Pollen-cones of *Pinus bungeana* Zucc. ex Endl. (Pinaceae, Coniferales): Do they indicate a pseudanthial origin?

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**ABSTRACT**

Even today, the evolutionary origin of coniferous pollen-cones is still controversial and conflicting theories about the identity of their microsporangiophores exist. Previous studies strongly suggest that the simple pollen-cone structure of some Taxaceae s.l. is most likely derived from a compound structure and each microsporangiophore represents a lateral, however markedly reduced flower. To test if a similar evolutionary pathway remembering the pseudanthium concept sensu Wettstein applies also for Pinaceae, normal shaped and abnormal pollen-cones of *Pinus bungeana* (Pinaceae) are investigated with SEM and paraffin microtome technique. *Pinus sylvestris*, which is the type species of the genus, is used as another example. The early development of bisporangiate microsporangiophores starts with two distinct primordia. They fuse in basal parts and form a common stalk. The distal parts remain free and each develops a stalk, a distinct phyllom-like scutellum and one abaxial microsporangium. In some bisporangiate microsporangiophores two monosporangiate microsporangiophores are inserted laterally at the common stalk, which forms a distinct terminal apex. Other microsporangiophores bear a subunit in form of a second, however, aborted microsporangium in a lateral position at the base of the common stalk. It is suggested that the bisporangiate microsporangium is not a staminate leaf in the sense of a microsporophyll, but a dorsiventral synangium consisting at least of two fused microsporangia. In this case each microsporangiophore corresponds to a markedly reduced cone (= flower) which however has lost its phyllom (= subtending leaf). Similar as shown for *Torreya* the simple pollen-cone structure in Pinaceae is thus derived from a pseudanthial (= compound) origin.

1. Introduction

*Pinus* is one of the largest genera among living conifers (Krüssmann, 1983; Eckenwalder, 2009; Farjon, 1984, 2010) with *Pinus sylvestris* as the type species (IPNI, 2024). In many textbooks, the genus is frequently called pollen-cones, the female, ovuliferous seed-cones. While the seed-cones, which are either male or female. The male, staminate ones are

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\[ \text{Conifers} = \text{Evolution} \]

\[ \text{Pollen-cones} \]

..corr.

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type (Fig. 9) is derived from an ancestral radial (= perisporangiate, Fig. 9) one (e.g. Worsdell, 1901; Dupler, 1919; Dlhouš, 1937); (2) perisporangiate microsporangiophores are radial syndiagnia formed by several fused hyposporangiate microsporangiophores (e.g. Thomson, 1940; Wilde, 1975; Mundry and Mundry, 2001; Dörken et al., 2011; Dörken and Nimsch, 2022; V.M. Dörken; V.M. Dörken, 2023). The latter concept was strongly supported by investigations carried out in Taxaceae s.l. In contrast to Pinaceae, Taxaceae s.l. show a great structural diversity with compound pollen-cones, that correspond to an inflorescence equivalent structure and simple pollen-cone that correspond to a flower equivalent structure and dorsiventral (= hyposporangiate) and radial (= perisporangiate) microsporangiophores (Fig. 9; Wilde, 1975; Page 1996; Mundry and Mundry, 2001; Dörken et al., 2011; Schulz et al., 2014; Dörken and Nimsch, 2023; Dörken, 2020, 2023). Thus, an evolutionary transition series from compound pollen-cones in Cephalotaxus to simple ones in Taxus and Torreya was proposed and the perisporangiate microsporangiophores have been interpreted as lateral, however markedly reduced cones (Fig. 9). Reduction of the perisporangiate microsporangiophores developed at the tips of Taxus pollen-cones (Fig. 9) leads to a Pinaceae like hyposporangiate one.

One might assume, that the hyposporangiate microsporangiophore in Pinaceae is also the result of a reduction process similar to the transition from Cephalotaxus to Torreya (Fig. 9). However, in contrast to Taxaceae s.l. pollen-cone, Pinaceae appear rather homogenous throughout. All pollen-cone are simple, flower equivalent structures carrying numerous dorsiventral, hyposporangiate microsporangiophores, each with 2 abaxial pollen-sacs (= microsporangia) and a terminal phylloid-like structure (= scutellum) (Dallimore and Jackson, 1966; Krüssmann, 1983; Page, 1990; Eckenwalder, 2009; Farjon, 2016; Dörken, 2020).

To get new insights into the evolution of pineaceous reproductive structures, the morphology and anatomy of pollen-cones of Pinus bungeana is investigated by SEM and microtome technique. In addition to normal shaped pollen-cones also teratological ones are included, which have numerous anomalies that are markedly different form the usual type and the common situation in Pinus. As another example Pinus sylvestris as type species of the genus, is additionally examined. In the different molecular phylogenies the position of both investigated taxa shows some variation. But all agree that Pinus sylvestris belongs to subgenus Pinus and P. bungeana to subgenus Strobus. Additionally in all phylogenetic trees, both species are not placed in a basal position (Zeb et al., 2022; Xia et al., 2023).

2. Material and methods

2.1. Material

Pollen-cone of Pinus bungeana Zucc. ex Endl. were collected from trees growing in the forest arboretum Freiburg-Günterstal, Freiburg i. Br. (Germany). Date of collection was 11.04.2020. Pollen-cone Pinus sylvestris were collected on 08.05.2023 from a tree growing on the campus of the University of Konstanz, Konstanz (Germany).

2.2. Methods

Freshly collected material was photographed and then fixed in FAA (100 ml FAA = 90 ml ethanol 70 % + 5 ml acetic acid 96 % + 5 ml formaldehyde solution 37 %) before being stored in 70 % ethanol. The anatomy was studied from sections using the classical paraffin technique and subsequent astrable/safranin staining (Gerlach, 1984). For scanning electron microscopy (SEM), the FAA-fixed material was dehydrated in formaldehyde dimethyl acetel (FDA) for 24 h (Gerstberger and Leins, 1978) and subsequently critical-point-dried. Sputter-coating was performed using a sputter coater SCD 50 Bal-tec (Balzers, Liechtenstein). The specimens were examined with an Auriga Zeiss TM (Zeiss, Germany). Macrophotography was carried out with a digital camera (Canon PowerShot IS2) and microphotography with a digital microscope (Keyence VHX 500F, Keyence, Japan) equipped with a high-precision VH mounting stand with X-Y stage and bright-field illumination (Keyence VH-S5).

2.3. Special terms

- ad-/abaxial: Here the reference axis is always the axis of the entire cone.

Flower: The definition of the term flower has been intensively debated in literature and numerous definitions exist. A representative spectrum of definitions is available in Bateman et al. (2006). In this present study, the term flower is used for a morphologically clearly delimited unbranched short shoot-like axis, which carries fertile leaves (microsporophylls) which bear the reproductive organs (Wettstein, 1935; Weberling, 1989; Hess, 2019; Stützel, 2021).

Compound pollen-cones: In this study, the terms inflorescence and compound are used only for staminate reproductive units developed from a single bud, the whole unit enclosed by bud scales (e.g. Cephalotaxus and Pseudotaxus, Fig. 9). Clusters of staminate cones each with its own bud scales (e.g. Sciadopitys verticillata or Juniperus drupacea) (Dörken, 2019; Dörken and Nimsch, 2023) are not treated as compound pollen-cones here.

Microsporangiophore: Structure bearing the microsporangia; here, the term sporophyll or microsporophyll is not used to avoid a priori homology statement.

Phyrophyll: A leaf bearing an auxillary shoot (Briggs and Johnson, 1979; Stützel and Trovó, 2013); mostly simple; often markedly smaller when developed in the floral region above the typical trophophylls (Wagenitz, 2008).

Scutellum: The terminal phylloid-like structure developed on the stalk of the microsporangiophores is termed scutellum.

Synangium: Group of fused sporangia (Wagenitz, 2008).

3. Results

3.1. Pinus bungeana

Mature pollen-cones are clustered in basal parts of a present year’s long shoot. There is a sylleptic flux of the long shoot axis, the basal pollen-cones and the subsequent vegetative short shoots (Fig. 1A, B). Each pollen-cone is inserted in the axil of a brownish membranous pherophyll (Fig. 1B). The base of each pollen-cone is surrounded by several membranous, brownish bud scales (Fig. 1B). The pollen-cones are 1–1.5 (–2) cm long and 0.4–0.5 cm in diameter. There are numerous spirally arranged microsporangiophores. Most microsporangiophores are hyposporangiate (= dorsiventral) and consist of a stalk, a small terminal scutellum and two abaxial pollen-sacs (= microsporangia). The size and shape of the scutellum varies markedly between the microsporangiophores. In numerous microsporangiophores a scutellum is absent (Figs 1B-D, 2), or has a small spine-like (Figs 3D, 4D) or leaf-like (Fig. 5A, B) shape.

The microsporangiophores are inserted directly on the cone axis, pherophylls within the pollen-cone are absent (Figs 1C, D; 2A, B, 3A). The microsporangia are fused to the stalk of the microsporangiophore (Fig. 2A, B). In numerous cases this stalk branches dichotomously near the base, so that two stalks are formed, each bearing a single abaxial microsporangium (Fig. 2C, D). In these cases, the two microsporangia of the microsporangiophore are only partly fused or entirely free (Fig. 2B-D).

The formation of such bisporangiate microsporangiophores with free microsporangia starts with the formation of two, non-axillary primordia on the cone axis. The two primordia fuse in basal parts and form a common stalk (Fig. 4A, B). Even in earliest ontogenetic stages, each primordium shows a differentiation into a short stalk, a terminal scutellum and one abaxial microsporangium (Fig. 4C). In subsequent
developmental steps the stalk of each unit elongates markedly so that
the microsporangia are finally distantly from each other and each with
a small adaxial, distal scutellum (Fig. 4D). In top view of such micro-
sporangiophores, the common stalk of the microsporangiophore and its
basal dichotomous branching are well visible even at maturity (Fig. 4E,
F).
In numerous other bisporangiate microsporangiophores the common
stalk is unbranched and its tip is well visible as a distinct apex. There are
two lateral monosporangiate lateral subunits inserted in basal parts on
the stalk, which are separated from each other by the apex of the
common stalk (Fig. 5). In addition, numerous compound micro-
sporangiophores composed of two bisporangiate subunits were found.
These secondary microsporangiophores were mostly aborted (Figs 4, 5).
When developed, the second microsporangiophores consist each of a
short stalk, a short but distinct terminal scutellum and two micro-
sporangia (Figs 6C-F, 7A-D). In some cases, these lateral micro-
sporangiophores or subunits consist just of a stalk and a single microsporangium (Fig. 6A, B). In one case such an additional lateral
microsporangiophore was found, where the stalk branches in distal parts
dichotomously in two stalks, each of them carries a terminal micro-
sporangium, a scutellum is absent (Fig. 6E, F).

Also, several monosporangiate microsporangiophores are developed,
which consist of a short stalk and a single sporangium (Figs 1C, D, 2E, F,
3F). These microsporangia are inserted either more or less basal to
(Fig. 3E) or terminal on the stalk (Fig. 3C, D, F). In rare cases the
microsporangia are sessile and a distinct stalk is absent (Fig. 3F). The
monosporangiate microsporangiophores often lack a scutellum (Figs 2E,
F, 3F). If a scutellum is developed, then it is formed as a small, adaxial tip
located terminal on the microsporangium (Fig. 3D).
In other cases, there is a small lateral outgrowth at or below the stalk
of the microsporangiophore, which is visible as a small, but distinct
bulge (Fig. 7E, F).

3.2. Pinus sylvestris

Pollen-cones of Pinus sylvestris are formed in basal parts of this year’s
long shoots. There is a sylleptic flush of the long shoot axis, the basal
pollen-cones, the subsequent vegetative short shoots and the distal seed-
cones (Fig. 8A). The pollen-cones are each inserted in the axil of a small
membranous long shoot leaf. They are (0.5-) 1–1.5 (–2) cm long and
0.4–0.5 cm in diameter. There are numerous membranous bud scales
surrounding the base of each pollen-cone. The pollen-cone consist of
**Fig. 2.** *Pinus bungeana,* morphology of microsporangiophores (SEM-images). (A-D) Bisporangiate microsporangiophores with two microsporangia. (A) The microsporangiophores are non-axillar and the short stalk is inserted directly at the cone axis; (B-D) Varied types of fusion of microsporangia. (B) Nearly entirely fused. (C) Weakly fused. (D) Not fused. (E & F) Monosporangiate microsporangiophores with a single microsporangium. (E) Front view. (F) Lateral view; the stalk is quite short and the sporangium is nearly sessile on the cone axis.
Fig. 3. *Pinus bungeana*, anatomy of microsporangiophores (microtome sections). (A-C) Bisporangiate microsporangiophores. (A) Microsporangia in a distal position on the stalk (longitudinal section); they are strongly fused; the microsporangioaphore is supplied by a single vascular bundle strand; a pherophyll is absent. (B) Cross section; sporangia only slightly fused. (C) Bisporangiate microsporangioaphore with a terminal sporangium and a second smaller one inserted at the base of the common stalk (longitudinal section); (D-F) Longitudinal sections of monosporangiate microsporangiophores. (D) Only few microsporangiophores have a terminal scutellum; the sporangia are developed terminal on a short stalk. (E) Abaxial sporangium developed in a basal position on the stalk; the distal part of the stalk is free. (F) Sessile sporangium; the stalk is nearly entirely reduced.
Fig. 4. *Pinus bungeana*, ontogeny of a bisporangiate microsporangiophore (SEM-images). (A-C) Early ontogenetic stages; there are two primordia, which fuse in basal parts and form a common stalk (A); already in the earliest ontogenetic stage each forms a terminal scutellum and a microsporangium that is inserted below the stalk (B); in subsequent developmental steps the stalk of each half elongates and the size of the sporangium and the terminal scutellum become markedly increased (C). (D-F) Mature microsporangiophore. (D) The microsporangia are fused parallel to the stalk and the phyllom-like scutellum is located adaxial in distal parts on each microsporangium. (E-F) Adaxial view of a bisporangiate microsporangiophore; in basal parts the stalk of the microsporangiophore branches in two strands, each carrying a single microsporangium below; each stalk terminates with a spine-like scutellum. (E) Overview. (F) Detail of E.
numerous spirally arranged hyposporangiate microsporangiophores (Fig. 8B). Each consists of a central stalk, a terminal, large foliate scutellum and two abaxial microsporangia (Fig. 8C-G). The microsporangia are fused to the terminal scutellum and to the stalk of the microsporangiophore. There is no sharp margin separating the microsporangia from the scutellum (Fig. 8B, D, H, I). The dehiscence line of the sporangia is longitudinal and parallel to the stalk of the microsporangium (Fig. 8D-I). The microsporangiophores are attached directly to the cone axis. Pherophylls within the pollen-cone are absent (Fig. 8C). In addition to the majority of bisporangiate microsporangiophores some were found with exceptional three (Fig. 8H) or four (Fig. 8I) microsporangia. Apart from the higher number of microsporangia, all other features of these teratological microsporangiophores correspond to those of the usual type.

4. Discussion

Usually pollen-cones of Pinus and all other Pinaceae are quite homogenous structures with the same basic structure. Differences refer mainly to the size of the pollen-cones, the number of microsporangiophores and the size and shape of the scutellum (Schulz et al., 2014; Dörken and Nimsch, 2015, 2019, 2021; Dörken, 2020). Therefore, it is difficult to develop evolutionary scenarios about the origin of staminate reproductive structures in this group. So, the existing differences are basically used for species identification but their evolutionary significance is seen as very limited.

The microsporangiophores are set spirally on an unbranched axis and the generally two microsporangia open with a longitudinal slit. This makes them similar to a bisporangiate stamen in angiosperms and so they are generally seen as microsporophylls with the two pollen-sacs shifted from the lateral margins to the abaxial side like in extrors stamens (Zimmermann, 1959 p. 445). The occasional occurrence of three or four microsporangia per pinaceous microsporangiophore is generally not seen as a problem and treated as the ancestral state similar to tetrasporangiate and bisporangiate stamens in angiosperms. The tip of this unit is compared to a connective tip as also known from some angiosperms. As it is usually rather hard and curved towards the cone apex (more or less right angle to microsporangium and stalk), it is termed scutellum. The hitherto known variability within Pinus and within Pinaceae is generally limited.
Fig. 6. *Pinus bungeana*, compound microsporangiophores (SEM-images); several monosporangiate microsporangiophores were found which carry a second, however, rudimentary microsporangiophore in basal parts. (A) Early ontogenetic stage of a basal rudimentary second microsporangiophore; it has a distinct stalk and a single terminal microsporangium; phyllom-like structures are absent. (B) Detail of A. (C-F) Monosporangiate microsporangiophores carrying a rudimentary bisporangiate microsporangiophore at their base. (C-D) The rudimentary basal microsporangiophore consists of a short stalk, two microsporangia and a distinct terminal phyllom-like scutellum. (C) Overview. (D) Detail of C. (E-F) The rudimentary basal microsporangiophore consists of a short stalk and two microsporangia; a distinct terminal phyllom-like scutellum is absent; the distal part is free and branches in two units, each carrying a single microsporangium below. (E) Overview. (F) Detail of E.
Fig. 7. *Pinus bungeana*, compound microsporangiophores (SEM-images); fully developed bi- (A & B) or monosporangiate microsporangiophore (C-D) carrying a second, however, rudimentary lateral microsporangiophore in basal parts. (A-B) The basal rudimentary second microsporangiohore has a distinct stalk and a single terminal sporangium; phyllom-like structures are absent. (A) Overview. (B) Detail of A. (C-D) The rudimentary basal microsporangiophore consists of a short stalk, two microsporangia and a distinct terminal phyllom-like scutellum. (C) Overview. (D) Detail of C. (E-F) Bisporangiate microsporangiophore with one well-developed and one aborted sporangium; lateral to the base of stalk of the microsporangium there is a small bulge. (E) Overview. (F) Detail of E.
The identity of the coniferous scutellum is still controversial (compare discussion in Schulz et al., 2014). The situation in *P. bungeana* differs markedly from *P. sylvestris*. In *P. sylvestris* it is a leaf-like, entire, adaxial structure developed terminal on the central stalk of the microsporangiophore (Fig. 8B-I). The abaxial microsporangia are fused with the stalk of the microsporangiophore, but also to the terminal scutellum. Thus, in *P. sylvestris* the scutellum is not a feature of a single microsporangium. In the investigated material of *P. bungeana* the situation is completely different. In most cases, the scutellum is entirely absent, but when it is still developed it is not terminal on the stalk, but placed on the adaxial surface of each microsporangium. The position of the scutellum on the adaxial surface of each microsporangium and not terminal on the stalk excludes *a priori* its identity as a leaf tip and this runs into great difficulties in explaining the microsporangiophore as a simple staminate leaf in the sense of a microsporophyll as it is widely done (e.g. Coulter and Chamberlain, 1917; Dluhosch, 1937; Pilger, 1960; Mirov, 1967; Sporne, 1965; Liu, 1971; Krüssmann, 1983; Page, 1990; Farjon, 1984, 2010; Taylor et al., 2009). The investigated pollen-cones of *P. bungeana* are exceptional in so far, as in addition to typical *Pinus*-like shaped bisporangiate microsporangiophores also several monosporangiate ones were found. Some of them (Fig. 2E, F) are symmetric to the median plane and can thus hardly be explained as the result of a loss of one of the sporangia in a bisporangiate microsporangiophore. Branched microsporangiophores in which each stalk carries a single sporangium, each with its own scutellum are also difficult to fit with the microsporophyll concept as is also the case for microsporangiophores which form an...
additional microsporangiophore on the common stalk. All this excludes an homology with a simple microsporophyll. This leads to the question, whether teratologies like these abnormal microsporangiophores are of any information at all. We feel that these exceptional microsporangiophores are useful, if we find a concept (morphological and developmental), in which the normal and the abnormal microsporangiophores fit as well. Such a concept would be better than one, that can explain only the normal type and leaves the exceptions as not understandable and outside our concepts.

Based on the results gained in usual shaped and abnormal pollen-cones /microsporangiophores we suggest that the entire microsporangiophore is a synangium. It is composed of several fused hyposporangiate microsporangiophores. In this case the entire unit otherwise treated as a leaf-homologon corresponds to a markedly reduced lateral cone (= flower equivalent structure) and the entire pollen-cone to a compound structure. In this case, the documented abnormal microsporangiophores would be atavistic forms indicating the pseudanthial origin of today's simple pollen cones. This theory is well supported by the fact that also some of the investigated microsporangiophores (Fig. 5) consist of a central stalk and two monosporangiate subunits/microsporangiophores, which are attached in basal parts lateral to the common stalk. The apex of the common stalk is still visible as a small, but distinct tip placed between the lateral microsporangiophores.

It would be very helpful to have a full ontogeny of such microsporangiophores. However, this is only possible if we can expect the same structure always in the same position as it is the case when we study floral ontogenies in angiosperms. This enables us to reconstruct the ontogeny from stages of different microsporangiophores from different samples. Despite the fact that abnormal microsporangiophores are very frequent in *P. bungeana*, their position and type does not follow a predictable pattern. Therefore, it remains somewhat hazardous to align different stages to an ontogenetic sequence.

In typical shaped microsporangiophores, the common axis is markedly reduced so that the inserted microsporangiophores are fused and form a dorsiventral synangium. The ontogeny of the bisporangiate microsporangiophores strongly suggests the microsporangiophores as a synangium, consisting of at least two fused microsporangiophores. In *P. bungeana* the microsporangiophore is not formed by a single primordium, as it would be the case when it just represents a simple staminate leaf. It originates from two separate primordia (Fig. 4) which fuse congenital in basal parts and form a common stalk (Fig. 4A, B). The distal, free parts develop each into a distinct own stalk carrying each a terminal adaxial scutellum and an abaxial microsporangium (Fig. 4C-F). Thus, the bisporangiate microsporangiophore is most likely a fusion product of two monosporangiate microsporangiophores.

In summary, serious evidence was found elucidating the *P. bungeana* microsporangiophores as dorsiventral synangia that are markedly reduced lateral simple cones (= flowers). In consequence this means that the simple flower-like structure of *Pinus* pollen-cones is a secondary feature derived from a pseudanthial origin as it was shown for other coniferous groups, e.g. Taxaceae s.l. (Mundry and Mundry, 2001; Dörken et al., 2011; Schulz et al., 2014; Dörken, 2020; 2023; Dörken and Nimsch, 2023). The non-axillary position of microsporangiophores and the absence of pherophylls are not necessarily a contradiction, that discards a pseudanthial origin. A loss of pherophylls resulting in non-axillary flowers is common among some seed-plants. There are numerous cases of distantly related angiosperms that are lacking pherophylls in their inflorescences, e.g. the heads of some Asteraceae (Engler, 1954) and Ericaceae (Rubland, 1903; Stützel, 1984; Trovo et al., 2010; Stützel and Trovo, 2013), the spike inflorescences of Araceae, Acorus (Acoraceae) and several alismatids (Buzgo, 2001). Moreover, the flowers of most Brassicaceae also lack noticeable pherophylls (Nikolov, 2019). Thus, non-axillary flowers are not uncommon in angiosperms and in this group, it is not questioned that they are derived from an axillary branching pattern. However, compound pollen-cones are rare in conifers and developed only in some Taxaceae s.l. In Taxaceae s.l. a full transition series from compound pollen-cones (in *Cephalotaxus* via *Pseudotaxus* to simple pollen-cones (in *Taxus* and *Torreya*) is suggested (Fig. 9). It could be demonstrated, that the pollen-cones of *Taxus* and *Torreya* species, which appear morphological and ontogenetically flower-like, are however, phylogenetically, derived from a pseudanthial origin. In both taxa each lateral microsporangiophore corresponds therefore to a strongly reduced lateral simple pollen-cone (= flower) which lost its pherophyll (Fig. 9; Mundry and Mundry, 2001; Dörken et al., 2011; Dörken and Nimsch, 2016, 2023; Dörken, 2023).

The random mutations found in microsporangiophores of *P. bungeana* may appear as potentially indicative of past evolutionary history of male reproductive structures in *Pinus*. However, in particular the bi-branch microsporangiophores as well as bi-branch with each branch bearing two microsporangia reminds strongly to the situation in Araucariaceae. In Araucariaceae it is highly likely that each microsporangiophore is a complex and compact fusion product of numerous bisporangiate microsporangiophores, which form a dorsiventral synangium (Dörken, 2024a) as is also suggested for several Podocarpaceae (Dörken, 2024a; Dörken & Stützel in preparation). Thus, also each araucariaceous and podocarpaceous microsporangiophores corresponds to a strongly reduced lateral pollen-cone (= flower) and the entire pollen-cones are regarded as derived from a pseudanthial origin. This demonstrates well that the present study is not an isolated observation but might elucidate a more general evolutionary pattern in coniferous pollen cones.

The situation in taxaceeous and araucariaceous and podocarpaceous pollen-cones demonstrates well, that the simple flower-like pollen-cone structure can be easily derived from pseudanthial origin by a simple loss of pherophylls and the reduction of microsporangia per microsporangiophore (Mundry and Mundry, 2001; Dörken et al., 2011; Dörken and Nimsch, 2016; 2023; Dörken, 2023, 2024a,b). Thus, the documented abnormal microsporangiophores of *P. bungeana* are rather atavistic forms indicating the origin from a composed pollen-cone (= inflorescence) what is today a simple pollen-cone (= flower) in regard to structure and ontogeny than being just meaningless mutations. However, they reinforce the idea that similar, parallel evolutionary processes have taken place in the different coniferous groups, from a former open compound situation to a simple flower-like one, with microsporangiophores that are representing either radial or dorsiventral synangia.

In previous studies, pollen-cone anomalies in different Pinaceae (Cathaya, *Pinus* and *Tsuga*) were documented, showing several cases where instead of the typical bisporangiate microsporangiophores, multisporangiate ones were found, or even radial microsporangiophores were developed instead of hyposporangiate ones (Dörken and Nimsch, 2015; Dörken, 2017). It seems that the bisporangiate type, which is the common one in pineaceous pollen-cone, is derived from a multi-sporangiate ancestral condition, which originates most likely from several fused hyposporangiate microsporangiophores. Thus, the pineaceous microsporangiophores may appear as microsporophylls today, as they are generally described (Bonga, 1974; Krüssmann, 1983; Farjon, 1984, 2016; Gifford and Forster, 1989; Page, 1990; Wang et al., 2000; Sharma and Khanduri, 2002; Taylor et al., 2009; Williams, 2009; Zhao et al., 2011; Song et al., 2012). However, in a phylogenetic context they are better seen as markedly reduced lateral pollen-cones (= flowers) and the simple pollen-cone structure is therefore a secondary feature derived from a pseudanthial origin.

5. Conclusion

Pollen-cone and microsporangiophores of *Pinus bungeana* were investigated with SEM and microtome technique. In addition to usual type bisporangiate microsporangiophores also abnormal ones were investigated. These include monosporangiate sporangiophores, bi-branch ones as well as bi-branch with each branch bearing two microsporangia. In the context of abnormal microsporangiophores
in other Pinaceae as well as in the context of the transition series known from Taxaceae s.l. (Mundry and Mundry, 2001; Dörken et al., 2011; Dörken and Nimsch, 2023) or the suggested pseudanthial origin in Araucariaceae (Dörken, 2024b), this suggests that the staminate cones in Pinaceae appearing today as unbranched and flower-like are phylogenetically derived from branched systems in the sense of a pseudanthial concept.

CRediT authorship contribution statement

Veit Martin Dörken: Writing – original draft, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Thomas Stützel: Writing – review & editing, Validation, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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