

VIEWPOINT

Evolution of the coniferous seed scale

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- **Background** The Florin model is the commonly accepted theory of coniferous seed scale evolution. It describes the derivation of extant seed scale morphology from the morphology of fossil conifers via the reduction of complex to simple axillary structures. In this framework the seed scale is composed of a reduced lateral shoot with fertile and sterile appendages which are interpreted as leaf homologues.
- **Scope** The Florin model has three crucial problems that we address here: (1) the original derivation series does not take the ontogeny of extant conifers into account, (2) it cannot explain the morphology of all extant conifers and (3) Taxaceae were originally excluded. Examination of seed cones of extant conifers shows that ovules occur in three different positions in the cone: in an axillary position, replacing a leaf or terminating the cone axis. By interpreting the fertile appendage or seed-bearing structure as a leaf, not all positions are possible. The exclusion of Taxaceae from conifers is in stark contrast to recent molecular phylogenetic studies, which include Taxaceae in conifers as sister to Cupressaceae. Therefore, the Florin model does not offer an adequate explanation for taxaceous morphology.
- **Conclusion** We conclude that the seed-bearing structure of conifers cannot be interpreted as homologous to a leaf. In the interpretation we present here, the seed-bearing structure is the modified funiculus of the ovule, multiples of which laterally fuse to form the seed scale. The seed scales of all extant conifers can be derived from a *Cunninghamia*-like morphology via fusion and reduction of individual funiculi.

Key words: Conifer, Florin model, seed-cone morphology, character evolution.

INTRODUCTION

The interpretation of the coniferous seed cone and seed scale by Rudolf Florin (1931, 1951) and the model named after him are still the basis for interpreting coniferous seed cones today. In the Florin model the seed scale of extant and fossil conifers comprises up to three fused parts, i.e. a stalked ovule, sterile appendages and a rudimentary axis. In the time since its inception the Florin model has been criticized and revised by several authors. For example, Schweitzer (1963) criticized the presence of stalked ovules and presented a re-interpretation without them, whereas Clement-Westerhof (1988) revised the attachment of the ovule to the fertile appendage. However, the core of the Florin model, a continued fusion of the constituent parts and the presence of a rudimentary lateral axis and sporophylls, has always remained despite revisions.

In this viewpoint we present a new interpretation of the coniferous seed scale that challenges these core principles of the Florin model. To achieve this, we incorporate insights gained from palaeobotany, and ontogenetic and phylogenetic studies into a new model of conifer seed scale evolution.

In the past the term seed scale has been used for a variety of parts in the seed cone. To avoid confusion and misinterpretation we will use the following terms for structures (Supplementary Data Fig. S1):

- **Cone unit:** repeating structure on a coniferous seed cone comprising a single bract and all axillary structures
- **Seed scale:** a single or multiple structures axillary to a bract, the entirety of all seed-bearing structures, which may be fused to various degrees
- **Seed-bearing structure:** a single structure supporting the ovule/seed, part of the seed scale, which may be conspicuous or reduced to only an ovule

THE FLORIN MODEL AND ITS PROBLEMS

In our view the Florin model deals with two separate parts of the evolution of the coniferous seed scale: (1) the morphological interpretation of the constituent parts of the seed scale, and (2) the mechanisms by which those parts evolved from the Carboniferous onwards (Florin, 1951, 1954). Morphologically the coniferous seed scale is currently interpreted as a lateral short shoot in the axil of the bract. This short shoot can have multiple appendages that are currently widely interpreted as leaves and sporophylls (Clement-Westerhof, 1988; Rothwell *et al.*, 2011). In extant conifers all appendages and the short shoot are fused together or reduced so that only the sporophylls are visible. For example, the seed scale of Pinaceae in the Florin

TEXT BOX

In our model of seed scale evolution, the seed scale of crown conifers evolved from multiple free ovule + seed-bearing structure units like those found in *Cunninghamia* and Permian Voltzian Voltziales, e.g. *Pseudovoltzia*. We see the ovule + seed-bearing structure unit as the ovule + funiculus. The unit inserts directly in the axil of the bract without a lateral short shoot, instead of a bract, or terminally on the cone axis. Together, ovule + funiculus represent a single fertile telome, an undifferentiated axial structure that is neither shoot nor leaf. The morphology of extant conifers can be derived by modification of the funiculus from a lobe-like ancestral form, e.g. as found in *Cunninghamia* and Permian Voltzian Voltziales. The modifications include, for example, lateral fusion of the recurved funicle to form a continuous scale (Pinaceae), reduction of the number of ovule + funiculus units and envelopment of the ovule by the aril-like funiculus (Podocarpaceae). A size reduction of the funiculus with or without a shift of the ovule onto the cone scale leads to complete lack of a scale-like seed scale (Cupressaceae s.s.). Sterile ovules may form scale-like units which are also termed the seed scale (*Cryptomeria*, *Taxodium*, *Glyptostrobus*), but these are not homologous to the seed scales addressed here.

model comprises at least two sporophylls (one for each ovule) and a short shoot, which are completely fused together to form the typical scale-like form (Mundry, 2000). The other extreme is the cone units of, for example, *Cupressus* L., in which the short shoot is reduced so drastically that only the individual ovules remain visible (Jagel and Dörken, 2015). From a mechanistic perspective our current understanding of seed scale evolution has not changed since the descriptions by Florin. He inferred that the seed scale of extant conifers can be derived from the seed scale of Palaeozoic conifers via fusion and reduction (Florin, 1951). Although the specifics of fossils and possible derivation series have been debated, the mechanism of fusion and reduction from the complex seed scale of Palaeozoic conifers to the simple seed scale of extant conifers has never been doubted (Clement-Westerhof, 1988; Meyen, 1997; Rothwell *et al.*, 2011; Escapa *et al.*, 2013; Leslie *et al.*, 2018).

In our view the Florin model has three problems. The first arises from the genus *Cryptomeria* (Thunb. ex L. f.) D. Don, a cupressaceous conifer. In his derivation series from Palaeozoic to extant conifers, Florin (1951) interpreted the morphology of the seed scale of *Cryptomeria* as the most basal one in conifers. He inferred that the ‘teeth’ that close the cone of *Cryptomeria* are the seed-bearing structure and are homologous to the appendages (leaf homologues) found in the seed scale of the Permian conifer *Pseudovoltzia* Florin and the seed-bearing structures of all other extant conifers (Florin, 1951). Ontogenetic studies of coniferous seed scales have shown that in all examined taxa with a conspicuous seed-bearing structure, the ovule develops after and on the former (e.g. Takaso and Tomlinson, 1991; Tomlinson, 1992; Herting and Stützel, 2020). However, the development of *Cryptomerias*’ ‘teeth’ only starts after the ovules are well developed, and the ‘teeth’ are initiated abaxial to ovules, as seen from the cone axis (Farjon and

Garcia, 2003). The position and time of initiation of the ‘teeth’ suggest that they are best interpreted as a sterile second row of ovules. Additionally, seed scales with multiple rows of ovules can be found in taxa that are both more basal and more derived within Cupressaceae s.l., such as *Sequoia* (Luer) (Luer, 1992) and *Cupressus* (Jagel and Dörken, 2015), respectively. Thus, the ‘teeth’ of Taxodiaceae [*Cryptomeria*, *Glyptostrobus* (Stanton ex D. Don) K. Koch, *Taxodium* L. C. Rich.] are not homologous to the seed-bearing structures of the other extant conifers, and the derivation series originally proposed by Florin (1951) is not suitable to homologize the seed scales of fossil and extant conifers.

The second problem of the Florin model is that it cannot explain the morphology of all extant conifer seed scales. The most prominent example are the cones of *Juniperus* L. Ontogenetic and morphological studies of *Juniperus* cones show that the ovules can occur in three principal positions in the cone: (1) axillary to a bract, (2) continuing cone phyllotaxis instead of a bract, and (3) terminal on the cone axis (Schulz *et al.*, 2003). Additionally, ovules in all three positions may occur mixed within the same cone. If mixed, those in the axil of a bract are basal within the cone to those that take the position of a cone scale. Schulz *et al.* (2003) suggested a terminal brachyblast (short shoot) consisting of lateral ovules and also or exclusively an ovule terminating the cone axis. Most importantly, the terminal position of an ovule is not reconcilable with the basic assumption in the Florin model that seed-bearing structures of conifers are sporophylls, because a leaf can never terminate an axis (Marilau, 1890). Therefore, not all existing seed cone morphologies can be explained within the framework of the Florin model.

The third problem for the Florin model is the family Taxaceae. Taxaceae are problematic for the Florin model for two reasons. First, similar to *Juniperus* the ovules of taxaceous taxa are found in a terminal position (Harris, 1976; Rövekamp and Stützel, 1999). Second, in the presentation of his model Florin (1951) himself noted that some Taxaceae do not fit within it. Consequently, Florin (1954) separated *Cephalotaxus* as a family of its own, excluded taxads from Coniferales and placed them in their own order Taxales. This separation has been disproven and Taxaceae have been included in the conifers since at least the molecular phylogenetic studies of the past 20 years (e.g. Stefanovic *et al.*, 1998; Leslie *et al.*, 2012). This means that the model used for describing conifer seed scale evolution must also explain Taxaceae morphology. Leslie *et al.* (2018) extended the Florin model by proposing a disassociation between the ovule and the supporting bract, and shift of the ovule into a terminal position. However, the underlying problem is not resolved because, as stated above, in the framework of the Florin model the ovule is situated on a sporophyll. Thus, even if the sporophyll is inconspicuous, it can never be found in terminal position as a leaf homologue.

In summary, ontogenetic and phylogenetic studies have revealed that the Florin model cannot explain the diversity of extant conifer seed scale morphology. The seed-bearing structure of extant conifers must fulfil the following criteria: (1) may take axillary, leaf or terminal position; (2) and interpretation should be applicable over the course of the whole ontogeny.

THE NEW INTERPRETATION

Keeping the aforementioned criteria in mind, we interpret the coniferous seed-bearing structure as the ovule and its stalk – the funiculus (see text box). Consequently, the seed scale is either just the funiculus, when there is only one ovule (e.g. *Araucaria* Juss.), or the fusion of at least as many funiculi as there are ovules (e.g. *Pinus* L.). The ovule is a stalked nucellus mantled by the integument, with the nucellus being homologous to the megasporangium of ferns. Thus, the ovule is essentially a stalked sporangium, as found in ferns or taxa that pre-date the development of the cormus, i.e. the plant body is differentiated in root, shoot and leaves. In the telome theory, each sporangium is formed by a single fertile telome, an undifferentiated axial structure (Zimmermann, 1930). Reproductive structures are exposed to environmental selection pressure only a rather short phase of the life cycle. Additionally, their precise function is essential for the survival of the species and these structures tend to be very conservative during evolution. Therefore, we interpret the seed-bearing structure, i.e. ovule and funiculus, as a single fertile telome. Accordingly, the seed scale, which is formed by one to many seed-bearing structures, comprises one to many fertile telomes. Being neither shoot nor leaf, it is unrestricted by the principles of phyllotaxis, and may occur in all positions outlined above. This means that in the most common case of an axillary position of the seed-bearing structures, they insert directly axillary without a lateral short shoot.

In contrast to the Florin model in its current iteration, our interpretation of the seed-bearing structure meets both criteria set above. First, the retention of its telome characteristics allows the funiculus to occur in all observable positions of the ovule in extant conifers, even if they occur mixed [e.g. *Juniperus phoenicia* L. (Jagel, 2001)]. Second, ontogenetically the funiculus always precedes the ovule. It may be very short and grow in length only later, but as the part attaching the ovule to the plant it is present earlier than all structures characterizing the ovule (e.g. Tomlinson, 1992; Farjon and Garcia, 2003; Herting and Stützel, 2020).

In our 2020 paper on the ontogeny of the seed scale of *Araucaria araucana* (Molina) K.Koch, we briefly showed that the seed scales of Araucariaceae, Pinaceae, Podocarpaceae and Sciadopityaceae can be derived from a *Cunninghamia* R.Br. ex A.Rich.-like morphology if the funiculus is assumed to be the seed-bearing structure (Fig. 1) (Herting and Stützel, 2020). Note in the following that we shorten terms such as *Cunninghamia*-like morphology to just *Cunninghamia* for readability purposes. We use extant taxa for a comparative analysis of the ontogeny and morphology of the cone units. The outcome is then used to infer a possible development of structures from the fossil record. In other words, the morphology and ontogeny of extant taxa used in our derivation series serves as a stand-in for possible fossil forms. Therefore, the order of taxa in our derivation series is not representative of our understanding of conifer phylogeny. We consider the morphology of the cone unit of *Cunninghamia*, a phylogenetically derived taxon (e.g. Spencer *et al.*, 2015; Leslie *et al.*, 2018), as the most basal in extant conifers. *Cunninghamia* and many Permian Voltzian Voltziales (e.g. Florin, 1951; Schweitzer, 1963) share crucial morphological features of the cone unit: (1) a one to one relationship of ovules and seed-bearing structures, (2) unfused seed-bearing

structures and (3) inverted seeds. Therefore, we chose the morphology of *Cunninghamia* as the basal morphology in our analyses. This can be risky, however, because heterobathmic effects should be considered. We agree with Spencer *et al.* (2015) that the ontogeny is crucial information for ascertaining homology. Thus, we use extant taxa instead of fossils because this approach allows us to incorporate the ontogeny of the cone units into the analyses. Ontogenetic data is rarely available in the fossil record, especially concerning the time frame in the ontogeny we focus on, which is from bud break to pollination. Ontogenetic stages found in the fossil record are usually from later stages of development, for example development of the seed in *Manifera talaris* Looy et Stevenson (Looy and Stevenson 2014). We use ontogenetic data because they have seldom been used in studies presenting derivation series, which focused on deriving extant from fossil taxa (e.g. Florin, 1951; Rothwell *et al.*, 2011).

The seed scale of Pinaceae may be derived from a *Cunninghamia*-like morphology through *Sciadopitys* Sieb. & Zucc., via lateral fusion of the funiculi and a heterochronic shift ('Zeitkorrelationsänderung' *sensu* Ihlenfeldt, 1971), resulting eventually in the lateral congenital fusion of the funiculi (Fig. 1A) (Herting and Stützel, 2020). On the other hand, Araucariaceae are derived from *Cunninghamia* through Podocarpaceae, via reduction of the number of ovules per cone unit and the envelopment of the ovule by an adaxial outgrowth of the funiculus (Fig. 1C) (Herting and Stützel, 2020).

Here we expand on that derivation series and show that the coniferous taxa without a conspicuous seed scale can be derived from *Cunninghamia*. These taxa are most of Cupressaceae *s.l.* and Taxaceae. *Cunninghamia* has one lobe-like modified funiculus per ovule and the ovules are turned inwards after pollination (Farjon and Garcia, 2003). These lobe-like modified funiculi are successively reduced until they are no longer detectable in taxa such as *Cupressus*, where the ovules emerge directly in the axil of the bract and are not turned in after pollination (Fig. 1B). The most extreme reduction can be observed in the cones of *Juniperus squamata* Buch.-Ham. ex D.Don, which at maturity comprise a single whorl of bracts and a single ovule terminal on the cone axis (Jagel and Dörken, 2015). An intermediate form is found in *Taiwania* Hayata; here the funiculi are reduced compared to *Cunninghamia*, but are still observable (Farjon and Garcia, 2003). The reduction of the conspicuous modified funiculus can be explained by a shift of timing in the ontogenetic sequence. The emergence of the funiculus and the ovule on it are moved closer together until they become indistinguishable. This is a prime example of a 'basal abbreviation of the ontogenetic sequence' ('basale ontogenetische Abbreviation' *sensu* Ihlenfeldt, 1971), which means that steps early in the ontogeny are skipped.

In Taxaceae the ovule emerges terminally on a second- or third-order branch and is preceded by one or two whorls of leaves (Röwekamp and Stützel, 1999). Thus, we consider this second- or third-order branch with the terminal ovule to be the cone of Taxaceae and use it for comparison with conifer cones. The cone morphology of Taxaceae is very similar to that of some species of *Juniperus* (e.g. *J. squamata*), which comprise a terminal ovule and, in *J. squamata*, one whorl of bracts. Therefore, the fertile structure of Taxaceae may be derived from

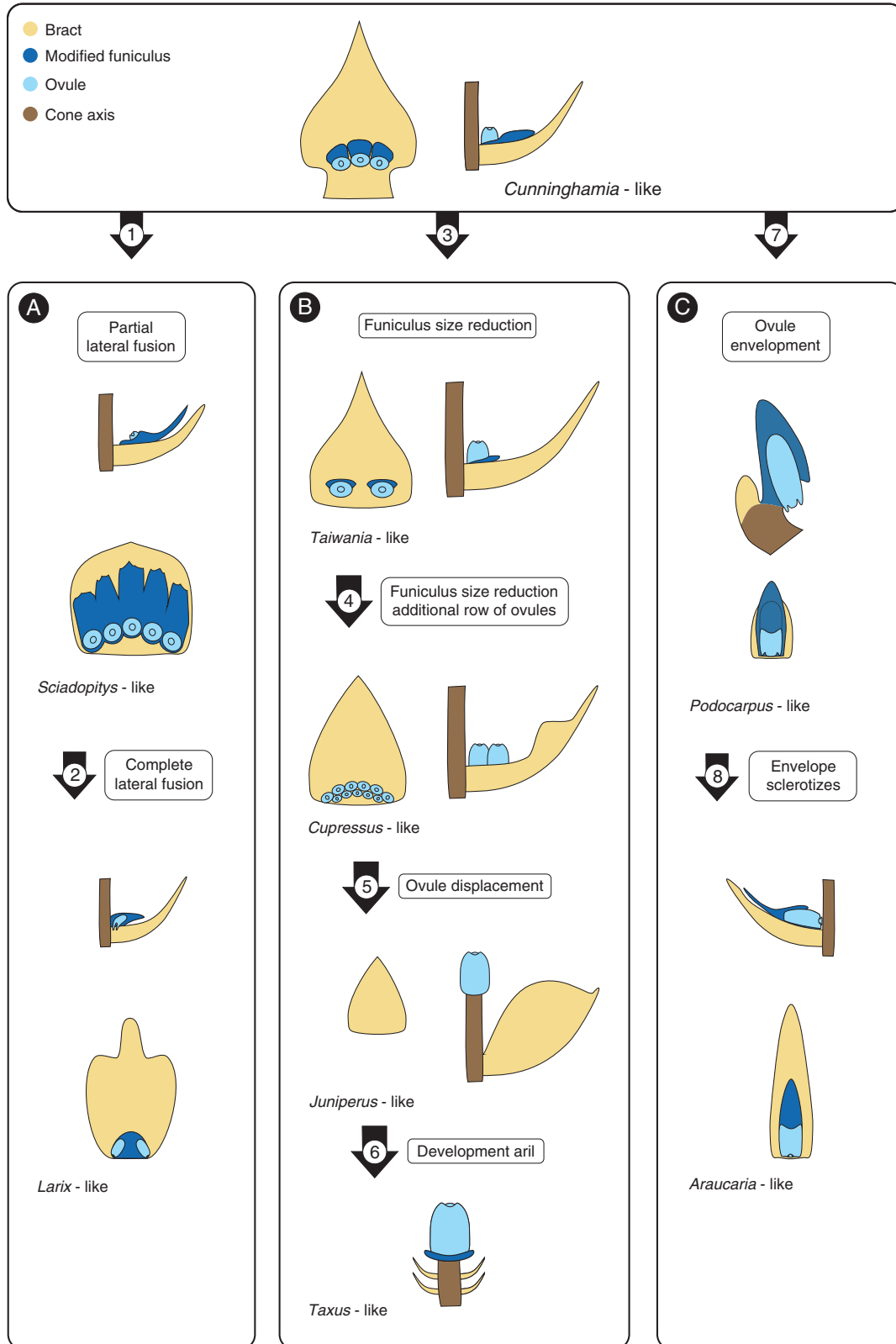


FIG. 1. Expanded derivation series of extant conifer seed scale morphology. The morphology of all extant conifers can be derived from a *Cunninghamia*-like form in one of the three pathways shown. The Pinaceae-like form (represented here by *Larix*) (A), with a continuous scale supporting more than one ovule, can be derived via: first the postgenital partly fusion of funiculi (1) to form a *Sciadopitys*-like scale; and second the congenital complete lateral fusion of funiculi to form a continuous scale (2). The Taxaceae-like form (represented here by *Taxus*) (B), with a single terminal ovule, can be derived via size reduction of the funiculus first to a ridge abaxial of the ovule (3) as in *Taiwania*; second to inconspicuousness (4), in a *Cupressus*-like form; thirdly, via the reduction to a single ovule and the

Cunninghamia similarly to *Juniperus* (Fig. 1B). The strongly reduced cones with terminal ovules of Taxaceae and *Juniperus* are an example of parallel evolution in conifers. The aril of Taxaceae is a further indication of the presence of the funiculus because the aril is defined as an outgrowth of the funiculus (Marilaun, 1890). This definition leads to an interesting observation concerning Podocarpaceae (except *Phyllocladus* L.C.Rich & A.Rich) and Araucariaceae. In both families an adaxial outgrowth distal to the ovule envelops or envelops and turns the ovule; the only difference to the aril of Taxaceae is the sequence of emergence in the ontogeny and it appears ‘one-sided’ due to its position (Tomlinson, 1992; Herting and Stützel, 2020). In Podocarpaceae (except *Phyllocladus*) and Araucariaceae, the outgrowth emerges before pollination, whereas in Taxaceae and *Phyllocladus* the aril emerges after pollination (Tomlinson *et al.*, 1989; Röwekamp and Stützel, 1999). This again can be explained by a heterochronic shift during the ontogeny; thus, we conclude that the aril of Taxaceae and *Phyllocladus* and the enveloping tissue in Podocarpaceae and Araucariaceae evolved in parallel from the funiculus.

In this new framework, we expect certain trait combinations to occur in crown conifers, while some other combinations should not occur. As outlined above, the funiculus is functionally linked to the turning of the ovule. Thus, we expect that a conspicuous funiculus is always paired with an inward facing ovule, e.g. in Pinaceae or Podocarpaceae, which is also suggested by ancestral state reconstructions of crown conifers (Herting *et al.*, 2020). Consequently, an inconspicuous funiculus should always occur together with an outward facing ovule, e.g. in Cupressaceae *s.s.* Other combinations, such as a conspicuous funiculus with an outward-facing ovule, should not occur in this framework of interpretation.

In summary, we have shown that the seed-bearing structure is best interpreted as a modified funiculus. Hence, the seed scale is best interpreted as the fusion product of at least as many funiculi as there are ovules. Based on this interpretation, the seed scales of all extant conifers can be derived from a morphology similar to that of *Cunninghamia* and that the aril of Taxaceae and the enveloping tissues of podocarps and Araucariaceae are homologous. The structures termed seed scale in *Cryptomeria*, *Taxodium* and *Glyptostrobus* are not homologous to the seed scale of other conifers discussed here.

THE MODIFIED FUNICULUS

During the ontogeny of taxa with conspicuous funiculi, the mechanisms of modification of the funiculi are revealed. A notable difference in such taxa is the position relative to the cone axis of the ovule on its funiculus. Although the ovule is always adaxially attached, the offset from the cone axis varies, e.g. directly axillary in Pinaceae, or recaulescently shifted on the bract in *Cunninghamia* (Mundry, 2000; Farjon and Garcia, 2003). Additionally, a

conspicuous modified funiculus always occurs together with ovules or seeds that are turned inwards (Tomlinson, 1992; Mundry, 2000; Jagel and Dörken, 2014; Herting *et al.*, 2020; Herting and Stützel, 2020). A factor in the modification of the funiculus is the available space in the bud, especially in taxa with cones comprising many cone units. The growth restriction enforced by this confined space results in friction between emerging ovules and the superadjacent bracts (Fig. 2B). Continued intercalary growth of the bracts then leads to turning over of the ovule and elongation of the funiculus into a scale-like form (Fig. 2C). The influence of spatial constraint within the bud on the morphology of emerging organs has been shown for angiosperm leaves, e.g. *Acer pseudoplatanus* (Kobayashi *et al.*, 1998; Couturier *et al.*, 2009, 2011, 2012; Edwards *et al.*, 2016). Couturier *et al.* (2011), in particular, show in their ‘kirigami theory’ that the shape of leaves is determined by packing in the bud and contact between successive leaves. A similar influence of friction can be observed on proximal leaves of the inflorescence of *Drimys maritima* (L.) Stearn; through friction with the bulb during inflorescence emergence the proximal leaves are distinctly shaped like an upward pointing hook, while leaves that develop after emergence are linear to lanceolate shaped, with intermediate forms between (Fig. 3). This comparison is not intended to infer homology between the funiculus of conifers and the leaves, but to illustrate that friction within buds can influence the morphology of the emerging plant organ. Depending on when the cone axis extends, breaking contact between the ovule and the superadjacent bract, the ovule is either facing outwards or inwards during pollination. The resulting gap between the bracts must subsequently be closed to protect the developing seed, and in some conifers this is done by an enlarging and sclerotizing funiculus (e.g. Pinaceae) or a thickening sclerotizing bract (e.g. *Cunninghamia*) (Figs. 2A, B). If the funiculus remains short, closure of the cone after pollination may be achieved by a ventral thickening or bulge of the cone scale (*Cupressus*, *Sequoiadendron* J.Buchholz). In the latter case the micropyle may be directed to the cone axis (*Sequoiadendron*) or to the periphery, depending on whether the intercalary growth of the cone scale takes place basal (*Sequoiadendron*) or distal to the insertion of the funiculi. This is an example of the same function being performed by different morphological structures. Another example is the turning over of the ovule in Podocarpaceae. Here the ovule is turned by an outgrowth of the funiculus, not by friction within the bud. The funicular outgrowth subsequently envelops the developing ovule and ensures protection of the seed during endozoochorous dispersal (Tomlinson, 1992). These examples show that the morphology of the funiculus is highly variable and that its modifications are tightly linked either to pollination or to seed dispersal. The disparity observed between the seed cones and the modified funiculi probably stems from multiple functional demands on a seed cone (summarized in Leslie and Losada, 2019).

displacement of this ovule to the apex of the cone axis, as found in some species of *Juniperus* (5); and lastly, through the development of an aril and size reduction of the bract (6). The Araucariaceae-like form (represented here by *Araucaria*) (C), with a scale enveloping a single ovule, can be derived via: first the reduction of the number of ovules to one per cone unit and envelopment of that ovule by its funiculus (7), resembling a *Podocarpus*-like morphology; and second the enveloping tissue becoming sclerenchymatic (8). Yellow: bract; light blue: ovule; dark blue: funiculus and outgrowths of the funiculus; brown: cone axis. Figure expanded from Herting and Stützel (2020).

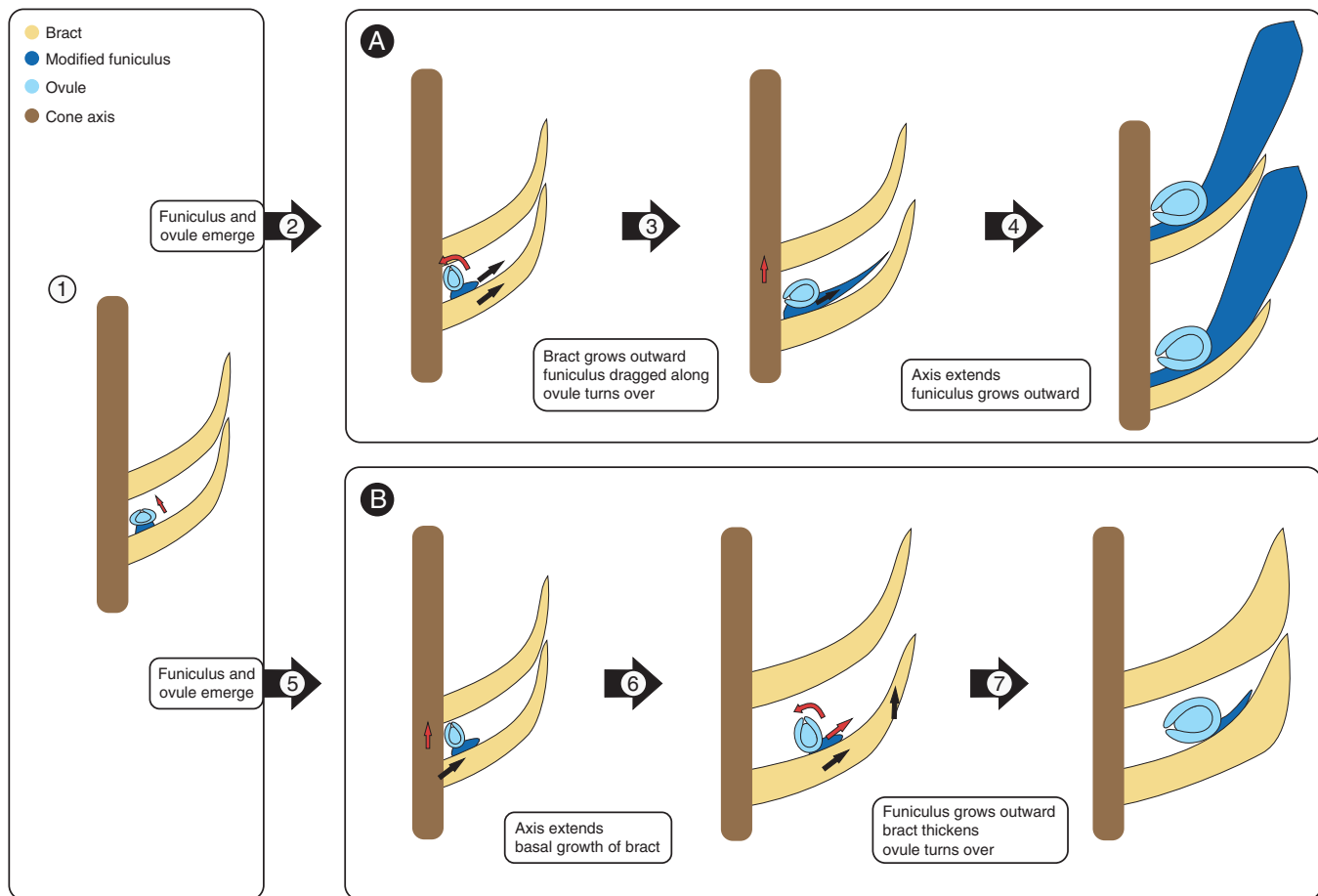


FIG. 2. Possible ways of modification of the funiculus in taxa with a morphology like Pinaceae (A) and *Cunninghamia* (B). In both cases the ovule and the funiculus emerge and grow upwards towards the next bract until the ovule hits the next bract (1, red arrow). In the Pinaceae-like morphology (A) growth in the part of the bract distal from the funiculus drags along the funiculus extending it towards the tip of the bract (2, black arrows). The funiculus is dragged along by friction and the ovule is turned by friction with the next bract (2, red arrow). After the bud breaks, the cone axis extends for pollination (3, red arrow) and the funiculus expands into the opening space (3, black arrow). The funiculus then expands, exceeding the bract and closing the cone by thickening and sclerotizing (4). In the *Cunninghamia*-like morphology (B), the ovule and funiculus are moved towards the tip of the bract by growth of the bract basal from the funiculus (5, black arrow). Additionally, the cone opens via elongation of the cone axis (5, red arrow). The opening space is closed after pollination by thickening and elongation of the bract (6, black arrows). The elongation additionally repositions the ovule and funiculus distally onto the bract. The funiculus extends slightly and the ovule turned via this growth and friction with the next bract (6, red arrows). As a result, the cone is closed by the bracts and the modified funiculus remains comparatively small (7). Yellow: bract; light blue: ovule; dark blue: funiculus and outgrowths of the funiculus; brown: cone axis.

IMPACT OF THE INTERPRETATION

Early-divergent fossil conifers are usually split into Walchian Voltziales and Voltzian Voltziales (Taylor *et al.*, 2009) (Supplementary Data Fig. S2). The former occur exclusively in the Palaeozoic, whereas the latter have been described from the Permian to the Cretaceous. According to the Florin model the seed scale of Voltzian Voltziales comprises an axillary dwarf shoot with fertile and sterile leafy appendages. However, in phylogenetic reconstructions, Voltzian Voltziales and extant conifers form a clade (Rothwell *et al.*, 2005; Herrera *et al.*, 2020). Thus, it is necessary to re-investigate whether the inference of an axillary dwarf shoot is necessary to explain the morphology of Voltzian Voltziales. Voltzian Voltziales and extant conifers share the adaxial (relative to the cone axis) and subterminal attachment of the ovule on the seed-bearing structure. Additionally, there are always at least as many appendages as ovules in Voltzian Voltziales, similar to the one-to-one of ovule to funiculus in *Cunninghamia* (Schweitzer, 1963; Looy and

Stevenson, 2014; Herrera *et al.*, 2015). We infer that the fertile appendages of Voltzian Voltziales are the funiculi of the ovules and are homologous to the funiculi of extant conifers. Thus, the seed-bearing structure of Voltzian Voltziales and extant conifers is only the funiculus. Similar to extant conifers, the funiculi of Voltzian Voltziales can be observed in various stages of fusion in different taxa, from partly fused in *Pseudovoltzia* (Schweitzer, 1963), to almost completely fused in *Majonica* Clement-Westerhof (Clement-Westerhof, 1987), and to completely fused in *Compsostrobus* Delevoryas & Hope (Delevoryas and Hope, 1987). Additionally, the ovules of Voltzian Voltziales are found in a similar position on the funiculi as in extant conifers, e.g. near the apex in *Pseudovoltzia* and *Cunninghamia* (Schweitzer, 1963; Farjon and Garcia, 2003), or near the base in *Krassilovia* Herrera, Shi, Leslie, Knopf, Ichinnorov, Takahashi, Crane et Herendeen and in Pinaceae (Mundry, 2000; Herrera *et al.*, 2015).

In contrast to Voltzian Voltziales, Walchian Voltziales have a clearly distinguishable axillary dwarf shoot, which has spirally

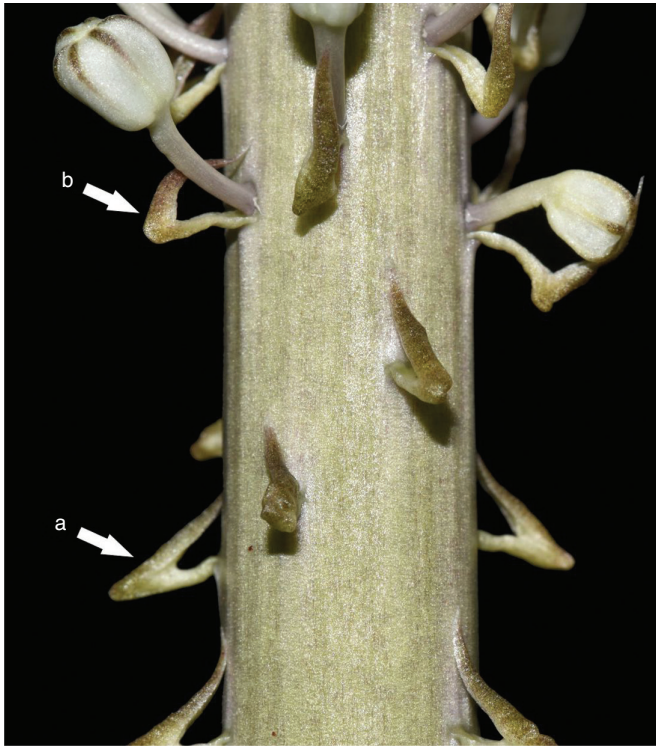


FIG. 3. Photograph of the proximal part of the inflorescence of *Drimia maritima*. Arrow a: hook-like proximal leaf with a typical fusion of the adaxial sides, which are the result of friction with the bud during emergence of the inflorescence. Arrow b: leaf further apical in the inflorescence; the upward pointing tip is still present, but there is no further adaxial fusion.

arranged leaves and stalked ovules interspersed with the leaves (summarized in Taylor *et al.*, 2009). In our new framework of interpretation, the stalk of the ovule of Walchian Voltziales is the funiculus. The funiculus of Walchian Voltziales is recurved towards the cone axis in most taxa, so that the ovule points inwards, e.g. *Ortiseia* Clement-Westerhof (Clement-Westerhof, 1984). Superficially this seems reminiscent of Voltzian Voltziales or extant conifers. However, the funiculus of Walchian Voltziales is recurved towards its abaxial side relative to its supporting axis (axillary dwarf shoot), rather than the adaxial side in Voltzian Voltziales and extant conifers. The three groups of conifers have in common that their ovules are attached subterminally on the funiculus and that the ovule faces towards the cone axis. Additionally, the funiculus of Walchian Voltziales can show severe modifications in the chalazal regions, such as horn-like outgrowths in *Ortiseia* (Clement-Westerhof, 1984); this demonstrates the modifiability of the funiculus.

In addition to fossil conifers, Gnetophytes should be considered in this new framework because some molecular phylogenetic studies infer a close relationship between conifers and Gnetophytes (Magallón and Sanderson, 2002; Ran *et al.*, 2010; Zhong *et al.*, 2010; Burleigh *et al.*, 2012). For this we follow the interpretation of the gnetalean ‘flower’ by Mundry and Stützel (2004), which infers that the ‘flower’ sits terminally on an almost completely reduced lateral axis and is preceded by one (*Ephedra* L.) or two (*Gnetum* L., *Welwitschia* Hook f.) pairs of decussate leaves (Takaso and Bouman, 1986; Mundry and Stützel, 2004; Yang, 2004). Multiples of these ‘flowers’

form the cone-like inflorescence of Gnetophytes. The morphology of the gnetalean ‘flower’ is strikingly similar to that of *J. squamata* or Taxaceae; both have a terminal ovule that is preceded by one (*Juniperus*) or two (Taxaceae) whorls of leaves. In contrast to Taxaceae, Gnetophytes lack an arillus and thus an implicit sign of the funiculus. Nonetheless, the Gnetophytes may be derived from a *Cunninghamia*-like morphology in a similar fashion to Taxaceae, as outlined above (Fig. 1). That means that one gnetalean ‘flower’ would be homologous to a single coniferous seed cone. Therefore, from a purely morphological standpoint there is merit in the inclusion of Gnetophytes into conifers. However, this complex is best resolved in a dedicated study of the comparative morphology of Gnetophytes and conifers.

CONCLUSION

Interpreting the coniferous seed scale as the fused funiculi remedies the discrepancies between the interpretation of the morphology of coniferous female cone units and the reconstructed phylogenies. Previous interpretations of coniferous reproductive morphology carried with them erroneous assumptions dating back decades. These assumptions have not been addressed, such as the initial exclusion of Taxaceae from conifers. In the framework presented above, all female cone units are homologous, as they may all be derived from a common ancestral morphology. Interpreting the seed-bearing structure as the funiculus opens new perspectives from which to study conifer evolution and possibly taxa such as Gnetophytes or *Gingko*. We strongly advocate re-investigation of extant and fossil conifers in the framework provided here, to further uncover mechanisms of the modification of the funiculus.

SUPPLEMENTARY DATA

Supplementary data are available online at <https://academic.oup.com/aob> and consist of the following. Fig. S1: Explanatory drawings of the constituent parts of the coniferous seed scale. Fig. S2: Example comparison between the cone units of Walchian and Voltzian Voltziales.

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