

## Review Paper

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# The rudimentary embryo: an early angiosperm invention that contributed to their dominance over gymnosperms

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**Abstract**

In this review, we explore the origin of the rudimentary embryo, its relationship to other kinds of plant embryos and its role in the diversification of angiosperms. Rudimentary embryos have a length:width ratio of  $\leq 2.0$ , and they have organs, including cotyledon(s) and a primary root. A literature survey failed to reveal rudimentary embryos in the pre-angiosperms, suggesting that this kind of embryo is an angiosperm invention. Although proembryos of some gymnosperms and angiosperms have a length:width ratio of  $\leq 2.0$ , they have not formed meristems or organs. Thus, rudimentary embryos are not proembryos. During the development of rudimentary embryos in monocots and dicots (all non-monocots), the growth pattern of the epicotyledonary cells differs, resulting in differences in the placement of the shoot meristem and in one *versus* two cotyledons, respectively, but the embryo size is similar. Rudimentary embryos grow inside the seed prior to germination, which is true for linear-underdeveloped embryos, including those in some gymnosperms. Rudimentary embryos served as the starting point for the great diversification of embryos, and ultimately of seeds, in angiosperms, and they are still present in many families of extant angiosperms. The rudimentary embryo is part of the syndrome of changes, including increased speed of pollen germination and pollen tube growth, simplification of the female gametophyte, development of endosperm and elimination of multiple embryo production from each zygote, that distinguish angiosperm seed production from that of gymnosperms. We conclude that the rudimentary embryo was one of many new developments of angiosperms that contributed to their great success on earth.

**Introduction**

A rudimentary embryo is small and has organs and grows inside the seed prior to germination. Martin (1946) placed the rudimentary embryo at the base of his family tree of seed phylogeny, and he listed the Aquifoliaceae, Araliaceae, Magnoliaceae, Ranunculaceae and Papaveraceae as examples of families with a rudimentary embryo. Today, we know that seeds of the most-basal extant angiosperm *Amborella trichopoda* also have a rudimentary embryo (Fogliani et al., 2017). Martin provided no clues about the origin of the rudimentary embryo but did give a hint about the relationship between the rudimentary and other kinds of embryos when he wrote, ‘... there is also clear evidence of ancestral relation of the Rudimentary type to many of the Linear seeds’ [p. 524]. Furthermore, he noted that rudimentary and linear embryos as well as intermediate embryos occur in the Apiaceae and Ranunculaceae. It should be noted that these comments do not include any monocot families. Furthermore, Martin included only angiosperms in his family tree of seed phylogeny. He said, ‘Gymnosperms were excluded from the diagram for the reason that they are not well adapted to depiction in a family tree for seeds; the group lacks representation in the Basal division and, therefore, would have to be illustrated as a trunk suspended in air or at least separated from its theoretical original base’ [p. 524].

It has been 77 years since the publication of Martin’s (1946) classic paper, and during this time much has been learned about the geological/fossil history, phylogenetic relationships and morphology/development of plants. Thus, an evaluation of the available information potentially could provide new insights into the origin of the rudimentary embryo and its relationship to other kinds of embryos. The purpose of this review is to seek answers to the following eight questions: (1) How is a rudimentary embryo distinguished from other kinds of embryos? (2) Do any pre-angiosperms have a rudimentary embryo? (3) Is the rudimentary embryo a proembryo? (4) Do rudimentary embryos differ in dicots (as used here, it refers to all non-monocot angiosperms) and monocots, and if so how? (5) When do embryos in pre-angiosperms and angiosperms grow? (6) What is the relationship between the rudimentary embryo and other kinds of angiosperm embryos? (7) How does seed production differ between

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gymnosperms and angiosperms? (8) Is the rudimentary embryo a new development ('invention') of angiosperms and did it contribute to the diversification and success of angiosperms?

We hypothesized that (1) the rudimentary embryo originated in the angiosperms, (2) underdeveloped embryos occur only in seed plants, (3) the rudimentary embryo is closely related to linear embryos, (4) rudimentary embryos in dicots and monocots differ in development/morphology but not in size and (5) the diversification of angiosperm embryos from the rudimentary embryo contributed to the success of angiosperms on earth.

### What is a rudimentary embryo?

Martin (1946) described the rudimentary embryo as 'Embryo small, globular to oval-oblong; seeds generally of medium size or larger; cotyledons are usually rudimentary and obscure but sometimes they are evident, making the embryos appear like miniatures of the Linear or Spatulate types. The group is not entirely clear-cut since most of the families concerned have some genera that merge into the Linear type and a few inclined toward the Broad' [p. 519]. Also, he said of the rudimentary embryo 'Endosperm, if present, not definitely starchy except among a few linear-embryoed forms; embryo not peripheral: Embryo minute in medium to large seeds' [p. 521]. Martin did not specify an embryo length.

To gain a better understanding of the morphological traits of rudimentary embryos, the length (L) and width (W) of the embryo in the 48 species of angiosperms Martin (1946) listed as having a rudimentary embryo were measured in the drawings he provided in his paper. Mean ( $\pm$ SE) embryo L:W ratio for the 48 species is  $1.50 \pm 0.08$ . The L:W ratios of embryos in seeds of *Aconitum napellus*, *Clematis columbiana* and *Thalictrum polyg-onum* were 3.0, 3.0 and 3.5, respectively, but the L:W ratio for embryos of the other 45 species was  $\leq 2.0$ . Martin said that the embryo in seeds of *Smilax glauca* and *Paeonia brownii* was linear, and the L:W ratio was 3.0 for both of these species. If the three species with a L:W ratio of  $\geq 3.0$  are excluded, then the L:W ratio for the remaining 45 species is  $1.39 \pm 0.06$ . Of these 45 species, 5 are monocots and 40 are dicots, and the L:W ratio (mean  $\pm$  SE) of the monocots and dicots is  $1.18 \pm 0.08$  and  $1.41 \pm 0.06$ , respectively.

For Martin's seeds with a rudimentary embryo, the embryo length (E):seed length (S) ratio (mean  $\pm$  SE) is  $0.11 \pm 0.01$ . For comparison, the E:S ratio of freshly matured seeds of *A. trichopoda* is  $0.08 \pm 0.01$ , and it grows to  $0.48 \pm 0.07$  just prior to radicle emergence (Fogliani et al., 2017).

### Do any pre-angiosperms have a rudimentary embryo?

Niklas et al. (2016) hypothesized that major evolutionary transformations have occurred in land plants, which lead to the development of different kinds of embryogenesis and embryos. Thus, a survey of the general embryo morphology of bryophytes, lycophytes, monilophytes (ferns and fern allies) and gymnosperms was conducted. Particular attention was given to the kinds of organs present in the embryo and to the general shape of the embryo.

The first cell division of the zygote of mosses and liverworts (bryophytes) is transverse in relation to the axis of the archegonium, giving rise to an apical (epibasal) and basal (hypobasal) cell within the venter (base) of the archegonium. The epibasal cell divides transversally, resulting in an embryo with three

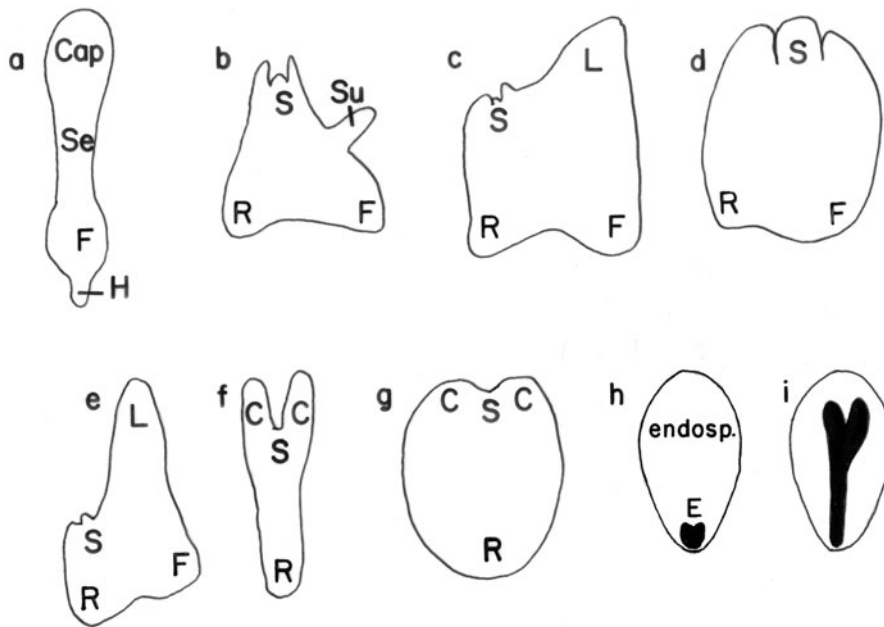
cells. The upper cell (adjacent to the neck of the archegonium) produces the capsule, the middle cell the seta and foot and the lower cell a haustorium (Bower, 1935; Schertler, 1979; Kato and Akiyama, 2005; Ligrone et al., 2012). In hornworts, the first division of the zygote is vertical, and then other cell divisions give rise to a three-tiered embryo, with the upper tier producing the capsule and the lowest tier the foot (Ligrone et al., 2012). The bryophyte embryo is relatively long and narrow, and as the development of the capsule begins the embryo becomes greatly elongated (Fig. 1a). Bryophyte embryos do not have a root meristem.

The embryo of lycophytes and monilophytes also develops inside an archegonium. The embryo has a shoot apex, one or more primary leaves (no cotyledons), a foot and a root, and it may, or may not, have a suspensor. The foot serves as a 'suctorial or nursing organ' (Foster and Gifford, 1959). Eventually, the developing sporophyte becomes detached from the foot via a separation layer of cells between the shoot and foot. The root meristem is lateral to the main axis of the embryo (Fig. 1b–e), which differs from the embryo of seed plants in which the root and shoot have the same vertical axis (Fig. 1f, g). The root–shoot portion of a lycopod or fern embryo is somewhat elongated, but the presence of the foot increases its overall width. In contrast to a lycopod or fern embryo, the rudimentary embryo of angiosperms has a vertical root–shoot axis and one or two cotyledons (i.e. monocot and dicot, respectively) (Figs 1g and 2a, d).

In gymnosperms, the female gametophyte develops within the confines of an ovule that is attached to the sporophyte, and nourishment for the developing gametophyte and embryo comes from the sporophyte. With the exception of a proembryo in *Plectilopsermum elliotii* (Glossopteridales) (Taylor and Taylor, 1987), embryos have not been found in fossil ovules or seeds of the early gymnosperms (Table 1), although much effort has been made to find fossil embryos (e.g. Gould and Delevoryas, 1977; Ryberg and Taylor, 2013). The absence of embryos has caused much speculation about seed development in early gymnosperms (Reed, 1939; Long, 1974/1975; Rothwell, 1982), but no definite answers to the question of why these fossils do not contain an embryo have been found. However, fossil megaspores of a lycopod with a megagametophyte and embryo have been found in the Upper Carboniferous (Westphalian A) at Burnley, England (Stubblefield and Rothwell, 1981), suggesting that the lack of embryos in fossil seeds of early gymnosperms may be due to the lack of an embryo and not lack of fossilization *per se*. We will return to this point later.

Fossil ovules of seed ferns (Lagenospermosida) have been collected from the Devonian and fossil seeds of Medullosales (seed ferns) and Cordaitales (coniferophytes) from the Middle Pennsylvanian (Table 1). The earliest gymnosperm embryos (Voltziales and coniferophyte) are from the uppermost Pennsylvanian and lowermost Permian, and they were elongated (linear) and polycotyledonous (Mapes et al., 1989). Embryos have been found in fossil seeds of Voltziales, Bennettitales and Coniferales from the Late Pennsylvanian to Late Cretaceous, and all of them are elongated and have two cotyledons, except *Pitystrobis beardii* with eight cotyledons.

Embryos in the 13 families of extant gymnosperms (Araucariaceae, Cupressaceae, Cephalotaxaceae, Cycadaceae, Ephedraceae, Ginkgoaceae, Gnetaceae, Pinaceae, Podocarpaceae, Sciadopityaceae, Taxaceae, Welwitschiaceae and Zamiaceae) are formed in the female gametophyte that develops in the ovule. The female gametophyte has much stored food that is subsequently used by the growing embryo(s). In all the extant families,



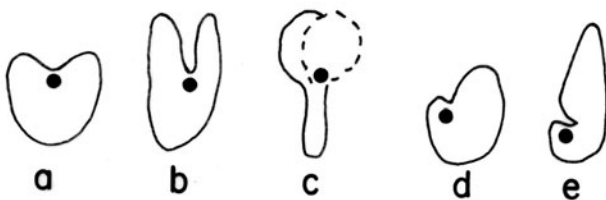
**Figure 1.** Diagrams showing parts of embryos (not to scale) of liverwort (a), *Selaginella* (b), fern (c), *Equisetum* (d), *Isoetes* (e), gymnosperm (Zamiaceae) (f), angiosperm (*Ilex* with rudimentary embryo) (g), longitudinal section of seed with a rudimentary embryo at time of dispersal showing small size of embryo in relation to endosperm (h) and the same seed with a rudimentary embryo (black) that has grown prior to germination (i). Modified from Schertler (1979), Bruchmann (1912), Hofmeister (1979), Walker (1921), La Motte (1937), Woodenberg et al. (2014), Hu (1976) and Martin (1946), respectively. C, cotyledon; Cap, capsule; E, embryo; endosp., endosperm; F, foot; H, haustorium; L, leaf; R, root; S, shoot; Se, seta; Su, suspensor.

the embryos have cotyledons, usually two but sometimes more, and the embryo is several times longer than wide. Embryos of some species of Cupressaceae and Ephedraceae are spoon-shaped (spatulate) (Martin, 1946), but nevertheless they are longer than wide. In the Cephalotaxaceae, Cycadaceae, Ginkgoaceae, Podocarpaceae, Taxaceae and Zamiaceae, the linear embryos have a low E:S ratio (Martin, 1946), and they grow inside the seed prior to germination. Thus, the embryo in these six families is underdeveloped (Baskin and Baskin, 2014), but the length of the embryo is longer than that of a rudimentary embryo.

In our survey of embryos in the non-seed plants and the gymnosperms, we did not find a group of pre-angiosperm plants with an embryo matching the characteristics of a rudimentary embryo. Thus, based on available information, we conclude that rudimentary embryos are not found in the pre-angiosperms. However, we would like to emphasize that more searching for embryos in fossil seeds of early gymnosperms is needed. Perhaps, fossil seeds of some early gymnosperms stored in a museum drawer have an embryo that could be revealed via synchrotron radiation X-ray tomography (see Friis et al., 2015).

### Is the rudimentary embryo a proembryo?

A proembryo in seeds of both gymnosperms and angiosperms is the product of the first stages of embryogenesis, and it is smaller



**Figure 2.** General shape of underdeveloped embryos in seeds of dicots: rudimentary (a), linear-underdeveloped (b) and spatulate-underdeveloped (c) and monocots: rudimentary (d) and linear-underdeveloped (e). • indicates position of shoot meristem.

than a mature embryo. Thus, we ask if proembryos of gymnosperms and angiosperms have the same size and general morphology as rudimentary embryos?

The L:W ratio of proembryos in the 13 families of extant gymnosperms ranges from 1.2 (Taxaceae) to 7.6 (Cephalotaxaceae) (Table 2). However, the ratio varies within a family as indicated by a range of 1.2–2.7 for the Taxaceae and of 1.4–3.9 for the Zamiaceae. The mean L:W ratio of the 48 species with a rudimentary embryo in Martin's (1946) paper is 1.5; thus, some gymnosperm taxa have a proembryo that fits into the size range of rudimentary embryos. However, the early proembryo stages of most gymnosperms are free-nuclear (see Rudall and Bateman, 2019), with the exception of *Gnetum* (Johansen, 1950), *Sequoia sempervirens* (Buchholz, 1939) and *Welwitschia mirabilis* (Pearson, 1909, 1910), which are cellular. A free-nuclear stage occurs in the early embryogenesis of the lower vascular plants, but it is not known in angiosperms (Foster and Gifford, 1959). However, nuclear and helobial endosperm formation in angiosperms seeds are free-nuclear, while cell wall formation keeps pace with cell division in cellular endosperm formation of angiosperms (Gifford and Foster, 1989).

In contrast to gymnosperms, the proembryo of angiosperms is cellular, and, as frequently illustrated in the botanical literature (e.g. Gifford and Foster, 1989), it is globular in shape. For example, the L:W ratio of the proembryo in various angiosperms is: (1) dicots – *Aconitum soongaricum*, 1.1 (Butuzova et al., 1997), *Capsella bursa-pastoris*, 0.8 (Raghavan and Torrey, 1963), *Phlox drummondii*, 1.1 (Miller and Wetmore, 1945), *Pisum* sp., 1.0 (Reeve, 1948) and *Strombosia ceylanica*, 1.0 (Agarwal, 1963); and (2) monocots – *Crocus thomasii*, 1.4 (Chichiricco, 1989), *Lomandra longifolia*, 1.5 (Ahmad et al., 2008), *Sagittaria variabilis*, 1.3 (Schaffner, 1897), *Scilla autumnalis*, 1.4 (Coşkun and Ünal, 2010) and *Zephyranthes drummondii*, 1.2 (Church, 1916).

In both gymnosperms (Johansen, 1950) and angiosperms (Raghavan, 1986), the signal that the proembryo stage has ended is the initiation of meristems and organs such as cotyledon primordia. Although proembryos of some gymnosperms and angiosperms are small enough to fit into the size range of

**Table 1.** Information about fossil ovules, seeds and embryos of gymnosperms from the Upper Devonian to Late Cretaceous

Order	Species	Age	Fossil has ovule/seed/embryo; embryo size (mm)	Ovule or seed size (mm)	References
Lagenospermopsida	<i>Cosmosperma polyloba</i>	Upper Devonian	Ovules	Ovule: 3.7–4.7 long, 1.6–2.2 wide	Liu et al. (2017)
Not determined	<i>Latisemenia longshania</i>	Late Devonian	Ovules	Ovule: 5.3–10.7 long, 2.4–5.3 wide	Wang et al. (2015)
Cordaitales	<i>Cordaites annularis</i>	Middle Pennsylvanian	Seeds <sup>a</sup>	Seed: 10–11 long, 9–11 wide	Šimůnek et al. (2009)
Cordaitales	<i>Cordaianthus duquesnensis</i>	Late Pennsylvanian	Ovules	Ovule: 0.1–0.3 long, 0.1 wide	Rothwell (1982)
Cordaitales	<i>Wangjunia microfolia</i>	Middle Permian	Seeds <sup>a</sup>	Seed: 5.4–5.5 long, 4.1–4.3 wide	Backer et al. (2019)
Medullosales	<i>Pachytesta muncii</i>	Lower Pennsylvanian	Seeds <sup>a</sup>	Seed: 30 long, 20 wide	Cichan and Taylor (1981)
Medullosales	<i>Hexapterospermum delevoryii</i>	Middle Pennsylvanian	Seeds <sup>a</sup>	Seed: 25 long, 13 wide	Taylor (1966)
Lagenostomales	<i>Conostoma oblongum</i>	Upper Pennsylvanian	Seeds <sup>a</sup>	Seed: 4 long, 2.5 wide	Reed (1939)
Trigonocarpales	<i>Pachytesta gigantea</i>	Upper Pennsylvanian	Seeds <sup>a</sup>	Seed: 70 long, 30 wide	Reed (1939)
Cycadales	Cycads, new genus A, new genus B	Lower Permian	Ovules/seeds	No data	Mamay (1969)
Cycadales	<i>Beania gracilis</i>	Jurassic	Seeds <sup>a</sup>	Seed: 7–15 long, 7–13 wide	Harris (1941)
Ginkgoales	<i>Sphenobaiera</i>	Upper Permian	Ovules/seeds	No data	Fischer et al. (2010)
Ginkgoales	<i>Schmeissneria microstachys</i>	Late Triassic–Early Jurassic	Ovules	Ovule: 2.5–3.5 long, 2.2–2.6 wide	Kirchner and van Konijnenburg-van Cittert (1994)
Glossopteridales	Glossopterid	Late Permian	Ovules	Ovule: 1.8 long, 0.5–0.9 wide	Taylor and Taylor (1992)
Glossopteridales	<i>Plectilopsermum elliotii</i>	Permian	Seeds	Seed: 3.1–4.1 long, 2.2–2.8 wide	Smoot and Taylor (1986), Taylor and Taylor (1987)
Glossopteridales	<i>Plectilopsermum elliotii</i>	Permian	Proembryo: 0.3 long, 0.1 wide	Seed: 2.2–4.1 long, 1.6–2.5 wide	Smoot and Taylor (1986); Taylor and Taylor (1987)
Glossopteridales	<i>Pachytestopsis tayloriorum</i>	Late Permian	Ovules	Ovules: 5–11 long, 5–10.1 wide	McLoughlin et al. (2018)
Voltziales	Walchian conifer	Uppermost Pennsylvanian or lowermost Permian	Linear-full polycotyledonous embryo: 2.5 long, slender	No data	Mapes et al. (1989)
Voltziales	<i>Emporia cryptica</i>	Late Pennsylvanian	Elongated and polycotyledonous embryo: 0.5 long, 0.2 wide	Seed: 2.4–7.9 long, 1.4–1.8 wide	Hernandez-Castillo et al. (2009)
Voltziales	<i>Parasciadopitys aequata</i>	Early Middle Triassic	Linear-full embryo (with 2 cotyledons): 0.2 long, 0.1 wide	Seed: 0.6 long, 0.2 wide	Schwendemann et al. (2010)
Bennettiales	<i>Westersheimia pramelreuthensis</i>	Upper Triassic	Linear-full embryo (with 2 cotyledons): 1.3 long, 0.4 wide	Seed: 1.6 long, 1.4 wide	Pott (2016)

Coniferales	<i>Pararaucaria patagonica</i>	Jurassic	Linear-full embryo (with 2–8 cotyledons): 4.0 long, 1.2 wide	Seed: 2.3–2.9 long, 1.0–1.3 wide	Stockey (1977)
Coniferales	<i>Araucaria sphaerocarpa</i>	Middle Jurassic	Linear-full embryo (with 2 cotyledons): 7.0 long, 1.5 wide	Seed: 9.4 long, 3.0–5.1 wide	Stockey (1980)
Bennettitales-Erdtmanitales-Gnetales	<i>Rothwellia foveata</i>	Early to middle Albian (Cretaceous)	Linear-full embryo (with 2 cotyledons): 0.6 long, 0.2 wide	Seed: 0.8–1.1 long, 0.7–0.9 wide	Friis et al. (2019)
Bennettitales	<i>Cycadeoidea maccafferyi</i>	Campanian (Late Cretaceous)	Linear-full embryo (with 2 cotyledons): 2.4 long, 0.6 wide	Seed: 12–19 long, 2.1–4.1 wide	Rothwell and Stockey (2002)
Bennettitales	<i>Cycadeoidea dartoni</i>	Upper Cretaceous	Linear-full embryo (with 2 cotyledons): 1.5 long, 0.5 wide	Seed: 1.8 long, 0.6 wide	Wieland (1916)
Coniferales	<i>Araucaria mirabilis</i>	Middle to Late Jurassic	Linear-full embryo (with 2 cotyledons): 2.0 long, 0.3 wide	Seed: 8–13 long, 2–6 wide	Stockey (1975)
Coniferales	<i>Pityostrobus beardii</i>	Campanian (Late Cretaceous)	Elongated embryo (with 8 cotyledons) <sup>b</sup>	Seed: 7.0 long, 3.5–4.0 wide	Smith and Stockey (2002)
Coniferales	<i>Araucaria famii</i>	Mid-Cretaceous	Spatulate embryo (with 2 cotyledons): 3.4–5.4 long, 1.1–1.8 wide	Seed: 4.4–6.8 long, 3.3–5.1 wide	Stockey and Rothwell (2020)
Coniferales	<i>Araucaria nihongi</i>	Late Cretaceous	Linear-full embryo (with 2 cotyledons) <sup>c</sup>	Seed: 3.0–3.3 long, 2.3 wide	Stockey et al. (1992)

<sup>a</sup>No evidence was provided that an embryo was present; thus, the structure may have only been an ovule.

<sup>b</sup>Only part of the embryo is shown in a longitudinal section of megagametophyte tissue.

<sup>c</sup>Embryo had 'two long straight cotyledons....'

**Table 2.** Examples of the length:width ratios of proembryos in the families of extant gymnosperms

Family	Proembryo length: width ratio	References
Araucariaceae	1.4, 2.4	Owens et al. (1995)
Cupressaceae	2.8	Johansen (1950)
	2.1	Doyle (1961–1963)
Cephalotaxaceae	7.6	Doyle (1961–1963)
Cycadaceae	3.6	Biswas and Johri (1997)
Ephedraceae	1.5	Johansen (1950)
Ginkgoaceae	1.9	Wang et al. (2011)
Gnetaceae	1.8	Johansen (1950)
Pinaceae	2.1	Buchholz (1918)
	1.8	Johansen (1950)
Podocarpaceae	1.8, 2.3	Doyle (1961–1963)
Sciadopityaceae	2.7	Doyle (1961–1963)
Taxaceae	2.7	Johansen (1950)
	1.3	Doyle (1961–1963)
	1.2	Schneckenburger (1993)
Welwitschiaceae	1.6	Pearson (1910)
Zamiaceae	2.7	Chamberlain (1910)
	3.2	Sedgwick (1924)
	3.9	Johansen (1950)
	1.4	Schneckenburger (1993)

Martin's rudimentary embryo, they are not rudimentary embryos due to lack of cotyledon primordia. Furthermore, in angiosperms, the source of food for the developing embryo changes as the embryo advances from a globular to a heart-shaped embryo. The young globular angiosperm embryo receives nutrients from the seed coat via the suspensor, while the heart-shaped embryo begins to use nutrients from the endosperm, at which time the suspensor degenerates (Lafon-Placette and Köhler, 2014).

### Dicot versus monocot embryos

Clearly, there are differences between embryos in dicots and monocots, for example, two (typically) *versus* one cotyledon, respectively, but is this the only difference? During embryogenesis of monocots and dicots, the epicotyl and cotyledon(s) come from derivatives of the apical (terminal) cell (*ca*) that results from the first division of the zygote. In dicots, initiation of the epicotyl and cotyledonary centres of growth begins when derivatives of the apical cell reach the octant stage. The octant stage may consist of four cells each in tiers *l* and *l'* or eight cells may be in tier *q* (Johri et al., 1992). In a dicot embryo, the epicotyl comes from the central cells of the *q* tier (with eight cells) or from the *l* (terminal) tier of four cells, depending on the species (Swamy and Krishnamurthy, 1977). The cells that give rise to the cotyledons in a dicot embryo are on opposite sides of the *q* tier of cells, or they are the four cells in tier *l'*. The epicotylary cells grow

very slowly, while the cells that give rise to the cotyledons grow rapidly forming a cotyledon on each side of the epicotylary centre (Swamy and Krishnamurthy, 1977; Johri et al., 1992).

During embryogenesis of the monocot embryo, the apical (terminal) cell resulting from the first division of the zygote divides by formation of a vertical wall, as seen in dicots. One of the two cells becomes the epicotylary centre and the other one the cotyledonary centre (Swamy and Krishnamurthy, 1977). Cells of the epicotylary centre divide very slowly, while those in the cotyledonary centre divide relatively rapidly, causing the growing cotyledon to push the epicotylary cells to the side of the embryo (Swamy, 1963; Lakshmanan, 1972, 1977, 1978; Swamy and Krishnamurthy, 1977; Guignard, 1984; Johri et al., 1992). Thus, the epicotyl and cotyledon(s) in both dicots and monocots are derived from the apical cell that results from the first division of the zygote. However, subsequent cell production and growth in the dicot and monocot embryo lead to the epicotyledonary cells being on the top and side of the embryo, respectively.

### Underdeveloped (differentiated) embryos in the seeds of dicots and monocots

In seeds with an underdeveloped embryo, not including undifferentiated embryos such as occurs in Orchidaceae (Yeung, 2022), the embryo is small in relation to the size of the seed, and a relatively large amount of endosperm is present. Furthermore, the embryo grows inside the seed prior to radicle emergence (germination) (Nikolaeva, 1969). Three kinds of underdeveloped embryos are found in dicots (rudimentary, linear-underdeveloped and spatulate-underdeveloped), and two occur in monocots (rudimentary and linear-underdeveloped).

In dicot seeds with a rudimentary embryo, the two cotyledons are small projections (bumps), one on each side of the apical meristem (Fig. 2a). In the linear-underdeveloped embryo, the top of the somewhat elongated (linear) cotyledons extends above the shoot meristem by one-third to one-half the full length of the embryo (Fig. 2b). In the spatulate-underdeveloped embryo, the two cotyledons are rounded and are about one-half the length of the embryo (Fig. 2c).

In the monocot rudimentary embryo, the height of the tip of the cotyledon above the shoot meristem (bud) is about equal to that of the height of the bud from the base of the embryo. That is, the bud is on the side of the embryo, halfway between the top and bottom (Fig. 2d). In the linear-underdeveloped monocot embryo, the bud is on the side of the embryo but relatively close to the base of the embryo; it is only about one-third of full embryo length above the base of the embryo (Fig. 2e). Thus, the tip of the elongated cotyledon projects well above the shoot meristem on the side of the embryo.

### When do embryos grow?

Spores are the dispersal unit for bryophytes, lycophytes and monilophytes, and seeds (gymnosperms) or seeds plus enclosing structures (angiosperms) are the dispersal unit in seed plants. Both spores and seeds can be dormant at maturity (Niklas, 2008), and various treatments such as dry storage (afterripening) and cold moist stratification may be required to break dormancy of spores (Kott and Britton, 1982; Whittier, 1987; Haupt et al., 1988; McLetchie, 1999; Sabovljević et al., 2016) and seeds (Baskin and Baskin, 2014); these treatments suggest the presence of physiological dormancy in both spores and seeds.

Non-dormant spores germinate and produce a gametophyte that grows on/in the soil or inside the megaspore (that is on/in the soil) of some species. As gametophytes mature, they produce one or more archegonia, each containing an egg that potentially will be fertilized, resulting in the formation of a zygote. The first division of the zygote occurs between 1 h and 10 d after fertilization, depending on the species (see Ward, 1954). After the first division of the zygote, the embryo increases in size via cell division, and organs are formed. The young sporophyte rapidly exceeds the size of the archegonium and emerges from it. Thus, there is relatively little delay between the time of first division of the zygote and appearance of the young sporophyte.

In gymnosperm and angiosperm seeds, the gametophyte develops inside an ovule that is attached to the sporophyte. After egg formation and fertilization, mitotic divisions of the zygote and the resulting cells lead to formation of an embryo; an ovule with an embryo inside is called a seed. The size of the embryo at the time of seed maturation varies with the species, and (in relation to size of the whole seed) it ranges from very small (rudimentary, linear-underdeveloped, spatulate-underdeveloped; together referred to as underdeveloped embryos) to very large (e.g. linear-full, spatulate, bent, folded and investing).

In the case of angiosperm seeds with a rudimentary, linear-underdeveloped or spatulate-underdeveloped embryo, the embryo has organs but additional growth and differentiation occur prior to germination (radicle emergence). That is, after the seeds are dispersed and are imbibed, the embryo grows inside the seed, using the stored food reserves. Rudimentary, linear-underdeveloped and spatulate-underdeveloped embryos are known to occur in 31, 83 and 27 families of dicots, respectively, and rudimentary and linear-underdeveloped occur in 5 and 27 families of monocots, respectively (Martin, 1946; Baskin and Baskin, unpublished embryo database). However, a family may have more than one kind of underdeveloped embryo, for example, Apiaceae, Araliaceae, Dilleniaceae, Myristicaceae and Papaveraceae. In gymnosperms, linear-underdeveloped embryos occur in the Cephalotaxaceae, Cycadaceae, Ginkgoaceae, Podocarpaceae, Taxaceae and Zamiaceae, and this is the only kind of underdeveloped embryo in these families; the embryo grows inside the seed prior to germination (Devillez, 1978; Dehgan and Schutzman, 1983, 1989; Nikolaeva et al., 1985 (see Rosbakh et al., 2020 for English translation of this book); Del Tredici, 2007; Ferrandis et al., 2011; Yang et al., 2011).

### Relationship between the rudimentary and other kinds of angiosperm embryos

First, we will consider the ANA grade of angiosperms, which includes Amborellales (A), Nymphaeales (N) and Austrobaileyales (A). Phylogenetic analyses based on 1594 nuclear genes have recovered '... full support for *Amborella* being sister to all other extant angiosperms, followed successively by Nymphaeales and Austrobaileyales ...' (Yang et al., 2020). There are three kinds of embryos in the ANA grade: two are underdeveloped (Amborellales and Austrobaileyales) and one fully developed although small (Nymphaeales) (Baskin and Baskin, 2007a, 2021). Seeds of Amborellales have a rudimentary embryo (Fogliani et al., 2017), and those of Austrobaileyales have a linear-underdeveloped embryo (Endress, 1980; Losada et al., 2017).

Seeds of Nymphaeales were reported by Martin (1946) to have a broad embryo, and when they are viewed in profile, they are wider than tall. However, much research has been done on

**Table 3.** Number of dicot angiosperm families with rudimentary or linear-underdeveloped embryos and number of dicot angiosperm families with a combination of rudimentary or linear-underdeveloped embryos and other kinds of embryos

Rudimentary or Linear-underdeveloped	Rud.	LU	SU	LF	Bent	Folded	Invest.	Spat.	Undiff.
Rudimentary	9 <sup>a</sup>	16 <sup>b</sup>	0	0	1	0	0	3	1
Linear-underdeveloped	16 <sup>b</sup>	33 <sup>c</sup>	8	16	2	1	1	17	5

Abbreviations: Rud, rudimentary; LU, linear-underdeveloped; SU, spatulate-underdeveloped; LF, linear-full; Invest., investing; Spat., spatulate; Undiff., undifferentiated.

<sup>a</sup>Nine families with only a rudimentary embryo.

<sup>b</sup>Sixteen families with both a rudimentary embryo and a linear-underdeveloped embryo.

<sup>c</sup>Thirty-three families with only a linear-underdeveloped embryo.

seeds with broad embryos, for example, in the monocot families Eriocaulaceae, Mayacaceae and Xyridaceae (see Baskin and Baskin, 2018), and it is now clear that the broad embryo only differentiates organs (shoot and root) after part of it is pushed to the outside of the seed (Ramasmamy et al., 1981; Corredor et al., 2015); this is also true in Hydatellaceae (Tucket et al., 2010; Friedman et al., 2012). In contrast to the mostly undifferentiated broad embryo of Eriocaulaceae, Hydatellaceae and other families, the embryo of Nymphaeales is cup-like with thick hemispherical cotyledons surrounding leaf primordia (Haines and Lye, 1975; Titova and Batygina, 1996). There is little or no embryo growth inside the seed prior to beginning of the germination process (Baskin and Baskin, 2007a, 2021). During seed germination of Nymphaeales, the base of the cotyledons elongates pushing the leaf primordia and terminal part of the hypocotyl to the outside of the seed; the distal end of the cotyledons remains inside the seed and acts as a haustorium (Okada, 1925; Haines and Lye, 1975; Povilus et al., 2015). The cup-like embryo of Nymphaeales has not been placed on Martin's (1946) family tree of seed phylogeny, and its relationship to rudimentary and linear-underdeveloped embryos is not known.

The rudimentary embryo is placed at the base of Martin's (1946) tree, and the linear embryo is placed above it. Martin's linear category includes linear-full and linear-underdeveloped embryos in both monocot and dicot families. To the right of the rudimentary embryo, along the base of his tree, we find the capitate, broad (as found in Eriocaulaceae, Mayacaceae and Xyridaceae) and lateral embryos. To look for relationships between the rudimentary embryo and other kinds of angiosperm embryos, all families in the Baskin and Baskin plant embryo database (257 families) were surveyed for presence of underdeveloped embryos: rudimentary, linear-underdeveloped and spatulate-underdeveloped. If a family with underdeveloped embryos also had other kinds of embryos, these kinds of embryos were recorded. Since monocots have some kinds of embryos not found in dicots, monocots and dicots were evaluated separately.

A total of 177 families were recorded for dicots and 7, 33, 51 and 5 have only rudimentary, linear-underdeveloped, linear-full or spatulate-underdeveloped embryos, respectively. The other 81 families in the database have a combination of kinds of embryos. The rudimentary embryo is found in 12 families that also have a linear-underdeveloped embryo but in a few or no families with other kinds of embryos (Table 3). On the other hand, although many (33) families have only a linear-underdeveloped embryo, this kind of embryo can be found in families that also have linear-full, spatulate-full or undifferentiated embryos. A few linear-underdeveloped embryos are found in families with bent, folded or investing embryos.

Of the 80 families of monocots in the database, 15, 29, 9, 7, 1 and 6 have only a linear-underdeveloped, linear-full, board, capitate, lateral and undifferentiated embryo, respectively. The other 13 families

have a combination of kinds of embryos: 5, rudimentary + linear-underdeveloped; 6, linear-underdeveloped + linear-full; and 2, linear-full + capitate. Thus, for both dicots and monocots, the rudimentary embryo is more likely to be found in families with a linear-underdeveloped embryo than in families with other kinds of embryos. The five families of monocots with both rudimentary and linear-underdeveloped embryos include the Arecaceae, Haemodoraceae, Liliaceae, Melanthiaceae and Stemonaceae (Martin, 1946).

### Rudimentary embryos and palaeohistory of seeds

Arnold (1938, 1949) concluded that in ovules of the pteridosperms and Cordaitales a rest period occurred after fertilization, which was marked by formation of a well-developed/durable integument. After the rest period, the ovule with a zygote inside it was dispersed from the plant. Later, Miller and Brown (1973) suggested that '... production of embryos before seed dispersal may have evolved as an adaptation to climatic conditions to enhance seedling survival rather than as a better way of manufacturing an embryo'. It seems reasonable that a step between ovules with only a zygote and seeds with a large well-developed embryo when they are dispersed would be seeds with a small embryo (with organs) and stored food to supply the early stages of growth.

In the history of seed plants, can we find a sequence of ovules with only a zygote, followed by seeds with small embryos and finally seeds with large well-developed embryos? In the Cycadopsida, we will consider the pteridosperms, cycads and Bennettitales. The pteridosperms (Devonian) presumably had ovules with only a zygote (Arnold, 1938, 1949). Based on the facts that (1) living cycads have a linear-underdeveloped embryo, and (2) features of gymnosperms were highly developed by the Permian (Wachtler, 2016), it is presumed that seeds of cycads (Permian) had a linear-underdeveloped embryo. Finally, seeds of the Bennettitales (Triassic) had a linear-fully developed embryo (Table 1). In the Coniferopsida, we will consider Cordaitales, Ginkgoales and Pinales. The sequence of advancement is Cordaitales (Mississippian; McLoughlin, 2020) with ovules containing only a zygote (Arnold, 1938, 1949) → Ginkgoales (Permian) with a linear-underdeveloped embryo, based on *Ginkgo biloba* (Martin, 1946) → Pinales (Coniferales) (Triassic) with linear-underdeveloped, linear-fully developed and spatulate embryos (Martin, 1946). However, Martin (1946) indicated that the shape and size of the cotyledons in gymnosperm linear-underdeveloped and spatulate embryos differed somewhat from those in angiosperms.

The presence of a small embryo in seeds of early angiosperms is consistent with small embryos in seeds of early gymnosperms. However, as noted above, a rudimentary embryo has not been found in fossil seeds of early gymnosperms. Thus, we conclude that the rudimentary embryo is an angiosperm 'invention'. If at

some point in the future the rudimentary embryo is found in seeds of an ancient gymnosperm, it seems that such a discovery would provide a good clue as to which group of ancient gymnosperms was the ancestor of angiosperms.

The fossil record indicates that seeds were small during most of the Cretaceous (Tiffney, 1984; Eriksson et al., 2000; Sims, 2012; Friis et al., 2015). For seeds from seven Late Cretaceous field-collection sites, average seed volume was 1.7 mm<sup>3</sup> (Tiffney, 1984); the size of *A. trichopoda* seeds is 3.3 mm<sup>3</sup> (Feild et al., 2004). In the early part of the Paleogene, both median seed size and the range of seed sizes increased (Tiffney, 1984; Eriksson et al., 2000; Benton et al., 2021). Furthermore, as seed size increased the rate of species diversification of angiosperms increased (Igea et al., 2017; Benton et al., 2021). Moles et al. (2005a,b) concluded that species divergence of angiosperms was more closely related to plant growth form than to other variables such as climate, latitude, net primary productivity, leaf area index and method of seed dispersal.

A factor that has not been considered in the divergences of angiosperms is the development of different kinds of embryos and the change from seeds with a large amount to endosperm at seed maturity to those with little or no endosperm at seed maturity. However, the analysis of embryo size in seed plants by Forbis et al. (2002) found that the underdeveloped embryo is primitive and that the E:S ratio has increased in both gymnosperms and angiosperms. Using data from Moles et al. (2005a) on seed mass for various orders of angiosperms, we can obtain a preliminary glimpse of the possible magnitude of change in seed mass as embryo size increased. The endospermous seeds in the orders Amborellales, Apiales, Aquifoliales, Austrobaileyales, Liliales, Piperales, Ranunculales and Trochodendrales have small either rudimentary and/or linear-underdeveloped embryos (Martin, 1946) and a mean seed mass of 6.69 mg (Moles et al., 2005a). However, the eight orders of fabids (Celastrales, Cucurbitales, Fabales, Fagales, Oxalidales, Malpighiales, Rosales and Zygophyllales) with little or no endosperm and large linear-full developed, spatulate, bent, investing and/or folding embryos (Martin, 1946) have a mean seed mass of 38.4 mg (Moles et al., 2005a). Thus, overall, it seems that seeds with small, underdeveloped embryos are smaller (i.e. lower volume and mass) than those with large, fully developed embryos. Do the small seeds of the early angiosperms mean that plants produced a relatively large number of seeds that may have enhanced colonization of new habitats (e.g. Leishman, 2001)?

### Rudimentary embryos and diversification of angiosperm embryos

Plant taxonomists have long considered angiosperm plant families whose seeds have an underdeveloped embryo and a large amount of endosperm to more primitive than those whose seeds have a fully developed embryo and little or no endosperm (e.g. Bessey, 1915). Fossil seeds from Early Cretaceous deposits in eastern North America and Portugal had much endosperm and tiny embryos, including rudimentary embryos in *Canrightiopsis* and linear-underdeveloped embryos in *Anacostia* and *Appomattoxia* (Friis et al., 2015). As mentioned above, seeds of the most-basal extant angiosperm *A. trichopoda* have a rudimentary embryo (Tobe et al., 2000), which is physiologically dormant, that is, the seeds have morphophysiological dormancy (Fogliani et al., 2017). In an investigation of the dormant state transitions for 14,000 taxa in 318 families, Willis et al. (2014) concluded that

morphophysiological dormancy was the ‘most likely ancestral state of seed plants’. With all these facts as background information, we see no reason to dispute Martin’s (1946) placement of the rudimentary embryo at the base of his family tree of seed phylogeny.

According to Martin (1946), the rudimentary embryo has served as the base or starting point for the diversification of embryos in angiosperms. Rudimentary and linear embryos occur together in at least 29 angiosperm families (Baskin and Baskin, embryo database). This association of rudimentary and linear embryos is not surprising, since Martin (1946) concluded that the progression of development of the different kinds of embryos was rudimentary → linear → spatulate → bent → folded, or it was from rudimentary → linear → spatulate → investing. The occurrence of rudimentary and linear embryos in the same families suggests a strong relationship between the two kinds of embryos. In addition, linear and spatulate embryos in the same families, for example, Boraginaceae, Caprifoliaceae, Hypericaceae, Loganiaceae, Plantaginaceae, Rubiaceae and Solanaceae, suggest a relationship between these two kinds of embryos. Furthermore, a relationship between spatulate and bent, investing and folded embryos is suggested by their occurrence in the same families, for example, Acanthaceae, Burseraceae, Fabaceae, Malpighiaceae, Phyllanthaceae and Rosaceae (Martin, 1946).

Although rudimentary embryos occur in the most-basal extant angiosperm, they are not restricted to the basal angiosperms. Rudimentary embryos are known to occur in 38 families and 25 orders of angiosperms (Martin, 1946; Baskin and Baskin, embryo database), and they occur in woody as well as in herbaceous perennials and annuals (Baskin and Baskin, 2014). Rudimentary embryos occur in seeds of the magnollids, commelinids, lamiids and campanulids and various other clades but not those in the fabids and malvids. Thus, rudimentary embryos are present in seeds of many families and orders of angiosperms and in species with various life forms growing in a diversity of habitats. The relatively wide occurrence of rudimentary embryos throughout the angiosperms suggests that a small embryo in an endospermous seed is not a detriment for lineage survival.

For both gymnosperms and angiosperms, we can think of ecological situations where the length of time for successful seed development is limited, for example, onset of drought and closure of the canopy in deciduous forests in spring. The production of seeds with an underdeveloped embryo with much stored food in the female gametophyte of gymnosperms or endosperm of angiosperms would permit relatively rapid seed development and maturation. Furthermore, the embryo could continue to grow after seed dispersal, using the stored food reserves in the seed. In addition, the timing of onset of favourable environmental conditions for plant growth, such as temperature and soil moisture, could help time growth of the embryo and thus germination to a season when conditions are favourable for seedling survival and growth (Baskin and Baskin, 2014).

Many examples of species with rapid seed development and underdeveloped embryos are found in the deciduous forests of eastern North America. Of the 127 species of herbs (mostly perennials) growing on the forest floor (see Braun, 1950), 59 (46.5%) of them produce seeds with an underdeveloped embryo, either rudimentary or linear-underdeveloped (Baskin and Baskin, 2014). These species flower and set seeds in early spring during the short period of high photosynthetic irradiance on the forest floor and warm temperatures prior to leaf emergence and canopy closure. Furthermore, seeds of most of these species have morphophysiological dormancy, that is, the underdeveloped embryo



has physiological dormancy, which is broken during the summer and/or winter following seed dispersal (Baskin and Baskin, 2014). Nonogaki et al. (2022) found a delay of a germination gene in *A. trichopoda*, which indicates an early association between the rudimentary embryo and physiological dormancy.

### Advantages of seed formation in angiosperms versus gymnosperms

Many changes have occurred in angiosperms, including increased rate (speed) of seed formation, simplification of the female gametophyte, development of a new tissue (endosperm) for food storage for the embryo and time when it is formed (after fertilization/zygote formation) and elimination of the production of multiple embryos from each zygote, that enhance seed production compared to gymnosperms.

A significant decrease in the time from pollen dispersal until seed dispersal has long been thought to have played a role in the origin and diversification of angiosperms (see Williams, 2012a). Two important aspects of the increase in speed of angiosperm seed formation are an increase in the speed of pollen germination and of pollen tube growth compared to gymnosperms (Williams, 2008, 2012a). After gymnosperm pollen is in the pollen chamber of the ovule, germination does not occur for hours or days (Gnetophyta), a week (conifers and *Ginkgo*) or several months (cycads), and this along with slow pollen tube growth results in a delay of fertilization of the egg for 10 h to more than 1 year, depending on the species (Fernando et al., 2010). However, angiosperm pollen on the stigma germinates quickly compared to pollen of gymnosperms. In a survey of pollen germination after deposition on the stigma in 131 species of angiosperms in 65 families, Williams (2012b) found that germination occurred within about 1 min to >60 h, depending on the species. Interestingly, the time intervals between pollination and fertilization (i.e. presence of sperm in female gametophyte) for *A. trichopoda*, *Austrobaileya scandens* and *Nuphar sepala* are 12, 13 and 24 h, respectively (Williams, 2008, 2009). *In vitro* pollen tube growth rates of gymnosperms are 5–20  $\mu\text{m h}^{-1}$ , and those of angiosperms are 10 to >20,000  $\mu\text{m h}^{-1}$ , with monocots generally having higher rates than eudicots (Williams, 2012a).

Although many living (and fossil) gymnosperms have (had) relatively small ovules at the time of pollination, gymnosperm ovules are larger than angiosperm ovules at the time of fertilization (Leslie and Boyce, 2012). Gymnosperm ovules increase in size by the time of fertilization because a large female gametophyte generally is required for egg formation. On the other hand, the angiosperm ovule at the time of fertilization is small and consists of only a few cells. In gymnosperms, much food has been stored in cells of the female gametophyte by the time fertilization occurs, but in angiosperms, endosperm formation is not initiated until double fertilization has occurred (Baroux et al., 2002; Leslie and Boyce, 2012). Thus, if fertilization does not occur an aborted ovule represents a greater loss ('cost') to a gymnosperm than to an angiosperm plant.

Although seeds with more than one embryo do occur in angiosperms (polyembryony), in general the fertilized egg in an angiosperm female gametophyte gives rise to a single embryo. In gymnosperms, however, there is a phase in embryogenesis during which multiple embryos derived from the same zygote are growing and presumably competing for food stored in the female gametophyte (Buchholz, 1918, 1939; Johansen, 1950; Foster and Gifford, 1959). For example, in *Pinus*, the zygote gives rise to

four cells, each of which becomes an embryo with a long, often twisted, suspensor. Furthermore, at the base of each suspensor, opposite the end to which the embryo is attached, a (rosette) cell is initiated, and each rosette cell has the potential to develop into an embryo. Thus, eight embryos can be produced from a single zygote. Rosette embryos mostly do not develop and quickly die, but some with elongated cells that look like a suspensor have been observed (Buchholz, 1918). In general, only one embryo survives, and the terminal embryo usually is the successful one; sometimes, the second rather than the terminal embryo survives. Programmed cell death has been shown to be an important factor in the death of subordinate embryos in *Pinus* (Vuosku et al., 2009).

### Concluding thoughts

From our review, we conclude that underdeveloped embryos occur only in seed plants. The rudimentary embryo originated in the angiosperms, and linear embryos are closely related to it. Rudimentary embryos in dicots and monocots differ in development/morphology, but their size is the same. The diversification of angiosperm embryos from the rudimentary embryo contributed to the success of angiosperms on earth.

It seems reasonable that the chances of offspring survival are increased if the dispersal unit contains an embryo *versus* only a zygote. Seeds of the oldest extant gymnosperms (Cycadales and Ginkgoales) contain a small linear-underdeveloped embryo, and the most-basal extant angiosperm (*Amborella*) has a small rudimentary embryo. In the case of gymnosperms, embryo diversification has resulted in the formation of linear-fully developed and somewhat spatulate embryos. However, the rudimentary embryo of angiosperms has directly/indirectly given rise to 13 new kinds of embryos in angiosperms (Martin, 1946; Baskin and Baskin, 2007b, 2018), that is, counting the linear-underdeveloped and spatulate embryos of angiosperms that differ somewhat from these two types of embryos found in seeds of gymnosperms. Diversification of embryos, along with increased embryo and seed size, are a part of the syndrome of changes in angiosperms that have increased the speed and efficiency of seed production compared to gymnosperms. Thus, efficient seed production may be one of the reasons for the eventual dominance of angiosperms over gymnosperms (Condamine et al., 2020). Finally, we fully agree with Martin's (1946) placement of the rudimentary embryo as the base of his family tree of seed phylogeny of angiosperms.

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