Salpin, M., Schnyder, J., Baudin, F., Suan, G., Suc, J.-P., Popescu, S.-P., Fauquette, S., Reinhardt, L., Schmitz, M.D., and Labrousse, L., 2018, Evidence for subtropical warmth in Canadian Arctic (Beaufort-Mackenzie, Northwest Territories, Canada) during the early Eocene, in Piepjohn, K., Strauss, J.V., Reinhardt, L., and McClelland, W.C., eds., Circum-Arctic Structural Events: Tectonic Evolution of the Arctic Margins and Trans-Arctic Links with Adjacent Orogens: Geological Society of America Special Paper 541, Chapter 27, https://doi.org/10.1130/2018.2541(27).

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Supplemental Text

Pollen grains recorded from the Caribou Hills sections are particularly well-preserved. Such a high-level of preservation is probably due in part to the sedimentary context but also to the non-agressive techniques used in the processing for extracting palynomorphs. In particular, HNO₃ attacks, often employed, were excluded because they seriously damage the envelope of pollen grains (i.e., the exine). This situation allows a detailed examination of the morphological characters of the pollen grains that can be compared to those kept in modern pollen collections and/or shown in published photographs. Below, we provide an accurate description, illustrated by photographs, of some critical pollen grains benefiting from a botanical identification. To summarize, this approach challenges for elevating pollen floras at the same step of botanical relevance than macrofloras, at least at the genus level (see Text-Tables 1–2).

The followed nomenclature in pollen morphology is that published by Punt et al. (2007) according to the LO-analysis technique of observation at the transmitted light microscope (TLM) (Erdtman, 1952). The suffix '-type' is used to indicate that the concerned pollen

morphology exists in several taxa (genera or species). The prefix 'cf.' means that the selected taxon has the nearest morphology with the fossil pollen. The Plant List website documents the present-day accepted botanical taxa and synonymies (<u>www.theplantlist.org</u>). All the photographs shown in Text-Fig. 7 and Plates 1–6 were taken by J.-P. Suc except for Figures 21–23 of Plate 3 which were taken by Z. Zheng. The origin of the compared modern pollen grains is indicated when available.

Cathaya, Pinaceae (Text-Fig. 7k–l; Plate 1, Figs. 1–3).

This is a bisaccate haploxylonoid pollen (i.e., with an almost continuous sacci–corpus outline). The alveolar structure of sacci (ectexine) shows only two layers, the small and large alveoli with relatively thick and short walls. The floor of each saccus is covered with granules. At TLM, the surface of the corpus appears smooth (i.e., psilate). Small spinules are however scattered on this surface, being only observable at the scanning electronic microscope (SEM) at high-magnification as shown in Text-Figure 7k–l.

This pollen is close to that of the only living species, *Cathata argyrophylla* Chun & Kuang (Plate 1, Figs. 4–6; Plate 2, Figs. 1–2), as described and illustrated by Erdtman (1965), Van Campo and Sivak (1972) and Sivak (1975). *Cathaya argyrophylla* is today restricted to eight altitudinal isolated localities in subtropical Southern China.

Cathaya pollen is already known from the Arctic Paleogene (Liu and Basinger, 2000; Grímsson et al., 2014; Suan et al., 2017).

Generally, *Cathaya* is erroneously included in the *Pinus* haploxylon-type, which, despite its haploxylonoid shape, shows three kinds of (small, medium-sized and large) alveoli with thin walls. This fossil genus (or group of fossil *Pinus* species) has no granulate floor of sacci and, in addition, has a vertucate sculpture of its corpus (Suc et al., 2004) as illustrated in Text-Figure 7m–n.

Pinus haplostellate-type, Pinaceae (Plate 1, Fig. 12).

This bisaccate pollen has a diploxylonoid shape (i.e., with a discontinuous sacci–corpus outline). It shows the common occurrence in *Pinus* of three layers of increasing size alveoli within the sacci. It is characterized by large granules on the internal face of the leptoma (i.e., the germinal zone) (Sivak and Raz, 1976). This pollen cannot be confused with that of *Picea*, which has large granules inside the leptoma but an haploxylonoid shape and a weakly increase in size of the saccus alveoli.

This pollen type only concerns about twenty modern species of *Pinus* listed by Sivak and Raz (1974), inhabiting diverse mountain environments.

This pollen type is indicated in the Arctic Eocene by Suan et al. (2017).

Dacrydium-type, Podocarpaceae (Plate 1, Figs. 7-9).

This bisaccate pollen has a haploxylonoid shape with an almost complete continuity of sacci which are not protruding far beyond the corpus. Ectexine of sacci is made of very large alveoli only.

Such a pollen is characteristic of the *Dacrydium*-type pollen (Podocarpaceae) (Erdtman, 1965; Sivak, 1975). The modern pollen of *Dacrydium taxoides* Brongn. & Gris (= *Falcatifolium taxoides* (Brongn. & Gris) (Plate 1, Figs. 10–12) is almost similar to some specimens of Caribou Hills. *Dacrydium* is today distributed in Southeastern Asia and Oceania.

Dacrydium has been indicated in a middle Eocene macroflora from Kamchatka (Budantsev, 1990). *Dacrydium* is also known in New Zealand since the mid-Eocene (Pocknall, 1989). Pollen grains related to *Dacrydium* are mentioned from the Paleocene of the Seymour Island (Antarctic Peninsula) by Askin (1989).

Podocarpus-type, Podocarpaceae (Plate 1, Figs. 13–15).

Pollen grains ascribed to this type are bisaccate and diploxtlonoid, with the size of each saccus larger than that of the corpus. The alveolar system of the sacci is made of two layers: small alveoli and very large ones, the long, thick and sinuous walls of which run up to the floor of sacci (Sivak, 1975).

The Carribou Hills *Podocarpus*-type pollen can be compared to that of the modern species *P*. *nagi* (Thunb.) Pilg. (= *Nageia nagi* (Thunb.) Kuntze) (Plate 1, Figs. 16–18). According to Erdtman (1965), the *Podocarpus*-type pollen exists in some other genera of Podocarpaceae. *Podocarpus* lives today in temperate to subtropical regions of the Far East, Africa, America and Austrlasia.

The occurrence of *Podocarpus* pollen in the Paleocene of the Seymour Island in the Antarctic Peninsula is documented by Askin (1989). *Podocarpus* pollen is also indicated in the late Eocene of New Zealand (Pocknall, 1989). *Podocarpus* is also a component of an early Eocene macroflora from Tasmania (Carpenter et al., 2012). Based on an extensive study of an Eocene macroflora from England and after a review of the *Podocarpus* fossil records, Greenwood et al. (2013) recommend, in agreement with Nichols and Brown (1992), to designate these fossil pollen as '*Podocarpidites*' and to consider them as belonging to fossil genera of Pinaceae or Podocarpaceae. However, the caution expressed by Greenwood et al. (2013) can be understood after looking for the '*Podocarpidites*' photographs published by Nichols and Brown (1992), showing a pollen devoid of comprehensive morphological examination. We conclude that the high-quality of preservation of the Carribou Hills pollen grains support our naming as *Podocarpus*-type.

Cupressaceae.

For a long time, several palynologists group inaperturate Gymnosperm pollen grains in the 'TCT' taxonomic unit (i.e., 'Taxodiaceae-Cupressaceae-Taxaceae': e.g., Manum, 1962; Frederiksen et al., 2002; Bouchal et al., 2016). This restricted botanical identification should be abandoned because the precise examination of exine ornamentation based on LO-analysis allows the distinction between the 'TCT' components whatever the occurrence or absence of a papilla (Reyre, 1968):

• 'Taxodiaceae' (i.e. the 'taxodioid' Cupressaceae) pollen shows a composite heteromorphic sculpture of ectexine, with less abundant large verrucae than the small ones in which they are integrated. This character is observable at TLM and very clear at SEM.

Two subgroups of pollen types are commonly distinguished: pollen grains with a large more or less hooked papilla with a relatively thick exine resemble the modern pollen of *Sequoia* (Plate 3, Fig. 13), *Cryptomeria* (Plate 3, Fig. 12), *Metasequoia* (Plate 3, Fig. 14) or *Cunninghamia*; those with a small papilla and thin exine refer to modern *Glyptostrobus* (Plate 3, Figs. 21–23) and *Taxodium* (Plate 3, Figs. 19–20) (Zagwijn, 1960).

Many of the pollen grains recorded at Caribou Hills have been ascribed to the *Sequoia*-type (Plate 3, Fig. 11) while many others to the *Glyptostrobus-Taxodium*-type (Plate 3, Figs. 15–18) as also supported by their exine ornamentation at SEM (Text-Fig. 7i–j of a fossil grain to be compared to *Glyptostrobus pensilis* in Plate 2, Figs. 3–4). The occurrence of this taxon in the Caribou Hills pollen record is consistent with the sedimentological and paleoenvironmental coastal context. The modern species of *Glyptostrobus* and *Taxodium* live in subtropical swamps, possibly in coastal environment.

Thus, the concept of a *Metasequoia/Glyptostrobus* cluster as conceived for northern Canada pollen floras by Ridgway et al. (1995) should decline. Occurrence of *Glyptostrobus* has been indicated in Eocene macrofloras of the Canadian High Arctic (Greenwood and Basinger, 1994; Harrington et al., 2011; Eberle and Greenwood, 2012). *Glyptostrobus* and *Taxodium* are

mentioned in a middle Eocene pollen flora from West Greenland (Grímsson et al., 2014). Mixed pollen grains of *Glyptostrobus*, *Taxodium* and *Metasequoia* are labelled from late Paleocene-early Eocene deposits in the Ellesmere Island (Arctic Canada) without reliable morphological argument (Kalkreuth et al., 1996). Glyptostrobus and Metasequoia are also mixed in an early Eocene pollen flora from Alaska without neither morphological description nor photograph (Frederiksen et al., 2002). Zaporozhets and Akhmetiev (2013) mention both Glyptostrobus and Taxodium in a middle-upper Eocene pollen flora from the West Siberian Platform, an occurrence supported by reliable photographs. The Glyptostrobus-Taxodiumtype is also recorded in the Eocene from the Arctic Siberia (Suan et al., 2017). Solving the above reported succession of confusions in pollen floras ('TCT' concept. Metasequoia/Glyptostrobus taxonomic cluster), the identification of Glyptostrobus-Taxodium-type pollen grains benefits from a reliable morphological examination and adequate photographs.

• Cupressaceae (i.e. the *Cupressus-Juniperus*-type) pollen, devoid of papilla, shows a double heteromorphic sculpture made of two ectexine layers: the lower level is composed of small numerous glomeruli, the upper layer is composed of grouped or not larger verrucae (Reyre, 1968). These characters are obvious at TLM (Plate 3, Figs. 5–7: *Cupressus dupreziana*; Plate 3, Fig. 8–10: *Juniperus oxycedrus*).

Such pollen grains were frequently recorded at Caribou Hills (Plate 3, Figs. 1–4). Cupressaceae with the *Cupressus-Juniperus*-type pollen grow in various conditions, from subtropical to boreal environments.

Pollen grains of the *Cupressus-Juniperus*-type are usually included in the 'TCT' group (e.g., Frederiksen et al., 2002; Bouchal et al., 2016). It is however indicated in Eocene deposits from the West Siberian Platform (Zaporozhets and Akhmetiev, 2013) and the Arctic Siberia (Suan et al., 2017).

• Taxaceae pollen, devoided of papilla too, shows a simple isomorphic but heterometric sculpture of ectexine, with verrucae overlying a smooth surface (Reyre, 1968). Such a pollen was not recorded at Caribou Hills.

Avicennia, Acanthaceae (Text-Fig. 7a–d; Plate 4, Figs. 1–11).

The concerned specimens show equiaxal to slightly longiaxal tricolpate (Text-Fig. 7a; Plate 4, Figs. 1–3) or tricolporate (Plate 4, Figs. 4–7) pollen grains characterized by long and largely opened colpi (without costae) that makes the polar area very small and the pollen close to be syncolp(or)ate (Text-Fig. 7c-d; Plate 4, Figs. 8–11). Tricolporate pollen grains show a slightly elongated endoaperture along the polar axis, which does not pass the edges of colpus at the pollen equator (Plate 4, Figs. 6–7). An homobrochate semitectate reticulum constitutes the exine sculpture with dense muri, a little larger than luminae, which are characterized by a polygonal and slightly elongated outline (Text-Fig. 7a–d; Plate 4, Figs. 1–2, 4–5, 8, 10–11). Thickness of muri somewhat increases toward the poles that reduces the size of luminae (Text-Fig. 7c–d; Plate 4, Figs. 8). Colpi are bordered by a thin margo where reticulum is smaller (Text-Fig. 7a, c–d; Plate 4, Figs. 1–2, 8). The structure of the semi-tectate ectexine shows dense columellae with large head constituting the tectum overlying a thinner endexine (Plate 4, Figs. 3, 6, 9, 11). At SEM, general shape and exine sculpture can be observed in finer detail showing, in particular, the smooth surface of the tectum somewhat prominent above the columellae (Text-Fig. 7b, d).

These characters, whatever the pollen is colpate or colporate, are those of the modern *Avicennia* pollen (also supported by a similar size), which unique morphology has been extensively described (Mukherjee and Chanda, 1973) and documented by many photographs at TLM and SEM (Thanikaimoni, 1987; Mao et al., 2012). Indeed, the *Avicennia* (colpate or colporate) pollen displays numerous characters that discard any confusion with pollen grain of

other genera. Using both TLM and SEM, the fossil pollen grains have been compared with those of five living species of *Avicennia* (Acanthaceae), selected after meticulous examination of modern pollen photographic atlases. Among them, three species displays pollen morphologies (with a colpate or colporate apertural system) very close to the Caribou Hills *Avicennia* pollen grains: *A. nitida* Jacq. synonym of *A. germinans* (L.) L. (Plate 2, Figs. 7–8; Plate 4, Figs. 12–18); *A. alba* Blume synonym of *A. marina* (Forssl.) Vierh. (Plate 4, Figs. 19–22); *A. officinalis* L. (Plate 2, Figs. 5–6; Plate 4, Figs. 23–25). All the *Avicennia* species contribute today to the mangrove ecosystem in tropical regions, the limits of which they may exceed thanks to favourable conditions (warm marine currents).

Avicennia pollen from the Arctic Eocene has been identified and described for the first time by Suan et al. (2017). However, after checking published photographs, we consider that *Avicennia* is probably present in other pollen records where it was mentioned under an artificial name because of poor or false morphological examination (*'Arecipites microreticulates'* from IODP Hole 302-4A: Sluijs et al., 2009: in Fig. S3; *'Tricolpites* sp. 2' from Franklin Bluffs in North Alaska: Frederiksen et al., 2002: Plate 3, Figs. 1–2).

Juglandaceae.

Apart from *Platycarya* and *Carya*, two kinds of triporate pollen grains have been considered at TLM within the *Engelhardia* complex, as supported by SEM observation after comparison with modern taxa (Stone and Broome, 1975):

- *Alfaroa*-type (Text-Fig. 7e–f) with an ornamentation made of relatively coarse and dense spinules, which also can correspond to a fossil genus.
- *Engelhardia* (Text-Fig. 7g-h) with ornamentation made of small and uniformly distributed spinules.

Alfaroa grows in montane and submontane tropical rain forests in Central America. *Engelhardia* is a component of the Asian evergreen sclerophyllous broad-leaved (subtropical) forests.

According to pollen records, the possible occurrence of *Alfaroa* in Eocene from Colorado has been suggested by Leopold and Clay-Poole (2001) and discussed by Bouchal et al. (2016). *Engelhardia* is commonly labelled in the high-latitude Eocene pollen floras (e.g.: Ridgway et al., 1995; Frederiksen et al., 2002; Jahren, 2007; Suan et al., 2017).

Buxus bahamensis-type, Buxaceae (Plate 5, Figs. 1–2).

This longiaxial pollen has three long ectoapertures (colpi) borderd by costae, which may include two-three endoapertures each (pores), delimited by a thin annulus. The ornamentation is a homobrochate semitectate reticulum with muri of equal size than luminae.

This pollen corresponds to the *Buxus bahamensis*-type, defined by Köhler (1981) and established by Bessedik (1983) as an element of the former *Nagyipollis* complex. The pollen of the reference species *B. bahamensis* Baker is shown in Plate 5 (Figs. 3–4). The modern species showing this pollen type live in the tropical Central America (Bessedik, 1983). This pollen type, recorded in the Eocene deposits from Arctic Siberia (Suan et al., 2017), is frequent in Paleogene sediments from Western Europe (Bessedik, 1983).

Ilex floribunda-type, Aquifoliaceae (Plate 5, Figs. 5-7).

This longiaxial tricolporate pollen type is described by Lobreau-Callen and Suc (1972). Its ornamentation is made of homogenous large clavae with respect to the shape, size and distribution. Endexine is a little thicker than ectexine. For comparison, the pollen of the species *I. floribunda* Reissek ex Maxim. is illustrated in Plate 5 (Figs. 8–10). *Ilex* species showing this pollen type are components of undergrowth in subtropical regions.

This taxon has been mentioned in the Eocene of Arctic Siberia by Suan et al. (2017). The photograph published by Ridgway et al. (1995: Fig. 12M) from the North Canada Eocene may correspond to the *I. floribunda*-type. The same comment concerns the Plate 2 – Figures 2–3 of Frederiksen et al. (2002) from the Alaska Eocene.

Amanoa, Phyllanthaceae (Plate 5, Figs. 11–16).

The pollen is equiaxial to breviaxial, tricolporate with long colpi (ectoapertures) and relatively rectangular endoapertures. Its ornamentation is a heterobrochate reticulum with large luminae. As the pollen is semitectate, the simplicolumellate muri are not all joined in a non rectilinear outline. Columellae are relatively high with a bulging head and a thin membrane may connect the muri. These characters correspond to the pollen of *Amanoa* (Erdtman, 1952; Punt, 1962).

The pollen of *Amanoa caribaea* Baker Krug & Urb. (Plate 5, Figs. 17–22) is shown for comparison. The genus *Amanoa* is found today in tropical South America, West Indies and Africa.

The pollen from the Alaska Eocene, illustrated under the name *Tricolpites* sp. 1 by Frederiksen et al. (2002: Plate 2, Figs. 15–17), might be ascribed to *Amanoa*.

Bombax-type, Malvaceae (Plate 5, Figs. 23–27).

Few rare pollen grains of CH2 show the common morphology of Bombacaceae: breviaxial pollen with a circular to triangulate polar view, interaperturate with three very short ectoapertures and circular endoapertures surrounded by a large annulus; semitectate pollen; heterobrochate simplicolumellate reticulum with large luminae as ornamentation at the pole and smaller luminae in the mesocolpium, decreasing more in the margines.

As pointed out by Erdtman (1952), Robyns (1963, 1971), Tsukada (1964), and Fuchs (1967), a more or less similar morphology is developed in several genera from the Bombacaceae: *Bombax, Pseudobombax, Eriotheca, Bernoullia, Ceiba, Aguiaria.* For this reason, although the Caribou Hills pollen grains are very similar to those of some modern species of *Bombax* (see for comparison *B. ceiba*: Plate 5, Figs. 28–30), we label them as *Bombax*-type. These genera grow today in tropical regions, especially in South America.

Frederiksen et al. (2002) group several pollen grains from the North Alaska Eocene within the pseudo-genus '*Bombacacidites*' as did Askin (1989) for the Antarctica Eocene, with almost the same significance than our *Bombax*-type also identified in the North Siberian Eocene (Suan et al., 2017). Similarly, Pross et al. (2012) designate this pollen type from the Antarctic early Eocene within the Bombacoideae sub-family. It is noteworthy that Gruas-Cavagnetto (1987) distinguished five genera (*Pseudobombax, Eriotheca, Aguiaria, Bombax* and *Ceiba*) according to the pollen in the Eocene of the Basin of Paris.

Itea, Iteaceae (Plate 6, Figs. 1–2).

One diporate, subisopolar and bilaterally symmetrical small pollen grain was recorded in the CH2 section. The pores are circular and bordered by a thin annulus. The ectexine ornamentation is scabrate.

It is close to the pollen of *Itea* described by Erdtman (1952) and Lieux (1982), here represented by the species *I. ilicifolia* Oliv. (Plate 6, Figs. 3–4). *Itea* species are shrubs inhabiting swamps in Eastern Asia and southeastern North America.

Itea pollen was reported from the mid-Eocene of West Greenland (Grímsson et al., 2014) and from the Eocene of England (Gruas-Cavagnetto, 1976).

Distylium, Hamamelidaceae (Plate 6, Figs. 5–11).

Angulaperturate and tricolpate pollen grains with irregular edges of short colpi often covered by a granular membrane have been commonly recorded in the Caribou Hills samples. Their ornamentation is a heterobrochate fine reticulum with equal size of muri and luminae.

This pollen corresponds to the description of the *Distylium* pollen published by Erdtman (1952), Endress (1977) and Bogle and Philbrick (1980), as illustrated by the comparison with *D. chinense* (Franch. Ex Hemsl.) Diels (Plate 6, Figs. 12–18). *Distylium* lives today in similar conditions to those of *Engelhardia*.

Occurrence of this genus in the North Siberia Eocene is documented by Suan et al. (2017). The small size pollen from mid-upper Eocene of the West Siberian Platform shown by Zaporozhets and Akhmetiev (2013: Plate I, Fig. 26), indicated as *Fothergilla gracilis*, could belong to *Distylium*.

Cuphea, Lythraceae (Plate 6, Figs. 19–22).

Some breviaxial tricolporate and syncolpate pollen grains were recorded in the Caribou Hills. These small pollen grains have an oval-triangular shape in polar view and show slightly protuberant endoapertures (pores) resulting in a small vestibulum. At the pole, colpi are bordered by an external thick costa. Their thin exine has a finely striate ornamentation.

These pollen grains correspond to the description and illustration of *Cuphea* published by Erdtman (1952) and Graham and Graham (1967), as supported by the comparison with the pollen of the modern species *Cuphea dipetala* (L.f.) Koehne (Plate 6, Figs. 23–25).

The modern species of *Cuphea*, herbs or bushes, grow in warm-temperate to tropical regions of America.

To our knowledge, this is the first identification of this taxon in the Arctic Eocene.

Additional References with respect to those following the main text.

- Askin, R.A., 1989, Endemism and heterochroneity in the Late Cretaceous (Campanian) to Paleocene palynofloras of Seymour Island, Antarctica: implications for origins, dispersal and palaeoclimates of southern floras. In: Origins and evolution of the Antarctic biota, Crame, J.A. (ed.), Geological Society Special Publication, 47, p. 107– 119.
- Bessedik, M., 1983, Le genre *Buxus* L. (*Nagyipollis* Kedves 1962) au Tertiaire en Europe occidentale: évolution et implications paléogéographiques. Pollen et Spores, 25 (3–4), p. 461–486.
- Bogle, A.L., Philbrick, C.T., 1980, A generic atlas of Hamamelidaceaeous pollens. Contribution to the Gray Herbarium, 210, p. 29–103.
- Bouchal, J.M., Zetter, R., Denk, T., 2016, Pollen and spores of the uppermost Eocene Florissant Formation, Colorado: a combined light and scanning electron microscopy study. Grana, 55 (3), p. 179–245.
- Budantsev, L.Yu, 1990, Occurrence of Macclintockia kowatschensis leaves in the Eocene deposits in western Kamchatka. Botanical Journal, 75 (6), p. 851–858.
- Endress, P.K., 1977, Evolutionary trends in the Hamamelidales-Fagales-Group. Plant Systematics and Evolution, Supplement 1, p. 321–347.
- Erdtman, G., 1952, Pollen morphology and plant taxonomy. Angiosperms. Almqvist and Wiksell, Stockholm, 539 p.
- Erdtman, G., 1965, Pollen and spore morphology / Plant taxonomy. Gymnospermae, Bryophyta. Almqvist and Wiksell, Stockholm, 108 p.
- Graham, A., Graham, S.A., 1967, Pollen morphology and taxonomy of *Cuphea* (Lythraceae). Review of Palaeobotany and Palynology, 3, p. 155–162.
- Greenwood, D.R., Hill, C.R., Conran, J.G., 2013, *Prumnopitys anglica* sp. nov. (Podocarpaceae) from the Eocene of England. Taxon, 62 (3), p. 565–580.

- Gruas-Cavagnetto, C., 1976, Etude palynologique du Paléogène du sud de l'Angleterre. Cahiers de Micropaléontologie, 1, p. 1–49.
- Gruas-Cavagnetto, C., 1987, Nouveaux éléments mégathermes dans la palynoflore éocène du Bassin Parisien. Mémoires et Travaux de l'Ecole Pratique des Hautes Etudes, Institut de Montpellier, 17, 207–233.
- Köhler, E., 1981, Pollen morphology of the West Indian Central American species of the genus *Buxus* L. (Buxaceae) with reference to taxonomy. Pollen et Spores, 23 (1), p. 37– 91.
- Leopold, E.B., Clay-Poole, S., 2001, Florissant leaf and pollen floras of Colorado compared: climatic considerations. *In* Evanoff, E., Gregory-Wodzicki, K.M., Johnson, K.R. (eds.), Fossil flora and stratigraphy of the Florissant Formation, Colorado, Denver Museum of nature and Sciences, series 4 (1), p. 17–69.
- Lieux, M.H., 1982, An atlas of pollen of trees, shrubs, and woody vines of Louisiana and other southeastern states, Part IV. Sapotaceae to Fabaceae. Pollen et Spores, 24 (3–4), p. 331–368.
- Lobreau-Callen, D., Suc, J.-P., 1972, Présence de *Microtropis fallax* (Celastraceae) dans le Pléistocène inférieur de Celleneuve (Hérault). Comptes Rendus de l'Académie des Sciences de Paris, ser. D, 275 (13), p. 1351–1354.
- Manum, S., 1962, Studies in the Tertiary flora of Spitsbergen, with notes on Tertiary floras of Ellesmere Island, Greenland and Iceland. Norsk Polarinstitutt Skrifter, 125, 127 p.
- Mukherjee, J., Chanda, S., 1973, Biosynthesis of Avicennia L. in relation to taxonomy. Geophytology, 3, p. 85–88.
- Nichols, D.J., Brown, J.L., 1992, Palynostratigraphy of the Tullock Member lower Paleocene of the Fort Union Formation in the Powder River Basin Montana and Wyoming. Bulletin of the U.S. Geological Survey, 1917, p. F1–F35.

- Pocknall, D.T., 1989, Late Eocene to Early Miocene vegetation and climate history of New Zealand. Journal of the Royal Society of New Zealand, 19 (1), p. 1–18.
- Pross, J., Contreras, L., Bijl, P.K., Greenwood, D.R., Bohaty, S.M., Schouten, S., Bendle, J.A., Röhl, U., Tauxe, L., Raine, J.I., Huck, C.E., van de Flierdt, T., Jamieson, S.S.R., Stickley, C.E., van de Schootbrugge, B., Escutia, C., Brinkhuis, H., Integrated ODP Expedition 318 Scientists, 2012, Persistent near-tropical warmth on the Antarctic continent during the early Eocene epoch. Nature, 488, p. 73–76.
- Punt, W., 1962, Pollen morphology of the Euphorbiaceae, with special reference to taxonomy. Wentia, 7, p. 1–116.
- Punt, W., Hoen, P.P., Blackmore, S., Nilsson, S., Le Thomas, A., 2007, Glossary of pollen and spore terminology. Review of Palaeobotany and Palynology, 143, p. 1–8.
- Reyre, Y., 1968, La sculpture de l'exine des pollens des Gymnospermes et des Chlamydospermes et son utilisation dans l'identification des pollens fossiles. Pollen et Spores, 10 (2), p. 197–220.
- Robyns, A., 1963, Contribution à l'étude monographique du genre *Bombax* s.l. Grana Palynologica, 4 (1), p. 73–77.
- Robyns, A., 1971, On pollen morphology of Bombacaceae. Bulletin du Jardin Botanique National de Belgique, 41, p. 451–456.
- Sivak, J., 1975, Les caractères de diagnose des grains de pollen à ballonnets. Pollen et Spores, 17(3), p. 349–421.
- Sivak, J., Raz, P., 1976, Le critère de détermination des *Pinus* haplostellés et diplostellés d'après les grains de pollen. Revue de Micropaleontologie, 18 (4), p. 259–263.
- Stone, D.E., Broome, C.R., 1975, Juglandaceae A. Rich. Ex. Kunth. World pollen and spore flora, 4, p. 1–35.

- Suc, J.-P., Fauquette, S., Popescu, S.-M., 2004, L'investigation palynologique du Cénozoïque passe par les herbiers. Actes du Colloque "Les herbiers: un outil d'avenir. Tradition et modernité", Villeurbanne. Edit. Association française pour la Conservation des Espèces Végétales, Nancy, p. 67–87.
- Thanikaimoni, G., 1987, Mangrove palynology. Institut Français de Pondichéry,, Travaux de la Section Scientifique et technique, 24, p. 1–100.
- Tsukada, M., 1964, Pollen morphology and identification III. Modern and fossil tropical pollen with emphasis on Bombacaceae. Pollen et Spores, 6 (2), p. 393–462.
- Van Campo, M., Sivak, J., 1972, Structure alvéolaire de l'ectexine des pollens à ballonnets des Abietaceae. Pollen et Spores, 14 (2), p. 115–141.
- Zagwijn, W.H., 1960, Aspects of the Pliocene and early Pleistocene vegetation in the Netherlands. Mededelingen van de Geologische Stichting, ser. C, 3 (1, 5), p. 1–78. Plate captions.
- Plate 1. Photographs at TLM of some fossil and modern bisaccate pollen grains of Gymnosperms.
- Figs. 1–3, Cathaya (Pinaceae), section CH2, sample 17.
 - Scale bar = 5 μ m.
 - Distal view, LO-analysis showing the structure of sacci.
 - 1, Focus on small alveoli.
 - 2, Focus on large alveoli.
 - 3, Optical section showing the finely granular floor of sacci.
- Figs. 4–6, *Cathaya argyrophylla* Chun & Kuang (Pinaceae), slide 559 of the GeoBioStratData modern pollen collection, specimen recolted in the Hua Ping Nature Reserve, Guangxi Province (China).

Scale bar = 5 μ m.

Distal view, LO-analysis showing the structure of sacci.

4, Focus on small alveoli.

5, Focus on large alveoli.

6, Optical section showing the finely granular floor of sacci.

Figs. 7–8, Dacrydium-type (Podocarpaceae), section CH2, sample 20.

Scale bar = $10 \mu m$.

Profile view, LO-analysis.

- 7, Focus on alveoli of the sacci.
- 8, Focus on ornamentation of the corpus.

Fig. 9, Dacrydium-type (Podocarpaceae), section CH2, sample 18.

Scale bar = $10 \ \mu m$.

Profile view.

Focus on ornamentation of the corpus and optical section of the sacci.

Figs. 10–11, Dacrydium taxoides Brongn. & Gris (= Falcatifolium taxoides (Brongn. & Gris) de Laub.

(Podocarpaceae), slide 304 of the GeoBioStratData modern pollen collection.

Scale bar = $10 \ \mu m$.

Profile view, LO-analysis.

- 10, Focus on alveoli of the sacci.
- 11, Focus on ornamentation of the corpus.

Fig. 12, Pinus haplostellate-type (Pinaceae), section CH2, sample 25.

Scale bar = $10 \ \mu m$.

Profile view.

Focus on the granular leptoma.

Figs. 13–14, Podocarpus-type (Podocarpaceae), section CH1, sample 43.

Scale bar = $10 \ \mu m$.

Proximal view, LO-analysis showing the structure of sacci.

13, Focus on small alveoli.

- 14, Focus on large alveoli.
- Fig. 15, Podocarpus-type (Podocarpaceae), section CH1, sample 50.

Scale bar = $10 \mu m$.

Distal view.

Focus on large alveoli and their junction with the floor of corpus.

Figs. 16–18, *Podocarpus nagi* (Thunb.) Pilg. (= *Nageia nagi* (Thunb.) Kuntze) (Podocarpaceae), slide 315 of the GeoBioStratData modern pollen.

Scale bar = $10 \ \mu m$.

16-17, Proximal view, LO-analysis.

16, Focus on small alveoli.

- 17, Focus on large alveoli and their junction with the floor of corpus.
- 18, Distal view. Focus on large alveoli and their junction with the floor of corpus.

Plate 2. Photographs at SEM of pollen of some modern species.

Figs. 1–2, *Cathaya argyrophylla* Chun & Kuang (Pinaceae), specimen collected in the Hua Ping Nature Reserve, Guangxi Province (China).

1, Pollen grain in proximal view showing the haploxylonoid outline of sacci and corpus (scale $bar = 20 \ \mu m$).

4, Detail showing the small spinules on its corpus (scale bar = 3 μ m). For comparison with fossil pollen, see Text-Fig. 71–m.

Figs. 3–4, *Glyptostrobus pensilis* (Staunton ex D.Don) K.Koch (Cupressaceae), specimen n° 6974 from the Herbarium of the Xiamen University (China), collected near Fuzhou, Fujian Province (China).

3, General view of a pollen grain (scale bar = $10 \ \mu m$).

4, Detail of the ectexine composite heteromorphic ornamentation (large vertucae integrated within numerous smaller ones) (scale bar = 1 μ m).

For comparison with fossil pollen, see Text-Fig. 7i-j.

Figs. 5–6, *Avicennia officinalis* L. (Acanthaceae), specimen n° 312 from the Herbarium of the C. Bernard University (Lyon, France), collected near Mindanao, the Philippines Islands.
5, A pollen grain in equatorial view showing the three apertures (scale bar = 2 μm).
6, Detail of its reticulate ornamentation in the mesocolpium (scale bar = 1 μm).
For comparison with fossil pollen, see Text-Fig. 7a–b.

Figs. 7–8, Avicennia nitida Jacq. (= Avicennia germinans (L.) L.) (Acanthaceae), specimen n° 312 from the Herbarium of the C. Bernard University (Lyon, France), collected near Nueva Gerona, Isla de Pinos, West Indies.

7, A pollen grain in polar view showing the small polar area (scale bar = $2 \mu m$).

8, Detail of its reticulate ornamentation at the pole (scale bar = 1 μ m).

For comparison with fossil pollen, see Text-Fig. 7c-d.

Plate 3. Photographs at TLM of some fossil and modern inaperturate pollen grains of Gymnosperms. Scale bar = $10 \mu m$.

Figs. 1-2, Cupressus-Juniperus-type (Cupressaceae), section CH2, sample 6.

- 1, Focus on verrucae constituting the ornamentation of ectexine.
- 2, Focus on the base of verrucae.

Figs. 3-4, Cupressus-Juniperus-type (Cupressaceae), section CH2, sample 12.

- 3, Focus on verrucae constituting the ornamentation of ectexine.
- 4, Focus on the base of verrucae.
- Figs. 5–7, *Cupressus dupreziana* A. Camus (Cupressaceae), slide 468 of the GeoBioStratData modern pollen.
 - 5, Focus on verrucae constituting the ornamentation of ectexine.
 - 6, Focus on the base of verrucae.
 - 7, Optical section.

Figs. 8–10, *Juniperus oxycedrus* L. (Cupressaceae), slide 470 of the GeoBioStratData modern pollen collection.

- 8, Focus on verrucae constituting the ornamentation of ectexine.
- 9, Focus on the base of verrucae.
- 10, Optical section.

Fig. 11, Sequoia-type (Cupressaceae), section CH1, sample 54.

Optical section showing the composite verrucate sculpture and the large papilla.

Fig 12, Cryptomeria fortunei Hooibr. ex Billain (= Cryptomeria japonica (Thunb. Ex L.f.) D.Don) (Cupressaceae), slide 649 of the GeoBioStratData modern pollen collection, collected on Luofu Mount, Guangdong Province (China).

Optical section showing the composite verrucate sculpture and the large papilla.

- Fig 13, Sequoia gigantea (Lindl.) Decne. (= Sequoiadendron giganteum (Lindl.) J.Buchholz) (Cupressaceae), slide 16 of the GeoBioStratData modern pollen.Optical section showing the composite verrucate sculpture and the large papilla.
- Fig. 14, *Metasequoia glyptostroboides* Hu & W.C.Cheng (Cupressaceae), slide 60331 of the ISEM modern pollen collection.

Optical section showing the composite verrucate sculpture and the papilla.

- Fig. 15, *Glyptostrobus-Taxodium*-type (Cupressaceae), section CH1, sample 46. Optical section showing the composite verrucate sculpture and the small papilla.
- Fig. 16, *Glyptostrobus-Taxodium*-type (Cupressaceae), section CH2, sample 35. Optical section showing the composite verrucate sculpture and the small papilla.
- Fig. 17, *Glyptostrobus-Taxodium*-type (Cupressaceae), section CH2, sample 27. Optical section showing the composite verrucate sculpture and the small papilla.
- Fig. 18, *Glyptostrobus-Taxodium*-type (Cupressaceae), section CH1, sample 40. Optical section showing the composite verrucate sculpture and the small papilla.
- Figs. 19–20, *Taxodium distichum* (L.) Rich. (Cupressaceae), slide 818 of the GeoBioStratData modern pollen collection, specimen n° 157314 of the Herbarium of the Sun Yat-sen University (Guangzhou, China), collected near Metter, Georgia (USA).

Optical section showing the composite verrucate sculpture and the small papilla.

- Figs. 21–23, *Glyptostrobus pensilis* (Staunton ex D.Don) K.Koch (Cupressaceae), slide 2018-FJ04 of the Sun Yat-sen University (Guangzhou, China), collected in the Dongshan Nature Reserve, Fujian Province, China.
 - 21, Surface of the composite verrucate sculpture.
 - 22, Optical section showing the small papilla.
 - 23, Optical section of another pollen grain showing the small papilla.

Fig. 24, Sciadopitys (Sciadopityaceae), section CH2, sample 33.

Focus inside the vertucate ornamentation and optical section.

Plate 4. Photographs at TLM of some fossil and modern pollen grains of *Avicennia* (Acanthaceae). Scale bar = $10 \mu m$.

Figs. 1-3, Avicennia (Acanthaceae), section CH2, sample 6.

Equatorial view, LO-analysis.

- 1, Focus on the reticulate ornamentation of ectexine.
- 2, Focus on the base of luminae.
- 3, Focus on a colpus, optical section.

Figs. 4–7, Avicennia (Acanthaceae), section CH2, sample 20.

Equatorial view (mesocolpium), LO-analysis.

- 4, Focus on the reticulate ornamentation of ectexine.
- 5, Focus on the base of luminae.
- 6, Focus on two colpori (profile view).

7, Optical section.

Figs. 8-9, Avicennia (Acanthaceae), section CH2, sample 18.

Polar view, LO-analysis.

- 8, Focus on the reticulate ornamentation of ectexine and base of luminae and colpi.
- 9, Focus on the polar area and optical section.

Figs. 10–11, Avicennia (Acanthaceae), section CH2, sample 18.

Polar view, LO-analysis.

- 11, Focus on the reticulate ornamentation of ectexine and base of luminae and colpi.
- 12, Focus on the polar area and optical section.
- Figs. 12–18, Avicennia nitida Jacq. (= Avicennia germinans (L.) L.) (Acanthaceae), slide 878 of the GeoBioStratData modern pollen collection, specimen n° 312 from the Herbarium of the C. Bernard University (Lyon, France), collected at Nueva Gerona, Isla de Pinos, West Indies..
 Polar view, LO-analysis.
 - 12, Focus on the reticulate ornamentation of ectexine.
 - 13, Focus on the base of luminae, colpi and polar area.
 - 14, Optical section.

Equatorial view (mesocolpium), LO-analysis.

- 15, Focus on the reticulate ornamentation of ectexine.
- 16, Focus on the base of luminae.
- 17, Focus on two colpori (profile view).
- 18, Optical section.
- Figs. 19–22, Avicennia alba Blume (= Avicennia marina (Forssk.) Vierh.) (Acanthaceae), slide 873 of the GeoBioStratData modern pollen collection, specimen n° 2209 from the Herbarium of the C. Bernard University (Lyon, France), collected in Java.

Equatorial view, LO-analysis.

- 19, Focus on the reticulate ornamentation of ectexine.
- 20, Focus on the base of luminae.
- 21, Focus on a colporus (front view).
- 22, Focus on two colpori (profile view) and optical section.
- Figs. 23–25, Avicennia officinalis L. (Acanthaceae), slide 877 of the GeoBioStratData modern pollen collection, specimen n° 312 from the Herbarium of the C. Bernard University (Lyon, France), collected near Mindanao, the Philippines Islands.
 - Polar view, LO-analysis.
 - 23, Focus on the reticulate ornamentation of ectexine.
 - 24, Focus on the base of luminae, colpi and polar area.
 - 25, Optical section.

Plate 5. Photographs at TLM of some fossil and modern pollen grains of Angiosperms.

Scale bar = $10 \mu m$.

Figs. 1-2, Buxus bahamensis-type (Buxaceae), section CH1, sample 50.

Equatorial view, LO-analysis.

1, Focus on the reticulate ornamentation of ectexine and a colpus showing two endoapertures (front view).

2, Optical section.

Figs. 3–4, Buxus bahamensis Baker (Buxaceae), slide 41147 of the ISEM modern pollen collection, specimen n° 138 from the Herbarium of the University of Montpellier (France), collected near Nassau, New Providence Island, the Bahamas.

Equatorial view, LO-analysis.

3, Focus on the reticulate ornamentation of ectexine and a colpus showing three endoapertures (front view).

- 4, Optical section.
- Figs. 5–7, *Ilex floribunda*-type (Aquifoliaceae), section CH2, sample 25.

Equatorial view (mesocolpium), LO-analysis.

- 5, Focus on the clavate ornamentation of ectexine.
- 6, Focus on the base of clavae and a colporus (front view).
- 7, Optical section.
- Figs. 8–10, *Ilex floribunda* Reissek ex Maxim. (Aquifoliaceae), slide 22956 of the ISEM modern pollen collection, specimen n° 378 from the Herbarium of the Muséum National d'Histoire Naturelle (Paris, France), collected in the Spiritu Santo Province, Brazil.

Equatorial view (mesocolpium), LO-analysis.

- 8, Focus on the clavate ornamentation of ectexine.
- 9, Focus on the base of clavae and a colporus (front view).
- 10, Optical section.

Figs. 11–13, Amanoa (Phyllanthaceae), section CH2, sample 4.

Equatorial view, LO-analysis.

- 11, Focus on the reticulate ornamentation of ectexine.
- 12, Focus on the base of luminae and a colporus (front view).
- 13, Optical section.

Figs. 14–16, Amanoa (Phyllanthaceae), section CH2, sample 18.

Polar view, LO-analysis.

- 14, Focus on the reticulate ornamentation of ectexine.
- 15, Focus on the base of luminae.
- 16, Optical section.
- Figs. 17–22, Amanoa caribaea Baker Krug & Urb. (Phyllanthaceae), slide 41784 of the ISEM modern pollen collection, collected in the Caribbean Islands (Dominican Republic), specimen n° 603 of the Egger collection, Herbarium of the University of Washington, Seattle (USA). Equatorial view, LO-analysis.
 - 17, Focus on the reticulate ornamentation of ectexine and a colporus (front view).
 - 18, Focus on the base of luminae and a colporus (front view).
 - 19, Optical section.
 - Polar view, LO-analysis.
 - 20, Focus on the reticulate ornamentation of ectexine.
 - 21, Focus on the base of luminae.
 - 22, Optical section.

Figs. 23-24, Bombax-type (Malvaceae), section CH2, sample 6.

Polar view, LO-analysis.

- 23, Focus on the reticulate ornamentation of ectexine and the three colpori.
- 24, Focus on the base of luminae and the three colpori, ooptical section.

Figs. 25–26, Bombax-type (Malvaceae), section CH2, sample 4.

Polar view, LO-analysis.

- 25, Focus on the reticulate ornamentation of ectexine and the three colpori.
- 26, Focus on the base of luminae and colpori, optical section.

Figs. 27, Bombax-type (Malvaceae), section CH2, sample 4.

Polar view.

Focus on the reticulate ornamentation of ectexine and the three colpori.

Figs. 28–30, *Bombax ceiba* L. (Malvaceae), slide 10603 of the ISEM modern pollen collection, sample
n° 8032 of the J.F. Rock collection, Herbarium of the University of Hawaii, Honolulu (Hawaii).

Polar view, LO-analysis.

27, Focus on the reticulate ornamentation of ectexine and the three colpori.

28, Focus on the base of luminae and colpori.

29, Focus on colpori and optical section.

Plate 6. Photographs at TLM of some fossil and modern pollen grains of Angiosperms (continued). Scale bar = $10 \ \mu m$.

Figs. 1–2, Itea (Iteaceae), section CH2, sample 22.

Equatorial view, LO-analysis.

- 1, Focus on the scabrate ornamentation of ectexine.
- 2, Focus on the two pores, optical section.

Figs. 3–4, *Itea ilicifolia* Oliv. (Iteaceae), slide 27173 of the ISEM modern pollen collection, sample n°
325 of the E. Wilson collection, Herbarium of the Royal Botanic Gardens Kew (United Kingdom), collected in the Western Hubei Province (China).

Equatorial view, LO-analysis.

3, Focus on the scabrate ornamentation of ectexine.

4, Focus on the two pores, optical section.

Figs. 5–7, Dystilium (Hamamelidaceae), section CH1, sample 46.

Equatorial view (mesocolpium), LO-analysis.

- 5, Focus on the reticulate ornamentation of ectexine.
- 6, Focus on the base of luminae and two colpi (profile view).
- 7, Optical section.
- Figs. 8–11, Dystilium (Hamamelidaceae), section CH2, sample 35.

Polar view, LO-analysis.

- 8, Focus on the reticulate ornamentation of ectexine.
- 9, Focus on the base of luminae.

10, Focus on colpi

- 11, Optical section and polar area.
- Figs. 12–18, Distylium chinense (Franch. Ex Hemsl.) Diels (Hamamelidaceae), slide 13996 of the ISEM modern pollen collection, sample n° 3929 of the J. Cavaleni collection, Herbarium of Geneva, collected in the Guizhou Province (China).

Equatorial view (mesocolpium), LO-analysis.

- 12, Focus on the reticulate ornamentation of ectexine.
- 13, Focus on the base of luminae and two colpi (profile view).
- 14, Optical section.
- Polar view, LO-analysis.
- 15, Focus on the reticulate ornamentation of ectexine.
- 16, Focus on the base of luminae.
- 17, Focus on colpi.
- 18, Optical section and polar area.

Figs. 19–20, Cuphea (Lythraceae), section CH1, sample 42.

Polar view, LO-analysis.

19, Focus on the striate ornamentation and syncolporate apertures.

20, Focus on the syncolporate apertures and optical section.

Figs. 21–22, Cuphea (Lythraceae), section CH1, sample 32.

Polar view, LO-analysis.

21, Focus on the striate ornamentation of ectexine and syncolpate apertures.

22, Focus on the syncolporate apetures and optical section.

Figs. 23–25, *Cuphea dipetala* (L.f.) Koehne (Lythraceae), slide 610 of the GeoBioStratData modern pollen collection and slide 5456 of the ISEM modern collection, specimen collected in Peru. Polar view, LO-analysis.

23, Focus on the striate ornamentation of ectexine.

- 24, Focus on the syncolporate apertures.
- 25, Optical section.

























