

The evolutionary relevance of vegetative long-shoot/short-shoot differentiation
in gymnospermous tree species

von
Veit Martin Dörken

1. Auflage

The evolutionary relevance of vegetative long-shoot/short-shoot differentiation in gymnospermous tree species –

schnell und portofrei erhältlich bei [Dörken
beck-shop.de](http://beck-shop.de) DIE FACHBUCHHANDLUNG

Schweizerbart, E. 2012

Verlag C.H. Beck im Internet:

www.beck.de

ISBN 978 3 510 48032 6

4 Discussion

4.1 Correlation between shoot differentiation and deciduousness

The results show a distinct correlation between deciduousness and vegetative shoot differentiation. Almost all of the investigated deciduous angiospermous tree species have a shoot differentiation. Only in less than 1 % of the deciduous taxa is it absent. In most of the evergreen angiospermous tree species a shoot differentiation is also absent. Most of the evergreen angiospermous taxa with a shoot differentiation show metamorphosis of the long-shoot leaves as they occur in *Berberis*. In all *Berberis*-species, the long-shoot leaves are metamorphosed to thorns. Due to this, the development of short-shoots is the only possibility to develop assimilating foliage. Therefore the shoot differentiation in spite of an evergreen habit is extremely necessary in this group.

Regarding the results for recent gymnospermous tree species in comparison to angiospermous trees, such a close angiosperm-like correlation between shoot differentiation and deciduousness does not exist. In this group, deciduousness is a rare feature today. The nine investigated deciduous taxa show a distinct shoot differentiation. Due to this, deciduousness in gymnosperms is always closely correlated with shoot differentiation. However, the shoot differentiation varies from angiospermous tree species also by being developed in several evergreen taxa.

4.2 Correlation between long- and short-shoots

In general, there is some ambiguity using the terms “long-shoot” and “short-shoots”. Regarding the length-frequency diagrams, two different types of shoot-differentiations exist. In some species, especially in most shoot-differentiated gymnosperms – e.g., *Cedrus* (Fig. 9D), *Larix* (Fig. 9F) and *Ginkgo* (Fig. 9E) – the dimorphism in length between long- and short-shoots is so extreme that intermediary forms are generally absent. The diagram shows a significant gap between both types of shoots. This gap can be absent, but then the two peaks have to be separated by a distinct local maximum. However, in other shoot-differentiated taxa, intermediate forms between long- and short-shoots are present, e.g., *Quercus phellos* (Fig. 8C), *Nothofagus obliqua* (Fig. 6J) or *Nothofagus dombeyi* (Fig. 6H). But

the diagrams for these taxa show two significant peaks, one pronounced and narrow short-shoot peak and one significant shorter and much wider long-shoot peak. In some groups – e.g., the sequoioid and taxodioid Cupressaceae (Gymnospermae) – long- and short-shoots are only separated by a small gap or a distinct local minimum. It seems that, in these groups, the terms “long-” and “short-shoot” were used for different reasons and not only according to their relative length. In shoot-differentiated Cupressaceae – e.g., *Glyptostrobus* (Fig. 15B), *Metasequoia* (Fig. 15C) and *Taxodium* (Fig. 15F) – the short-shoots are abscised at the end of the vegetation period together with the inserted leaves as a unit. The long-shoots are persisting. Due to this, long-shoot leaves are abscised separately. These results are conform to the definition given by BÖCHER (1964), who defined the short-shoots in *Metasequoia* “...as the ultimate unbranched shoots which always have closely spaced, distichously arranged leaves, are always shed and never produce buds or any kinds of phellogenesis...”.

The results of the present investigation show that the terms “long-shoot” and “short-shoot” should only be used if the short-shoots are standing in a definite position to the long-shoot. The total length of a shoot cannot be used as the single criterion for classification of both types of shoots (WAGENITZ 2008). Due to this, the terms “long-” and “short-shoots” are correlative and cannot be used independent from each other as it is frequently done. Never the less it is not unusual that in textbooks and determination keys (e.g., MELCHIOR & WERDERMANN 1954; SCHULTZE-MOTEL 1992; SCHÜTT et al. 2002; BRESINSKY et al. 2008) phrases like “...has only long-shoots...” for descriptions for *Picea* and *Abies* are used. This might be explained by the fact that in length-frequency diagrams the entire diagram, for homogenous shoots of non-differentiated taxa matches perfectly with the long-shoot part in diagrams of shoot-differentiated taxa. For both types of shoots, the diagram shows a wide range with a maximum in more or less in middle part. Following this, the term “long-shoot” for non-shoot-differentiated taxa is used on only a comparative basis, without relation to the true morphological situation in the branching system. But it should be taken into account that long-shoots are similar to the monomorphic shoots in non-differentiated shoot systems. Regarding the results of the annual investment in shoot biomass per cm² leaf area, no differences can be found between the two types of shoots.

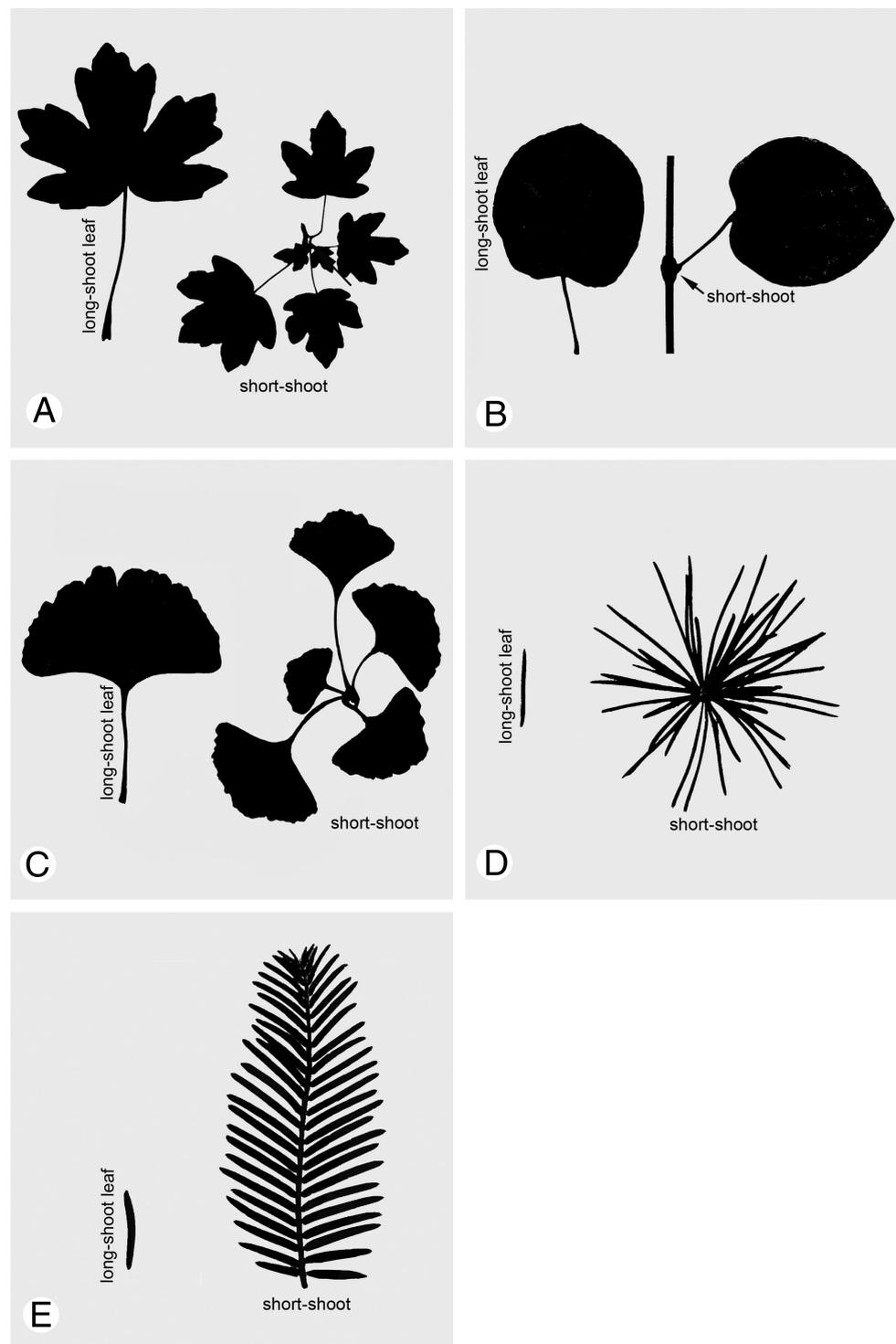


Fig. 34: Short-shoot types in angiospermous (A, B) and gymnospermous tree species (C–E). **A:** *Acer campestre* representing the common type of short-shoots in angiospermous tree species; short-shoots with several leaves; the total leaf area similar to the leaf area of a single long-shoot leaf; **B:** *Cercidiphyllum japonicum* representing the *Cercidiphyllum*-type of short-shoots; each short-shoot develops only a single-leaf per year that equals a long-shoot leaf in area and shape; **C:** *Ginkgo biloba*; the *Ginkgo*-type complies for the situation typical for angiospermous tree species; **D:** *Larix decidua* representing the Pinaceae-type; several leaves per short-shoot; shoot axis strongly reduced; **E:** *Metasequoia glyptostroboides* representing the Cupressaceae-type with several leaves inserted on a well developed short-shoot axis, internodes visual; terminal bud absent; in D and E the total leaf area of a short-shoot exceeds the leaf area of a single long-shoot leaf by about the factor 80.

Regarding the length-frequency diagrams for the investigated angiospermous tree species, they show that, in most taxa, intermediary forms between long- and short-shoots exist. Exceptional in *Cercidiphyllum* (Fig. 6D) and *Tetracentron* (Fig. 8H), the dimorphism is so distinct that intermediary forms are absent. Both taxa have only weakly developed short-shoots, each with only a single folious leaf per year (cataphylls excepted) which equals the long-shoot leaf in area and shape (Fig. 2).

The length-frequency diagrams show that in the investigated gymnospermous families Pinaceae and Ginkgoaceae the dimorphism is so distinct that intermediate forms between both types of shoots are absent. Only in Cupressaceae types – e.g., *Metasequoia* (Fig. 9G), *Sequoia* (Fig. 10D) and *Taxodium* (Fig. 10E) – intermediate forms exist. In these taxa the differences in length between long- and short-shoots are not as significant. Long-shoots have nearly only double the length of short-shoots.

Long- and short-shoots show significant differences in annual investment in shoot biomass. In angiospermous tree species, the annual investments in shoot biomass vary greatly in interspecific comparisons. The largest difference is represented by *Cercidiphyllum japonicum*, with its typical single-leaved short-shoots (Tab. 3). The values for annual investment in shoot biomass also vary significantly in interspecific comparisons in gymnospermous tree species. In this group, the greatest difference exists in *Ginkgo biloba*. *Metasequoia glyptostroboides* and *Taxodium distichum* illustrate only slight differences between both types of shoots.

In angiospermous (Fig. 11A–C) as well as in gymnospermous tree species (Fig. 11D–F), the shoot differentiation is strongly influenced by the individual's age. In both groups, the shoot differentiation is well developed in the middle part of the crown development (Fig. 11B, E). In mature trees, all shoots are more or less homogenous and short-shoot-like (Fig. 11C, F). One big difference exists between angiospermous and gymnospermous tree species: The number of short-shoots at young angiospermous trees (Fig. 11A) is reverse to the situation on young gymnospermous trees. Even at young gymnosperms, short-shoots significantly dominate the shoot system (Fig. 11D).

The results show different types of shoot differentiations in angiospermous and gymnospermous trees. In angiospermous tree species, two different types of shoot differentiation exist. First, the most common is found in all shoot-differentiated species (Fig. 34A), except *Cercidiphyllum* and *Tetracentron*. Between long- and short-shoots, several intermediary forms are devel-

oped. Several leaves are inserted on each short-shoot. These leaves are distinctly smaller than the long-shoot leaves. The second type of shoot-differentiation in angiosperms shows a strict dimorphism in shoot differentiation without intermediary forms between long- and short-shoots (Fig. 34B). At the short-shoots, only a single leaf is inserted, whose area and shape perfectly mirror the long-shoot leaf. This type of shoot differentiation is very rare and only exists in *Cercidiphyllum* and *Tetracentron*. Within gymnosperms, three different types of shoot differentiation can be found. Metamorphoses like e.g., cladode formations are excluded here. The first type of gymnospermous shoot differentiation is herein referred to as Pinaceae-type, with a strict dimorphism in long- and short-shoots (Fig. 34D). Intermediary forms are absent. The short-shoots have no visual internodes. The assimilating leaves are needle-like. This type of shoot differentiation can be found in *Cedrus*, *Larix*, *Pinus* and *Pseudolarix*. The second one, the Ginkgoaceae-type, also has a strict shoot dimorphism between both types of shoots. Intermediary forms are absent (Fig. 34C). However, the leaves are folious with a dichotomous branching of veneration. This type of shoot differentiation is represented only by *Ginkgo biloba*. The third one is the Cupressaceae-type (Fig. 34E). Several intermediate forms are developed between long- and short-shoots. Short-shoots have visual internodes and needle leaves. Short-shoot leaves are not abscised separately. They are abscised together with the short-shoot axis as a unit. The long-shoot leaves, however, are abscised separate from the individuals.

4.3 Correlation between long- and short-shoot leaves

The results show that in angiospermous as well as in gymnospermous tree species several leaves are inserted at a short-shoot (Tab. 4). Single-leaved short-shoots are limited to *Cercidiphyllum* (Cercidiphyllaceae, Angiospermae) and *Tetracentron* (Tetracentraceae, Angiospermae) and are generally absent in gymnosperms except *Pinus monophylla*. In angiospermous tree species, long-shoot leaves generally have a significantly larger area than the short-shoot leaves (Tab. 5). In gymnospermous tree species, only *Ginkgo biloba* (Tab. 5) shows a similar situation as exists in angiospermous tree species. In shoot-differentiated gymnospermous tree species short-shoot leaves are slightly larger as long-shoot leaves.

In the investigated angiospermous trees, the annual investment in shoot biomass per long- and short-shoot leaf varies strongly in interspecific comparisons (Tabs 6, 7). In angiospermous trees without shoot differentiation the annual investment in shoot biomass per leaf also ranges significantly in interspecific comparisons (Tab. 9). In the investigated gymnosperms, the annual investments in shoot mass per long-shoot leaf vary only slightly in interspecific comparisons contrasting to angiospermous tree species (Tab. 6). Contrasting to annual investments in shoot biomass per single short-shoot leaf in angiospermous tree species, gymnosperms show only slightly variations in interspecific comparisons (Tab. 7).

Regarding the values for 1 cm² long- and short-shoot leaf area in angiospermous tree species (Tab. 6), the annual investments in shoot biomass vary only slightly in interspecific comparisons. The annual investment in shoot biomass for 1 cm² short-shoot leaf area is always 10⁻¹ less than the annual investments in shoot biomass for 1 cm² long-shoot leaf area. In angiospermous trees without shoot differentiation (Tab. 9), the annual investment in shoot biomass per cm² leaf area also varies only slightly in interspecific comparisons. The values are similar to the annual investments in shoot biomass for 1 cm² long-shoot leaf area. In angiospermous tree species, a significant correlation between annual investments in shoot biomass and leaf area exists, and it seems that all investigated taxa are equally well adapted to the annual leaf fall. In this respect, *Cercidiphyllum japonicum* represents the “optimal” shoot differentiation of all investigated tree species.

In contrast to the homogenous situation in angiospermous tree species, the situation in gymnosperms differs significantly (Tab. 6). Regarding the values for annual investments in short-shoot biomass per cm² leaf area (Tab. 7), the interspecific comparisons show, however, only slight variations. Gymnosperms without shoot differentiation have, in interspecific comparisons, a distinct variation in the annual investment in the shoot mass per single leaf. Regarding, however, the annual investment in shoot biomass per 1 cm² leaf area in taxa without short-shoot differentiation (Tab. 9), the values are more or less monomorphic with only low variations. It seems that distinct correlations between annual investments in shoot biomass per leaf area exist only for short shoots and for homogenous shoots in non-differentiated shoot systems. In gymnospermous tree species no correlations between long-shoots and long-shoot leaves, as can be found in angiospermous tree species, exists. It might be possible that in previous times the long-shoot leaves in most gymnosper-

mous groups had larger leaf areas than today. In this case the situation in these previous gymnospermous tree species could have been similar to the situation in recent angiospermous tree species. This hypothesis is supported by the fact that sometimes well developed long-shoot leaves are presented in taxa which generally have only rudimentary developed long-shoot leaves (see also 4.5.2.6).

In angiospermous as well as in gymnospermous tree species the annual investment in shoot biomass for short-shoot leaves is distinctly less compared to the annual investment in shoot biomass for long-shoot leaves. In angiospermous tree species, the annual savings vary, in interspecific comparisons, from 60–96.7 % and in gymnosperms from 92.5–97.5 % (Tab. 10). This is of greatest interest especially in deciduous taxa, because here the annual investments in the foliage are significantly higher than those in evergreen taxa.

Another remarkable correlation exists between the leaf area of a single long-shoot leaf compared with the total leaf area of an entire short-shoot. In angiospermous tree species, the leaf area of a single long-shoot leaf is almost exactly the same as the total leaf area of an entire short-shoot (Tab. 11). In over 70 % of the investigated angiospermous taxa, the values vary in interspecific comparisons from 1:0.5 to 1:1.5. Extreme values with 1:0.3 or 1:2.5 have been only exceptionally measured. It is remarkable that the number of leaves per short-shoot is reverse proportional to the leaf area of the single-leaf. If the single short-shoot leaf is small, the number of inserted leaves per short-shoot is high. If the single-leaf is large, the number of inserted leaves per short-shoot is less. This applies also when short-shoots develop only one leaf per year. In this case, long- and short-shoot leaves perfectly equal each other in area and shape (*Cercidiphyllum* and *Tetracentron*). In gymnospermous tree species, such correlations do not exist. In this group, the total leaf area of a short-shoot is the multiple of the area of a single long-shoot leaf (Tab. 11). The values therefore vary in interspecific comparisons from 1:48 to 1:80.

The results show, that in angiospermous tree species, the long-shoot leaf will be replaced by the foliage of an entire short-shoot in nearly the same position in the following vegetation period but with significantly less annual investment in shoot mass. In this respect, only *Ginkgo biloba* represents an angiospermous-like situation. This could be explained by the large area of the single folious leaves. In the investigated gymnospermous tree species with only needle leaves (except *Pinus*), the leaf area of a single long-shoot leaf is nearly similar to the leaf area of a single short-shoot leaf (Tab.

11). In *Pinus* the long shoot leaves represent only rudimentary bracts.

The former results pose the question if anatomical and physiological differences exist between both types of leaves. Long-shoots mainly construct the crown and are only developed in the peripheral region of the crown. Short-shoots, however, are only developed in the inner region of the crown. They fill the crown secondarily. Due to this, it could have been assumed that long-shoot leaves are generally sun leaves and short-shoot leaves shade leaves. However, the anatomical investigations show no significant differences in the structure of both types of leaves. Of special interest are the thickness of palisade and spongy parenchyma. Sun leaves usually have more layers of palisade parenchyma, while in shade leaves the palisade parenchyma is thin and consists mostly only of a single layer. The results of the anatomical investigations show that there is no strict border concerning sun and shade leaves versus long- and short-shoot leaves (Figs 12, 13, 14).

In angiospermous tree species, the total leaf area of a short-shoot is equal to the single leaf area of a long-shoot leaf (Tab. 11). For evincing possible differences in the assimilation rates between a single long-shoot leaf and the total leaf area of an entire short-shoot, the total chlorophyll content has been measured. Taxa where the total leaf area of an entire short-shoot exceeds the leaf area of a long-shoot leaf, as well as taxa with single-leaved short-shoots were focused in this physiologic investigation. The results show that the total chlorophyll content of a long-shoot leaf matches more or less with those of all leaves of an entire short-shoot (Tab. 12B).

In angiospermous tree species, the results of the morphological, anatomical, and physiological investigations of leaves indicate that a long-shoot leaf is functionally replaced perfectly by all leaves of a short-shoot in the following vegetation period. Therefore, the shoot differentiation in deciduous trees is an important evolutionary adaptation to the annual leaf fall. Due to this, in evergreen species, there is no need to develop such a dimorphism in the shoot system. This could mean that recent evergreen taxa with distinct shoot differentiation could reflect a secondary feature. In this case, the shoot differentiation in combination with an evergreen habit could be best explained as reminiscent of a deciduous ancestor.

4.4 Shoot abscission and its evolutionary meaning

It seems not uncommon, that plants abscise old and dysfunctional organs actively, e.g., shoots, leaves, flowers. In most cases, special abscission tissues are developed (WITTA 1996; RUST & ROLOFF 2002, 2004; WILSON et al. 1998a, b; RUST et al. 2004; BURROWS et al. 2007). Shoot abscission is widely spread within angiospermous and gymnospermous tree species. To detect possible evidence that the shoot abscission in Cupressaceae should be used as an indicator for ancient deciduousness in this group, the process of shoot abscission in distantly related taxa (*Larix decidua*, Gymnospermae and *Quercus robur*, Angiospermae) was investigated.

4.4.1 Shoot abscission in *Quercus robur*, Fagaceae (Angiospermae)

In *Quercus robur*, a well developed abscission structure exists at the base of lateral branchlets (Fig. 24A). Thus, the lateral branchlets will be abscised at a special predefined breaking point. Below the base of the lateral shoot, a distinct annular furrow is detectable (Fig. 23B). In this zone, the xylem of the lateral shoot is only weakly developed and distinctly interrupted by a strongly developed abscission tissue. It consists of small living parenchymatic cells (Fig. 24A), which are rich in cellulose and poor in lignin. Due to this, the parenchyma is only less differentiated in the abscission zone. Due to the interrupted xylem of this region, the water flow occur only symplastically (Fig. 25).

Especially older trees with less annual growth of the shoots show an increase of shoot abscission. In mature trees, the shoot and leaf hydraulic conductance is significantly lower on weakly growing than on strongly growing shoots. In this context, the nodes and the abscission zones generally represent bottlenecks to the water flow in a shoot. Due to this, assimilation rates of older individuals are increased by reducing the hydraulic conductance of shoots (RUST & ROLOFF 2002, 2004; RUST et al. 2004). The annual abscission in *Quercus robur* affects only shoots with a hydraulic disadvantage compared to the assimilation rates. In *Quercus*, the abscission of leaved shoots is an important self-cleaning process for adjusting the canopy structure to keep the water balance.

4.4.2 Shoot abscission in *Larix*, Pinaceae (Gymnospermae)

The removal of shoots in *Larix* takes place without a special abscission structure or tissue (Fig. 21). The results of the anatomic investigations show that it is a passive process and should be therefore not called “abscission” as it is frequently done. Lateral shoots die back and remain dead on the axis for years. The shoots are passively removed from the individual by strong winds or by snow and ice mostly in winter. Due to this, a distinct stump of the lateral shoot always remains on the axis with an irregular breaking point (Fig. 21A). It seems that this passive shoot removal in *Larix decidua* is an important process in the self-cleaning process of the crown, to get rid of old and dysfunctional shoots, as is also the case for *Quercus robur*. It also has no evolutionary meaning for the initial hypothesis of this study.

4.4.3 Shoot abscission Cupressaceae (Gymnospermae)

Shoot abscission is very common in gymnospermous tree species and exists in several recent taxa. The abscission affects different types of shoots: short-shoots (e.g., *Metasequoia*, *Sequoia*), branches of second and third order (e.g., *Agathis*, *Araucaria*), or even primary branches (e.g., *Wollemia*). Studies in *Agathis* and *Araucaria* show that an active shoot abscission is an old feature in Araucariaceae BURROWS et al. (2007).

In *Metasequoia* (Fig. 35), all short-shoots with inserted needle leaves are shed in autumn (Fig. 15). In contrast to long-shoot leaves, short-shoot leaves are not abscised separately in this taxon. Remarkably, the same type of abscission also exists in evergreen Cupressaceae e.g., *Sequoia* (Fig. 36). But in evergreen taxa, the abscission of short-shoots takes place only in an irregular manner. It is remarkable that the short-shoot abscission in evergreen Cupressaceae happens in the same time when deciduous gymnospermous as well as angiospermous tree species shed their leaves. All Cupressaceae have distinct abscission structure below the base of the short-shoots or below the base of small lateral branchlets (Fig. 17). The basal parts of the short-shoots are greatly proliferated by parenchyma in the cortex, which is rich in cellulose and poor in lignin. This feature also exists in other groups; e.g., Araucariaceae (e.g., WILSON et al. 1998 a, b; BURROWS et al. 2007). In Cupressaceae a deep annular furrow is developed below the short-shoot base, representing a predefined breaking point. However, a special abscission tissue, as is developed in *Quercus robur*, is absent. In the region where the later abscission will take place, any changes

in the parenchyma can be detected. This is conform to BÖCHER (1964), who described the abscission of short-shoots in *Metasequoia* without any special separation layer. The short-shoots are cut off by the phellogen of the persisting long-shoots.

In Cupressaceae, the abscised short-shoots are replaced by serial descended accessory buds in the following vegetation period (Fig. 20). Serial buds are typical for deciduous and generally absent in evergreen taxa. In contrast to deciduous taxa, in typical evergreen taxa the inner part of the crown is leafless. Therefore, the occurrence of descended serial accessory buds in evergreen Cupressaceae is remarkable. The shoot abscission in evergreen Cupressaceae can generally be regarded as a self-cleaning process of the crown, to get rid of older short-shoots with reduced functionality (as is also the case for *Quercus robur* and *Larix decidua*). But in contrast to *Quercus* and *Larix*, the abscised short-shoots of Cupressaceae are replaced in nearly the same position. This renewal mode is very uncommon for evergreen taxa but widely spread within deciduous taxa. In evergreen Cupressaceae, this renewal mode could be best understood as a reminder of a deciduous ancestry. In this case, the deciduous condition of *Metasequoia glyptostroboides* would represent the primitive feature, while the morphologically very similar, but evergreen *Sequoia sempervirens* would represent the derived condition. This hypothesis is supported by the results of PITTERMANN et al. (2010), who have worked on the relationships between xylem safety and hydraulic efficiency in Cupressaceae and the evolution of the pit membrane. Their results show that drought tolerance in cupressoid as well as in callitroid clade represents a derived feature that has evolved in both groups separately from each other. Due to this result, it would not be very unlikely that a secondary adaptation to drought has led to the recent evergreen habit of *Sequoia sempervirens*. It might be possible that a mediteranisation of the climate with a short but not complete dormancy in summer and a continuous but cool or frosty period in winter could be the reason for shifting from deciduous to evergreen. BURROWS et al. (2007) explain the shoot abscission in *Wollemia nobilis* (Araucariaceae) also as an adaptive strategy restricted to the water supply to the foliage. In this context, the hydraulic conductivity of the xylem plays an important role, as is also described for *Quercus*.

The development of serial descended accessory buds in evergreen Cupressaceae (Gymnospermae) cannot only help to understand the evolutionary pathway from a possible deciduous ancestor towards the recent evergreen habit, but could also lead to a better

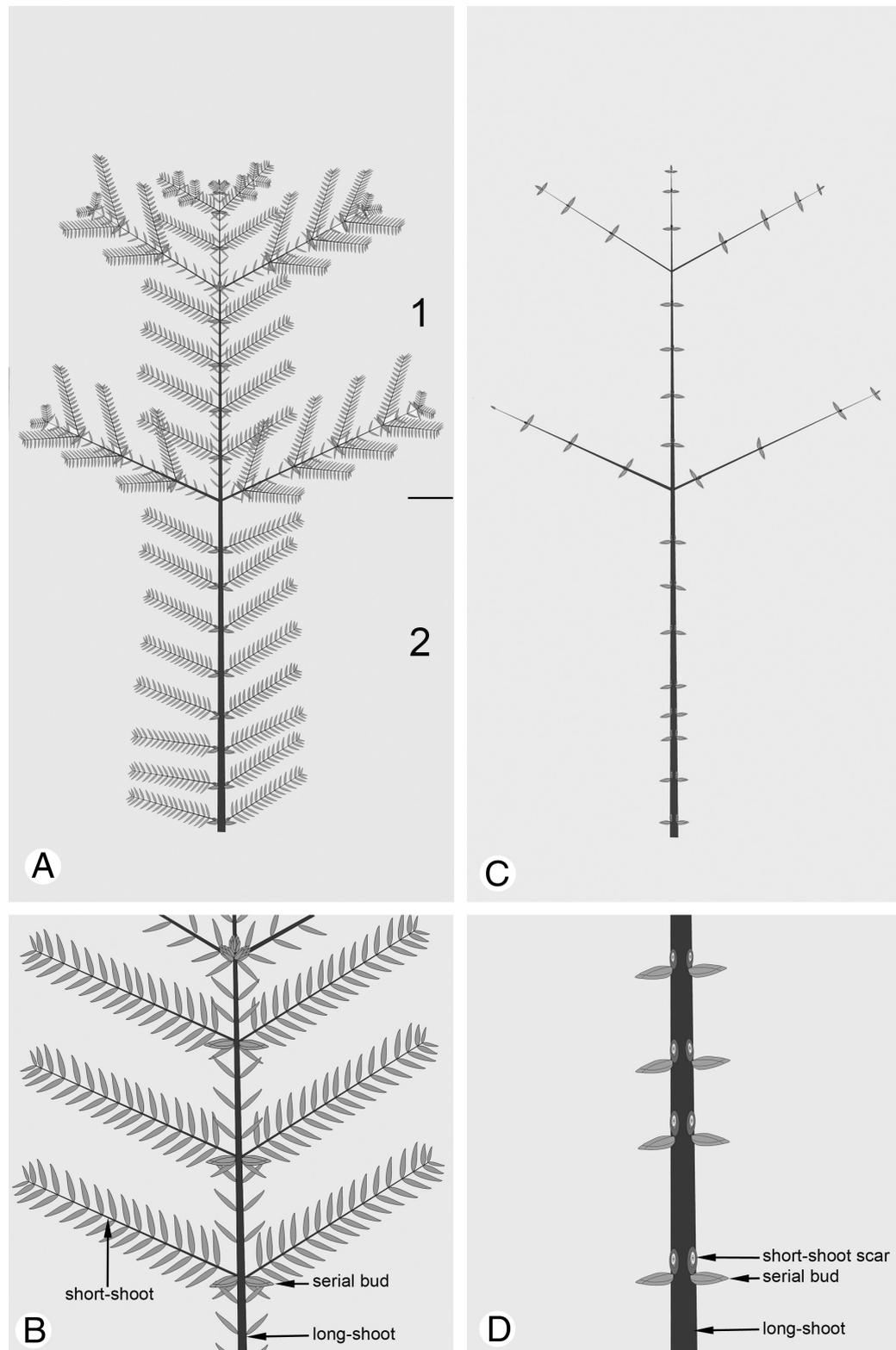


Fig. 35: Shoot abscission in *Metasequoia glyptostroboides* (deciduous); **A:** two-years-old branching system before abscission; **B:** detail of a long-shoot of the present year; a short-shoot as well as a serial descended accessory bud are inserted in the axil of each long-shoot leaf; **C:** two-years-old branching system after short-shoot abscission; in *Metasequoia* the annual abscission affects all short-shoots; **D:** detail of C; below the short-shoot scar a serial descended accessory bud is inserted, which forms in the next vegetation period again a short shoot in nearly the same position.

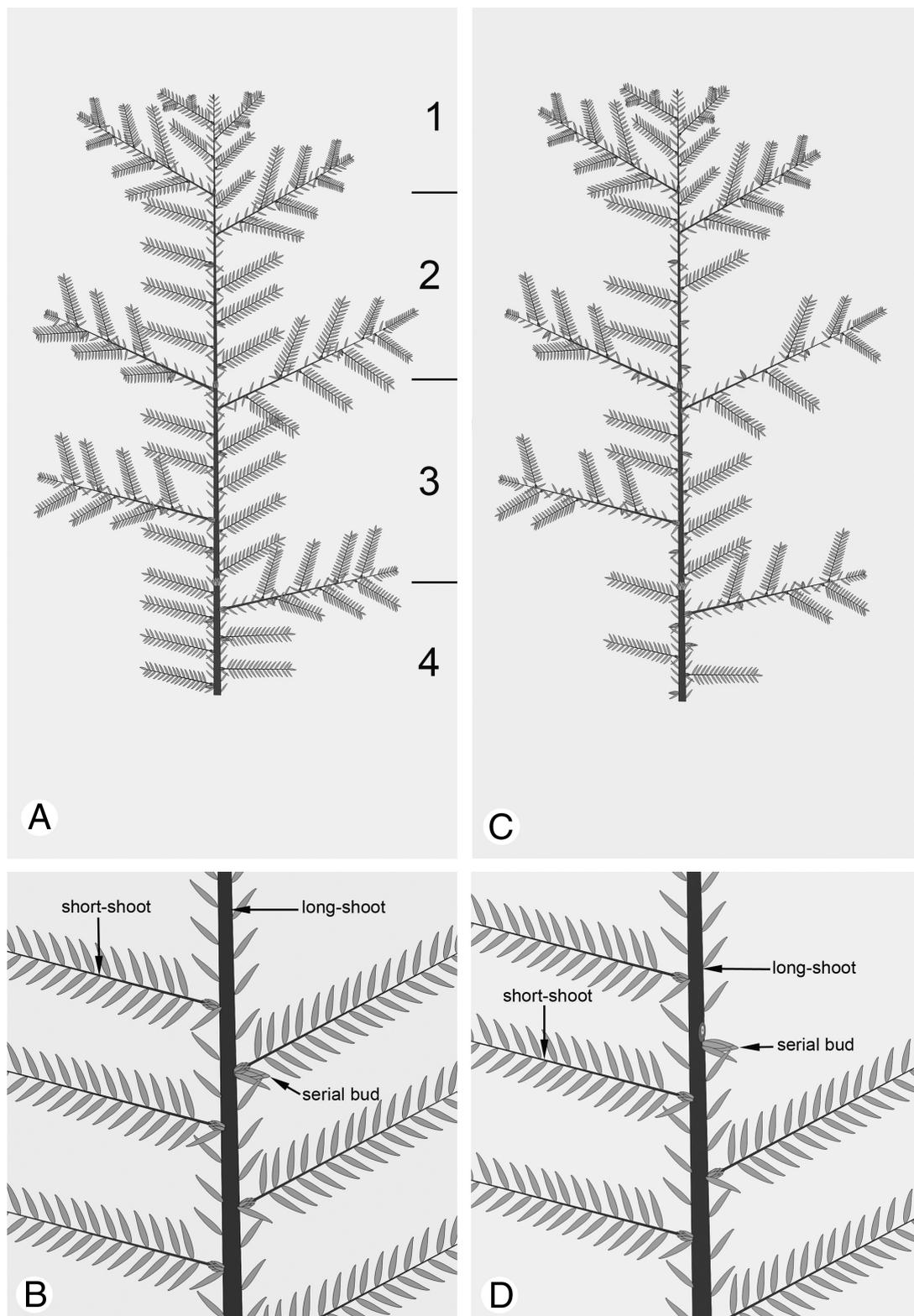


Fig. 36: Shoot abscission in *Sequoia sempervirens* (evergreen); **A:** four-years-old branching system before the annual abscission of short-shoots takes place; **B:** detail; in the axil of some long-shoot leaves a short-shoot as well as a serial descended accessory bud is inserted; **C:** branching system after short-shoot abscission; in *Sequoia* the annual abscission affects only some of the oldest short-shoots, the others remain on the tree; **D:** detail of C; short-shoot scar with a serial descended accessory bud below.

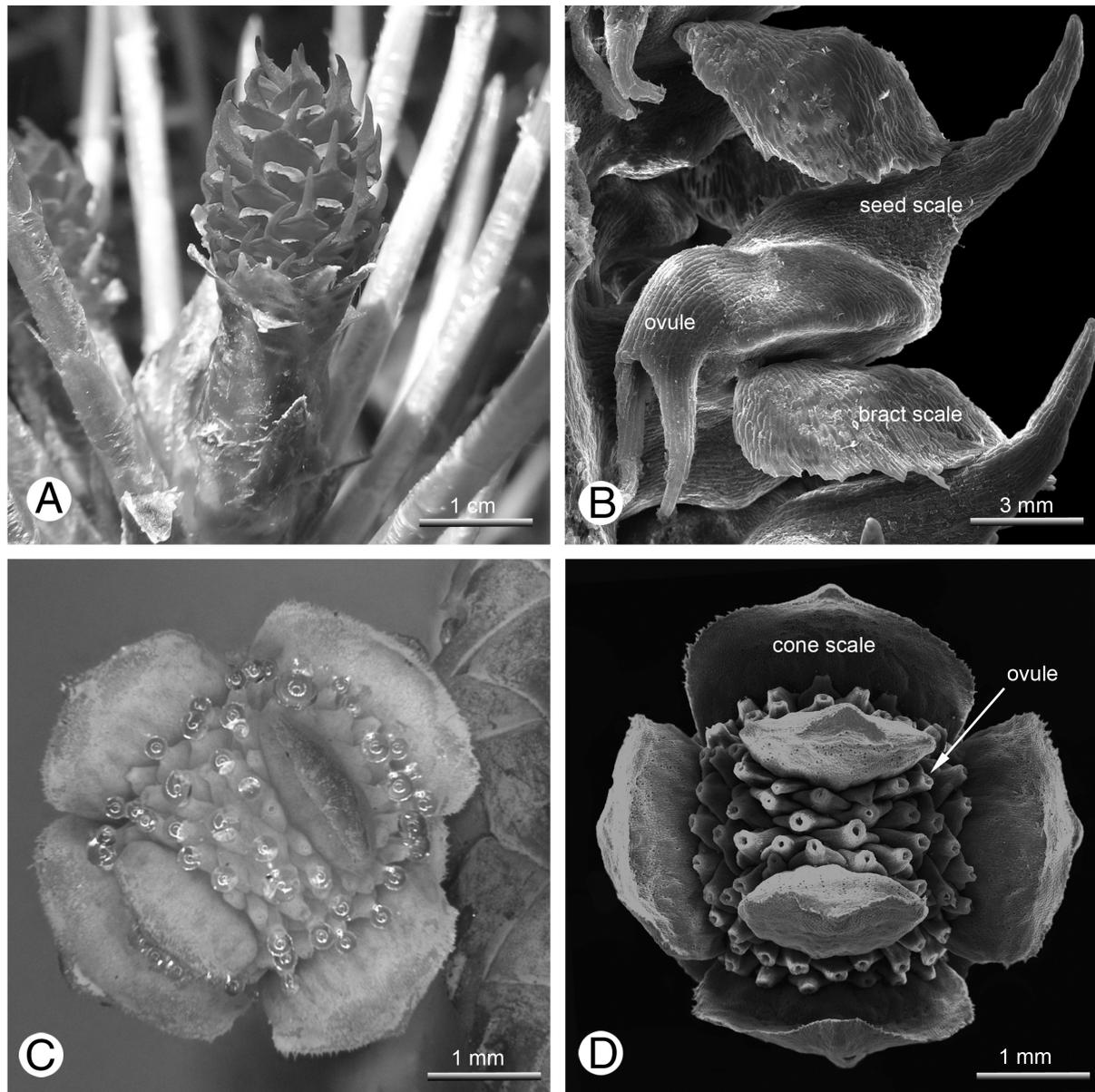


Fig. 37: Seed cones; **A, B:** seed cone of *Pinus mugo* at pollination time (**A**); seed cone with two types of scales; in the axil of the bract scale the seed scale is inserted; the seed scale is a greatly reduced short-shoot carrying the two ovules (**B**); **C, D:** seed cone of *Cupressus arizonica* at pollination time (**C**); the seed scale is greatly reduced to the ovules and only the bract scale can be recognized; in the axil of each cone scale several rows of ovules are inserted, which can be regarded as originated from a serial descended accessory bud; the ovule-carrying short-shoot axis is completely reduced.

understanding of reproductive structures, especially the female seed cones in Cupressaceae. In conifers, the cones consist of two types of cone scales. These are the bract scales in which axils the ovule-carrying seed scales are inserted (SCHUHMAN 1902; HERZFELD 1914; FLORIN 1954; SCHWEITZER 1963). Due to this, in recent taxa the bract scale has to be morphologic a reduced leaf, while the seed scale represents a reduced and

condensed short-shoot with phylloclade character. In Pinaceae, both types of scales are distinctly developed and can easily be detected (Fig. 37A, B). Due to this, a female seed cone in Pinaceae represents a branched system, which compromises an inflorescence in angiospermous taxa (STÜTZEL & RÖWEKAMP 1997; MUNDRY 2000). In contrast to Pinaceae, bract and seed scales cannot be detected in the seed cones in most genera of

Cupressaceae. Only one type of cone scales exists in this group today. The seed scales are strongly reduced to the ovules and can only be recognized as rudiments in a few recent taxa. Due to this, the seed cones in Cupressaceae consist of only one type of scales, which are called “cone scales” in the following. Like the seed cones in Pinaceae, the seed cones in Cupressaceae are also branched systems. In the axils of the cone scales in Cupressaceae, several ovules are inserted (Fig. 37C, D), sometimes in more than one row of ovules (TAKASO 1992; JAGEL 2002; FARJON & GARCIA 2003). The rows are developed centrifugally descent. Each row could be interpreted as a remainder of an ovule-carrying short-shoot, however with a completely reduced shoot axis. In this case, each row of ovules can be regarded as originating from a serial bud (JAGEL & STÜTZEL 2001a, b, 2003; JAGEL 2002; SCHULZ & STÜTZEL 2006). The results of this study show that serial buds are not uncommon and more widely spread in gymnosperms than they were previously believed to be. Due to this, the hypothesis that several rows of ovules in Cupressaceae seed cones are originated from several serial descended accessory buds gets strong support by proving serial buds in the vegetative shoot system.

4.5 Evolutionary implications for different groups

4.5.1 Angiospermous trees

The origin of deciduousness in angiospermous tree species appeared first at lower middle latitudes in the Northern Hemisphere during the late Cretaceous. It seems that it was a response to a changing climate with seasonal absence of rainfall, marginal to the tropical zone. Following this, deciduousness has evolved in this group as an adaptation to seasonal drought. Furthermore, it was also an advantageous adaptation for cooler climates and a longer photoperiodic in higher latitudes. In these areas, a seasonal leaf fall is a great advantage during cool periods when the uptake of nutrients is generally reduced (e.g., AXELROD 1966; WOLFE 1987). Deciduousness has evolved as a consequence of a new seasonal climate. Shoot differentiation in combination with evergreen habit (e.g., *Nothofagus dombeyi*, *Acer sempervirens*) is best explained as representing phylogenetic intermediate forms. The recent shoot differentiation can be regarded as reminiscent of a previous deciduous ancestor. Following this, different evolutionary scenarios for angiospermous tree species are

considerable, as suggested below. Next to the results of this study, also the evolutionary history (e.g., centre of origin and geographical spreading) of a taxon has to be included by suggesting evolutionary scenarios.

4.5.1.1 *Cercidiphyllum* (Cercidiphyllaceae, Angiospermae)

In *Cercidiphyllum*, the shoot dimorphism is extreme. Intermediary forms between both types of shoots are never present. Furthermore, long- and short-shoot leaves equal each other in area and shape. The values for the annual investments in shoot biomass per cm² leaf area are about 10⁻¹ less compared to all other investigated deciduous taxa. Due to this, *Cercidiphyllum japonicum* represents the absolute optimum in its shoot differentiation. TITMAN & WETMORE (1955) described all buds in *Cercidiphyllum* as getting potential short-shoots and that many of them get greatly developed as long-shoots on young plants and decrease with the onset of flowers.

Reconstructions of fossil Cercidiphyllaceae e.g., *Joffrea speirsii* (CRANE & STOCKEY 1984, 1986), a *Cercidiphyllum*-like, deciduous ancestor of *Cercidiphyllum* (late Palaeocene, Alberta, Canada) shows even a distinct shoot differentiation. But contrasting to the modern *Cercidiphyllum*, several short-shoot leaves were inserted on each short-shoot. Due to this, the single-leaved short-shoots of the modern *Cercidiphyllum japonicum* would represent a derived feature, resulting from strong and continuously reductions of short-shoot leaves to optimize the annual investments in shoot biomass per leaf. *Cercidiphyllum* as a phylogenetic old angiospermous taxon impressively illustrates that the character evolution does not need parallelly comply for the species evolution. An open question remains however, why this advantageous type of shoot differentiation is only restricted to two distantly related taxa (*Cercidiphyllum* and *Tetracentron*) and has not evolved in other recent angiospermous tree species.

4.5.1.2 *Nothofagus* (Nothofagaceae, Angiospermae)

Nowadays, about 35 *Nothofagus*-species exist. This genus has a very disjunct distribution range with species in S-America, Tasmania, SE-Australia, New Guinea and New Caledonia (KUBITZKI et al. 1993). *Nothofagus* is one of those Gondwana-taxa which are documented best in the fossil record. Its biogeographical distribution in time and space has been studied several times (e.g., SCHLINGER 1974; FLEMMING & BARRON 1966; HILL et al. 1996; NELSON & LADIGES 2001; SWENSON et al.