Botanical Journal of the Linnean Society, 2021, **195**, 380–419. With 15 figures.

REVIEW

Diversity, development and evolution of archegonia in land plants

DMITRY D. SOKOLOFF[1,*] and MARGARITA V. REMIZOWA[1,2]

[1]*Biological Faculty, M.V. Lomonosov Moscow State University, 119234 Moscow, Russia*
[2]*Faculty of Biology and Biotechnologies, National Research University Higher School of Economics, Moscow, Russia*

Received 21 February 2020; revised 13 July 2020; accepted for publication 24 July 2020

We review the diversity and development of archegonia, the female reproductive organs of land-plant gametophytes. The archegonium is a uniquely land-plant structure, and studies of its evolution benefit from use of a comparative approach in a phylogenetic context. Archegonia of most land plants share a common developmental motif, here termed a T-shaped pattern. A primary axial cell produces a primary cover cell and a central cell by horizontal division. The upper cell usually divides vertically and the lower one horizontally. In mosses such as *Atrichum*, the T-shaped stage is shifted towards the end of archegonium development, whereas in vascular plants it appears at the beginning of development, but these stages are still probably homologous. The fully exposed archegonia are traditionally viewed as an ancestral (plesiomorphic) condition in land plants, but there is no direct support for this view. We speculate that the fully exposed condition is derived and synapomorphic for setaphytes (mosses and liverworts). The fully sunken hornwort archegonia may be similar to the ancestral type of land-plant archegonia. Developmental evidence suggests that archegonium necks of setaphytes and tracheophytes are not homologous to each other. The neck wall of pteridophytes is composed of four-celled tiers, and one such tier is present in gymnosperms with motile male gametes. Neck-cell arrangement is much more plastic in archegonia of gymnosperms with sperm cell delivery by pollen tube (siphonogamy), in which the neck plays a role similar to pollen-tube transmitting tissue of angiosperms. Angiosperm synergids are probably homologues of gymnosperm neck cells, and the angiosperm egg cell is probably homologous to the ventral canal cell of gymnosperms. Developmental genetic bases of archegonium diversity in land plants remain to be understood. Even descriptive developmental data are currently missing or controversial for some key lineages of land plants.

ADDITIONAL KEYWORDS: asymmetric cell divisions – embryo sac – ferns – hornworts – liverworts –lycopsids – mosses – neck – seed plants – venter.

INTRODUCTION

The presence of a multicellular diploid generation (sporophyte) in addition to the haploid generation (gametophyte) distinguishes land plants from their closest relatives, the streptophyte algae. The occurrence of a sporophyte embryo and regulated transfer of nutrients from gametophyte to sporophyte (matrotrophy) are also among the key characters of land plants (Graham & Wilcox, 2000). There are no direct data for the origin of the land-plant life cycle and elucidating its evolution remains a fundamental problem (Kato & Akiyama, 2005; Bennici, 2008; Niklas & Kutschera, 2009, 2010; Kato, 2010; Gerrienne & Gonez, 2011; Kenrick, 2017; Cox, 2018; Sousa *et al.*, 2019). Evolution of the land-plant embryo is also enigmatic in many respects, but it is of great importance in understanding differences between major groups of embryophytes. The land-plant zygote remains in the same location as the egg cell from which it derived, and positional information from surrounding structures is essential for the patterning and orientation

*Corresponding author. E-mail: sokoloff-v@yandex.ru

of the embryo. In bryophytes, pteridophytes and most gymnosperms, the egg cell occurs in an archegonium, which also represents a land-plant specific organ. It is timely to assemble data on the diversity of land-plant archegonia, because such data may be useful in resolving some general aspects of land-plant evolution, including the evolution of the embryo.

Both male and female sexual organs (antheridia and archegonia, respectively) of the land-plant gametophyte are multicellular and develop by three-dimensional growth with precisely regulated cell divisions in different planes, although Niklas & Kutchera (2010) used developmental genetic evidence to support their hypothesis that land-plant antheridia and archegonia are homologous with charophyte gametangia. Three-dimensional growth is specific to gametangia and other organs of land plants, but not charophytes. Recent studies have provided clues for understanding its developmental regulation (Perroud *et al.*, 2014; Olsen *et al.*, 2015; Moody, 2019).

Recent decades have provided important new molecular phylogenetic data elucidating relationships among major lineages of land plants (Fig. 1), although precise rooting of the entire group remains problematic. Among the most remarkable conclusions of many recent phylogenetic and phylogenomic studies is the notion of a sister-group relationship between mosses and liverworts (Cox *et al.*, 2014; Wickett *et al.*, 2014; Gitzendanner *et al.*, 2018; Puttick *et al.*, 2018; Sousa *et al.*, 2019, 2020; see also Hedderson, Chapman & Rootes, 1996) forming a clade called setaphytes (Renzaglia, Villarreal & Garbary, 2018). In the late 20th century, the paraphyletic nature of bryophytes (hornworts, liverworts and mosses) was widely accepted based on morphology (e.g. Kenrick & Crane, 1997) and molecular phylogenetic data (e.g. Qiu and Palmer, 1999). In pre-cladistic times and terminology, similar ideas were expressed in a form that the vascular plants (tracheophytes) have arisen from bryophytes (e.g. Smith, 1955). Nowadays, the status of bryophytes

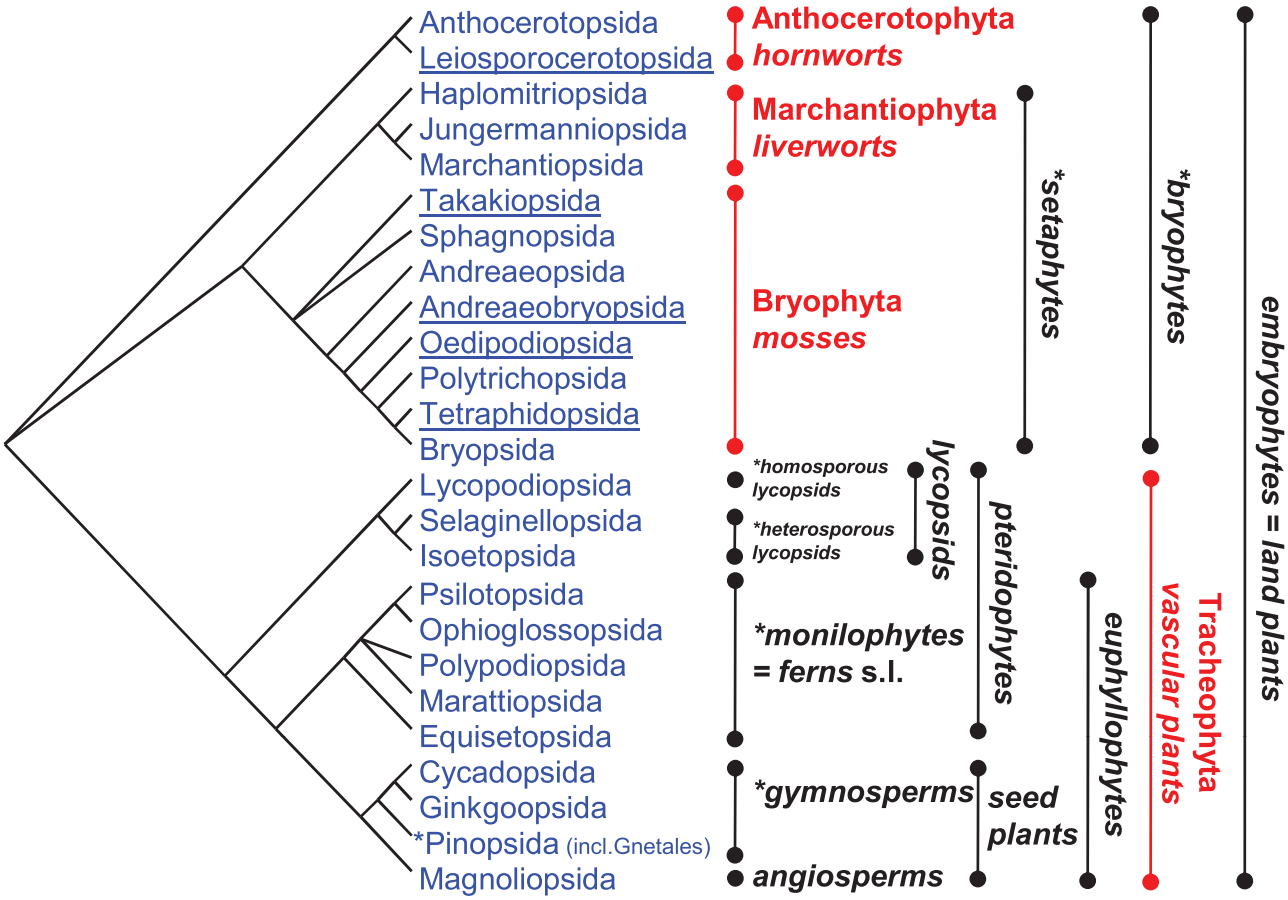


Figure 1. Major groups of extant land plants and their names used in this paper. Left, simplified diagram of relationships among classes of land plants as revealed by molecular phylogenetic data. Blue, classes. Red, phyla. Informal names italicized. Asterisks indicate groups for which monophyly may need re-consideration using the fossil record. Classes for which complete data on archegonium development are currently not available are underlined.

seems to be unresolved (Cox, 2018). The majority of recent phylogenetic studies (all based on molecular data, and excluding vast numbers of extinct fossil taxa) support the monophyly of bryophytes or, at least, do not reject this hypothesis (Cox *et al.*, 2014; Wickett *et al.*, 2014; Gitzendanner *et al.*, 2018; Puttick *et al.*, 2018; Sousa *et al.*, 2019; Bell *et al.*, 2019); other (mostly less recent) studies continue to indicate bryophyte paraphyly (Samigullin *et al.*, 2002; Chang & Graham, 2011; Shaw, Szövényi & Shaw, 2011; Ruhfel *et al.*, 2014; see also Renzaglia *et al.*, 2000; Ligrone, Duckett & Renzaglia, 2012). The remaining controversies in relationships between the three bryophyte lineages and the tracheophytes are mostly related to the rooting of the land-plant tree, whereas the unrooted pattern of (mosses + liverworts) + (tracheophytes + hornworts) is relatively stable (Cox, 2018; Bell *et al.*, 2019). The report on a draft hornwort genome further supports bryophyte monophyly, with hornworts sister to liverworts and mosses (Zhang *et al.*, 2020). Clearly, recent phylogenetic evidence requires re-thinking possible evolutionary scenarios of key morphological characters in land plants.

There is no recent review on the diversity and possible evolution of archegonia covering bryophytes and tracheophytes, although this topic is covered in several important textbooks and discussed in lecture courses around the world. Detailed information on archegonium development in various taxa has accumulated in the 19th and early 20th centuries. For example, von Janczewski (1872) published a classical account on the developmental morphology of land-plant archegonia (although not illustrated) and Campbell (1918) provided a detailed systematic review of the structure and development of free-sporing land plants. Still, the question of archegonium evolution is far from being resolved (Renzaglia *et al.*, 2000), especially in the light of new ideas in phylogenetics. The present review is aimed at stimulating further discussion in this field.

TERMINOLOGY AND NOMENCLATURE

Definitions of the most important terms used in the paper are provided in Table 1. Full scientific names of all species and genera mentioned in the text are provided in the online Supporting Information. Synonyms are indicated there when old names that are currently out of use are employed in original publications discussed here. As we review structure and development of archegonia across all land plants, use of certain general classification is required. Chase & Reveal (2009) proposed a classification in which all land plants are recognized as a class Equisetopsida with 14 extant subclasses. This classification provided no details on lower rank taxa within these subclasses (except for angiosperms). Standard classifications are currently available for all major groups of land plants. Those for gymnosperms (Christenhusz *et al.*, 2011) and flowering plants (APG IV, 2016) follow the general idea of Chase & Reveal (2009), but the standard classification of pteridophytes (PPG I, 2016) recognizes lycopsids and ferns (as monilophytes) as two distinct classes. Standard classifications of liverworts (Crandall-Stotler, Stotler & Long, 2009), mosses (Goffinet, Buck & Shaw, 2008) and hornworts (Renzaglia, Villarreal & Duff, 2008) recognize each of these bryophyte groups as a distinct phylum with two or more classes. The problem of taxonomic ranks as such has no scientific solution, but taxonomic ranks should be coordinated in different parts of a classification. In our opinion, recognizing three bryophyte phyla is appropriate, and tracheophytes (vascular plants) should be accepted as the fourth phylum of the land plants (Fig. 1). The classification with four phyla recognizes the four basic groups of land plants so that each phylum is clearly monophyletic according to molecular and morphological evidence. Further splitting of vascular plants into more than one phylum is problematic especially when the huge diversity of Palaeozoic fossils is considered. Figure 1 summarizes concepts of major groups of extant land plants used here. Monophyly of some groups (e.g. ferns) is largely based on molecular phylogenetic evidence and may be sensitive to non-representative taxon sampling caused by complete extinction of some key lineages. We use taxa of the rank of order and below according to standard classifications (Goffinet *et al.*, 2008; Renzaglia *et al.*, 2008; Crandall-Stotler *et al.*, 2009; Christenhusz *et al.*, 2011; APG IV, 2016), except that *Ephedra* L., *Gnetum* L. and *Welwitschia* Hook.f. are recognized as an order, Gnetales. Tracheophyte classes other than Polypodiopsida, Pinopsida and Magnoliopsida contain only one extant order each, and we use ordinal names to follow standard classifications (Christenhusz *et al.*, 2011; PPG I, 2016) as far as possible.

STRUCTURE AND DEVELOPMENT OF ARCHEGONIA IN MAJOR GROUPS OF LAND PLANTS

Archegonia of all land plants develop from a single initial cell, which is situated at the primary morphological surface (terminology: Endress, 2006) of the gametophyte, thus they are always exogenous (see Renzaglia *et al.*, 2008). The main parts of the archegonium are the venter and the neck. The venter houses the egg cell and the ventral canal cell (these are always sister cells), and the neck usually encloses a row of neck canal cells (all normally derived from the

Table 1. Glossary

Antheridium (of land plants): male sexual organ (gametangium) developing several or many motile male gametes (spermatozoids), with cells producing gametes forming a continuous tissue surrounded by at least one layer of sterile gametophytic tissue. So-called antheridia of charophycean algae do not fit this definition as the cells forming male gametes are arranged in iniseriate filaments rather than 3D tissue.

Archegonium: female sexual organ (gametangium) developing an egg cell that is initially surrounded by at least one cell layer of continuous gametophytic tissue.

Archegonium proper (in mosses and liverworts): the main part of the archegonium that does not include its stalk and apperas after a transition of the apical cell from a two-sided to a three-sided shape.

Basal cell(s): a cell or group of cells derived from the archegonium initial and situated below the egg cell.

Canal cells: archegonium cells that normally disintegrate before fertilization to form a canal through which the motile male gamete reaches the egg cell.

Central cell (in embryo sac): the largest cell of the angiosperm female gametophyte producing an endosperm after fusion with a male gamete.

Central cell (in young archegonium): the lower cell derived from a horizontal division of the primary axial cell (when a basal cell is absent). Alternatively, the lower cell divides horzontally to form a basal cell and a central cell, the latter being closer to the primary cover cell.

Cover cells: cells situated at the distal side of the archegonium in bryophytes that are formed by vertical divisions of the primary cover cell or its derivative. The cover cells separate from each other before fertilization to open a neck canal.

Embryo sac: female gametophyte of angiosperms.

Gametophyte: normally haploid generation in the life cycle of land plants developing male and female gametes through mitosis.

Jacket: in bryophytes, archegonial cells surrounding the egg cell and canal cells; in tracheophytes, histologically differentiated cells surrounding the egg cell irrespective of their origin.

Neck: long or short distal part of the archegonium aimed in attraction and delivery of male gametes to the egg cell. Before fertilization, a neck canal is formed by disintegration of neck canal cells.

Neck mother cell: term often used for the primary cover cell of tracheophytes.

Polar nuclei (nucleus): nuclei or nucleus in the central cell of angiosperm embryo sac.

Primary axial cell: in bryophytes, the cell that appears in the centre of young archegonium after three unequal (=asymmetric) vertical or obliquely vertical divisions of the archegonium initial cell. In our view, the so-called archegonium initial of tracheophytes is homologous with the primary axial cell of bryophytes.

Primary cover cell: the upper cell derived from a horizontal division of the primary axial cell.

Primary jacket cells: three peripheral cells formed after three unequal divisions of the archegonium initial in bryophytes. Their further divisions produce an outer wall (jacket) surrounding the egg and canal cells.

Sporophyte: normally diploid generation in the life cycle of land plants developing spores through meiosis.

Synergids: cells of angiosperm embryo sac situated close to the egg cell and facilitating attraction of pollen tubes and release of male gametes.

Tier: a group of cells lying in the same plane (a tier of neck cells lies in a plane perpendicular to the archegonium axis in tracheophytes).

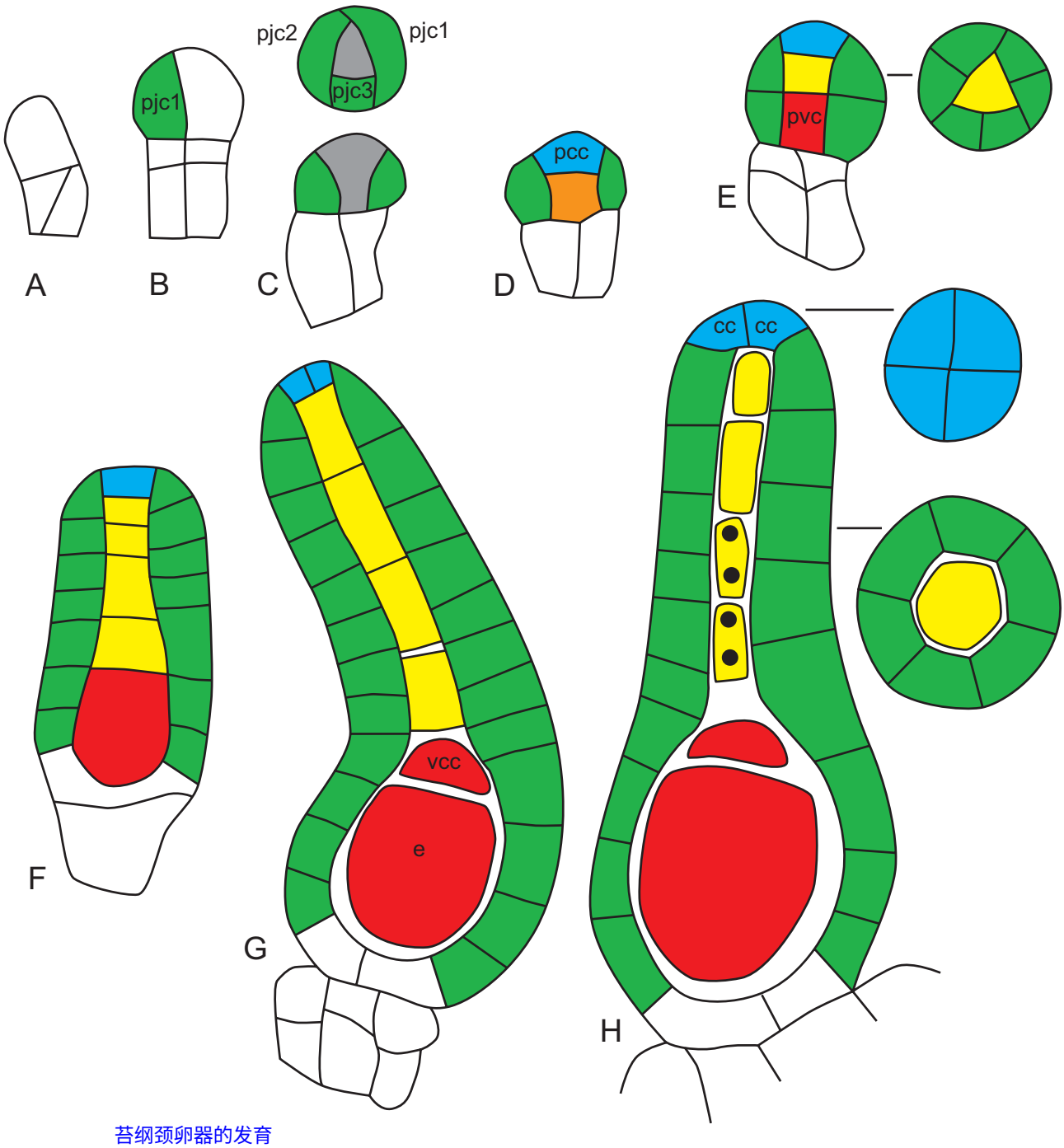
Venter: proximal part of the archegonium containing the egg cell.

Ventral canal cell: canal cell that is developmentally sister to the egg cell. A possibility of its further divisions to form multiple ventral canal cells (in homosporous lycopsids) is disputable.

same initial cell). The canal cells normally disintegrate before fertilization to form a canal through which the motile male gamete reaches the egg cell. In hornworts and tracheophytes, the venter and sometimes the entire archegonium (e.g. in hornworts and gymnosperms) is congenitally united with surrounding tissue, so that it is sunken into the gametophyte body. Mosses and liverworts are the only land plants possessing fully exposed archegonia with a free venter. Systematic description of diversity of land-plant archegonia is provided below. Variation of major characters across land plants is summarized in Table 2.

ARCHEGONIA OF LIVERWORTS 苔纲

Schuster (1966, 1984) summarized the diversity of structure and development of archegonia in liverworts and emphasized the significance of these characters in characterization of higher-level taxa in the group. In all liverworts, the initial cell of the archegonium undergoes a periclinal division (i.e. the wall between the two daughter cells is parallel to the surface of the gametophyte). The outer daughter cell, which is free-bulging above the gametophyte surface, then produces the archegonium proper, sometimes after



苔纲颈卵器的发育

Figure 2. Archegonium development in liverworts: *Marchantia polymorpha*. Line drawings of longitudinal and transverse sections simplified and modified from Durand (1908). Colouring indicates cell lineages. Green, primary jacket cells (pjc1, pjc2, pjc3, numbered in sequence of their origin) and cells derived from them. Grey, primary axial cell, which produces a primary cover cell and a central cell. Blue, primary cover cell (pcc) and cells derived from it. Orange, central cell, which produces a primary ventral cell (pvc) and primary neck canal cell (in E, yellow). All neck canal cells (yellow) are derived from the primary neck canal cell. Some of them may become binucleate (H). Nuclei (black dots) are only shown in cells with more than one nucleus. Red, primary ventral cell (pvc), ventral canal cell (vcc) and egg cell (e).

Table 2. Basic features of archegonium morphology and embryo polarity in classes of land plants. Classes with insufficient data on archegonium development are not included (underlined names in Fig. 1). See Figure 13 for evolutionary interpretations of character evolution

	Archegonium venter embedded (E) or free (F)	First division of the initial cell of the archegonium proper: horizontal (H) or unequal (obliquely) vertical, followed by two other unequal vertical divisions (3V)	First division of the primary cover cell: horizontal (H), vertical (V) or oblique (O)	Multiplication of tiers of cells derived from the primary cover cell (=pteridophyte-type neck)	Neck canal cells	Ventral canal cell: single (1), possibly multiple (?M), possibly absent (?0), ventral canal cell nucleus remains in the same cell as egg nucleus (N)	Embryo polarity: exoscopic (Ex) or endoscopic (En)*
Anthocerotopsida	E	3V	H(?)	-	+	1	Ex
Haplomitriopsida	F	3V	V	-	+	1	Ex
Jungermanniopsida	F	3V	V	-	+	1	Ex
Marchantiopsida	F	3V	V	-	+	1	Ex
Sphagnopsida	F	3V	V	-	+	1	Ex
Andreaeopsida	F	3V	O	-**	+	?0	Ex
Polytrichopsida	F	3V	O	-**	+	1	Ex
Bryopsida	F	3V	O/?V	-**	+	1	Ex
Lycopodiopsida	E	H	V	+	+	?M	En
Selaginellopsida	E	H	V	+	+	1	En
Isoëtopsida	E	H	V	+	+	1	En
Psilotopsida	E	H	V	+	+	1	Ex
Ophioglossopsida	E	H	V	+	+	1/?0	En/Ex
Polypodiopsida	E(F)	H(1-2V***)	V	+	+	1	En/Ex
Marattiopsida	E	H	V	+	+	1	En
Equisetopsida	E	H	V	+	+	1	Ex
Ginkgoopsida	E	H	V	-	-	1	En
Cycadopsida	E	H	V	-	-	N(1)	En
Pinopsida (including Gnetales)	E	H	V/H	+/-	-	1/N	En

* In exoscopic polarity, the apical pole of the embryo (ultimetely producing a sporangium in bryophytes or sporangia in tracheophytes) develops close to the neck end of the archegonium; in endoscopic polarity, the apical pole of the embryo develops close to the base of the archegonium (Niklas, 2008; Sokoloff *et al.*, 2015). When zygote division is vertical (so-called prone type; Johnson & Renzaglia, 2009), derivatives of the two upper and two lower cells of the four-celled embryo are considered to distinguish between the exoscopic and endoscopic types.

** Although the distal part of the neck wall is derived from the primary cover cell in mosses such as *Andreaea*, *Plagiomnium* and *Atrichum* and thus coloured blue in Fig. 5, the mode of its development differs from that in the tracheophyte neck.

*** One or two unequal oblique vertical divisions resulting in the origin of the archegonium initial in *Actinostachys* (Bierhorst, 1968, 1975) strongly resemble the first division(s) of the archegonium initial in bryophytes.

another periclinal division (e.g. Hutchinson, 1915a; Campbell, 1959), or alternatively the initial cell directly produces the archegonium proper without any periclinal divisions (Campbell, 1916). The inner cell ultimately produces the stalk of the archegonium. The outer cell undergoes a series of three vertical (i.e. parallel to the axis of the archegonium) or almost vertical unequal divisions at 120° angles to each other resulting in a larger primary axial cell surrounded by three primary jacket cells. In the 'open type' of archegonium development (the term is introduced here), these three divisions are vertical and the distal part of the primary axial cell remains at the surface of the archegonium (Figs 2, 3A–E). In the 'closed type' of archegonium development, the three divisions are obliquely vertical, so that their planes intersect above the primary axial cell (Fig. 3F–H). Thus, the primary axial cell is completely surrounded by the three primary jacket cells in the closed type (hence the name proposed here). In the open type, the primary axial cell divides horizontally (i.e. perpendicular to the axis of the archegonium) and unequally to form a smaller upper cell (the primary cover cell) and a larger lower cell (the central cell). When subsequent

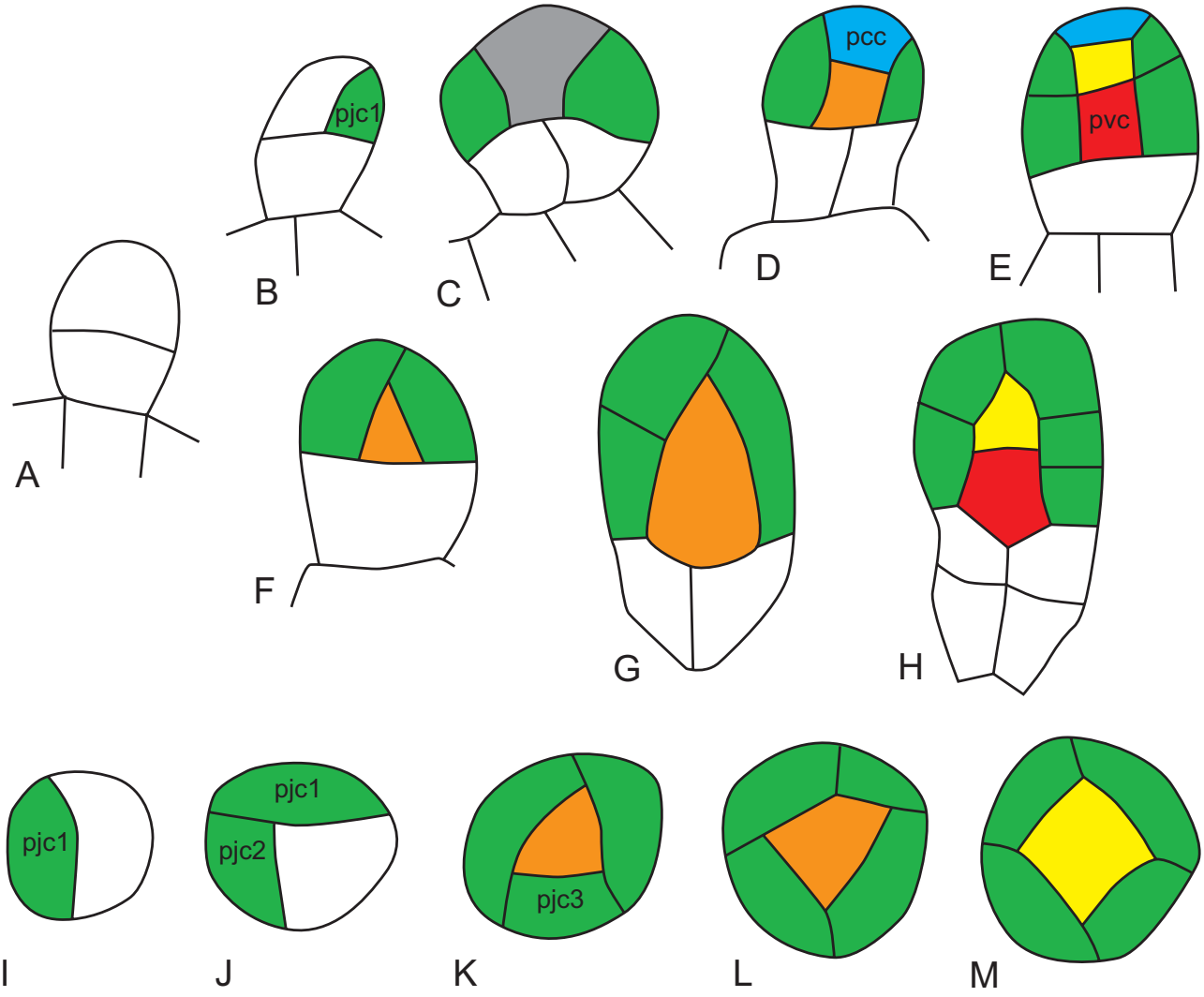


Figure 3. Two types of early archegonium development in liverwort *Haplomitrium*. Both types may be found within a species. A–E, open type. A, F–H, closed type. I–M, Transverse sections, which are similar in archegonia developing according to either type. Line drawings modified from D.H. Campbell (1920), E.O. Campbell (1959) and Bartholomew-Began (1991). Green, primary jacket cells (in B–D, F, J–L; numbered in sequence of their origin as pjc1, 2, 3) and cells derived from them. Grey, primary axial cell, which produces a primary cover cell (blue, pcc) and a central cell (orange). The central cell produces a primary ventral cell (red, pvc) and primary neck canal cell (yellow).

divisions of the primary cover cell take place, they are equal and vertical (Fig. 2G, H). As a result, a group of two (e.g. Haupt, 1920) or much more commonly four (Durand, 1908; Campbell, 1918; Schuster, 1966, 1992a; Shimamura, 2016) cover cells is formed. In some cases, the four cover cells undergo one or two additional divisions (Campbell, 1918). For example, in *Riccia* L. each of the four cover cells divide by radial walls usually once, so that the complete number is normally eight (Campbell, 1918), although sometimes only six or as many as ten cells are formed (von Janczewski, 1972). The cover cells separate from each other just before maturation of the archegonia, probably owing to a breaking down of the middle lamellae that connect them (Schuster, 1992a).

The primary axial cell (in the open type) or the central cell (in the closed type) undergoes a series of horizontal divisions to produce a proximal egg cell and a distal series of canal cells (Fig. 2). The first division gives rise to a primary ventral cell (terminology of Schuster, 1966; also called secondary central cell or venter canal cell) and a primary neck canal cell. The former ultimately produces the egg cell and the ventral canal cell (athough this division may be much delayed: e.g. Schuster, 1966; Shimamura, 2016) and the latter gives rise to the neck canal cells. The number of neck canal cells varies from up to 40 in *Haplomitrium* Nees (Campbell, 1959) to as few as four, e.g. in the model liverwort *Marchantia polymorpha* L. (Durand, 1908; Shimamura, 2016), or rarely two [in *Sphaerocarpos* (Micheli) Boehm. ex Ludwig (Schuster, 1992a, but see Campbell, 1918)]. According to Durand (1908), some neck canal cells are ultimately binucleate in *Marchantia* L. The primary jacket cells divide in different planes to form the jacket. The jacket is formed by one cell layer in the neck (i.e. the neck wall) and by two (sometimes one or more than two) cell layers in the venter.

The current phylogeny-based classification of liverworts (Marchantiophyta) recognizes three classes with the following relationships: Haplomitriopsida (Marchantiopsida + Jungermanniopsida) (Crandall-Stotler *et al.*, 2009). Haplomitriopsida are species-poor compared with two other classes and include only three genera (Crandall-Stotler *et al.*, 2009): *Haplomitrium* Nees (Haplomitriaceae), *Treubia* Goebel and *Apotreubia* S.Hatt. & Mizut. (Treubiaceae). Most liverworts possess the open type of archegonium development. The closed type is found in *Haplomitrium* (Campbell, 1920; Campbell, 1959; Bartholomew-Began, 1991), *Apotreubia* (Renzaglia, 1982) and in a late-divergent member of Marchantiopsida, *Monoclea* Hook. (Note that only the open type is found in *Treubia insignis* Goebel, Campbell, 1916). In *Haplomitrium* and *Apotreubia*, the closed type occurs with the open type (Campbell, 1920; Renzaglia, 1982; Bartholomew-Began, 1991). Both developmental patterns can sometimes be found in the same species [*Haplomitrium blumei* (Nees) R.M.Schust. Campbell, 1920] and even in the same accession in *H. mnioides* (Lindb.) R.M.Schust (Bartholomew-Began, 1991) and *Apotreubia nana* (S.Hatt. & Inoue) S.Hatt. & Mizut. (see figs 26, 27 in Renzaglia, 1982). However, Campbell (1959) found only the closed type in *H. gibbsiae* (Stephani) R.M.Schust. In archegonia of *Haplomitrium* developing according to the open type, the primary cover cell apparently remains undivided (Bartholomew-Began, 1991) or it undergoes the quadrant division typical to most liverworts, and there may be a limited number of secondary divisions in the quadrant cells (Campbell, 1920). Also, Campbell (1920) reported an archegonium of the open type with four canal cells and no cover cell. In *Monoclea* (a genus of one or two closely related species: Campbell, 1987), the closed type was described by Campbell (1954) for the New Zealand material, but Johnson (1904) illustrated the open type for his material from Jamaica, although the earliest stages were not available in the latter case.

Unlike other liverworts, early archegonium and antheridium development are remarkably similar to each other in *Haplomitrium* (Campbell, 1920; Campbell, 1959; Bartholomew-Began, 1991) and possibly in *Apotreubia* (see Inoue, 1960; Renzaglia, 1982). Even variation in the presence vs. absence of a cover cell is shared by archegonia and antheridia in *Haplomitrium* (Bartholomew-Began, 1991). This similarity is traditionally viewed as a primitive (plesiomorphic) condition, an important argument for placement of *Haplomitrium* at the beginning of the liverwort classification (Campbell, 1920; Campbell, 1959; Schuster, 1966; Schljakov, 1975; Bartholomew-Began, 1991; Renzaglia *et al.*, 2007; Crandall-Stotler *et al.*, 2009). On the other hand, Filin (2009) suggested that the closed pattern of development shared by antheridia and archegonia of *Haplomitrium* could be a derived condition related to progenesis in evolution of liverwort gametangia. Indeed, this developmental pattern allows the earliest possible ontogenetic differentiation of the primary axial cell (in archegonia) and the primary androgonial cell (in antheridia). We agree that the similarity between male and female structures as such cannot guarantee their plesiomorphic nature. Meyen (1984, 1988) highlighted that such similarities may appear by a secondary shift of developmental progams from one sex to the other and provided hypotheses on the roles of this phenomenon (called gamoheterotopy, but see Sokoloff & Timonin, 2007) in the evolution of seed plants. Importantly, it seems that the closed type of archegonium development occurs together with a similar type of early antheridium development only in *Haplomitrium*. In *Monoclea*, early antheridium

development is totally different from that of the archegonium and matches the pattern characteristic of antheridia of other Marchantiopsida (Campbell, 1954).

The number of neck wall cells observed in cross section is an important taxonomic character in liverworts (Schuster, 1966). Early in development, the neck wall is always composed of tiers each formed by three cells (Fig. 2C, K). In most Marchantiopsida, at a certain stage every neck wall cell undergoes a vertical division so that the mature neck wall consists of tiers, each formed of six cells (Fig. 2E). In most Jungermanniopsida, such vertical division takes place in two of three cells of a tier, so that the mature neck has only five rows of neck wall cells. There are several remarkable exceptions from the general pattern of differences between Marchantiopsida and Jungermanniopsida (Schuster, 1984, 1992a). In Blasiaceae (*Blasia* L. and *Cavicularia* Stephani) five or six rows of neck wall cells occur (Renzaglia, 1982). Blasiaceae are currently viewed as an early-divergent member of Marchantiopsida according to molecular phylogenetic data (Crandall-Stotler *et al.*, 2009). Campbell (1954) described six cell rows in *Monoclea*, which is consistent with its placement in Marchantiopsida, but Johnson (1904) found (five) six to eight rows in his material of *Monoclea*. Haupt (1918) reported that in *Pallavicinia lyellii* (Hook.) Gray (Jungermanniopsida) the neck canal cells are surrounded by a neck wall of five cells (in cross section), although frequently one or more of these may divide. These divisions apparently occur late in development, because in this illustration of the neck with six cells in transverse section, two cells are much smaller than the others. Thus, the condition with six rows found in this species is not homologous to that in Marchantiopsida. In Metzgeriaceae (Jungermanniopsida), there are five or six rows (Renzaglia, 1982). The most substantial deviations from the five-seriate condition of Jungermanniopsida are found in some thalloid genera (Renzaglia, 1982; Schuster, 1992a) currently classified in families Petalophyllaceae (Pelliidae) and Aneuraceae (Metzgeriidae, Crandall-Stotler *et al.*, 2009). Among the two genera of Petalophyllaceae, *Petalophyllum* Nees & Gottsche ex Lehmann, has six rows of neck wall cells and *Sewardiella* Kashyap has five (six) to eight rows (Renzaglia, 1982). Necks with six or seven (or more) rows of wall cells are found in all four currently recognized genera of Aneuraceae (see Schuster, 1992a, 1999; Crandall-Stotler *et al.*, 2009; Preußing *et al.*, 2010). The monospecific New Zealand genus *Verdoornia* R.M.Schust. (Aneuraceae) is unique in having short archegonia with no clear boundary between the venter and the neck. Furthermore, unlike all other setaphytes, the archegonia of *Verdoornia* are sessile with a broad base directly continuous with the thallus tissue (Schuster, 1999). The orifice of the mature archegonium is formed by eight to 12 cells, but the cell rows are not pronounced. Based on the illustrations of Schuster (1999), late cell divisions are chaotic in the jacket of *Verdoornia*. There are no developmental data for *Verdoornia*. Apart from many mature archegonia, Schuster (1999) found a single structure, presumably an immature archegonium, with five peripheral cells and one internal cell visible just below the summit. This arrangement might suggest that the archegonium of *Verdoornia* develops from something resembling a typical archegonium of Jungermanniopsida. Phylogenetic data (Crandall-Stotler *et al.*, 2009) suggest that the variation found in Aneuraceae is probably a derived condition.

Although species-poor, Haplomitriopsida are diverse in the number of neck wall cells. In *Haplomitrium*, only one cell of each tier undergoes a vertical division, and a neck wall of four rows of cells is produced (Fig. 3L, M). There is an equivalent process in antheridium development in *Haplomitrium* (Bartholomew-Began, 1991). Renzaglia (1982) illustrated the earliest stages of archegonium development in *Apotreubia nana*, with the same transition from three to four peripheral cells in cross section, but subsequent development is unknown. In *Haplomitrium*, additional vertical divisions sometimes take place in the older neck wall cells in the distal region of the archegonium to form a few tiers of neck wall cells composed of five or six cell rows (Bartholomew-Began, 1991) or even six to ten cell rows (Campbell, 1959), although the proximal part of the neck still has only four rows.

Campbell (1916) described (but did not illustrate) the formation of six rows of neck wall cells in *Treubia insignis* in the same way as in Marchantiopsida. With subsequent vertical divisions in older archegonia, the number of cell rows sometimes reaches as many as nine, especially in the lower part of the neck (Campbell, 1916; see also Renzaglia, 1982).

Archegonia of mosses 藓纲

Some moss archegonia are the largest and the most complex (in terms of cell number) among the archegonia of land plants. Disentangling a complete pattern of cell divisions during archegonium development requires considerable effort, and descriptions provided by some early authors are thus controversial and published data vary as to their completeness. Apparently, the most detailed and well-documented accounts are those of Bryan (1915, 1917) for *Sphagnum subsecundum* Nees (Sphagnopsida) and *Atrichum angustatum* (Brid.) Bruch & Schimp. (Polytrichopsida) and Holferty (1904) for *Plagiomnium cuspidatum* (Hedw.) T.Kop. (Bryopsida). Kühn (1870) provided data on *Andreaea*

rupestris Hedw. (Andreaeopsida). Bryan (1915, 1917) and Holferty (1904) also provided useful analyses and criticism of previous publications.

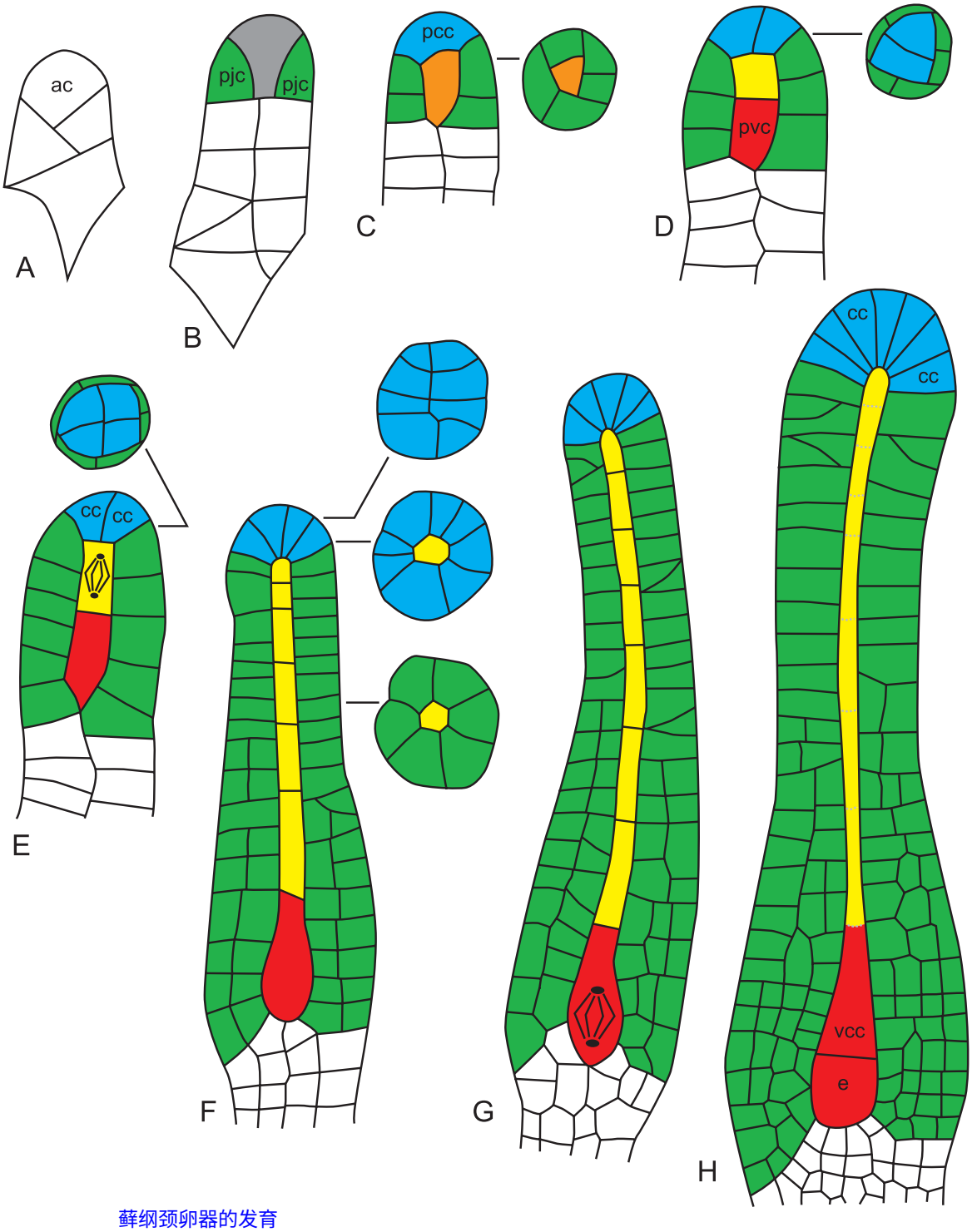
In the first phase of archegonium development (Figs 4A, 5A), there is an apical cell with two cutting faces producing a filament of a few cells (in *Sphagnum* L., the filament is sometimes formed by transverse divisions of the apical cell in the terminal archegonium of a cluster: Bryan, 1915). Their divisions produce a massive stalk of the archegonium. Subsequently, the apical cell changes its activity (Figs 4B, C, 5B) and three obliquely vertical divisions produce peripheral cells (primary jacket cells) surrounding a cell that is triangular in cross section (the primary axial cell). With these three divisions, formation of the archegonium proper is initiated. Vertical divisions of the primary jacket cells normally results in six rows of neck wall cells (Goffinet *et al.*, 2008; sometimes five in *Sphagnum*, Campbell, 1940). Jacket cell divisions take place in all three planes in the venter, so that its wall is multilayered in mosses. The primary axial cell then divides horizontally (i.e. transversely to the archegonial axis) producing the primary cover cell outside and the central cell inside. Subsequent horizontal division of the central cell forms the primary neck canal cell and the primary ventral cell. The former produces neck canal cells and the latter produces the egg cell and the ventral canal cell. The above aspects of archegonium development appear to be conserved among mosses (Campbell, 1918, 1940).

In *Sphagnum subsecundum* (Fig. 4), the primary cover cell exhibits an early vertical and equal division, followed by equal vertical divisions of the daughter cells, so that four cover cells are formed. Each of these undergo another vertical (but neither radial nor tangential) division (Bryan, 1915). As pointed out by Bryan (1915), at older developmental stages, the cells of the cover and the neck usually cannot be separated with any degree of certainty and no accurate statement as to the final number of cells produced by the cover can be made. However, at least in a series of transverse sections illustrated by Bryan (1915, fig. 57, redrawn here as Fig. 4F) the border of the cover is clearly visible: below it the neck wall is composed of six jacket cells, above it the uppermost neck canal cell is surrounded by eight cover cells. *Sphagnum subsecundum* has up to nine neck canal cells, all derived from divisions of the primary neck canal cell. None of them is produced from derivatives of the cover cell (Bryan, 1915).

In *Atrichum angustatum* (Fig. 5), the pentagonal primary cover cell undergoes a series of divisions similar to those in the initial cell of the archegonium proper (Bryan, 1917), so that there are apparently three obliquely vertical divisions at *c*. 120° to each other, producing three peripheral cells (here called additional primary jacket cells, their further divisions add cells to the neck wall) followed by a horizontal division. The lower daughter cell resulted from the horizontal division (here called additional primary neck canal cell) exhibits further divisions, producing neck canal cells, and the upper daughter cell exhibits another round of divisions similar to those in the initial of the archegonium proper. Bryan (1917) documented at least three rounds of such divisions of the primary cover cell, but the actual number of rounds apparently varies and may exceed this figure. The primary cover cell of *Atrichum angustatum* can be viewed as an apical initial cell with four triangular cutting faces: three lateral and one proximal. Note that this shape and mode of division is apparently not recorded in any monoplex apical meristems of thallus or shoot in gametophytes and sporophytes of any land plants. At a certain stage of development, the uppermost cell of the archegonium radically changes the pattern of divisions: it undergoes an equal and vertical division followed by vertical divisions perpendicular to the first one in each of the daughter cells. This pattern corresponds exactly to the typical behaviour of the primary cover cell of *Sphagnum* as well as most liverworts and hornworts. As in these taxa, a quadrant of cover cells is formed in *Atrichum angustatum*. Each of the four cover cells exhibits further vertical division(s), although these are not radial but tend to be parallel to one of the previous vertical cutting faces (Bryan, 1917).

The major growth of the archegonium neck of *Atrichum angustatum* is intercalary. The cells of the neck canal row (the number of which varies from *c*. 50 to as many as 86) have a double origin. The lower cells are formed by divisions of the primary neck canal cell, the upper cells through divisions of the three or more initials cut from the base of the primary cover cell (Bryan, 1917). Some late cell divisions in the neck canal row are vertical rather than horizontal. Thus, the canal row is generally multiple in its upper part and occasionally throughout in *Atrichum angustatum* (Bryan, 1917). Data of Holferty (1904) for *Plagiomnium cuspidatum* largely agree with those for *Atrichum angustatum*. The description of Kühn (1870) for *Andreaea rupestris* also agrees with data for *Atrichum angustatum*, except that the cells derived from horizontal divisions of the uppermost cell of young archegonium are said to differentiate directly into neck canal cells, without additional divisions. *Andreaea rupestris* has relatively few neck canal cells, and these form a single row. There is no direct evidence of the presence of a ventral canal cell in *Andreaea rupestris* (Kühn, 1870; Smith, 1955).

Ruhland (1924) and Campbell (1940) suggested that the pattern described above for *Atrichum angustatum* (sometimes with minor differences) characterizes all mosses except *Sphagnum* (see also Burr, 1939; Goffinet *et al.*, 2008). Note that detailed



薛纲颈卵器的发育

Figure 4. Archegonium development in moss *Sphagnum subsecundum*. Line drawings of longitudinal and transverse sections modified from Bryan (1915). Mitotic divisions in some cells are indicated. Colouring indicates cell lineages. Green, primary jacket cells (pjc) and cells derived from them (note that the bottom boundary of these cell lineages cannot be precisely identified in E–H). Grey, primary axial cell, which produces a primary cover cell and a central cell. Blue, primary cover cell (in C) and cover cells derived from it (cc). Orange, central cell, which produces a primary ventral cell (red, pvc) and primary neck canal cell (yellow). All neck canal cells (yellow) are derived from the primary neck canal cell. The primary ventral cell produces an egg (e) and a ventral canal cell (vcc), at the stage when the neck canal cells are disintegrating (H).

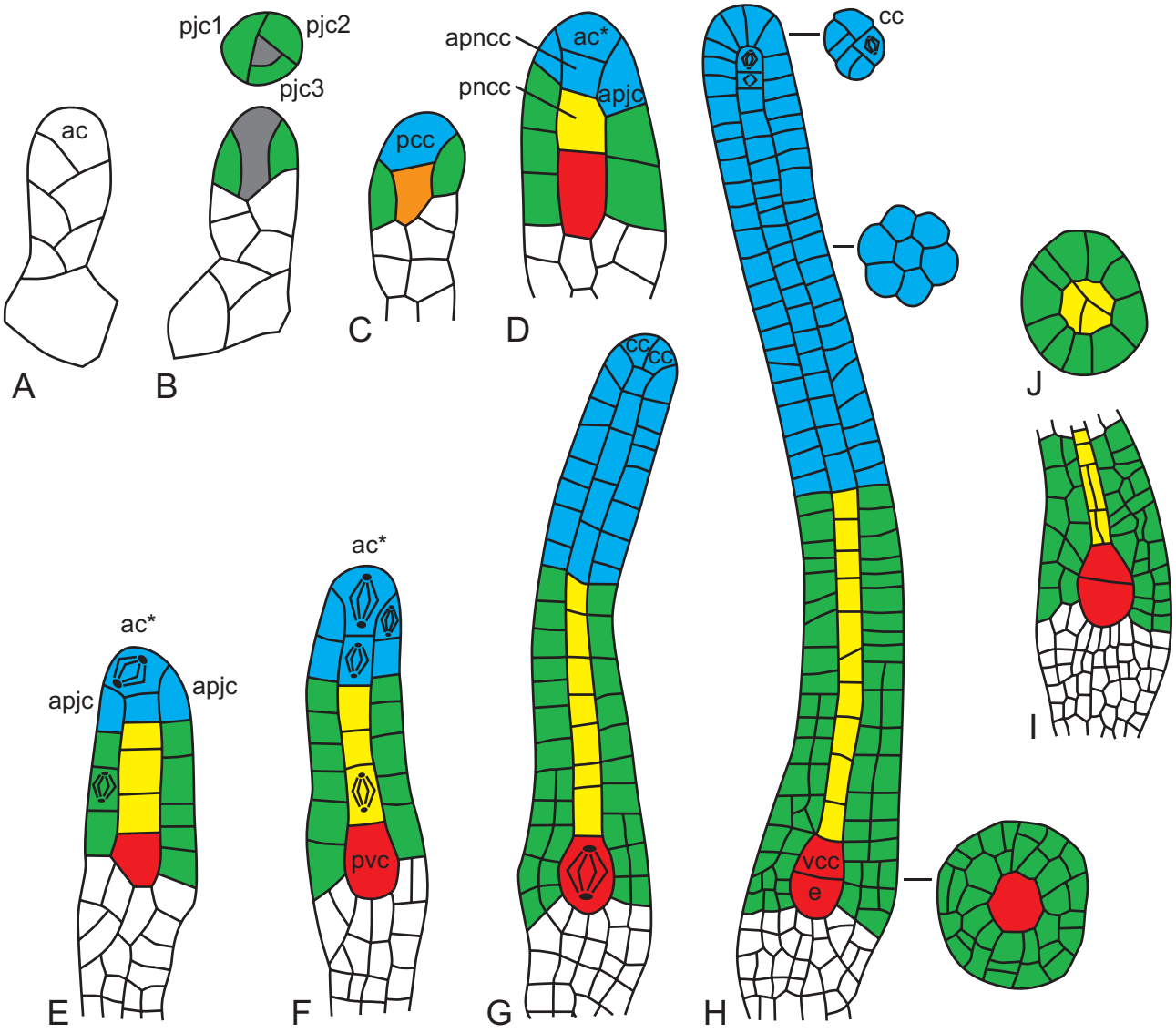


Figure 5. Archegonium development in moss *Atrichum angustatum*. Line drawings of longitudinal and transverse sections modified from Bryan (1917). Mitotic divisions in some cells are indicated. Colouring indicates cell lineages. Green, primary jacket cells (in B, C) and cells derived from them. Grey, primary axial cell, which produces a primary cover cell and a central cell. Blue, primary cover cell (in C) and cells derived from it (in D–H). Orange, central cell, which produces a primary ventral cell (red) and primary neck canal cell (yellow, D). As can be seen from D–H, not all cells of the neck wall are derived from the primary jacket cells. The upper part of the neck wall is derived from the primary cover cell. The boundary between these cell lineages (green and blue) cannot be precisely identified at later developmental stages. It is shown here as arbitrary. Similarly, not all neck canal cells are derived from the primary neck canal cell (yellow), but those in the distal part of the neck (blue) are derived from the primary cover cell (E–H). Again, a boundary cannot be precisely traced at late stages of development. J is a transverse section of archegonium similar to that in I cut in the middle part of the neck. Note more than one row of neck canal cells. ac, two-sided apical cell before development of the archegonium proper; ac*, apical cell cutting off four rows of daughter cells, one row by periclinal divisions (apncc) and three rows by oblique vertical divisions (apjc); apjc, additional primary jacket cell; apncc, additional primary neck canal cell; cc, cover cell; e, egg cell; pcc, primary cover cells; pjc1, 2, 3, primary jacket cells in sequence of their origin; pncc, primary neck canal cell; vcc, ventral canal cell; pvc, primary ventral cell.

accounts of archegonium development and even definitive structure are still missing for many key taxa (Fig. 1), most importantly for *Takakia* S.Hatt. & Inoue and *Andreaeobryum* Steere & B.M.Murray (Schuster, 1997; Ignatov *et al.*, 2016). As Sphagnales and *Takakia* are putatively the two earliest-diverging moss lineages (Chang & Graham, 2011; Shaw *et al.*, 2011) and development of the archegonium proper of *Sphagnum* resembles that of the open type development of archegonia in liverworts, it is tempting to suggest that the characters found in *Sphagnum* are plesiomorphic for mosses. However, the picture seems to be more complex, and patterns of development may be related to the neck length and the number of neck canal cells rather than to higher-level phylogeny. Lal & Bhandari (1968) provided data on archegonium development in *Physcomitrium immersum* Sullivant (Funariaceae) suggesting a developmental pattern similar to that in *Sphagnum subsecundum*. This species has not more than seven neck canal cells. The model moss *Physcomitrella patens* (Hedw.) Bruch & Schimp. is relatively close to *Physcomitrium immersum* and also has relatively few neck canal cells, but recent studies of archegonium development in *Physcomitrella patens* do not provide relevant information regarding the developmental roles of the primary cover cell (Kofuji *et al.*, 2009; Landberg *et al.*, 2013). Kofuji & Hasebe (2014) recognized eight types of stem cells in the life cycle of *Physcomitrella patens*, including the archegonium stem cell that produces several cells in two rows before formation of the archegonium proper. In this terminology, *Atrichum angustatum* possesses yet another type of stem cell, the primary cover cell, but the question of its potential occurrence in *Physcomitrella patens* has not been investigated.

Before fertilization, moss archegonia open by separation of the uppermost cells. Details of this process were nicely described and illustrated by Zielinski (1909), but without a reference to whether all separating cells are derived from the quadrant of cover cells. Early in development, the distalmost cells of the archegonium wall are similar to the more proximal cells of the neck wall. All these cells contain starch. Later in development, the distalmost cells no longer possess starch grains but accumulate mucilage. The distalmost cells then increase in size due to swelling of the mucilage, and the cuticle breaks by longitudinal cracks at the tip of the archegonium. The resulting strips of cuticle roll back, together with the distalmost cells that remain attached to it, but separate from each other. Although the formation of cracks is rather irregular, often four cuticle strips are formed (Zielinski, 1909; Landberg *et al.*, 2013), possibly according to the primary division of the cover into the four sectors derived from the quadrant stage. Illustrations of Sharma & Chopra (1964) suggested that most cells separating from each other at archegonium dehiscence belong to the neck wall, at least in *Lyellia crispa* R.Br. (Polytrichaceae), because the quartet cover cells are still undivided in mature archegonia of this species. The process of distal opening is similar in moss antheridia and archegonia (Zielinski, 1909). In *Physcomitrella patens*, *PpSHI* genes are required for the apical opening of both antheridia and archegonia (Landberg *et al.*, 2013).

Although the ventral canal cell normally disappears before fertilization, there are records of its occasional persistence in mature archegonia in various mosses. For example, Lal, Kaur & Chauhan (1982) found that in *Physcomitrium immersum*, 2–3% of mature archegonia have a persistent ventral canal cell that remains healthy and retains its original size. The persistent ventral canal cell becomes rounded, freely suspended along with the egg in a mucilaginous substance and almost as large as the egg cell. Ultrastructure of the ventral canal cell in these cases is similar to that of a young egg (Lal *et al.*, 1982). In *Sphagnum* (Bryan, 1915, 1920; Ruhland, 1924), the ventral canal cell is variable in size and fate. It may ultimately disintegrate, but sometimes the egg cell disintegrates instead and the ventral cell acts as a female gamete. Apparently, in rare cases both cells can be fertilized. Sometimes, up to four or even six female gametes are formed in *Sphagnum*. Bryan (1920) reported occasional fusion of the ventral canal cell and the egg cell in *Sphagnum subsecundum*. The fusion of the protoplasts is followed by the fusion of the nuclei.

Archegonia of hornworts 角苔

The structure and development of hornwort archegonia was studied in detail by Renzaglia (1978) who also summarized previously published data (see also Renzaglia *et al.*, 2008). Archegonium development (Fig. 6) starts with three unequal anticlinal divisions of a cell situated at the dorsal surface of the thalloid gametophyte. The initial cell does not project above the gametophyte surface, and the archegonium remains completely embedded in surrounding gametophyte tissue throughout its development. Planes of the three anticlinal divisions of the initial cell are located at 120° angles to each other, resulting in a larger primary axial cell surrounded by three primary jacket cells. Each of the three primary jacket cells undergo one longitudinal division and a number of transverse divisions, giving rise to the six rows of neck jacket cells of a one- to two-layered venter jacket in the mature archegonium (Renzaglia, 1978; Renzaglia *et al.*, 2008). The primary axial cell divides transversely (the plane of division is parallel to the surface of the gametophyte). The

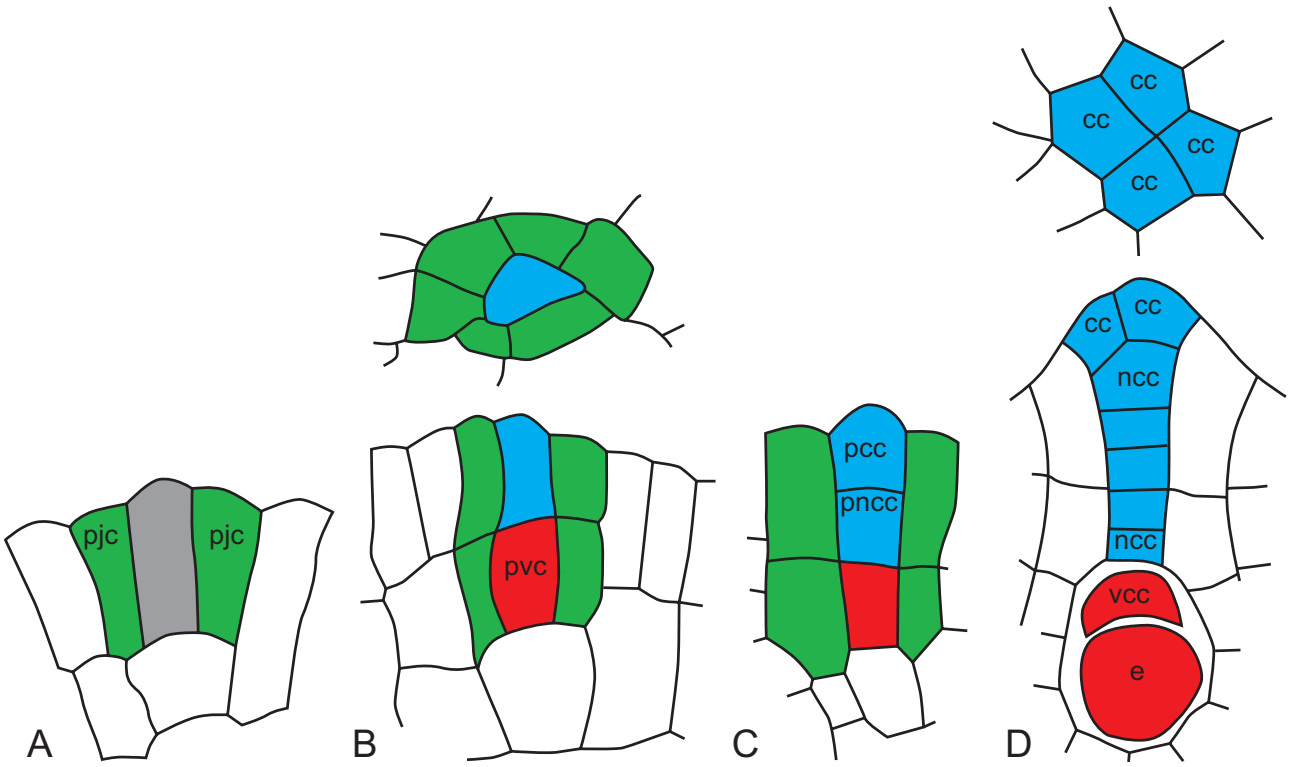


Figure 6. Archegonium development in hornworts. Modified from longitudinal sections of *Anthoceros* cf. *gemmulosus* (Bharadwaj as reproduced in Schuster, 1992b), with transverse section in B modified from Renzaglia (1978, *Anthoceros punctatus*) and transverse section in D modified from Campbell (1898, *Dendroceros* sp.). Colouring indicates cell lineages. Green, primary jacket cells (pjc) and cells derived from them. There are three primary jacket cells, but only two are visible in A. Each primary jacket cell produces two rows of jacket cells. Thus, six cells are visible in transverse section in B. Blue, cover cells (cc) and neck canal cells (ncc), primary cover cell (pcc) and primary neck canal cell (pncc), and their mother cell (in B). Note that the idea of the common origin of neck canal cells and cover cells in hornworts (Campbell, 1918) has not been tested in detail in recent studies. Red, primary ventral cell (pvc) that produces an egg (e) and a ventral canal cell (vcc).

inner cell is the primary ventral cell. The outer cell further divides transversely, producing an outer cell, which is the primary cover cell, and an inner cell, which is the primary neck canal cell (Campbell, 1918). [Smith (1955) stated that the primary canal cell is sister to the primary venter cell but failed to note the alternative interpretation and lacked convincing illustrations.] The primary cover cell divides vertically and equally and usually each of the daughter cells further divide vertically perpendicular to the plane of the first division, forming a quadrant of cover cells. In some cases, the second division does not occur in one or both daughter cells, and the mature archegonium has only two or three cover cells (Campbell, 1918; Renzaglia, 1978; Schuster, 1984, 1992b). When three cover cells are present, they may be unequal in size (Schuster, 1992b). Hornwort cover cells may have more numerous chloroplasts than neighbouring epidermal cells (Schuster, 1992b). In mature archegonia, the cover cells project strongly above the surrounding cells of the gametophyte; their walls become partially mucilaginous, which causes them to separate readily, and they are finally shed (Campbell, 1918). After shedding of the cover cells, the six distal neck jacket cells protrude slightly from the thallus surface and are overarched by a layer of mucilage (e.g. Proskauer, 1948; Renzaglia *et al.*, 2008).

The primary neck canal cells produce a row of neck canal cells. The primary ventral cell enlarges considerably and ultimately divides into an egg cell and a ventral canal cell. The timing of this division varies relative to the development of the neck canal cell. Sometimes, the primary ventral cell divides as late as after the neck canal cells have begun to disintegrate (Renzaglia, 1978). The two resulting cells are of approximately equal size, or the ventral canal cell appears a little larger than the egg (Renzaglia, 1978).

Renzaglia (1978) highlighted the considerable uniformity in archegonium morphology among hornwort genera. A deviation from the pattern described above is found in *Nothoceros aenigmaticus*

J.C.Villarreal & K.D.McFarland in which there are only two or three delicate cover cells per archegonium (a condition also found in other taxa), lying over a ring of (six-) seven or eight (-ten) cells that bound the archegonial canal (Schuster, 1992b, c). All archegonia studied by Schuster were unfertilized. The figures exceeding the typical hornwort six rows of the neck jacket cells result from secondary cell divisions (Schuster, 1992c).

孢子维管植物（蕨类）

Archegonia of free-sporing vascular plants (pteridophytes)

The structure and development of archegonia in vascular plants were reviewed by Gifford & Foster (1989). We follow their terminology in naming cells in archegonia of tracheophytes. We employ the orders of ferns and lycopsids according to PPG I (2016). Note that many of the key lineages are absent from this classification, because they are extinct.

In tracheophytes (Figs 7–11), the initial cell of the archegonium is located at the level of other epidermal cells and its first division is periclinal, so that a smaller outer and a larger inner cell are formed (Gifford & Foster, 1989; Renzaglia *et al.*, 2000). The upper of the two first-formed cells is the primary cover cell. The lower cell either functions directly as a central cell (Figs 7, 8A–G) or first divides to form a basal cell and a central cell (Fig. 8H–S), the latter being closer to the primary cover cell (or the neck). At least the venter or sometimes the entire archegonium is embedded into gametophyte tissue in pteridophytes. Entirely exposed archegonia are found in some species of *Schizaea* Sm. (Schizaeales), but the most important publications (Britton & Taylor, 1901; Bierhorst, 1968) unfortunately did not provide sufficient informative illustrations of archegonium development in these species.

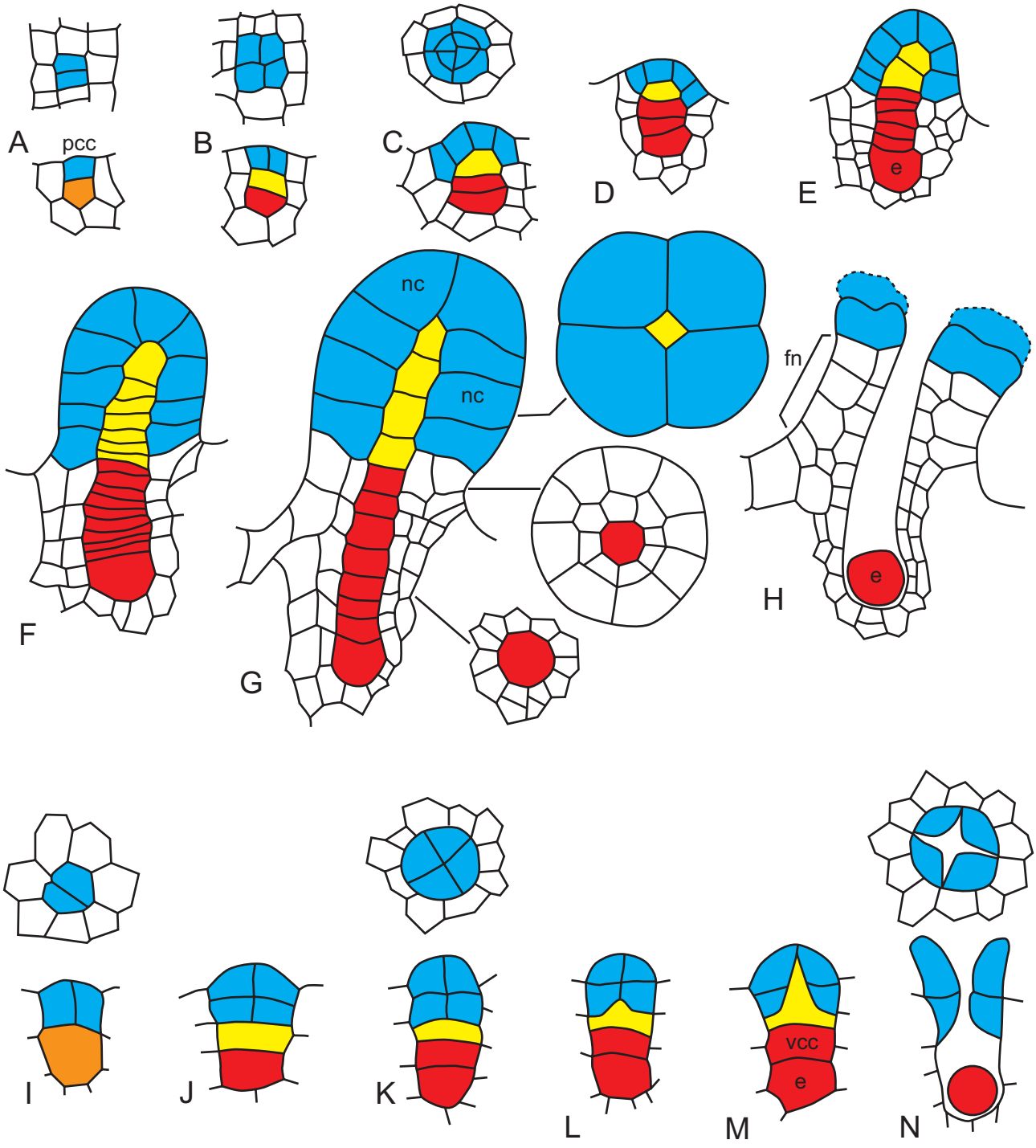
Cells derived from the primary cover cell

The primary cover cell always divides anticlinally into two equal cells, and these further divide equally and anticlinally, so that a plate of four cells is formed (Figs 7B, 8O) in the same way as in the cover of most bryophytes. In tracheophytes, these cells act as four neck initials. By further divisions (Figs 7, 8), they form the four vertical rows of cells of the archegonial neck (Gifford & Foster, 1989; Renzaglia *et al.*, 2000).

The neck canal cell(s) and the neck cells derived from the primary cover cell exhibit a remarkable and coordinated unequal growth. The wall between the primary cover cell (the four neck initials) and the central cell (the primary canal cell) is at first flat and horizontal (Figs 7A, B, I–K, 8A–C, H, I, N). At later stages, the canal cells lie between the four rows of neck cells, at least in the proximal part of the neck.

The degree of projection of the neck from the surface of the gametophyte varies among pteridophyte groups and there is no strict correlation with the number of cell tiers. Only slightly projected necks are characteristic of Marattiales (Fig. 8A–M), some Ophioglossales and heterosporous lineages (Campbell, 1907, 1940; Haupt, 1940; Bierhorst, 1971). Almost the entire neck or its basal tiers can be embedded in gametophyte tissue. The embedded versus projected nature of the neck apparently depends on patterns of cell divisions during neck development. Details of the actual divisions of the four quadrant cells and their daughter cells are rarely illustrated. The cell divisions that are responsible for a transition from a four-celled to an eight-celled neck are often initially vertical (so the divisions are anticlinal) or oblique, but with subsequent unequal growth of the neck cells, the dividing walls become horizontal (e.g. Buchtien, 1887; Bruchmann, 1908a). In *Angiopteris evecta* (G.Forst.) Hoffm. (Marattiales), after the oblique first division (Fig. 8D), a transition takes place from an eight-celled to a 12-celled neck by divisions in cells of the lower tier (Fig. 8F), resulting in an embedded neck (Haupt, 1940). In *Ptisana* Murdock (Marattiales) (Fig. 8L), further transition from a 12- to 16-celled neck is performed by divisions in cells of the middle tier (Stokey, 1942). When the lower part of the neck is embedded and the upper part is projecting, the eight-celled stage is followed by divisions in both tiers (e.g. Bruchmann, 1904).

The occurrence of four cell rows in the neck wall is the typical condition for all pteridophyte groups and the only condition found in all studies of younger developmental stages. There are reports of further divisions of neck cells. In *Lycopodium clavatum* L., Lang (1899) reported that subsequent divisions in one or more of the four rows may incease the number of rows, and Bruchmann (1898) noted the occasional occurrence of five rows of neck cells. However, neither author provided any illustrations supporting such observations, despite many published illustrations of the typical condition with four rows (Treub, 1884, 1890; Lang, 1899; Bruchmann, 1908a; Bruce, 1979b). In *Amauropelta hakgalensis* Holttum (Thelypteridaceae, Polypodiales), the proximal tier consists of eight cells (apparently by vertical divisions of the four primary cells) while each of the four subsequent tiers has four cells (Tigerschiöld, 1989). Various divisions in the basal tier of neck cells occur in some other ferns. In *Macrothelypteris torresiana* (Gaudich.) Ching (Thelypteridaceae), the distalmost of four to six neck cell tiers have three, seldom four, cells that are not triangular but irregularly shaped with an asymetrically



石松类

Figure 7. Archegonium development in lycopsids. A–H, *Diphasiastrum complanatum*, modified from Bruchmann (1908a). I–N, *Selaginella kraussiana* (top views of gametophyte with archegonium neck) and *S. martensii* (longitudinal sections), modified from Bruchmann (1908b). Colouring indicates cell lineages. Blue, cells derived from the primary cover cell. Orange, central cell, which produces a primary ventral cell (red) and a primary neck canal cell (yellow). Interpretation of cell lineages derived from the primary ventral cell and the primary neck canal cell is problematic in *Diphasiastrum* and other homosporous lycopsids. We follow a hypothesis of Bruchmann (1908a) on the occurrence of multiple ventral canal cells in D–G, but this hypothesis certainly requires further testing. e, egg cell; fn, false neck; nc, neck wall cells; pcc, primary cover cell; vcc, ventral canal cell.

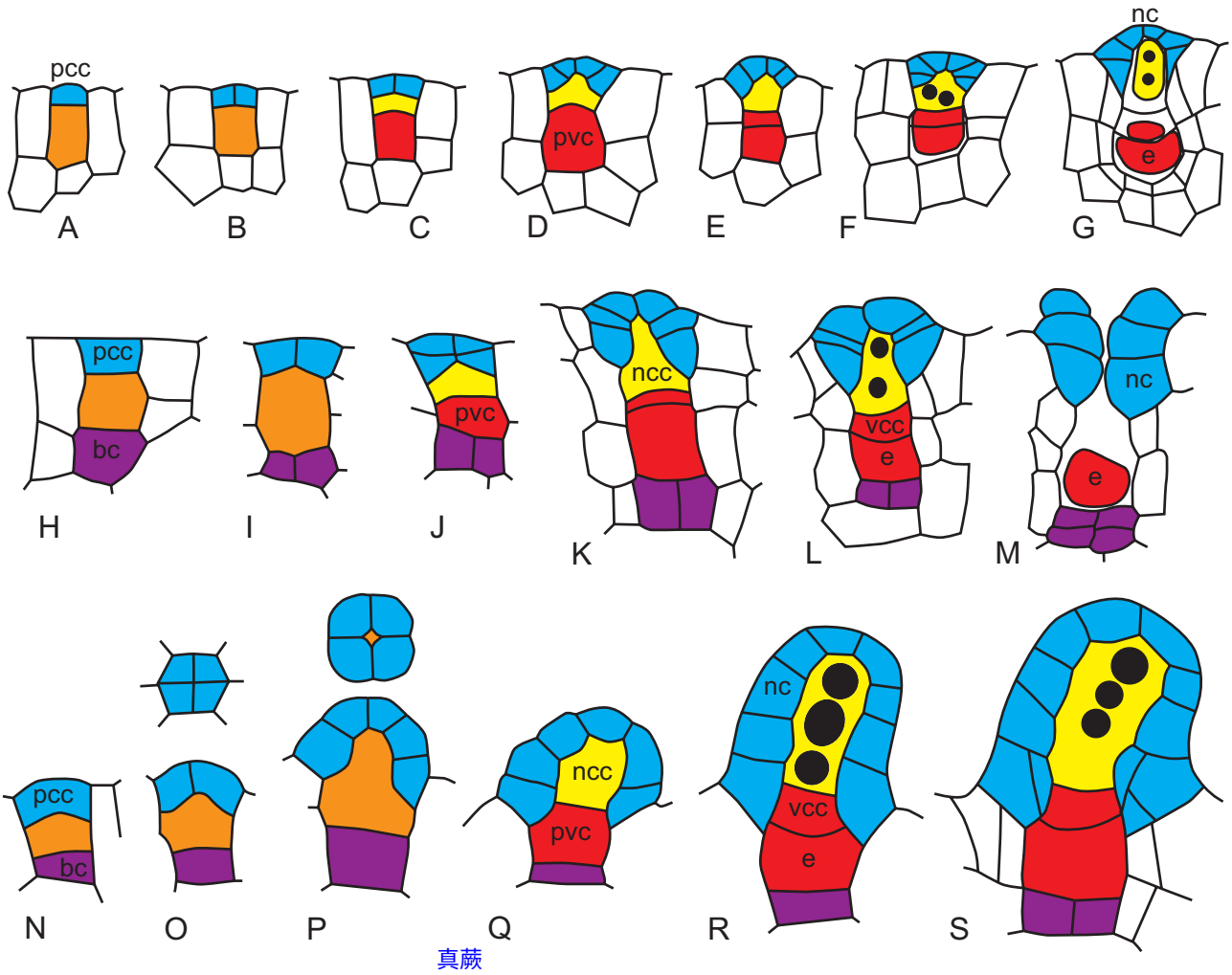


Figure 8. Archegonium development in monilophytes. A–G, *Angiopteris evecta* (Marattiales), modified from Haupt (1940). H–M, *Ptisana sambucina* (Marattiales), modified from Stokey (1942). Longitudinal sections in N–S, *Diplazium expansum* (Polypodiales), modified from Atkinson (1967), transverse sections in O, P, *Dryopteris filix-mas* (Polypodiales), modified from Kny (1895). Colouring indicates cell lineages. Blue, primary cover cell (pcc) and neck wall cells (nc) derived from it. Orange, central cell, which produces a primary ventral cell (red, pvc) and a neck canal cell (yellow, ncc). The primary ventral cell produces an egg cell (e) and a ventral canal cell (vcc). The latter becomes two- or three-nucleate (the nuclei are shown only in this cell). Violet, basal cell (bc) and cells derived from it.

positioned apical projection (Tigerschiöld, 1989). Use of scanning electron microscopy documented the sporadic occurrence of irregular neck-cell arrangement in some fern species (Elmore & Adams, 1976; Nester, 1985). In *Pteridium aquilinum* (L.) Kühn, abnormal archegonia with neck cells not arranged in orderly tiers were occasionally observed on older gametophytes (Elmore & Adams, 1976). In *Schizaea*, each neck cell (except those of the terminal tier) divides longitudinally to cut a small cell facing the neck canal, so that four small inner and four large outer neck cells can be seen in a cross section (Bierhorst, 1967).

There are differences among and sometimes within taxa in the number of tiers of the neck, i.e. in the number of cells in each of the four vertical rows (Table 3). Data available in the literature on the number of tiers of neck cells should be used with caution, even for well-investigated taxa. For example, Duckett (1973) noted that various earlier authors had reported two or three, three to five, three or four and two to four tiers in species of *Equisetum* L. subgenus *Equisetum*, but on the basis of his detailed studies concluded that mature archegonial necks are always composed of three tiers each of four cells and it is impossible to clearly distinguish a fourth tier from the other cells of the gametophyte cushion surrounding the venter. Does this mean that a fourth tier is always absent? The same condition (three tiers) was reported

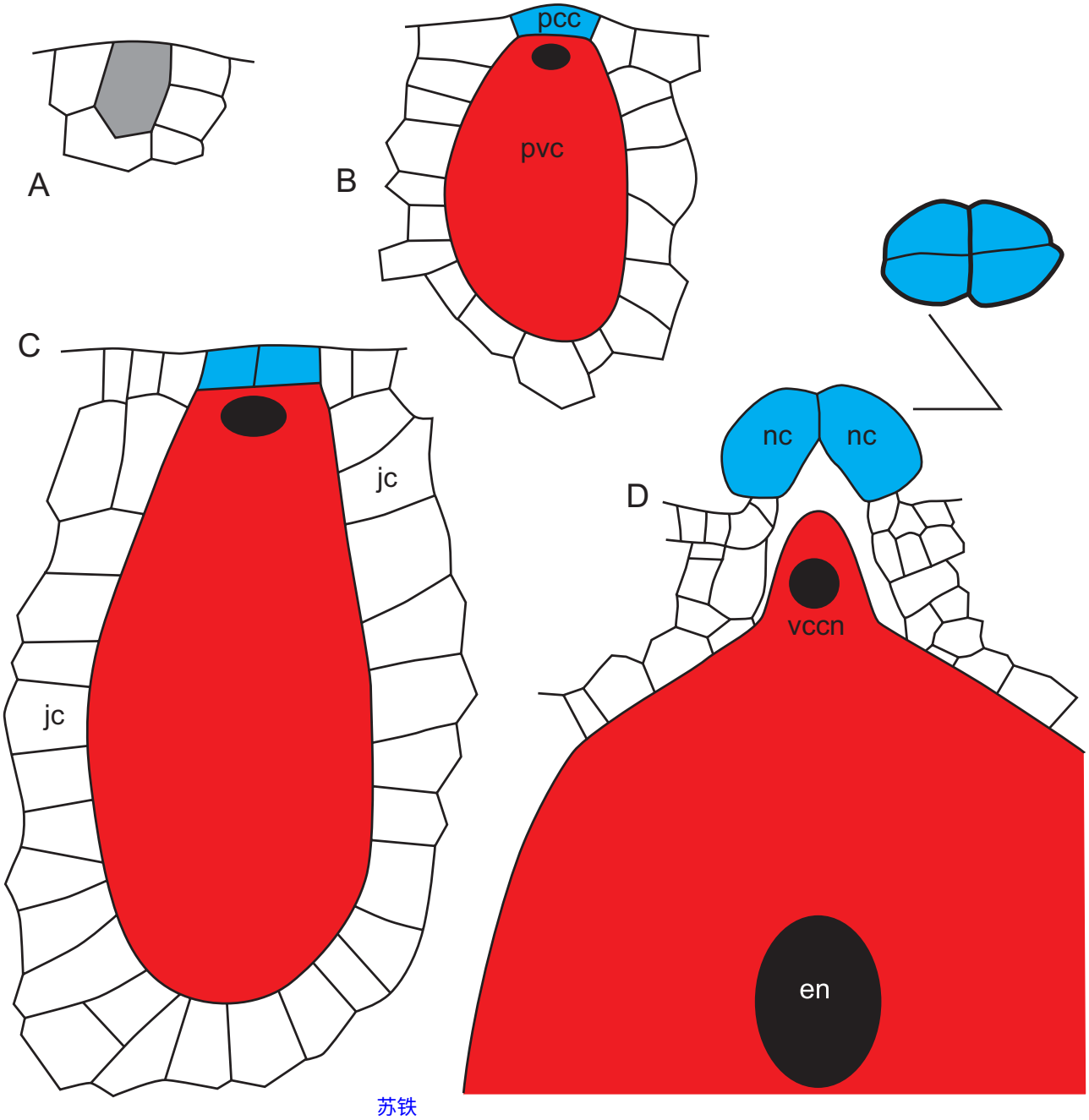


Figure 9. Archegonium development in cycads. A–C, *Dioon edule*, modified from Chamberlain (1935). D (longitudinal section and transverse section of neck cells), *Zamia integrifolia*, modified from Bryan & Evans (1957). Colouring indicates cell lineages. Grey, primary axial cell, which produces a primary cover cell (blue) and a primary ventral cell (red). The primary cover cell divides anticlinally to produce four neck cells in single tier. The nucleus of the primary ventral cell divides to form the egg nucleus and the ventral canal cell nucleus. Nuclei are only shown in this cell. en, egg nucleus; jc, jacket cells (derived from cells surrounding the archegonium inital); nc, neck cell; pcc, primary cover cell; pvc, primary ventral cell; vccn, ventral canal cell nucleus.

for Eurasian and North American species of *Equisetum* subgenus *Hippochaete* (Milde) Baker (Duckett, 1979) and the South American *E. bogotense* Kunth (Hauke, 1968), recently segregated as *Equisetum* subgenus *Paramochaete* Christenh. & Husby (Christenhusz *et al.*, 2019). Duckett & Pang (1984) studied a South American species of *Equisetum* subgenus *Hippochaete*, *E. giganteum* L. They concluded that in subgenus

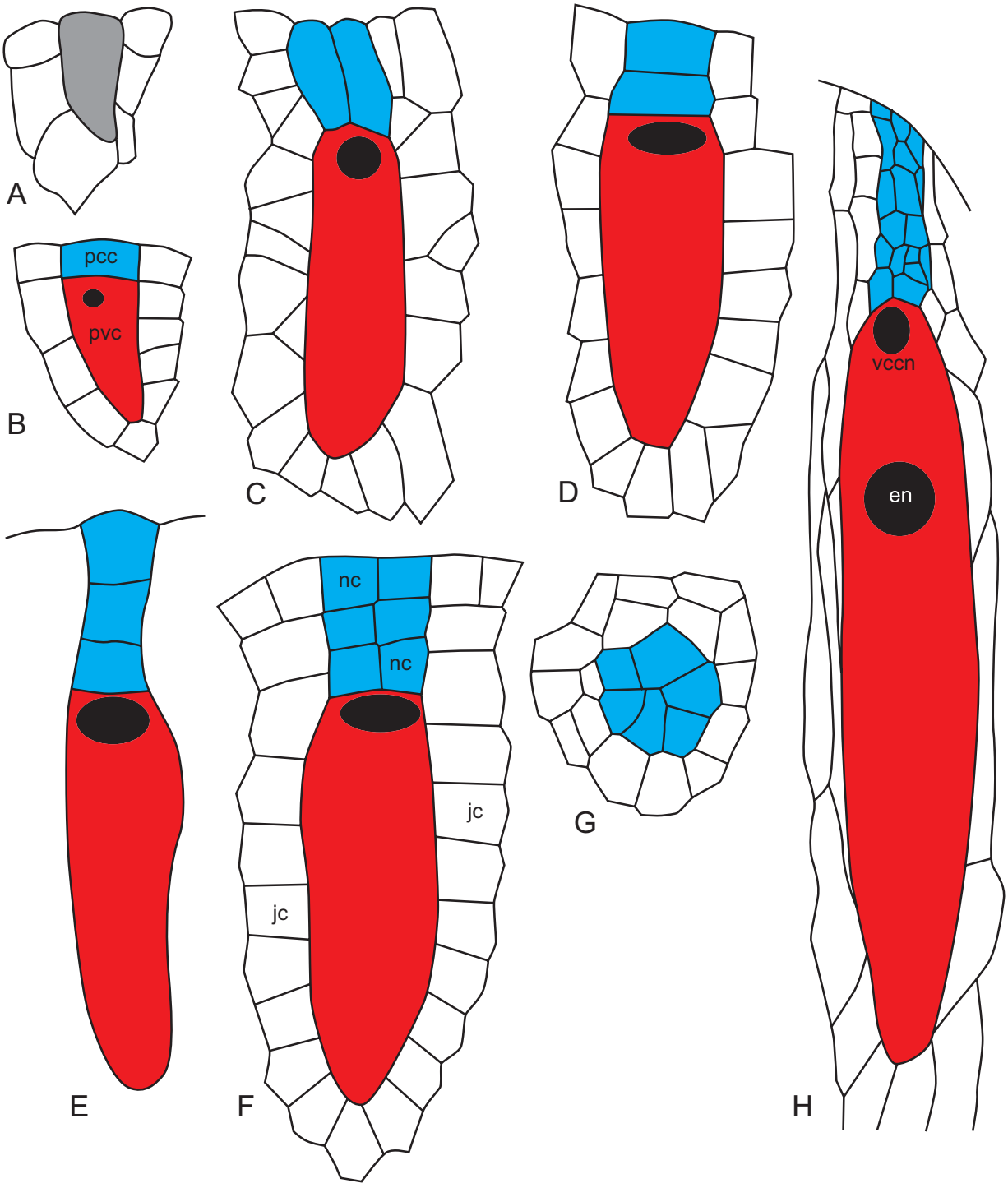
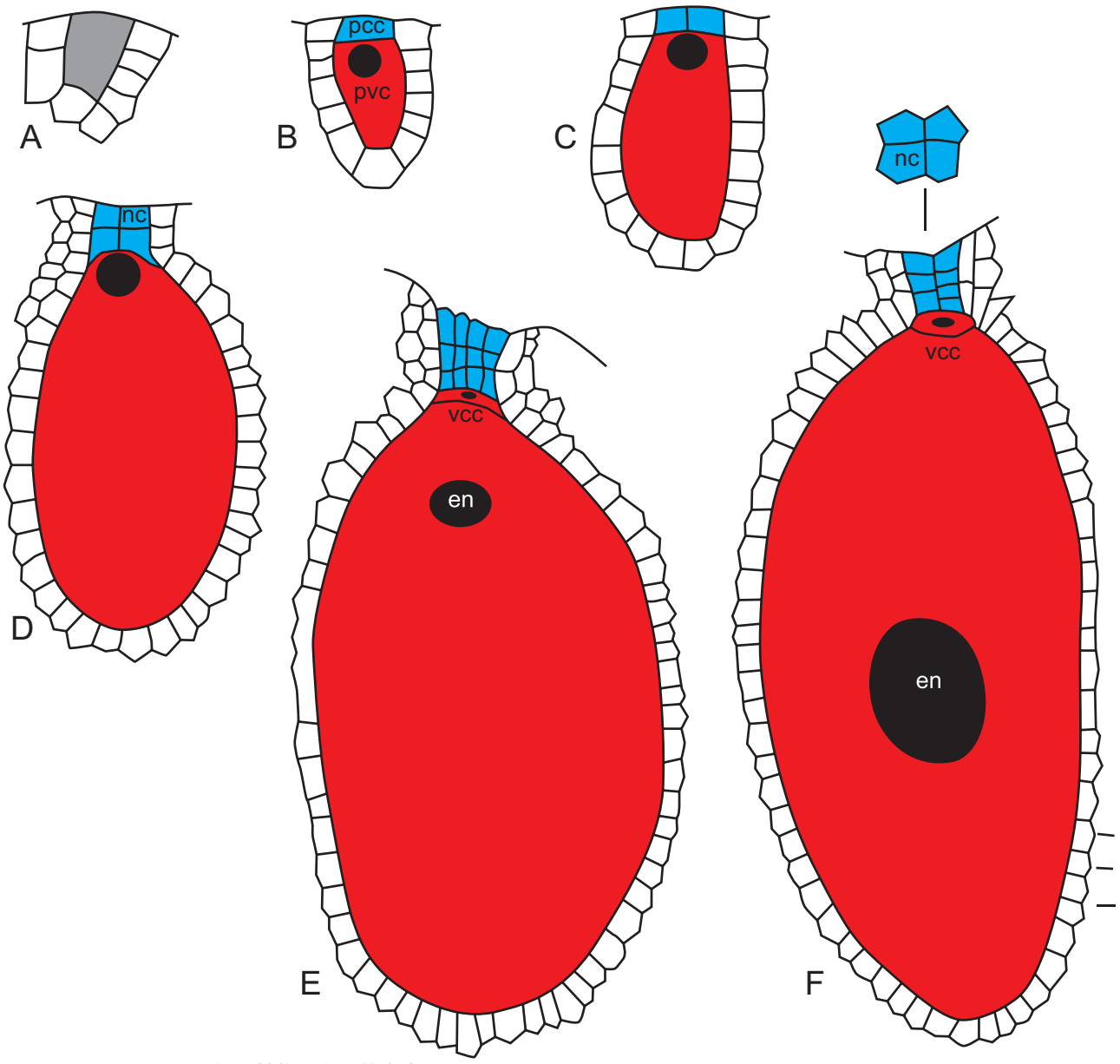


Figure 10. Archegonium development in gymnosperms: *Ephedra* (Ephedrales). Modified from Land (1904), Everett (1951) and Maheshwari (1935). Colouring indicates cell lineages. Grey, primary axial cell, which produces a primary cover cell (blue) and a primary ventral cell (red). The first division of the primary cover cell is either vertical (C) or more commonly horisontal (D). Sometimes, two horizontal divisions take place (E). The nucleus of the primary ventral cell divides into the egg nucleus and the ventral canal cell nucleus. Nuclei are only shown in this cell. In reality, there may be more nuclei in the female gamete, because the polyploid nuclei of the jacket cells penetrate into it (Friedman, 1990). en, egg nucleus; jc, jacket cells (derived from cells surrounding the archegonium inital); nc, neck cells; pcc, primary cover cell; pvc, primary ventral cell; vccn, ventral canal cell nucleus.



裸子植物颈卵器的发育

Figure 11. Archegonium development in gymnosperms: *Picea abies* (Pinales), modified from Miyake (1903). Colouring indicates cell lineages. Grey, primary axial cell, which produces a primary cover cell (blue) and a primary ventral cell (red). The primary cover cell divides anticlinally to produce four neck cells in single tier. These four cells may divide then only periclinally to form vertical rows (F) or also anticlinally, so that up to eight vertical rows are formed (of which four are visible in E). The primary ventral cell develops a large egg cell (its nucleus is shown) and a small ventral canal cell. en, egg nucleus; nc, neck cells; pcc, primary cover cell; pvc, primary ventral cell; vcc, ventral canal cell.

Hippochaete 'in all but *E. giganteum* the protruding archegonial necks comprise two or three tiers of cells. However, in *E. giganteum* only the terminal tier stands above the dorsal surface of the cushion (Duckett & Pang, 1984: 30)'. These statements cast doubt on conclusions regarding the stability of tier number in *Equisetum*; indeed, figures 8T and 8R in Duckett (1973) show the occurrence of only two tiers in *E. arvense* L. (subgenus *Equisetum*).

The necks of pteridophyte archegonia are either straight or curved. The latter condition is common in many leptosporangiate ferns, in which the direction of curvature (towards or more commonly away from the apex of the gametophyte) is usually taxonomically

Table 3. Variation of characters of archegonium morphology in pteridophytes

Order (PPG I, 2016) and class recognized here (Fig. 1)	Basal cell	Neck canal cells	Tiers of true neck cells	References
Lycopodiales (Lycopodiopsida)	absent	1–10 (in the true neck; up to 10 more canal cells in the venter)	3–5	Treub 1884, 1890; Bruchmann, 1898, 1908a, 1910; Lang, 1899; Bruce, 1979a, b; Whittier, 1981, 2003, 2006; Whittier & Webster, 1986
Isoëtales (Isoëtopsida)	absent	1 with 1 nucleus (sometimes with 2 nuclei)	4	La Motte, 1933; Campbell, 1940; Bierhorst, 1971
Selaginellales (Selaginellopsida)	absent	1 with 1 nucleus	2–3	Bruchmann, 1908b, 1912; Bierhorst, 1971
Equisetales (Equisetopsida)	absent (occasional presence reported by Campbell, 1940)	2, often side by side	(?2)3(?4)	Buchtien 1887; Hauke, 1968; Duckett, 1973, 1979; Duckett & Pang, 1984
Psilotales (Psilotopsida)	absent	1 (with 2 nuclei) or 2	6	Bierhorst, 1971
Ophioglossales (Ophioglossopsida)	present	1 (with 2 nuclei, apparently sometimes 1 with 1 nucleus) or 2	4–8	Bruchmann, 1904, 1906; Campbell, 1907, 1940; Bierhorst, 1971; Nayar & Kaur, 1971
Marattiales (Marattiopsida)	Present or absent	1 (with 2 nuclei) or 2	3–4	Campbell, 1940; Haupt, 1940; Stockey, 1942; Bierhorst, 1971
Osmundales (Polypodiopsida)	present	1 (with 2 nuclei) or 2	5–7	Campbell, 1892; Bierhorst, 1971; Cao *et al.*, 2012
Hymenophyllales (Polypodiopsida)	present	1 with 2 nuclei	4–9	Stokey, 1948; Bierhorst, 1971
Gleicheniales (Polypodiopsida)	present or absent	1 (with 2–4 nuclei) or 2	5–14	Stokey, 1945, 1950; Campbell 1940; Bierhorst, 1971
Schizaeales (Polypodiopsida)	present or absent	1 (with 2–4 nuclei)	3–9	Bierhorst, 1967, 1968, 1971, 1975; Nayar & Kaur, 1971; Nester, 1985
Salviniales (Polypodiopsida)	absent	1 (with 1 nucleus or with 2 nuclei side by side)	2–4	Bierhorst, 1971
Cyatheales (Polypodiopsida)	present or absent	1 (with 2–4 nuclei) or 4	4–8	Stokey, 1930; Bierhorst, 1971; Nayar & Kaur, 1971; Cao *et al.* 2011
Polypodiales (Polypodiopsida)	usually present	1 with 2(3) nuclei; sometimes up to 4 cells	3–8	Javalgekar & Mahabale, 1959; Bierhorst, 1971; Nayar & Kaur, 1971; Tigerschiöld, 1989; Mendoza, Pérez-García & Riba, 2002; Hu & Liu, 2012; Martínez, Chambi & Avilés, 2014.

significant (e.g. Bierhorst, 1971). When a neck is curved, two rows of neck wall cells usually possess more cells than two other rows (e.g. Momose, 1968).

There are diverse modes of neck opening in mature archegonia, but most commonly the rows of neck cells or the cells of the terminal tier split apart to release the contents of the neck canal which clears a passageway from the egg to the outside (e.g. Whittier & Peterson, 1980). In *Equisetum* (Hauke, 1968; Duckett, 1973, 1979; Duckett & Pang, 1984), the four cells of the terminal tier elongate at maturity, separate from each other and bend away from the neck canal. They may also twist spirally after or even before separation. The degree of elongation and twisting of the terminal cell varies, reaching a maximum in *E. fluviatile* L. and *E. bogotense* (which belong to different subgenera) where it is also accompanied by especially strong elongation of subterminal neck cells. In these two species, the behaviour of antheridia before and during dehiscence resembles that of the archegonia (Hauke, 1968; Duckett, 1979). In most Ophioglossales, archegonia dehisce by separation of the four terminal neck cells, but in one collection of *Botrychium virginianum* (L.) Sw., many archegonia showed separation, then lateral radiation of the four rows of cells, down to about four cells from the distal end (Bierhorst, 1971). Similar behaviour of the neck is illustrated for *Dipteris* Reinw. (Gleicheniales) (Stokey, 1945). In *Stromatopteris* Mett. (Gleicheniales) and some Lycopodiales, the basal one or two cells in each row of neck cells develop thickened walls separating them from more distal neck cells, which become lost by cellular disintegration (Bierhorst, 1971; Bruce, 1972).

False neck

Some Lycopodiales (i.e. homosporous lycopsids) possess a long neck in which the basal region lacks the characteristic tracheophyte condition of four vertical rows of cells, as more rows and more than one cell layer can be seen (Bruchmann, 1898, 1908a, 1910; Lang, 1899; Bierhorst, 1971; Bruce, 1979a). This basal region results from divisions of cells surrounding the archegonial initial rather than from the primary cover cell (Lang, 1899). In Lycopodiales, the primary cover cell apparently always produces about four tiers, each composed of four cells. The proximal part not derived from the primary cover cell (Fig. 7G, H) should be better termed a false neck, because this region is not strictly homologous with the archegonium neck of other vascular cryptogams (Lang, 1899). Additional anticlinal and periclinal divisions at the base of the neck are also reported in *Botrychium* Sw. (Ophioglossales, Bierhorst, 1971), but it is more likely that the basal part of the neck is embedded in gametophyte tissue (Bruchmann, 1906). Cell divisions around the base of the neck are found in some other ferns and at least in some cases the dividing cells are the four basal neck cells derived from the primary cover cell (see Bierhorst, 1971), and thus no false neck is formed.

Basal cell and venter jacket

A basal cell is not reported for any lycopsids (e.g. Bruchmann, 1898, 1908a, 1910; Lang, 1899; Bierhorst, 1971) and may be a synapomorphy of ferns (Johnson & Renzaglia, 2009). Its presence or absence in ferns is unstable (Table 3) and the character may vary within a family or even a genus (Gifford & Foster, 1989). In Marattiales, the presence or absence of a basal cell was found to be unstable at the species level in *Angiopteris smithii* Racib. (Stokey, 1942), although in some other species of the family it was either consistently present or consistently absent in samples examined (Haupt, 1940; Stokey, 1942). Often one or two further vertical (anticlinal) divisions of the basal cell take place (Nayar & Kaur, 1971). In the latter case, a quadrant of cells adjacent to the egg cell is formed (Bell, 1961). There are species where the basal cell does not divide or the occurrence of its division is unstable (e.g. Stokey, 1930). In *Ptisana sambucina* (Blume) Murdock, Stokey (1942) illustrated a vertical section with four cells almost certainly derived from the basal cell (Fig. 8M), these form two regular tiers (see also Campbell, 1940 on *Botrychium*). It is unclear from the description whether each tier really has four cells. In *Hymenophyllum* Sm. (Hymenophyllaceae), three types of division of the basal cell are documented: a horizontal division, a vertical division and a horizontal division followed by a vertical one in the cell adjoining the venter (Stokey, 1948). In *Cyathea horrida* (L.) Sm., Stokey (1930) found two basal cells in oblique arrangement so that they were apparently not products of division of a primary basal cell; these cells were likely derived from two successive divisions of the inner cell of a two-celled young archegonium.

Formation of more than one basal cell by successive divisions of the inner cell of a two-celled young archegonium was demonstrated by Bierhorst (1975) in *Actinostachys wagneri* (Selling) C.F.Reed (Schizaeales). Here, the archegonium initial is established by an oblique vertical unequal division of a superficial cell of the gametophyte (there are two such divisions in other species studied of this genus: Bierhorst, 1968). The small cell becomes the archegonium initial. It has a triangular shape in vertical section. The initial divides periclinally, and the outer cell produces a neck of four cell rows in the usual way, but the inner cell undergoes about four unequal oblique divisions in different planes, cutting off what can be interpreted as multiple basal cells. These cells further divide in

different planes and differentiate as jacket cells (see below). The remaining central cell divides to form a neck canal cell and a ventral cell, producing the egg and the ventral canal cell.

The basal part of the pteridophyte archegonium may possess a conspicuous jacket derived from cells adjacent to the archegonial initial (e.g. Isoëtales: Bierhorst, 1971; Lycopodiales: Lang, 1899; Bruchmann, 1908a). In *Diphasiastrum digitatum* (Dill. ex A.Braun) Holub, the tissue surrounding the venter is the only place in the gametophyte where starch is present (Bruce, 1979a). A jacket is present in many ferns, and when a basal cell is present, the jacket is partially derived from the basal cell. However, the presence of a basal cell is by no means required for jacket development in ferns. For example, in *Angiopteris* Hoffm. (Marattiales, Fig. 8G), each gametophyte cell adjacent to the axial row of cells divides unequally to produce a smaller jacket cell (Haupt, 1940). Another example is *Schizaea elegans* (Vahl) Sw., in which the proximal part of the jacket is not related ontogenetically to the axial row but is composed of cells derived from others external to the venter that are not traceable to the archegonial initial, whereas the distal part of the jacket appears by oblique divisions of the four basal neck cells (Bierhorst, 1975).

The presence of a basal cell in archegonium development allows a shift of archegonium initiation into the youngest part of a thalloid gametophyte where the thallus is still only one cell thick. Without a basal cell and its derivatives, the egg cell would appear at the gametophyte surface. In a range of leptosporangiate ferns, including the model plant *Ceratopteris* Brongn., archegonium initiation occurs in the part of the young gametophyte that is one cell thick, always involving a basal cell (e.g. Nayar, 1968; Yang, Cao & Wang, 2009).

Cells derived from the central cell

The central cell divides horizontally to produce an inner primary ventral cell and an outer primary neck canal cell. The primary neck canal cell divides to produce two or more neck canal cells or remains undivided and acts directly as a neck canal cell (which may contain more than one nucleus). Data on variation in the number of the neck canal cells are summarized in Table 3. Literature reports of the occurrence of single binucleate cell should be taken with caution, as cell division sometimes takes place late in development, just before disintegration of the neck canal cells. For example, despite earlier records of the sporadic occurrence of single binucleate neck canal cell in *Equisetum*, the detailed studies of Duckett (1973, 1979) based on extensive material on most species of the genus revealed the constant occurrence of two cells. *Equisetum* is of interest with respect to the relative position of the neck canal cells. The division of the mother cell is often median and vertical, thus producing two equal half conical neck canal cells and sometimes it is oblique and the two resulting cells are unequal in shape (Duckett, 1973, 1979). The sporadic occurrence of vertical divisions during the formation of the canal cells occurs in some other pteridophytes, especially in Lycopodiales (e.g. Lyon, 1904; Spessard, 1922; Whittier, 1981), but these occur together with the typical condition of single row of canal cells. In *Salvinia*, the two nuclei of single binucleate neck canal cell are located side by side (Arnoldi, 1909; Bierhorst, 1971).

The primary ventral cell normally produces a basally situated egg cell and a ventral canal cell. In some Ophioglossales, the primary ventral cell is believed to function directly as an egg, but these data need further confirmation (see Smith, 1955; Gifford & Foster, 1989). Bruchmann (1904, 1906) found no evidence of formation of a ventral canal cell in *Ophioglossum vulgatum* L. and *Botrychium lunaria* Sw. (Ophioglossales). On the other hand, Campbell (1907) reported a ventral canal cell in at least one archegonium of *Ophioderma pendulum* (L.) C.Presl and found apparent traces of it in some other archegonia, although that the ventral cell is extremely difficult to demonstrate in *Ophioglossum s.l.* because of its transient nature. The presence of a ventral canal cell is also difficult to prove in *Danaea* Sm., although it is present and conspicuous in other genera of Marattiales (Campbell, 1940).

Interpretation of the canal cells in Lycopodiales is intriguing. Edgerley (1914) suggested the absence of a ventral canal cell in the New Zealand species she studied, although these developmental data are not supported by illustrations. Some Lycopodiales possess numerous canal cells (ten to 20 in *Diphasiastrum complanatum* (L.) Holub; Bruchmann, 1908a), and the most extensive studies of these species were performed > 100 years ago (Bruchmann, 1898, 1908a, 1910; Lang, 1899). According to Bruchmann (1908a), of the two cells derived from the central cell in *D. complanatum*, the upper one produces canal cells located in the true neck, whereas the lower one produces an egg cell and numerous ventral canal cells. More than half of the canal cells are ventral canal cells in *D. complatanum* (Bruchmann, 1908a). In a related species, *D. digitatum* (Dill. ex A.Braun) Holub, Whittier (1981) found that most canal cells are located in the sunken part of the archegonium. For *Lycopodium clavatum* L., Bruchmann (1898) suggested that the lower of the two cells derived from the central cell divides more than once before producing the egg. Since that time, the idea of multiple ventral canal cells occurring in some homosporous lycopsids has apparently not been critically reviewed using original observations. This idea could be questioned because (1) all other land plants normally possess only one ventral canal cell and

(2) Bruchmann (1908a) did not illustrate all cell division events in the ventral part of the archegonium. While describing archegonium development of *L. clavatum* with six to eight canal cells, Lang (1899) noticed that the lowest of these cells could not be distinguished with any certainty as a ventral canal cell, since the material was insufficient to view all successive cell divisions. On the other hand, some observations provide indirect support for the interpretation of Bruchmann (1908a), including differences between upper and lower canal cells in published images of archegonia of Lycopodiales. For example, two upper canal cells are much larger than five lower canal cells in plates 3–17 of Bruchmann (1898, *L. clavatum*); the wall between these two groups of canal cells is oblique and located just at the level of transition between false neck and true neck. Bryan (1917) found the occurrence of an oblique wall between canal cells in moss archegonia to be a good indication of the boundary between canal cells of different origins. Whittier (2003) illustrated numerous small canal cells in the sunken part of the archegonium in *Diphasiastrum sitchense* (Rupr.) Holub (including the false neck) and a large canal cell with a large nucleus (or several nuclei?) in the true neck (see also Whittier, 2006). Normally, only one ventral canal cell develops in pteridophytes, but, for example, Stokey (1930) reported a binucleate ventral canal cell in the fern *Thyrsopteris elegans* Kunze (Cyatheales).

Developmental relationships between the ventral canal cell and the egg cell are functionally important in many polypodioid ferns (Polypodiopsida in Fig. 1 = Polypodiidae in PPG I, 2016), in which there is an egg envelope and a fertilization pore. The pore is formed in the egg cell in a narrow area of its prolonged contact with the ventral canal cell. Polypodioid ferns differ in the structure of the egg envelope, which is assumed to be formed from membranes inside the egg plasmalemma or from material accumulated outside it (Cao, Yang & Wang, 2009; Cao, Wang & Bao, 2010; Cao, Dai & Wang, 2011, 2012). Only one spermatozoid can penetrate into the egg through the fertilization pore (Cao *et al.*, 2009). An early-diverging member of Polypodiopsida, *Osmunda* L. (Osmundales), lacks a typical egg envelope and fertilization pore, but it has another mechanism preventing entrance of more than one spermatozoid. Immediately after fertilization, a large vesicle covered by plasmalemma extrudes from the egg cell towards the archegonium neck and provides a physical barrier for other male gametes (Cao *et al.*, 2016). The absence of egg envelope and fertilization pore is also reported for *Lygodium* Sw. (Schizaeales) (Cao *et al.*, 2017).

Fossil record of pteridophyte archegonia

Apart from Rhynie fossils (see below), fossil tracheophyte archegonia are known from heterosporous plants. Important data are accumulated on structure and development of archegonia in Carboniferous heterosporous lycopsids *Flemingites* Carruthers, *Mazocarpon* M.J.Benson and *Chaloneria* K.B.Pigg & G.W.Rothwell (e.g. Brack, 1970; Brack-Hanes, 1978; Gordon, 1910; Pigg, 1983; Pigg & Rothwell, 1983; Stevens *et al.*, 2010). Among extant heterosporous lycopsids, *Selaginella* P.Beauv. has an archegonium neck with two or three cell tiers, whereas *Isoëtes* L. has four cell tiers (Table 3). Archegonia with one to four tiers of of neck cells are documented from Carboniferous fossils (each tier with four cells like in other pteripdophytes). The differences in the number of tiers at least in most cases indicate different developmental stages rather than taxon-specific characters, and fully developed archegonia resemble those of extant *Isoëtes* rather than those of *Selaginella*. Some archegonia with fewer than four tiers are on young developmental stages (their central cell is still undivided), whereas the others show evidence of disintegration of the upper cell tier(s), which takes place in extant relatives on archegonim dehiscence before fertilization (La Motte, 1933; Brack, 1970; Brack-Hanes, 1978).

裸子植物

Archegonia of gymnosperms

Recognizing an archegonium is impossible in *Gnetum* and *Welwitschia* (Carmichael & Friedman, 1996; Friedman, 2015). Archegonium development in other gymnosperms is essentially similar to that of pteridophytes, although neck canal cells and a basal cell are absent (Chamberlain, 1935; Maheshwari & Sanwal, 1963; Singh, 1978; Gifford & Foster, 1989; Zhang & Zheng, 2016). One or more archegonium initials are located at the micropylar end of the female gametophyte or sometimes [e.g. in *Microcycas* (Miq.) A.DC.] also on its lateral and even chalazal side (Maheshwari & Sanwal, 1963; Biswas & Johri, 1997). The first division is periclinal (Figs 9B, B, 10B). The outer cell (the primary cover cell, also called the neck mother cell) produces a neck, and the lower cell (which is much larger) produces the egg and the ventral canal cell (e.g. *Ginkgo* L., *Pinus* L.) or a binucleate female gamete. In the latter case, the ventral canal nucleus either ultimately disappears (e.g. in cycads) or sometimes undergoes a fusion with a male nucleus, whereas another male nucleus fuses with the egg nucleus (e.g. in *Abies* Mill.: Hutchinson, 1915b). Regular double fertilization of this type is found in *Ephedra* spp. (Friedman, 1990). There exists some doubt as to whether a ventral canal nucleus is regularly formed in *Taxus canadensis* Marshall (Biswas & Johri, 1997).

Gymnosperms with motile male gametes (cycads and *Ginkgo*) have four neck cells (Fig. 9D). The primary cover cell divides anticlinally, resulting in two neck cells. They divide once again just before

fertilization, to form four neck cells (Bryan & Evans, 1957; Norstog, 1972; Singh, 1978; Steyn, Strydom & Botha, 1996; Biswas & Johri, 1997; Stevenson, 2013). The time interval between the first and two subsequent divisions is much longer than between primary cover cell formation and its first division (about 70 days vs. five to eight days in *Ginkgo*: Wang *et al.*, 2014). Archegonium opening appears soon after formation of the four cells (in two to three days in *Ginkgo*, Wang *et al.*, 2014).

In cycads, the neck cells become large and turgid and project into the archegonial chamber by the time of fertilization (sometimes the entire apex of the archegonium is elevated above the level of the female gametophyte), and finally the large spermatozoids pass through a narrow opening between the neck cells (Bryan & Evans, 1957; Steyn *et al.*, 1996; Biswas & Johri, 1997). At the time of fertilization, the cycad neck is bisymmetric, as two pairs of cells are clearly visible in top view (Bryan & Evans, 1957; Norstog, 1972; Takaso *et al.*, 2013). This differs from the radial symmetry of the neck apex commonly found in pteridophytes. The difference correlates with much larger temporal gap between the division of the primary neck cells and its daughter cells in cycads. Schizogenous cell separation takes place in cycads along the longer diameter between the two cell pairs, leaving a linear gap with a narrow orifice in the centre (Norstog, 1972; Takaso *et al.*, 2013). Accumulated evidence convincingly demonstrate that the entire neck is exposed in cycads, in contrast with the embedded nature of the neck in *Ephedra* and conifers. Cycad neck cells are apparently involved in release of secretion in the archegonial cavity before fertilization. Female gametophytic secretion appears to initiate and synchronize spermatozoid development with archegonium maturation (Takaso *et al.*, 2013). The neck cells shrivel soon after fertilization (Biswas & Johri, 1997).

The female gametophyte of *Ginkgo* has two archegonia. The plane of the first anticlinal division of the primary cover cell is the same in the two archegonia (Lee, 1955; Wang *et al.*, 2014), fitting the bilateral nature of the ovule. The plane of division passes through the two achegonia and the tentpole of the female gametophyte. It takes about 30 days for the two cells to project above the gametophyte surface by swelling (Wang *et al.*, 2014). The neck cells together form a hemispherical projection over the surface of the female gametophyte (Lee, 1955). Division is oblique in each daughter cell, so that a monosymmetric neck of two outer and two inner cells is formed (Lee, 1955; Zhang *et al.*, 2013; Wang *et al.*, 2014). These oblique divisions take place simultaneously with division of the central cell of the archegonium; they are also synchronized with male gamete formation (Zhang *et al.*, 2013). During opening of the neck, the extremely turgid outer neck cells are extruded towards the archegonial chamber and the inner neck cells are pushed to two sides (Wang *et al.*, 2014). The archegonial opening it thus oblique rather than perpendicular to the archegonium. According to Lee (1955), the egg cell pushes through the disintegrated ventral canal cell to form a beak that separates the four neck cells, thus forming a small opening at the top of the archegonium (see also Zhang *et al.*, 2013). According to Hori & Miyamura (1997), the neck canal opens mainly through swelling and reflexing of the neck cells. The flagellated male gamete of *Ginkgo* has an extraordinary elasticity, since it is strongly stretched during its passage through a gap between the neck cells, which is much narrower than the spermatozoid (Hori & Miyamura, 1997). The sperm cell does not enter directly into the cytoplasm of the egg, but first into the receptive cavity formed in the place of degenerated ventral canal cell (Hori & Miyamura, 1997). The narrow opening of the archegonium is still visible after fertilization, when all four neck cells have become distinctly shrivelled (Wang *et al.*, 2014). The neck cells of *Ginkgo* have a secretory function to facilitate fertilization (Wang *et al.*, 2014).

Some fossil gymnosperms with preserved archegonia are known (e.g. Stidd & Cosentino, 1976). Data on the fine structure of the female and male gametophytes in anatomically preserved fossil glossopterid ovules from the Late Permian of Queensland, Australia (Nishida *et al.*, 2004) are of special importance, because phylogenetic analyses place glossopterids outside the clade (or clades) containing all extant gymnosperms, but closer to angiosperms (e.g. Hilton & Bateman, 2006; Doyle, 2012; see also Rudall, 2006). Nishida *et al.* (2004) provided convincing evidence of zooidogamy in *Glossopteris homevalensis* K.B.Pigg & McLoughlin and illustrated archegonia with two neck cells. Based on their observations, Nishida *et al.* (2004) concluded that it is unlikely that the neck cells divided further before fertilization to produce four neck cells as in *Ginkgo* or cycads.

Ephedra is the only member of Gnetales (=Gnetidae in Christenhusz *et al.*, 2011) possessing archegonia (Fig. 10). The archegonium neck of *Ephedra* is the most massive among gymnosperms if not among tracheophytes. It may contain up to 50 cells (Everett, 1951). A peculiar feature of neck development in *Ephedra coryi* E.L.Reed, *E. trifurca* Torr. ex S.Watson and *E. foeminea* Forssk. (=*E. campylopoda* C.A.Mey.) is that the first division of the primary cover cell is periclinal (horizontal), and a vertical row of two cells is formed (Land, 1904; Everett, 1951). Division of the primary cover cell is either vertical or horizontal in *E. foliata* Boiss. ex C.A.Mey. (Maheshwari, 1935). At least occasionally, a row of three cells is formed in

E. coryi (Everett, 1951). Subsequently, as described by Everett (1951), both periclinal and anticlinal divisions take place in the neck cells over a rather short period of time while the central cell is enlarging. The result is a neck composed of four or five vertical columns each composed of eight to ten superposed cells (Everett, 1951). Land (1904) illustrated a tier of six cells. Cell arrangement in the neck becomes irregular by late developmental stages (Land, 1904; Everett, 1951; Maheshwari, 1935).

In conifers, the first division of the primary cover cell is usually vertical (but see comments on *Tsuga* (Endl.) Carrière, below). In most cases, each of the two cells divide anticlinally, so that a tier of four cells is formed. This is the final stage of development in most archegonia of *Pinus strobus* L. and in many other conifers (Ferguson, 1904; Zhang & Zheng, 2016). In some conifers such as Taxaceae (including Cephalotaxaceae: Christenhusz *et al.*, 2011), the number of cell divisions is generally low, and a tier of two to four neck cells is formed (Biswas & Johri, 1997). In some conifers (especially in Podocarpaceae and Araucariaceae, i.e. Araucariales: Christenhusz *et al.*, 2011), additional vertical divisions often take place and the mature archegonium has a tier of more than four neck cells. In *Araucaria* Juss., the neck is dome-shaped, comprising *c.* 12 wedge-shaped cells in a single tier, and a narrow passage is left in the centre; frequently, the entire neck is shed (Biswas & Johri, 1997). In Podocarpaceae, the neck is formed of four to six cells in *Afrocarpus gracilior* (Pilg.) C.N.Page and *Podocarpus nivalis* Hook. and ten to 15 cells in *Prumnopitys andina* (Poepp. ex Endl.) de Laub (Biswas & Johri, 1997). However, in *Dacrycarpus dacrydioides* (A.Rich.) de Laub (Podocarpaceae), many irregular tiers of neck cells are present, resembling the condition in *Ephedra* (Singh, 1978). In some *Pinus* spp., each of the four first-formed neck cells exhibit periclinal divisions, and two or several tiers of four cells are formed (Ferguson, 1904). In *Picea abies* (L.) H.Karst (Fig. 11), vertical and horizontal divisions of the first-formed neck cells produce necks with four to eight rows of cells, with two to four cells in each row (Miyake, 1903). Careful studies have revealed that although one tier of four cells is the typical condition in *P. strobus*, occasional further divisions may produce a neck with six or eight cells in one tier or two tiers of four cells in this species, or reportedly only three neck cells may be present (Ferguson, 1904).

The archegonium neck of *Fokienia hodginsii* A.Henry & H H.Thomas (Cupressaceae) has four cells, but their arrangement varies according to the presence of one of three patterns of cell division. The initial division of the primary cover cell is always vertical, but the second division can be vertical in both cells, horizontal in both cells or vertical in one cell and horizontal in the other cell (Chen & Wang, 1980, cited in Zhang & Zheng, 2016).

Murrill (1900) described remarkable variation in the archegonium neck of *Tsuga canadensis* (Pinaceae). He found two neck cells as a common condition, but necks with three and four cells were also present. Planes of cell division varied. The first division of the primary cover cell was transverse, longitudinal and most commonly oblique. A neck with four cells in a vertical row was found (Murrill, 1900).

In *Pinus* and many other conifers, as the archegonia grow the entire female gametophyte continues to increase in size and cell number, several layers of cells being formed above the archegonia, except over their neck cells (Ferguson, 1904; Biswas & Johri, 1997; Owens & Morris, 1990). As a result, an opening appears in the female gametophyte, leading from the neck cells of each archegonium to the nucellar cap. In the last stages of gametophyte development preceding fertilization, the sides of this tubular cavity often become very closely crowded together so that the passage is obscured (Ferguson, 1904). Archegonium position at the base of a funnel-shaped canal is found in Carboniferous ovules that apparently belong to cordaites, an extinct group related to conifers (Stidd & Cosentino, 1976).

The neck cells of conifers and *Ephedra* play important roles during pollen-tube growth. There is evidence of secretory activity (Owens & Morris, 1990). Pollen-tube growth does not destroy the neck cells, in least some conifers (Ferguson, 1904; Zhang & Zheng, 2016), but neck cell degeneration forming a passage for pollen tubes occurs in some taxa (Cupressaceae: Biswas & Johri, 1997). Studies of fertilization in *Pinus contorta* Douglas ex Loudon showed the pollen tube both separating and destroying the neck cells (Owens, Simpson & Molder, 1982). Developmental studies of the ultrastructure of neck cells in *Ephedra* revealed their functional similarity with angiosperm pollen-tube transmitting tissue (Moussel, 1972, see also Singh, 1978). In *Ephedra*, pollen tubes grow between neck cells and through their thick walls, which are composed of rather lax material (Moussel, 1972). There are also examples in conifers of pollen-tube entry through the lateral side of the archegonium rather than through the neck (Biswas & Johri, 1997).

In most gymnosperms, the cells adjacent to the developing archegonium divide to form small, darkly stained jacket cells that remain active throughout the development of the archegonium (Biswas & Johri, 1997; Zhang & Zheng, 2016). At the final developmental stage, cytoplasmic material of jacket cells, including their nuclei, may penetrate the egg or the binucleate central cell in conifers and *Ephedra* (e.g. Friedman, 1990; Biswas & Johri, 1997). In Cypressaceae *s.l.* and sometimes in *Ephedra*, archegonial complexes

are formed, in which several archegonia developing from adjacent initial cells are enclosed within a single common jacket (Maheshwari & Sanwal, 1963; Biswas & Johri, 1997; Stevenson, 2013).

被子植物潜在的颈卵器
Potential archegonia of angiosperms

The female gametophytes of angiosperms are highly reduced. As in other seed plants, their development starts with a coenocytic phase (see Rudall & Bateman, 2019). In all angiosperms except *Amborella* Baill., cellularization takes place after all the nuclear divisions are complete, at least in the egg apparatus (Friedman, 2006; Rudall, 2006). The question of whether the eight-nucleate, seven-celled Polygonum-type female gametophyte (Fig. 12H–L) found in most mesangiosperms (and in all other types of angiosperm embryo sacs) possesses any traces of archegonia is highly problematic. The problem has been reviewed in detail elsewhere (e.g. Favre-Duchatre, 1984; Friedman & Williams, 2003, 2004; Rudall, 2006; Friedman & Ryerson, 2009). One of the most plausible hypotheses is based on the occurrence of a four-nucleate Nuphar-type female gametophyte (Fig. 12D–G) in two (of three) orders forming the early-diverging grade of angiosperms (Friedman & Williams, 2003, 2004). The Nuphar-type female gametophyte has just one developmental module with four nuclei. The Polygonum-type has two such modules with identical sequences of nuclear divisions (Friedman & Williams, 2003, 2004). Each module provides one of the two polar nuclei. One polar nucleus is the sister cell to the egg nucleus and another polar nucleus is sister to the nucleus of one of three synergids (Fig. 12H–L). As proposed by Friedman & Williams (2003, 2004), the four-celled condition is ancestral for angiosperms, and the Polygonum-type female gametophyte evolved through a modular duplication. This duplication of the developmental programme explains the widely discussed similarity between structures located on opposite sides of the Polygonum-type female gametophyte. The developmental sequence of the Nuphar-type female gametophyte (Fig. 12D–G) strongly resembles that of the simplest possible gymnosperm archegonium (Fig. 12A–C), with the only difference being that in the Nuphar-type cell walls do not appear until after all nuclear divisions. Thus, it is possible that in the angiosperm stem lineage the entire female gametophyte is reduced to a single archegonium. This theory agrees with the hypothesis that the angiosperm synergids are gymnosperm neck-cell homologues (Rudall, 2006, and references cited therein). Another important point is that the angiosperm egg cell seems to be homologous with the ventral canal cell of gymnosperms, whereas the gymnosperm egg cell seems to be homologous with the central cell possessing a polar nucleus in the Nuphar-type female gametophyte (Fig. 12). This proposal agrees with observations that in rare cases, the ventral canal cell can act as an egg in some free-sporing land plants and can be fertilized along with the egg in some gymnosperms (see above).

Interpretation of the female gametophyte of *Amborella*, the putative sister to all other extant angiosperms, is especially problematic. Up to the seven-celled, eight-nucleate stage, embryo sac development is the same in the Polygonum-type and *Amborella*. However, one of three small cells at the micropylar pole divides further in *Amborella* to produce an egg cell and a third synergid, which is a unique condition among angiosperms (Friedman, 2006; Friedman & Ryerson, 2009; Flores-Tornero *et al.*, 2019). Tobe, Gensel & Hass (2000) described only two synergids in *Amborella*, but the study was not specifically focused on the structure of the egg apparatus and the illustrations provided are not convincing. Friedman (2006) suggested that the extra division found in *Amborella* could be homologous with the division in gymnosperm archegonium producing the egg and the ventral canal cell (or a binuclear female gamete). This idea was questioned by Rudall (2006), but further developed by Niklas, Cobb & Kutschera (2016). They suggested that the egg apparatus of *Amborella* is homologous with a simple four-celled gymnosperm archegonium. In their interpretation, the two first-formed synergids of *Amborella* are neck cells, the last-formed synergid of *Amborella* is the ventral canal cell and the egg cells of *Amborella* and gymnosperms are homologues. We disagree with the hypothesis of Niklas *et al.* (2016), because it contradicts the sequence of nuclear divisions in angiosperm embryo sacs (Fig. 12D–M). Indeed, a polar nucleus is sister to the egg nucleus in most angiosperms. In *Amborella*, a polar nucleus appears to belong to the same lineage as the egg nucleus and the nucleus of the last-formed synergid (open black circles in Fig. 12H–M). One could try to rescue the hypothesis of Niklas *et al.* (2016) by assuming the occurrence of a basal cell similar to that of ferns, producing a polar nucleus in angiosperms. Alternatively, one could view the final cell division in the female gametophyte of *Amborella* as homologous with the first division of the archegonium initial in gymnosperms. However, all these hypotheses are highly speculative. Friedman & Ryerson (2009) plausibly suggested that transitions to a Polygonum-type female gametophyte took place separately in Amborellales and mesangiosperms. According to Friedman & Ryerson (2009), subsequent to the evolution of a seven-celled, eight-nucleate Polygonum-type female gametophyte in Amborellales, a peramorphic increase in egg apparatus cell number took place and led to the unique situation in which there are three synergids in *Amborella*. The late cell

被子植物中整个雌配子体退化为一个颈卵器

借助于中央细胞的无配子生殖&买麻藤的“双受精”

珠孔侧的三个小细胞之一（原本的卵器中的一个细胞）进一步分裂形成一个卵细胞和3个助细胞

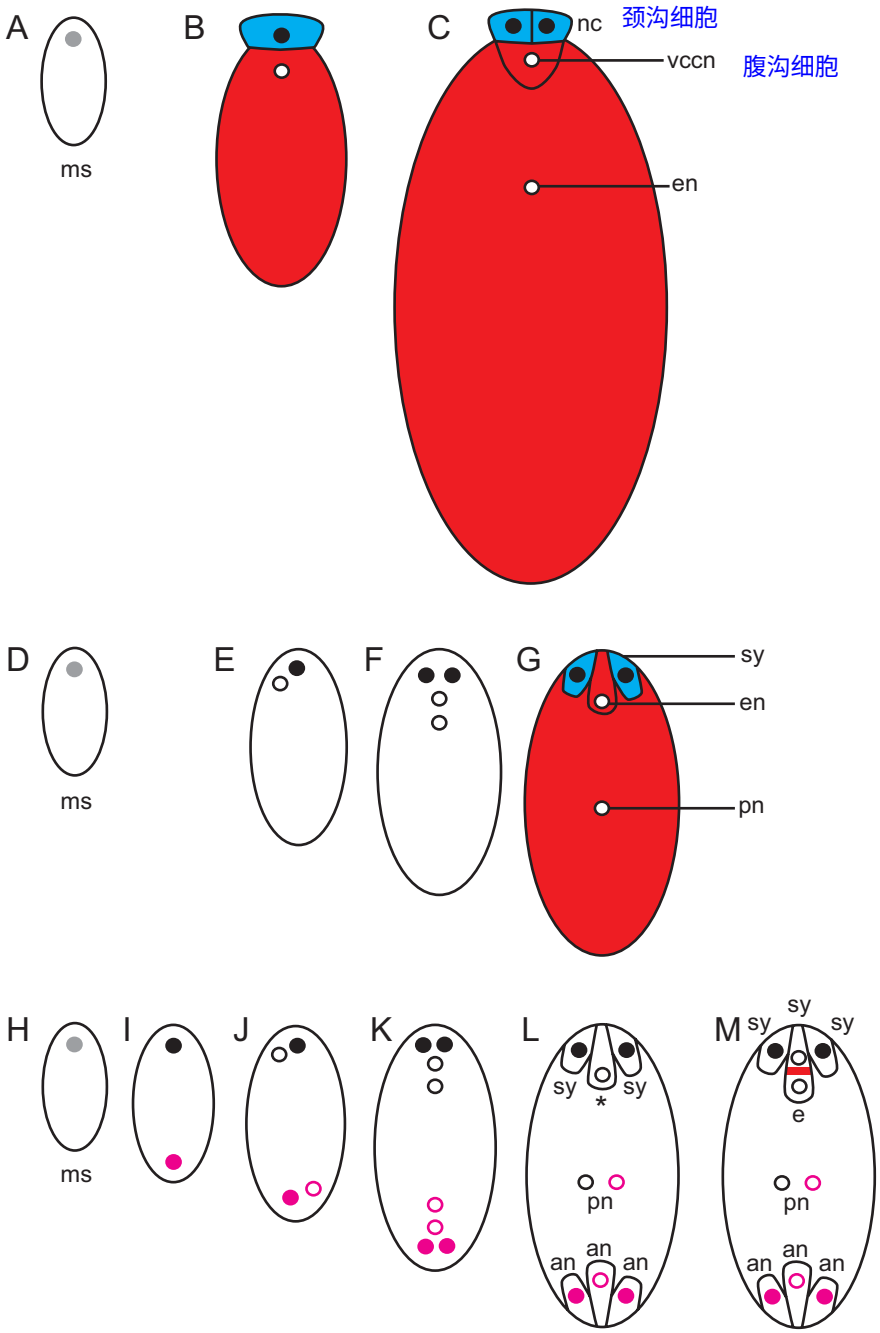


Figure 12. A–G, Comparative diagrams of development of the simplest possible gymnosperm archegonium (A–C) and the Nuphar-type angiosperm embryo sac found in early-divergent angiosperm orders Nymphaeales and Austrobaileyales (D–G), modified from Sokoloff (2009). Colouring in B, C, G follows the scheme in Figures 9–11. This comparison suggests possible homologies between angiosperm synergids and gymnosperm neck cells. The angiosperm egg cell seems to be homologous with the ventral canal cell of gymnosperms. The gymnosperm egg cell seems to be homologous with the central cell with polar nucleus in the Nuphar-type female gametophyte. H–L, Diagram of development of eight-nucleate, seven-celled Polygonum-type female gametophyte that is common across mesangiosperms. H–M, Diagram of development of female gametophyte in *Amborella* (based on Friedman, 2006; Friedman & Ryerson, 2009). Cell wall formed in the last stage of embryo sac development in *Amborella* is red in M. Different symbols showing nuclei in A–C, D–G and H–M indicate nuclear lineages as evidenced by sequence of mitotic divisions (see also Fig. 14). an, antipodal; e, egg cell; en, egg nucleus; ms, megaspore; nc, neck cell; pn, polar nucleus or polar nuclei; sy, synergid; vccn, ventral canal cell nucleus; asterisk, egg cell of the Polygonum-type female gametophyte and mother cell of the third synergid and the egg cell in *Amborella*.

division in the egg apparatus of *Amborella* is similar to cell divisions resulting in multiplication of antipodals in some grasses (Rudall, 2006; see also Anton & Cocucci, 1984).

Fully exposed archegonia as a synapomorphy of setaphytes

Mosses and liverworts represent almost the only land plants possessing fully exposed archegonia with a free venter. This condition occurs as an extremely rare exception and certainly represents a derived condition in a few ferns possessing filamentous adult gametophytes such as *Schizaea* spp. (Britton & Taylor, 1901; Bierhorst, 1968; Nayar & Kaur, 1971). Furthermore, the solitary archegonium developing in the highly reduced female gametophyte of the heterosporous fern *Marsilea* L. could be viewed as fully exposed because there is only one cell layer surrounding the egg cell, although these surrounding cells are not derived from the archegonium inital (Bierhorst, 1971).

The fully exposed archegonia are traditionally viewed as an ancestral (plesiomorphic) condition in land plants (e.g. Campbell, 1918; Smith, 1955; Kenrick & Crane, 1997; Ligrone *et al.*, 2012). However, apart from theoretical considerations and 'common sense' there is no direct support for this view. The female organs of streptophyte algae such as Coleochaetophyceae and Charophyceae are fundamentally different from land-plant archegonia, because they are not based on three-dimensional growth (their growth is essentially filamentous) and those of Coleochaetophyceae are unicellular at the time of fertilization (although an envelope is formed after fertilization). The currently accepted closest land-plant outgroup, Zygnematophyceae (e.g. Wickett *et al.*, 2014), does not possess any female reproductive organs because of isogamy. We believe that the female organs of Coleochaetophyceae and Charophyceae cannot readily be used for outgroup comparison, even though some aspects of developmental regulation (MADS-box gene expression) are shared with land-plant archegonia (Niklas & Kutschera, 2010).

In our view, the character 'female gametangia exposed vs. at least basally embedded in the gametophyte tissue' cannot be defined for any streptophyte outgroup because none of these outgroups possesses gametophytes with cells organized in three-dimensional tissue. Therefore, the character should be scored as unknown in land-plant outgroups. As with the problem of inferring the morphology of the ancestral angiosperm flower (Endress & Doyle, 2009; Sauquet *et al.*, 2017), use of a 'bottom-up' approach (*sensu* Bateman, Hilton & Rudall, 2006) is problematic in inferring the evolution of land-plant archegonia. Parts of land-plant archegonia cannot be precisely homologized with those of the female organs of streptophyte algae in the same way as parts of angiosperm flowers cannot be traced unequivocally to particular structures in the reproductive organs of other seed plants. Therefore, in both cases, a 'top-down' approach is probably the only practicable solution, although less than ideal. As the rooting of land plants is problematic and in the absence of useful data on the outgroups, it is necessary to study character evolution using unrooted trees, while taking into account different rooting options (Fig. 13).

As outlined in the Introduction, many recent phylogenetic studies suggest that mosses and liverworts form a clade (called setaphytes). We speculate that fully exposed archegonia represent a synapomorphy of the setaphyte clade. Indeed, a growing body of publications supports the idea of sister relationships between the tracheophyte and bryophyte clades (with hornworts being sister to setaphytes). With this topology, assuming an uncertain condition for the outgroups, it is more parsimonious to have archegonia with an embedded venter as the plesiomorphic condition in land plants (Fig. 13A, rooting 1). The same conclusion can be made with the hornwort-basal phylogeny found in some other recent studies (Fig. 13A, rooting 2). Finally, if setaphytes are sister to the rest of land plants (Fig. 13A, rooting 3), it is equally parsimonious to keep fully exposed archegonia as a derived or an ancestral state in land plants. Only in the liverwort-basal topology (Fig. 13A, rooting 4) is it likely that the fully exposed archegonia are ancestral in land plants, but this topology does not receive support in most recent molecular phylogenetic studies (Cox *et al.*, 2014; Wickett *et al.*, 2014; Gitzendanner *et al.*, 2018; Puttick *et al.*, 2018; Sousa *et al.*, 2019; Bell *et al.*, 2019; Zhang *et al.*, 2020).

Thinking of functional aspects of reproduction in early land plants, it does not appear impossible that they possessed partially or even completely embedded archegonia. Following the evolutionary acquisition of true parenchymatous growth, it seems to be adaptively significant to have an egg cell located inside a gametophyte tissue with a canal leading to it, as in archegonia of extant hornworts. Such a system would defend the egg cell from desiccation.

What kinds of morphological transformations were potentially responsible for a transition to fully exposed archegonia in the setaphyte stem group? We hypothesize that they were similar to those leading to the exposed archegonia of *Marsilea* and especially *Schizaea*, namely miniaturization of structures bearing archegonia. In *Marsilea*, the entire female gametophyte is reduced, which is a common trend associated with heterospory (Bateman & DiMichele, 1994). In *Schizaea*, miniaturization of structures bearing archegonia is associated with filamentous type

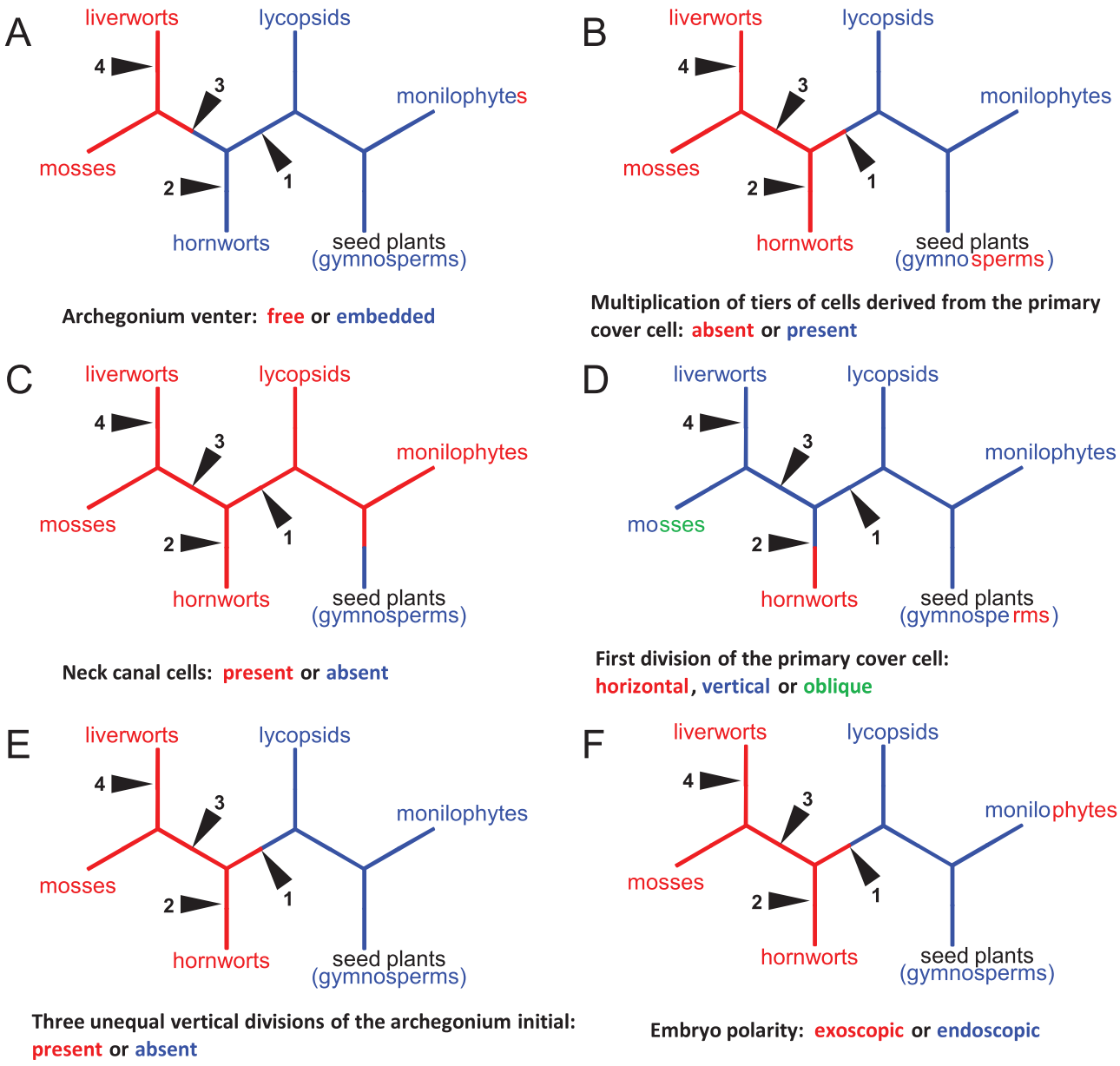


Figure 13. Possible evolutionary transformations of six characters related to archegonium and embryo development in land plants (see Table 2). Character distribution is shown using an unrooted tree of land plants (e.g. Cox, 2018) and assumes that character evolution followed maximum parsimony. Four possible points or rooting land plant phylogeny are indicated by arrowheads and numbered. Selecting any of these four options does not change character optimizations, because all six characters should be treated as uncertain in the outgroups. Colours indicate character states as described in the legend. When two character states are recorded in a group, the name of the group is shown by two colours. As recognizing archegonia in angiosperms is problematic, we only consider gymnosperm archegonia with respect to seed plants in these analyses.

of prothallium. Archegonia of *Schizaea* are produced in clusters either directly on the filaments or on small lateral cushions formed by the division of a short unicellular archegoniophore (Nayar & Kaur, 1971).

We speculate that stalks of archegonia of mosses and liverworts are highly reduced and miniaturized axes, each developing a single archegonium. The moss archegonium stalk (but not the archegonium proper) has a two-sided apical cell that resembles apical cells found elsewhere in bryophytes. The stalk is especially massive in some early-divergent mosses such as *Takakia* and *Andreaeobryum* (Ignatov *et al.*,

2016). Variation in archegonium morphology occurs in *Takakia lepidozioides* S.Hatt. & Inoue, with some archegonia possessing a long stalk interpreted as resembling a leaf segment (Mizutani, 1967), but it equally resembles a stem of *Takakia*. In another early-divergent moss genus, *Andreaea* Hedw., the archegonium stalk enlarges greatly after fertilization and produces a so-called pseudopodium (Roth, 1969).

Most extant setaphyte species are acrogynous, i.e. the first archegonium in a group is derived from the apical cell of a shoot or thallus. This feature seems to be restricted to setaphytes, at least among extant land plants. The anacrogynous condition is known in some groups of mosses and liverworts, including such basal lineages as Haplomitiopsida, *Takakia* and *Andreaeobryum* (e.g. Schuster, 1984; Ignatov *et al.*, 2016). If our interpretation of archegonium stalks as highly reduced and miniaturized axes is correct, then in a sense all setaphytes are acrogynous, even those traditionally interpreted as anacrogynous. It is possible that the acrogynous condition was also present in the setaphyte stem group. We hypothesize that these plants possessed a single terminal archegonium per axis. Increase in the number of archegonia was possible by producing large numbers of small axes, each bearing an archegonium. Having a group of archegonia was possibly important to secure fertilization of at least one of them. This scenario is purely speculative, but in the absence of direct data it is useful to have at least a hypothesis.

Potential homologies in archegonium development across land plants

The differences between archegonia of extant bryophytes and tracheophytes were clearly summarized by Renzaglia *et al.* (2000). In bryophytes, development of the archegonium (or the archegonium proper) starts with three longitudinal divisions of an initial cell to form a central triangular axial cell surrounded by three peripheral cells. The peripheral cells form the walls of the neck (or its basal part) and the venter, whereas the axial cell gives rise to the neck canal cells, the ventral canal cell and the egg. The neck wall is difficult to distinguish from surrounding gametophyte tissues in hornworts because of their sunken archegonia, but its developmental origin is the same as in setaphytes. In extant tracheophytes, the first division of the epidermal initial cell is transverse. In pteridophytes (Renzaglia *et al.*, 2000), the upper cell develops a neck wall, which invariably has four rows of cells. The lower cell produces the neck canal cells, the ventral canal cell and the egg.

A common groundplan of all land-plant archegonia can be found by considering the occurrence of cover cells in most bryophytes (Campbell, 1895, 1918, 1940; Smith, 1955), although they are absent in the sporadic 'closed type' of archegonium development found in Haplomitriopsida and perhaps in *Monoclea*. Typically, the primary cover cell undergoes an equal anticlinal division, followed by another anticlinal division in the perpendicular plane. As a result, a tier of four cover cells is formed that is most probably homologous with the neck of tracheophytes (Campbell, 1895, 1918, 1940; Smith, 1955). The multicellular neck wall develops by multiplication of tiers of cells derived from the primary cover cell in pteridophytes and many conifers (Figs 7A–G, 13B). To simplify, there is a common developmental pattern across most land-plant archegonia, but (1) the three initial unequal anticlinal divisions are absent (lost?) in tracheophytes (Fig. 13E) and (2) the necks of setaphytes and tracheophytes are not homologous with each other. Considering the diagram of archegonium development in *Atrichum angustatum* (Fig. 5), one may suggest that its neck has an 'intermediate' morphological nature, because its lower part is coloured green (as in liverworts and *Sphagnum*, Figs 2, 4) and its upper part is coloured blue (as in tracheophytes, Figs 7–11). The 'blue' part of the neck wall is indeed derived from the primary cover cell in *Atrichum angustatum*, but the mode of its development is entirely different from that in tracheophytes. Instead of being derived from

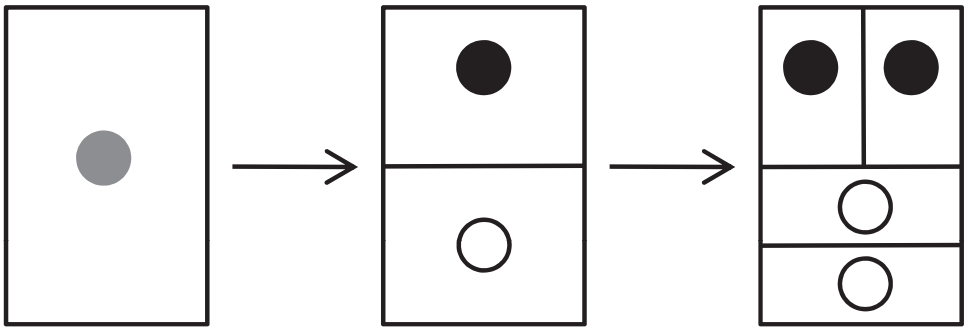


Figure 14. Diagram of a T-shaped developmental pattern. Symbols used for cell nuclei are the same as in Figures 12 and 15.

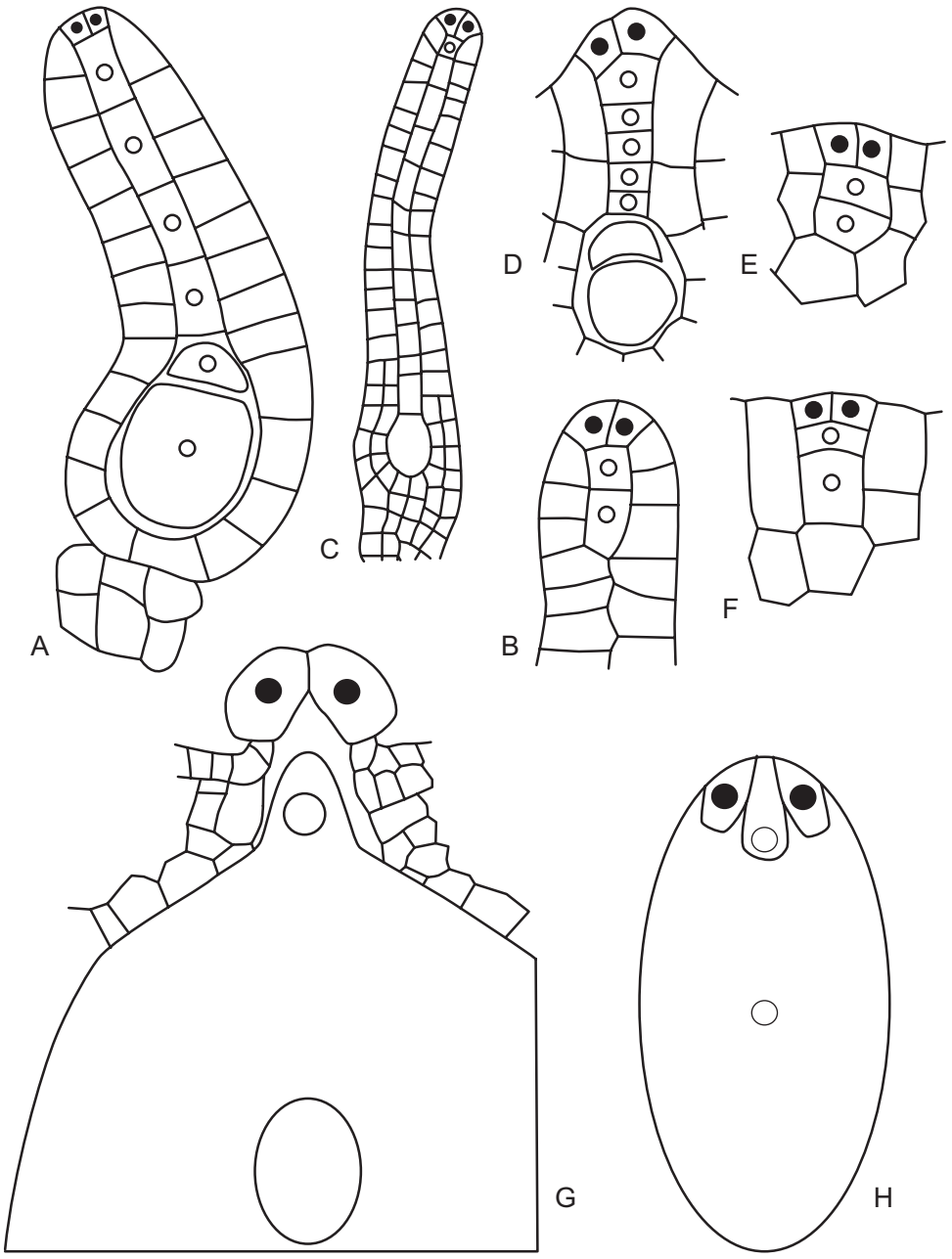


Figure 15. T-shaped pattern in archegonium development of non-angiosperm land plants (A–G) and angiosperm embryo sac (H). A general diagram of the T-shaped pattern is provided in Figure 14. Nuclei are only shown in cell lineages derived from the T-shaped pattern. Symbols used for the nuclei (hollow and solid circles) indicate their origin from the lower and upper cell of a two-celled stage, respectively. These symbols are the same as in Figures 12 and 14. For each group, only a key developmental stage that is most appropriate to show the T-shaped pattern is illustrated (can it be interpreted as a phylotypic stage? – see Niklas *et al.*, 2016). A, liverwort *Marchantia polymorpha* (Fig. 2A). B, moss *Sphagnum subsecundum* (Fig. 4D). C, moss *Atrichum angustatum* (Fig. 5G). D, hornwort *Dendroceros* sp. (Fig. 6D). E, clubmoss (homosporous lycopsid) *Diphasiastrum complanatum* (Fig. 7B). F, fern *Angiopteris evecta* (Fig. 8C). G, gymnosperm *Zamia integrifolia* (Fig. 9D). H, Diagram of Nuphar-type female gametophyte (embryo sac) that is found in two of three orders of of the early-diverging angiosperm grade (Fig. 12G). In pteridophytes and gymnosperms, the T-shaped pattern is realized in first divisions of the archegonium initial. In angiosperms with Nuphar-type of embryo sac, this pattern encompasses the entire development of the female gametophyte. In bryophytes, the T-shaped pattern takes place after cutting off the three primary jacket cells (liverworts and some mosses such as *Sphagnum*) or even later in development. The differences in timing of appearance of the T-shaped pattern across land plants can be regarded as heterochronies.

two equal vertical divisions of the primary cover cell with subsequent multiplication of cell tiers (the tracheophyte condition, Fig. 13B), the upper part of the neck wall develops in *Atrichum angustatum* and in some other mosses through cutting off what we call additional primary jacket cells (Fig. 5D, E). The additional primary jacket cells are formed by unequal oblique vertical divisions of the primary cover cell (this oblique condition in Fig. 13D) in the same way as the primary jacket cells are being cut off from the archegonium inirial (Fig. 5B).

These data lead us to a hypothesis that the fully sunken hornwort archegonia are similar to the ancestral type of land-plant archegonia, except for the unusual origin of their neck canal cells (Fig. 6), which appears to be a derived condition.

Campbell (1895, 1918, 1940) and Smith (1955) viewed several aspects of hornwort morphology, including archegonium morphology, as transitional between those of other bryophytes and tracheophytes; they discussed the possible origin of tracheophytes through hornworts. Sister relationships between hornworts and tracheophytes were revealed in some subsequent studies, and sunken archegonial venters were viewed as a potential synapomorphy of the two groups (e.g. Ligrone *et al.*, 2012). The scenario proposed by Campbell (1895) of archegonium evolution from the setaphyte exposed type through the hornwort completely embedded type to the tracheophyte type with an exposed neck involves loss and regain of an exposed neck on a different morphological basis. In our view, it is easier to imagine that different groups (setaphytes and tracheophytes) acquired an exposed neck in parallel in two different ways.

Early archegonium evolution and fossil record

Hypotheses on the evolution of land-plant archegonia should accommodate knowledge of the fossil record. Unfortunately, no early land plant has been studied with respect to archegonium development. Mature archegonia are described in Devonian fossils from Rhynie, which are the oldest known land-plant fossils with a well-documented life cycle (e.g. Taylor, Kerp & Hass, 2005). Their sporophytes dominated in the life cycle and were polysporangiate, so that these taxa are commonly placed in a grade leading to the (core) tracheophyte clade (Kenrick & Crane, 1997; Kenrick, 2017). Gametophytes of the Rhynie plants possessed archegonia with a sunken venter and a massive free neck that possessed tiers of eight or more cells (Remy, Gensel & Hass, 1993). This differs from the typical tracheophyte condition of four cells per tier. Necks with so many cells per tier are known in a few extant conifers and a few liverworts, but this could be a homoplastic similarity. If the currently accepted phylogenetic placement of the Rhynie fossils is correct and the knowledge of their archegonia is complete, then it is possible that the similarity between the bryophyte cover cells and the tracheophyte neck represents a case of parallel evolution. One could imagine the origin of this similarity through evolutionary fixation of early developmental stages with two successive equal anticlinal divisions of the uppermost cell of young archegonium. In this scenario, we hypothesize that the two successive equal anticlinal divisions of the uppermost cell were followed by more cell divisions ultimately producing the massive neck with tiers of eight or more cells in the Rhynie plants. Another possibility is that the Rhynie plants belonged to the stem group of land plants and appeared before the divergence of bryophytes and tracheophytes (see Remy *et al.*, 1993), which agrees with the absence of unequivocal bryophytes in Rhynie and older fossils. If so, the condition of four cells per tier at the archegonium apex would be a synapomorphy of all extant land plants. Finally, it is possible that what we currently understand as archegonium necks in Rhynie fossils are in reality their proximal parts, whereas their distal parts abscised during archegonium opening. As far as we understand it, published images illustrate open archegonia. It is even possible that the apparently massive necks found in these fossils are false necks similar to those of some extant Lycopodiales.

Evolutionary transformations of developmental pathways

Several patterns of such transformations can be inferred.

1. Loss or gain of the earliest developmental stages. This pattern includes the loss (or gain?) of three unequal divisions of the archegonium initial forming primary jacket cells. Another example is the gain of a special pattern of unequal cell division(s) leading to the formation of the archegonium initial in the fern genus *Actinostachys* Wall. (Bierhorst, 1968, 1975).
2. Prolongation of development by adding new types of cell division. This is the pattern associated with the origin of the tracheophyte neck through multiplication of tiers of cells derived from the primary cover cell (a scenario that is unequivocal with rooting 2, 3, 4 and equivocal, but in our view plausible with rooting 1 in Fig. 13B). The hypothesis of Friedman & Ryerson (2009) on the origin of the embryo sac in *Amborella* also falls into this group.
3. Multiplication of developmental programmes. This pattern is illustrated by the behaviour of the primary cover cell in mosses such as *Plagiomnium cuspidatum* and *Atrichum angustatum*. The primary

cover cell of these plants reiterates a pattern of divisions of the initial cell of archegonium proper, and this process is repeated more than once. This resembles the theory of modular duplication in the evolution of angiosperm embryo sac.

4. Insertion of developmental stage: appearance of a basal cell in ferns. Patterns of subsequent division of the basal cell in some ferns resemble those of the cover cell. This aspect needs further exploration, as this mirrored repetition somewhat resembles the similarity between the two developmental modules in the Polygonum-type embryo sac of angiosperms.
5. Deletion of developmental stage: loss of neck canal cell(s) in seed plants (Fig. 13C).
6. Changes in sequence of cell divisions without strong effect on definitive structure. To this category belongs the difference between hornworts and other land plants in the origin of the primary neck canal cell and also the change from vertical to horizontal division of the primary cover cell in *Ephedra* (Fig. 13D).
7. Loss of developmental stability. This pattern is nicely illustrated by strong variation in neck structure in conifers and *Ephedra*, which is related to functional changes, as the neck no longer forms a canal, but operates like angiosperm pollen-tube transmitting tissue.

Developmental genetic bases of these transformations remain to be understood. Apparently, they should be related to regulation of patterns of equal and unequal cell divisions and establishment of their division planes (e.g. Abrash & Bergmann, 2009; Rasmussen, Humphries & Smith, 2011). Apart from the use of molecular genetic tools in model plants, a broad comparative approach in a phylogenetic context including extant and fossil plants will be useful. At the moment, even descriptive information is still missing or insufficient for some key extant lineages of land plants (Fig. 1). Remarkably, as outlined above, descriptive knowledge on patterns of cell divisions in archegonium development is incomplete for the model moss *Physcomitrella patens*.

CONCLUSIONS

We suggest reconsidering traditional views on the ancestral nature of fully exposed archegonia in land plants. Our hypothesis fits current ideas on potential sister relationships between tracheophytes and bryophytes, but it could also be accommodated with some other ideas on rooting land the plant-phylogeny. It will be interesting to reconsider several other characters related to the life cycle of land plants. For example, the exoscopic embryo development found in bryophytes (Table 2) is traditionally considered ancestral in land plants (Niklas & Kutschera, 2009; Johnson & Renzaglia, 2009), but the idea of monophyletic bryophytes allows consideration of the potentially plesiomorphic nature of the endoscopic type (Fig. 13F, rooting 1). Endoscopic development creates a spatial constraint for further sporophyte development. Different ways of overcoming this constraint are known in various tracheophytes (Johnson & Renzaglia, 2009; Sokoloff *et al*., 2014, 2015). It is possible that the evolutionary history of the land-plant embryo should be read as a 'search' for potential ways of overcoming the problems created by its endoscopy, the most 'radical' way would be a switch to exoscopy.

We believe that patterns of archegonium development are more compatible with each other among land plants than patterns of embryo development. If homologies between the four-nucleate Nuphar-type embryo sac and the gymnosperm archegonium are correct (Fig. 12), then this developmental module (*sensu* Friedman & Williams, 2003) fits the pattern found in most land plants of the initial divisions of the central cell (horizontal) and primary cover cell (vertical). We propose to designate this type of development as a T-shaped pattern (Fig. 14) and predict that future comparative studies of its regulation will help in deeper understanding of land-plant evolution (Fig. 15).

ACKNOWLEDGEMENTS

We are grateful to Vladimir Filin, Michael Ignatov, Paula Rudall, Alexander Shmakov and Alexander Timonin for helpful discussions and suggestions.

FUNDING

The work is supported by Russian Foundation for Basic Research (project 18-04-00797, angiosperms) and carried out in accordance with Government order for the Lomonosov Moscow State University (project AAAA-A16-116021660045-2, non-angiosperm land plants).

REFERENCES

Abrash EB, Bergmann DC. 2009. Asymmetric cell divisions: a view from plant development. *Developmental Cell* **16:** 783–796.

Anton AM, Cocucci AE. 1984. The grass megagametophyte and its possible phylogenetic implications. *Plant Systematics and Evolution* **146:** 117–121.

APG IV. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* **181:** 1–20.

Arnoldi W. 1909. Beiträge zur Morphologie der Keimung von *Salvinia natans*. *Flora* **100:** 121–139.

Atkinson LR. 1967. The gametophyte of *Diplazium*. *Phytomorphology* **17:** 99–109.

Bartholomew-Began SE. 1991. Morphogenetic re-evaluation of *Haplomitrium* Nees (Hepatophyta). *Bryophytorum Bibliotheca* **41:** 1–297 + 508 figs.

Bateman RM, DiMichele WA. 1994. Heterospory: the most iterative key innovation in the evolutionary history of the plant kingdom. *Biological Reviews* **69:** 345–417.

Bateman RM, Hilton J, Rudall PJ. 2006. Morphological and molecular phylogenetic context of the angiosperms: contrasting the 'top-down' and 'bottom-up' approaches used to infer the likely characteristics of the first flowers. *Journal of Experimental Botany* **57:** 3471–3503

Bell D, Lin Q, Gerelle WK, Joya S, Chang Y, Taylor ZN, Rothfels CJ, Larsson A, Villarreal JC, Li F-W, Pokorny L, Szövényi P, Crandall-Stotler B, DeGironimo L, Floyd SK, Beerling DJ, Deyholos MK, von Konrat M, Ellis S, Shaw AJ, Chen T, Wong GK-S, Stevenson DW, Palmer JD, Graham SW. 2019. Organellomic data sets confirm a cryptic consensus on (unrooted) land-plant relationships and provide new insights into bryophyte molecular evolution. *American Journal of Botany* **107:** 1–25.

Bell PR. 1961. Interaction of nucleus and cytoplasm during oogenesis in *Pteridium aquilinum* (L.) Kuhn. *Proceedings of the Royal Society of London. Series B. Biological Sciences* **153:** 421–432.

Bennici A. 2008. Origin and early evolution of land plants. *Communicative and Integrative Biology* **1:** 212–218.

Bierhorst DW. 1967. The gametophyte of *Schizaea dichotoma*. *American Journal of Botany* **54:** 538–549.

Bierhorst DW. 1968. Observations on *Schizaea* and *Actinostachys* spp., including *A. oligostachys*, sp. nov. *American Journal of Botany* **55:** 87–108.

Bierhorst DW. 1971. *Morphology of vascular plants*. New York: Macmillan.

Bierhorst DW. 1975. Gametophytes and embryos of *Actinostachys pennula*, *A. wagneri*, and *Schizaea elegans*, with notes on other species. *American Journal of Botany* **62:** 319–335.

Biswas C, Johri BM. 1997. *The gymnosperms*. Berlin, Heidelberg: Springer.

Brack SD. 1970. On a new structurally preserved arborescent lycopsid fructification from the lower Pennsylvanian of North America. *American Journal of Botany* **57:** 317–330.

Brack-Hanes SD. 1978. On the megagametophytes of two lepidodendracean cones. *Botanical Gazette* **39:** 140–146.

Britton EG, Taylor A. 1901. Life history of *Schizaea pusilla*. *Bulletin of the Torrey Botanical Club* **28:** 1–19.

Bruce JG. 1972. Observations on the occurrence of the prothallia of *Lycopodium inundatum*. *American Fern Journal* **62:** 82–87.

Bruce JG. 1979a. Gametophyte of *Lycopodium digitatum*. *American Journal of Botany* **66:** 1138–1150.

Bruce JG. 1979b. Gametophyte and young sporophyte of *Lycopodium carolinianum*. *American Journal of Botany* **66:** 1156–1163.

Bruchmann H. 1898. *Über die Prothallien und die Keimpflanzen mehrerer europäischer Lycopodien, und zwar über die von* Lycopodium clavatum, L. annotinum, L. complanatum *und* L. Selago. Gotha: Perthes.

Bruchmann H. 1904. Ueber das Prothallium und die Keimpflanze von *Ophioglossum vulgatum* L. *Botanische Zeitung* **62:** 227–247.

Bruchmann H. 1906. Über das Prothallium und die Sporenpflanze von *Botrychium lunaria* Sw. *Flora* **96:** 203–230.

Bruchmann H. 1908a. Das Prothallium von *Lycopodium complanatum* L. *Botanische Zeitung* **66:** 169–181.

Bruchmann H. 1908b. Vom Prothallium der groβen Spore und von der Keimesentwicklung einiger *Selaginella*-Arten. *Flora* **99:** 12–51.

Bruchmann H. 1910. Die Keimung der Sporen und die Entwicklung der Prothallien von *Lycopodium clavatum* L., *L. annotinum* L. und *L. Selago* L. *Flora* **101:** 220–267.

Bruchmann H. 1912. Zur Embryologie der Selaginellaceen. *Flora* **104**:180–224.

Bryan GS. 1915. The archegonium of *Sphagnum subsecundum*. *Botanical Gazette* **59:** 40–56.

Bryan GS. 1917. The archegonium of *Catharinea angustata* Brid. (*Atrichum angustatum*). *Botanical Gazette* **64:** 1–20.

Bryan GS. 1920. The fusion of ventral canal cell and egg in *Sphagnum subsecundum*. *American Journal of Botany* **7:** 223–230.

Bryan GS, Evans RI. 1957. Types of development from the central nucleus of *Zamia umbrosa*. *American Journal of Botany* **44:** 404–415.

Buchtien O. 1887. Entwicklungsgeschichte des Protallium von *Equisetum*. *Bibliotheca Botanica* **8:** 1–49.

Burr IL. 1939. The development of the antheridium, archegonium, and sporogonium of *Cyathophorum bulbosum* (Hedw.) C.M. *Transactions and Proceedings of the Royal Society of New Zealand* **68:** 437–456.

Campbell DH. 1892. On the prothallium and embryo of *Osmunda claytoniana*, L., and *O. cinnamomea*, L. *Annals of Botany* **6:** 49–94.

Campbell DH. 1895. The origin of the sexual organs of the Pteridophyta. *Botanical Gazette* **20:** 76–78.

Campbell DH. 1898. On the structure and development of *Dendroceros* Nees. *Journal of the Linnean Society, Botany* **33:** 467–478.

Campbell DH. 1907. Studies on the Ophioglossaceae. *Annales du Jardin botanique de Buitenzorg* **21:** 138–194.

Campbell DH. 1916. The archegonium and sporophyte of *Treubia insignis* Goebel. *American Journal of Botany* **3:** 261–273.

Campbell DH. 1918. *The structure and development of mosses and ferns (Archegoniatae), 3rd edn*. London: Macmillan.

Campbell DH. 1920. Studies in some East Indian Hepaticae. *Calobryum blumei*, N. ab E. *Annals of Botany* **34:** 1–12.

Campbell DH. 1940. *The evolution of the land plants (Embryophyta).* Stanford: Stanford University Press.

Campbell EO. 1954. The structure and development of *Monoclea forsteri*, Hook. *Transactions of the Royal Society of New Zealand* **82:** 237–248.

Campbell EO. 1959. The structure and development of *Calobryum gibbsiae* Steph. *Transactions of the Royal Society of New Zealand* **87:** 243–254.

Campbell EO. 1987. *Monoclea* (Hepaticae); distribution and number of species. *Bryologist* **90:** 371–373.

Cao J-G, Dai X-F, Dai X-L, Wang Q-W. 2016. Observations on fertilization and a novel cytological mechanism for preventing polyspermy in the fern *Osmunda japonica*. *International Journal of Plant Sciences* **177:** 287–293.

Cao J-G, Dai X-L, Wang Q-X. 2011. Archegonial development and oogenesis of the fern *Plagiogyria euphlebia* and their phylogenetic significance. *American Fern Journal* **101:** 231–240.

Cao J-G, Dai X-L, Wang Q-X. 2012. Cytological features of oogenesis and their evolutionary significance in the fern *Osmunda japonica*. *Sexual Plant Reproduction* **25:** 61–69.

Cao J-G, Guo Y-D, Cao Y-C, Wang Q-X. 2017. Studies on oogenesis of the fern *Lygodium japonicum*. *American Fern Journal* **107:** 124–135.

Cao JG, Wang QX, Bao WM. 2010. Formation of the fertilization pore during oogenesis of the fern *Ceratopteris thalictroides*. *Journal of Integrative Plant Biology* **52:** 518–527.

Cao JG, Yang NY, Wang QX. 2009. Ultrastructure of the mature egg and fertilization in the fern *Ceratopteris thalictroides*. *Journal of Integrative Plant Biology* **51:** 243–250.

Carmichael JS, Friedman WE. 1996. Double fertilization in *Gnetum gnemon* (Gnetaceae): its bearing on the evolution of sexual reproduction within the Gnetales and the anthophyte clade. *American Journal of Botany* **83:** 767–780.

Chamberlain CJ. 1935. *Gymnosperms. Structure and evolution*. Chicago: University of Chicago Press.

Chang Y, Graham SW. 2011. Inferring the higher-order phylogeny of mosses (Bryophyta) and relatives using a large, multigene plastid data set. *American Journal of Botany* **98:** 839–849.

Chase MW, Reveal JL. 2009. A phylogenetic classification of the land plants to accompany APG III. *Botanical Journal of the Linnean Society* **161:** 122–127.

Christenhusz MJM, Bangiolo L, Chase MW, Fay MF, Husby C, Witkus M, Viruel J. 2019. Phylogenetics, classification and typification of extant horsetails (*Equisetum*, Equisetaceae). *Botanical Journal of the Linnean Society* **189:** 311–352.

Christenhusz MJM, Reveal JL, Farjon A, Gardner MF, Mill RR, Chase MW. 2011. A new classification and linear sequence of extant gymnosperms. *Phytotaxa* **19:** 55–70.

Cox CJ. 2018. Land plant molecular phylogenetics: a review with comments on evaluating incongruence among phylogenies. *Critical Reviews in Plant Sciences* **37:** 113–127.

Cox CJ, Li B, Foster PG, Embley TM, Civáň P. 2014. Conflicting phylogenies for early land plants are caused by composition biases among synonymous substitutions. *Systematic Biology* **63:** 272–279.

Crandall-Stotler B, Stotler RE, Long DG. 2009. Phylogeny and classification of the Marchantiophyta. *Edinburgh Journal of Botany* **66:** 155–198.

Doyle JA. 2012. Molecular and fossil evidence on the origin of angiosperms. *Annual Review of Earth and Planetary Sciences* **40:** 301–326.

Duckett JG. 1973. Comparative morphology of the gametophytes of the genus *Equisetum*, subgenus *Equisetum*. *Botanical Journal of the Linnean Society* **66:** 1–22.

Duckett JG. 1979. Comparative morphology of the gametophytes of *Equisetum* subgenus *Hippochaete* and the sexual behaviour of *E. ramosissimum* subsp. *debile*, (Roxb.) Hauke, *E. hyemale* var. *affine* (Engelm.) A.A., and *E. laevigatum* A. Br. *Botanical Journal of the Linnean Society* **79:** 179–203.

Duckett JG, Pang WC. 1984. The origins of heterospory: a comparative study of sexual behaviour in the fern *Platysoma microphyllum* R.Br. and the horsetail *Equisetum giganteum* L. *Botanical Journal of the Linnean Society* **88:** 11–34.

Durand EJ. 1908. The development of the sexual organs and sporogonium of *Marchantia polymorpha*. *Bulletin of the Torrey Botanical Club* **35:** 321–335.

Edgerly KV. 1914. The prothallia of three New Zealand lycopods. *Transactions the New Zealand Institute* **47:** 94–111.

Elmore HW, Adams RJ. 1976. Scanning electron microscopic observations on the gametophyte and sperm of the bracken fern, *Pteridium aquilinum* (L.) Kuhn. *New Phytologist* **76:** 519–522.

Endress PK. 2006. Angiosperm floral evolution: morphological developmental framework. *Advances in Botanical Research* **44:** 1–61.

Endress PK, Doyle JA. 2009. Reconstructing the ancestral angiosperm flower and its initial specializations. *American Journal of Botany* **96:** 22–66.

Everett TR. 1951. *Development of the seed of the joint fir,* Ephedra coryi. Unpublished MSc Thesis, Texas Technological College.

Favre-Duchatre M. 1984. Homologies and phylogeny. In: Johri BM, ed. *Embryology of angiosperms*. Berlin: Springer, 697–734.

Ferguson MC. 1904. Contributions to the knowledge of the life history of *Pinus* with special reference to sporogenesis, the development of the gametophytes and fertilization. *Proceedings of the Washington Academy of Sciences* **6:** 1–202.

Filin VR. 2009. Superdivisio Bryomorphae. In: Timonin AC, ed. *Botanika. Vol. 4, Part 1.* Moscow: Publishing Centre "Academia", 38–167 [in Russian].

Flores-Tornero M, Proost S, Mutwil M, Scutt CP, Dresselhaus T, Sprunck S. 2019. Transcriptomics of manually isolated *Amborella trichopoda* egg apparatus cells. *Plant Reproduction* **32:** 15–27.

Friedman WE. 1990. Sexual reproduction in *Ephedra nevadensis* (Ephedraceae): further evidence of double fertilization in a nonflowering seed plant. *American Journal of Botany* **77:** 1582–1598.

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

Friedman WE. 2015. Development and evolution of the female gametophyte and fertilization process in *Welwitschia*

mirabilis (Welwitschiaceae). *American Journal of Botany* **102:** 312–324.

Friedman WE, Ryerson KC. 2009. Reconstructing the ancestral female gametophyte of angiosperms: insights from *Amborella* and other ancient lineages of flowering plants. *American Journal of Botany* **96:** 129–143.

Friedman WE, Williams JH. 2003. Modularity of the angiosperm female gametophyte and its bearing on the early evolution of endosperm in flowering plants. *Evolution* **57:** 216–230.

Friedman WE, Williams JH. 2004. Developmental evolution of the sexual process in ancient flowering plant lineages. *Plant Cell* **16:** S119–S132.

Gerrienne P, Gonez P. 2011. Early evolution of life cycles in embryophytes: a focus on the fossil evidence of gametophyte/sporophyte size and morphological complexity. *Journal of Systematics and Evolution* **49:** 1–16.

Gifford EM, Foster AS. 1989. *Morphology and evolution of vascular plants*. New York: Freeman.

Gitzendanner MA, Soltis PS, Wong GK-S, Ruhfel BR, Soltis DE. 2018. Plastid phylogenomic analysis of green plants: a billion years of evolutionary history. *American Journal of Botany* **105:** 291–301.

Goffinet B, Buck WR, Shaw AJ. 2008. Morphology, anatomy, and classification of the Bryophyta. In: Goffinet B, Shaw AJ, eds. *Bryophyte biology, 2nd edn*. Cambridge: Cambridge University Press, 55–138.

Gordon WT. 1910. Note on the prothallus of *Lepidodendron veltheimianum*. *Annals of Botany* **24:** 821–822.

Graham LE, Wilcox LW. 2000. The origin of alternation of generations in land plants: a focus on matrotrophy and hexose transport. *Transactions of the Royal Society London B* **355:** 757–767.

Hauke RL. 1968. Gametangia of *Equisetum bogotense*. *Bulletin of the Torrey Botanical Club* **95:** 341–345.

Haupt AW. 1918. A morphological study of *Pallavicinia lyellii*. *Botanical Gazette* **66:** 524–533.

Haupt AW. 1920. Life history of *Fossombronia cristula*. *Botanical Gazette* **69:** 318–331.

Haupt AW. 1940. Sex organs of *Angiopteris evecta*. *Bulletin of the Torrey Botanical Club* **67:** 125–129.

Hedderson TA, Chapman RL, Rootes WL. 1996. Phylogenetic relationships of bryophytes inferred from nuclear-encoded rRNA gene sequences. *Plant Systematics and Evolution* **200:** 213–224.

Hilton J, Bateman RM. 2006. Pteridosperms are the backbone of seed-plant evolution. *Journal of the Torrey Botanical Society* **133:** 119–168.

Holferty GM. 1904. The archegonium of *Mnium cuspidatum*. *Botanical Gazette* **37:** 106–126.

Hori T, Miyamura S-I. 1997. Contribution to the knowledge of fertilization of gymnosperms with flagellated sperm cells: *Ginkgo biloba* and *Cycas revoluta*. In: Hori T, Ridge RW, Tulecke W, del Tredici P, Tremouillaux-Guiller J, Tobe H, eds. Ginkgo biloba*, a global treasure: from biology to medicine.* Tokyo: Springer, 67–84.

Hu N, Liu C. 2012. Ultrastructrual studies on axial row cell development in archegonium of *Nephrolepis cordifolia*. *Journal of Beijing Normal University (Natural Science)* **6:** 12 (abstract seen).

Hutchinson AH. 1915a. Gametophyte of *Pellia epiphylla*. *Botanical Gazette* **60:** 134–143.

Hutchinson AH. 1915b. Fertilization in *Abies balsamea*. *Botanical Gazette* **60:** 457–472.

Ignatov MS, Ignatova EA, Fedosov VE, Ivanov OV, Ivanova EI, Kolesnikova MA, Polevova SV, Spirina UN, Voronkova TV. 2016. *Andreaeobryum macrosporum* (Andreaeobryopsida) in Russia, with additional data on its morphology. *Arctoa* **25:** 1–51.

Inoue H. 1960. Studies in *Treubia nana* (Hepaticae) with special reference to the antheridial development. *Botanical Magazine (Tokyo)* **73:** 225–229.

von Janczewski E. 1872. Vergleichende Untersuchungen über die Entwicklungsgeschichte des Archegoniums. *Botanische Zeitung* **30:** 377–394, 401–420, 440–443.

Javalgekar SR, Mahabale TS. 1959. Germination of spores and prothalli in two species of *Nephrolepis*, *N. exaltata* Schott., and *N. acuta* Presl. *Proceedings of the National Institute of Science India* **25:** 333–338.

Johnson DS. 1904. The development and relationship of *Monoclea*. *Botanical Gazette* **38:** 185–205.

Johnson GP, Renzaglia KS. 2009. Evaluating the diversity of pteridophyte embryology in the light of recent phylogenetic analyses leads to new inferences on character evolution. *Plant Systematics and Evolution* **283:** 149–164.

Kato M. 2010. Evolution of primitive land plants: a review. *Bulletin of the National Museum of Natural Sciences, Series B.* **36:** 1–11.

Kato M, Akiyama H. 2005. Interpolation hypothesis for origin of the vegetative sporophyte of land plants. *Taxon* **54:** 443–450.

Kenrick P. 2017. Changing expressions: a hypothesis for the origin of the vascular plant life cycle. *Philosophical Transactions of the Royal Society of London B* **373:** 20170149.

Kenrick P, Crane PR. 1997. *The origin and early diversification of land plants: a cladistic study*. Washington: Smithsonian Institution.

Kny L. 1895. Entwicklung von *Aspidium filix-mas*. *Botanische Wandtafeln* **9:** 411–438.

Kofuji R, Hasebe M. 2014. Eight types of stem cells in the life cycle of the moss *Physcomitrella patens*. *Current Opinion in Plant Biology* **17:** 13–21.

Kofuji R, Yoshimura T, Inoue H, Sakakibara K, Hiwatashi Y, Kurata T, Aoyama T, Ueda K, Hasebe M. 2009. Gametangia development in the moss *Physcomitrella patens*. *Annual Plant Reviews* **36:** 167–181.

Kühn E. 1870. Zur Entwicklungsgeschichte der Andreaeaceen. *Mittheilungen aus dem Gesammtgebiete der Botanik (Leipzig)* **1:** 1–56.

La Motte C. 1933. Morphology of the megagametophyte and the embryo sporophyte of *Isoetes lithophila*. *American Journal of Botany* **20:** 217–233.

Lal M, Bhandari NN. 1968. The development of sex organs and sporophyte in *Physcomitrium cyathicarpum* Mitt. *Bryologist* **71:** 11–20.

Lal M, Kaur G, Chauhan E. 1982. An unusual archegonium with persistent ventral canal cell in *Physcomitrium cyathicarpum* Mitt. — an ultrastructural study. *Journal of Bryology* **12:** 293–295.

Land WJG. 1904. Spermatogenesis and oogenesis in *Ephedra trifurca*. *Botanical Gazette* **3:** 1–18.

Landberg K, Pederson ERA, Viaene T, Bozorg B, Friml J, Jönsson H, Thelander M, Sundberg E. 2013. The moss *Physcomitrella patens* reproductive organ development is highly organized, affected by the two *SHI*/*STY* genes and by the level of active auxin in the *SHI*/*STY* expression domain. *Plant Physiology* **162:** 1406–1419.

Lang WH. 1899. The prothallus of *Lycopodium clavatum*, L. *Annals of Botany* **13:** 279–317.

Lee CL. 1955. Fertilization in *Ginkgo biloba*. *Botanical Gazette* **117:** 79–100.

Ligrone R, Duckett JG, Renzaglia KS. 2012. Major transitions in the evolution of early land plants: a bryological perspective. *Annals of Botany* **109:** 851–871.

Lyon F. 1904. The evolution of the sex organs of plants. *Botanical Gazette* **37:** 280–293.

Maheshwari P. 1935. Contributions to the morphology of *Ephedra foliata* Boiss. I. The development of the male and female gametophytes. *Proceedings of the Indian Academy of Sciences* **1:** 586–601.

Maheshwari P, Sanwal M. 1963. The archegonium in gymnosperms: a review. *Memoirs of the Indian Botanical Society* **4:** 103–119.

Martínez OG, Chambi CJ, Avilés Z. 2014. Gametophytic phase of two Neotropical ferns, *Dennstaedtia globulifera* (Poir.) Hieron and *Hypolepis poeppigii* Mett. ex Maxon (Dennstaedtiaceae). *Plant Systematics and Evolution* **300:** 909–915.

Mendoza A, Pérez-García B, Riba R. 2002. Comparative research of gametophytes of *Olfersia alata* and *Olfersia cervina* (Dryopteridaceae). *American Fern Journal* **92:** 229–238.

Meyen SV. 1984. Basic features of gymnosperm systematics and phylogeny as evidenced by the fossil record. *Botanical Review* **50:** 1–111.

Meyen SV. 1988. Origin of the angiosperm gynoecium by gamoheterotopy. *Botanical Journal of the Linnean Society* **97:** 171–178.

Miyake K. 1903. On the development of the sexual organs and fertilization in *Picea excelsa*. *Annals of Botany* **17:** 351–372.

Mizutani M. 1967. A new knowledge of archegonia of *Takakia lepidozioides*. *Journal of Japanese Botany* **42:** 379–381.

Momose S. 1968. Prothallia of the ferns from Thailand. *Tonan Ajia Kenkyu (The Southeast Asian Studies)* **6:** 73–167.

Moody LA. 2019. The 2D to 3D growth transition in the moss *Physcomitrella patens*. *Current Opinion in Plant Biology* **47:** 88–95.

Moussel B. 1972. Etude en microscopie électronique des cols archégoniaux de *l'Ephedra distachya* L. *Comptes rendus hebdomadaires des séances de l'Académie des sciences. Série D* **274:** 3372–3374.

Murrill WA. 1900. The development of the archegonium and fertilization in the hemlock spruce (*Tsuga canadensis*, Carr.). *Annals of Botany* **14:** 583–607.

Nayar BK. 1968. The gametophyte and juvenile leaves of *Loxogramme*. *American Fern Journal* **58:** 19–29.

Nayar BK, Kaur S. 1971. Gametophytes of homosporous ferns. *Botanical Review* **37:** 295–396.

Nester JE. 1985. Scanning electron microscopy of antheridia and archegonia of *Anemia mexicana* Klotzsch. *American Journal of Botany* **72:** 777–780.

Niklas KJ. 2008. Embryo morphology and seedling evolution. In: Leck MA, Parker VT, Simpson RL, eds. *Seedling ecology and evolution*. Cambridge: Cambridge University Press, 103–129.

Niklas KJ, Cobb ED, Kutschera U. 2016. Haeckel's biogenetic law and the land plant phylotypic stage. *BioScience* **66:** 510–519.

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

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

Nishida H, Pigg KB, Kudo K, Rigby JF. 2004. Zooidogamy in the Late Permian genus *Glossopteris*. *Journal of Plant Research* **117:** 323–328.

Norstog K. 1972. Role of archegonial neck cells of *Zamia* and other cycads. *Phytomorphology* **22:** 125–130.

Olsen O-A, Perroud P-F, Johansen W, Demko V. 2015. DEK1; missing piece in puzzle of plant development. *Trends in Plant Science* **20:** 70–71.

Owens JN, Morris SJ. 1990. Cytological basis for cytoplasmic inheritance in *Pseudotsuga menziesii*. I. Pollen tube and archegonial development. *American Journal of Botany* **77:** 433–445.

Owens JN, Simpson SJ, Molder M. 1982. Sexual reproduction of *Pinus contorta*. II. Postdormancy ovule, embryo, and seed development. *Canadian Journal of Botany* **60:** 2071–2083.

Perroud P-F, **Demko V**, **Johansen W**, **Wilson RC**, **Olsen O-A, Quatrano RS. 2014.** Defective Kernel 1 (DEK1) is required for three-dimensional growth in *Physcomitrella patens*. *New Phytologist* **203:** 794–804.

Pigg KR. 1983. The morphology and reproductive biology of the sigillarian cone *Mazocarpon*. *Botanical Gazette* **144:** 400–413.

Pigg KR, Rothwell GW. 1983. Megagametophyte development in the Chaloneriaceae fam. nov., permineralized Paleozoic Isoetales (Lycopsida). *Botanical Gazette* **144:** 295–302.

PPG I. 2016. A community-derived classification for extant lycophytes and ferns. *Journal of Systematics and Evolution* **54:** 563–603.

Preußing M, Olsson S, Schäfer-Verwimp A, Wickett NJ, Wicke S, Quandt D, Nebel M. 2010. New insights in the evolution of the liverwort family Aneuraceae (Metzgeriales, Marchantiophyta), with emphasis on the genus *Lobatiriccardia*. *Taxon* **59:** 1424–1440.

Proskauer J. 1948. Studies on the morphology of *Anthoceros*. I. *Annals of Botany* **12:** 237–265.

Puttick MN, Morris JL, Williams TA, Cox CJ, Edwards D, Kenrick P, Pressel S, Wellman CH, Schneider H, Pisani D, Donoghue PCJ. 2018. The interrelationships of land plants and the nature of the ancestral embryophyte. *Current Biology* **28:** 733–745.

Qiu Y-L, Palmer JD. 1999. Phylogeny of early land plants: insights from genes and genomes. *Trends in Plant Science* **4:** 26–30.

Rasmussen CG, Humphries JA, Smith LG. 2011. Determination of symmetric and asymmetric division planes in plant cells. *Annual Review of Plant Biology* **62:** 387–409.

Remy W, Gensel PG, Hass H. 1993. The gametophyte generation of some early Devonian land plants. *International Journal of Plant Sciences* **154:** 35–58.

Renzaglia KS. 1978. A comparative morphology and developmental anatomy of the Anthocerotophyta. *Journal of Hattori Botanical Laboratory* **44:** 31–90.

Renzaglia KS. 1982. A comparative developmental investigation of the gametophyte generation in the Metzgeriales (Hepatophyta). *Bryophytorum Bibliotheca* **24:** 1–253.

Renzaglia KS, Duff RJ, Ligrone R, Shaw J, Mishler BD, Duckett JG. 2007. Bryophyte phylogeny: advancing the molecular and morphological frontiers. *Bryologist* **110:** 179–213.

Renzaglia KS, Duff RJ, Nickrent DL, Garbary DJ. 2000. Vegetative and reproductive innovations of early land plants: implications for a unified phylogeny. *Philosophical Transactions of the Royal Society of London B* **355:** 769–793.

Renzaglia KS, Villarreal JC, Duff RJ. 2008. New insights into morphology, anatomy, and systematics of hornworts. In: Goffinet B, Shaw AJ, eds. *Bryophyte biology, 2nd edn*. Cambridge: Cambridge University Press, 139–171.

Renzaglia KS, Villarreal JC, Garbary DJ. 2018. Morphology supports the setaphyte hypothesis: mosses plus liverworts form a natural group. *Bryophyte Diversty and Evolution* **40:** 11–17.

Roth D. 1969. Embryo und Embryotheca bei den Laubmoosen. Eine histogenetische und morphologische Untersuchung. *Bibliotheca Botanica* **129:** 1–49.

Rudall PJ. 2006. How many nuclei make an embryo sac in flowering plants? *BioEssays* **28:** 1067–1071.

Rudall PJ, Bateman RM. 2019. Coenocytic growth phases in land plant development: a paleo-evo-devo perspective. *International Journal of Plant Sciences* **180:** 607–622.

Ruhfel BR, Gitzendanner MA, Soltis PS, Soltis DE, Burleigh JG. 2014. From algae to angiosperms–inferring the phylogeny of green plants (Viridiplantae) from 360 plastid genomes. *BMC Evolutionary Biology* **14:** 23.

Ruhland W. 1924. Musci. Allgemeiner Teil. In: Engler A, ed. *Die natürlichen Pflanzenfamilien, 2nd edn*, *Vol. 10*. Leipzig: Engelmann, 1–100.

Samigullin TH, Yacentyuk SP, Degtjareva GV, Valiejo-Roman CM, Bobrova VK, Capesius I, Martin WF, Troitsky AV, Filin VR, Antonov AS. 2002. Paraphyly of bryophytes and close relationship of hornworts and vascular plants inferred from analysis of chloroplast rDNA ITS (cpITS) sequences. *Arctoa* **11:** 31–43.

Sauquet H, von Balthazar M, Magallón S, Doyle JA, Endress PK, Bailes EJ, de Morais EB, Bull-Hereñu K, Carrive L, Chartier M, Chomicki G, Coiro M, Cornette R, El Ottra JHL, Epicoco C, Foster CSP, Jabbour F, Haevermans A, Haevermans T, Hernández R, Little SA, Löfstrand S, Luna JA, Massoni J, Nadot S, Pamperl S, Prieu C, Reyes E, Santos P, Schoonderwoerd KM, Sontag S, Soulebeau A, Staedler Y, Tschan GF, Leung AWS, Schönenberger J. 2017. The ancestral flower of angiosperms and its early diversification. *Nature Communications* **8:** 16047.

Schljakov RN. 1975. *Hepatics. Morphology, phylogeny, classification [Pechenochnye mkhi: Morfologiya, filogeniya, klassifikatsiya]*. Leningrad: Nauka [in Russian].

Schuster RM. 1966. *The Hepaticae and Anthocerotae of North America east of the hundredth meridian, Vol. 1*. New York & London: Columbia University Press.

Schuster RM. 1984. Comparative anatomy and morphology of the Hepaticae. In: Schuster RM, ed. *New manual of bryology, Vol. 2*. Nichinan: Hattori Botanical Laborartory, 760–891.

Schuster RM. 1992a. *The Hepaticae and Anthocerotae of North America east of the hundredth meridian, Vol. 5*. Chicago: Field Museum of Natural History.

Schuster RM. 1992b. *The Hepaticae and Anthocerotae of North America east of the hundredth meridian, Vol. 6*. Chicago: Field Museum of Natural History.

Schuster RM. 1992c. On *Megaceros aenigmaticus* Schust. *Bryologist* **95:** 305–315.

Schuster RM. 1997. On *Takakia* and phylogenetic relationships of the Takakiales. *Nova Hedwigia* **64:** 281–310.

Schuster RM. 1999. *Verdoornia* and the phylogeny of the Metzgeriales. *Journal of Hattori Botanical Laboratory* **86:** 71–87.

Sharma PD, Chopra RS. 1964. The life history of *Lyellia crispa* R. Br. *Bryologist* **67:** 329–343.

Shaw AJ, Szövényi P, Shaw B. 2011. Bryophyte diversity and evolution: windows into the early evolution of land plants. *American Journal of Botany* **98:** 352–369.

Shimamura M. 2016. *Marchantia polymorpha*: taxonomy, phylogeny and morphology of a model system. *Plant and Cell Physiology* **57:** 230–256.

Singh H. 1978. *Embryology of gymnosperms*. Stuttgart: Borntraeger.

Smith GM. 1955. *Cryptogamic botany. Vol II. Bryophytes and pteridophytes*. New York: McGraw Hill Book Company.

Sokoloff DD. 2009. The most important morphological and biological features of angiosperms. In: Timonin AC, ed. *Botanika, Vol. 4*, *Part 2*. Moscow: Publishing Centre "Academia", 116–176 [in Russian].

Sokoloff DD, Remizowa MV, Conran JG, Macfarlane TD, Ramsay MM, Rudall PJ. 2014. Embryo and seedling morphology in *Trithuria lanterna* (Hydatellaceae, Nymphaeales): new data for infrafamilial systematics and a novel type of syncotyly. *Botanical Journal of the Linnean Society* **174:** 551–573.

Sokoloff DD, Rudall PJ, Bateman RM, Remizowa MV. 2015. Functional aspects of the origin and subsequent evolution of cotyledons in seed plants. *Botanica Pacifica* **4:** 35–47.

Sokoloff DD, Timonin AC. 2007. Morphological and molecular data on the origin of angiosperms: on a way to a synthesis. *Journal of General Biology* **68:** 83–97.

Sousa F, Civáň P, Brazão J, Foster PG, Cox CJ. 2020. The mitochondrial phylogeny of land plants shows support for Setaphyta under composition-heterogeneous substitution models. *PeerJ* **8:** e8995.

Sousa F, Foster PG, Donoghue PCJ, Schneider H, Cox CJ. 2019. Nuclear protein phylogenies support the monophyly of the three bryophyte groups (Bryophyta Schimp.). *New Phytologist* **222:** 565–575.

Spessard EA. 1922. Prothallia of *Lycopodium* in America. II. *L. lucidulum* and *L. obscurum* var. *dendroideum*. *Botanical Gazette* **74:** 392–413.

Stevens LG, Hilton J, Rees AR, Rothwell GW, Bateman RM. 2010. Systematics, phylogenetics, and reproductive biology of *Flemingites arcuatus* sp. nov., an exceptionally preserved and partially reconstructed Carboniferous arborescent lycopsid. *International Journal of Plant Sciences* **171:** 783–808.

Stevenson DW. 2013. Gymnosperms. *Annual Plant Reviews* **45:** 141–161.

Steyn EMA, Strydom DJF, Botha A. 1996. Fertilization and rejection of spermatozoids by egg cells in artificially pollinated ovules of *Encephalartos* (Zamiaceae). *Sexual Plant Reproduction* **9:** 175–185.

Stidd BM, Cosentino K. 1976. *Nucellangium*: gametophytic structure and relationship to *Cordaites*. *Botanical Gazette* **137:** 242–249.

Stokey AG. 1930. Prothallia of the Cyatheaceae. *Botanical Gazette* **90:** 1–45.

Stokey AG. 1942. Gametophytes of *Marattia sambucina* and *Macroglossum smithii*. *Botanical Gazette* **103:** 559–569.

Stokey AG. 1945. The gametophyte of *Dipteris conjugata*. *Botanical Gazette* **106:** 402–411.

Stokey AG. 1948. Reproductive structures of the gametophytes of *Hymenophyllum* and *Trichomanes*. *Botanical Gazette* **109:** 363–380.

Stokey AG. 1950. The gametophyte of the Gleicheniaceae. *Bulletin of the Torrey Botanical Club* **77:** 323–339.

Takaso T, Kimoto Y, John N. Owens JN, Kono M, Mimura T. 2013. Secretions from the female gametophyte and their role in spermatozoid induction in *Cycas revoluta*. *Plant Reproduction* **26:** 17–23.

Taylor TN, Kerp H, Hass H. 2005. Life history biology of early land plants: deciphering the gametophyte phase. *Proceedings of the National Academy of Sciences of the United States of America* **102:** 5892–5897.

Tigerschiöld E. 1989. Scanning electron microscopy of gametophyte characters and antheridial opening in some Ceylonese species of Thelypteridaceae. *Nordic Journal of Botany* **8:** 639–648.

Tobe H, Jaffre T, Raven PH. 2000. Embryology of *Amborella* (Amborellaceae): descriptions and polarity of character states. *Journal of Plant Research* **113:** 271–280

Treub M. 1884. Études sur les Lycopodiacées. 1. Le prothalle du *Lycopodium cernuum* L. *Annales du Jardin botanique de Buitenzorg* **4:** 107–138.

Treub M. 1890. Études sur les Lycopodiacées. IV. Le prothalle du *Lycopodium salakense*. *Annales du Jardin botanique de Buitenzorg* **8:** 141–150.

Wang D, Lu Y, Zhang M, Lu Z, Luo K, Cheng F, Wang L. 2014. Structure and function of the neck cell during fertilization in *Ginkgo biloba* L. *Trees* **28:** 995–1005.

Whittier DP. 1981. Gametophytes of *Lycopodium digitatum* (formerly *L. complanatum* var. *flabelliforme*) as grown in axenic culture. *Botanical Gazette* **142:** 519–524.

Whittier DP. 2003. The gametophyte of *Diphasiastrum sitchense*. *American Fern Journal* **93:** 20–24.

Whittier DP. 2006. Gametophytes of four tropical, terrestrial *Huperzia* species (Lycopodiaceae). *American Fern Journal* **96:** 54–61.

Whittier DP, Peterson RL. 1980. Archegonial opening in *Psilotum*. *Canadian Journal of Botany* **58:** 1905–1907

Whittier P, Webster TR. 1986. Gametophytes of *Lycopodium lucidulum* from axenic culture. *American Fern Journal* **76:** 48–55.

Wickett NJ, Mirarab S, Nguyen N, Warnow T, Carpenter E, Matasci N, Ayyampalayam S, Barker MS, Burleigh JG, Gitzendanner MA, Ruhfel BR, Wafula E, Der JP, Graham SW, Mathews S, Melkonian M, Soltis DE, Soltis PS, Miles NW, Rothfels CJ, Pokorny L, Shaw AJ, DeGironimo L, Stevenson DW, Surek B, Villarreal JC, Roure B, Philippe H, dePamphilis CW, Chen T, Deyholos MK, Baucom RS, Kutchan TM, Augustin MM, Wang J, Zhang Y, Tian Z, Yan Z, Wu X, Sun X, Wong GK-S, Leebens-Mack J. 2014. Phylotranscriptomic analysis of the origin and early diversification of land plants. *Proceedings of the National Academy of Sciences of the United States of America* **111:** 4859–4868.

Yang N-Y, Cao J-G, Wang Q-X. 2009. Formation and development of archegonium in the fern *Ceratopteris thalictroides* (L.) Brongn. *Journal of Wuhan Botanical Research* **27:** 569–573.

Zhang J, Fu X-X, Li R-Q, Zhao X, Liu Y, Li M-H, Zwaenepoel A, Ma H, Goffinet B, Guan Y-L, Xue J-Y, Liao Y-Y, Wang Q-F, Wang Q-W, Wang J-Y, Zhang G-Q, Wang Z-W, Jia Y, Wang M-Z, Dong S-S, Yang J-F, Jiao Y-N, Guo Y-L, Kong H-Z, Lu A-M, Yang H-M, Zhang S-Z, van de Peer Y, Liu Z-J, Chen Z-D. 2020. The hornwort genome and early land plant evolution. *Nature Plants* **6:** 107–118.

Zhang M, Zheng C-X. 2016. Archegonium and fertilization in Coniferopsida. *Trees* **30:** 75–86.

Zhang Z, Clayton SC, Cui K, Lee C. 2013. Developmental synchronization of male and female gametophytes in *Ginkgo biloba* and its neck mother cell division prior to fertilization. *Physiologia Plantarum* **147:** 541–552.

Zielinski F. 1909. Beiträge zur Biologie des Archegoniums und der Haube der Laubmoose. *Flora* **100:** 1–36.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Supplementary Material. Full scientific names of all species and genera mentioned in the paper.