

FOSSIL *CATHAYA* (PINACEAE) POLLEN FROM THE CANADIAN HIGH ARCTIC

Yu-Sheng Liu and James F. Basinger¹

Department of Geological Sciences, University of Saskatchewan, Saskatoon, Saskatchewan S7N 5E2, Canada

Palynological studies of the Eocene Buchanan Lake Formation, Axel Heiberg Island, Canadian High Arctic, have yielded pollen grains closely comparable to those of extant *Cathaya* Chun et Kuang, a paleoendemic conifer of southwestern China. These palynomorphs are assigned to *Cathaya gausseui* Sivak, which is here interpreted as the only species to which known fossil pollen of this genus can be assigned. Unless scanning electron microscopy is used, generic affinity cannot be determined with certainty. On the basis of light microscopy alone, *Cathaya*-like pollen fossils may be grouped into one form-taxon, *Pityosporites microalatus* (Potonié) Thomson et Pflug. The Eocene record from Canada provides convincing evidence for the occurrence of *Cathaya* in North America and is consistent with interpretations for warm climatic conditions in the Canadian Arctic in the Middle to Late Eocene. An appraisal of the available literature on fossil *Cathaya* and *Cathaya*-like pollen of Cretaceous to Recent age has been undertaken. The pre-Cretaceous record is difficult to evaluate. The genus *Cathaya* was apparently restricted to North America and East Asia during the Cretaceous but had dispersed to Europe, possibly via a North Atlantic land bridge, by the Early Tertiary. In the Neogene, *Cathaya* became widespread in North America, East Asia, and Europe. Late Tertiary climatic deterioration and Quaternary glaciation appears to have been responsible for extirpation of *Cathaya* from North America first (latest record Late Miocene), and then from Europe (Pleistocene). Therefore, the endemic distribution of extant *Cathaya* in China represents a remnant of a formerly widespread Asiatic population.

Keywords: *Cathaya*, Pinaceae, fossil, Eocene, arctic, Canada, evolution, pollen, biogeography.

Introduction

Cathaya argyrophylla Chun et Kuang (the “giant panda” of the plant kingdom) was formally described in 1958 by Chun and Kuang (1958; Ying et al. 1993). It is one of two monotypic genera of Pinaceae found in China and has been categorized as a paleoendemic, with a fossil history dating at least to the Cretaceous (Ferguson et al. 1997; Liu et al. 1997). It has commonly been held that *Cathaya* has been restricted to Eurasia (Florin 1963; Wang 1989; Farjon 1990; Ying et al. 1993), although many records of fossil pollen from North America have been proposed to be of *Cathaya* affinity (Sivak 1976; Thiele-Pfeiffer 1980; Mohr 1984; Liu et al. 1997). Misidentification of bisaccate grains as *Cathaya* and the classification of *Cathaya*-like grains under form-generic names that are of little botanical significance have been the sources of much of the difficulty in determination of past distribution. When we review the record of *Cathaya*-like pollen, we find a confusing nomenclatural history, with most palynomorphs misidentified as *Abietinaepollenites*, *Pinus Haploxylon*-type, and *Pityosporites*, even *Podocarpus* and *Podocarpidites* (see also Sivak 1976; Liu et al. 1997).

Megafossils of *Cathaya*, including leaves and ovulate cones, are known only from the Oligocene to Pliocene of Eurasia, primarily central and southern Europe, and are absent from China (Liu et al. 1996). The leaves and cones of *Cathaya* are distinctive and relatively easy to identify (Pant and Basu 1977;

Hu and Wang 1984; Mai 1994a, 1999; Walther 1999). To date, no megafossils of *Cathaya* have been reported from North America, and none have been found at the Axel Heiberg Island site, although megafossils of *Cathaya* are rare worldwide. Fortunately, pollen of extant *Cathaya* is distinctive, and identification can be confirmed by means of scanning electron microscopy (SEM) (Liu et al. 1997). It is on this basis that we can document the occurrence of *Cathaya* on Axel Heiberg Island. Although Caratini et al. (1972) assigned fossil pollen to the genus *Cathaya*, Sivak (1976) was the first to observe both Recent and fossil pollen of *Cathaya* using SEM and to provide clear documentation of diagnostic features of exine morphology that are essential for identification. Because Sivak's (1976) work has not been fully accepted (e.g., Wilkinson and Boulter 1980; Mohr 1984; Ashraf and Mosbrugger 1996), it will be necessary here to reexamine published data and newly found fossils.

The knowledge of fossil spores and pollen grains has been greatly enhanced by adoption of transmission electron microscopy (TEM) and SEM, contributing to reevaluation of the relevance of exospore-exine stratification and fine sculpture of the sporomorphs to interpretation of biological affinity, phylogeny, and phytogeography (Kedves 1982; Zetter and Hesse 1996; Ferguson et al. 1998; Kovar-Eder et al. 1998; Van der Burgh and Zetter 1998). In this article, we first summarize characteristics of Recent *Cathaya* pollen and tabulate data from other extant coniferous genera with bisaccate pollen. On the basis of numerous well-preserved (three-dimensional) pollen from the Eocene Buchanan Lake Formation, Axel Heiberg Island, Canadian Arctic Archipelago, we confirm a record of

¹ Author for correspondence; e-mail jim.basinger@sask.usask.ca.

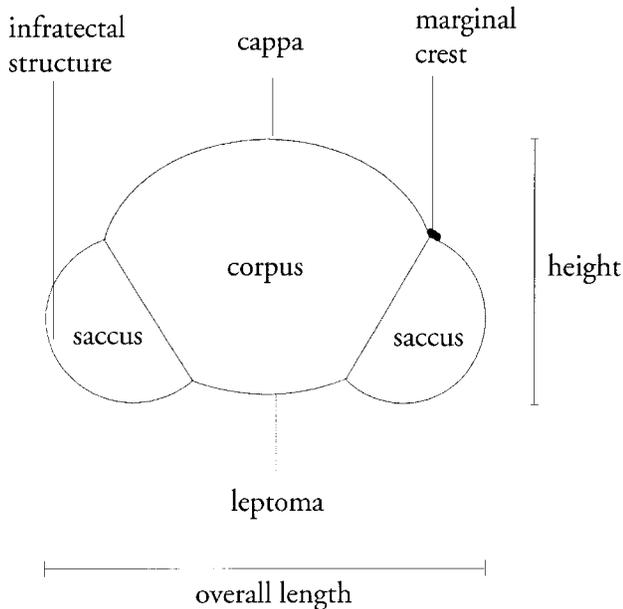


Fig. 2 Schematic figure showing key morphological features of bisaccate pollen in equatorial view.

size of the sacchi (Liu et al. 1997). Pollen grains of *Podocarpus*, in particular, may appear to share this feature with *Cathaya*, so that fossil bisaccate grains of this type, and with relatively large sacchi and small corpus, have commonly been mistakenly attributed to the genus *Podocarpus*, causing considerable confusion in the fossil literature (e.g., see Zheng 1987). *Podocarpus* pollen possess characteristically rugulate and/or psilate exine, by which they can be readily separated from *Cathaya*. Nevertheless, some species of *Podocarpus* share some other features with *Cathaya* (Pocknall 1981; Liu et al. 1997); for example, the cappa of the living *Podocarpus acutifolius* Kirk from New Zealand has spinules, although its exine is coarsely rugulate (Pocknall 1981).

The most definitive features for identification of living and fossil *Cathaya* pollen are seen only under SEM. *Cathaya* pollen grains have irregularly spaced spinules and perforations on the surface of both corpus and saccus, except for the leptoma area on the distal surface of the grain (Liu et al. 1997).

Although grains superficially resembling *Cathaya* have been reported from pre-Cretaceous rocks (e.g., Pocock 1962, pp. 62, 63, pl. 9, figs. 142–144, 146, pl. 10, figs. 157, 158; Rouse 1959, p. 316, pl. 1, figs. 13–16), they are too poorly preserved to allow biological assignment. Thus, the record of *Cathaya* is at this time restricted to the Cretaceous and Cenozoic.

History of Nomenclature of Fossil Pollen of *Cathaya*

The nomenclature of fossil *Cathaya* and *Cathaya*-like pollen has an extremely complex history. There are only a few cases in which the generic name *Cathaya* has been applied to fossil grains (Caratini et al. 1972; Sivak 1976; Klaus 1984; Nagy 1985; Liu et al. 1997; Meller et al. 1999), although some of these assignments appear to be inappropriate (e.g., Nagy 1985, p. 134, pl. 65, figs. 4, 5). In most cases, fossil grains resembling

Cathaya have been assigned to form taxa reserved for palynomorphs. The earliest description of *Cathaya*-like pollen was that of Potonié (1931), who described *Piceae-pollenites* (*sic*) *microalatus* Potonié from the Miocene of Germany. (Potonié also described *Piceae-pollenites* [*sic*] *alatus* Potonié at the same time, but we do not consider this taxon *Cathaya*-like; see below.) The species displays clear resemblance to *Cathaya*, but it must be recalled that living *Cathaya* was not discovered until 1958, so therefore was unknown to Potonié. Three years later, he renamed it *Pollenites microalatus* (Potonié) Potonié (1934), and later transferred it yet again, to the invalidly published form genus *Abietinae-pollenites* (Potonié 1951). Delcourt and Sprumont (1955) attempted to validate this generic name by formally transferring *Piceapollenites microalatus* Potonié to *Abietinaepollenites microalatus* (Potonié) ex Delcourt et Sprumont, but curiously did not cite or discuss earlier recombinations of Thomson and Pflug (1953), who had transferred Potonié's species, *P. microalatus* (Potonié) Potonié (1934), to the form genus *Pityosporites* Seward (1914). The recombination *Pityosporites microalatus* (Potonié) Thomson et Pflug clearly has priority. (Potonié [1951] refers to two subspecies or forms of this species, *minor* and *major*, which have also been recognized by Thomson and Pflug. Curiously, Potonié thought of the former as smaller, the latter as larger grains, while Thomson and Pflug described form *minor* as larger than form *major*.) Unfortunately, both recombinations have been adopted and used by different researchers for fossil grains of the *Cathaya* type, although fewer have used the superfluous combination of Delcourt and Sprumont (1955). It should be noted that we reject the additional materials that Delcourt and Sprumont (1955) attributed to this taxon, as it is not clear that their figured specimens are consistent with the concept for the species. Interestingly, Potonié (1975) himself did acknowledge the work of Caratini et al. (1972) in which *Cathaya* fossil pollen was first reported, but he was not inclined to revise his own work.

When Sivak (1976) applied the SEM to description of *Cathaya* fossil pollen from the Oligocene-Miocene of France, he noted the resemblance of both *Pityosporites microalatus* (Potonié) Thomson et Pflug and *Pityosporites alatus* (Potonié) Thomson et Pflug to *Cathaya* and suggested that dispersed pollen assigned to these species represent *Cathaya* as well. While we agree that *P. microalatus* is *Cathaya*-like, and we recognize this taxon as having nomenclatural priority for pollen of this type, we do not consider Potonié's (1931) illustrated material of *P. alatus* as either resembling or representing the genus *Cathaya* (see app. A). Unfortunately, it would appear that, in original descriptions of these two species and in subsequent interpretations (e.g., Krutzsch 1971; Thiele-Pfeiffer 1980), the major (only?) difference between the species concepts of *P. microalatus* and *P. alatus* is size, with the former being smaller than the latter. Nevertheless, it is clear that *P. alatus* must be rejected from the list of possible synonyms of *Cathaya*-like dispersed pollen grains.

In addition to the above binomials, the name "*Pinus Haploxyylon*-type" has long been used for *Cathaya*-like fossil pollen (e.g., Doktorowicz-Hrebicka 1960; Oszast 1960; Lona and Ricciardi 1961; Gray 1964; Hopkins 1969; Boulter and Craig 1979; Nghia 1974; Herter 1985). Rudolph (1935, pp. 254–255) first applied this name to *Cathaya*-like grains while

Table 1

Comparison of Bisaccate Coniferous Pollen Morphology from Extant Conifers

Genus	LM			SEM		References
	Breadth (μm)	Corpus	Saccus	Corpus	Leptoma	
<i>Abies</i>	115–185	Corpus elliptical in polar view; marginal crest absent; exine thick, sexine thicker than nexine; proximal exine tapering toward sacci	Size and shape variable, typically small in relation to corpus; sharp angular discontinuity at saccus-cappa junction; lumina smaller than of <i>Pinus</i>	Cappa sexine usually coarse; triradiate mark visible on the proximal surface in the American species only; not seen in other species	Smooth	Wodehouse 1935; Ueno 1958; McAndrews et al. 1973; Bagnell 1975; Weir and Thurston 1975; Moore et al. 1991; Wang et al. 1995
<i>Cathaya</i>	55–80	Corpus rhomboidal in polar view; marginal crest absent; exine thick, sexine thicker than nexine; proximal exine of even thickness	Size and shape highly variable; saccus-cappa junction smooth, without sharp angular discontinuity; muri of reticulum rather coarse, usually unconnected; sacci infratectate, unlike all other Pinaceae	Sexine spinulose and perforate	Verrucate	Sivak 1976; Klaus 1977, 1987; Xi and Wang 1989; Ying et al. 1993; Wang et al. 1995; Liu et al. 1997
<i>Cedrus</i>	50–80	Corpus elliptical in polar view; marginal crest absent; exine thick, sexine thicker than nexine; proximal exine of even thickness	Size and shape variable, typically smaller than corpus; widely separated with broad leptoma; saccus-cappa junction smooth, without sharp angular discontinuity; lumina of reticulum irregularly polygonal; muri undulate	Sexine rugulate, coarser than in <i>Pinus</i>	Finely rugulate	Wodehouse 1935; Erdtman 1943; Klaus 1978; Moore et al. 1991; Wang et al. 1995
<i>Keteleeria</i>	80–155	Corpus elliptical in polar view; marginal crest absent; exine thick, sexine thicker than nexine; proximal exine tapering toward sacci	Much smaller than corpus, widely separated with broad leptoma; sharp angular discontinuity at saccus-cappa junction; lumina irregularly polygonal	Sexine finely granular, delicate	Verrucate	Erdtman 1943; Ueno 1958; Wang et al. 1995
<i>Picea</i>	70–120	Corpus elliptical to circular in polar view; marginal crest absent; exine thick, sexine much thicker than nexine; proximal exine tapering toward sacci	Small to similar in proportion to corpus; saccus-cappa junction smooth, without sharp angular discontinuity; lumina irregularly polygonal	Sexine finely granular	Psilate, granulate or microverrucate	Erdtman 1943; Ueno 1958; McAndrews et al. 1973; Bagnell 1975; Weir and Thurston 1975; Birks 1978; Moore et al. 1991; Wang et al. 1995

Table 1
(Continued)

Genus	LM			SEM		References
	Breadth (μm)	Corpus	Saccus	Corpus	Leptoma	
<i>Pinus</i> , <i>Diploxylon</i> type	40–120	Corpus elliptical to circular in polar view; marginal crest present, may be well developed; exine thin, sexine same thickness as nexine; proximal exine of even thickness	Saccus size and shape variable, more or less contracted at base, appearing inflated; connection with cappa smooth, without obvious angles; lumina irregularly polygonal	Sexine granulate	Psilate or finely verrucate	Erdtman 1943, 1965; Ueno 1958; Hansen and Cushing 1973; McAndrews et al. 1973; Bagnell 1975; Weir and Thurston 1975; Sivak and Raz 1976; Klaus 1977, 1978; Moore et al. 1991; Wang et al. 1995
<i>Pinus</i> , <i>Haploxylon</i> type	40–12	Corpus elliptical to circular in polar view; marginal crest absent; exine thin, sexine same thickness as nexine; proximal exine of even thickness	Saccus size and shape variable; semicircular, broadly attached to the corpus; connection with cappa smooth, without obvious angles; lumina irregularly polygonal	Sexine granulate	Coarsely verrucate	Erdtman 1943, 1965; Ueno 1958; Hansen and Cushing 1973; McAndrews et al. 1973; Bagnell 1975; Weir and Thurston 1975; Sivak and Raz 1976; Klaus 1977, 1978; Moore et al. 1991; Wang et al. 1995
<i>Podocarpus</i>	35–90	Corpus rhomboidal, elliptical, or spheroidal; marginal crest present or absent; exine thin; proximal sexine of even thickness	Saccus typically large, may be larger than corpus; connection with cappa smooth, without obvious angles; lumina irregularly polygonal; muri of reticulum rough, connected or unconnected	Sexine finely to coarsely rugulate	Rugulate	Pocknall 1981
<i>Pseudolarix</i>	60–85	Corpus elliptical in polar view; marginal crest absent; exine thin, sexine thicker than nexine; proximal exine of even thickness	Saccus small, the two sacci joining the corpus with a wide angle; sharp angular discontinuity at saccus-cappa junction; lumina irregularly polygonal; muri of reticulum thin, commonly connected	Sexine rugulate and perforate	Finely granular	Erdtman 1943; Van Campo 1950; Ueno 1958; Ying et al. 1993; Wang et al. 1995

studying Neogene palynofloras from northern Bohemia, Czech Republic. Rudolph's (1935, p. 254, pl. 4, figs. 1–5) material has been interpreted as *Cathaya* by R. Zetter (personal communication, 1999). Earlier, Zagwijn (1960) had doubted that pollen being assigned to *Pinus Haploxylon*-type actually belonged to the genus *Pinus*, recognizing that morphology of these grains had no known counterpart among then known extant species of *Pinus*. He further pointed out that the name *Pinus Haploxylon*-type, originally thought to represent all *Pinus* subgenus *Haploxylon*, is therefore misleading (Zagwijn 1960, p. 64). Unfortunately, Zagwijn continued to use the name of *Pinus Haploxylon*-type, although he did so in the strict sense, as suggested by Doktorowicz-Hrebicka (1957).

Cathaya-like grains have also been assigned to a diversity of other genera, such as *Alisporites* (Felix and Burbridge 1973; Brideaux and McIntyre 1975), *Pinus* (Macko 1957; Khlonova 1961; Stanley 1965), *Podocarpus* (Macko 1957; Zaklinskaya 1957; Piel 1971), *Podocarpidites* (Zheng 1987), and *Punctabivesiculites* (Pierce 1961). Details are provided in appendix B.

Systematics

As discussed above, only SEM observation can confirm the assignment of fossil bisaccate pollen grains to the genus *Cathaya*. *Cathaya gausseui* Sivak, coined by Sivak (1976) on the basis of SEM observation, is applied to our Canadian fossil pollen. Sivak (1976) established 12 separate species of *Cathaya* to accommodate fossil pollen that he recovered from a single Oligo-Miocene boundary deposit in southwestern France. We consider 11 to be synonymous (rejecting *Cathaya zagwijnii* Sivak on the basis of figured materials). We have selected *C. gausseui* to represent this species because, among all of Sivak's species, this morphotype is the most abundant and most typical of the taxon. The form taxon *Pityosporites microalatus* is used for fossil pollen that lack confirmation of affinity by SEM but under LM bear sufficiently close resemblance to Recent *Cathaya* that affinity is highly probable (see app. B).

Order—Coniferales Jussieu, 1789

Family—Pinaceae Lindley, 1836

Genus—*Cathaya* Chun et Kuang, 1958

Species—*Cathaya gausseui* Sivak (Figs. 3a–4l)

Synonymy. The following specimens have been illustrated by SEM and can be confirmed from the published literature:

- 1976. *Cathaya erdtmanii* Sivak, p. 264, pls. 5, 6.
- 1976. *Cathaya vancampoae* Sivak, pp. 264, 266, pls. 7, 8.
- 1976. *Cathaya gausseui* Sivak, pp. 266, 268, pls. 9, 10.
- 1976. *Cathaya krutzschii* Sivak, pp. 268, 270, pl. 11.
- 1976. *Cathaya wilsonii* Sivak, pp. 270, 272, pl. 121.
- 1976. *Cathaya potonieii* Sivak, pp. 272, 274, pl. 13.
- 1976. *Cathaya scheuringii* Sivak, pp. 274, 276, pls. 14, 15.
- 1976. *Cathaya uenoi* Sivak, p. 276, pl. 16.
- 1976. *Cathaya millayi* Sivak, p. 278, pls. 17, 18.
- 1976. *Cathaya ponsii* Sivak, pp. 280, 282, pls. 20, 21.
- 1976. *Cathaya tingii* Sivak, pp. 282, 284, pl. 22.
- 1984. *Pityosporites microalatus* (Potonié) Thomson et Pflug,

Mohr, p. 55, pl. 6, figs. 1.1, 1.2.

- 1984. *Pityosporites alatus* (Potonié) Thomson et Pflug, Mohr, pp. 55, 56, pl. 6, figs. 2.1–2.3.
- 1996. *Pityosporites microalatus* (Potonié) Thomson et Pflug, Ashraf and Mosbrugger, pp. 6, 7, pl. 2, figs. 5, 6.
- 1997. *Cathaya zhejiangensis* Liu, Zetter et Ferguson, pp. 229, 230, pl. 1, figs. 1–6.
- 1999. *Cathaya* sp., Meller et al., p. 29, pl. 4, figs. 4–6.

Emended diagnosis. Pollen bisaccate, heteropolar; outline ovate or subcircular in polar view. Corpus outline circular to rhomboidal in polar view, with sacchi generally originating at the margin of the corpus. Sacchi variable in shape, from hemispherical to inflated; lumina formed by infractectal muri of the sacchi small and regularly arranged. Exine of corpus of even thickness in lateral view, without marginal crest. Under SEM, irregularly arranged spinules and perforations observed on the surface of both corpus and sacchi, with elements less dense on sacchi. Leptoma verrucate.

Description. Pollen grains are highly variable in size, with the corpus 30–55 μm in depth, 35–50 μm in breadth, and 30–35 μm in height, while sacchi are 35–55 μm in breadth and 20–25 μm in height (see fig. 2). In polar view the corpus is distinctly rhomboidal (figs. 3g, 4a). There seems to be no preponderance of hemispherical, as opposed to more inflated, sacchi (fig. 3b, 3d, 3g, 3j; fig. 4a, 4c, 4e, 4g, 4i). The lumina of sacchi are fine and regularly spaced (fig. 3a; fig. 4a, 4b). The surface of the leptoma is seen as verrucate, even under LM (fig. 3a, 3c, 3f). Exine of the corpus is ca. 1–1.5 μm thick; there is no thickening seen adjacent to the saccus attachment, and therefore there is no marginal crest (fig. 3g, 3j; fig. 4e, 4g). Randomly arranged spinules and perforations are observed under SEM to cover the entire surface (fig. 3e, 3i, 3k, 3l; fig. 4d, 4f, 4h, 4j, 4l), with the exception of the leptoma. The density of spinules and perforations is greatest on the cappa (fig. 3i, 3l; fig. 4f, 4h), while ornament is less dense on the surface of the sacchi (fig. 3e, 3h, 3k; fig. 4d, 4j, 4l).

Discussion. The fossil pollen of *Cathaya* from Axel Heiberg Island resemble very closely those of the living *C. argyrophylla* in size and morphology. In fact, there are essentially no differences between the living and fossil pollen of *Cathaya*. Furthermore, pollen of this type, as noted above and in table 1, can be distinguished from all other bisaccate grains.

Cathaya zhejiangensis, a species based on fossil pollen from the Miocene of east China, was similarly reported by Liu et al. (1997, p. 230) to be indistinguishable from living *Cathaya*, although they stated that the latter “are usually smaller than the fossils.” Nevertheless, pollen grains of living *Cathaya* have a wide range of size variation (see also Ying et al. 1993), and we do not consider size to be a useful character for recognizing the grains of the genus. Furthermore, saccus size and, therefore, overall dimensions, may be strongly biased by environmental conditions as well as experimental procedures (Wodehouse 1933; Runions et al. 1999).

Sivak (1976) reported 12 species of fossil *Cathaya* pollen from the same locality in southwestern France, although it is unlikely that so many “species” would coexist in the same region (Liu et al. 1997). On the basis of consideration of the variation of grain size and morphology in living *Cathaya*, as reported by Ying et al. (1993), and the recognition of diag-

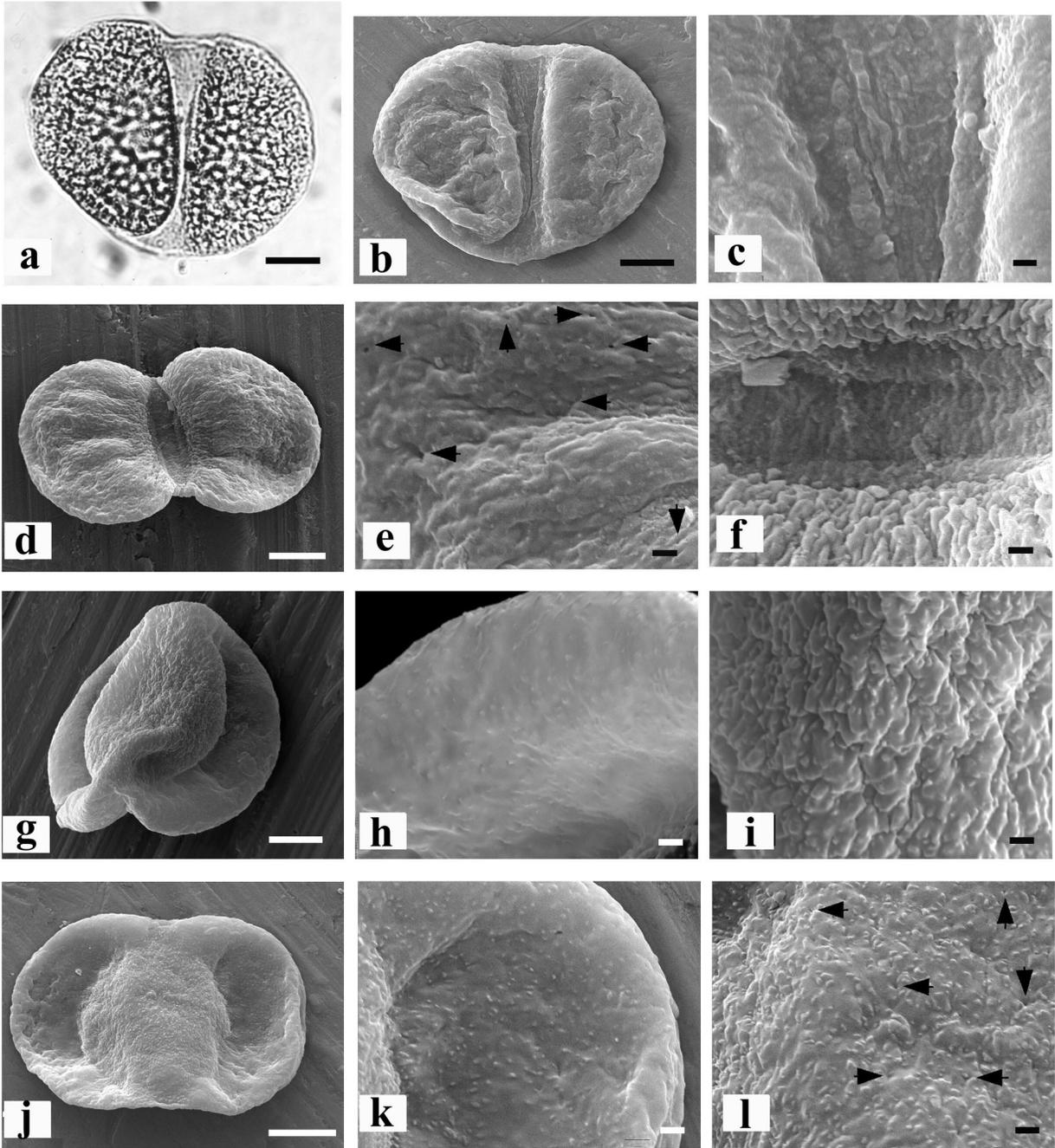


Fig. 3 *Cathaya gausseii* Sivak from Axel Heiberg Island. *a-c*, Single pollen grain under light microscopy (LM, bright-field) and scanning electron microscopy (SEM); US188-41cath1. *a*, LM; note connection between sacci and corpus (bar = 10 μ m). *b*, SEM; distal view (bar = 10 μ m). *c*, SEM; close-up of leptoma, showing verrucate sculpture (bar = 1 μ m). *d-f*, Single pollen grain under SEM; US188-23cath2. *d*, Distal view (bar = 10 μ m). *e*, Close-up of saccus. Note occurrence of irregularly arranged perforations (arrows) and spinules (bar = 1 μ m). *f*, Close-up of leptoma, showing verrucate sculpture (bar = 1 μ m). *g-i*, Single pollen grain under SEM; US188-20cath2. *g*, Proximal view. Note rhomboidal shape of corpus (bar = 10 μ m). *h*, Close-up of saccus, showing sparse spinules (bar = 1 μ m). *i*, Close-up of corpus. Note shrinkage and wrinkling of exine (bar = 1 μ m). *j-l*, Single pollen grain under SEM; US188-40cath1. *j*, Proximal view (bar = 10 μ m). *k*, Close-up of saccus, showing fine spinules (bar = 1 μ m). *l*, Close-up of corpus, showing perforations (arrows) and densely arranged spinules. Note that spinules of both saccus and corpus are similar, although they differ in density (bar = 1 μ m).

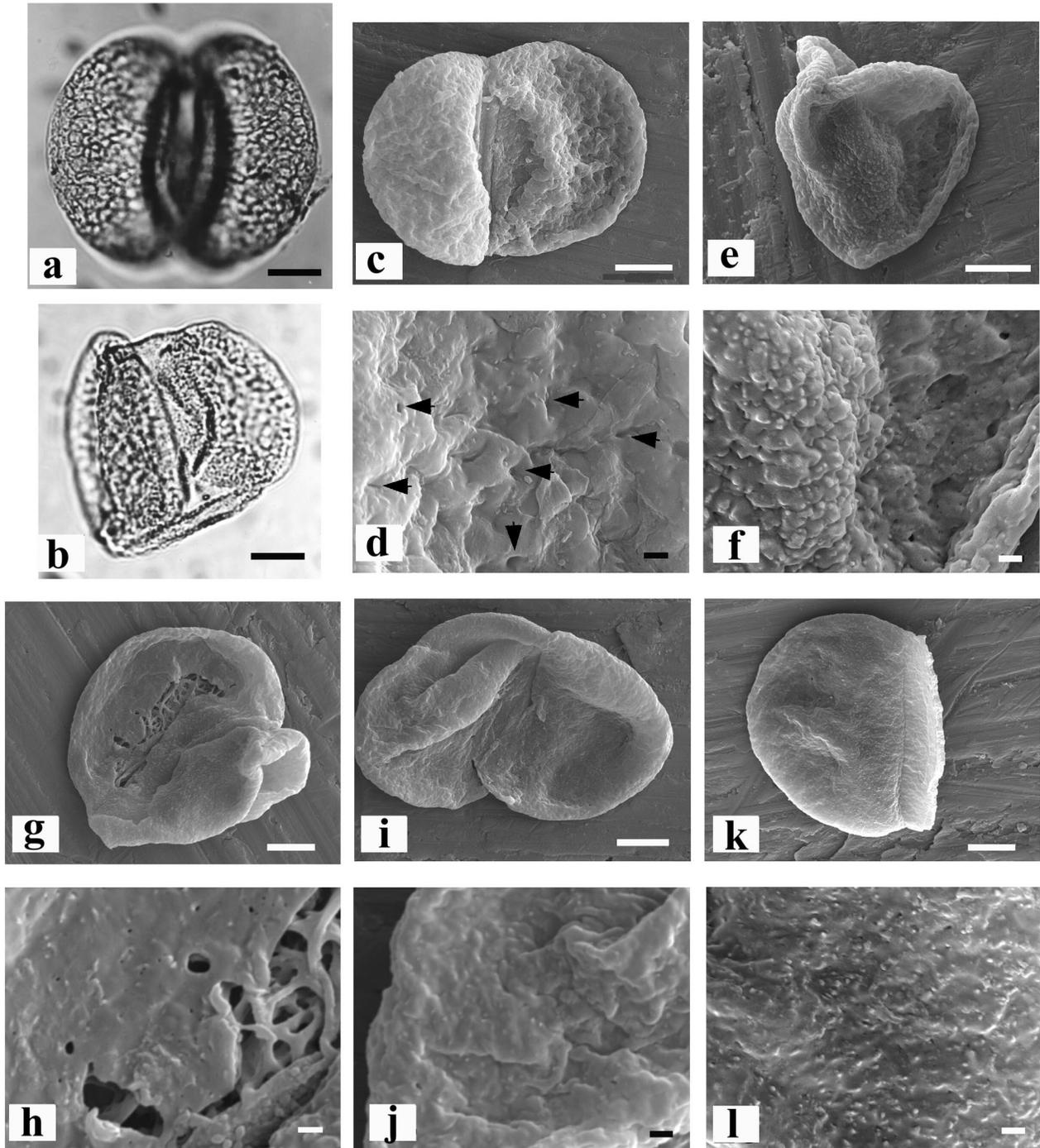


Fig. 4 *Cathaya gaussenii* Sivak from Axel Heiberg Island. *a*, Pollen under LM; US188-slide1 (bar = 10 μ m). *b*, LM; note connection between saccus and corpus; US188-slide2 (bar = 10 μ m). *c*, *d*, Single pollen grain under SEM; US188-40cath2. *c*, Distal view (bar = 10 μ m). *d*, Close-up of saccus, showing sparse occurrence of perforations (arrows) and spinules (bar = 1 μ m). *e*, *f*, Single pollen grain under SEM; US188-33cath1. *e*, Proximal-lateral view, showing absence of marginal crest (bar = 10 μ m). *f*, Close-up of junction between corpus and saccus. Note shrinkage and wrinkling of exine and absence of marginal crest (bar = 1 μ m). *g*, *h*, Single pollen grain under SEM; US188-23cath3. *g*, Distal view, showing broken saccus and folded corpus (lower right) (bar = 10 μ m). *h*, Close-up of saccus, showing the smooth surface of muri (bar = 1 μ m). *i*, *j*, Single pollen grain under SEM; US188-23cath1. *i*, Distal-lateral view. Note the relatively large sacci of this grain (bar = 10 μ m). *j*, Close-up of saccus, showing sparse perforations and spinules (bar = 1 μ m). *k*, *l*, Single saccus under SEM; US188-20cath1. *k*, Distal view of saccus (bar = 10 μ m). *l*, Close-up of saccus, showing irregularly arranged perforations and spinules (bar = 1 μ m).

nostic exine ornamentation, we consider as synonymous all of Sivak's species save one, *C. zagwinjii*. Exine ornamentation of *C. zagwinjii* appears granular (Sivak 1976, p. 278, pl. 19), excluding it from *Cathaya* (see app. A).

Cathaya antiqua Klaus (1984) was first established on the basis of pollen from the Miocene of Austria observed under LM. This record was later confirmed under SEM by R. Zetter (personal communication, 1999), who found no grounds for distinguishing this material from other grains assigned to *Cathaya*.

Some of the Axel Heiberg fossil pollen grains exhibit shrinkage of the exine (figs. 3i, 4f), which probably has been caused by experimental treatment. Klaus (1978) has reported similar phenomena while studying living alpine *Pinus* pollen grains.

Species—*Pityosporites microalatus* (Potonié)
Thomson et Pflug

Synonymy. The very numerous specimens referable to this taxon have not been examined by us personally. On the basis of extensive review of published figured materials, we have created a list of potential synonyms (app. B):

1931. *Piceae-pollenites microalatus* Potonié, p. 5, fig. 34.
1953. *Pityosporites microalatus* (Potonié) Thomson et Pflug f. *major* (Potonié) Thomson et Pflug, p. 67, pl. 5, fig. 53 (only).
1953. *Pityosporites microalatus* (Potonié) Thomson et Pflug f. *minor* (Potonié) Thomson et Pflug, p. 68, pl. 5, figs. 51, 57 (only).

Description. Pollen outline oval or circular in polar view, ca. 60–80 μm long. Bisaccate grains with sacchi hemispherical to inflated. Sacchi attached at the margin of the corpus. Sacchi reticulate, with regularly developed muri.

Discussion. As noted above, we retain the form-genus name of *Pityosporites* for all *Cathaya*-like dispersed pollen fossils for which no SEM data exist. We follow the recommendation of Thiele-Pfeiffer (1980) in the use of the species *P. microalatus* for these grains. Also, as noted above, *Abietinaepollenites microalatus*, although commonly used, is an inappropriate combination because *P. microalatus* has priority. We reject recognition of two forms, *major* and *minor*, by some authors, and combine both into a single species concept.

The literature is replete with assignments of *Cathaya*-like grains to a host of palynological taxa, but at the same time, there is a diversity of forms (i.e. biological taxa) that share these names. Therefore, it is necessary to consider each record of these taxa individually, with critical evaluation. The lists found in appendixes A (rejected records), B (potential synonyms), and C are meant to guide future researchers as well as to provide a basis for paleoecological and paleogeographic interpretations.

Paleoecological and Floristical Significance

Living *Cathaya argyrophylla* is an evergreen conifer inhabiting ridges in mountainous regions of southwest China, where the climate is warm and humid, with a mean annual temperature of 8.1°–18.1°C and annual precipitation of 1456–1543 mm. Forests of this region are typically evergreen broad-leaved

or mixed evergreen and deciduous broad-leaved (Ying and Li 1981; Ying et al. 1983). Associated species include evergreen Fagaceae (e.g., *Castanopsis platycantha*, *Castanopsis carlesii*, *Castanopsis eyrei*, *Castanopsis fabri*, *Quercus engleriana*, *Cyclobalanopsis glauca*, *Cyclobalanopsis oxyodon*, and *Lithocarpus cleistocarpus*), Theaceae (e.g., *Schima argentea*, *Schima superba*), and many other deciduous or evergreen plants, including *Pinus kwangtungensis*, *Fokienia hodginsii*, *Clethra fabri*, *Rhododendron bachii*, *Vaccinium fimbriicalyx*, *Blastus dunnianus*, *Carrierea calycina*, *Fagus engleriana*, *Sorbus* spp., *Prunus pilosiuscula*, *Liquidambar acalycina*, and *Pterostyrax psilophyllus*, etc. (Ying et al. 1983). On the basis of its modern distribution, *Cathaya* is interpreted as an element of humid moist subtropical climate (see Strahler and Strahler 1992). Little information is available on environmental tolerance of *Cathaya* because it is rarely cultivated.

The paleoenvironment of Axel Heiberg Island during the Eocene has been reconstructed as consistent with that of the region presently occupied by *Cathaya* (Basinger et al. 1994; McIver and Basinger 1999). Nevertheless, the Eocene polar flora had a different forest aspect, as broad-leaved evergreen trees were rare or absent, so that the associated taxa in the fossil flora (see full list in McIver and Basinger 1999) is rather different from those of extant *Cathaya* communities. Basinger et al. (1994) attribute this absence of broad-leaved evergreen elements to enforced deciduousness as a result of polar winter darkness. Evidence from European megafossils of *Cathaya* supports the interpretation of *Cathaya* as a humid subtropical to warm temperate element in the Tertiary (Mai and Walther 1988; Mai 1994a; Martinetto 1995; Meller et al. 1999).

The occurrence of *Cathaya* in the Buchanan Lake flora is notable because this genus is not known from other Arcto-Tertiary floras. Moreover, it adds a new taxon to the already diverse Pinaceae in the flora; at least seven of the 10 genera of extant Pinaceae make their appearance in this Eocene flora.

Paleogeographical History

That increasing numbers of plants with eastern Asiatic affinities are being recognized in Eocene polar Canadian floras is of considerable paleogeographical significance (Lepage and Basinger 1995; McIver and Basinger 1999). This is evidence that Recent restricted or endemic distributions of these genera in eastern Asia represent remnants of once widespread taxa. Ferguson et al. (1997) discussed some general patterns of geographical evolution of eastern Asiatic paleoendemics, many of which apparently first originated in the Northern Hemisphere in or before the Paleogene, dispersed to occupy an extensive region prior to the opening of the Atlantic, and then became severely restricted as a consequence of mid- to late Tertiary paleoclimatic deterioration. Quaternary glaciation has caused retreat to what amount in many cases to refugia (Ferguson et al. 1997). The fossil record of *Cathaya* indicates such a paleogeographical pattern (app. C).

The oldest record of *Cathaya*-like pollen that we recognize is from the Aptian to Albian, Northwest Territories, Canada (Brideaux and McIntyre 1975), although we acknowledge the difficulty in evaluating the pre-Cretaceous record. According to the data we have assembled, the Cretaceous record of *Cathaya* appears to indicate a mid- to high-latitude distribution

in both North America (Pierce 1961; Tschudy 1970; Brideaux and McIntyre 1975) and eastern Asia (Zaklinskaya 1957; Khlonova 1961; Takahashi 1988). While flora exchange across Beringia between western North America and eastern Asia (Lepage and Basinger 1995) appears to have been uninhibited, the influence of the intermittent inundation of interior North America by epeiric seas is not clear (fig. 5). During the Cretaceous the Western Interior Seaway at times fully divided the North American continent, extending from the Gulf of Mexico to the Beaufort Sea in the Arctic (Hamilton 1983). Nevertheless, the Cretaceous record of *Cathaya* appears largely confined to the *Aquillapollenites* floral province (Batten 1984). Dispersal southeastward into the *Normapolles* floral province (Batten 1984) may have been restricted.

There is no known Cretaceous fossil record of *Cathaya* in Europe. The Atlantic Ocean did not begin to open until early in the Late Cretaceous (Hamilton 1983), and land bridges existed in the north between Europe and North America until well into the Tertiary (Tiffney 1994; Lepage and Basinger 1995). Nevertheless, there must have been strong paleoenvironmental barriers to dispersal of many taxa into Europe. Lepage and Basinger (1995) found a similar distribution pattern

for *Pseudolarix*, another Chinese paleoendemic conifer. *Metasequoia* is also well documented in North America and East Asia in the Cretaceous, but apparently did not reach the European continent (Mai 1994b).

Cathaya did reach Europe during the Paleogene (fig. 6), probably from North America via either of two land bridges, the DeGeer Route linking North America and Fennoscandia or the Thulian Route linking south Greenland to Europe (McKenna 1972; Lepage and Basinger 1995). This may be supported by the occurrence of *Cathaya*-like pollen in the Norwegian Sea (ODP Leg 104) at the Paleocene-Eocene boundary (Boulter and Manum 1989) that are of similar size and morphology to those from Axel Heiberg. The European fossil record of *Cathaya* and *Cathaya*-like pollen is mostly from central Europe (Knobloch et al. 1996), particularly Germany (Potonié 1934; Thiele-Pfeiffer 1988; Ashraf and Mosbrugger 1996; Nickel 1996). Dispersal of *Cathaya* westward from Asia into Europe would have been blocked by the Turgai Strait throughout most of the early Tertiary (fig. 6), although free exchange between Asian and North American floras existed via the Beringian Corridor (McKenna 1972; Lepage and Basinger 1991). *Cathaya* apparently flourished in the North American Paleo-

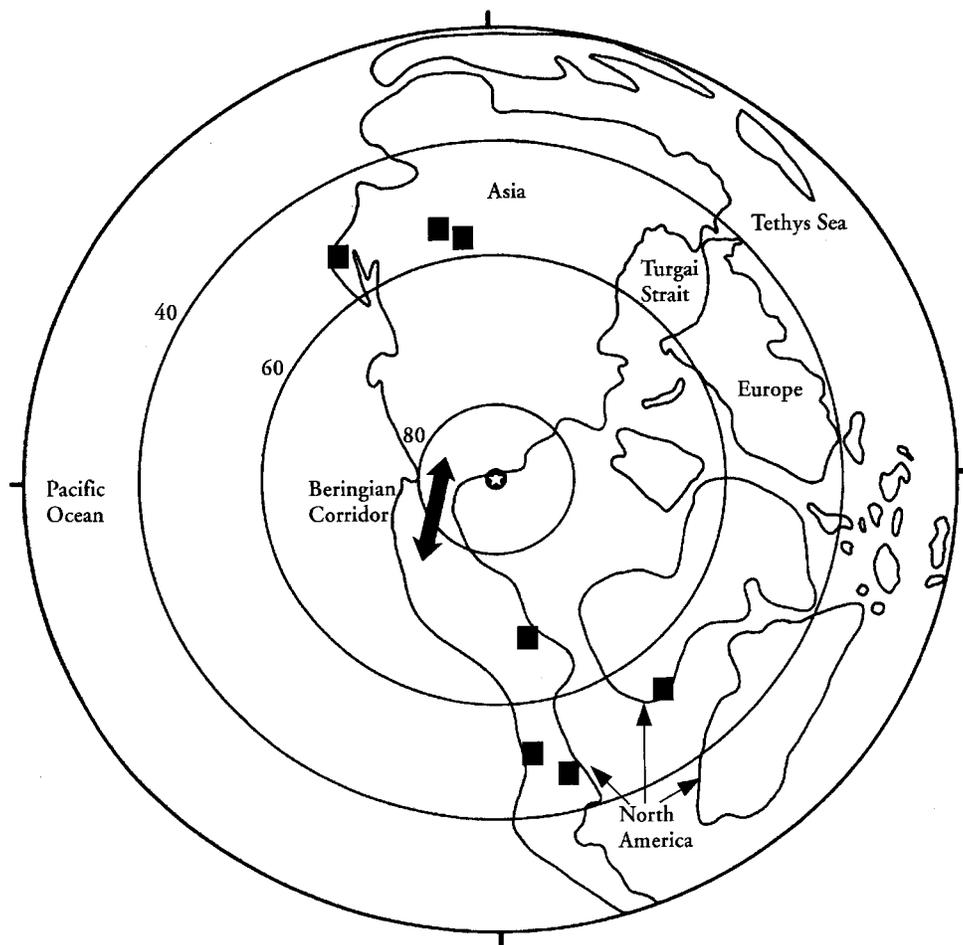


Fig. 5 Generalized paleogeographic reconstruction of Northern Hemisphere, polar projection, during the Late Cretaceous (ca. 90 million yr ago), showing occurrences of *Cathaya*-like pollen (solid squares). Star = North Pole. (Modified after Lepage and Basinger 1995.)

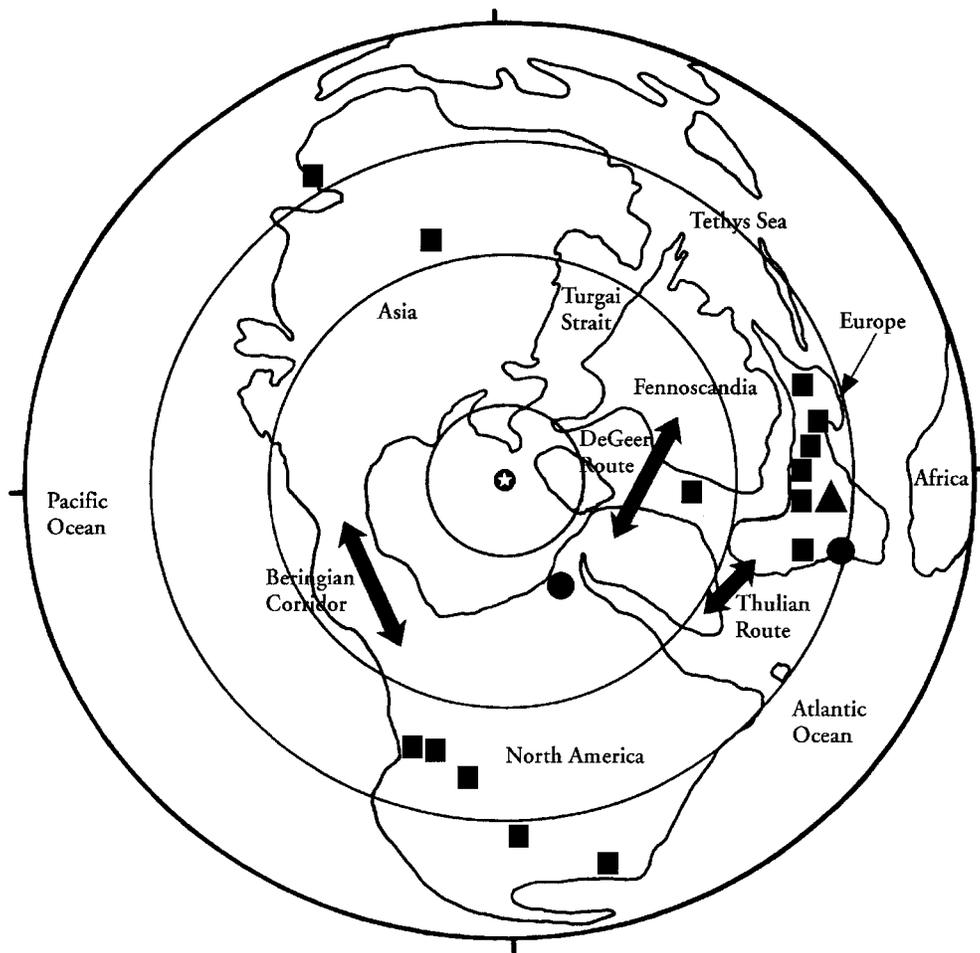


Fig. 6 Generalized paleogeographic reconstruction of Northern Hemisphere, polar projection, during the Paleogene (ca. 45 million yr ago), showing occurrences of *Cathaya gaussenii* pollen grains (solid circles), *Cathaya*-like pollen (solid squares), and megafossils of *Cathaya* spp. (triangle). Star = North Pole. (Modified after Lepage and Basinger 1995.)

gene, with records from western North America (Stanley 1965; Hopkins 1969; Rouse et al. 1970; Piel 1971), the southeastern United States (Tschudy and Van Loenen 1970; Frederiksen 1980), and the Canadian Arctic (this study). The Asiatic record of *Cathaya* is principally from the midlatitudes (Zaklinskaya 1957; Sun et al. 1989) (fig. 6).

Throughout the Neogene, *Cathaya* remained widely distributed in Asia, Europe, and North America (fig. 7). As a consequence of climatic cooling, it is likely that high-latitude land bridges may have become unavailable to *Cathaya*, a thermophilous plant, so that European, eastern Asian, and North American populations may have become isolated. Closure of the Turgai Strait in the Oligocene may have permitted floral exchange between Europe and Asia, although uplift of the Tibetan Plateau and subsequent drying of central Asia may have limited availability of this route. *Cathaya* apparently became extinct in North America during the Late Miocene (e.g., Martin and Rouse 1966; White et al. 1994) and in Europe during the Pleistocene (e.g., Lona and Ricciardi 1961). The population in Asia also was increasingly constricted during the Neogene, until during the Quaternary (e.g., Guan et al. 1989)

the genus was confined to mountainous regions of southwestern China, where it apparently escaped the most severe environmental effects of the Pleistocene Ice Age (Hu 1980).

The present relictual distribution apparently represents a remnant of the eastern Asian Tertiary population, as is also the case for *Glyptostrobus* (Florin 1963), *Metasequoia* (Chaney 1951), *Pseudolarix* (Lepage and Basinger 1995), and many others. The fossil record of *Cathaya* supports the hypothesis of Ying et al. (1993) that the origin of eastern Asian endemic genera may be attributed to the absence of extensive glaciation there during the Pleistocene, coupled with the great diversity in topography, climate, and ecological conditions that characterizes the region. These factors have combined to create an opportunity for persistence of a large number of once pan-boreal genera.

Acknowledgments

We thank Drs. Reinhard Zetter and David Ferguson for detailed discussion and invaluable advice, Dr. William Sargeant

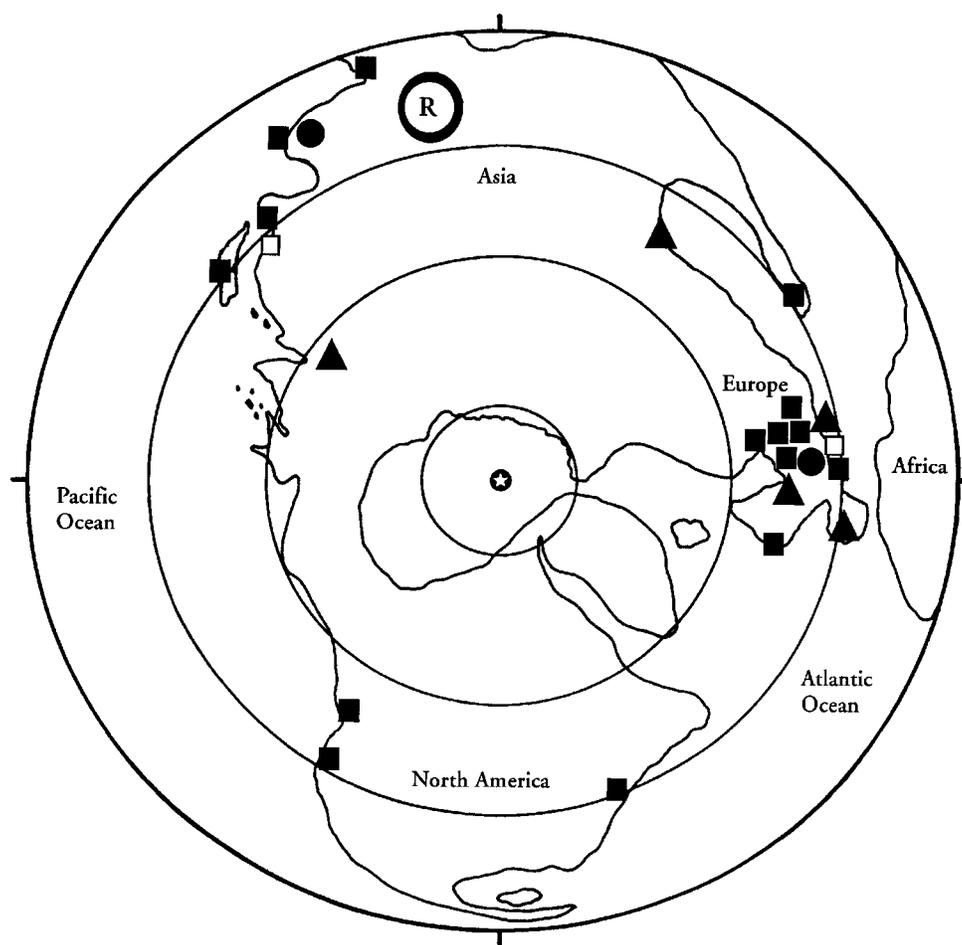


Fig. 7 Generalized paleogeographic reconstruction of Northern Hemisphere, polar projection, during the Neogene (ca. 15 million yr ago), showing occurrences of Neogene *Cathaya gausseii* pollen (solid circles), *Cathaya*-like pollen (solid squares), and megafossils of *Cathaya* spp. (triangles). Quaternary *Cathaya*-like pollen (open squares) and extant *Cathaya argyrophylla* (R) are also plotted. Star = North Pole. (Modified after Lepage and Basinger 1995.)

for providing access his library, and Dr. James White for providing information on geological age of Queen Charlotte Islands, British Columbia. Donna Postnikoff assisted with photography and Tom Bonli with SEM. This work was supported

by the Natural Sciences and Engineering Research Council of Canada IRG (0001334) and the Polar Continental Shelf Project of Natural Resources Canada (PCSP/ÉPCP publication 01599) to J. F. Basinger.

Appendix A

Rejected Fossil Records of *Cathaya*-Like Pollen Grains

1931. *Piceae-pollenites alatus* Potonié, p. 5, fig. 31 (Miocene, Germany). Attachment of sacchi to corpus not *Cathaya*-like.
1934. *Pollenites microalatus* (Potonié) Potonié: Potonié and Venitz (1934), p. 19, pl. 2, figs. 23, 24 (Miocene, Germany). Attachment of sacchi to corpus not *Cathaya*-like.
1953. *Pityosporites microalatus* (Potonié) Thomson et Pflug f. *major* (Potonié) Thomson et Pflug (in part), p. 67, figs. 50 (Middle Eocene, Helmstedter Oberflözgruppe, Germany), 52 (Eocene-Oligocene, Kassel, and Middle Oligocene–earliest Miocene, Marxheim, Germany), 54, 58 (Middle Oligocene–earliest Miocene, Kassel, Germany), 59 (Middle to Upper Pliocene, Braunkohlenlager v. Wallensen im Hils, Germany) only. Attachment of sacchi to corpus not *Cathaya*-like (figs. 50, 59) or no further comments to be made as only lateral views of the pollen illustrated (figs. 52, 54, 58).
1953. *Pityosporites microalatus* (Potonié) Thomson et Pflug f. *major* (Potonié) Thomson et Pflug (in part), p. 68, figs. 47, 48 (Danian[?]-Paleocene, Hannover, Germany), 49 (Senonian, Gradens, Germany), 55 (Middle

- Eocene, Helmstedter Oberflözgruppe, Germany), 56 (Middle Oligocene–earliest Miocene, Ville-Schoole, Germany) only. Attachment of sacci to corpus not *Cathaya*-like (fig. 55) or poor preservation (figs. 47–49, 56).
1955. *Abietinaepollenites microalatus* (Potonié) Delcourt et Sprumont, pp. 51–53, pl. 4, figs. 7a, b (Early Cretaceous, Belgium). Neither figured specimen appears to be consistent with the species concept.
1958. *Abietinaepollenites microalatus* Potonié: Couper, pp. 152–153, pl. 27, figs. 11–13 (Mesozoic, U.K.). Although figure 12 is much like *Cathaya*, the saccus lumina pattern is too coarse.
1962. *Abietinaepollenites microalatus* Potonié: Groot and Groot, p. 164, pl. 29, figs. 9, 10. (Paleocene, Maryland, U.S.A.). Because only lateral views of the pollen are preserved, it is not possible to make further comments.
1968. *Pityosporites microalatus* (Potonié) Thomson et Pflug: Elsik, p. 310, pl. 14, figs. 8–11 (Paleocene, Texas, U.S.A.). The lumina pattern of the saccus suggests that the fossils may not be related to *Cathaya*.
1968. *Pityosporites microalatus* (Potonié) Thomson et Pflug f. *major* Potonié: Nakoman (in part), p. 532, pl. 3, figs. 3, 5 only (Tertiary, Turkey). Insufficient detail available.
1969. *Abietinaepollenites microalatus microalatus* Potonié: Oltz, p. 133, pl. 40, fig. 72 (Cretaceous/Early Tertiary, Montana, U.S.A.). The specimens have much finer saccus lumina pattern than *Cathaya*.
1976. *Cathaya zagwijnii* Sivak, pp. 278, 280, pl. 19 (Oligocene–Miocene boundary, southern France). Exine sculpture is granular on corpus and saccus under SEM, with no resemblance to *Cathaya*.
1978. *Abietinaepollenites* cf. *A. microalatus microalatus* Potonié: Wilson 1978, p. 120, pl. 5, fig. 3. (Cretaceous–Paleocene boundary; Yukon and Northwest Territories, Canada). Insufficient detail available.
1978. *Cathaya* aff. *argyrophylla*, Zaklinskaya 1978, pl. 3, fig. 3 (Plio–Pleistocene, Timor). Insufficient detail available.
1985. *Abietinaepollenites microalatus* Potonié: Nagy, pp. 132–133, pl. 61, fig. 8; pl. 62, figs. 3, 4; pl. 62, figs. 5, 6 (Egerian–Pannonian, Hungary). Insufficient detail discernible on published photos.
1985. *Cathaya pulaensis* Nagy (in part), p. 134, pl. 65, figs. 4, 5 only (Upper Pannonian, Hungary). Attachment of sacci to corpus not *Cathaya*-like.
1989. *Abietinaepollenites microalatus* (Potonié) Thomson et Pflug f. *major* Potonié: Guan et al., p. 51, pl. 14, figs. 8, 9, 11, 12. Fossils lack features of *Cathaya*.
1989. *Abietinaepollenites microalatus* (Potonié) Thomson et Pflug f. *minor* Potonié, Guan et al., p. 51, pl. 14, figs. 1–7, 10, 15, 17. Fossils lack features of *Cathaya*.
1989. *Abietinaepollenites microalatus* (Potonié) Thomson et Pflug f. *major* Potonié: Sun et al. (in part), p. 45, pl. 8, fig. 12; pl. 10, fig. 1. Attachment of sacci to corpus not *Cathaya*-like.

Appendix B

Potential Synonyms of *Pityosporites microalatus* (Potonié) Thomson et Pflug

1931. *Piceae-pollenites microalatus* Potonié, p. 5, fig. 34.
1934. *Pollenites microalatus* (Potonié) Potonié, p. 49, pl. 2, fig. 4.
1935. *Pinus Haploxyylon*-type Rudolph, pp. 253, 254, 325, pl. 4, figs. 1–5, text-fig. 1c, d.
1951. *Abietinaepollenites microalatus* f. *minor* Potonié, p. 145, pl. 20, fig. 21.
1953. *Pityosporites microalatus* (Potonié) Thomson et Pflug f. *major* (Potonié) Thomson et Pflug (in part), p. 67, pl. 5, fig. 53 only.
1953. *Pityosporites microalatus* (Potonié) Thomson et Pflug f. *minor* (Potonié) Thomson et Pflug (in part), p. 68, pl. 5, figs. 51, 57 only.
1954. *Pinus* sp.: Leschik, p. 248, pl. 1, figs. 11, 12.
1957. *Pinus Haploxyylon*-type Rudolph: Rouse, p. 358, pl. 1, figs. 1, 2.
1957. *Pinus peuce* Griseb.: Macko, pp. 26–27, pl. 18, figs. 1–20; pl. 19, figs. 1–12.
1957. *Podocarpus sellowiformis* Zaklinskaya, p. 104, pl. 2, figs. 1, 2.
1957. *Podocarpus andiniformis* Zaklinskaya, p. 105, pl. 2, figs. 3–7.
1957. *Pinus protocembra* Zaklinskaya, p. 146, pl. 12, figs. 1, 2.
1959. *Pinus peuce* Griseb.: Macko, pl. 8, figs. 1–6; pl. 32, figs. 1–4.
1959. *Podocarpus* sp. 1–4: Macko, pl. 16, figs. 1–15.
1959. *Podocarpus standleyi* Buch. et Gray: Macko, pl. 2, figs. 9–12; pl. 39, figs. 5, 6.
1960. *Pinus Haploxyylon*-type Rudolph: Doktorowicz-Hrebnicka, pp. 199–200, 226, pls. 3–5, 18.
1960. *Pinus Haploxyylon*-type: Oszast, p. 15, pl. 5, figs. 3, 4.
1961. *Pinus haploxyylon*: Lona and Ricciardi, p. 95, pl. 1, fig. 2.
1961. *Pinus trivialis* (Naumova) Bolchovitina: Khlonova, pp. 61, 62, pl. 10, figs. 59, 59a.
1961. *Pinus insignis* (Naumova) Bolchovitina: Khlonova, p. 62, pl. 10, figs. 60, 60a.
1961. *Pinus subconcinna* (Naumova) Bolchovitina: Khlonova, pp. 62, 63, pl. 10, figs. 61, 61a.
1961. *Punctabivesiculites crassus* Pierce, p. 37, pl. 2, fig. 47.
1964. *Pinus* sp. *Haploxyylon*-type: Gray, pl. 1, fig. 3.
1965. *Pinus semicircularis* Stanley, pp. 277–278, pl. 39, figs. 8–10; pl. 40, figs. 1–7.
1966. *Pinus* sp.: Martin and Rouse (in part), pp. 191–192, fig. 45 only.
1968. *Pityosporites microalatus* (Potonié) Thomson et Pflug f. *minor* (Potonié) Thomson et Pflug: Nakoman (in part), p. 532, pl. 3, figs. 2, 6 only.
1968. *Pityosporites libellus* (Potonié) Nakoman, no description, pl. 4, figs. 1, 2.
1968. *Pityosporites subtiliexinatus* Trevisan: Kedves, pp. 324–325, pl. 1, fig. 45, pl. 2, figs. 1–5.
1969. *Pinus* sp. *Haploxyylon*-type: Hopkins, p. 1115, figs. 53,

- 54.
1969. *Pityosporites microalatus* (Potonié) Thomson et Pflug f. *minor* (Potonié) Thomson et Pflug: Kedves, p. 24, pl. 11, fig. 2.
1969. *Pityosporites microalatus* (Potonié) Thomson et Pflug f. *major* (Potonié) Thomson et Pflug: Kedves, p. 24, pl. 11, fig. 1.
1970. *Abietinaepollenites* sp.: Tschudy and Van Loenen, pl. 2, fig. 4.
1970. *Pinus Haploxylon*-type: Boulter and Chaloner, pp. 72–73, pl. 3, fig. F.
1970. cf. *Pinus semicircularis* Stanley: Tschudy, pl. 4, fig. 2.
1970. *Pinus strobipites* Wodehouse: Rouse et al. (in part), pl. 7, fig. 4 only.
1971. *Pinus* sp. 1 cf. *P. peuce* Griesb.: Piel, pp. 1902–1903, pl. 8, fig. 53.
1971. *Pityosporites microalatus* (Potonié) Thomson et Pflug: Krutzsch, pp. 48–51, pl. 1, figs. 1–19.
1971. *Pityosporites alatus* (Potonié) Thomson et Pflug: Krutzsch (in part), pp. 51–52, pl. 2, figs. 2, 3, 5, 7–10 only.
1971. *Pityosporites* sp. B: Krutzsch (in part), p. 56, pl. 4, figs. 5–8 only.
1971. *Podocarpidites libellus* (Potonié) Krutzsch, p. 128, pl. 32, figs. 1–15.
1971. *Podocarpidites podocarpoides* (Thiergart) Krutzsch, p. 130, pl. 33, figs. 1–11.
1974. *Pityosporites microalatus* (Potonié) Thomson et Pflug: Nghia, p. 58, pl. 7, figs. 8, 9.
1974. *Pinus tenuextima* Traverse: Takeuti, p. 106, pl. 1, figs. 3, 4.
1975. *Alisporites grandis* (Cookson) Dettmann: Brideaux and McIntyre, p. 16, pl. 3, fig. 29.
1978. *Pityosporites microalatus* (Potonié) Thomson et Pflug: Hochuli, p. 66, pl. 7, fig. 7.
1980. *Pityosporites microalatus* (Potonié) Thomson et Pflug: Chateauneuf, p. 88; Thiele-Pfeiffer, pp. 115–116, pl. 6, fig. 2.
1980. *Pityosporites alatus* (Potonié) Thomson et Pflug: Chateauneuf, p. 88, pl. 4, fig. 9; Thiele-Pfeiffer, p. 116, pl. 6, fig. 1.
1980. *Podocarpus? cappulatus* Frederiksen, pp. 34–35, pl. 4, figs. 17, 18.
1984. *Cathaya antiqua* Klaus, p. 318, pl. 8, figs. 8, 11, 12.
1985. *Abietinaepollenites microalatus* f. *minor* Potonié: Song et al., p. 81, pl. 24, figs. 15–18.
1985. *Cathaya gaussenii* Sivak: Nagy, pp. 133–134, pl. 64, figs. 2–7.
1985. *Cathaya pseudocristata* (Doktorowicz-Hrebnicka 1960) Nagy, p. 134, pl. 64, figs. 8, 9.
1985. *Cathaya pulaensis* Nagy (in part), p. 134, pl. 65, figs. 1–3 only.
1985. *Pinus Haploxylon*-type: Herter, p. 21, pl. 2, fig. 3.
1987. *Podocarpidites gracilis* Zheng, p. 612, pl. 2, figs. 1–4.
1987. *Podocarpidites* cf. *nageiaformis* (Zakl.) Krutzsch: Zheng (in part), pp. 612–613, pl. 2, fig. 21 only.
1988. *Pityosporites bisaccus* (Rouse) Takahashi, pp. 109, 110, pl. 14, fig. 8.
1988. *Pityosporites microalatus* (Potonié) Thomson et Pflug: Thiele-Pfeiffer, pp. 14–15, pl. 5, fig. 6.
1989. *Abietinaepollenites microalatus* f. *minor* Potonié: Sun et al. (in part), p. 45, pl. 10, figs. 4, 6 only.
1989. K BASIC SMALL BODY: Boulter and Manum, p. 675, pl. 3, figs. 1, 7, 9.
1989. K BASIC STRAIGHT: Boulter and Manum, p. 675, pl. 3, figs. 5, 11, 14.
1989. *Podocarpidites andiniformis* (Zakl.) Takahashi: Guan et al. (in part), p. 57, pl. 15, figs. 3, 4 only.
1994. *Abietinaepollenites baileyanus* (Traverse) Zhu: Traverse, p. 277, pl. 1, fig. 9.
1994. *Abietinaepollenites microalatus* Potonié ex Delcourt et Sprumont: Traverse, p. 277, pl. 1, fig. 10.
1994. *Pinuspollenites tenuextimus* (Traverse 1955) Traverse, p. 277, pl. 1, fig. 11.
1994. *Podocarpidites gracilis* Zheng: Zheng and Wang, pl. 1, fig. 15.
1996. *Pityosporites microalatus* (Potonié) Thomson et Pflug: Nickel, p. 33, pl. 7, figs. 9, 10.

Appendix C

Records of *Cathaya* and *Cathaya*-Like Fossils

- I. *Megafossils*: Chun and Kuang (1958) recognized one fossil species of *Cathaya*, *C. loehrii* (Engelhardt and Kinkel in 1908) Chun et Kuang, on the basis of fossil seed cones from Germany. Farjon (1992) documents the nomenclatural problems associated with this assignment, including reference to the original description of the type material by Geyler and Kinkel in (1887). Nevertheless, Farjon rejects this taxon as valid, and furthermore points out that the type material is lost, and in any event appears to have been more similar to *Pseudotsuga* than *Cathaya*. We follow the recommendation of Farjon and exclude this taxon from consideration.
- A. Oligocene:
1. *Cathaya* sp. Leaves: Late Oligocene; Kleinsaubernitz, Bautzen, eastern Germany (Walther 1999).
- B. Miocene:
1. *Cathaya roselti* Schneider. Leaves: Middle Miocene; Bluno, Niederlausitz, Germany (Schneider 1981; see also synonymy therein).
 2. *Cathaya bergeri* (Kirchheimer) Schneider. Leaves: Wiesa, Germany (Schneider 1981). Leaves and seed cones: Lower Miocene; Lusatica region, Saxony and Brandenburg, Germany (Mai 1999).
- C. Pliocene:
1. *Cathaya* sp. Seed cones: Miocene or Pliocene; Aldan River Valley, eastern Siberia, ca. latitude 62° (Florin 1963). Seed cones: Pliocene, Thüringen, Germany (Mai and Walther 1988).
 2. *Cathaya abchasica* Svehnikova. Leaves: Pliocene; east of Black Sea, Russia (Svehnikova 1964). Leaves: Pliocene; Thüringen, Germany (Mai and Walther 1988).

3. *Cathaya europaea* Svechnikova. Seed cones: Pliocene; east of Black Sea, Russia (Svechnikova 1964).
 4. *Cathaya bergeri* (Kirchheimer) Schneider. Gregor (1990) reported this species in floral lists for Spain and Italy.
 5. *Cathaya van-der-burghii* Gossmann. Seed cones: Pliocene; Bergheim/Niederrheinische Bucht, Germany (Gossmann 1991). Seed cones: Late Pliocene; Toskana, Italy (Mai 1994a). Seed cones: Pliocene; Piemonte, northwestern Italy (Martinetto 1995).
- II. *Pollen*: Pollen records below list names as applied by original authors. We consider all of these reports to be assignable to either the form taxon *Pityosporites microalatus* or to *Cathaya gausenii*, where warranted. Within categories, reports are listed from oldest to youngest.
- A. Cretaceous:
1. Asia:
 - a. *Pinus trivialis*, *P. insignis*, and *P. subconcinna*. Western Siberia, Russia. Cretaceous (Khlonova 1961).
 - b. *Podocarpus andiniformis* and *P. sellowiformis*. Pavlodar Irtysh Basin, Russia. Upper Cretaceous (Zaklinskaya 1957).
 - c. *Pityosporites bisaccus*. Honshu, Japan. Futaba Group, Tamayama Formation, Coniacian (Upper Cretaceous) (Takahashi 1988).
 2. North America:
 - a. *Alisporites grandis*. Horton River, District of Mackenzie, Canada. Aptian-Albian (Brideaux and McIntyre 1975).
 - b. *Pinus Haploxyylon*-type. Vancouver Island, western Canada. Comox Formation, Upper Cretaceous (Rouse 1957).
 - c. *Punctabivesiculites crassus*. Minnesota, U.S.A. Lower Upper Cretaceous (Dakota Group) (Pierce 1961).
 - d. cf. *Pinus semicircularis*. Montana, U.S.A. Tullock Member of Hell Creek Formation and Fort Union Formation, Cretaceous-Tertiary boundary (Tschudy 1970).
- B. Paleogene:
1. Asia:
 - a. *Abietinaepollenites microalatus* f. *minor*. Continental Shelf of East China Sea, China. Lower member of Linfeng Formation, Lower Paleocene (Sun et al. 1989).
 - b. *Pinus protocembra*. Pavlodar Irtysh Basin, Pavlodar City, Russia. Upper horizon of Lower Oligocene (Zaklinskaya 1957).
 2. North America:
 - a. *Pinus semicircularis*. Harding County, South Dakota, U.S.A. Cannonball Member, Fort Union Formation, Paleocene (Stanley 1965).
 - b. *Pinus* sp. *Haploxyylon*-type. Southwest British Columbia, Canada. Kitsilano Formation, Eocene (Hopkins 1969).
 - c. *Pinus strobipites*. British Columbia and adjacent Alberta, Canada. Middle Eocene (Rouse et al. 1970).
 - d. *Podocarpus? cappulatus*. Mississippi and western Alabama, U.S.A. Upper Eocene (Frederiksen 1980).
- e. *Abietinaepollenites* sp. (Diploxyylon type). Yazoo City, Mississippi, U.S.A. Upper Eocene (Tschudy and Van Loenen 1970).
- f. *Pinus* sp. 1, cf. *P. peuce*, and *Podocarpus* cf. *nubigenus*. British Columbia, Canada. Oligocene (Piel 1971).
3. Europe:
 - a. *Pityosporites subtilixinatus*. Paris Basin, France. Paleogene (Kedves 1968).
 - b. K BASIC SMALL BODY and K BASIC STRAIGHT. ODP Leg 104 in Norwegian Sea (Brito-Arctic igneous province flora). Paleocene-Eocene boundary (Boulter and Manum 1989).
 - c. *Pollenites microalatus*. Geiselal, Germany. Middle Eocene (Potonié 1934).
 - d. *Pityosporites microalatus* and *P. alatus*. Paris Basin, France. Eocene (Chateauneuf 1980).
 - e. *Pityosporites microalatus*. Messel, Darmstadt, western Germany. Middle Eocene (Thiele-Pfeiffer 1988).
 - f. *Pityosporites microalatus* f. *minor* and *P. microalatus* f. *major*. Dudar Coal Basin, Hungary. Middle Eocene (Kedves 1969).
 - g. *Pityosporites microalatus*. Messel, Darmstadt, western Germany. Middle Eocene (Thiele-Pfeiffer 1988).
 - h. *Pityosporites microalatus*. Upper Rhine Graben, western Germany. Upper Eocene–Middle Oligocene (Nickel 1996).
 - i. *Pityosporites microalatus* and *P.* sp. Tongrube Öbel NO, Netherlands. Upper Oligocene (Krutzsch 1971).
 - j. *Cathaya erdtmanii*, *C. van campoeae*, *C. gausenii*, *C. krutzschii*, *C. wilsonii*, *C. potonieii*, *C. scheuringii*, *C. uenoi*, *C. millayi*, *C. ponsii*, and *C. tingii*. Escornebeou, southwestern France. Oligocene-Miocene boundary (Sivak 1976).
 - k. *Pityosporites microalatus*. Central and western Paratethys region. Oligocene–early Miocene (Hochuli 1978).
- C. Neogene:
1. Asia:
 - a. *Cathaya zhejiangensis*. Ninghai County, Zhejiang Province, east China. Miocene (Liu et al. 1997).
 - b. *Pityosporites microalatus* f. *minor* and *P. libellus*. Seyitömer region, Turkey. Miocene (Nakoman 1968).
 - c. *Podocarpidites gracilis* and *P.* cf. *nageiaformis*. Zhangpu County, Fujian Province, southeast China. Middle–Late Miocene (Zheng 1987; Zheng and Wang 1994).
 - d. *Abietinaepollenites microalatus* f. *minor*. Shelf Basin of East China Sea, China. Heilongjing, Yuquan, and Santan Formations, Mio-Pliocene (Song et al. 1985).
 - e. *Pinus tenuextima*. Ichinoseki City, Iwate Prefecture, Japan. Kazawa Formation, Late Pliocene (Takeuti 1974).
 - f. *Podocarpidites andiniformis*. Central and eastern Bohai Sea, China. Guantao and Pingyuan Formations, Lower Miocene–Pleistocene (Guan et al.

- 1989).
2. North America:
 - a. *Abietinaepollenites baileyanus*, *A. microalatus*, and *Pinuspollenites tenuextimus*. Brandon Lignite, Vermont, U.S.A. Middle Early Miocene (Traverse 1994).
 - b. *Pinus* sp. *Haploxylon*-type. Oregon, U.S.A. Miocene (Gray 1964).
 - c. *Pinus* sp. Queen Charlotte Islands, British Columbia, Canada. Skonun Formation, Late Miocene (Martin and Rouse 1966; White et al. 1994).
 3. Europe:
 - a. *Pinus peuce*. Gliwice, Upper Silesia, Poland. Lower Miocene (Macko 1957); Lower Silesia, Poland. Miocene (Macko 1959).
 - b. *Cathaya* sp. Oberdorf, western Styria, Austria. Lower Miocene (Meller et al. 1999).
 - c. *Podocarpus* sp. 1–4 and *P. standleyi*. Lower Silesia, Poland. Miocene (Macko 1959).
 - d. *Podocarpidites libellus* and *P. podocarpoides*. Niderrheinisches Hauptfloe, Germany. Miocene (Krutzsch 1971).
 - e. *Pityosporites microalatus* and *P. alatus*. Wackersdorf/Oberpfalz, Germany. Miocene (Thiele-Pfeiffer 1980).
 - f. *Pityosporites microalatus*. Wallensen, Germany. Miocene (Thomson and Pflug 1953).
 - g. *Pityosporites alatus*. Ville, Rhein, Braunkohle, Germany. Miocene (Thomson and Pflug 1953).
 - h. *Pinus Haploxylon*-type. Upper Silesia, Poland. Miocene (Oszast 1960).
 - i. *Pinus Haploxylon*-type. Central Poland. Miocene (Doktorowicz-Hrebicka 1960).
 - j. *Cathaya gausсенii*, *C. pseudocristata*, and *C. pulaensis*. Hungary. Eger Formation, Miocene (Nagy 1985).
 - k. *Piceae-pollenites microalatus* and *P. alatus*. Grube Babina bei Muskau, Germany. Middle Miocene (Potonié 1931).
 - l. *Pinus Haploxylon*-type. Nowy Targ–Orawa Basin, West Carpathians, Poland. Upper Miocene (Nghia 1974).
 - m. *Pityosporites microalatus*. Lower Rhine Embayment, northwest Germany. Middle Miocene to Pliocene (Ashraf and Mosbrugger 1996).
 - n. *Pinus Haploxylon*-type. Schosnitz, Poland and Bohemia, Czech Republic. Upper Miocene and Pliocene, respectively (Rudolph 1935).
 - o. *Cathaya antiqua*. Lavanttal (Carinthia), Austria. Lower Sarmatian (Miocene) (Klaus 1984).
 - p. *Pityosporites microalatus* and *P. alatus*. Frechen and Fortuna Garsdorf, Germany. Upper Miocene–Lower Pliocene (Mohr 1984).
 - q. *Pinus* sp. Hünfeld/Hessen, Germany. Pliocene (Leschik 1954).
 - r. *Pinus Haploxylon*-type. Derbyshire, England. Pliocene (Boulter and Chaloner 1970).
 - s. *Pinus Haploxylon*-type. Horloff-Graben/Wetterau, Frankfurt am Main, Germany. Pliocene-Pleistocene (Herter 1985).
 - D. Quaternary:
 1. Asia:
 - a. *Podocarpidites andiniformis*. Central and eastern Bohai Sea, China. Pingyuan Formation, Pleistocene (Guan et al. 1989).
 2. Europe:
 - a. *Pinus Haploxylon*-type. Perugia, near Roma, Italy. Pleistocene (Lona and Ricciardi 1961).

Literature Cited

- Ashraf AR, V Mosbrugger 1996 Palynologie und Palynostratigraphie des Neogens der Niederrheinischen Bucht. Teil 2. Pollen. Palaeontogr Abt B 241:1–98.
- Bagnell CR Jr 1975 Species distinction among pollen grains of *Abies*, *Picea* and *Pinus* in the Rocky Mountain area (a scanning electron microscope study). Rev Palaeobot Palynol 19:203–220.
- Basinger JF 1991 The fossil forests of the Buchanan Lake Formation (Early Tertiary), Axel Heiberg Island, Canadian Arctic Archipelago: preliminary floristics and paleoclimate. Pages 39–65 in RL Christie, NJ McMillan, eds. Tertiary fossil forests of the Geodetic Hills, Axel Heiberg Island, Arctic Archipelago. Bull Geol Surv Can, vol 403.
- Basinger JF, DR Greenwood, T Sweda 1994 Early Tertiary vegetation of Arctic Canada and its relevance to paleoclimatic interpretation. Pages 175–198 in MC Boulter, HC Fisher, eds. Cenozoic plants and climates of the Arctic. NATO ASI series 1: global environmental change. Springer, Berlin.
- Batten DJ 1984 Palynology, climate, and the development of Late Cretaceous floral provinces in the Northern Hemisphere: a review. In PJ Brenchley, ed. Fossils and climate, special issue, Geol J 11: 127–163.
- Birks HJB 1978 Geographic variation of *Picea abies* (L.) Karsten pollen in Europe. Grana 17:149–160.
- Boulter MC, WG Chaloner 1970 Neogene fossil plants from Derbyshire (England). Rev Palaeobot Palynol 10:61–78.
- Boulter MC, DL Craig 1979 A Middle Oligocene pollen and spore assemblage from the Bristol Channel. Rev Palaeobot Palynol 28: 259–272.
- Boulter MC, SB Manum 1989 The Brito-Arctic igneous province flora around the Palaeocene/Eocene boundary. Proc Ocean Drilling Prog, Sci Results 104:663–680.
- Brideaux WW, DJ McIntyre 1975 Miospores and microplankton from Aptian-Albian rocks along Horton River, District of Mackenzie. Bull Geol Surv Can 252:1–85.
- Caratini C, M Van Campo, J Sivak 1972 Pollen de *Cathaya* (Abietaceae) au Tertiaire en France. Pollen Spores 14:169–172.
- Chaney RW 1951 A revision of fossil *Sequoia* and *Taxodium* in western North America based on the recent discovery of *Metasequoia*. Trans Am Philos Soc, NS, 40:171–263.
- Chateaufort JJ 1980 Palynostratigraphie et paleoclimatologie de l'éocène supérieur et de l'oligocène du Bassin de Paris (France). Thèse de Doctorat d'état ès Sciences Naturelles, Université Pierre et Marie Curie, Paris VI. Bureau de Recherches Géologiques et Minières, Mémoire du B.R.G.M. 116. 360 pp, 31 pls.
- Chun WY, KZ Kuang 1958 Genus novum Pinacearum ex Sina australi et occidentali. Bot Zh 43:461–470. (In Russian.)
- Couper RA 1958 British Mesozoic microspores and pollen grains: a systematic and stratigraphic study. Palaeontogr Abt B 103:75–179.
- Delcourt A, G Sprumont 1955 Les spores et grains de pollen du Wealdien du Hainaut. Soc Belg Geol Paleontol Hydrol Mem, NS 4, 5: 5–73.

- Doktorowicz-Hrebnicka J 1957 Index pollen spectra of Pliocene coal-bearing sediments. *Inst Geol Pr* 15:87–136.
- 1960 Correlation of brown coal seams from the provinces of Poznan and Bydgoszcz. *Biul Inst Geol* 157:69–133 (in Polish), 222–243 (in English).
- Eberle JJ, JE Storer 1999 Northernmost record of brontotheres, Axel Heiberg Island, Canada: implications for age of the Buchanan Lake Formation and brontothere paleobiology. *J Paleontol* 73:979–983.
- Elsik WC 1968 Palynology of a Paleocene Rockdale lignite, Milam County, Texas. I. Morphology and taxonomy. *Pollen Spores* 10:263–314.
- Engelhardt H, F Kinkelin 1908 Oberpliozäne Flora und Fauna des Untermainales, insbesondere des Frankfurter Klärbeckens. II. Unterdiluviale Flora von Hainstadt am Main. *Abh Senckenb Natforsch Ges* 29:150–306.
- Erdtman G 1943 An introduction to pollen analysis. *Chronica Botanica*, Waltham, Mass. 239 pp.
- 1963 Palynology and Pleistocene ecology. Pages 367–375 in Á Löve, D Löve, eds. *North Atlantic biota and their history*. Macmillan, New York.
- 1965 Pollen and spore: morphology and plant taxonomy. *Gymnospermae, Bryophyta: an introduction to palynology*. Vol 3. Almqvist & Wiksell, Stockholm. 191 pp.
- Farjon A 1990 *Pinaceae: drawings and descriptions of the genera*. Koeltz Scientific, Königstein. 330 pp.
- 1992 *Cathaya loebrii*, a misnomer for a Pliocene conifer cone. *Taxon* 41:721–723.
- Felix CJ, PP Burdridge 1973 A Maastrichtian age microflora from Arctic Canada. *Geosci Man* 7:1–30.
- Ferguson DK, YS Liu, R Zetter 1997 The paleoendemic plants of East Asia: evidence from the fossil record for changing distribution patterns. Pages 359–371 in NG Jablonski, ed. *The changing face of East Asia during the Tertiary and Quaternary*. Centre of Asian Studies, University of Hong Kong, Hong Kong.
- Ferguson DK, M Pinggen, R Zetter, C-C Hofmann 1998 Advances in our knowledge of the Miocene plant assemblage from Kreuzau, Germany. *Rev Palaeobot Palynol* 101:147–177.
- Florin R 1963 The distribution of conifer and taxad genera in time and space. *Acta Horti Bergiani* 20:121–312.
- Frederiksen NO 1980 Sporomorphs from the Jackson Group (Upper Eocene) and adjacent strata of Mississippi and western Alabama. Professional paper 1084, US Geological Survey. 75 pp.
- Geyler T, F Kinkelin 1887 Oberpliocän-Flora aus den Baugruben des Klärbeckens bei Niederrad und der Schleuse bei Höchst a. M. *Abh Senckenb Natforsch Ges* 15:1–49.
- Gossmann R 1991 Die Gattung *Cathaya* im rheinischen Jungtertiär. Paper presented at the Pan-European Paleobotanical Conference, Vienna, September 19–23.
- Gray J 1964 Northwest American Tertiary palynology: the emerging picture. Pages 21–30 in *Ancient Pacific floras*. University of Hawaii Press, Honolulu.
- Gregor H-J 1990 Contributions to the Late Neogene and Early Quaternary flora history of the Mediterranean. *Rev Palaeobot Palynol* 62:309–338.
- Groot JJ, CR Groot 1962 Some plant microfossils from the Brightseat Formation (Paleocene) of Maryland. *Palaeontogr Abt B* 111:161–173.
- Guan XT, HP Fan, ZC Song, YH Zheng 1989 Researches on late Cenozoic palynology of the Bohai Sea. Nanjing University Press, Nanjing. 152 pp. (In Chinese.)
- Hamilton W 1983 Cretaceous and Cenozoic history of the northern continents. *Ann Mo Bot Gard* 70:440–458.
- Hansen BS, EJ Cushing 1973 Identification of *Pinus* pollen of Quaternary age from the Chuska Mountains, New Mexico. *Bull Geol Soc Am* 84:1181–1200.
- Herter G 1985 Palynologische Untersuchungen der Pliozän/Pleistozän grenzsichten und eines (?prä-elsterzeitlichen) Interglazials im Horloff-Graben/Wetterau. *Palaeontogr Abt B* 195:1–128.
- Hochuli PA 1978 Palynologische Untersuchungen im Oligozän und Untermiozän der Zentralen und Westlichen Paratethys. *Beitr Palaeontol Oesterr* 4:1–132.
- Hopkins WS Jr 1969 Palynology of the Eocene Kitsilano Formation, southwest British Columbia. *Can J Bot* 47:1101–1131.
- Hu SY 1980 *The Metasequoia* flora and its phytogeographic significance. *J Arnold Arbor Harv Univ* 61:41–94.
- Hu YS, FH Wang 1984 Anatomical studies of *Cathaya* (Pinaceae). *Am J Bot* 71:727–735.
- Kedves M 1968 Études palynologiques des couches du tertiaire inférieur de la région parisienne. III. Pollens inaperturés, à ballonnets, polypliés, monocépés, disulqués, trichotomosulqués et proxaperturés. *Pollen Spores* 10:315–334.
- 1969 Palynological studies on Hungarian Early Tertiary deposits. Hungarian Academy of Sciences, Budapest. 22 pls., 84 pp.
- 1982 Palynology of the Thanetian layers of Menat. *Palaeontogr Abt B* 182:87–150.
- Khlonova AF 1961 Spory i pyl'tsa verkhnei poloviny verkhnego mela vostochnoi chasti zapadno-sibirskoi nizmennosti (Spores and pollen grains from upper part of upper Cretaceous, eastern of west Siberia). *Izd-vo Sibirskogo otd-niia AN SSSR, Novosibirsk*. 138 pp. (In Russian.)
- Klaus W 1977 Forschungsschwerpunkte der Paläobotanik und Palynologie der Universität Wien. *Rev Palaeobot Palynol* 23:303–330.
- 1978 On the taphonomic significance of tectonic sculpture characters in alpine *Pinus* species. *Grana* 17:161–166.
- 1984 Zur Mikroflora des Unter-Sarmat am Alpen-Südosstrand. *Beitr Palaentol Oesterr* 11:289–419.
- 1987 Einführung in die Paläobotanik. *Fossile Pflanzenwelt und Rohstoffbildung*, Band 1. Franz Deuticke, Wien. 314 pp.
- Knobloch E, M Konzalová, Z Kvaček 1996 Die obereozäne Flora der Staré Sedlo-Schichtenfolge in Böhmen (Mitteleuropa). *Rozpr Cesk Geol Ustavu*, vol 49. 260 pp, 64 pls.
- Kovar-Eder J, B Meller, R Zetter 1998 Comparative investigations on the basal fossiliferous layers at the opencast mine Oberdorf (Köflach-Voitsberg lignite deposit, Styria, Austria; Early Miocene). *Rev Palaeobot Palynol* 101:125–145.
- Krutzsch W 1971 Atlas der mittel- und jungtertiären dispersen Sporen- und Pollen- sowie der Mikroplankonformen des nördlichen Mitteleuropas. Lieferung 6. Coniferenpollen (Saccites und "Inaperturates"). Fischer, Jena. 234 pp.
- Lepage BA, JF Basinger 1991 Early Tertiary *Larix* from the Buchanan Lake Formation, Canadian Arctic Archipelago, and a consideration of the phytogeography of the genus. Pages 67–81 in RL Christie, NJ McMillan, eds. *Tertiary fossil forests of the Geodetic Hills, Axel Heiberg Island, Arctic Archipelago*. *Bull Geol Surv Can*, vol 403.
- 1995 Evolutionary history of the genus *Pseudolarix* Gordon (Pinaceae). *Int J Plant Sci* 156:910–950.
- Leschik G 1954 Die oberpliozäne Flora von Hünfeld (Hessen). *Senckenb Lethaea* 35:247–262.
- Liu YS, SX Guo, DK Ferguson 1996 Catalogue of Cenozoic megafossil plants in China. *Palaeontogr Abt B* 238:141–179.
- Liu YS, R Zetter, DK Ferguson 1997 Fossil pollen grains of *Cathaya* (Pinaceae) in the Miocene of eastern China. *Meded Ned Inst Toegepaste Geowetensch TNO* 58:227–236.
- Lona R, E Ricciardi 1961 Studio pollinologico stratigrafico su una serie lacustre pleistocenica dell' Italia centrale (Bacino di Gubbio, Perugia). *Pollen Spores* 3:93–100.
- Macko S 1957 Lower Miocene pollen flora from the valley of Klodnica near Gliwice (Upper Silesia). *Trav Soc Sci Lett Wroclaw, Ser B*, 88:1–313.
- 1959 Pollen grains and spores from Miocene brown coals in Lower Silesia. I. *Prace Wroclawskiego Towarzystwa Naukowego. Trav Soc Sci Lett Wroclaw, Ser B*, 96:1–178.

- Mai DH 1994a Fossile Koniferenreste in der meridionalen Zone Europas. Feddes Repert 105:207–227.
- 1994b Two conifers—*Tetraclinis* Mast. (Cupressaceae) and *Metasequoia* Miki (Taxodiaceae): relicts or palaeoclimatic indicators of the past. Pages 199–213 in MC Boulter, HC Fisher, eds. Cenozoic plants and climates of the Arctic. NATO ASI series 1: global environmental change. Springer, Berlin.
- 1999 Die untermiozänen Floren aus der Spremberger Folge und dem 2. Flözhorizont in der Laustiz. Teil I. Farnpflanzen, Koniferen und Monokotyledonen. Palaeontogr Abt B 250:1–76.
- Mai DH, H Walther 1988 Die pliozänen Floren von Thüringen, Deutsche Demokratische Republik. Quartärpaläontologie 7:55–297.
- Martin HA, GE Rouse 1966 Palynology of Late Tertiary sediments from Queen Charlotte Islands, British Columbia. Can J Bot 44: 171–208.
- Martinetto E 1995 Chronological and paleoenvironmental meaning of plant macrofossils in the stratigraphical framing of the “Villafranchiano” unit in some districts of the Piemonte region (NW Italy). PhD diss. Dipartimento di Scienze della Terra, Università degli Studi di Torino.
- McAndrews JH, AA Berti, G Norris 1973 Key to the Quaternary pollen and spores of the Great Lakes Region. Royal Ontario Museum, Life Sciences, Miscellaneous Publication, Toronto. 61 pp.
- McIntyre DJ 1991 Pollen and spore flora of an Eocene High Arctic forest, eastern Axel Heiberg Island, N.W.T. Pages 83–97 in RL Christie, NJ McMillan, eds. Tertiary fossil forests of the Geodetic Hills, Axel Heiberg Island, Arctic Archipelago. Bull Geol Surv Canada, vol 403.
- McIver EE, JF Basinger 1999 Early Tertiary floral evolution in the Canadian High Arctic. Ann Mo Bot Gard 86:523–545.
- McKenna MC 1972 Was Europe connected directly to North America prior to the middle Eocene? Pages 179–189 in T Dobzhansky, MK Hecht, WC Steere, eds. Evolutionary biology. Vol 6. Appleton-Century-Crofts, New York.
- Meller B, J Kovar-Eder, R Zetter 1999 Lower Miocene leaf, palynomorph, and diaspore assemblages from the base of the lignite-bearing sequence in the opencast mine Oberdorf, N Voitsberg (Styria, Austria) as an indication of “Young Mastixoid” vegetation. Palaeontogr Abt B 252:123–179.
- Mohr BAR 1984 Die Mikroflora der Obermiozänen bis Unterpliozänen Deckschichten der Rheinischen Braunkohle. Palaeontogr Abt B 191:29–133.
- Moore PD, JA Webb, ME Collinson 1991 Pollen analysis. 2d ed. Blackwell Scientific, Oxford. 216 pp.
- Nagy E 1985 Sporomorphs of the Neogene in Hungary. Geol Hung Ser Palaeontol, vol 47. 471 pp.
- Nakoman E 1968 Contribution à l'étude de la microflore tertiaire des lignites de Seyitömer (Turquie). Pollen Spores 10:521–556.
- Nghia TD 1974 Palynological investigation of Neogene deposits in the Nowy Targ–Orawa Basin (west Carpathians, Poland). Acta Palaeobot 15:46–81.
- Nickel B 1996 Palynofazies und Palynostratigraphie der Pechelbronn Schichten im nördlichen Oberrheinalgraben. Palaeontogr Abt B 240:1–151.
- Oltz DF Jr 1969 Numerical analyses of palynological data from Cretaceous and Early Tertiary sediments in east central Montana. Palaeontogr Abt B 128:90–166.
- Oszast J 1960 Pollen analysis of Tortonian clays from Stare Gliwice in Upper Silesia, Poland. Monogr Bot 9:3–47.
- Pant DD, N Basu 1977 A comparative study of *Cathaya argyrophylla* Chun et Kuang and three species of *Keteleeria* Carrier. Bot J Linn Soc 75:271–282.
- Piel KM 1971 Palynology of Oligocene sediments from central British Columbia. Can J Bot 49:1885–1920.
- Pierce RL 1961 Lower Upper Cretaceous plant microfossils from Minnesota. Univ Minn, Minn Geol Surv Bull, vol 42, 86 pp.
- Pocknall DT 1981 Pollen morphology of the New Zealand species of *Dacrydium* Solander, *Podocarpus* L'Heritier, and *Dacrycarpus* Endlicher (Podocarpaceae). N Z J Bot 19:67–95.
- Pocock SA 1962 Microfloral analysis and age determination of strata at the Jurassic-Cretaceous boundary in the western Canada plains. Palaeontogr Abt B 111:1–95.
- Potonié R 1931 Pollenformen aus tertiären Braunkohlen. Jahrb Preuß Geol Landesanstalt (Berlin) 52:1–7.
- 1934 Zur Mikrobotanik des eocänen Humodils des Geiseltsals. Arb Inst Palaeont Petrogr Brennsteine Preuß Geol L-A 4:25–125.
- 1951 Revision stratigraphisch Wichtiger Sporomorphen des mitteleuropäischen Tertiärs. Palaeontogr Abt B 91:131–151.
- 1975 Beispiele zur natürlichen Systematik der Sporen in Ergänzung von Synopsis der Sporee in situ 1962 und der Forschungsberichte aus den Jahren 1965, 1967 und 1970 sowie der Phylogenetischen Sporologie 1973. Fortschr Geol Rheinl Westfalen 25: 151–181.
- Potonié R, A Venitz 1934 Zur Mikrobotanik des miozänen Humodils der niederrheinischen Bucht. Arb Inst Palaeobot Petrogr Brennsteine 5:5–58.
- Punt W, S Blackmore, S Nilsson, A Le Thomas 1994 Glossary of pollen and spore terminology. Laboratory of Palaeobotany and Palynology Contributions, Ser 1, University of Utrecht. 71 pp.
- Ricketts BD 1991 The influence of sedimentation and Eureka tectonism on the fossil forest succession, eastern Axel Heiberg and Ellesmere Islands, Canadian Arctic Archipelago. Pages 1–27 in RL Christie, NJ McMillan, eds. Tertiary fossil forests of the Geodetic Hills, Axel Heiberg Island, Arctic Archipelago. Bull Geol Surv Canada, vol 403.
- 1994 Basin analysis, Eureka Sound Group, Axel Heiberg and Ellesmere Islands, Canadian Arctic Archipelago. Mem Geol Surv Can 439:1–27.
- Ricketts BD, DJ McIntyre 1986 The Eureka Sound Group of eastern Axel Heiberg Island: new data on the Eureka Orogeny. Geol Surv Pap, Mines Geol Branch Can 86-1B:405–410.
- Rouse GE 1957 The application of a new nomenclatural approach to Upper Cretaceous plant microfossils from western Canada. Can J Bot 35:349–375.
- 1959 Plant microfossils from Kootenay coal-measures strata of British Columbia. Micropaleontology 5:303–324.
- Rouse GE, WS Hopkins Jr, KM Piel 1970 Palynology of some Late Cretaceous and Early Tertiary deposits in British Columbia and adjacent Alberta. Geol Soc Am Spec Pap 127:213–246.
- Rudolph K 1935 Mikrofloristische Untersuchung tertiärer Ablagerungen im nördlichen Böhmen. Beih Bot Centralbl B 54:244–328.
- Runions CJ, KH Rensing, T Takaso, JN Owens 1999 Pollination of *Picea orientalis* (Pinaceae): saccus morphology governs pollen buoyancy. Am J Bot 86:190–197.
- Schneider W 1981 Nachweis der Pinaceen-Gattung *Cathaya* Chun & Kuang im 2. Lausitzer Flöz (Miozän). Z Geol Wiss 9:889–897.
- Seward AC 1914 Antarctic fossil plants. Nat Hist Rep Br Antarct Exp, Br Mus (Nat Hist) Geol 1:1–49.
- Sivak J 1976 Nouvelles espèces du genre *Cathaya* d'après leurs grains de pollen dans le Tertiaire du Sud de la France. Pollen Spores 18: 243–288.
- Sivak J, P Raz 1976 Le critere de determination des *Pinus* haplostelles et diplostelles d'après les grains de pollen. Rev Micropaleontol 18: 259–263.
- Song ZC, XT Guan, YH Zheng, ZR Li, WM Wang, ZH Hu 1985 A research on Cenozoic palynology of the Longjing Structural Area in the Shelf Basin of the East China Sea (Donghai) region. Anhui Science & Technology, Hefei. 209 pp. (In Chinese.)
- Stanley EA 1965 Upper Cretaceous and Paleocene plant microfossils and Paleocene dinoflagellates and hystrichosphaerids from north-western South Dakota. Bull Am Paleontol 49:179–384.

- Strahler AH, AN Strahler 1992 Modern physical geography. 4th ed. Wiley, New York. 638 pp.
- Sun MR, XY Sun, YN Zhao, DN Wang, ZR Li, ZH Hu, JR Xu, PF Mei 1989 Sporo-pollen. Pages 6–111 in Cenozoic paleobiota of the continental shelf of the East China Sea. Micropaleobotanical volume. Geological, Beijing. (In Chinese.)
- Svechnikova IN 1964 Predstavitel' roda *Cathaya* (Pinaceae) iz pliocena Abchazii (Representatives of family Pinaceae-Cathaya from Pliocene of Abchazii region). *Palaeontol Zh* 2:125–131. (In Russian.)
- Takahashi K 1988 Palynology of the Upper Cretaceous Futaba Group. *Sci Bull Fac Lib Arts Nagasaki Univ* 28:67–183.
- Takeuti S 1974 Geology and palynology of the hilly area southeast of Ichinoseki City, late Prefecture, Japan. *Sci Rep Tohoku Univ Second Ser (Geol)* 44:65–119.
- Thiele-Pfeiffer H 1980 Die Miozäne Mikroflora aus dem Braunkohlentagebau Oder bei Wackersdorf/Oberpfalz. *Palaeontogr Abt B* 174:95–224.
- 1988 Die Mikroflora aus dem Mitteleozänen Ölschiefer von Messel bei Darmstadt. *Palaeontogr Abt B* 211:1–86.
- Thomson PW, H Pflug 1953 Pollen und Sporen des mitteleuropäischen Tertiärs. *Palaeontogr Abt B* 94:1–138.
- Tiffney BH 1994 An estimate of the early Tertiary paleoclimate of the southern Arctic. Pages 267–295 in MC Boulter, HC Fisher, eds. *Cenozoic plants and climates of the Arctic*. NATO ASI series 1: global environmental change. Springer, Berlin.
- Traverse A 1955 Pollen analysis of the Brandon lignite of Vermont. US Bureau of Mines Report of Investigations, no 5151. 107 pp.
- 1994 Palynology geochronology of the Brandon Lignite of Vermont, USA. *Rev Palaeobot Palynol* 82:265–297.
- Tschudy RH 1970 Palynology of the Cretaceous-Tertiary boundary in the northern Rocky Mountain and Mississippi Embayment Regions. *Geol Soc Am Spec Pap* 127:65–111.
- Tschudy RH, SD Van Loenen 1970 Illustrations of plant microfossils from the Yazoo Clay (Jackson Group, Upper Eocene), Mississippi. Prof Pap US Geol Surv 643-E:1–5.
- Ueno J 1958 Some palynological observations of Pinaceae. *J Inst Polytechn Osaka City Univ Ser D Biol* 9:163–188.
- Van Campo M 1950 Recherches sur la phylogénie des Abiétinées d'après leurs grains de pollen. *Trav Lab For Toulouse Tome II*, vol 6. 183 pp.
- Van der Burgh J, R Zetter 1998 Plant mega- and microfossil assemblages from the Brunsumian of "Hambach" near Düren, B.R.D. *Rev Palaeobot Palynol* 101:209–256.
- Walther H 1999 Die Tertiärflora von Kleinsaubernitz bei Bautzen. *Palaeontogr Abt B* 249:63–174.
- Wang FH, NF Chien, YL Zhang, HQ Yang 1995 Pollen flora of China. Science, Beijing. 461 pp. (In Chinese.)
- Wang HS 1989 A study on the origin of spermatophytic genera endemic to China. *Acta Bot Yunnanica* 11:1–16. (In Chinese.)
- Weir GH, EL Thurston 1975 Scanning electron microscopic identification of fossil Pinaceae pollen to species by surface morphology. *Palynology* 1:157–165.
- White JM, L Marincovich Jr, R Higgs 1994 New Miocene fossil discoveries in the Skonun Formation, Queen Charlotte Islands, British Columbia, and implication for basin stratigraphy and climate. *Bull Geol Surv Can* 479:85–101.
- Wilkinson GC, MC Boulter 1980 Oligocene pollen and spores from the western part of the British Isles. *Palaeontogr Abt B* 175:27–83.
- Wilson MA 1978 Palynology of three sections across the uppermost Cretaceous/Paleocene boundary in the Yukon Territory and District of Mackenzie, Canada. *Palaeontogr Abt B* 166:99–183.
- Wodehouse RP 1933 Tertiary pollen. II. The oil shales of the Eocene Green River Formation. *Bull Torrey Bot Club* 60:479–522.
- 1935 Pollen grains: their structure, identification and significance in science and medicine. McGraw-Hill, New York. 574 pp.
- Xi YZ, FH Wang 1989 Pollen exine ultrastructure of extant Chinese gymnosperms. *Cathaya* 1:119–142. (In Chinese.)
- Ying TS, LQ Li 1981 Ecological distribution of endemic genera of taxads and conifers in China and neighbouring area in relation to phytogeographical significance. *Acta Phytotaxon Sin* 19:408–415. (In Chinese.)
- Ying TS, CG Ma, LQ Li, ZS Zhang, WX Zhang 1983 Studies on the *Cathaya* communities. *Acta Bot Sin* 25:157–170. (In Chinese.)
- Ying TS, YL Zhang, DE Boufford 1993 The endemic genera of seed plants of China. Science, Beijing. 824 pp.
- Zagwijn WH 1960 Aspects of the Pliocene and Early Pleistocene vegetation in the Netherlands. *Meded Geol Sticht Ser C-III* 1:1–78.
- Zaklinskaya ED 1957 Stratigraphic significance of pollen grains of gymnosperms of the Cenozoic deposits of the Irtysh Basin and of the Northern Aral Basin. *Acad Sci SSSR Works of the Geol Inst Contr* 6, Moscow. 184 pp. (In Russian.)
- 1978 Palynological information from Late Pliocene–Pleistocene deposits recovered by deep-sea drilling in the region of the island of Timor. *Rev Palaeobot Palynol* 26:227–241.
- Zetter R 1989 Methodik und Bedeutung einer routinemässig kombinierter lichtmikroskopischer und rasterelektronenmikroskopischer Untersuchung fossiler Mikroflora. *Cour Forschungsinst Senckenb* 109:41–50.
- Zetter R, M Hesse 1996 The morphology of pollen tetrads and viscin threads in some Tertiary *Rhododendron*-like Ericaceae. *Grana* 35: 285–294.
- Zheng YH 1987 Fossil pollen grains of Podocarpaceae from Upper Tertiary in Fujian. *Acta Palaeontol Sin* 26:604–615. (In Chinese.)
- Zheng YH, WX Wang 1994 Sequence of Miocene Fotan Group in SE Fujina and its palyno-assemblages. *Acta Palaentol Sin* 33: 200–216. (In Chinese.)