



The rise and demise of *Podozamites* in east Asia—An extinct conifer life style



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ABSTRACT

In the Late Triassic–Early Jurassic, forests dominated by *Podozamites*—an apparently deciduous, shoot-dropping conifer with broad, multi-veined leaves—were extensive in what were the mid-latitudes of eastern Asia. *Podozamites* was the only conifer in many forests of this region, and at times appeared to have formed an almost mono-specific vegetation. *Podozamites* appears to have been little-affected through the Triassic–Jurassic transition, but responded to climate changes later in the Jurassic. The Chinese region progressively dried through the Middle Jurassic and aridity had developed in some areas by the Late Jurassic–Early Cretaceous. The centre of distribution of *Podozamites* shifted north, to the Siberian region, where conditions remained wet. There, it typically coexisted with conifers having a diverse range of smaller leaf morphologies.

By the late Albian angiosperms had arrived in the Siberian area and risen to dominance. Some time after this event, *Podozamites* became extinct. This is significant, as it represents the permanent extinction of a unique lifestyle—a deciduous, broad-leaved and multi-veined conifer.

The broad history of *Podozamites* raises some interesting issues:

1. The existence of a large, dominantly deciduous vegetation at mid-latitudes in the Late Triassic–Early Jurassic is little discussed.
2. It is unexpected that as broad-leaved angiosperms took over, amongst the conifers it was the broad leaved, multi-veined *Podozamites* that became extinct. This is the morphology that might have been expected to compete with the apparently more shade-forming angiosperms. Instead, it was the smaller leaved and single-veined conifers that remained to coexist with the angiosperms.

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1. Introduction

Most extant conifers have foliage that is relatively small, and single-veined. These may be of different shapes (e.g. needle-like or flattened), or disposed in various ways on the shoot (e.g. spirally or in a flattened, pinnate way), but there are exceptions (e.g. *Agathis*, *Nageia*, and *Phyllocladus*). Most extant conifers are also evergreen, though again, there are exceptions (e.g. *Metasequoia* and *Taxodium*). Leaf morphology is generally (not just conifers) understood to reflect lifestyle and/or climatic constraints. For example, large leaves tend to reflect a warm and humid environment (Dolph and Dilcher, 1980; Parkhurst and Loucks, 1972; Taylor, 1975), whereas shape can reflect how a leaf was carried

on a branch (Givnish, 1979, 1984). The various types of conifer leaf-shape/shoot-type can all be seen as essentially different light-gathering strategies, and in the broader sense (i.e. whether they were deciduous or evergreen) as life-style. In the Mesozoic, there appears to have been a distinct and very successful conifer life-style that is now extinct. This was a conifer that had broad, flattened, multi-veined leaves, and was deciduous. The most common name for this kind of fossil is *Podozamites*. The disappearance of this previously successful life-style should be thought-provoking and the phenomenon may contribute to broader issues concerning conifer and angiosperm distribution.

Podozamites was established by Braun (1843) and now tends to be used in two different ways—one is as a pure morphogenus simply describing a fossil (presumed) conifer shoot with multi-veined leaves. Harris (1969) tried to clarify its use in this sense. In this broad sense, *Podozamites* is represented today by *Agathis* (Araucariaceae) and *Nageia* (Podocarpaceae). Harris (1935) warned against placing isolated fossil leaves into either *Podozamites* or *Phoenicopsis*. In the absence of any

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cuticle details, or if the specimens are only of single, unattached leaves, they are better referred to as *Desmiophyllum*. Isolated material of this form could, therefore, be either conifer or ginkgophyte.

Podozamites is also used in a more restricted sense—as a ‘genuine’ Linnaean genus. For example, in the Late Triassic–Late Jurassic of the Northern Hemisphere, *Podozamites* is regularly associated with the reproductive structures *Cycadocarpidium* and *Swedenborgia*, and some other less common forms (e.g. Oishi and Takahasi, 1936; Harris, 1937; Anderson, 1978). Assuming that they were connected, in this sense *Podozamites* can be viewed as a genus of a particular family, for example the Podozamitaceae, or more recently of the Voltziaceae or Podocarpaceae, but the taxonomy remains unsettled (Clement-Westerhof, 1987; Miller, 1999; Escapa et al., 2010; Dietl and Schweigert, 2011). Unfortunately, informative leaf cuticle has been published only from about four species of Northern Hemisphere *Podozamites*, as it is extremely thin. Two of these are from Greenland (Harris, 1935) and two from Siberia (Doludenko, 1967; Bugdaeva, 1995). Three of the species have a remarkable transverse orientation of the stomata that is reminiscent of *Taxodium*, although *Podozamites* does not have differentiated subsidiary cells. Recently, well-preserved *Podozamites* cuticle has been prepared directly from coal in the Barremian Chagdamyn Formation, of the Bureya Basin, Russian Far East (Fig. 1). However, most Eurasian workers, who have attempted to retrieve *Podozamites* cuticle, have remarked on how delicate it is. It is generally concluded that *Podozamites* in this narrow sense, was deciduous, and abscised whole shoots, a view consistent with it being especially targeted by insect herbivores (Ding et al., 2015). The broad-leaved, parallel-veined conifers from the Jurassic of the Southern Hemisphere that were assigned to *Podozamites* by Walkom (1921) or *Agathis* by White (1981) also show their fair share of insect damage (McLoughlin et al., 2015). It is notable that Harris seems to have changed his view about *Podozamites*. Although Harris (1969) promoted it as a pure morphogenus, Harris (1979) seemed to see it as a ‘genuine’ genus with a particular stomatal orientation (transverse). His new genus *Lindleycladus* could then be distinguished from *Podozamites* by its longitudinal stomatal orientation. There are other conifer genera that would fall into the broader scope of *Podozamites*, but which have been separated by morphological or cuticular differences, e.g. *Ferganiella* and *Liaoningocladus* (Sun et al., 2000).

What reproductive structures were associated with *Podozamites* in the Early Cretaceous is less clear. Both *Cycadocarpidium* and *Swedenborgia* were either extinct or highly restricted by this time. Bugdaeva's (1995) report of *Podozamites* and *Swedenborgia* from the Early Cretaceous of Siberia is the most recent for the reproductive structure. In the Early Cretaceous of Japan, the evidence of an attached ‘fruit’ shows that at least some *Podozamites*-type foliage was more-likely the Podocarpaceae genus *Nageia* (Kimura et al., 1988), and in the Early Cretaceous of Colombia *Podozamites* might have carried the *Pityostrobus* structure (van Waveren et al., 2002).

The fossil *Xenoxylon* was long ago suggested to be the wood of *Podozamites* (Nathorst, 1897), but more recent work (Philippe and Thevenard, 1996; Philippe et al., 2013; Oh et al., 2015) suggest several other, perhaps more likely candidates. The suggestion has also been made that *Podozamites* might have been herbaceous and “might have played an important and often underestimated role in the Mesozoic ecosystems possibly as a substantial part of dinosaur diet” (Gierliński et al., 2006). The pollen of *Podozamites* is unknown, though several bisaccate types that generally coexisted, such as *Pinuspollenites* and *Podocarpidites*, are reasonable candidates in the Northern Hemisphere. Bomfleur et al. (2011) isolated *Alisporites* pollen from *Switzianthus*, the probable pollen organ of *Heidiphyllum/Telemachus* in the Late Triassic of Antarctica. Bolkhovitina (1956) referred *Araucariacites australis* pollen grains to *Podozamites* (see also Tralau, 1968).

Southern Hemisphere (Gondwanan) Triassic occurrences of the *Podozamites* morphology have been found associated with reproductive structures related to *Cycadocarpidium* and *Swedenborgia*, e.g. *Telemachus* (Anderson, 1978; Axsmith et al., 1998; Escapa et al., 2010) and have proven similarly difficult to prepare cuticle. However, Early Cretaceous specimens have robust cuticle with a morphology that can place them in the Araucariaceae (Cantrill, 1991) and the Late Jurassic Talbragar forms are also associated with (but not connected to) araucarian cones and cone scales (Walkom, 1921; White, 1981).

Despite the variety of names and the uncertainty over the reproductive structures, there is a continuity of this morphology in the eastern Asian fossil record that is highly suggestive of a single, related group. In this paper we deal with *Podozamites* in that sense, assuming that it and related forms were a distinct taxon of the Asian Mesozoic.

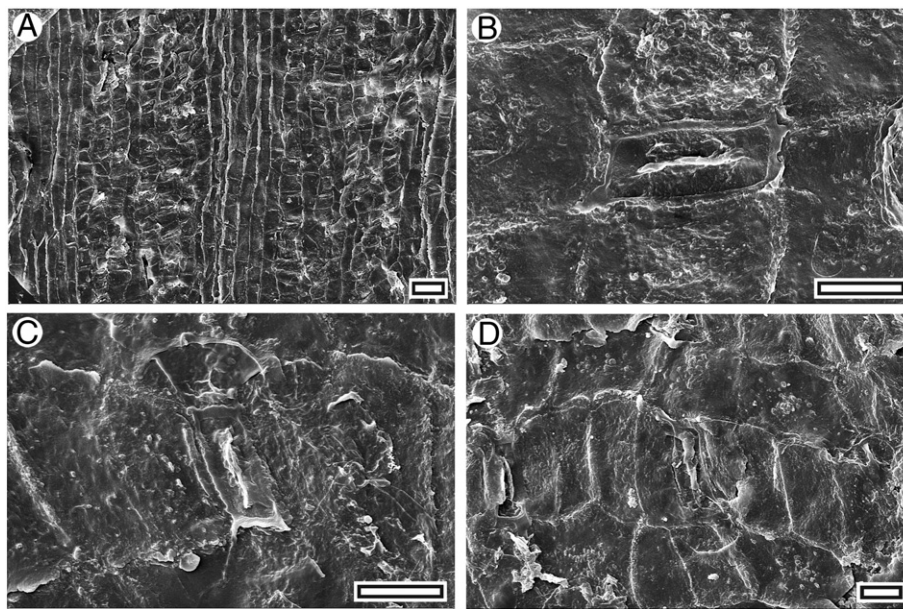


Fig. 1. Scanning electron microscopy images of *Podozamites* cuticle from the Chagdamyn Formation (Barremian) of the Bureya Basin, Russian Far East. A, inner view of lower leaf showing two stomatal zones separated by venal regions (scale = 40 µm). Stomata are transversally oriented. B, inner view of single stomatal complex (scale = 10 µm). C, inner view of single stomatal complex (scale = 10 µm). D, inner view of two stomatal complexes (scale = 10 µm).

Around 20 species of *Podozamites* have been recognised in eastern Asia, as well as morphologically similar taxa like *Ferganiella*, *Lindleycladus* and *Nageiopsis*. It is likely that some of the 'species' are merely morphological extremes or outliers and some workers prefer to classify them as varieties or 'forms'. *Podozamites* leaves ranged in size from about 15 mm long by 8 mm wide, to 160 by 40 mm. They could have up to 25 veins per 10 mm of leaf width, in some cases with as many as 34 veins across the full leaf width (Sun, 1993). Thicker veins commonly alternated with thinner 'interstitial' veins. *Podozamites* leaves were helically arranged on a shoot that could be distichously flattened, or not (Harris, 1935).

The purpose of this paper is to provide a broad review of the distribution of *Podozamites* (and similar forms) through the Mesozoic in eastern Asia (where there is a good plant fossil record through time and at a range of latitudes), and placing this in the context of the morphology of associated conifers, and the appearance of angiosperms. It is not a taxonomical review, but it hopes to stimulate some interest in this enigmatic conifer (or rather, group of conifers) and how it may contribute to some broader issues.

2. Methods

For this study 'eastern Asia' includes China, Japan, Korea, Mongolia, and eastern Siberia.

Distribution data for eastern Asian *Podozamites* (and similar genera) were gleaned from two different sources. One was specialist palaeobotanical literature (journals or books). The second was the Paleobiodiversity Database (PBDB; paleobiodb.org). Virtually all the PBDB Mesozoic records for China at present are from the series of 'Stratigraphic Tables'. These publications collate stratigraphic data on a provincial basis and include lists of plant fossils. These may be summaries for formations, or for specific levels of a measured section. Most specialist literature illustrates examples of *Podozamites* shoots (as compared with single leaves), and although the 'Stratigraphic Tables' are not illustrated, we assume that most records are correct.

We deliberately refer to other conifers in terms of leaf or shoot morphology, i.e., 'needle-leaves' (e.g. *Pityophyllum*), pinnate-leaves (e.g. *Elatocladus*, *Sequoia*), scale-leaves (e.g. *Brachyphyllum*, *Thuja*), and awl-leaves (e.g. *Pagiophyllum*) to emphasise generalities. We occasionally use Linnaean names of extant conifers when the aim is to emphasise taxonomic diversity.

To help understand not just where *Podozamites* grew, but also where it did not, plant fossil assemblages that lacked *Podozamites* were also noted. The distributions of terrestrial vertebrates (essentially 'dinosaurs') were also plotted. These tend to occur in facies where plant remains are absent—commonly 'red beds', which were probably deposited in more seasonal conditions than the coal-bearing facies with plant fossils. The distribution of evaporites, another suggestor of dry conditions, was also noted. These use the dataset of Boucot et al. (2013). Data were plotted on five palaeogeographic maps based on the reconstructions of Scotese (2014a,b). These are Late Triassic, Early Jurassic, Middle Jurassic, Late Jurassic, and Early Cretaceous. Present-day distribution coordinates were rotated using the software PointTracker (obtained from C.R. Scotese).

3. Results

3.1. Triassic

The oldest eastern Asian (and global) occurrence of *Podozamites* on the PBDB database is a single Early Triassic record, and there are then just five records for the Middle Triassic. However, *Podozamites* is not mentioned in palaeobotanical works over this time (e.g. Sun et al., 1995a), so the occurrences in the Atlas lists that the PBDB refers to might be interpreted as restricted occurrences. We note Ye (1979) recorded a Middle Triassic "*Desmiophyllum* sp. (*Glossophyllum?* sp.)",

and that might conceivably be a *Podozamites*. Other conifer morphologies were present in China, for example both scale and awl-leaves in the Early Triassic of Hainan Island (Zhou and Li, 1979).

Podozamites spread rapidly in the Late Triassic (the PBDB has over 70 records), with a concentration in South China, but extending north, into Siberia (Fig. 2). At this time, *Podozamites* had become a dominant plant in many lowland areas. There are few plant fossil assemblages from this time that do not include *Podozamites*. The most southern Late Triassic record for the region is Bintan Island, Indonesia (Wade-Murphy and van Konijnenburg-van Cittert, 2008; c. palaeolatitude 15° N). This contains scale-leaved conifers and an isolated leaf identified as *Podozamites*. However, this is currently an outlier, and most records are north of about 30° palaeolatitude. In China, one of the most southerly Late Triassic plant fossil records comes from Guangdong Province (Wang, 1993; palaeolatitude c. 33° N). This has prominent *Podozamites*, but also some pinnate and needle-leaved conifers. There was a similar situation further to the north, in Fujian Province (Zhou, 1978). In an early study of the Mesozoic flora across several Chinese provinces Sze (1933) found *Podozamites* to be by far the most widespread taxon. In a more restricted study on West Hubei, Sze (1949) also found *Podozamites* to be the most widespread taxon, closely followed by the sphenophytes. In the Late Triassic of the Sichuan Basin, Huang and Lu (1992) interpreted the ginkgophyte *Baiera* and *Podozamites* as forming the 'climax' of vegetation succession.

In the southwest Sichuan Basin flora of Baoding (Hsu et al., 1979; palaeolatitude c. 35° N), *Podozamites* was one of only two conifers (the other was the pinnate *Stachyotaxus*) and both appear to have been uncommon. However, further to the north of the basin (c. 41° S palaeolatitude), *Podozamites* was a major component in the Late Triassic. Li (1964, p. 165) noted that "the species of *Podozamites* form a most conspicuous feature of this flora". Ye et al. (1986) documented fossils from three stratigraphic levels across five localities, and found *Podozamites* to be one of the most widespread foliage taxa. Its frequency was just below that of the ferns *Cladophlebis/Todites* and the bennettitalean *Pterophyllum*, and similar to the sphenophytes and *Ctenis* and *Zamites* (cycad and bennettitale respectively). *Podozamites* and *Ferganiella* were almost the only conifers in these assemblages (Wang

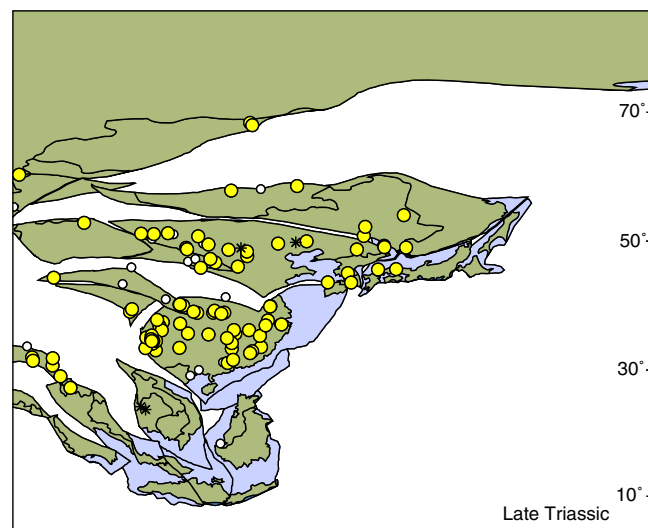


Fig. 2. Late Triassic distribution of *Podozamites* and similar taxa (large dots), along with plant fossil localities where *Podozamites* has not been recorded (small dots), and vertebrates chiefly dinosaurs (asterisks). Superimposed on a c. 210 Ma palaeogeographic configuration, supplied by C. Scotese. There are four isolated *Podozamites* occurrences above a palaeolatitude of 80° N. that are awkward to show on this projection. These are (and their PBDB collection number): Amga River (30,422), Cape Tsvetkova (30,416), Sincha River (30,524), and Unguokhtakh River (30,547).

et al., 2010). *Podozamites* was mostly the only conifer in Qinghai Province (He, 1980), although needle-leaved *Pityophyllum* is also reported. At a similar latitude to the west, *Podozamites* was a member of the Yenchang-type Flora of the Tarim Basin (palaeolatitude c. 40° N; Wu et al., 2000).

In the northeast of China, *Podozamites* was the most prominent conifer, but there were typically some other conifers as well—with pinnate and needle-leaved foliage, although not with scale-leaves (Sun, 1983; Sun, 1993). A similar situation prevailed in the Primorye region near the Chinese–Siberian border (palaeolatitude c. 48° N) where various *Podozamites* remained present throughout the Late Triassic, in association with pinnate conifer foliage but no scale-leaved examples (Volynets et al., 2008). P'an (1936) found abundant *Podozamites* in the Yenchang Formation of northern Shensi. This is in surprising contrast to the work of Sze (1956), in the same formation two decades later, who found no conifers at all.

In Japan and Korea, *Podozamites* was also common (Kim and Kimura, 1986; Chun, 1996; Kim, 2001), with Kimura and Kim (1989) making the interesting comment that particularly long and narrow *Podozamites* leaves are restricted to Late Triassic floras. This suggests that the physiognomy of the genus may have potential for interpreting palaeoclimate.

Most Late Triassic *Podozamites* records are south of a palaeolatitude of about 70° N, although many of the more northerly ones are only as lists in regional geological accounts. There are four records on the PDBD much further to the north (e.g. Gromov et al., 1980) but these need careful scrutiny.

3.2. Early Jurassic

Globally, there was an important vegetation turnover in response to the Triassic–Jurassic boundary event. In eastern Asia, several genera disappeared, and some new ones appeared. However, in the areas where it predominated in the Late Triassic, *Podozamites* appears to have remained untouched. Its latitudinal range was from at least 30°–70°. The common species remained and it still formed near monospecific assemblages. In Guangdong Province of southern China, it was absent in an assemblage documented by Wang et al. (2014), but further north, in Hunan, it remained the dominant conifer of the Early Jurassic (Zhou, 1984). In the Sichuan Basin, *Podozamites* was a common component of the earliest Jurassic Zhenzhuchong Formation (Ye et al., 1986; Huang, 2001) and at times it appears to have formed a monogeneric vegetation. Although several other conifers are known (scale, awl, pinnate and needle-leaved), these appear to have been rare (Ye et al., 1986).

On a broader time-scale, there are suggestions of a centripetal movement of *Podozamites* distribution, away from south-western China, and perhaps with some expanding to the north (Fig. 3). This movement probably reflects drying in the south-west. Coal there is replaced by more 'mottled' sediment with vertebrate remains, but coal becomes more extensive and thicker to the north and east.

In southern China, *Podozamites* has not been found in the Jinji Formation, where awl and pinnate conifers are the main types (Wang et al., 2014). In North Shensi, *Podozamites* continued through the Yanan–Isihihtsen (originally part of the Wayaopu Coal Series) Series and Chilio Series (Liu, 1956).

3.3. Middle Jurassic

By the Middle Jurassic, coal is abundant in northern China, particularly from early in the Middle Jurassic (Aalenian to Bajocian). However, southern China is dominated by the occurrence of extensive 'red beds' (Chan, 1938; Bien, 1941; Sheng et al., 1962; Nguyen and Sha, 2007) along with the absence of coal suggesting that rainfall had become distinctly seasonal across the southern part of the region. Plant fossils are essentially absent from there. Elsewhere, *Podozamites* remains a component of the known assemblages, although it is usually no longer

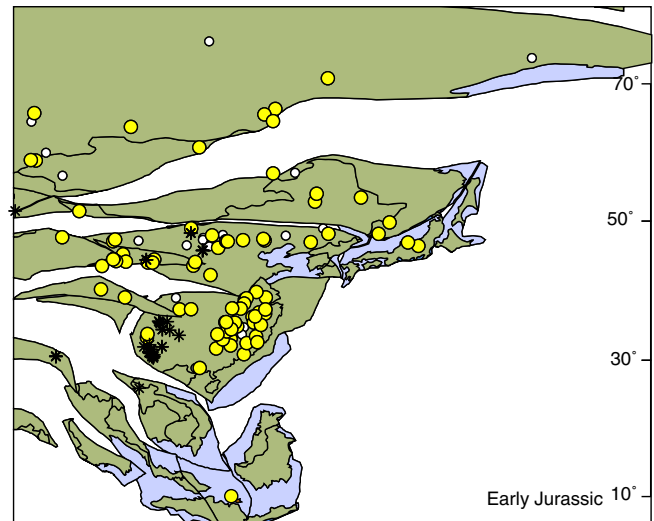


Fig. 3. Early Jurassic distribution of *Podozamites* and similar taxa (large dots), along with plant fossil localities where *Podozamites* has not been recorded (small dots), and vertebrates chiefly dinosaurs (asterisks). Superimposed on a c. 190 Ma palaeogeographic configuration supplied by C. Scotese.

dominant (Fig. 4). It occurs along with other conifers in the Turpan–Hamii Basin in the NW of China (Shang et al., 1999), the Junggar Basin (Sun et al., 2010; palaeolatitude c. 60°, see Sha et al., 2011, 2015), in the Beijing area (Zhang and Jiang, 2010), Sichuan (Yang, 1987), Qinghai Province (He and Wu, 1986), and the Daohugou fossil-bearing strata of Inner Mongolia and Liaoning Province (Na et al., 2015). In the Middle Jurassic coal measures of the Yima Formation, Henan, *Podozamites* was the most abundant of only three conifers, the others being *Parastorgaardia* and *Sewardiodendron* (Zeng et al., 1995; Yao et al., 1998). The Middle Jurassic Utano flora in Japan is a 'southern' type containing scale-leaved conifers, but no *Podozamites* (Kimura et al., 1986). The northern limit of *Podozamites* (with the exception of a scattered few records), appears to have contracted from the Early Jurassic, to a more clearly defined palaeolatitude of about 60°. North of this, various plant fossil

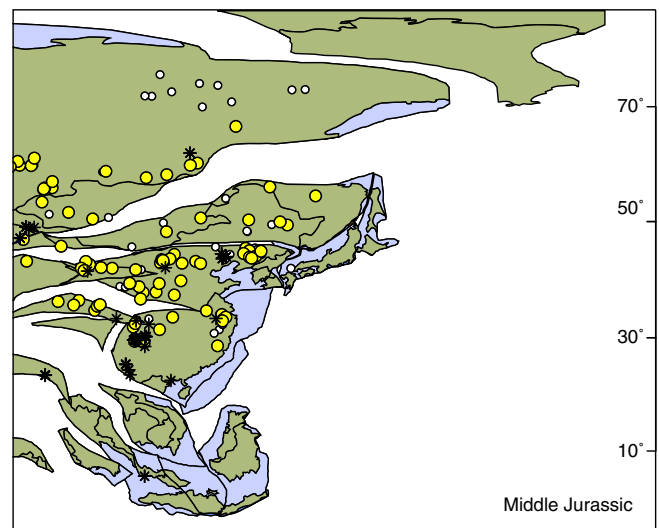


Fig. 4. Middle Jurassic distribution of *Podozamites* and similar taxa (large dots), along with plant fossil localities where *Podozamites* has not been recorded (small dots), and vertebrates chiefly dinosaurs (asterisks). Superimposed on a c. 170 Ma palaeogeographic configuration supplied by C. Scotese.

assemblages are known, but without *Podozamites*. Thus by this time, *Podozamites* does not appear to have included a polar distribution.

3.4. Late Jurassic

By the Late Jurassic, the western (more interior) Chinese region was clearly relatively dry, without coal, but with extensive red-beds. With a few exceptions, the plant fossil record from these regions all but vanishes. Plant fossils are found across Mongolia, but without *Podozamites*. The distribution of *Podozamites* fossils now had a distinctly north–south axis, along the eastern edge of China, and extending far up into Siberia (Fig. 5). Southern Chinese assemblages have scale-leaved conifers as the most important, or only conifers. They suggest a clear southern limit of *Podozamites* at around 20°, whereas the northern limit, remained at, or a little less than, 60°.

In general, by this time, conifers had become a dominant element of the flora (Zhou, 1995). The Hanshan Formation of Anhui Province includes possible *Podozamites*, alongside scaled-leaved conifers (Cao, 1985; Zhou, 1995). In the Shahezi Formation of north-eastern China, *Podozamites* existed alongside several other conifer morphologies. Extensive coal-swamps had retreated further to the north-east of China and neighbouring Siberia. In the Zeya River area, *Podozamites* coexisted with the needle-leaved conifers, which were the more widespread taxa (Vakhrameev, 1965; Lebedev, 1965). These were the only conifers except for rarer ones with awl-leaves. *Podozamites* was also present in the Bureya Basin (Vakhrameev and Doludenko, 1961; Krassilov, 1961; Markevich and Bugdaeva, 2014) as well as in the polar Lena Basin (Vakhrameev, 1961). The bulk of Siberia fell into Vakhrameev's (1987) Siberian floristic area, where for example, the pollen of *Classopollis*, was minor.

In Japan, fossil assemblages from this time can be recognised as falling into two distinct provinces—an 'outer' zone Ryoseki flora, and an 'inner' zone Tetori flora. The Tetori flora contains "varied and abundant" *Podozamites*, whereas the Ryoseki has none, having instead "varied and abundant" small scale-leaved conifers (Ohana and Kimura, 1995; Yabe et al., 2003; Matsukawa et al., 2006). These two floras could also be recognised on mainland eastern Asia, where the Tetori was more of a northern flora (Kimura, 1987). The sharp Japanese distinction appears to be the result of large-scale tectonics, moving the outer Ryoseki

rocks north, to juxtapose them with the Tetori (e.g. Isozaki, 1997; Tsukada, 2003).

3.5. Early Cretaceous

The southern limit of *Podozamites* moved north to about 30° N, while for much of the Early Cretaceous, the northern limit appears to have remained at or a little less than 60° (but see below). Evaporites and vertebrate remains became extensive, although there was a broad range of overlap geographically with *Podozamites* (not necessarily at exactly the same time).

Low-latitude fossil plant localities are few (Fig. 6), but include Malaysia (Kon'no, 1967; Yaacub and Said, 2002). These have a typical low-latitude assemblage where the conifers have scale-leaves, although Kon'no (1967) illustrated three multi-veined leaves that were identified as 'Nageiopsis?'—a *Podozamites* type of leaf.

Dry conditions continued over much of China in the Early Cretaceous, but in detail the geographical and temporal situation can be complex. In Eastern China, the Early Cretaceous floras of Fujian and Shandong Provinces include *Podozamites*, and some pinnate conifer taxa, but it is the scale and awl-leaved conifers that predominate (Liu, 1990; Cao et al., 1995; Wu, 2000; Deng et al., 2012). There is a similar situation on the east coast of China. For example, near Shanghai, conifers are abundant in the Early Cretaceous flora of Zhejiang (Cao, 1999), with scale or awl-leaves dominating the conifer component, and where *Podozamites* is only "very rare". Further north, in the outskirts of Beijing, P'an (1933) found *Podozamites*, along with pinnate and needle-leaved conifers. In mid-latitudes, angiosperms may have appeared as early as the Barremian (Li, 2003).

In the north-east of China, Deng et al. (2012) recognised three Early Cretaceous floras—the Jehol, Fuxin and Dalazi (these all lay at about 45° N at the time). Depending on the author, the Fuxin Formation is either not included in the Jehol Group (Zhou et al., 2003) or is the uppermost unit of the Jehol Group, with the Jehol Biota limited to the middle and lower units of the Jehol Group: the Jiufotang and Yixian formations (Sha, 2007; Pan et al., 2013). The Jehol flora studied by Deng et al. (2012) comes from the Jiufotang and Yixian formations, and the Fuxin flora from Fuxian Formation. The potential relevance to *Podozamites* is that the Fuxin Formation has prominent coal, in the Jiufotang Formation

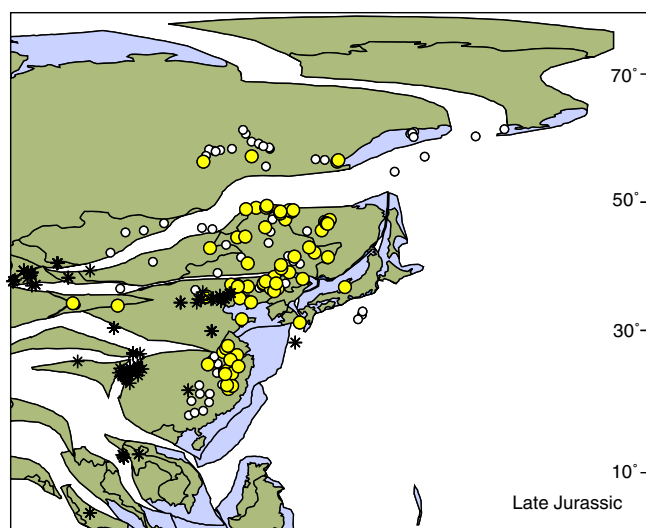


Fig. 5. Late Jurassic distribution of *Podozamites* and similar taxa (large dots), along with plant fossil localities where *Podozamites* has not been recorded (small dots), and vertebrates chiefly dinosaurs (asterisks). Superimposed on a c. 150 Ma palaeogeographic configuration supplied by C. Scotese.

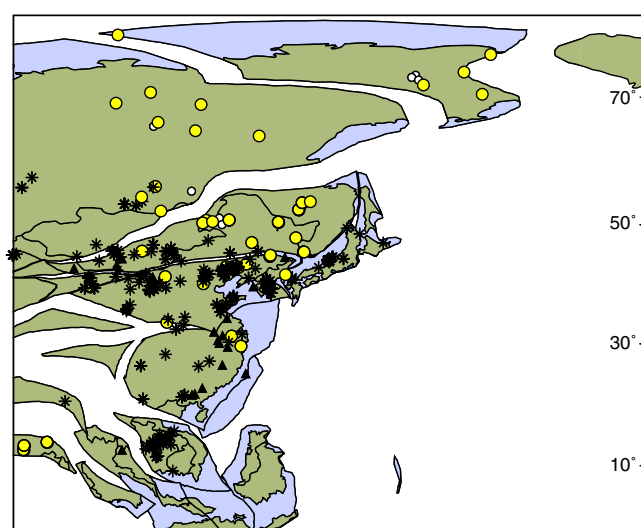


Fig. 6. Early Cretaceous distribution of *Podozamites* and similar taxa (large dots), along with plant fossil localities where *Podozamites* has not been recorded (small dots), vertebrates chiefly dinosaurs (asterisks) and evaporites (triangles). Superimposed on a c. 130 Ma palaeogeographic configuration supplied by C. Scotese.

coal is limited to the upper part (Sha, 2007), whereas coal is absent in the Yixian Formation. In the Yixian Formation, Wu (1999a) did not record *Podozamites*, although a relatively broad-leaved, single-veined conifer *Cephalotaxopsis* sp., was present along with scale- and pinnate-leaved conifers (Zhou et al., 2003). *Podozamites* was recorded from the Yixian Formation by Zheng et al. (2003), but as a component of a flora otherwise dominated by what they termed “xeric” conifers, with scale, awl, needle and pinnate foliage. A very similar mix of conifers was reported from NW China (Deng and Lu, 2008). In the Fuxin flora, *Podozamites* is diverse, and occurs with other conifers, but only rarely are these scale-leaved (Chen et al., 1988). The Dalazi flora is dominated by angiosperms and does not include coal (Du et al., 2008).

In Heilongjiang Province, bordering the Primorye region in the far north-east of China, *Podozamites* was present, along with pinnate and awl-leaved conifers (Oishi, 1935; Zhang and Xiong, 1983). Later floras in the same area have *Podozamites* together with pinnate and scale-leaved conifers, although not in the same layers (Zheng and Zhang, 1983).

In Inner Mongolia of northeast China the Early Cretaceous flora of Hailar is coal-bearing, and includes *Podozamites* together with needle and pinnate conifers (but no scale-leaved ones, Deng et al., 1997). The Early Cretaceous Zhonggou Formation of the Jiuquan Basin in NW China likewise has a rich coniferous flora. *Podozamites* was present, but as one genus of a diverse conifer assemblage that also included scale, pinnate and awl-leaved forms (Deng and Lu, 2008). Several of these taxa probably belong to Cheirolepidiaceae (Du et al., 2013). In Mongolia, Krassilov (1982) reported *Podozamites* and scale-leaved conifers, as the most widespread conifers. They occurred together and at times they were associated with *Araucaria* (with awl-like to more flattened leaf forms). Reproductive structures, such as *Pseudolarix*, suggested that *Podozamites* had also been associated with needle-leaved conifers.

In the Primorye region of southern Russian Far East, Krassilov (1967, 1973) reported *Podozamites* as “locally abundant” in the Valanginian, and present along with other conifers, in the lower part of the Barremian–Aptian Starosuchan Formation. Higher in the same formation, Bugdaeva et al. (2014) found the coals to be dominated by the dispersed cuticle of the pinnate *Elatides asiatica*. *Podozamites* appears to have been at least rare in this facies. Much further north, in what were then polar

regions, such as the Okhotsk–Chukotka Volcanic Belt, and typified by the Grebenka flora, there were very diverse conifers (although not scale-leaved) along with angiosperms, but *Podozamites* was apparently absent (Lebedev, 1992; Spicer et al., 2002).

Angiosperms began to appear in Siberian assemblages at the start of the Albian (Fig. 7). At this time they were small-leaved and apparently only a minor part of the vegetation. But by the late Albian they included large-leaved taxa and were a dominant part of the vegetation. The transition to angiosperm-domination was not simple, as emphasised by Vakhrameev (1991, p. 187) “certain localities continued to be inhabited and even dominated by the Early Cretaceous elements that disappeared later”. The late Albian Serta floral assemblage of western Siberia far to the north of the Junggar Basin, NW China (c. 54° N at the time), was discussed in detail by Golovneva and Shchepetov (2010). They concluded that it represents the first diversification of large-leaved angiosperms in the region. It was dominated by leaves of *Platanus*, along with abundant pinnate conifers, such as *Sequoia* sp., and common needle-leaved ones, but they found just a single impression of *Podozamites* sp. However, *Podozamites* was present in one of the most northerly Albian floras—Balyktakh River (palaeolatitude c. 80° N)—where it grew with both pinnate and needle-leaved conifers (Herman and Spicer, 2010).

In the Early Cretaceous of Japan, the evidence of an attached ‘fruit’ shows that at least some *Podozamites*-type foliage was attributable to the Podocarpaceae genus *Nageia* (Kimura et al., 1988).

3.6. Late Cretaceous

The Late Cretaceous features the absolute takeover of the angiosperms in many areas. Low latitude fossil assemblages from the eastern Asian area are uncommon, but include Hong Kong, and these have angiosperms along with scale and awl-shaped conifer leaves, but no *Podozamites* (Wu, 1999b). Red-beds were still prevalent, and the rare plant fossils associated with them include scale-leaved conifers (Liang, 2006; Li et al., 2015). Generally across the rest of China, the situation was similar (Sun et al., 1995b). Although angiosperms were abundant, conifers were also plentiful and diverse. They included a variety of pinnate and scale-leaved forms including extant taxa such as *Taxodium*,

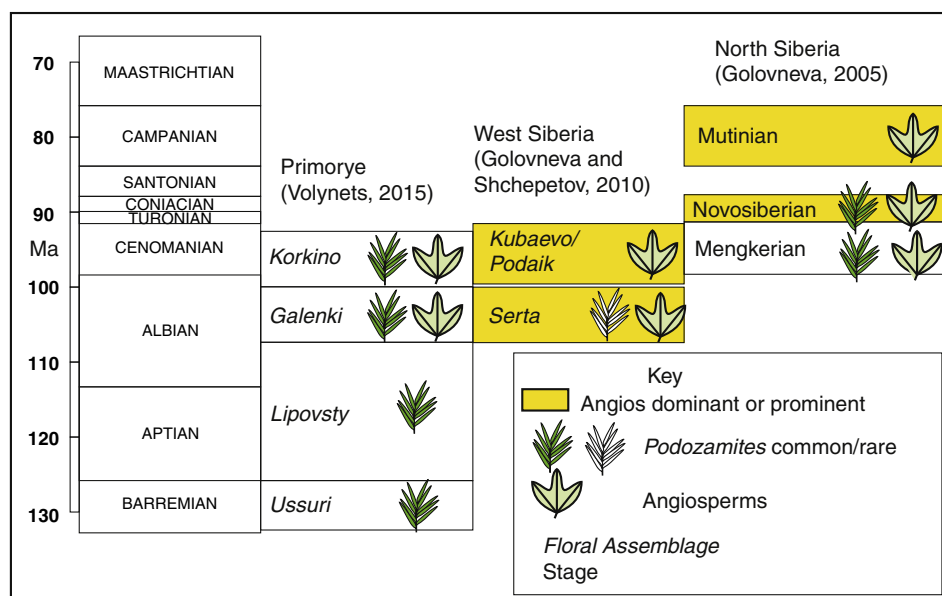


Fig. 7. A schematic interpretation of *Podozamites* and angiosperm distribution in Siberia around the mid-Cretaceous transition to an angiosperm-dominated flora. The figure is based on Golovneva (2005), Golovneva and Shchepetov (2010), and Volynets (2015). The basic point is that the arrival of angiosperms and the continuity of *Podozamites* varied within a time-zone of c. 15–20 Ma.

Podocarpus, *Sequoia*, *Metasequoia*, *Glyptostrobus*, and scale-leaved forms, such as *Thuja*. In general, the Late Cretaceous conifers of Siberia are a mixture of scale, awl and needle-leaves living with broadleaved angiosperms. An exception is the unusual conifer *Protophyllocladus*, which was a broad, flattened phylloclade, morphologically highly similar to its extant namesake, *Phyllocladus* (Nosova and Golovneva, 2014). In western Siberia (Golovneva and Shchepetov, 2010), the Kubaevo Floral Assemblage (palaeolatitude c. 74°, Cenomanian) was dominated by angiosperms along with diverse conifers including needle-leaved (*Pinus*, *Picea*, and *Cedrus*), pinnate (*Sequoia*), and scale-leaved forms. Broad-leaved flowering plants by this stage were dominant in terms of both abundance of fossils and generic diversity. Also in western Siberia, Golovneva and Nosova (2012) reported a single *Podozamites* from the otherwise angiosperm (platanoid) dominated Cenomanian Simonovo Formation.

Late Cretaceous *Podozamites* have been reported from a few, high-latitude floras (Fig. 8). These include the Arman flora (Herman, 2005, 2011; Herman et al., 2012; see also Filippova and Abramova, 1993, who dated it as Cenomanian) and Zarya flora (Shchepetov and Golovneva, 2014), both Turonian–Coniacian and situated at a palaeolatitude of c. 67–70°. It has also been reported from the Turonian–Coniacian Chauna Group, Okhotsk–Chukotka subregion (palaeolatitude c. 80°; Shchepetov, 1991; Belyi, 1977; Kelley et al., 1999).

The most northerly Albian–Cenomanian flora is Grebenka (palaeolatitude c. 78°). Filippova and Abramova (1993) listed *Podozamites*, although Spicer et al. (2002) did not. A range of pinnate and awl-leaved conifers were present, along with angiosperms. At a slightly higher latitude, the Turonian Flora of Novaya Sibir' (palaeolatitude c. 82°, Herman and Spicer, 2010), also lacks *Podozamites*, although notably, *Agathis* and *Desmiophyllum* were recorded. These grew with a diverse range of other conifers (needle, pinnate and scale leaves) and angiosperms. The far north-east Siberian Maastrichtian Flora of Amaam Lagoon (palaeolatitude c. 76°, Moiseeva, 2012) had only pinnate conifers in a diverse, angiosperm-dominated flora.

The most recent location of *Podozamites* is probably the Santonian–Campanian Topolevskaya Unit, from the Anadyr River, and, at a palaeolatitude of c. 81°, was one of the most polar (Herman, 2011). It should be kept in mind that some other multi-veined conifers persisted, but *Podozamites* was very restricted at the start of the late Cretaceous, and likely extinct by the end.

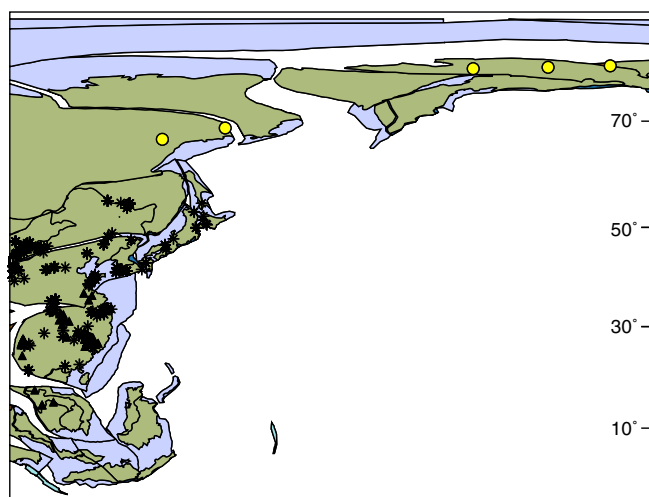


Fig. 8. Late Cretaceous distribution of *Podozamites* and similar taxa (large dots), vertebrates chiefly dinosaurs (asterisks) and evaporites (triangles). Superimposed on a c. 90 Ma palaeogeographic configuration supplied by C. Scotese. The datapoint of Golovneva and Nosova (2012) lies just to the west of the map boundary at c. 70° N.

4. Discussion

Podozamites distribution data suggest an origin and then rapid spread in the Middle Triassic. By the Late Triassic, *Podozamites* was widespread over eastern Asia perhaps from 15° and certainly from 30° S, to around 70° N. At this northernmost limit, *Podozamites* was in a polar environment (>66° N). The overwhelming abundance of *Podozamites* in some assemblages, or its consistent association with sphenophytes, suggests a nearly mono-dominant vegetation, or one where it grew over a ground-cover of sphenophytes (assuming it was a tree).

Its abundance in Early Jurassic assemblages in China contrasts with Greenland, where *Podozamites* appears to have suffered from the Triassic–Jurassic boundary event. *Podozamites* there was classified as 'broadleaved' by Belcher et al. (2010), and it was a member of the generally broad-leaved and potentially less fire-prone vegetation that existed in the Late Triassic. These authors concluded that the Early Jurassic vegetation in Greenland was more narrow-leaved and more fire-prone. So far, such a physiognomic change is not yet evident in eastern Asia. Fire, however, was at least sporadically present in mid-Mesozoic eastern Asia (Early Jurassic–Early Cretaceous, Yamazaki and Tsunada, 1982; Miao et al., 1989; He, 1995; Tanner et al., 2012), as it was in Greenland (Harris, 1926; Belcher et al., 2010). At the polar extreme of its range, *Podozamites* was part of a deciduous and evergreen community. The vegetation dynamics in these then warm regions have been the center of much attention (Beerling and Osborne, 2002; Osborne et al., 2004; Royer et al., 2005), but it appears that disturbance, probably primarily fire, seems to have been critical in maintaining the mix (Brentnall et al., 2005). Mid-latitude deciduous forests are of course widespread today, and the phenomenon is reasonably well understood (Monk, 1966; Chabot and Hicks, 1982; Aerts, 1995; Givnish, 2002). However, the existence of large, dominantly deciduous vegetation types in mid-latitudes, as suggested by *Podozamites*-dominance, does not seem to have been remarked upon before. Note that at times, *Podozamites* grew alongside diverse ginkgophytes (Deng et al., 2012) and it is generally accepted that they were also deciduous, although perhaps this relies a little too much on the habit of the one survivor, *Ginkgo* (Note that in contrast to *Podozamites*, both extant *Ginkgo* and the extinct ginkgophytes tended to have relatively robust cuticle). These mid-latitude deciduous forests would have grown in conditions quite different from those that promote deciduousness there today. This would have included an absence of cold polar air, and with an absence of polar ice caps, correspondingly more water in atmospheric circulation. Perhaps this mid-latitude deciduousness needs some attention as a phenomenon in its own right.

As the interior of China dried in the mid-late Jurassic there was an apparent contraction of *Podozamites* distribution towards the coast and out of the polar region. Plant fossil assemblages in general become much rarer in these times, so a simple map of *Podozamites* distribution can be misleading. Reflecting the broad change away from carbonaceous and relatively acidic sediments, vertebrate remains (typically including dinosaurs) become more prevalent. The few plant fossil assemblages known from these drier regions tend not to have *Podozamites*, suggesting that it did respond negatively to drier conditions.

The Jurassic–Cretaceous saw a distinct northwards contraction of various plant taxa in the eastern-Asia region, or at least of their distribution 'centroids'. A regional multivariate analysis for the Jurassic by Rees et al. (2000) quantified the distribution centroids of the scale-leaved conifer *Brachyphyllum* and of *Podozamites*. This resulted in a 'floral gradient' score of 9 for *Brachyphyllum*, whereas *Podozamites* scored 72. The higher the score, the more polar, and hence cooler, was the distributional 'centroid' of the genus. Cheirolepidiaceae, commonly with scale leaves, has long been associated with dry conditions, although it was probably not restricted to these (Alvin, 1982; Pole, 2000; Pole and Philippe, 2010; Tosolini et al., 2015). The scale-leaved conifers were almost restricted to low latitudes in the Late Triassic, but later their limit expanded north into 'territory' that had been dominated by *Podozamites*.

The dry conditions of the Early Cretaceous were probably detrimental to *Podozamites* and likely explain its local absences. However, there are growing arguments for cold conditions in eastern Asia as well (Amiot et al., 2011; Oh et al., 2015; Yang et al., 2013). In the Cretaceous, the tectonically-induced east–west division between the Tetori and Ryoseki floras in Japan continued. A similar distinction was recognised in the Primorye region of Siberia (Golozoubov et al., 1999) although the distribution of *Podozamites* here seemed less rigid. On mainland East Asia, the natural gradient was more clearly a north–south one. Spicer et al. (1993) used multivariate statistics to show that the relative distribution of genera ‘centroids’ in Asia was basically the same in both the Early and Late Cretaceous as it had been in the Jurassic (despite the appearance of angiosperms). Saiki and Wang (2003) selected *Podozamites* as one of their ten ‘climate-indicator’ plants for the Early Cretaceous of China. They found it to be a representative taxon of the ‘Northern type’ floristic province, where it tended to occur with the Ginkgoales. It was not as restricted as the Ginkgoales were though, and some *Podozamites* still occurred in the south. Saiki and Wang (2003) found *Podozamites* contrasted in its distribution with the scale-leaved ‘frenelopsid’ Cheirolepidiaceae conifers, which were typically in the south. The scale-leaved conifer morphology, especially in the earlier Mesozoic of eastern Asia is generally associated with equatorial regions—areas that were relatively hot and dry in contrast with presumed cooler and wetter conditions favouring *Podozamites*. Although some of them occur in the north, amongst *Podozamites* localities, in almost all cases they are still mutually exclusive. It is instructive that although at the level of a ‘locality’, taxa such as *Podozamites* and scale-leaved conifers may occur together, where the finer details of stratigraphy are given, they are commonly found to occur in different beds. Thus it may be that in these areas of regional overlap, the two morphologies

may be occupying different habitats. On a broader scale, if *Podozamites* occurs with other conifers, it is with scale-leaved ones in the south, and with needle-leaved or pinnate ones in the north.

A detailed distribution of *Podozamites* in the mid-Cretaceous is unclear, partly due to the paucity of data in the south. But at face-value, *Podozamites* shows signs of both retreating towards the north—and expanding its distribution back into polar latitudes.

Sometime later in the mid-Cretaceous, the ‘classic’ *Podozamites* became more or less extinct in eastern Asia (although it may have lingered on in some localities). This extinction meant that an entire lifestyle that once dominated—a deciduous conifer with broad, multi-veined leaves—vanished forever. The remains of broad, multi-veined conifers do appear scattered through the subsequent fossil record, and occur today (e.g. *Agathis* and *Nageia*), but these are evergreen.

The end of *Podozamites* is broadly coincident in time with the rise to dominance of angiosperms, although angiosperms did not achieve dominance simultaneously across eastern Asia, and in some cases *Podozamites* co-existed with them for a period. Nevertheless, angiosperms were mostly dominant, and *Podozamites* was absent. However, several relatively high-latitude Cretaceous floras were particularly rich in conifer genera. It remains to be seen if this is, or partly is, an artefact of taxonomy—with earlier specimens tending to be lumped into morphogenera. Nevertheless, scale-leaved conifers appear to have expanded their range northward and joined the high-latitude conifer ensemble, an area where they seem to have been entirely absent before.

The extinction of *Podozamites* can be placed into the broader, global context whereby conifers in general (and other gymnosperms) apparently lost ground as angiosperms advanced. This is the topic of much discussion (e.g. Bond, 1989; Lusk et al., 2003; Pittermann et al., 2005;

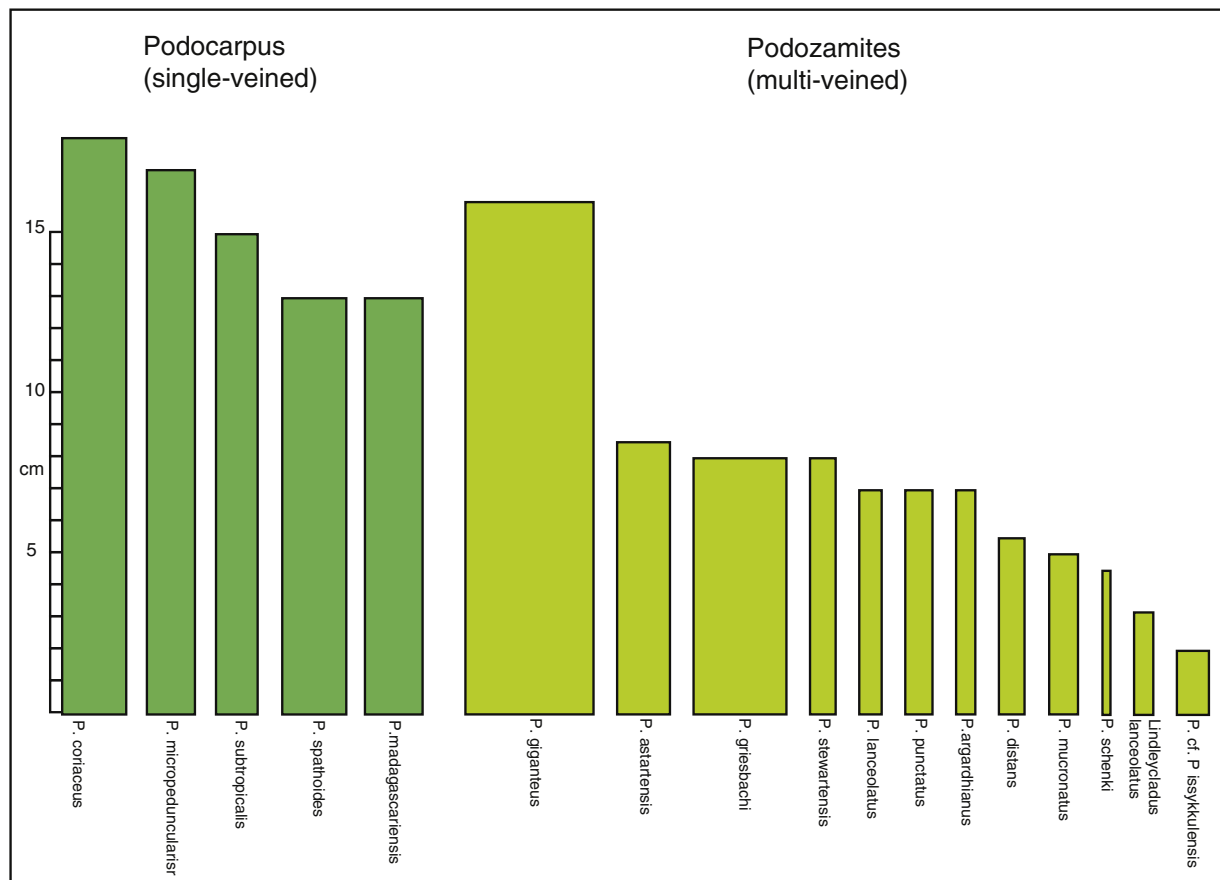


Fig. 9. Comparative sizes of a range of *Podozamites* leaves (multi-veined) with the largest extant *Podocarpus* leaves (single veined). The rectangles represent average length and widths. *Podocarpus* data from Farjon (2010). The basic point is that if distance from mid-vein is limiting, at least some *Podozamites* leaves might be expected to have been larger.

Sperry et al., 2006), and one line of research has focussed on the Podocarpaceae. This conifer family is usual in that members commonly co-exist in angiosperm-dominated forests, and can grow exceptionally large leaves. Brodribb et al. (2012) have suggested that part of the reason for their continuing success is their large leaves. This gives them a competitive ability in the shaded forest floor. This explanation is reasonable, however, in the case of *Podozamites* versus angiosperms, it is remarkable not just that it was this broad-leaved conifer that vanished, but that it was the much smaller leaved conifer taxa (the needle-leaved, pinnate and scale-leaves) that remained and co-existed with angiosperms for the next 100 Myrs or so.

It is worth considering comparing the range in leaf size of *Podozamites* with extant *Podocarpus*—the conifer genus with some of the largest leaves today. In general, the largest *Podozamites* leaves are similar to the largest *Podocarpus* (Fig. 9). The maximum inter-vein distances achieved by *Podozamites* were in the order of a millimetre, and were commonly much less. The margin of a medium-sized *Podocarpus* leaf is about 5 mm from the vein, and is about 10 mm in the largest (e.g. *Podocarpus spathoides*). Large extant *Podocarpus* leaves may well have reached the physiological limit of width for single-veined leaves, but it is curious that *Podozamites*, having many veins, did not in some way expand to take advantage of this.

The coincidence of *Podozamites* demise and the rise of angiosperms may turn out to have been just that—a coincidence. For instance, the

combination of multiple veins and deciduousness might have made them vulnerable to certain climate changes, such as declining rainfall. The highly restricted range of extant *Ginkgo*, probably the nearest living analogue to *Podozamites*, may be instructive in that respect (per. comm. D.K. Ferguson). As a thin-leaved conifer with apparently no physical defensive features, *Podozamites* and other broadleaved conifers suffered from “elevated levels” of insect consumption. As Ding et al. (2015) demonstrated, the feeding strategy of insects on these conifers changed markedly over the Mesozoic. It cannot be ruled out that this may have eventually contributed to their demise, but *Podozamites* had countered this evolving force for millions of years—and when it did become extinct, it was surrounded by presumably palatable deciduous angiosperms.

Finally, *Podozamites* was just one of several taxa that show an apparent poleward movement (part migration and part contraction) over the Mesozoic in the Northern Hemisphere (e.g. Caytoniales, *Equisetites*, *Hausmannia*, *Nilssonia*, *Phoenicopsis*, *Sagenopteris*; see the PBDB). A similar trend is apparent in the Southern Hemisphere, where in some cases, it extended into the Cenozoic (e.g. Bennettitales, Corystospermales, Ginkgoales and Cheirolepidiaceae; Carpenter and Hill, 1999, McLoughlin et al., 2008, 2011; Barreda et al., 2012). Seen in this context the Cretaceous expansion of angiosperms towards the poles (Axelrod, 1959; Crane and Lidgard, 1989; Drinnan and Crane, 1989) might be seen as less an invasion of higher

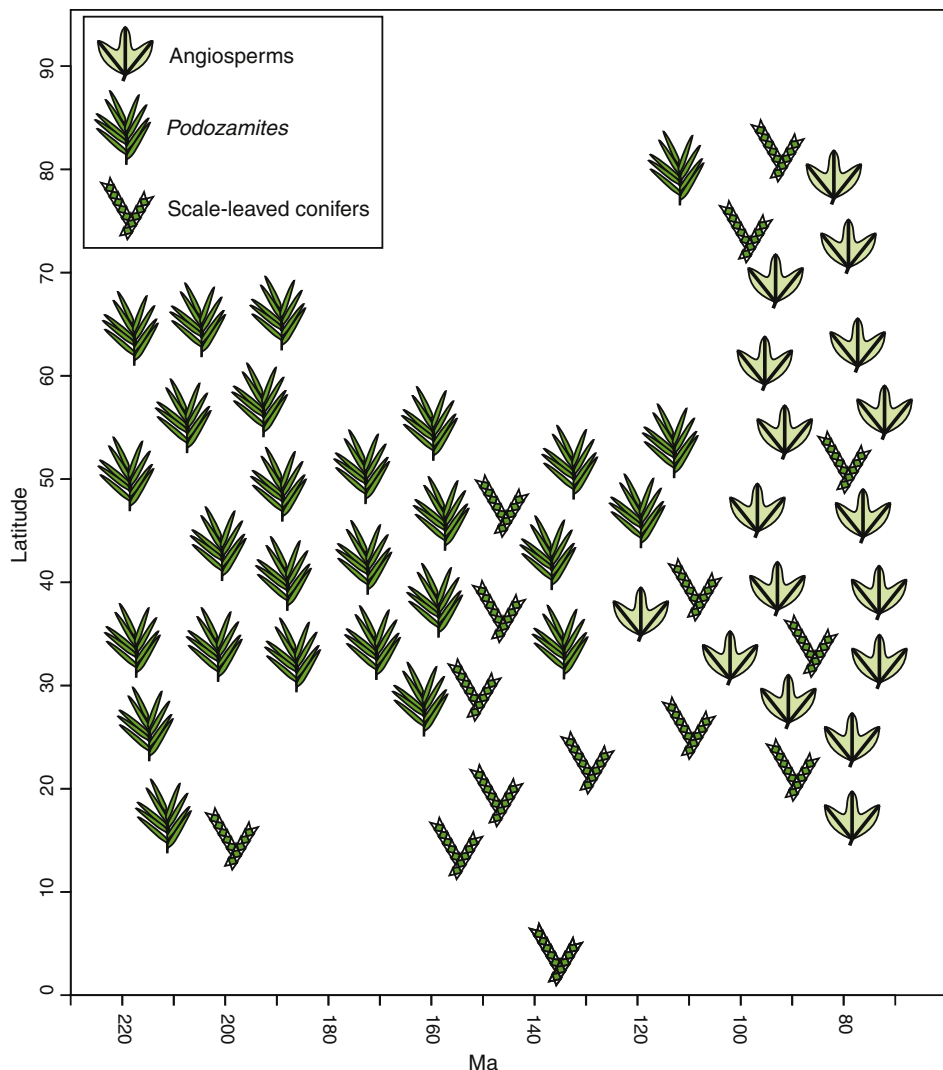


Fig. 10. Schematic summary of the distribution of East Asian *Podozamites*, scale-leaved conifers and angiosperms through time and space.

latitude vegetation, than as being one component of a broader movement.

5. Conclusions

After being uncommon earlier in the Triassic, *Podozamites* became widespread across eastern Asia at mid-latitudes in the Late Triassic. At this time it was frequently the only conifer in fossil assemblages and in some assemblages it was overwhelmingly dominant. In terms of the broader ranges of conifers, *Podozamites* tended to be bordered on its equatorial side by scale-leaved conifers, and by pinnate, awl, or needle-leaved conifers on the polar side.

Podozamites did not seem to be much affected by the Triassic–Jurassic boundary event, remaining dominant in some assemblages just after. However, as the Jurassic progressed, at least its fossil record contracted out of central China in response to drying. By the Early Cretaceous there had been a general shift in the ‘centroid’ of *Podozamites* distribution to the north of China and Siberia. It was in the mid-Cretaceous that angiosperms made their appearance and rapidly (although not synchronously) became dominant, and at roughly the same time *Podozamites* became extinct. The spread of angiosperms may well have an implication for *Podozamites* extinction. However, if it does, it raises some interesting questions concerning how conifer morphologies compete with angiosperms. We summarise this history of eastern Asian *Podozamites* distribution along with the scale-leaved conifer shoot morphology and angiosperms in a schematic diagram (Fig. 10). The history of *Podozamites* distribution highlights two main questions and suggests a foci for some future research:

1. The existence of an extensive deciduous forest at mid-latitudes in the Late Triassic–Early Jurassic does not seem to have been remarked on before. Although disturbance, probably primarily involving fire seems to be the explanation for both deciduous and evergreens coexisting in the polar regions, this explanation for lower latitudes is an open question. We recommend one focus to be on clarifying the fire-history of the eastern Asian region. This may be a key to understanding the existence of deciduous forests at mid-latitudes.
2. The end of *Podozamites* appears somehow linked with the rise of angiosperms. Whether or not they caused it, it is remarkable that this broad-leaved conifer vanished at about that time, and was replaced with much smaller leaved taxa. This suggests that we need to know more about the competitive abilities of scale-leaved conifers, and to model how broad-leaved, multi-veined and deciduous conifers may have interacted. Considering *Ginkgo* as a *Podozamites* analogy may be very useful here. A further key may be the details of those Siberian assemblages where *Podozamites* ‘hung on’ for different times with a variety of other conifers in angiosperm-dominated vegetation. Fundamental to this, is establishing whether *Podozamites* was a tree or a herb. Despite being such an important plant, we still do not know what wood fossil is associated with it.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2016.02.037>.

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