn2@cornell.edu) and Edward D. Cobb are affiliated with the Plant Biology Section of the School of Integrative Plant Biology at Cornell University, in Ithaca, New York. Ulrich Kutschera is affiliated with the Institute of Biology at the University of Kassel, in Germany.