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Research paper

Revision of the genus *Cunninghamites* (fossil conifers), with special reference to nomenclature, taxonomy and geological age

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ABSTRACT

The genus *Cunninghamites* was originally described for fossil sterile foliage. The inclusion of fertile material, and the debate about the nomenclature and taxonomy of *Cunninghamites* have initiated its revision. Revision has shown that only six species undoubtedly belong to *Cunninghamites*. Ovuliferous cones of *Cunninghamites oxycedrus* and *Cunninghamites squamosus* have been added to the diagnoses of these species. Based on the ovuliferous cones, *Cunninghamites* belongs to the Cupressaceae s.l.
After revision of *Cunninghamites*, it can geographically be confined to the Northern Hemisphere, mainly Europe and North America. The stratigraphic range of the genus now starts at the Valanginian–Hauterivian and can be extended upwards to the Maastrichtian.

1. Introduction

Since the early 19th century numerous fossil plants and plant fragments from all geological times and from all over the world have been discovered and described. As a result a large amount of fossil genera have been erected, modified, abandoned and reused. Species within these genera have also undergone the same process of assignment and reassignment to extinct, as well as, extant genera. Due to these changes in the use of genera, some are not used in accordance with their original diagnosis. One of these genera is the conifer genus *Cunninghamites*.

Presl (in Sternberg, 1838) erected a genus for fossil sterile foliage with a high similarity to the extant species *Cunninghamia lanceolata* (Lambert) Hooker; "Ramuli foliaque illis *Cunninghamiae sinensis* quam maxime analogi". The protologue clearly indicates *Cunninghamites* as a fossil genus for sterile twigs; however, currently two species of the genus are described with attached cones (e.g. Kvaček, 1999; Rüffle and Trostheide, 2000) and one species with associated cones.

In the original description of *Cunninghamites* (Presl in Sternberg, 1838, p. 203) the type species has not been clearly indicated. Two species have been simultaneously described: *Cunninghamites dubius* (pl. 33, Fig. 8) and *Cunninghamites oxycedrus* (pl. 48, Fig. 3 and pl. 49, Fig. 1). *Cunninghamites dubius* was described first, implicating that this material might be regarded as the type species; the International Code of Nomenclature for Algae, Fungi and Plants (Miller et al., 2011), however, does not prescribe this. Saporta (1884) stated that this species might possibly represent sterile twigs of *Palyssia braunii* Endlicher, and Schenk (1890) confirmed this. Due to its reassignment to *Palyssia*, *C. dubius* cannot be the type species. Thus, *C. oxycedrus* has been designated as the type species of the genus by Seward (1919).

The suggestion of botanical affinity with the extant genus *Cunninghamia*, implied by the name *Cunninghamites*, has been debated in literature. Corda (in Reuss, 1846) used the name *Cunninghamia* instead of *Cunninghamites* for the description of *Cunninghamia elegans* (=*Cunninghamites lignitum*) without explanation or reference to the nomenclatural issue. *Cunninghamites* was compared to *Dammara* and subsequently assigned to the family Dammaraceae (=Araucariaceae) (Corda in Reuss, 1846). *Cunninghamia elegans* was reassigned to *Cunninghamites* by Endlicher (1847). Zeiller (1905) supported the use of *Cunninghamites* and suggested that it is an intermediate between the extant genera *Cunninghamia* and *Dammara* (=*Agathis*). Other authors (e.g. Seward, 1919; Kräusel, 1922) suggested the use of *Elatocladus* to distinguish *Cunninghamites* from the extant genus *Cunninghamia*.

The absence of botanical affinity with extant *Cunninghamia* does not create the need to reassign all the material as *Cunninghamites* as it merely states the morphological resemblance to the extant genus. The name *Cunninghamites* has been validly and legitimately published and thus can be used.

Comparison to *Cunninghamia* and related genera, however, can be used to investigate the taxonomic position of the genus. The leaf base and number of vascular bundles of *Cunninghamia* are distinctively different from *Cunninghamites*. *Cunninghamiostrobus* has also been related to *Cunninghamites*; however, these permineralised cones cannot be compared without leaf material present. The details preserved in the compression fossils, are different from the details in

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the permineralised cones. Both the associated and attached cones of *Cunninghamites* are more elliptical, and considerably larger than those of *Cunninghamiostrobus*, and bear fewer seeds than *Cunninghamiostrobus* (Miller, 1975; Kvaček, 1999). Leaves described for *Cunninghamiostrobus* are not attached, but they show a high similarity to *Cunninghamia* (Brink et al., 2009).

The first reference of associated cones is by Göppert (1850). The cones he described as similar to *Cunninghamia* have been found associated with sterile twigs of *Cunninghamites oxycedrus* from Niederschöna (Germany). Velenovský and Viniklář (1926) were the first to describe attached ovuliferous cones under the illegitimate name of *Kettneria elegans*.

The systematic position of *Cunninghamites* highly agrees with the 'taxodiaceous' clades of the family Cupressaceae s.l., although Araucariaceae has been suggested as a possibility. The leaf arrangement and ovuliferous cones born singly and terminally, having two to nine ovules on the adaxial side of the cone scales, are characteristics of the Cupressaceae and can all be found in *Cunninghamites*.

Cunninghamites has been described from the Triassic to the Maastrichtian. However, to date most Triassic and Jurassic species have been removed from *Cunninghamites* and attributed to *Palyssia* and/or *Elatocladus* (e.g. Feistmantel, 1877; Barale, 1978). Therefore, it is now restricted to the Cretaceous. The lectotype of the type species *Cunninghamites oxycedrus*, selected by Kvaček and Straková (1997), has been described from the "Grünsand" (Greensand) of Niederschöna (Saxony, Germany). This locality is in the basalmost part of the Bohemian Cretaceous Basin (Čech et al., 1980; Uličný and Špičáková, 1996; Voigt et al., 2008), stratigraphically belonging to the Cenomanian (Late Cretaceous). Two other major species, *Cunninghamites lignitum* and *Cunninghamites squamosus*, also originate from the Late Cretaceous. The lectotype of *C. lignitum* was described from the locality of Mšeno, from the Peruc–Korycany Formation of the Bohemian Cretaceous Basin (Kvaček, 1999). The holotype of *C. squamosus* was described from the Heidelberg Formation (Santonian) of Quedlinburg in the Subhercynian Basin (Heer, 1871). Species of an older age should be carefully examined to determine whether a botanical relationship can be established with the genus *Cunninghamites*.

These problems with the nomenclature of *Cunninghamites*, as well as the uncertainty of its botanical affinity have led to the present revision. The current status of *Cunninghamites* will be assessed and diagnoses will be emended to create a coherent generic concept. The geological occurrences of *Cunninghamites* will be reviewed to better understand its stratigraphic range. We will attempt to reconstruct the evolutionary lines of *Cunninghamites* and discuss its botanical affinity.

2. Material and methods

Fossil material, particularly type material, from several historical collections was studied.

Collections in the following institutions were studied:

- Institut für Geologie und Paläontologie, Westfälische Wilhelms-Universität Münster (Germany)
- Bavarian State Collections of Palaeontology and Geology, Munich (Germany, numbered with prefix BSPG)
- Museum für Mineralogie und Geologie, Senckenberg Naturhistorische Sammlungen Dresden (Germany, numbered with prefix MMG)
- Museum für Naturkunde, Berlin (Germany, numbered with prefix MB Pb)
- Institut Royal des Sciences Naturelles de Belgique, Brussels (Belgium)
- Netherlands Centre for Biodiversity Naturalis, Leiden (The Netherlands, numbered with prefix JMS)
- Natuurhistorisch Museum Maastricht (The Netherlands, numbered with prefix NHMM)
- Geologisk Museum, Statens Naturhistoriske Museum, Copenhagen (Denmark, numbered with prefix MGUH)
- Naturhistorisches Museum Wien (Austria)
- Národní muzeum Praha (Czech Republic, numbered with prefix NMP)
- Naturhistoriska riksmuseet Stockholm (Sweden, NRS).

The specimens were studied with the aid of a dissecting microscope and, where possible and necessary, cuticle preparations were made. For this purpose, small pieces of the coalified leaf material were macerated in Schulze's reagent ($KClO_3$ and 30% HNO_3) and neutralised with either 5% ammonia or KOH. The cuticles were then separated into the ad- and abaxial cuticle with the aid of needles, mounted in glycerine jelly and sealed with paraplast. For SEM studies separate needles cleaned in HF and rinsed in water were mounted on aluminium stubs using nail polish, coated by gold and studied using Hitachi S-4300 and JEOL JSM 6380 field emission scanning electron microscopes.

3. Systematic palaeobotany

Order Coniferales
Family Cupressaceae
Genus *Cunninghamites* Presl (in Sternberg, 1838)

Emended diagnosis: Conifer shoots, bearing helically arranged, linear–lanceolate, dorsoventrally flattened leaves with three to five ribs (probably indicating veins); leaves diverging from shoot, widest at their basal third, apex acuminate. Older branches showing conspicuous leaf base cushions.

Leaf cuticle showing monocyclic to incompletely dicyclic stomata arranged in two bands. Papillae absent on ordinary epidermal cells and subsidiary cells. Leaf base cushion cuticle bearing isodiametric epidermal cells and few stomata.

Pollen cone born singly and terminally; conical; covered by short, helically arranged microsporophylls with imbricating distal ends.

Ovuliferous cone born singly and terminally; mature cone ovoid, bearing helically arranged cone scales, peltate, cone scales bearing up to four seeds.

Remarks on nomenclature: More recent descriptions of *Cunninghamites* have included fertile parts in the generic diagnosis (e.g. Kvaček, 1999). Although the protologue indicates that *Cunninghamites* is a genus for fossil sterile twigs, the inclusion of fertile parts is supported by the current authors. *Cunninghamites lignitum* and *Cunninghamites squamosus* have been described with attached ovuliferous cones (Kvaček, 1999; Rüffle and Trostheide, 2000). In addition, the type species *Cunninghamites oxycedrus* may have small ovuliferous cones (von Ettingshausen, 1867; Kunzmann, 2001) and a pollen cone was included in the diagnosis of this species (Kunzmann, 2001).

The proposed emendations of the International Code of Botanical Nomenclature (now International Code of Nomenclature for Algae, Fungi and Plants) – deletion of the concept of morphogenus and the introduction of the concept of a fossil-genus (Cleal and Thomas, 2010) – allow the inclusion of different fossil organs in the same genus. Following the acceptance of this proposal at the 2011 International Botanical Congress in Melbourne, Australia (Melbourne Code) we include the ovuliferous and pollen cones as part of the *Cunninghamites* generic concept.

Cunninghamites material has most often been reassigned to the fossil genus *Elatocladus* Halle (1913). The emended diagnosis of *Elatocladus* by Harris (1979) states: "Fossil conifer shoot bearing elongated, dorsiventrally flattened leaves with a single vein. Leaves divergent from stem". *Elatocladus* differs from *Cunninghamites* in several characteristics (Kvaček, 1999): (1) the contraction of the leaf base, which is absent in *Cunninghamites*, (2) in *Elatocladus* only one rib (a resin canal or vein) per needle is present, where there are up to

five present in *Cunninghamites*, (3) the conspicuous leaf base cushions of *Cunninghamites* are absent in *Elatocladus*.

Discussion: The leaf margin has been eliminated from the previous diagnosis of *Cunninghamites* (Kvaček, 1999) because it is a differentiating characteristic between some species within the genus and not a character of the genus itself. The absence of papillae on epidermal cells was previously not included, but emphasises the possible relationship with the 'basal' Cupressaceae s.l. (i.e. former Taxodiaceae).

The most probable taxonomic position of *Cunninghamites* is with the 'basal' Cupressaceae s.l. The ovoid shape, and often single and terminally born ovuliferous cones are characteristic of this family. The suggested affinity to the Araucariaceae is less likely since these cones are subglobular to ovoid, and bear only one seed per cone scale. *Cunninghamites* bears up to 4 seeds per scale, which is between two to numerous seeds on the adaxial side of the scale; which is the range of seeds per scale in the Cupressaceae s.l.

3.1. Species considered belonging to Cunninghamites

Cunninghamites oxycedrus Presl in Sternberg, 1838
Plate I, 1–2; Plate II, 3

Selected synonymy:

1838 *Cunninghamites oxycedrus* Presl in Sternberg; Presl in Sternberg, p. 203, pl. 48, Fig. 3a–c; pl. 49, Fig. 1a–c.
?1867 *Cunninghamites sternbergii* Ettingshausen; von Ettingshausen, p. 246, pl. 1, Figs. 4–6.
1997 *Cunninghamites oxycedrus* Presl in Sternberg; Kvaček and Straková, p. 116, pl. 39, Figs. 1, 3.
2001 *Cunninghamites oxycedrus* Presl in Sternberg; Kunzmann, p. 424–425, pls. 1–8.

Lectotype: MMG Ns 180, Presl in Sternberg, 1838: pl. 48, Fig. 3a,b (selected by Kvaček and Straková, 1997: pl. 39, Fig. 3).

Syntype: NMP F642, Presl in Sternberg, 1838: pl. 49, Fig. 1a,b (selected by Kvaček and Straková, 1997: pl. 39, Fig. 1; herein pl. II, 3).

Epitype: MMG Ns 13 (figured in Kunzmann, 2001: pl. 5, Figs. 1–4 and pl. 6, Figs. 1–5; herein pl. I, 2), here designated.

Geographic occurrence of the type material: Niederschöna in Saxony, Germany.

Stratigraphic occurrence: Niederschöna-Formation, Lower to Middle Cenomanian, Upper Cretaceous. This formation is located in the same sub-basin (Lausitz-Jizera Sub-Basin of the Bohemian Cretaceous Basin) as, and of identical age to, the Peruc–Korycany Formation (Voigt et al., 2008).

Emended diagnosis: Conifer shoot, leaves borne helically and diverging radially, arranged densely and overlapping. Leaf blade linear–lanceolate to lanceolate–ovate, dorsoventrally flattened, markedly variable in length, widest at the basal third. Leaf base decurrent, narrowing slightly at attachment. Apex acuminate, margin serrate. Up to five ribs (probably indicating veins) visible on impressions of the leaf lamina. Older branches showing conspicuous leaf base cushions.

Leaf epistomatic, adaxial cuticle with two bands of monocyclic to incompletely dicyclic stomata surrounded by 4–6 subsidiary cells, stomata irregularly placed and variously orientated, but often longitudinally. Abaxial cuticle without stomata, showing elongate epidermal cells. Papillae absent on ordinary epidermal cells and subsidiary cells. Leaf base cushion bearing isodiametric epidermal cells and few stomata.

Pollen cone born singly and terminally, conical, covered by short, helically arranged microsporophylls with imbricating distal ends.

Description: *Cunninghamites oxycedrus* has been described in detail by Kunzmann (2001). Leaf blade 20–30 mm long and 1.5–4 mm wide, tapering in an acute apex. Young leaves do not show conspicuous leaf base cushions, but mature leaves do. The leaf base cushions are epistomatic, bearing only a few stomata.

Remarks on nomenclature: The type specimens of *Cunninghamites oxycedrus* were selected in an earlier publication by Kvaček and Straková (1997). After this publication it was discovered that lectotype NMP F2612 was mistakenly catalogued in the collections of the National Museum Prague. Subsequently the specimen was returned to Senckenberg Naturhistorische Sammlungen Dresden where it is now stored as MMG Ns 180.

The selection of MMG Ns 180 as the lectotype of *Cunninghamites oxycedrus* is based on the representation of the typifying characteristics this specimen displays. The syntype NMP F642 has a possible attached male cone (Plate I, 3); microsporophylls are indistinct and no pollen has been isolated so far.

Specimen MMG Ns 13 (Plate I, 1) from Niederschöna, the type locality, is designated here as an epitype since it shows epidermal characteristics not visible or preserved in the lectotype.

Discussion: The major characteristic distinguishing *Cunninghamites oxycedrus* from other species of the genus, in particular *Cunninghamites lignitum* and *Cunninghamites squamosus*, is the serrate leaf margin (Plate I, 2). The arrangement of the stomata on the adaxial side of the leaf (Plate I, 1) distinguishes *C. oxycedrus* from *C. squamosus*.

As suggested by Kunzmann (2001), the putative ovuliferous cone of *Cunninghamites oxycedrus*, originally described as *Cunninghamites sternbergii* by von Ettingshausen (1867), is excluded from the diagnosis. Whether or not the cones are attached to twigs of *C. oxycedrus* is debatable. The material figured by von Otto (1854, pl. 8, Fig. 7), which shows the best characteristics to confirm the affiliation of the species, is apparently missing and cannot be re-examined. The cones are approximately 25 by 15 mm in size as compared to the cones of *Cunninghamites lignitum* and *Cunninghamites squamosus*, which are considerably smaller and more ovoid in shape.

Distribution: *Cunninghamites oxycedrus* is only known from the type locality, Niederschöna, Saxony, Germany (Cenomanian).

Cunninghamites lignitum (Sternberg) Kvaček, 1999
Plate I, 3–4; Plate II, 5–6

Selected synonymy:

1825 *Lycopodiolites lignitum* Sternberg; Sternberg, tentamen p. 8.
1846 *Cunninghamia elegans* Corda in Reuss; Corda in Reuss, p. 93, pl. 49, Figs. 29–31.
1846 *Cunninghamia planifolia* Corda in Reuss; Corda in Reuss, p. 93, pl. 50, Figs. 1–3.
1847 *Cunninghamites elegans* (Corda) Endlicher; Endlicher, p. 201.
1847 *Cunninghamites planifolius* (Corda) Endlicher; Endlicher, p. 41.
1885 *Cunninghamia stenophylla* Velenovský; Velenovský, p. 15, pl. 5, Figs. 5, 10, 16.
1926 *Kettneria elegans* (Corda) Velenovský et Viniklář; Velenovský and Viniklář, p. 11, 38, pl. 1 Figs. 12–15, pl. 3, Fig. 6.
1999 *Cunninghamites lignitum* (Sternberg) Kvaček; Kvaček, p. 131–136, pls. 4–6.

Basionym: *Lycopodiolites lignitum* Sternberg; Sternberg, 1825, tentamen p. 8.

Lectotype: NMP F636, Sternberg, 1825: 8 (tentamen); Kvaček, 1999: pl. 4, Fig. 1a.

Epitype: NMP F2708a (figured in Kvaček, 1999: pl. 5, Fig. 2; herein pl. II, 6), here designated.

Geographic occurrence of the type material: Mšené ('Mseno') near Litoměřice ('Litomeritz'), Bohemia, Czech Republic.

Stratigraphic occurrence: Peruc–Korycany Formation, Lower to Middle Cenomanian, Upper Cretaceous. This formation is located in the same sub-basin (Lausitz-Jizera Sub-Basin of the Bohemian Cretaceous Basin) as, and of identical age to, the Niederschöna-Formation.

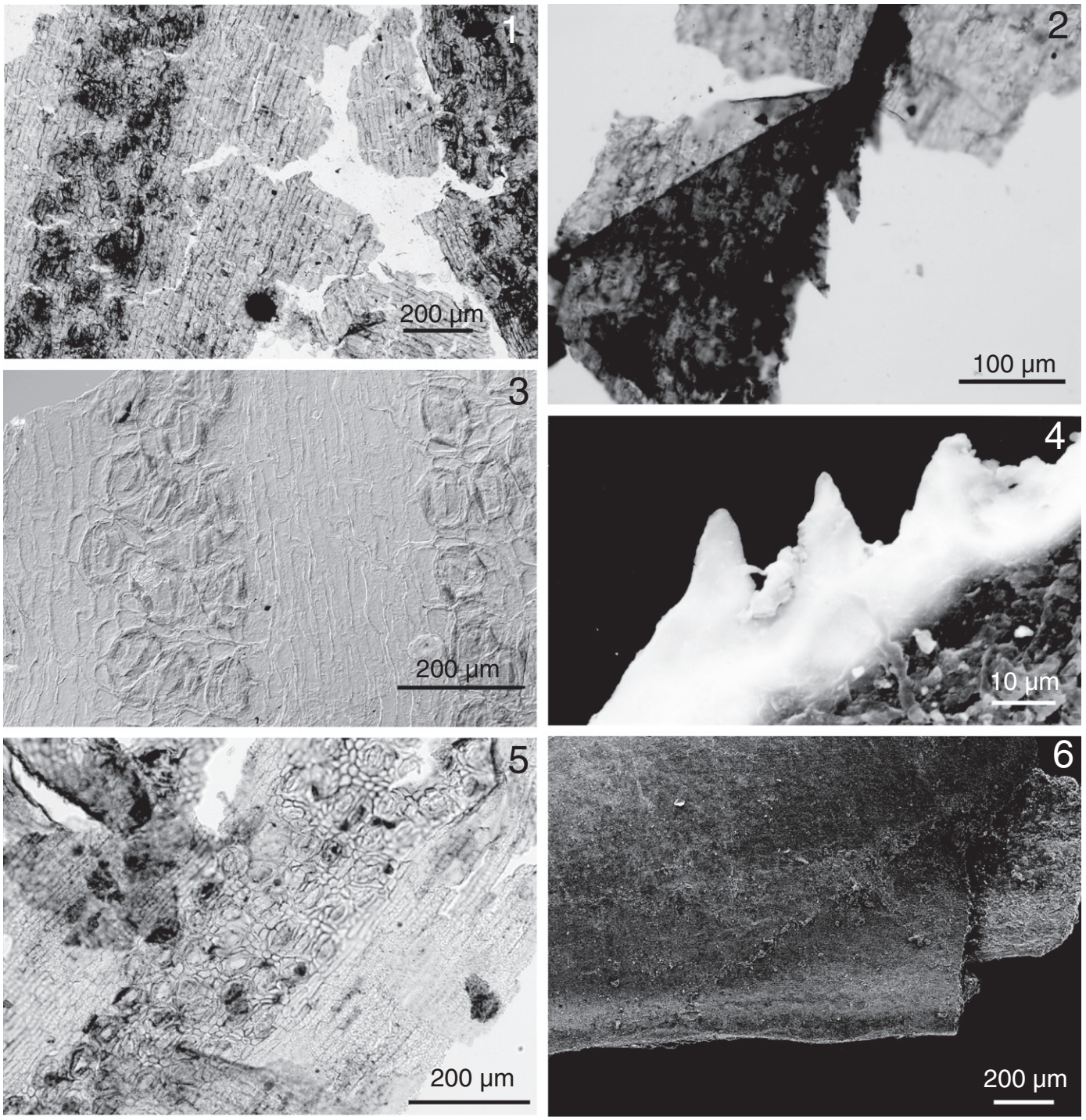


Plate I. Cuticle remains of *Cunninghamites* species.

1. Cuticle preparation of *Cunninghamites oxycedrus* showing adaxial side with stomatal band (MMG Ns13; Niederschöna, Germany; Cenomanian).
2. Cuticle preparation of *Cunninghamites oxycedrus* showing serrate margin (MMG NS63:2; Niederschöna, Germany; Cenomanian).
3. Cuticle preparation of *Cunninghamites lignitum* showing adaxial side with stomatal bands (NMP F2278; Pecínov, Czech Republic; Cenomanian).
4. SEM photograph of *Cunninghamites lignitum* showing irregularly serrulate margin (NMP F2833; Pecínov, Czech Republic; Cenomanian).
5. Cuticle preparation of *Cunninghamites squamosus* showing abaxial side with stomatal band (JMS 52309; Swalmen, the Netherlands; Santonian).
6. SEM photograph of *Cunninghamites squamosus* showing entire margin and vein (JMS 52340; Cottesen, the Netherlands; Santonian).

Emended diagnosis: Conifer shoot, axis straight, branching occasionally, leaves born helically, diverging at 20° to 50° from the axis and overlapping. Apical part of axis formed by dense, overlapping needles forming a bud. Leaf blade linear–lanceolate, dorsoventrally flattened, markedly variable in length, widest at its basal third. Apex acuminate, margin irregularly serrulate. Three to five ribs (probably indicating veins) on impressions of the leaf lamina. Older branches showing conspicuous leaf base cushions.

Leaf blade epistomatic, adaxial cuticle with two bands of monocyclic to incompletely dicyclic stomata surrounded by 4–6 subsidiary cells.

Abaxial cuticle without stomata, showing elongate epidermal cells. Papillae absent on ordinary epidermal cells and subsidiary cells. Leaf base cushion amphistomatic, showing isodiametric epidermal cells and few irregularly placed and variously oriented stomata surrounded by four subsidiary cells.

Ovuliferous cone born singly and terminally; mature cone ovoid, bearing helically arranged cone scales; scales peltate, with long stalk and large hexagonal head terminating in an excrescence, bearing up to four oval, wingless seeds.

Description: *Cunninghamites lignitum* was described by Kvaček (1999) in detail, including the attached ovuliferous cone. Kvaček (1999) described the leaves as hypostomatic, but there are no stomata on abaxial side of the leaf blade, only on and in the vicinity of the leaf base cushions are stomata present on both sides. The leaf base cushion is characterised as amphistomatic; on the abaxial side stomata are present, as well as on the adaxial side directly adjacent to the axis.

Remarks on nomenclature: *Cunninghamites lignitum* is the most common species and is described from various European localities. It often has been identified as *Cunninghamia elegans* or *Elatocladus elegans*. Kvaček (1999) demonstrated that this widely used epithet is illegitimate and emended the species.

Kvaček (1999) also included *Cunninghamites oxycedrus* in this species. However, this is debatable and even though the species are very similar and occur in comparable geological formations, their leaf margin and arrangement of the stomata differ. *Cunninghamites lignitum* is serrulate with teeth irregular both in distribution and size (up to 15 μm; Plate I, 4). They are distinctly smaller than the regularly distributed teeth of *C. oxycedrus* (app. 50 μm; Plate I, 2). In both species the stomata are situated on the adaxial side of the leaf (Plate I, 1 and 3). However, on and near the leaf base of *C. lignitum* stomata are present on both sides, where *C. oxycedrus* only has stomata on the abaxial side of the leaf base cushion. Since no conclusive evidence has shown overlap between the two species, current authors decided that both species remain separate.

The pollen cone included in the diagnosis by Kvaček (1999) has been removed, since this material belongs to *Cunninghamites oxycedrus* (Plate II, 3). In the present study an epitype is added to the type material of *Cunninghamites lignitum* to include the ovuliferous cone (NMP F2078a, Plate II, 6). The ovuliferous cone was first described as *Kettneria elegans* by Velenovský and Viniklář (1926). The dimensions of the ovuliferous cones of *C. lignitum* (55–65 mm long by 25–35 mm wide), are considerably larger than the putative cone of *C. oxycedrus* (25 mm long by 15 mm wide). The cone consists of helically arranged hexagonal to polygonal cone scales bearing four seeds each.

Kräusel (1922) included *Cunninghamites planifolius* in his *Elatocladus elegans* from the Late Cretaceous of the Netherlands without indicating a reason. This *E. elegans* however, is not identical with *Cunninghamites lignitum*, but conspecific with *Cunninghamites squamosus* (Bosma et al., 2009). Although the holotype is missing, *C. planifolius* can be considered identical to *C. lignitum* based on gross morphology and co-occurrence in the type locality (Kvaček, 1999).

Velenovský (1885) already mentioned the possibility that his species *Cunninghamia stenophylla* is identical with *Cunninghamia elegans* (=*Cunninghamites lignitum*). Kräusel (1922) also indicated this reassignment as very probable. Here we formally include *C. stenophylla* in *C. lignitum*; the original separation was based on the fact that *C. stenophylla* is more slender than *C. lignitum*. As Zeiller (1905) already indicated, the study of a more extensive collection of material shows that *C. stenophylla* falls within the size range of *C. lignitum*.

Distribution: Sterile foliage assigned to *Cunninghamites lignitum* has only been described from the European continent (e.g. Italy and Bohemia; Bozzi, 1891; Kvaček, 1999). The species is confined to localities of Cenomanian age.

Cunninghamites squamosus Heer
Plate I, 5–6; Plate II, 4 and 7

Selected synonymy:

1871 *Cunninghamites squamosus* Heer; Heer, p. 9, pl. 1, Figs. 5–7.
1880 *Cunninghamites recurvatus* Hosius et von der Marck; Hosius and von der Marck, p. 178, pl. 37, Figs. 143, 144.
1905 *Cunninghamites pulchelles* Knowlton; Knowlton, p. 136, pl. 16, Fig. 1.
1910 *Cunninghamites elegans* (Corda) Endlicher; Berry, p, 186, pl. 20, Figs. 1–4.
1919 *Elatocladus elegans* (Corda) Seward; Seward, p. 433, Figs. 804, 805.
1922 *Elatocladus elegans* (Corda) Seward; Kräusel, p. 10–18, pl. 1, Figs. 4–10; pl. 2, Figs. 1–5; pl. 3, Figs. 1,2; Textfigs. 4,5.
1925 *Cunninghamites elegans* (Corda) Endlicher; Berry, p. 33.
2000 *Elatocladus elegans* (Corda) Seward; Rüffle and Trostheide, p. 434, pl. 1, Fig. 6; pl. 2, Fig. 2; pl. 3, Fig. 1.
2009 *Cunninghamites squamosus* Heer; Bosma et al., p. 486–489, Fig. 4c–f; Fig. 5.

Lectotype: BSPG coll. Univ. Würzburg no. 6166 (ex coll. Schenk), Heer, 1871; pl. 1, Fig. 5, here designated.

Epitypes: MB Pb 2003/776a (figured in Rüffle and Trostheide, 2000: pl. 2, Fig. 2; herein pl. II, 4), here designated. JMS 52309 (figured in Bosma et al., 2009: Figs. 4C–F, herein pl. I, 5), here designated.

Geographic occurrence of the type material: "Altenburg" near Quedlinburg, Saxony-Anhalt, Germany.

Stratigraphic occurrence: Heidelberg Formation, Upper Santonian, Upper Cretaceous (Niebuhr et al., 2007).

Emended diagnosis: Conifer shoot, leaves born helically and diverging radially, leaves arranged densely and overlapping. Leaf blade linear–lanceolate to lanceolate–ovate, dorso-ventrally flattened, markedly varying in length, widest at the basal third. Leaf base decurrent, narrowing slightly at attachment; axis with conspicuous leaf base cushion. Leaf apex acuminate, margin entire. Three to five ribs (probably indicating veins) on impressions of the leaf lamina.

Leaf blade hypostomatic, abaxial cuticle with two bands of monocyclic to incompletely dicyclic stomata surrounded by 4–6 subsidiary cells. Adaxial cuticle showing elongate epidermal cells. Stomata irregularly placed and variously orientated but often longitudinally. Papillae absent on ordinary epidermal cells and subsidiary cells. Leaf base cushion amphistomatic, cuticle bearing isodiametric epidermal cells and few stomata.

Ovuliferous cone born singly and terminally, mature cone ovoid, bearing helically arranged cone scales, peltate with hexagonal head.

Description: Sterile material of *Cunninghamites squamosus* has extensively been described by Bosma et al. (2009). The addition of American material to the species has increased the length of the leaves to 65 mm. The leaf base cushion is characterised as amphistomatic; on the abaxial side stomata are present, as well as on the adaxial side directly adjacent to the axis.

The ovuliferous cones are ovoid and born singly and terminally on leafy shoots. Cones are 45–63 mm long and 30–42 mm in diameter, containing more than 34 (up to 52) peltate cones scales. Cone scales are helically arranged, diverging at right angles. The cone scales are 15–21 mm long and up to 12 mm wide at the base of the rectangular to hexagonal head. The basal part of the scales is cuneate to pedicellate. The head of the cone scale shows several radial ribs and terminates in an excrescence up to 2.5 mm long. At least two impressions of wingless seeds are visible on the scales.

Remarks on nomenclature: *Cunninghamites squamosus* (Plate II, 7) morphologically resembles *Cunninghamites lignitum* and *oxycedrus*. The distinction between the three species can be made based on the leaf margin and stomatal arrangement. *Cunninghamites squamosus* has

an entire leaf margin (Plate I, 6), whereas *C. lignitum* and *C. oxycedrus* are respectively irregularly serrulate and serrate. The leaf blade of *C. squamosus* is hypostomatic (Plate I, 5), in contrast to the epistomatic leaf blades of *C. oxycedrus* and *C. lignitum*. The arrangement of stomata on the leaf base cushion differs between the species; *C. oxycedrus* has epistomatic leaf base cushions, while in *C. lignitum* and *C. squamosus* they are amphistomatic. The epitype of *C. squamosus*, JMS 52309 (Plate I, 5), clearly shows the amphistomatic character of the leaves of *C. squamosus*, as well as the entire margin.

The age of the sediments in which *Cunninghamites squamosus* occurs (viz. Santonian to Maastrichtian), is younger than the sediments in which both *Cunninghamites lignitum* and *Cunninghamites oxycedrus* are found (viz. Cenomanian).

Discussion: The type material of *Cunninghamites recurvatus* is not detailed enough to establish the characteristics of the leaf margin. In addition, cuticle preparations could not be obtained thereby making it impossible to determine the arrangement of the stomata, which is a diagnostic character of the species. The inclusion of *C. recurvatus* is solely based on gross morphology and the origin of the material; i.e. Campanian sediments from Legden (Germany).

Another Campanian species, *Cunninghamites pulchellus*, has been included in the genus for the same reason. Knowlton (1905) made the suggestion earlier when he described this species; "[it] may possibly be a smaller branchlet of *C. elegans* with the leaves slightly recurved" (Knowlton, 1905, p. 136). The distinction between *Cunninghamia elegans* and *Cunninghamites squamosus* was not made at that time.

Halamski (2012) described *Cunninghamia elegans* from two new localities; Potylicz (Ukraine, Upper Campanian) and Chełm (Poland, Upper Maastrichtian). Based on the age of the specimens, they are most probably conspecific with *Cunninghamites squamosus*. The preservational state of this material does not permit cuticular analysis or further investigation of the leaf margin.

Berry (1925) described *Cunninghamia elegans* from various North American localities. All available material from the American continent is interpreted as the same species. The leaves are distinctly longer (up to 65 mm; Berry, 1910) than *Cunninghamites lignitum*. The age of the localities varies from Santonian to Maastrichtian, which may suggest that these specimens are not conspecific to *C. lignitum*. Based on the length of the leaf blade and the indication the geological age gives about conspecifity, the current authors reassign the American material to *Cunninghamites squamosus*.

Bosma et al. (2009) described an ovuliferous cone, which is associated with and possibly belongs to *Cunninghamites squamosus*. Unfortunately, the base of the cone is not present, so attachment to twigs of this species cannot be established.

This ovuliferous cone is in complete agreement with cones from Quedlinburg (type locality of *Cunninghamites squamosus*) described as *Elatocladus elegans* (Rüffle and Trostheide, 2000), thus inclusion of the specimen from the Netherlands in the species is possible. Further unpublished material from Quedlinburg includes several twigs with both complete and incomplete ovuliferous cones attached. These are housed in Stockholm (NRS) as part of the Richter collection. The material only comprises impressions of ovuliferous cones without coalified remains or impressions of seeds.

The first figured specimen of the ovuliferous cone (Rüffle and Trostheide, 2000; pl. 2, Fig. 2; herein Plate II, 4) is designated here as an epitype. This specimen clearly shows the attachment of the cone to a twig with the distinct characteristics of the species.

Distribution: *Cunninghamites squamosus* has been described from Santonian, Campanian and Maastrichtian localities from the United States (e.g. Knowlton, 1905; Berry, 1925) and Western Europe (e.g. Bosma et al., 2009) and possibly in the border area of Poland (Maastrichtian) and Ukraine (Campanian; Halamski, 2012).

Cunninghamites ubaghsii Debey ex Ubaghs
Plate II, 1

Selected synonymy:

1885 *Cunninghamites Ubaghsi* De Bey; Ubaghs, p. 28.
2004 *Cunninghamites* sp.; Van der Ham and Van Konijnenburg — Van Cittert, p. 28, Fig. 7.
2004 *Cunninghamites ubaghsii* Debey ex Ubaghs; Van der Ham et al., p. 94, Figs. 3–6.

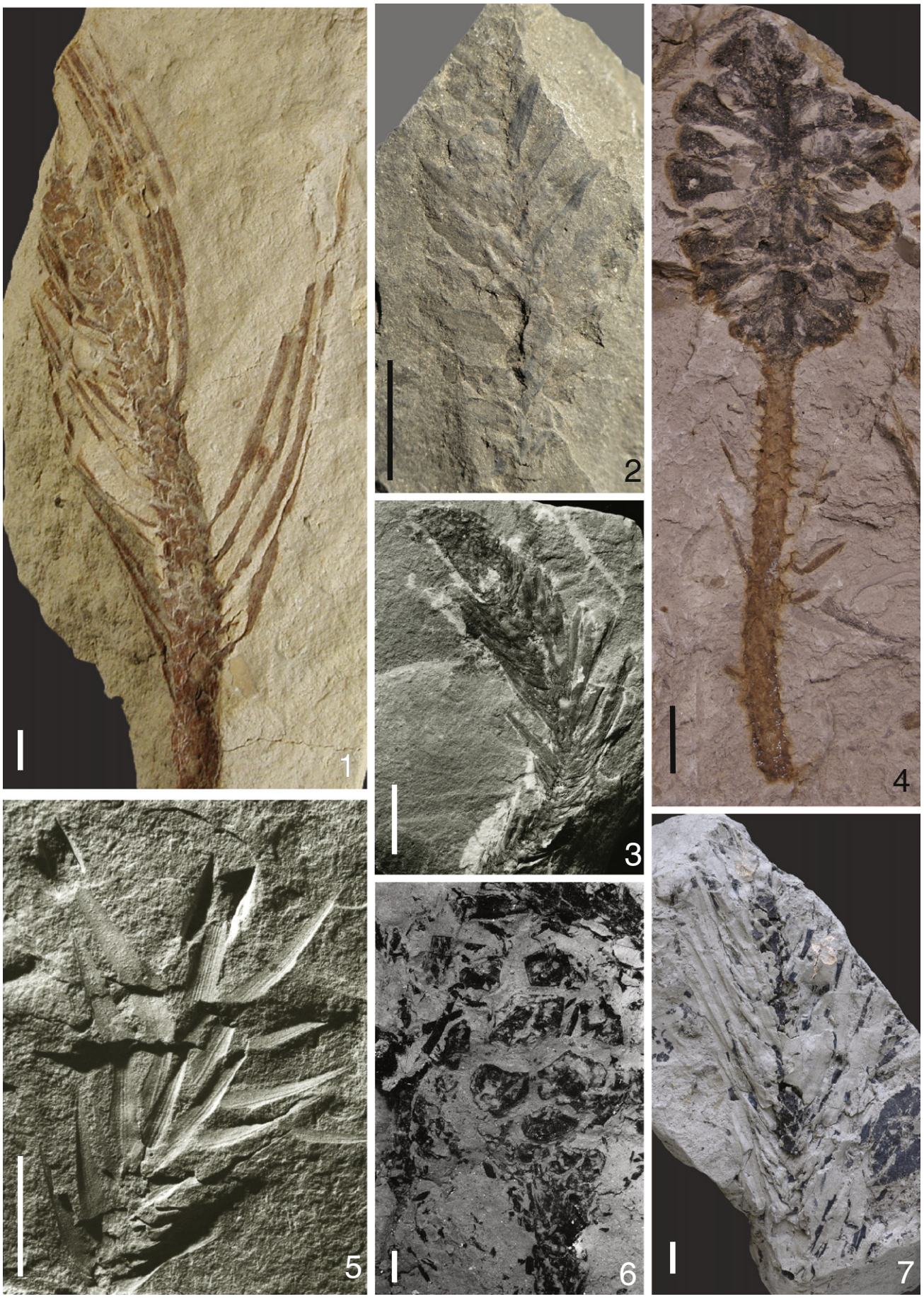
Holotype: IRSNB-Paleobot. b4318, Van der Ham et al., 2004: Fig. 3.
Geographic occurrence of the type material: quarry near Kunrade, The Netherlands.
Stratigraphic occurrence: Kunrade Chalk (Maastricht) Formation, Late Maastrichtian, Late Cretaceous.
Diagnosis: Shoot with spirally arranged leaves spreading in all directions. Free leaf portion dorsiventrally flattened, linear, up to ca. 120 mm long and 4–5 (max. 7) mm wide, hardly or not constricted arising from a conspicuous, obovoid–rhomboidal leaf base cushion of 5–7 by 4–6 mm.
Description: *Cunninghamites ubaghsii* has extensively been described by Van der Ham et al. (2004). The known fragments of *C. ubaghsii* are relatively long, 17 and 18 cm. Leaves are up to 120 mm long, without visible apices. Specimens do show the characteristic leaf base cushions or scars on the places where the leaves have been detached.
Discussion: *Cunninghamites ubaghsii* has distinctly longer leaves than all other species of *Cunninghamites*. This species can be included in the genus based on the conspicuous leaf base cushions and leaf scars on the branches (Plate II, 1) typical for *Cunninghamites*. The anatomy of the cuticle could not be determined due to the lack of suitable material.
Halamski (2012) described *Cunninghamites ubaghsii* from an upper Campanian locality in Eastern Poland, Krasnobród. Previously this species was only known from the Maastrichtian of the Netherlands.
Distribution: *Cunninghamites ubaghsii* has been described from southern Limburg, The Netherlands (Maastrichtian; Van der Ham et al., 2004) and Krasnobród, Poland (Campanian; Halamski, 2012).

Cunninghamites borealis Heer
Plate II, 2

Selected synonymy:

1882 *Cunninghamites borealis* Heer; Heer, p. 55, pl. 29, Fig. 12.
1890 *Torreya borealis* Heer; Schenk, p. 331 pro parte.
1926 *Elatocladus smittiana* (Heer) Seward; Seward, p. 103 pro parte.

Holotype: MGUH 5800, Heer, 1882; pl. 29, Fig. 12, 12b (herein Plate II, 2).
Geographic occurrence of the type material: Asuk, Greenland.
Stratigraphic occurrence: Kingittoq Member, Atane Formation, Cenomanian, Late Cretaceous (Boyd, 1992).
Emended diagnosis: Conifer shoot, leaves born helically, diverging and overlapping. Leaf blade linear–lanceolate, apex acuminate, at least three ribs visible on impressions of leaf lamina. Leaf base decurrent.
Description: *Cunninghamites borealis* has only been properly described by Heer (1882). The holotype, which is the only available fragment, is a slender axis approximately 40 mm long. The leaves are helically arranged and vary in length from 6 to 13 mm and are 2 mm wide. The leaves show leaf base cushions, which are not as conspicuous as in the other species of the genus, and have at least three ribs. The base of the leaf is not constricted, but it is not clearly visible in this specimen. No cuticles could be prepared from the material.
Remarks on nomenclature: Originally Heer (1882) spelled the name of this species with one 'n' (*Cuninghamites*), but he does compare it to the other *Cunninghamites* species. Schenk (1890) described the species using a double 'n'.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Schenk (1890) reassigned *Cunninghamites borealis* to *Torreya borealis* Heer (1883) from the Atane Formation. *Torreya borealis* however lacks the conspicuous leaf base cushions, has a constricted leaf base, and the apex of the leaf is more rounded.

Seward (1926) reassigned the material of *Cunninghamites borealis* without any explanation to *Elatocladus smittiana*. That taxon, however, lacks the conspicuous leaf base cushion characteristic for *Cunninghamites*. Moreover, *E. smittiana* has only been described from Lower Cretaceous localities, which makes reassignment to this species less likely. Therefore, we recognise this material as *C. borealis*.

Discussion: In the original species description, Heer (1882) described it as having leaves similar to *Cunninghamia*. The leaves were characterised as multi-veined and with distinct median vein. However, the sole indication of the distinct median vein is probably caused by a fold in the leaf lamina or overlapping leaves (Plate II, 2). There are at least three ribs visible on the impression of the leaf lamina.

Heer (1882) extensively compares *Cunninghamites borealis* to the other species *Cunninghamites lignitum*, *Cunninghamites oxycedrus*, and *Cunninghamites squamosus*. The leaves of *C. borealis* are shorter and do not end in an elongated, pointed apex (Plate II, 2) as in *C. lignitum*. Compared to *C. oxycedrus*, this species has a more pronounced midrib and wider leaf base. *Cunninghamites squamosus* can be distinguished by its more slender leaves.

Distribution: *Cunninghamites borealis* has only been described from the type locality, Asuk, Greenland (Cenomanian) (Heer, 1882).

Cunninghamites priscus Eichwald

Synonymy:

1844 undeterminable plant-remains; Auerbach, p. 148, pl. 4, Fig. 3.
1861 *Cunninghamites prisca* Eichwald; Eichwald, p. 311.
1865 *Geinitzia prisca* (Eichwald) Eichwald; Eichwald, p. 48, pl. 3, Fig. 19a–c.

Holotype: unknown repository, Auerbach, 1844: pl. 4, Fig. 3.

Geographic occurrence of the type material: Klin, near Moscow, Russia.

Stratigraphic occurrence: Formation unknown; Valanginian–Hauterivian, Early Cretaceous.

Diagnosis: Sterile twigs cylindrical with narrow, elongated leaves. Leaves with acute apex showing a dorsal median keel. Leaf base cushion widened and amplexicaul (after Eichwald, 1865).

Description: The type material could not be studied because the repository is unknown. The original figure by Auerbach (1844) shows a short branch with possible leaf scars. No further description has been given and the figured specimen does not show any other characteristics. The first description of *Cunninghamites priscus* (Eichwald, 1861) only referred to Auerbach's material as being identical.

Eichwald (1865) figures a different specimen in a later publication, which shows a short twig densely covered with leaves. The leaves are approx. 23 mm long and 1 mm wide, helically arranged, and show a distinct median rib. The base of the leaf forms an amplexicaul leaf base cushion.

Discussion: The original publication by Auerbach (1844) appears to figure a different specimen than Eichwald (1861 and 1865) described. However, Eichwald (1861) specifically refers to the material of Auerbach and added new material from a Ukrainian locality (Tatarowo).

Eichwald (1865) reassigned the material to *Geinitzia* (as *Geinitzia prisca*), a combination that was already suggested in the original description of the species (Eichwald, 1861). The absence of the rhomboidal leaf scars in the type specimen was the argument for reassigning it to *Geinitzia*. The characteristic scars are absent in the figured specimen, due to the fact that all the leaves are still present. It is however possible that older branches do show the leaf scars, however, the unknown repository of the material makes reinvestigation impossible. The conspicuous leaf base cushions in this material are not typical for *Geinitzia* (Kunzmann, 2010), but are most similar to those of *Cunninghamites*.

Cunninghamites priscus differs from *Elatidopsis cryptomerioides* from the Kunraad sandstones, because the apex of the latter species is less elongated (Eichwald, 1865). The two species are also of different ages; *C. priscus* is Early Cretaceous and *E. cryptomerioides* is from the Late Cretaceous. This difference in age is another argument, although less valuable, against the two species being conspecific.

Based on the pronounced leaf base cushions and elongate leaf apex the present authors accept *Geinitzia prisca* as belonging to the genus *Cunninghamites*.

Distribution: *Cunninghamites priscus* is known from the type locality Klin, and also from Litkarino (both near Moscow, Russia) and Tatarowo (Ukraine), all Valanginian–Hauterivian (Early Cretaceous).

3.2. Species formerly described as Cunninghamites, but excluded here from the genus

Currently in the literature two other species of *Cunninghamites* have been described. However, based on their descriptions and figured specimens they can easily be excluded from *Cunninghamites*. Reassignment to another genus is problematic due to the unknown repository of the type material.

Conifer shoot of unknown affinity, formerly described as *Cunninghamites dubiosus* Feistmantel.

Synonymy:

1863 ?*Cunninghamites inaequifolius* Oldham et Morris; Oldham and Morris, pl. 33, Figs. 3,4.
1877 *Cunninghamites dubiosus* Feistmantel; Feistmantel, p. 140.
1957 *Cunninghamites dubiosus* Feistmantel; Kryshtofovich, p. 512.

Basionym: *Cunninghamites dubiosus* Feistmantel; Feistmantel, p. 140.

Holotype: unknown repository (probably Geological Survey of India), Oldham and Morris, pl. 33, Figs. 3,4.

Geographic occurrence of the type material: Brindabun, India.

Stratigraphic occurrence: Rajmahal Group, Lower Jurassic (McDougall and McElhinny, 1970).

Diagnosis: Leaves helically arranged, rigid, linear–lanceolate, with one vein. Leaf base constricted and decurrent (after Feistmantel, 1877).

Description: Feistmantel (1877) describes his new species minimally and indicates the species will possibly be further described in another publication. The assignment of this species to *Cunninghamites*

Plate II. Macrofossil remains of *Cunninghamites* species, bar is 10 mm.

1. Sterile foliage of *Cunninghamites ubaghsii* (NHMM, collection Nieuwenhuis, no. 8e; Maastricht, the Netherlands; Maastrichtian).
2. Holotype of *Cunninghamites borealis* (MGUH 5800; Asuk, Greenland; Cenomanian).
3. Lectotype of *Cunninghamites oxycedrus* with pollen cone (NMP F642; Niederschöna, Germany; Cenomanian).
4. Epitype of *Cunninghamites squamosus* with ovuliferous cone (MB Pb 2003/776a; Quedlinburg, Germany; Santonian).
5. Sterile foliage of *Cunninghamites lignitum* (NMP F640; Mšené, Czech Republic, Cenomanian).
6. Epitype of *Cunninghamites lignitum* with ovuliferous cone (NMP F2708a; Pecínov, Czech Republic; Cenomanian).
7. Sterile foliage of *Cunninghamites squamosus* (JMS 52343; Swalmen, the Netherlands; Santonian).

is based on the leaves and 'other characteristics' shown in the figures. The figures are part and counterpart and show a short branch of which no measurements are given. There are remnants of intact leaves, which are broad at the base and end in a very sharp apex. The base of the leaf is not clearly visible, but does not show the typical leaf base cushions. On the branch where no leaves are attached, the rhomboidal scars are absent.

Remarks on nomenclature: As Feistmantel (1877) already mentioned in his description of the species, the figured material is very 'imperfect' and characteristics are not clearly visible. The type material was originally figured as a possible *Cunninghamites inaequifolius* by Oldham and Morris (1863) from Brindabun (India).

Feistmantel decided to create a new species because the smaller leaves, in size equal to *Cunninghamites inaequifolius*, are probably only leaf fragments. This statement is probably correct. However, based on the figured specimen and short description, this is not *Cunninghamites*. The characteristic leaf base cushion or leaf scar is not present in this specimen. The current authors believe the material should not be attributed to the genus, however, without examination of the material the species cannot be reassigned.

Apart from a listing by Kryshtofovich (1957), the species has never been further cited in the literature.

Distribution: The conifer shoot formerly described as *Cunninghamites dubiosus* has only been described from the locality Brindabun (India).

Cf. *Pagiophyllum* sp., formerly described as *Cunninghamites australis* Tenison-Woods.

Synonymy:

1883 *Cunninghamites australis* Tenison-Woods; Tenison-Woods, p. 139, pl. 3, Figs. 1–3; pl. 4, Fig. 1.
?1910 cf. *Pagiophyllum* sp.; Arber, p. 27.

Holotype (of *Cunninghamites australis*): unknown repository (probably Macleay Museum, University of Sydney), Tenison-Woods, 1883: pl. 3, Figs. 1–3; pl. 4, Fig. 1.

Geographic occurrence of the type material: Rosewood, Ipswich, Queensland, Australia.

Stratigraphic occurrence: Ipswich coal, Late Triassic (Day et al., 1983).

Diagnosis: Leaves linear, elongated, with an acute apex. Base of the leaves decurrent, margin entire. Male strobili elongated, cylindrical, curved, born terminally in clusters (after Tenison-Woods, 1883).

Description: Tenison-Woods (1883) did not describe in detail the material of this species, hence no exact measurements are available. The species is described as highly similar to *Cunninghamia* based on the male 'amenta' (catkin or strobili), which are born in terminal clusters. The strobili are elongated, cylindrical, and approximately 20 mm long. Comparable structures have not been described for *Cunninghamites*.

Remarks on nomenclature: *Cunninghamites australis* has been assigned to the genus based on the high similarity of the male strobili to those of the extant genus *Cunninghamia*. Tenison-Woods (1883) states: 'In the specimens found at Rosewood, Ipswich, there are two to three with male amenta in terminal clusters which are figured here rendering the identification of the genus much more certain'. This statement is incorrect, since the described strobili are similar to the extant genus *Cunninghamia*, and not to *Cunninghamites*. The possible male cone of *Cunninghamites oxycedrus* is born terminally and singly, whereas there is a cluster of two or more terminal male cones in *C. australis*. The shape of the structure is also distinctly different in that it is cylindrical instead of conical.

The assignment to *Cunninghamites* based on the resemblance to *Cunninghamia* is incorrect since there is no well established botanical relationship between the species. The geological age of the material, Late Triassic, also indicates it is less likely to have botanical affinity with the extant genus. Furthermore, based on the description, *Cunninghamites australis* does not show any of the diagnostic characters of the genus. Tenison-Woods also compared *C. australis* to *Cunninghamites inaequifolius*, which has been reassigned to *Elatocladus confertus*.

The figured specimens and description of the genus do not indicate the presence of a conspicuous leaf base cushion or rhomboidal leaf scar. As Arber (1910) already suggested, the leaf material is probably a *Pagiophyllum*. However, without examination of the original material, which is in an unknown repository, this species cannot be reassigned with certainty.

Distribution: *Cunninghamites australis* has only been described from the locality, Rosewood, Ipswich (Queensland, Australia) (Tenison-Woods, 1883).

3.3. Species excluded from the genus Cunninghamites by previous authors

Several other species previously described as *Cunninghamites* have already been excluded from the genus by different authors. The Jurassic species *Cunninghamites confertus* from Bindrabun (India) (Oldham and Morris, 1863) was only figured and not described in its original publication. It was reassigned to *Palyssia conferta* by Feistmantel (1877) and ultimately to *Elatocladus confertus* by Halle (1913).

In the same publication Oldham and Morris (1863) described a species named *Cunninghamites inaequifolius* from the same locality. The distinction between the two species is dubious and thus Feistmantel (1877) also reassigned this species to *Palyssia*. Hence *C. inaequifolius* is now recognised as *Elatocladus confertus*.

Cunninghamites dubius from Bamberg (Germany; Keuper, Triassic) has been described by Presl (in Sternberg, 1838), together with the type species *Cunninghamites oxycedrus*. Saporta (1884) stated that this species might be possibly the sterile twigs of *Palyssia braunii*; Schenk (1890) confirmed this.

The Upper Jurassic species from Cerin (France), *Cunninghamites microphyllus*, has been described by Saporta and Marion (1873). Although the species was not figured by Saporta and Marion, Barale (1978) reassigned it to *Elatocladus microphyllus* based on the description.

From the Lower Jurassic (Liassic) from Bayreuth (Germany) *Cunninghamites sphenolepis* has been described (Braun, 1843). Nathorst (1908) reassigned this species to *Palyssia sphenolepis*, the type species of *Palyssia*.

Geinitz (1849) named fossil remains from the Turonian Strehlen Formation (Plänerkalk horizon) in Dresden–Strehlen as *Cunninghamites mantellii* and listed *Pinus* leaves published by Mantell (1822) as a synonym. Unfortunately, he did not figure any specimen nor give any diagnosis. Von Otto (1854) described and figured a specimen from the type locality of his private collection, mentioning that it is not a very well preserved specimen. This specimen might be considered the holotype, unfortunately the repository is unknown.

Specimens labelled by Geinitz as *Cunninghamia mantellii* that were donated by Geinitz and Steinla (in 1858) to the Museum für Mineralogie und Geologie (Dresden, Germany) were determined by the palaeontologist P. Suhr (Freiberg, Saxony) in 1985 as the ichnofossil *Lepidenteron* (*Terebellum*) *mantellii*. This specimen shows needle-like structures that are light brown coloured impressions on light grey limestone without any visible stem remains. However, the distribution of the structures suggests that they could be attached to a stem, which is not visible due to the dense cover they form. The current curator of palaeozoology Dr. M. Willmsen, a specialist in Cretaceous invertebrates, confirms this determination (LK pers.comm, 2011).

The current authors consider the species *Cunninghamia mantellii* as an ichnofossil until von Otto's original specimen is found, or additional new material of *Cunninghamites* is indeed present in that horizon.

Table 1
Overview of *Cunninghamites* species, their current name, geologic age and geographic distribution ([1]Presl in Sternberg, 1838; [2]von Ettingshausen, 1867; [3]Kvaček, 1999; [4]Endlicher, 1847; [5]Heer, 1871; [6]Kräusel, 1922; [7]Hosius and von der Marck, 1880; [8]Knowlton, 1905; [9]Ubaghs, 1885; [10]Heer, 1882; [11]Eichwald, 1861; [12]Feistmantel, 1877; [13]Tenison-Woods, 1883; [14]Oldham and Morris, 1863; [15]Saporta and Marion, 1873; [16]Braun, 1843; [17]Geinitz, 1849).

Original name	Current name	Age	Geographical distribution
Cunninghamites oxycedrus[1]	*Cunninghamites oxycedrus*	Cenomanian	Niederschöna, Germany
?*Cunninghamites sternbergii*[2]			
Cunninghamites lignitum[3]	*Cunninghamites lignitum*	Cenomanian	Europe (e.g. Czech Republic and Italy)
Cunninghamites elegans ex parte[4]			
Cunninghamites planifolius[4]			
Cunninghamites squamosus[5]	*Cunninghamites squamosus*	Santonian/Campanian	North America (e.g. Judith River Beds) and Europe (e.g. The Netherlands and Poland)
Cunninghamites elegans ex parte[6]			
Cunninghamites recurvatus[7]			
Cunninghamites pulchellus[8]			
Cunninghamites ubaghsii[9]	*Cunninghamites ubaghsii*	Campanian/Maastrichtian	The Netherlands; Poland
Cunninghamites borealis[10]	*Cunninghamites borealis*	Cenomanian	Asuk, Greenland
Cunninghamites prisca[11]	*Cunninghamites priscus*	Valanginian–Hauterivian	Moscow, Russia; Ukraine
Cunninghamites dubiosus[12]	Conifer shoot of unknown affinity	Early Jurassic	Rajmahal Hills, India
Cunninghamites australis[13]	cf. *Pagiophyllum* sp.	Middle Jurassic	Ipswich, Australia
Cunninghamites confertus[14]	*Elatocladus confertus*	Early Jurassic	Rajmahal Hills, India
Cunninghamites inaequifolius[14]			
Cunninghamites microphyllus[15]	*Elatocladus microphyllus*	Upper Jurassic	Cerin, France
Cunninghamites dubius[1]	*Palyssia braunii*	Keuper, Triassic	Bamberg, Germany
Cunninghamites sphenolepis[16]	*Palyssia sphenolepis*	Early Jurassic	Bayreuth, Germany
Cunninghamites mantellii[17]	Ichnofossil	Cenomanian	Strehlen, Germany

4. Comprehensive summary

The genus *Cunninghamites* is characterised by the linear–lanceolate leaves with a distinct leaf base cushion. When leaves have been detached from the branch, a typical rhomboidal scar is visible. Leaves show three to five equally sized ribs that probably indicate veins (Plate I, 6). However, a midrib or prominent midvein cannot be distinguished. Originally, *Cunninghamites* was described as a fossil genus for sterile twigs with a high resemblance to the extant genus *Cunninghamia* (Presl, in Sternberg, 1838). In later publications fertile material has been described, which has been included in the diagnosis. Ovuliferous cones for *Cunninghamites lignitum* were first published as *Kettneria elegans* by Velenovský and Viniklář (1926). Kvaček (1999) included this material, combined with newly collected material, in *C. lignitum*. Rüffle and Trostheide (2000) included ovuliferous cones from Quedlinburg in *Elatocladus elegans* (=*Cunninghamites squamosus*). The morphology of these ovuliferous cones indicates that *Cunninghamites* is distinct from *Cunninghamia*. However, based on the shape of the ovuliferous cones and number of seeds per scale, *Cunninghamites* can be assigned to the 'basal' Cupressaceae s.l.

In contrast to the clear difference between the ovuliferous cones of *Cunninghamia* and *Cunninghamites*, leaf material of *Cunninghamites* is similar to that of *Cunninghamia*. The sterile material can be distinguished only by the absence of a conspicuous leaf base cushion and corresponding leaf scars in *Cunninghamia*.

Cunninghamiostrobus is often compared with *Cunninghamites*, however, these permineralised ovuliferous cones are considerably narrower and longer. The leaf material associated with *Cunninghamiostrobus* is amphistomatic, but neither the stomatal arrangement (i.e. stomatal bands) (Miller, 1975, 1990), nor the type of leaf margin is known. The characteristic leaf base cushion and leaf scars have not been described for *Cunninghamiostrobus*.

The most commonly used comparison in the literature is with the genus *Elatocladus*. As Kvaček (1999) already indicated, that *Elatocladus* can be distinguished by the contraction of the leaf base, the absence of leaf base cushions, and the single rib indicating a midvein.

Leaves of *Elatides*, as well as *Geinitzia*, are smaller and usually falcate, and do not show the conspicuous leaf base cushions and corresponding scars. The ovuliferous cone of *Elatides* is narrower and has three to five seeds, compared up to four in *Cunninghamites*.

Since the designation of the genus *Cunninghamites*, 19 species of *Cunninghamites* have been published in the literature (see Table 1). Before the current revision five *Cunninghamites* species have been included in one of the other species of *Cunninghamites* and five species reassigned to other genera, either *Palyssia* or *Elatocladus*. The current publication reduces the remaining nine species to six. Two species should be excluded from the genus, but reassignment to another genus cannot be done without extensive study of the type material, which is currently unavailable. One species, *Cunninghamia mantellii*, is an ichnofossil, and should be treated as such until the original material is found or additional specimens are collected.

The 6 species considered here to belong to *Cunninghamites* can be distinguished from each other based on leaf margin, arrangement of the stomata, and morphology of the leaf (see Table 2). *Cunninghamites ubaghsii* is clearly distinguished by the long leaves (up to 120 mm), *Cunninghamites borealis* is characterised by the shorter and more rounded apex. *Cunninghamites priscus* has 1 rib and much narrower leaves (1 mm wide) than the other species. *Cunninghamites oxycedrus*, *Cunninghamites lignitum*, and *Cunninghamites squamosus* are very similar. Based on the leaf margin (respectively serrate, irregularly serrate,

Table 2
Comparison of leaf characteristics for the 6 species currently assigned to *Cunninghamites*.

	Dimensions of leaf (mm)		Leaf margin	Stomatal arrangement		Ribs
	Length	Width		Leaf blade	Leaf cushion	
Cunninghamites oxycedrus	20–30	1.5–4	Serrate	Epistomatic	Epistomatic	Up to 5
Cunninghamites lignitum	12–24	1–2	Irregularly serrulate	Epistomatic	Amphistomatic	3–5
Cunninghamites squamosus	10–65	1–4	Entire	Hypostomatic	Amphistomatic	3–5
Cunninghamites ubaghsii	Up to 120	4–7	Entire?	?	?	1?
Cunninghamites borealis	10–35	3	Entire?	?	?	5
Cunninghamites priscus	23	1	Entire?	?	?	1?

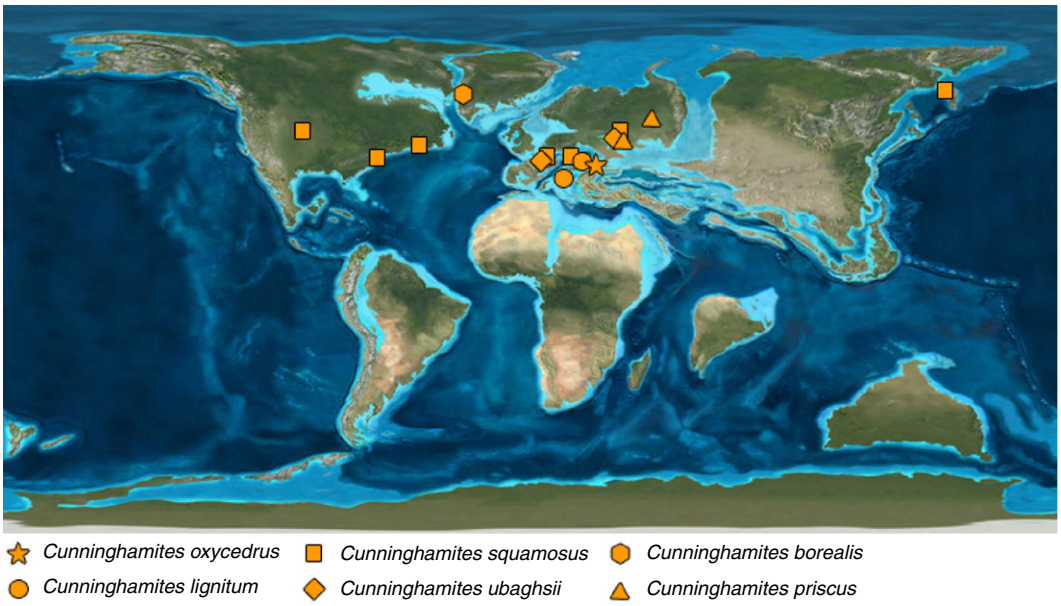

Fig. 1. Geographic distribution of *Cunninghamites* (continental configuration Maastrichtian). After Blakey (2012).

and entire) and stomatal arrangement of both the leaf blade (respectively epistomatic, epistomatic, and hypostomatic) and the leaf base cushion (respectively epistomatic, amphistomatic, and amphistomatic), the three species can be distinguished.

The geographic distribution of *Cunninghamites* is confined to the Northern Hemisphere (Fig. 1); from Central North America to Russia (Moscow). In the literature there is only one reference made about an occurrence of the genus in Asia; material that possibly belongs to *Cunninghamites squamosus* from the Haman Formation (Late Albian) of Korea (Kimura, 2000). However, this material is only listed in the publication and lacks further description or illustration. Further specimens of *C. squamosus* have been described from both North America and Europe. The other species are confined to their type locality or other European locations. In contrast, *Cunninghamia* only occurs in southeastern Asia.

The distribution through time is also limited with most species occurring during the Late Cretaceous (Fig. 2). The most common species, *Cunninghamites lignitum*, as well as, *Cunninghamites oxycedrus* and *Cunninghamites borealis* are described from the Cenomanian.

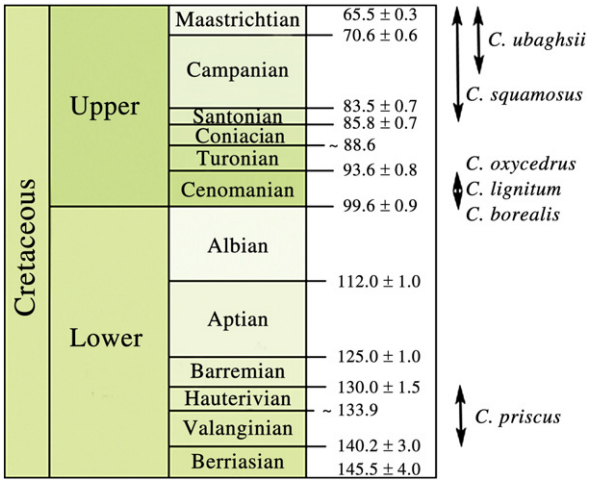

Fig. 2. Stratigraphic distribution of *Cunninghamites*.

Cunninghamites squamosus is mainly known from the Santonian, but extends up to the Maastrichtian, while *Cunninghamites ubaghsii* from the Maastrichtian. The Russian species, *Cunninghamites priscus*, is stratigraphically older, occurring during the Early Cretaceous (Valanginian–Hauterivian).

After the present revision, *Cunninghamites* consists of six species from localities confined to the Northern Hemisphere. In terms of geologic age, *Cunninghamites* only occurs during the Cretaceous and becomes extinct during the Maastrichtian.

Botanical affinity to the extant genus *Cunninghamia* or other fossil genera cannot be determined, although the genus can be affiliated with the same family, the Cupressaceae s.l.

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