Seed cone proliferation in *Cupressus vietnamensis* (Cupressaceae) and its evolutionary meaning

Abstract

Teratological seed cones of *Cupressus vietnamensis* (Farjon & T.H. Nguyên) Silba showing apical and axillary vegetative proliferations were investigated. This showed that the apical proliferation represents a simple elongation of the cone axis. A full transitional series from basal fertile peltate cone scales to the distal, decussate, sterile scaly trophophylls at the proliferation was documented. The investigations of the axillary proliferations show that here ovules are replaced by a homologous vegetative axillary shoot. It is suggested that the primitive condition of the Cupressaceae seed cones was an open, loose, polyaxial inflorescence, before the ovuliferous short shoot (= seed scale) was strongly reduced, so that in most derived Cupressaceae the seed scale is reduced to its ovules, which finally leads to the formation of the compact seed cone structure in living Cupressaceae.

Keywords: *Cupressus vietnamensis*, seed cone, morphology, anatomy, proliferation, evolution, teratology.

1 Introduction

Typical coniferous seed cones are characterized by the so called bract/seed scale complex. The bract scale represents a leaf which is carrying an axillary ovuliferous short shoot, the seed scale (Takaso & Tomlinson 1992; Jagel & Stützel 2001, 2003; Jagel 2002; Farjon & Ortiz-Garcia 2003; Schulz & Stützel 2007; Dörken 2011). Thus, the coniferous seed cones represent polyaxial, compound structures fulfilling the definition of an inflorescence (Schuhmann 1902; Herzfeld 1914; Pilger 1926; Florin 1951, 1954; Schweitzer 1963; Farjon 1984, 1990, 2005, 2010; Stützel & Röwekamp 1997, 1999; Mundry 2000; Farjon & Ortiz-Garcia 2003; Eckenwalder 2009). However, both types of cone scales can be distinguished so clearly from each other as two separate structures only in Pinaceae. In other coniferous groups, the bract/seed scale complex is strongly reduced and modified so that finally only one type of cone scales is developed, which represents either a fusion product of the bract and seed scale as is e.g. the case in Araucariaceae (e.g. Eckenwalder 2009; Farjon 2010), or the cone scale represents exclusively the bract scale, while the seed scale is completely reduced to its ovules as is typical for several Cupressaceae s.str. (e.g. Page 1990; Gadek *et al.* 2000; Jagel & Stützel 2001; Schulz & Stützel 2007; Jagel & Dörken 2014, 2015a, 2015b; Dörken 2011; Dörken & Jagel 2014, 2017). Among several Cupressaceae s.str. the ovules are inserted in a single or in several rows. These axillary rows of ovules are regarded as descending accessory short shoots. In the typical shaped seed cones of Cupressaceae s.str. no vegetative portions of the ovule-carrying seed scale are visible.

By chance teratological seed cones of *C. vietnamensis* showing different types of proliferations were found and their morphology and anatomy is investigated here. The structures of these proliferated seed cones are of greatest interest to gain new results helping towards a better understanding of the evolutionary pathway of seed cones in Cupressaceae and their original branching pattern.

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2 Material and Methods

2.1 Material

Teratological seed cones showing an apical vegetative proliferation were received from the Bedgebury Pinetum (UK). Seed cones showing axillary vegetative proliferations were collected in the living collection of Hubertus Nimsch (Bollschweil, Germany). In both cases, the cones were collected from trees cultivated as pot-plants.

2.2 Methods

Freshly collected material was photographed and then fixed in FAA (100 ml FAA = 90 ml 70% ethanol + 5 ml acetic acid 96% + 5 ml formaldehyde solution 37%) before being stored in 70% ethanol. The leaf-anatomy was studied from serial sections using the classical paraffin technique and subsequent astrablue/safranin staining (Gerlach 1984). Macrophotography was accomplished using a digital camera (Canon PowerShot IS2) and microphotography with a digital microscope (Keyence VHX 500F) equipped with a high-precision VH mounting stand with X-Y stage and bright-field illumination (Keyence VH-S5).

3 Results

3.1 Teratological seed cones with an apical proliferation

The basal part of these proliferated seed cones has the typical *C. vietnamensis* seed cone morphology (Figs 1A-D), with two pairs of fertile cone scales. Each cone scale carries axillary 2(-3) ovules, which are arranged in a single row. The apex of the cone axis remained vegetative and formed an apical distinct foliar proliferation (Fig. 1). The apex of the proliferated shoot axis remains vegetative. However, the duration of the proliferation is closely correlated to the life span of the seed cone. At maturity, the seed cone dries out and the cone axis and cone scales shrink to release the seeds. In consequence, also the apical proliferation dries. The apical proliferation is sterile (Figs 1A-C). The leaves at the proliferation show a full transitional series from basal peltate leaves showing the shape of typical cone scales to distal scaly, decussate trophophylls, which can be distinguished in lateral and median leaves (Fig. 1F), as is typical for the vegetative parts of *C. vietnamensis*. The basal fertile cone scales and also the cone scale like basal leaves inserted at the proliferation are peltate shaped, but do not represent peltate leaves in the classical sense. A meristematic fusion of marginal leaf tissues leading to the formation of a meristematic cross zone above the petiole lacks in both. The peltate leaf shape is caused by a strongly ventral bulge, which starts development soon after pollination to close the cone. Thus, the distal part of the cone scale becomes finally shield like, carrying the leaf tip as a more or less conspicuous central spike on its back (Figs 1A-D). While maturing the cone scales and the cone scale like leaves at the proliferation become strongly lignified. Within the leaves inserted at the proliferation, the formation of this ventral bulge is more and more reduced so that the peltate shape of the lower cone scales and the sterile cone scale like leaves gets lost so that finally the scaly trophophylls, lacking a meristematic swelling, are formed.

3.2 Teratological seed cones with an axillary proliferation

One seed cone was found, showing a vegetative proliferation inserted in the axil of a distal cone scale (Figs 2 & 3). Within this cone scale the axillary row of ovules is completely replaced by a sterile, scale-leaved shoot axis (Figs 3A & 3C). Each, the axillary proliferation and the cone scale are supplied by an own vascular bundle strand, which enter the vascular bundle of the cone axis in separate strands. The vascular bundle of the cone scale is collateral with xylem located towards adaxial and phloem towards abaxial. The vascular bundle of the proliferation is concentric and similar to those of the cone axis with inner xylem and outer phloem (Figs 3A & 3C). The apex of the proliferation remains vegetative and a possible further growth would be possible. However, the duration of the proliferation is closely correlated to the life span of the seed cone and is therefore limited to about max. 18 months. The leaves inserted at the axillary proliferation show the morphology and anatomy of typical trophophylls of *C. vietnamensis*: scaly, decussate, inverse

bifacial, distinguishable in lateral and median leaves (Figs 2A & 2F). Transitional leaves between the peltate shaped cone scales and the scaly trophophylls at the proliferation lack. Except for the axillary proliferation, the seed cone shows the typical conditions of *C. vietnamensis*: two decussate fertile cone scales, each carrying 2(-3) ovules, which are arranged in a single axillary row per cone scale. The ovule and the cone scale are each supplied by an own vascular bundle strand, which enter the concentric bundle of the cone axis by a separate strand. In basal parts the collateral bundle strand supplying the cone scale branches dichotomously once. One of the strands ends shortly below the tip of the cone scale, the other one supplies the strongly swollen ventral bulge (Fig. 3B).

4 Discussions

Within the genus *Cupressus* the Vietnamese taxon *C. vietnamensis* and the north-western Pacific coast *C. nootkatensis* D.Don can be regarded as the most primitive taxa. Thus, it is assumed that they still represent several primitive features in their vegetative and reproductive structures as well. Within seed cones of *C. vietnamensis* their small size, the low number of cone scales and ovules per cone scale and in the entire seed cone, the arrangement of ovules in mostly merely a single axillary row and a more or less columella like seed cone apex are regarded as primitive (Dörken & Jagel 2017). Within the other most derived *Cupressus* species the seed cones are much larger, with a significantly higher number of cone scales and ovules (Jagel 2002; Eckenwalder 2009; Jagel & Dörken 2014, 2015a, 2015b). In most derived *Cupressus* species ovules are arranged in several axillary rows per cone scale. A distinct columella like apex is missing in most taxa and the apex of the cone axis is only flat or gets completely lost by forming the distal pair of cone scales. Thus, within the genus *Cupressus* a tendency towards larger seed cones developing a significantly increased number of ovules per cone scale and in the entire seed cone is observable (e.g. Jagel 2002; Jagel & Dörken 2014, 2015a, 2015b; Dörken & Jagel 2017). Due to the loss of a meristematic apex the seed cones of the most derived *Cupressus* species are of limited growth and cannot undergo a further development.

Within seed cones of several coniferous groups including basal taxa of the Cupressaceae *s.l.* sterile distal elements are developed, which form together with the apex of the cone axis a so called “terminal piece”. Within Cupressaceae a tendency to reduce such sterile terminal elements is observable, so that finally the distal cone scales become fertile, as is the case for e.g. all taxa of the genus *Cupressus* and all Callitroid Cupressaceae (e.g. Jagel 2002; Jagel & Dörken 2014, 2015a, 2015b; Dörken & Jagel 2017). The reduction of the sterile distal elements leads also to a strong reduction of the seed cone apex. In taxa showing a sterile “terminal piece”, apical proliferations are quite frequently developed as is the case for e.g. Pinaceae, Araucariaceae or Sciadopityaceae. Also within the basal Cupressaceae, especially in taxa of the former Taxodiaceae (now merged into the Cupressaceae *s.l.*) apical proliferations are not uncommon (e.g. Tosh & Powell 1986; Caron & Powell 1991; Jagel & Stützel 2001; Farjon, 2008; Owens 2008; Bateman *et al.* 2011; Dörken 2011; Rudall *et al.* 2011). In most derived Cupressaceae lacking a sterile “terminal piece” e.g. *Cupressus* and all Callitroideae such apical proliferations are unusual, and within these taxa the reduction of the distal vegetative elements including a meristematic apex of the cone axis prevents such a vegetative proliferation. Thus, it is not surprising that until now, no report of proliferated *Cupressus* seed cones existed.

The evolutionary meaning of such proliferations is, however, still highly controversial. In general, apical vegetative proliferations of seed cones are quite useless for suggesting evolutionary scenarios, because they represent only a simple vegetative elongation of the cone axis, however with a significant change in the internode length and in the size and shape of leaves. In most cases this change is quite abrupt and transitional structures leading from the basal fertile cone scales to the trophophylls inserted distally at the proliferation usually lack. The leaves inserted at the apical proliferations usually show the morphology of typical trophophylls of the respective species (Dörken 2011). Thus, the apical proliferation illustrated in Fig. 1 is special because here several intermediary scales are developed. The shape of the basal most sterile leaves inserted at the apical proliferation is quite similar to the lower fertile peltate cone scales. The subsequent leaves get more

and more similar in size and shape to the typical scaly trophophylls of *C. vietnamensis*, which can be distinguished in lateral and median leaves. It could be shown that the peltation of the cone scales and the cone scale like sterile leaves inserted at the proliferated shoot axis is not caused by a meristematic fusion of marginal leaf tissues leading to the formation of a meristematic cross zone above the petiole as is the case for peltate leaves in the classical sense (Troll 1932; Franck 1976; Natho *et al.* 1990; Gleissberg *et al.* 2005; Throm 2007; Bresinsky *et al.* 2008; Leins & Erbar 2008, 2010; Fukushima & Hasebe 2014). The peltation of cone scales in *C. vietnamensis* is caused by a strongly ventral bulge, which development starts soon after pollination to close the cone. Due to this strong swollen ventral bulge the cone scales are finally peltate-like, carrying the tip of the cone scale as a more or less conspicuous central mucro on its back (Figs 1A-D). The transitional series from basal fertile cone scales via peltate sterile cone scale-like intermediary scales to distal sterile scaly trophophylls at the apical proliferation is characterized by a continuously reduction of this ventral bulge, which is finally lacking in the distal scaly trophophylls. Thus, these leaves are scaly and not peltate. These intermediary scales demonstrate quite well all structural changes occurring between typical shaped fertile cone scales and sterile scaly trophophylls.

The monomorphic tissue of the ventral bulge differs strongly from those of the cone scale by showing larger, thin-walled cells and lacking a differentiation into palisade and spongy parenchyma (Figs 3A-B). Due to these anatomical differences and the presence of a clear boundary-layer between the tissue of the cone scale and the ventral bulge both appear as different separate structures at the first glace and the ventral bulge might be interpreted as representing the seed scale. In this case the cone scale would represent a fusion product of the bract and seed scale. However, the late point of development and the vasculature within the ventral bulge definitively exclude this. The ventral bulge is always formed later than the ovules and even after pollination. Thus, it cannot produce or carry the ovules. Furthermore, it does not have its own independent vascular strand bundle. The vascular bundle strand supplying the ventral bulge results from one basal, dichotomous branching of the collateral bundle strand supplying the cone scale. This and the collateral structure of the vascular bundle, which is typical for a leaf, exclude the shoot character of this bulge. If the ventral bulge would reflect an ovuliferous short shoot, then it would be likely that its vasculature is concentric as is typical for a shoot axis, and that it is not formed by a dichotomous branching of a collateral one. Thus, the cone scale and its secondary developed ventral bulge are not representing a fusion product of the bract and seed scale. The cone scale represents exclusively a leaf (= bract scale), which is carrying axillary the ovuliferous short shoot (= seed scale), which is however reduced to the ovules. The formation of the ventral bulge is urgently needed to close the cone soon after pollination, so that the ovules can develop well protected within the closed cone (Jagel & Dörken 2014, 2015a, 2015b).

In contrast to apical proliferations, which are representing just a simple vegetative elongation of the cone axis, axillary proliferations are, however, quite important for suggesting evolutionary scenarios and to gain new insides into the original branching pattern of the respective type of coniferous seed cones. However, such axillary proliferations are exceptionally rare. By chance one of the investigated teratological *C. vietnamensis* seed cones showed such an axillary proliferation, which was inserted exactly in the same position where normally the axillary row of ovules is developed. A comparable vegetative axillary proliferation of seed cones was described for *Metasequoia glyptostroboides* Hu & W.C.Cheng (Cupressaceae, Coniferales) (Neubauer 1976; Dörken 2011). Dörken (2011) showed that the developmental sequence of the inserted leaves at the axillary proliferated shoot axis is similar with those of the ovules which are arranged in a single axillary row. Thus, Dörken (2011) suggested that such axillary proliferations are representing a homologous replacement of a single row of ovules by a sterile axillary foliar short shoot. The leaf-like structures inserted at the proliferated shoot axis were suggested to represent sterile leaf-like shaped ovules. Furthermore, Dörken's investigations of such axillary proliferations clearly show that ovules can occur in the position of leaves and perfectly replace them in the orientation and general structure. This is an important finding, because it can explain the occurrence of non-axillary ovules as they occur in some Cupressaceae genera, e.g. *Tetraclinis* or *Juniperus* (Jagel & Dörken

2014, 2015a, 2015b). Contrasting to *Metasequoia* with leaves arranged in two parastichies, in *Cupressus vietnamensis* four parastichies are developed, which makes it quite difficult to explain the scale leaves at the proliferated shoot axis as leaf like shaped sterile ovules as is suggested for *Metasequoia*, because in *Cupressus vietnamensis* significant differences in the developmental sequence of ovules and trophophylls exist. Despite this, the axillary vegetative proliferations of *C. vietnamensis* can be regarded as an atavism, which might reflect the primitive condition in Cupressaceae seed cones with an ovuliferous short shoot showing an elongated shoot axis which was inserted in the axil of a leaf. In most derived Cupressaceae the axis of the ovuliferous shoot is strongly reduced so that the ovuliferous short shoot is reduced to its ovules, as is also suggested by e.g. Jagel (2002), Jagel & Dörken (2014, 2015a, 2015b) or Dörken & Jagel (2017). Thus, these axillary proliferations found in *C. vietnamensis* seed cones leads to the hypothesis that the original structure of cupressaceous seed cones was a more open, loose inflorescence which was strongly reduced and modified so that finally the compact seed cones of living Cupressaceae species was formed.

5 Conclusion

Teratological seed cones of *C. vietnamensis* were investigated showing two types of vegetative proliferations, apical and axillary. It was shown that the apical proliferation represents just a vegetative elongation of the cone axis, which maintained a longer period of growth, and was not used up by the formation of the distal cone scales. However, the apical proliferation shows a full transitional series from basal most cone scale-like sterile peltate leaves to distal most decussate scaly trophophylls which show all structural changes from a sterile trophophyll to a fertile peltate cone scale. The axillary proliferation, however, is regarded to represent an atavism and it is suggested that the primitive condition of cupressaceous seed cones was an open and loose, polyaxial inflorescence, which became strongly reduced, so that in most derived Cupressaceae species the ovuliferous axillary short shoot (= seed scale) is reduced to its ovules so that finally a compact seed cone is formed.

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Bibliography

Bateman, R.M., J. Hilton & P.J. Rudall (2011). Spatial separation and developmental divergence of male and female reproductive units in gymnosperms, and their relevance to the origin of the angiosperm flower. *In:* Wanntorp, L. & L. P. Ronse DeCraene (eds): *Flowers on the tree of life:* 8-48. Systematics Association, Special Vol. 80. Cambridge University Press, Cambridge.

Bresinsky, A., C. Körner, J.W. Kadereit, G. Neuhaus & U. Sonnewald (2008). *Strasburger Lehrbuch der Botanik.* 36th ed. Spektrum, Heidelberg.

Caron, G.E. & G.R. Powell (1991). Proliferated seed cones and pollen cones in young black spruce. *Trees* 5: 65-74.

Dörken, V.M. (2011). Proliferating seed cones in *Metasequoia glyptostroboides* Hu & Cheng (Cupressaceae *s.l.*, Coniferales) elucidate the evolution of seed cones and ovules in Cupressaceae s.l. *Feddes Repert.* 122: 409-420.

Dörken, V.M. & A. Jagel (2017). Morphology, anatomy and morphogenesis of seed cones of *Cupressus vietnamensis* (Cupressaceae) and its taxonomic and systematic implications. *Flora* 230: 47-56.

Dörken, V.M. & A. Jagel (2014). Orientation and withdrawal of pollination drops in the Cupressaceae s. l. (Coniferales). *Flora* 209: 34-44.

Eckenwalder, J.E. (2009). *Conifers of the World*. Timber Press, Portland.
Farjon, A. & S. Ortiz-Garcia (2003). Cone and ovule development in *Cunninghamia* and *Taiwania* (Cupressaceae sensu lato) and its significance for conifer evolution. *Amer. J. Bot.* 90: 8-16.
Farjon, A. (1984). *Pines, drawings and descriptions of the genus* Pinus. Brill, Leiden.
Farjon, A. (1990). *Pinaceae. Drawings and descriptions of the genera* Abies, Cedrus, Pseudolarix, Keteleeria, Nothotsuga, Tsuga, Cathaya, Pseudotsuga, Larix *and* Picea. Koeltz Scientific Books, Königstein.
Farjon, A. (2005). *A monograph of Cupressaceae and* Sciadopitys. Royal Botanic Gardens, Kew.
Farjon, A. (2008). *A natural history of conifers*. Timber Press, Portland.
Farjon, A. (2010). *A handbook of the world's conifers*. Vol. I & II. Brill, Leiden.
Florin, R. (1951). Evolution in cordaites and conifers. *Acta. Horti Berg.* 17: 7-37.
Florin, R. (1954). The female reproductive organs of conifers and taxads. *Biol. Rev. Cambridge Philos. Soc.* 29: 367-389.
Franck, D.H. (1976). The morphological interpretation of epiascidiate leaves: An historical perspective. *Bot. Rev.* 42: 345-388
Fukushima K. & M. Hasebe (2014). Adaxial-abaxial polarity: The developmental basis of leaf shape diversity. *Genesis* 52: 1-18.
Gadek, A.P., D.L. Alpers, M.M. Heslewood & C.J. Quinn (2000). Relationships within Cupressaceae sensu lato: a combined morphological and molecular approach. *Amer. J. Bot.* 87: 1044-1057.
Gerlach, D. (1984). *Botanische Mikrotomtechnik, eine Einführung*. 2nd ed. Thieme, Stuttgart.
Gleissberg, S., E.P. Groot, M. Schmalz, M. Eichert, A. Kölsch & S. Hutter (2005). Developmental events leading to peltate leaf structure in *Tropaeolum majus* (Tropaeolaceae) are associated with expression domain changes of a YABBY gene. *Developm. Genes Evol.* 215: 313-319
Herzfeld, S. (1914). Die weibliche Koniferenblüte. *Österr. Bot. Z.* 64: 321-358.
Jagel, A. & V.M. Dörken. (2014). Morphology and morphogenesis of the seed cones of the Cupressaceae - part I: Cunninghamioideae, Athrotaxioideae, Taiwanioideae, Sequoioideae, Taxodioideae. *Bull. Cupressus Conservation Proj.* 3: 99-121.
Jagel, A. & V.M. Dörken. (2015a). Morphology and morphogenesis of the seed cones of the Cupressaceae - part II: Cupressoideae. *Bull. Cupressus Conservation Proj.* 4: 51-78.
Jagel, A. & V.M. Dörken. (2015b). Morphology and morphogenesis of the seed cones of the Cupressaceae - part III: Callitroideae. *Bull. Cupressus Conservation Proj.* 4: 91-108.
Jagel, A. & Th. Stützel (2003). On the occurrence of non-axillary ovules in *Tetraclinis articulata* (Vahl) Mast. (Cupressaceae s.str.). *Feddes Repert.* 114: 497-507.
Jagel, A. (2002). *Morphologische und morphogenetische Untersuchungen zur Systematik und Evolution der Cupressaceae s.l. (Zypressengewächse)*. PhD-thesis, Ruhr-University Bochum.
Jagel, A., & Th. Stützel (2001). Zur Abgrenzung von *Chamaecyparis* Spach und *Cupressus* L. (Cupressaceae) und die systematische Stellung von *Cupressus nootkatensis* D. Don [= *Chamaecyparis nootkatensis* (D. Don) Spach]. *Feddes Repert.* 112: 179-229.
Leins, P. & C. Erbar (2008). *Blüte und Frucht: Morphologie, Entwicklungsgeschichte, Phylogenie, Funktion, Ökologie*. 2nd edn. Schweizerbart´sche Verlagsbuchhandlung, Stuttgart.
Leins, P. & C. Erbar (2010). *Flower and fruit: morphology, ontogeny, phylogeny, function and evolution*. Schweizerbart´sche Verlagsbuchhandlung, Stuttgart.
Mundry, I. (2000). Morphologische und morphogenetische Untersuchungen zur Evolution der Gymnospermen. *Biblioth. Bot.* 152.
Natho, G., Müller C, Schmidt H (1990). *Morphologie und Systematik der Pflanzen. Teil 2 (L-Z).* UTB Gustav Fischer Verlag, Stuttgart.
Neubauer, H. F. (1976). Über Zapfen und Zapfenmißbildungen bei *Metasequoia*. *Bot. Jahrb. Syst.* 95: 321-326.
Owens, J.N. (2008). *The reproductive biology of western larch*. The Inland Empire Tree Improvement Cooperative, Victoria (B.C.).

Page, C.N. (1990). Gymnosperms. *In:* Kubitzky, K. (ed.): *The Families and Genera of Vascular Plants* 1: 279-391. Springer, Berlin, Heidelberg.
Pilger, R. (1926). Coniferae. *In:* Engler, A., *Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten insbesondere der Nutzpflanzen*, Engelmann, Leipzig.
Rudall, P.J., J. Hilton, F. Vergara-Silva & R.M. Batmemann (2011). Recurrent abnormalities in conifer cones and the evolutionary origins of flower-like structures. *Trends Pl. Sci.* 16: 151-159.
Schuhmann, K. (1902). Ueber die weiblichen Blüten der Coniferen. *Verhandl. Bot. Ver. Prov. Brandenburg* 44: 5-79.
Schulz, Ch. & Th. Stützel (2007). Evolution of taxodiaceous Cupressaceae. *Org. Divers. Evol.* 7: 124-135.
Schweitzer, H.J. (1963). Der weibliche Zapfen von *Pseudovoltzia liebeana* und seine Bedeutung für die Phylogenie der Koniferen. *Palaeontographica Abt. B* 113: 1-29.
Stützel, Th. & I. Röwekamp (1997). Bestäubungsbiologie bei Nacktsamern. *Palmengarten* 61(2): 100-110.
Stützel, Th. & I. Röwekamp (1999). Bestäubungsbiologie bei Nacktsamern (Gymnospermen). *In:* Zizka, G. & S. Schneckenburger, Blütenbiologie - faszinierendes Miteinander von Pflanzen und Tieren. *Kleine Senckenberg-Reihe* 33: 107-117.
Takaso, T. & P.B. Tomlinson (1992). Seed cone and ovule ontogeny in *Metasequoia*, *Sequoia* and *Sequoiadendron* (Taxodiaceae, Coniferales). *Bot. J. Linn. Soc.* 109: 15-37.
Throm, G. (2007). *Grundlagen der Botanik*, 2te Aufl. Nikol, Hamburg.
Tosh, K.J. & G.R. Powell (1986). Proliferated, bisporangiate, and other atypical cones occurring on young, plantation-grown *Larix laricina*. *Can. J. Bot.* 64: 469–475.
Troll, W. (1932). Morphologie der schildförmigen Blätter. *Planta* 17: 153-314.

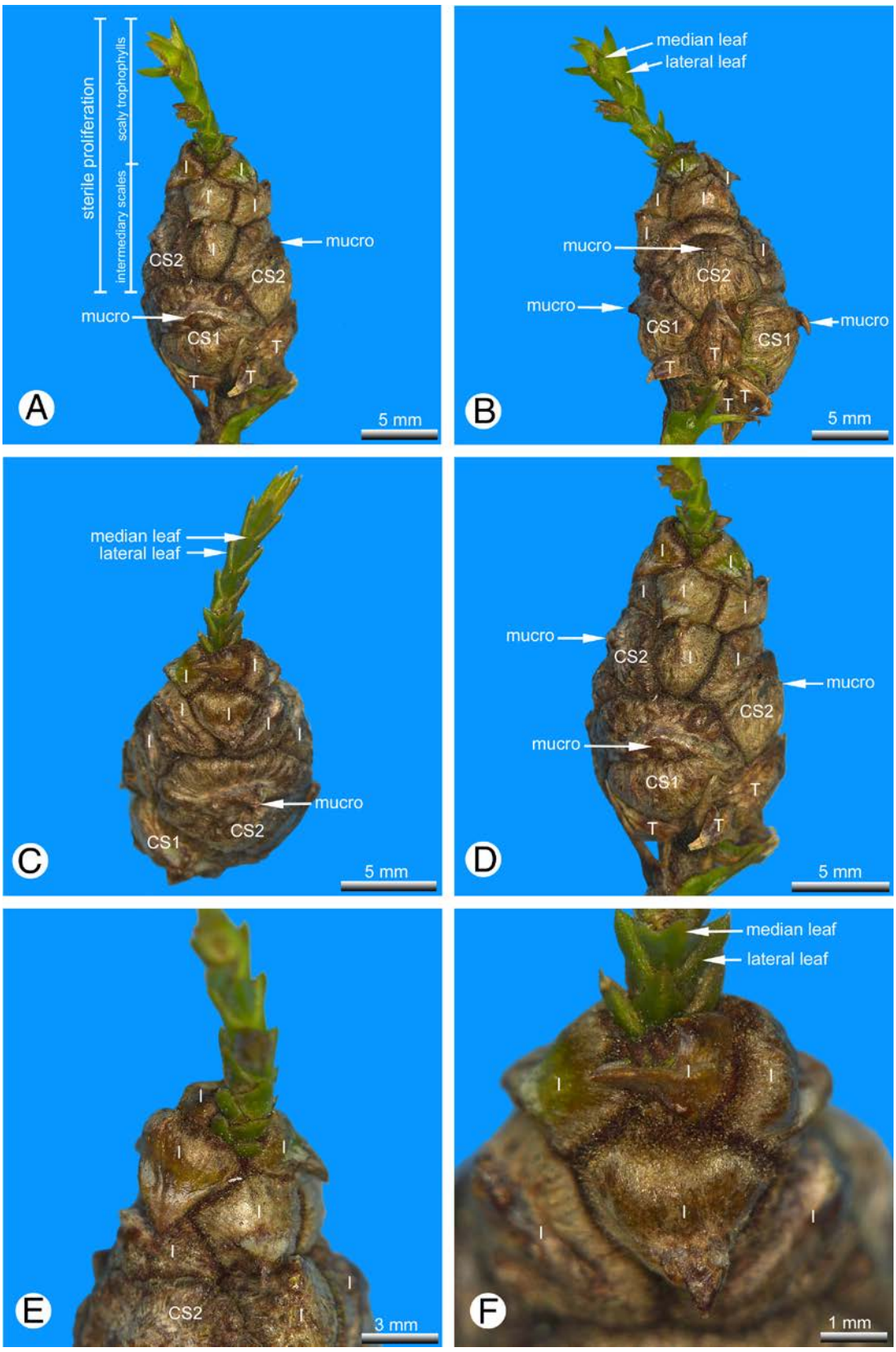

Fig. 1: *Cupressus vietnamensis*, apical proliferation.

A-D: Seed cone in different views; **E-F:** Detail of the distal part, showing several intermediary leaves leading towards the scaly trophophylls at the proliferation (CS1 = first pair of fertile cone scales; CS2 = second pair of fertile cone scales; I = intermediary scales; T = transitional leaf).

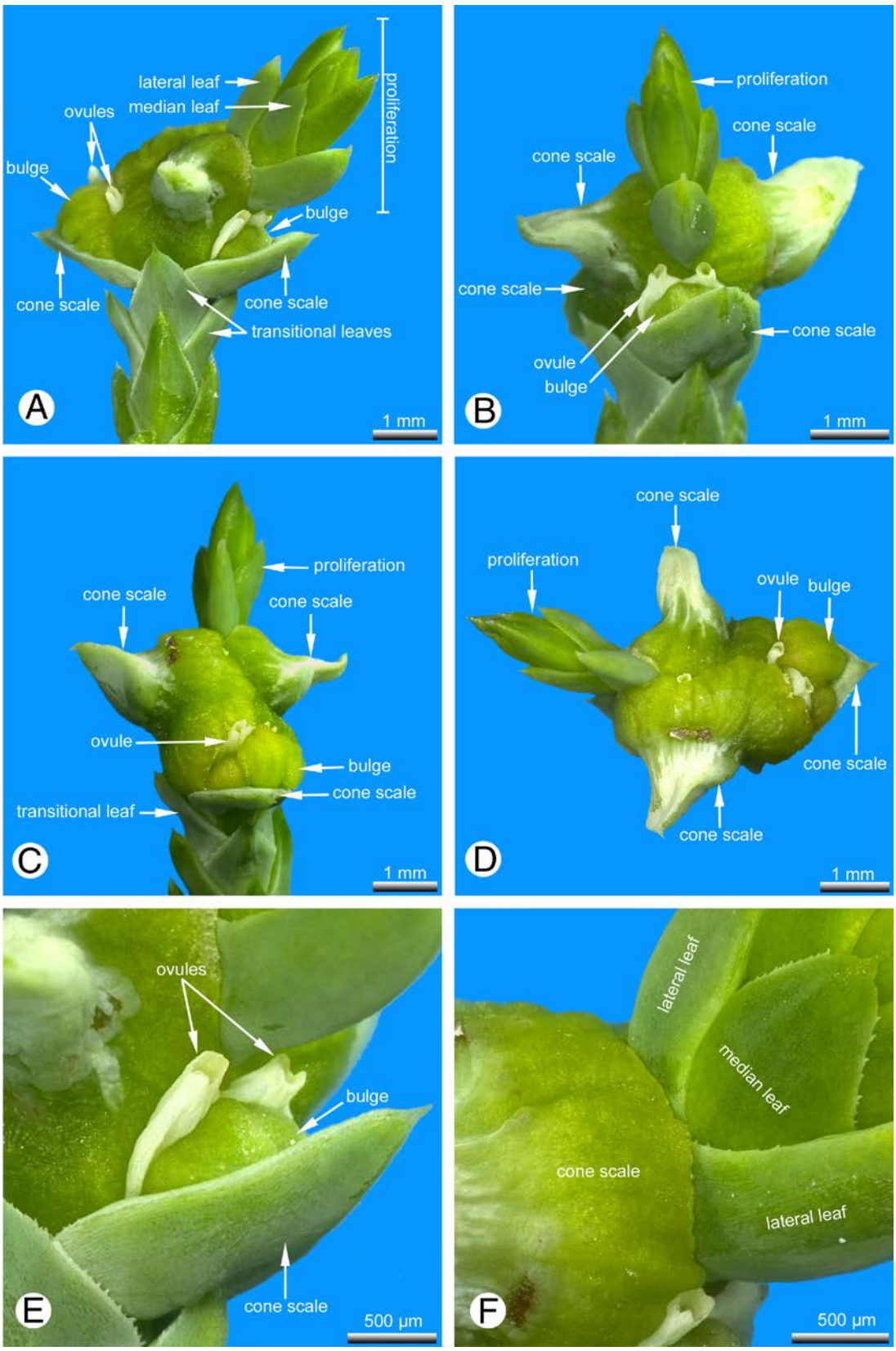

Fig. 2: *Cupressus vietnamensis*, axillary proliferation in one of the distal cone scales. **A-D:** Proliferated seed cone in different views; **E:** Detail of a cone scale of the lower pair with two ovules and a distinct ventral bulge; **F:** Basal part of the proliferation.

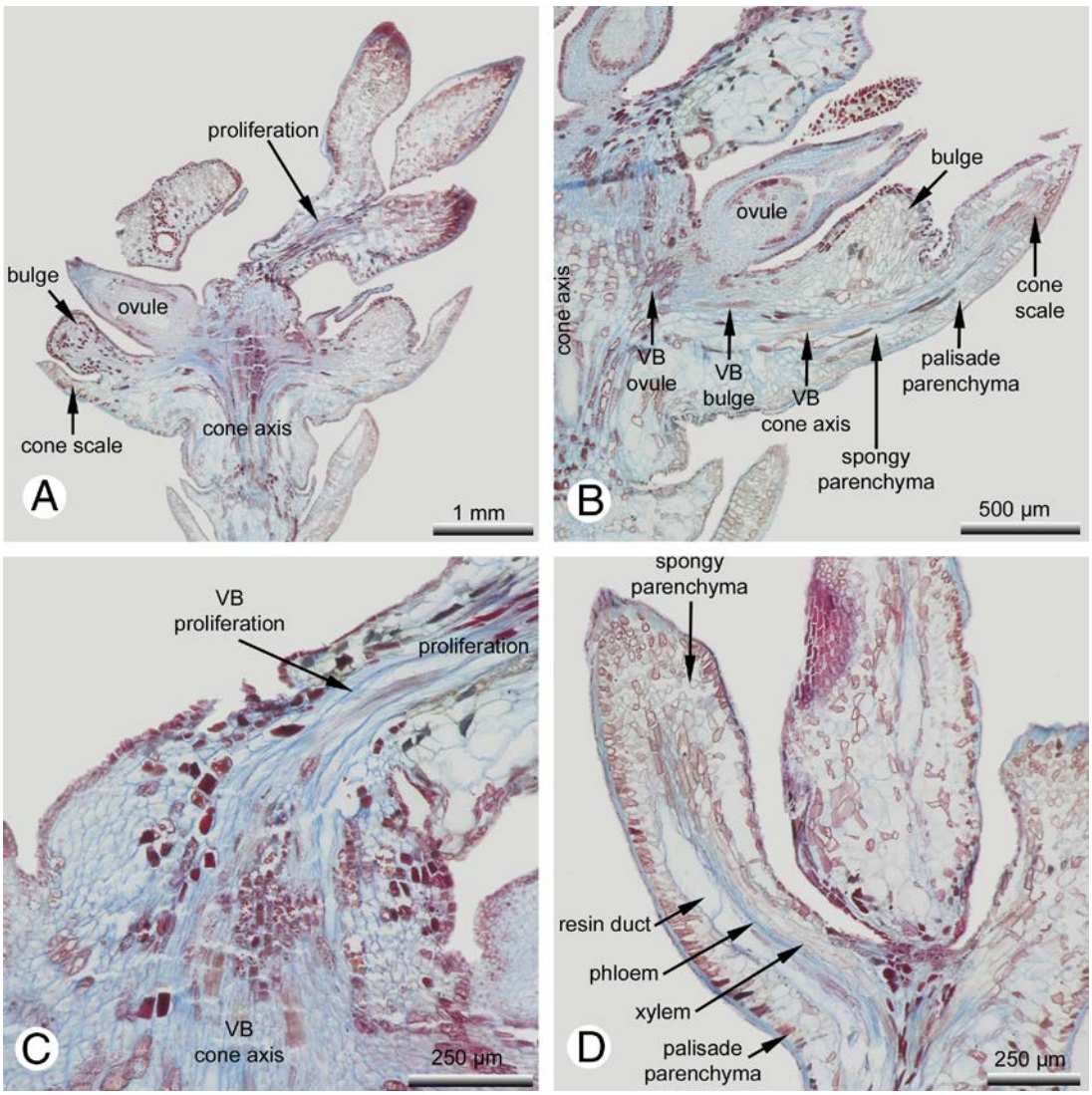

Fig. 3: *Cupressus vietnamensis*, anatomy (longitudinal sections) of the seed cone illustrated in Fig. 2.

A: Median section of the cone axis showing the basal fertile pair of cone scales and the axillary proliferation in the subsequent pair of cone scales; **B:** Detail of a fertile cone scale of the lower pair, each the ovule, the ventral bulge and the cone scale are supplied by a separate vascular bundle (VB); **C:** Detail of A; vascular detail of the transitional zone between the cone axis and the proliferation; **D:** Detail of a scaly trophophyll inserted at the proliferation.