



## NOVELTIES ON *DOLIOSTROBUS* (DOLIOSTROBACEAE), AN EXTINCT CONIFER GENUS OF THE EUROPEAN PALAEOGENE

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**Abstract.** The circumscription and affinities of *Doliosobus* MARION are re-evaluated. This conifer genus shares some characteristics with the Cupressaceae s.l. and the Araucariaceae. Distinct features of its wood anatomy combined with the properties of seeds (basal-laterally winged, typically one per cone scale) stress the independent position of this conifer within the Pinopsida, which is expressed by the definition of a new family. Besides *Doliosobus*, the Doliosobaceae, fam. nova includes one morpho-species: *Araucariacites europaeus* KRUTZSCH (dispersed pollen). The relationship to the morpho-species *Podocarpoxylo helmstedtianum* GOTTWALD (trunk wood) remains ambiguous. The genus is treated as monospecific (*D. taxiformis* (STERNBERG) Z. KVAČEK emend. KUNZMANN with three varieties *D. taxiformis* (STERNBERG) Z. KVAČEK var. *taxiformis*, var. *sternbergii* MAI et WALTHER ex Z. KVAČEK and var. *hungaricus* (RÁSKY) Z. KVAČEK et HABLY) occurring in the Palaeogene of Europe.

■ Conifers, Doliosobaceae, Palaeogene, Europe, affinities.

### INTRODUCTION

More than 30 years ago, first accounts reporting new records of *Doliosobus* from the Palaeogene of North Bohemia were published, including a short paper in this journal (Bůžek et al. 1968a, b, 1969). As new views and data have been accumulated about this curious extinct conifer since, it is appropriate to summarize them and add new facts about its still controversial systematic position, as well as to rectify the inconsistencies in the nomenclature. This article is a preliminary report of a broader treatment planned for the future, which is based on the study of many type and additional specimens from the European Palaeogene. The possible Cretaceous ancestors that are usually referred to as “*Dammara*” *borealis* HEER are mentioned only marginally being under the study of other colleagues (A. Boyd, L. Kunzmann, M. Popa, and others).

The following abbreviations are used to designate respective collections:

- NM – National Museum, Prague
- ČGÚ – Czech Geological Survey (former Český geologický ústav, recently re-named as Česká geologická služba), Prague
- PR – Botanical Institute, Academy of Sciences of the Czech Republic, Průhonice
- DB – Headquarters of the Bílina Mine, Bílina
- BP – Hungarian Natural History Museum, Budapest
- NHMW – Naturhistorisches Museum, Wien
- IBUG – Botanisches Institut der Universität, Graz
- MMG – Staatliche Naturhistorische Sammlungen, Museum für Mineralogie und Geologie, Dresden
- SM.B – Forschungsinstitut und Museum Senckenberg, Frankfurt am Main

- BMNH – British Natural History Museum, London
- E – Royal Botanic Garden, Edinburgh
- P – Muséum National d’Histoire Naturelle, Paris
- NHRMS – Swedish Museum of Natural History, Stockholm
- K – Royal Botanic Gardens, Kew
- PE – Botanical Institute of the Chinese Academy of Sciences, Beijing

## MATERIAL AND METHODS

The following previously described records of *Doliosobus* have been re-considered together with the additional, newly recovered material: Trupelník Hill, Kučlín (Kutschlin), N Bohemia, twig impressions, partly with (?) pollen cones, detached cone scales, Late Eocene diatomite (Menzel 1901, Bůžek et al. 1968a, Kunzmann 1999 – NM, BP, MMG, IBUG, NHMW, DB); Mrtvý Vrch Hill, Kostomlaty (Kostenblatt), N Bohemia, twigs, cone scales, Late Eocene marl (Kvaček 2002 – DB); Hlinná and Lbín (cores Úc 9, Lb 1), N Bohemia, twigs, cone scales, seeds, Late Eocene claystone (Bůžek et al. 1968a, Kvaček 2002 – ČGÚ); Häring, Tyrol, twigs including the type of *D. taxiformis*, cone scales, Late Eocene (?) – Early Oligocene marl (Kvaček 1971, Kunzmann 1999 – NM, NHMW, MMG, P); Messel, Hessen, twigs, cone scales, Middle Eocene oil shale (Wilde 1989 – SM.B); Phoenix-Nord, Groitzsch, Kayna-Süd, Profen, Königsau, Weissester Basin, twigs, partly with (?) pollen cones, cone scales, Middle and Late Eocene sieved material (Mai et Walther 1985 – MMG); Kiseged Hill, Eger and Budapest-Szepevölgy, N Hungary, twigs and cone scales including the type of *D. taxiformis* var. *hungaricus*, Early Oligocene shale (Rásky 1943, Kvaček et Hably 1998 – BP); Célas, Alais Basin, S France, twigs, cone scales including the lectotype of *D. sternbergii* (Marion 1884, 1888, Kvaček 1971, Kunzmann 1999, Kvaček 2002 – BMNH, NHRMS, P). It is unfortunate that most of the original collections described and partly figured by Marion (1888) from the Alais Basin are missing (Kunzmann 1999).

Cuticle (testa) preparations have been made from carbonised compressions of twigs, cone scales and seeds from the core Úc-9 at Hlinná and compared with the other cuticle preparations from the previous studies (Bůžek et al. 1968a, Kvaček 1971). Wood sections of a branchlet from the Geiseltal (Bůžek et al. 1968a) and of a trunk from Kučlín (Březinová et al. 1994) were compared with the data published by Rüffle et Süß (2001).

The extant Araucariaceae and Cupressaceae s.l. have been studied in the herbaria at E, PE and PR as well as on the comparative material of seed cones supplied from PR and K. The collection of conifer leaf cuticles housed at the Charles University, Faculty of Science has been consulted as well.

A standard camera (Practica SMX) with the Microtar Lense 25 mm attached and the Phase-contrast Light Microscopy (Carl Zeiss, Nfjpk) have been used for the graphic documentation.

## SYSTEMATIC PART

The affinity of *Doliosobus* is re-assessed below in view of a newly recognized peculiar branch wood structure (Rüffle et Süß 2001) and properties of the seed cone and the seed. The new data corroborate an isolated position of *Doliosobus* among other conifers, and require this extinct genus to be accommodated in an independent family of the Coniferopsida (= Pinopsida).

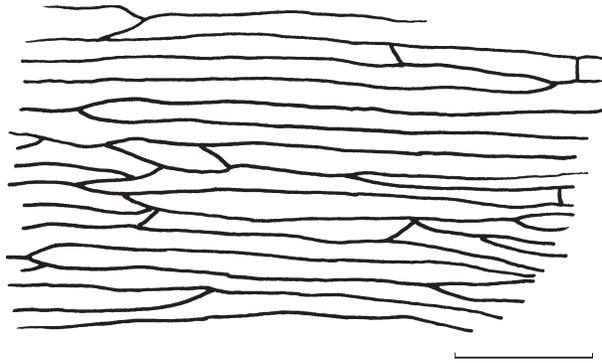


Fig. 1 *Doliostrobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, cuticle of the seed testa, Hlinná (ČGÚ Úc 9–31/1). Scale bar = 50  $\mu$ m.

Order Coniferales

Family **Doliostrobaceae** *fam. nova*

Type: *Doliostrobus sternbergii* MARION, *nom. illegit.* (*D. taxiformis* (STERNBERG) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK).

Trees (?) distinct in the wood structure with abietoid pitting of tracheids and doliostroboïd (not bordered) pits in the cross field of branch wood, and lacking ray tracheids as well as resin channels. Foliage shoots bearing polymorphic, helically arranged needle leaves – longer acicular to falcate and shorter appressed. Seed cones similar to those of *Agathis* (Araucariaceae) disintegrating at maturity into individual scales; cone scales flat, widely obtrullate to obovate in the outline, apparently simple, with several longitudinal ridges corresponding to resin ducts, typically with an apical spiny process; seeds free, inverse, one per scale (aberrantly two), with one large basal or basal-lateral wing and occasionally with an additional opposite  $\pm$  smaller wing. Pollen of the *Araucariacites* type.

Remarks: *Doliostrobus* cannot be accommodated into the Cupressaceae s.l. (including Taxodiaceae), as some authors maintain (Mai 1976, in Mai et Walther 1985, Kunzmann 1999), because all taxodioids, and also most cupressoids differ in having typically two and more seeds per cone scale in the seed cones, which do not usually shatter into single cone scales. (*Taxodium* seed cones disintegrate mostly into groups of scales.) The basal single wing of the seeds of *Doliostrobus* is unique among the conifers and can be easily derived from the double basal-lateral wings of *Agathis* by the fusion of the wings. Indeed, in aberrant cases of the double winged seeds in *Agathis australis* the wings are closely set together and nearly fused (Pl. I: 4). All taxodioids, contrary to cupressoids, share with the Doliostrobaceae (and the Araucariaceae) inverse seeds, but differ in having seeds with marginal narrow wings or a single apical-lateral wing in *Glyptostrobus* (see Fig. 3 a, b) or being wingless. Also the structure of the branch wood of *Doliostrobus* is typical of the new family and is not shared with any other conifer group. Most important are “doliostroboïd” pits of the cross-fields (1–5 unequally large pits  $\pm$  roundish-elliptical and not bordered), as well as the combination of other characters – axial parenchyma and growth rings distinct, abietoid pits on radial and tangential tracheid walls present, rays uniseriate, mostly 1–3 cells high, horizontal walls without pitting, ray tracheids and resin channels absent (Rüffle et Süß 2001). The Doliostrobaceae at the

present stage of knowledge was endemic to the Northern Hemisphere, where it possibly derived from the Araucariaceae as an offshoot during the late Mesozoic. Unfortunately, various representatives of the Araucariaceae occurring in the Cretaceous of the Northern Hemisphere are rather poorly known. We are not well informed particularly on the development of their wood structure. The Doliostroboaceae decidedly differ in this respect from the Araucariaceae that all possess, as far as we know, the *Araucarioxylon*-type of wood with densely crowded pitting of tracheids.

***Doliostrobus* MARION (1888), *nom. cons. prop.***

Lectotype selected here: *Doliostrobus sternbergii* MARION, *nom. illegit.* (BMNH – V. 1439, Kvaček 1971: pl. 31, fig. 7, re-illustrated in Pl I: 3).

Marion (1884) described this genus on the basis of the specimens from Célas, at first assuming their identity with *Araucarites sternbergii* GOEPPERT from the Palaeogene marl at Häring. He was unaware of the fact that this binomen, taken as the basionym, is ambiguous being also based on a lycopod cone (*Araucaria sternbergii* CORDA  $\equiv$  *Lepidostrobus sternbergii* (CORDA) NĚMEJC – see Bůžek et al. 1968b). Later on, Marion (1888) re-named the material from Célas as a new species *Doliostrobus sternbergii* MARION, hesitating to identify it with similar foliage shoots known from other sites under *Araucarites sternbergii* – (Marion 1888: 2 – “Nous conservons comme appellation spécifique l’*épithète Sternbergii*, sans vouloir cependant affirmer dès maintenant l’identité de notre conifère avec les diverses empreintes designées jusqu’ici sous le nom d’*Araucarites Sternbergii*”). To stabilize the status and the typification of this genus, its name (in the sense of Marion 1888) was proposed for conservation (Kvaček in press).

The detailed review of the *Doliostrobus* records given by Kunzmann (1999) is followed here by accepting only a single species *D. taxiformis*, which has several local populations (variants) that differ only in subtle details. The ancestral taxa, possibly related to *Doliostrobus* from various Late Cretaceous sites of the Northern Hemisphere (e.g. “*Dammara*“ *borealis* HEER complex, “*Dammara*“ *macrosperma* HEER emend. BOYD 1992) require further studies. *D. rerollei* MARION (1884, 1888) is excluded from this genus because its holotype represents an ambiguous, most probably an angiosperm remain of uncertain affinity.

One morpho-taxon is included to the newly established family Doliostroboaceae parallel to *Doliostrobus*: *Araucariacites europaeus* KRUTZSCH (1971) – dispersed pollen confined to the Middle and Upper Eocene of Europe. Contrary to the statement of Kunzmann (1999) this type of pollen accompanies the *Doliostrobus* megafossils at most sites in N Bohemia (Konzalová 1981, Kvaček 2002).

The affinities of *Podocarpoxyylon helmstedtianum* GOTTWALD (1966) are problematic. This trunk wood shares many characteristics with branches of *Doliostrobus*, e.g. the lack of resin ducts, the disposition of abietoid pitting etc., but differs in having one or more cupressoid (not “doliostroboid”) pits in cross-fields. According to C. Privé-Gill and J. Sakala (personal communication) this difference may not be due to discrepancies between the structure of the branch and trunk wood of the same plant. Their view supports the notion of Ruffle et Süß (2001), that the trunk wood of *Doliostrobus* is in fact not known. The problem must be resolved in the future by more extensive studies of coniferous wood in the European Palaeogene. In any case, at Kučlín in N Bohemia a large trunk of *P. helmstedtianum* was found not directly attached, but in a close association

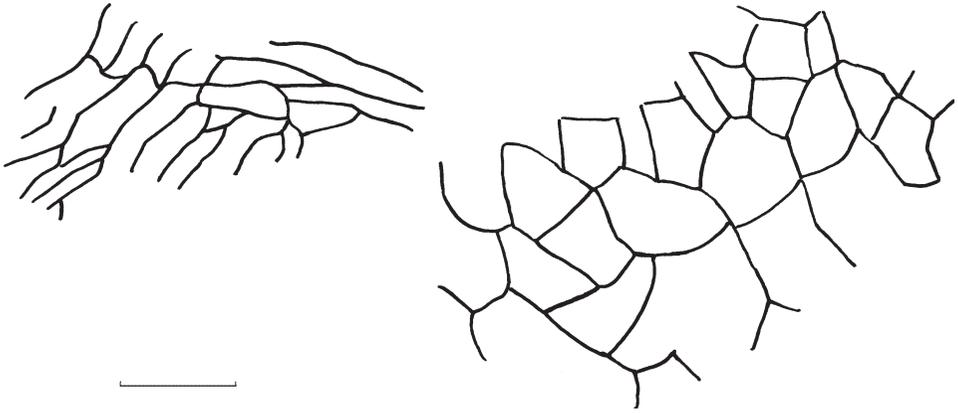


Fig. 2 *Doliostrobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, cuticle of two layers of the seed wing, Hlinná (ČGÚ Úc 9-31/1). Scale bar = 50  $\mu$ m.

with large branches and cone scales of *Doliostrobus* in the soft diatomite at the bottom of this deposit (Březinová et al. 1994). The Middle Eocene site Helmstedt, the type locality of *P. helmstedianum*, has yielded foliage shoots and detached cone scales of *Doliostrobus* as well (Wilde 1989).

***Doliostrobus taxiformis* (STERNBERG) Z. KVAČEK emend. KUNZMANN**

Pl. I: 1–3, pl. II: 1–5, 8, pl. III: 1–4, pl. IV: 1–7, figs. 1–2, 3c

*Cystoseirites taxiformis* STERNBERG, Vers. Fl. Vorw. 5–6: 35. pl. 18. figs. 1–3. 1833.

*Araucarites sternbergii* GOEPPERT ex ENDLICHER, Syn. Conif. 301. 1847, *nom illegit. superfl.*

*Doliostrobus sternbergii* MARION, Ann. Sci. Geol. 20(3): 19. pl. 1. figs. 1–8. pl. 2. figs. 9–19. 1888, *nom. illegit.* (non (CORDA) MARION 1884).

*Araucarites taxiformis* (STERNBERG) KNOBLOCH, N. Jb. Geol. Pal. Mh. 1964: 601. 1964.

*Doliostrobus taxiformis* (STERNBERG) Z. KVAČEK, Palaeontographica B 135: 118. 1971.

For further synonymy see Kunzmann (1999).

Large foliage shoots and branches have been recovered at Célas, Kučlín and Häring (Marion 1888, Kunzmann, personal communication – this paper, Pl. I: 1), suggesting a possible arborescent growth habit of *Doliostrobus*. The branching system is less regular than in *Araucaria*, more similar to taxodioids (see also Marion 1888: 9). The branch wood obtained from the Geiseltal (Bůžek et al. 1968a, Rüffle 1976) is distinct in the “doliostroboid” cross-field pitting similar to the Podocarpaceae and *Pinus*, and differing from the Pinaceae by absent resin ducts (Rüffle et Süß 2001). Di(-tri)morphic leaves (acicular, falcate, scale-like) resemble morphologically the foliage of *Araucaria* sect. *Eutacta* or some taxodioids, e.g., *Cryptomeria*. The leaves are amphistomatic. The stomata are consistently amphicyclic, resembling those of *Araucaria* sect. *Eutacta* and also *Taiwania*. That is why the sterile twigs of *Doliostrobus taxiformis* were misinterpreted for the latter genus (“*Taiwania*” *araucarioides* SVESHNIKOVA – see Bůžek et al. 1968a, Rüffle 1976). Small differences between

local populations of *D. taxiformis* in the topography of stomata, as well as the distinctness of crystal cavities are better explained as an ecotypic variation and expressed by infraspecific taxa (Mai et Walther 1985, Kunzmann 1999).

Immature pollen cones (?) are broadly ovoid, sessile, about 3 mm long and grow axially in groups of 2–4, which are concentrated on tips of twigs (Marion 1888: pl. 1, fig. 2, this paper, Pl. IV: 6–7). The cones consist of many crowded simple and narrow imbricate scales. They have not yielded any pollen *in situ* so far. A similar arrangement of pollen cones can be seen in *Cunninghamia* or *Cryptomeria*. The material from Célas included also detached pollen cones (Marion 1888: 11, pl. 2, fig. 19). According to Marion's opinion the figured specimens are only fertile pollen-bearing parts of longer structures, which grew in bunches on the tips of twigs (Marion 1888: pl. 1, fig. 6). This notion cannot be verified until the original or topotypical material is available. Similar structures have not been noticed elsewhere. *Doliosobus* differs in having the pollen cones crowded on the tips of twigs from its Late Cretaceous ancestors, as far as it can be assumed from the single so far described instance from the Senonian of Zliv, S Bohemia. A large foliage shoot accompanied by the "*Dammara*" *borealis*-type of cone scales was recovered there with a solitary sub-terminal pollen cone attached (Němejč et Kvaček 1975: pl. 2, fig. 7 – NM F 1826 and 1827). This pollen cone yielded pollen *in situ* of the *Araucariacites*-type (ibid. pl. 17, figs. 4–6).

Immature seed cones (Mai et Walther 1985: pl. 6, figs. 1–2, Phoenix Nord Mine, Late Eocene of the Weissester Basin) were originally globular, but became well flattened by the fossilisation. They attain about 15 mm in diameter and include about 60–80 helically arranged imbricate cone scales (Kunzmann 1999: 78). The same structure is indicated for bigger detached seed cones from Célas, which were found at various stages of disintegration. One juvenile cone was terminally attached to a foliage shoot (Marion 1888: pl. 2, fig. 9A). Kunzmann (1999: pl. 15, fig. 1) reported and figured a still larger detached seed cone in the state of disintegration from Häring. The seed cones fully shatter at maturity, like in all three genera of the Araucariaceae and in contrast to the Cupressaceae s.l. The single case of disintegrating seed cones of *Taxodium* is an exception among taxodioids. However, the seed cones of swamp cypress mostly fall into groups of scales, rarely into individual cone scales. The detached cone scales of *Doliosobus* are flat. They vary in the form and the size according to their position within the cone and the maturity of the cone (Marion 1888: 11–12, this paper – Pls. II: 1–5, 8, IV: 1–5). In the cross section they show an arrangement of resin ducts and vascular bundles similar to *Cunninghamia* (Mai 1976: 97). The largest cone scales were found in the Early Oligocene deposits of Hungary and Romania and these populations are usually treated on that basis as a separate variety (Petrescu et al. 1989, Kvaček et Hably 1998). The mature cone scales are preserved usually without seeds, flat, thicker in the upper part (Pl. IV: 2), occasionally with an indistinct depression after the seed (Pl. IV: 1). In rare cases, the seeds were found attached to the cone scales (Pls. II: 1–3, 8, IV: 4–5). Large cone scales (probably from the middle part of the mature cone) always carry only a single seed body or show a single trace of the funicle, partly asymmetrically positioned below the half of the scale length (Kunzmann 1999: text-fig. 15.5). The seeds from Kučlín attached to the cone scales and preserved as impressions did not leave traces of the wing, which was apparently too delicate to survive the fossilisation. Only in one specimen (Kunzmann 1999: text-fig. 15.4g, MMG Kin 17 – present paper, Pl. II: 8) the wing partly stretches beyond the base of the scale as a narrow rim. In this particular case Kunzmann (1999) suggests that two seeds

may be present, but in my opinion the longitudinal line across the seed body corresponds apparently to the dehiscence. Seeds are mostly not preserved on the compressions of cone scales from the Weisselster Basin. In two immature cone scales (Groitzsch, MMG – coll. Mai 10602), a small oval seed body (Pl. IV: 5) and a seed body accompanied by another impression (Pl. IV: 4), respectively have been noticed. The seed in both cases is starting to produce a wide basal wing, which is not fully developed. Some other small cone scales probably from the cone base, obtained by washing (e.g. from the Kayna-Süd Mine), show often depressions on their sides, but no traces of seeds (Pl. IV: 3). These scales were sterile and the depressions were formed mostly on the abaxial side due to overlapping of neighbouring scales within the cone, like in *Agathis*, and – contrary to the opinion of Mai (1976, in Mai et Walther 1985) – not after two seeds.

Well-preserved seeds of *Doliosobus* were first illustrated from Célas (Marion 1888). Another suite of winged seeds was recovered in the Late Eocene shale at Hlinná and Lbín in N Bohemia in the association of and partly attached to the cone scales (Bůžek et al. 1968a). At Célas (Marion 1888: pl. 2, fig. 18, Kunzmann 1999: pl. 14, fig. 2, this paper, Pl. I: 2, Fig. 3 c right) the wing is basal, broadly elongate to rounded, stretching towards the micropyle continuously on one side of the seed by a very narrow border. In N Bohemia, the wing is basal-lateral, short, broadly oval, decurrent towards the micropyle on mostly both sides of the seed, on one side broadly and continuously, on the other side incompletely, in one case forming the second smaller wing (Pl. III: 1–4, Fig. 3 c middle). The carbonised substance of the seed and the wing (specimen No. ČGÚ Úc 9–31) has yielded the cell structure. The testa consists of narrow long elongate parallel-sided straight-walled cells 7–10 µm wide. One layer of the wing shows narrow parallel-sided cells grouped in series oblique to each other; the surface near the edge reflects polygonal, mostly isodiametric straight-walled cells c. 30–50 µm across (Figs. 1–2).

We are not informed about the form of the winged seeds from other localities of *Doliosobus*. Only one poorly preserved specimen (BMNH – V. 17516) was described in the association of several cone scales and twigs of *Araucarites gurnardii* FLORIN from the Bembridge Marl (Reid et Chandler 1926: pl. 2, fig. 19). It has an about 8 mm long wing attached basally to the small seed body and matches the smaller specimens from Célas (e.g. Marion 1888: pl. 2, fig. 18 c). According to Kunzmann (1999: 78, 104) the seeds illustrated by Mai et Walther (1985: pl. 5, figs. 18–20) as coming from a cone of *Doliosobus*, were released in fact from another cone of *Chamaecyparites hardtii* (GOEPP.) ENDL. included in the same sample.

The most significant evidence of *Doliosobus taxiformis* is the occurrence of typical seed cone scales or seeds. Mere foliage impressions, as cited, e.g., from the Palaeocene of Menat (Piton 1940), and some other sites of the European Palaeogene require cuticular revisions to get at least some leaf anatomical data. All reports of *Doliosobus* from the Neogene are misidentifications (cf. Givulescu 1988). But even many reliable records cannot be all attributed to the so far distinguished varieties listed below, because they have not been characterized completely.

***Doliosobus taxiformis* (STERNBERG) Z. KVAČEK var. *taxiformis***

*Doliosobus taxiformis* (STERNBERG) Z. KVAČEK var. *taxiformis* MAI et WALTHER, Abh. Staatl. Mus. Mineral. Geol. 33: 25. 1985, *nom. inval.* (ICBN Art. 32.6, 37.1)

Type: *Cystoseirites taxiformis* STERNBERG, 1833: pl. 18, fig. 2 (NM E 25), Häring – Lectotype selected by Knobloch (1968).

The diagnostic features are expressed in the mostly longitudinal arrangement of large stomata and the lack of distinct crystal cavities in the leaf cuticle (Mai et Walther 1985), although these characters are not very stable, as rightly pointed out by Kunzmann (1999). Another gross morphological difference seen on the branches from Häring, unlike most other populations, is in the prevailing form of robust acicular needle leaves with a very long free part. In general, the polymorphy of leaves is only slightly expressed at Häring.

Occurrence: Häring, Austria (Kvaček 1971, Kunzmann 1999), Late Eocene (?) to Early Oligocene.

***Doliosirobus taxiformis*** (STERNBERG) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK

*Doliosirobus taxiformis* var. *sternbergii* MAI et WALTHER, Abh. Staatl. Mus. Mineral. Geol. 33: 25.1985, *nom. inval.* (ICBN, Art. 37.1)

*Doliosirobus sternbergii* MARION, Ann. Sci. Geol. 20(3): 19. pl. 1. figs. 1–8. pl. 2. figs. 9–19.1888, *nom. illegit.*

Lectotype designated here: BMNH V. 1439 (as *Doliosirobus sternbergii* MARION (1888), *nom. illegit* – Kvaček 1971: pl. 31, fig. 7, present paper Pl. I: 3).

This variety differs from *D. taxiformis* var. *taxiformis* in having large and distinct crystal cavities in the leaf cuticle and smaller stomata, which are on the adaxial leaf side mostly tightly spaced, and obliquely/perpendicularly arranged to the leaf length in short rows. This variety was invalidly published without the designation of the type (Mai et Walther 1985) and is validated here. Besides the type locality Célas, most other occurrences in the European Eocene probably belong to this variety, like *D. gurnardii* (FLORIN) BŮŽEK, HOLÝ et Z. KVAČEK and *D. certus* BŮŽEK, HOLÝ et Z. KVAČEK (see Kunzman 1999). The population of *Doliosirobus taxiformis* from Célas differs from the record in N Bohemia in the longer and basally oriented wings (cf. Pls. I: 2 vs. III: 1–4, Fig. 3 c right vs. middle). Therefore the latter may deserve an independent status. The earliest species name related to this taxon is *Embothrites cuneatus* ETTINGSHAUSEN (1868) based on a cone scale from Kučlín (the type specimen missing).

Occurrence: Célas, Alais Basin (Marion 1884, 1888), Bembridge (Reid et Chandler 1926), Weisselster Basin (Rüffle 1976, Mai et Walther 1985), Kučlín, Kostomlaty, Hlinná and Lbín, N Bohemia (Bůžek et al. 1968 a), all Late Eocene; Messel, Geiseltal (Mai 1976, Rüffle 1976, Wilde 1989). Middle Eocene.

***Doliosirobus taxiformis*** (STERNBERG) Z. KVAČEK var. *hungaricus* (RÁSKY) Z. KVAČEK et HABLY

*Araucaria hungarica* RÁSKY, Föld. Közl. 73: 524. pl. 22. fig. 1. 1943.

*Doliosirobus hungaricus* (RÁSKY) BŮŽEK, HOLÝ et Z. KVAČEK, Palaeontographica B 123: 155. 1968a.

*Doliosirobus taxiformis* (STERNBERG) Z. KVAČEK var. *hungaricus* (RÁSKY) PETRESCU, GIVULESCU et TODORAN, in Petrescu, Olig. Transylv. Bas. 166. pl. 2. figs. 8–9. 1989, *comb. inval.* (ICBN Art. 33.3).

*Doliosirobus taxiformis* var. *hungaricus* (RÁSKY) Z. KVAČEK et HABLY, Acta Palaeobot. 38: 6. pl. 1. figs. 1–2. 1998.

Holotype: *Araucaria hungarica* RÁSKY, 1943: 524, pl. 22. fig. 1 – BP 61.18.1. Budapest -Szépvölgy, clay pit of Czillagehegy.

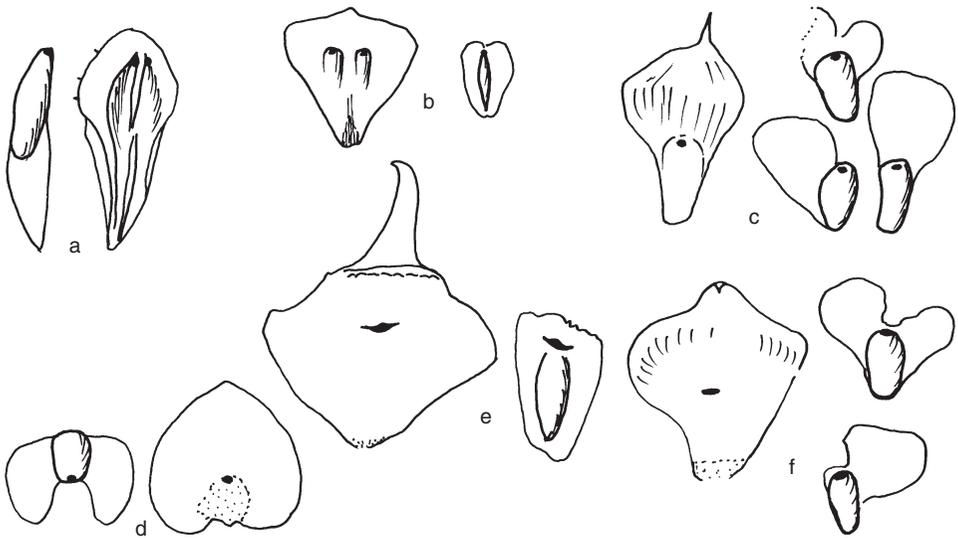


Fig. 3 Schematic diagrams of cone scales and seeds in selected representatives of the Cupressaceae s.l., Araucariaceae and *Doliostrobus*: a *Glyptostrobus pensilis* (STAUTON ex D. DON) K. KOCH, b *Taiwania cryptomerioides* HAYATA, c *Doliostrobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, d *Tetraclinis articulata* (VAHL) MAST., e *Wollemia nobilis* W. G. JONES et al., f *Agathis australis* (D. DON) LOUD. The hilum and the attachment scar of seeds on the seed scales shown as black spots.

The epidermal structure has not been obtained as yet. The variety differs from the others by a slightly larger maximum size of the seed cone scales. The suggested reduction to the varietal rank by Petrescu et al. (1989) was invalidly published because the basionym was not fully cited as required by the nomenclatural rules.

Occurrence: Budapest-Szépvölgy, Eger- Kiseged hill, Tard clay Fm. (Rásky 1943, Kvaček et Hably 1998), Buzuşa Basin (Petrescu et al. 1989) Early Oligocene.

## CONCLUSIONS

In vegetative organs (branching pattern, leaf morphology and anatomy, wood structure) and pollen cones, *Doliostrobus* (Doliostroboaceae) recalls taxodioids (Cupressaceae s.l.). The associated pollen is, however, more similar to araucarians. The cone scales of *Doliostrobus* have often been compared with those of the *Cunninghamia-Taiwania* group (Mai 1976, Mai et Walther 1985, Kunzmann 1999). However, the typical normal condition of a single seed per cone scale found in *Doliostrobus* is not compatible with the Cupressaceae s.l.

The most peculiar similarity of *Doliostrobus* and the Araucariaceae, namely *Agathis*, is in the morphology of seeds. In both genera they are free, inverse and basally or lateral-basally single- or double-winged (Pls. II: 3, 6–7, III: 1–6, Fig. 3 c, f). Among Cupressaceae s.l., the only case of basally and laterally double- (triple-) winged seeds is in *Tetraclinis* (Fig. 3 d), but the seeds are erect, as in all cupressoids. In other genera of Cupressaceae s.l., the seeds are either wingless (e.g. *Taxodium*, *Juniperus*, *Platykladus*), or with a narrow peripheral rim (most genera), rarely with an apical-lateral single wing (e.g., *Libocedrus*, *Austrocedrus*, *Diselma*, *Glyptostrobus*) or unequal apical-lateral two wings

(e.g. *Calocedrus*, *Fokienia*). The most similar seed body is seen in *Glyptostrobus* (Fig. 3 a), but its two inverse seeds per scale are oriented with the micropyle and the apical wing towards the scale base (Henry et McIntyre 1926), not erect, as erroneously shown by Kunzmann (1999: text-fig. 10.9 c). The cone scale of *Doliosobus* is simple, with a thorn-like process similar to that of *Wollemia* (Araucariaceae – Pl. II: 9, Fig. 3 e), the latter differing in the seed with a peripheral winged rim (Jones et al. 1995: fig. 1). Contrary to *Taiwania* (Fig. 3 b), the cone scale of *Doliosobus* is mostly without any seed depression on the ventral side and has a distinct dorsal rib continuing into an apical process, which is stretching from the cone (Pl. II: 4, Fig. 3 c).

The megafossils of *Doliosobus* are regularly associated with the dispersed pollen of the *Araucariacites*-type (Konzalová 1981, Kvaček 2002). It is an unusual morpho-species described as *A. europaeus* Krutzsch (1971) and occurring in the Middle-Late Eocene deposits of Central Europe. KRUTZSCH (l.c.) hesitated to accept this pollen type as a representative of the true Araucariaceae due to the differences in the sculpture of the exine (densely collumelate and fine foveolate tectum in the surface view appearing as a  $\pm$  granulate and undulate pattern). *A. europaeus* differs from the pollen of Cupressaceae s.l. in its larger size and the mentioned sculpture.

The family Doliosobaceae is similar in some characters to both the Araucariaceae and the Cupressaceae s.l. It is obviously near to the former family, from which it probably derived, although it differs from araucarians in the wood structure. The objective evaluation of its relationship would require a more extensive comparison of representatives of the three groups by a cladistic analysis. This is intended later, after the Cretaceous Araucariaceae, Cupressaceae s.l. and Doliosobaceae are more fully known.

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## EXPLANATION OF THE PLATES

### Pl. I

- 1 *Doliosobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, foliage shoot, Kučlín (MMG *Kin 1*), × 0.9
- 2 *Doliosobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, detached mature seed, Célas (NHRMS *S 105288*), × 6
- 3 *Doliosobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, detached cone scale, Célas (LECTOTYPE – BMNH *V. 1439*), × 4
- 4 *Agathis australis* (D. DON) LOUD., double-winged seed with tightly set wings, Waipona Forest, New Zealand (K, *Farjon, March 2002*), × 3.5

### Pl. II

- 1 *Doliosobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, adaxial surface of a cone scale with attached seed, Kučlín (NM *G 2432a*), × 4
- 2 *Doliosobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, broad cone scale with attached seed, Kučlín (IBUG *Ettingshausen 6460*), × 3
- 3 *Doliosobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, cone scale with double-winged seed, Hlinná (ČGÚ *Úc 9–13*), × 4
- 4 *Doliosobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, counterpart of fig. 1 showing abaxial surface, Kučlín (NM *G 2432b*), × 4
- 5 *Doliosobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, small cone scale, Kučlín (DB *s.n.*), × 4
- 6 *Agathis australis* (D. DON) LOUD., cone scale with one-winged seed from an immature cone, cult. (PR, *Kučera 358*), × 3.5
- 7 *Agathis australis* (D. DON) LOUD., cone scale with double-winged seed, cult. (PR, *Kučera 358*), × 4
- 8 *Doliosobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, adaxial surface of a cone scale with attached seed showing a small part of the wing beyond the scale outline, Kučlín (MMG *Kin 17*), × 4
- 9 *Wollemia nobilis* W.G. JONES, HILL et ALLEN, two cone scales, Wollemi National Park, Australia (E *Jones, Allen and Turton NSW 392965*), × 3

### Pl. III

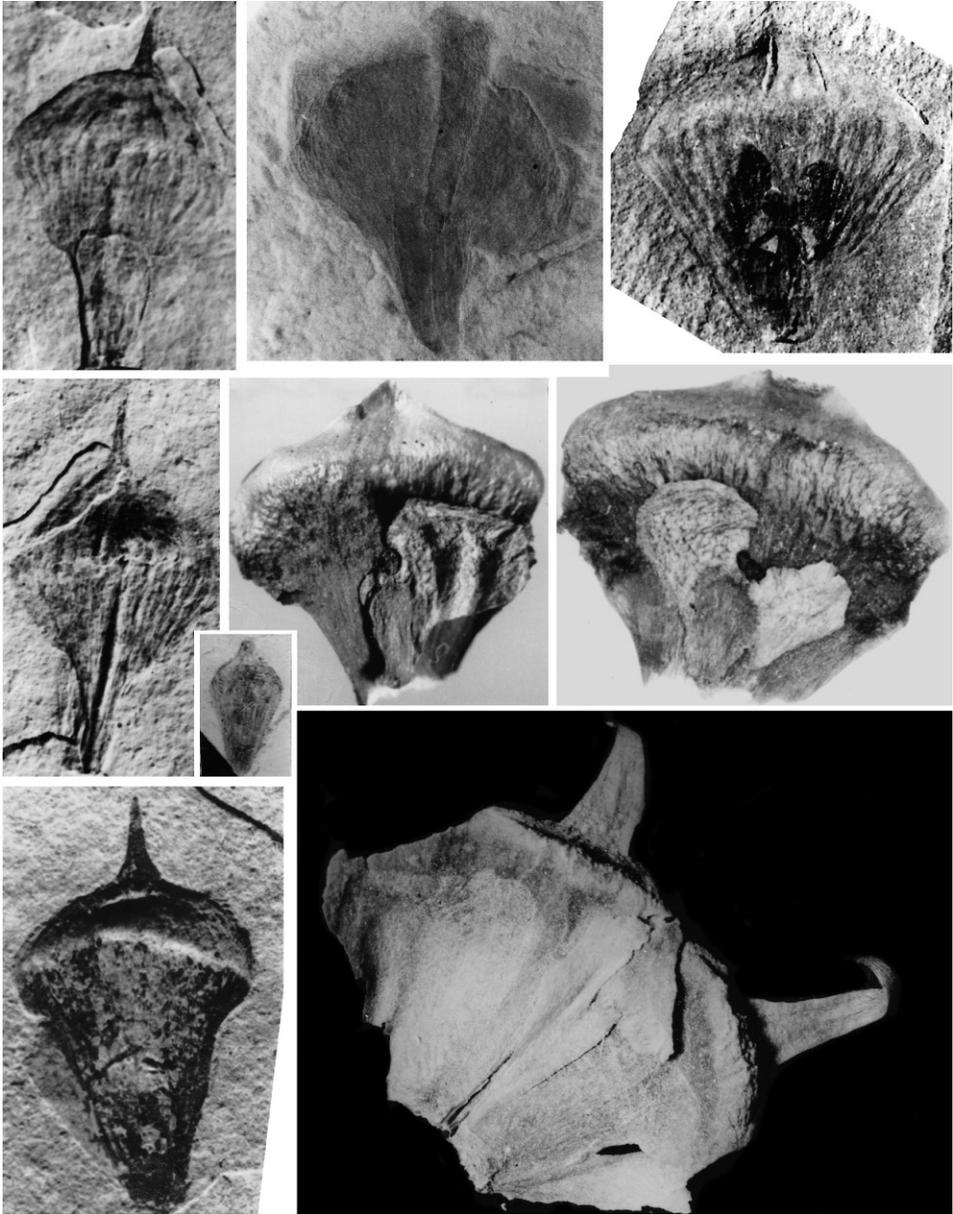
- 1 *Doliosobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, detail of double-winged seed on the cone scale, Hlinná (ČGÚ *Úc 9–13*), × 10
- 2 *Doliosobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, detached seed, Hlinná (ČGÚ *Úc 9–5.4*), × 10
- 3 *Doliosobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, detached seed, Lbín (ČGÚ *Lb 1–9*), × 10
- 4 *Doliosobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, detached seed, Hlinná (ČGÚ *Úc 9–31*), × 10
- 5 *Agathis australis* (D. DON) LOUD., one-winged seed, cult. (PR *Kučera 358*), × 10

### Pl. IV

- 1 *Doliosobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, larger cone scale with a seed impression, Kayna Süd (MMG *Mai 5819a*), × 10
- 2 *Doliosobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, larger cone scale from the abaxial side, Profen (MMG *Mai 5839a*), × 10
- 3 *Doliosobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, small cone scale with impressions by adjacent scales on the abaxial side, Kayna Süd (MMG *Mai 5819a*), × 10
- 4 *Doliosobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, aberrant cone scale with the seed and an adjacent impression after the second seed (?), Groitczsch (MMG *Mai 10602*), × 10
- 5 *Doliosobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, fragmentary cone scale with an immature winged seed, Groitczsch (MMG *Mai 10602*), × 10
- 6 *Doliosobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, short twig with (?) pollen cones, Königsau (MMG *Mai 2909b*), × 4
- 7 *Doliosobus taxiformis* (STERNB.) Z. KVAČEK var. *sternbergii* MAI et WALTHER ex Z. KVAČEK, detail of (?) pollen cones, Königsau (MMG *Mai 2909b*), × 9



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