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Cretaceous and Paleogene Fagaceae from North America and Greenland: evidence for a Late Cretaceous split between *Fagus* and the remaining Fagaceae

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ABSTRACT. Modern lineages of the beech family, Fagaceae, one of the most important north-temperate families of woody flowering plants, have been traced back to the early Eocene. In contrast, molecular differentiation patterns indicate that the *Fagus* lineage, Fagoideae, with a single modern genus, evolved much earlier than the remaining lineages within Fagaceae (Trigonobalanoideae, Castaneoideae, Quercoideae). The minimum age for this primary split in the Fagaceae has been estimated as 80 ± 20 Ma (i.e. Late Cretaceous) in recently published, time-calibrated phylogenetic trees including all Fagales. Here, we report fagaceous fossils from the Campanian of Wyoming (82–81 Ma; Eagle Formation [Fm]), the Danian of western Greenland (64–62 Ma; Agatdal Fm), and the middle Eocene of British Columbia (ca 48 Ma; Princeton Chert), and compare them to the Fagaceae diversity of the recently studied middle Eocene Hareøen Fm of western Greenland (42–40 Ma). The studied assemblages confirm that the *Fagus* lineage (= Fagoideae) and the remainder of modern Fagaceae were diverged by the middle Late Cretaceous, together with the extinct Fagaceae lineage(s) of *Eotrigonobalanus* and the newly recognised genus *Paraquercus*, a unique pollen morph with similarities to both *Eotrigonobalanus* and *Quercus*. The new records push back the origin of (modern) *Fagus* by 10 Ma and that of the earliest Fagoideae by 30 Ma. The earliest Fagoideae pollen from the Campanian of North America differs from its single modern genus *Fagus* by its markedly thicker pollen wall, a feature also seen in fossil and extant Castaneoideae. This suggests that a thick type 1 foot layer is also the plesiomorphic feature in Fagoideae although not seen in any of its living representatives. The Danian *Fagus* pollen of Greenland differs in size from those of modern species but is highly similar to that of the western North American early Eocene *F. langevinii*, the oldest known beech so far. Together with the *Quercus* pollen record, absent in the Campanian and Danian formations but represented by several types by the middle Eocene, this confirms recent dating estimates focussing on the genera *Fagus* and *Quercus*, while rejecting estimates from all-Fagales-dated trees as too young. The basic Castaneoideae pollen type, still found in species of all five extant genera of this putatively paraphyletic subfamily, represents the ancestral pollen type of most (modern) Fagaceae (Trigonobalanoideae, Castaneoideae, Quercoideae).

KEYWORDS: oldest modern Fagaceae, dispersed pollen, scanning electron microscopy, plant evolution, Campanian, Danian

INTRODUCTION

With ten genera, five of which are monotypic (*Chrysolepis*, *Notholithocarpus*, and the Trigonobalanoideae *Colombobalanus*, *Formanodendron*, and *Trigonobalanus*), the Fagaceae are a relatively small eudicot (eurosid) family. Despite this, they are one of the most important Northern Hemispheric tree families. The family includes genera that are dominant or common elements in mesophytic-temperate forests (*Castanea*, *Fagus*, *Quercus*), commonly are codominant in the Laurisilva (*Castanopsis*, *Quercus*), or may be found as accessory elements in tropical lowland and mid-altitude forests (*Castanopsis*, few *Quercus*, *Lithocarpus*). *Fagus* and *Quercus* are among the most economically important north-temperate deciduous trees. Oak (*Quercus*) is the largest tree genus in the Northern Hemisphere, with more than 400 accepted species. Except for the position of *Fagus* as a genetically distinct sister to the remainder of the family (Manos et al. 2001; Fig. 1 based on the oligogene data used by Li et al. 2004), the intergeneric relationships have remained unclear to some degree (Manos et al. 2008, Oh & Manos 2008, Grimm & Denk 2010). The main problem of molecular phylogenies is that the signal in the commonly used chloroplast data, also used in all-Fagales dating approaches (Sauquet et al. 2012, Xiang et al. 2014, Xing et al. 2014, Larson-Johnson 2016), appears to be decoupled from the systematic and phylogenetic relationships in Fagaceae. Highly similar to identical plastid haplotypes can be found in different genera, and are commonly shared by otherwise distinct, based on morphology and nuclear sequence data, evolutionary lineages. This is well documented for the largest genus *Quercus* at various levels (Kanno et al. 2004, Neophytou et al. 2010, Simeone et al. 2013, Simeone et al. 2016b), but also for *Fagus* species in China (Zhang et al. 2013) and Japan (Fujii et al. 2002). A similar situation is found in *Nothofagus* (Acosta & Premoli 2010, Premoli et al. 2012), a South American genus of the Nothofagaceae, a family of four modern genera (Heenan & Smissen 2013) representing the first branch in the Fagales subtree (Stevens 2001 onwards, Li et al. 2004, APG III 2009). Hence, phylogenetic research on the largest genus, *Quercus*, has increasingly focussed on the nuclear genome (Manos et al. 2001, Denk et al. 2005, Oh & Manos 2008, Grimm & Denk 2010, Hipp et al. 2014, Hubert et al. 2014, Hipp and co-workers, work in progess). Essentially, the compiled molecular data indicate that the Castaneoideae (*Castanea*, *Castanopsis*, *Chrysolepis*, *Lithocarpus*, *Notholithocarpus*) are a paraphyletic group comprising genera more (*Castanea*, *Castanopsis*, *Notholithocarpus*) or less (*Chrysolepis*, *Lithocarpus*) close to *Quercus.* The Eurasian *Castanea* and *Castanopsis* are likely sister genera, and share plastids with affinity to the 'Old World' or mid-latitude clade of oaks (*Quercus* Group Cerris, Cyclobalanopsis and Ilex), and *Notholithocarpus* is particularly close to the 'New World' or high-latitude clade of oaks (*Quercus* Group Lobatae, Protobalanus, Quercus; Manos et al. 2008, Simeone et al. 2016b). The three monotypic trigonobalanoid genera *Colombobalanus*, *Formanodendron*, and *Trigonobalanus*, are strongly isolated from this complex and from each other, and probably represent a species-depleted sister lineage to the core Fagaceae, i.e. Castaneoideae + Quercoideae (Manos et al. 2001, Manos et al. 2008, Oh & Manos 2008, Grimm & Denk 2010). The family's type genus, *Fagus* (beech), is a distant relative of the other Fagaceae: the phylogenetic-genetic distance between *Fagus* and the most recent common ancestor of all other Fagaceae is equal to or higher than that between, for example, Juglandaceae and Myricaceae or Betulaceae and Ticodendraceae (monotypic)/Casuarinaceae (Fig. 1, see also File S2[*]; Simeone et al. 2016a). However, the oldest unambiguous records of all modern genera with a studied fossil record consistently fall into the same time, the Eocene (see fig. 14 in Grímsson et al. 2015).

Because of parallelisms and convergent evolution, the rich macrofossil record of the Fagaceae has been difficult to assess for molecular dating analyses, particular when these are exclusively based on chloroplast data that are incongruent with relationships suggested by nuclear sequences (e.g. Xiang et al. 2014, Larson-Johnson 2016). On the other hand, pollen morphologies are highly conserved within the Fagaceae (Tab. 1), and diagnostic when studied using high-resolution scanning electron microscopy (Praglowski 1982, 1984, Harada et al. 2003, Denk & Grimm 2009b). The recognition that pollen morphology is highly diagnostic for molecularly supported infrageneric groups of oaks (Denk & Grimm 2009b) eventually led to the reconciliation of the fossil record and molecular dating estimates (Hubert et al. 2014, Grímsson et al. 2015). Remarkably, recent studies providing dated trees for the Fagales (Sauquet et al. 2012, Xiang et al. 2014, Xing et al. 2014, Larson-Johnson 2016) did not make use of the fossil pollen record of Fagaceae or most other Fagales. Considering all available evidence (macro-, meso- and microfossil record; phylogenetic relationships inferred using nuclear data sets), it is clear that the modern genera and main intrageneric lineages of oaks were evolved by the Eocene

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[*] File S2 available on page http://botany.pl/images/ibwyd/acta_paleo/Acta_Paleobot_56_2_Grimsson_et_al_S2.pdf

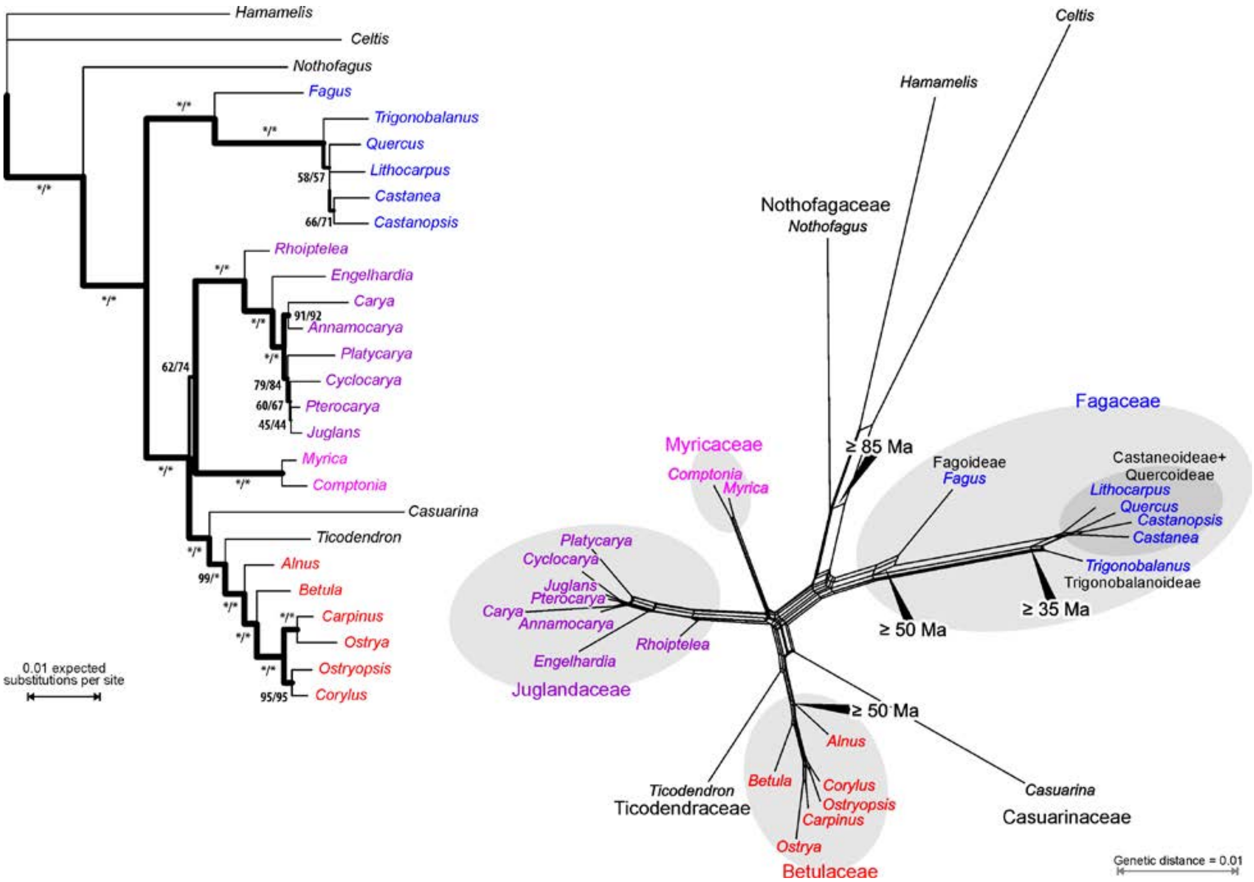

Fig. 1. Phylogenetic inferences highlighting the absolute genetic relatedness of most Fagales genera, based on the matrix by Li et al. (2004). Shown is a phylogenetic network based on model-based distances (right) and a traditional maximum likelihood tree (left; values at branches indicate non-parametric bootstrap support from a partitioned and unpartitioned analysis). The tree equals the cladogram shown in Li et al. (2004), which still is the basis for the classification of the order (Stevens 2001 onwards; APG III 2009). Note the substantial genetic (phylogenetic network) and phylogenetic distance (maximum likelihood tree) between *Fagus* and other Fagaceae, matching that of interfamily distances in the rest of the Fagales. Selected minimum age constraints used in all-Fagales dating studies are indicated. See File S2 for details on methodology and data

(Hubert et al. 2014, Grímsson et al. 2015; and references therein) and that all modern Fagaceae genera formed during the Paleogene.

Grímsson et al. (2015) documented a pollen flora rich in Fagaceae from the late middle to early late Eocene (42–40 Ma) Hareøen Fm, Qeqertarsuatsiaq Is. (Hareøen), western Greenland, including (i) *Fagus*, (ii) *Eotrigonobalanus*, an extinct Fagaceae lineage, (iii) representatives of the Castaneoideae including pollen with affinity to modern species of *Castanea* and possibly *Castanopsis*, and (iv) several types of ancestral and derived (modern) oak (*Quercus*) pollen. Here we investigate the diversity of Fagaceae in a ca 20 Ma older formation from the same geographic region, the Danian (early Paleocene), 64–62 Ma, Agatdal Fm (Grímsson et al. 2016b), complemented by palynological data from Campanian and Eocene localities of (north-)western North America studied for the first time using SEM.

The earliest fossil record of Fagaceae dates back to the Coniacian (Takahashi et al. 2008, Denk & Tekleva 2014). Reproductive structures of Coniacian Fagaceae have pollen that is very similar to modern pollen of Castaneoideae. This pollen type continues to be the most common Fagaceous pollen throughout the Cretaceous and Paleocene. Therefore, we were particularly interested in assessing the pollen diversity of Fagaceae representing this time period. We compare Campanian, Danian, and Eocene Fagaceae assemblages and discuss possible biological affinities of the leaf type *Fagopsiphyllum*. The likely convergent evolution of deciduous leaves in the Fagaceae at different time periods is briefly discussed. We recognise a new extinct Fagaceae genus, *Paraquercus*, based on fossil pollen from the Upper Cretaceous of Wyoming, and the Eocene of British Columbia and western Greenland. Our findings are furthermore discussed in the light of previously proposed molecular

Table 1. Traditional classification and main pollen types of Fagaceae

Subfamily	Status	Genus	Infrageneric group, informal subgenus	Shape	P (µm)	E (µm)	P/E
Fagoideae	monophyletic	*Fagus*	Subgenus Engleriana	spheroidal	28–37	32–33	0.86–1.11
			Subgenus Fagus	spheroidal	33–42	35–44	0.86–1.14
Trigonobalanoideae	monophyletic	*Colombobalanus*		prolate	25–31	18–21	1.23–1.55
		Formanodendron		spheroidal	23–29	25–29	0.88–0.96
		Trigonobalanus		spheroidal	25–28	23–26	1.10–1.18
Castanoideae	paraphyletic	*Castanea*		prolate	14–19	10–16	1.25–1.70
		Castanopsis		prolate	16–23	10–17	1.35–2.00
		Chrysolepis		prolate			
		Lithocarpus		prolate to spheroidal	13–24	10–17	1.12–2.08
		Notholithocarpus		prolate	17–19	9–14	1.4
Quercoideae	probably monophyletic	*Quercus*	Group Cyclobalanopsis	spheroidal	19–33	17–33	1.00–1.12
			Group Cerris	spheroidal	26–40	24–38	1.05–1.08
			Group Ilex	spheroidal to prolate	18–38	14–34	1.10–1.29
			Group Protobalanus	prolate	20–30	14–23	1.30–1.43
			Group Quercus	spheroidal	23–50	21–46	1.07–1.10
			Group Lobatae	prolate	36–42	22–26	1.60–1.63

divergence estimates for the Fagaceae subtree, which vary remarkably depending on the data sets used for inference (Tab. 2).

MATERIAL AND METHODS

PALAEOPALYNOLOGICAL SAMPLES

The investigated material originates from four different localities: the Late Cretaceous (Campanian) Eagle Fm, Elk Basin, Wyoming (palynological samples); the early Paleocene (Danian) Agatdal Fm (and/or Eqalulik Fm), Nuussuaq Basin, western Greenland (macrofossils and palynological samples); the middle Eocene (late Ypresian) Allenby Fm, Princeton Basin, British Columbia (palynological samples); and the middle Eocene (latest Lutetian, early Bartonian) Hareøen Fm (macrofossils and palynological samples), Nuussuaq Basin.

GEOLOGICAL BACKGROUND

The Elk Basin is a valley bordering the Wyoming-Montana state boundary in the north-western United States (44°59′N/108°52′W; see File S1[**]). The Elk Basin is a breached and eroded anticline comprising several outcrops with both marine and terrestrial Upper Cretaceous to Paleogene sedimentary rocks. The Campanian Eagle Fm is divided into two units: a lower unit, the Virgelle Sandstone Member and an upper unit, the Upper Eagle Beds (Hicks 1993, Van Boskirk 1998). All plant macrofossils described by Van Boskirk (1998) and the palynological samples used for this study originate from the upper part of the Upper Eagle Beds. Biostratigraphic, magnetostratigraphic, and chronometric dating studies (see Hicks 1993, Van Boskirk 1998) suggest that the plant-bearing unit of the Eagle Fm is of early Campanian age (82–81 Ma). For a more detailed geological background and previous work on the palaeoflora see Hicks (1993), Van Boskirk (1998), and Manchester et al. (2015).

The material of the early Paleocene (Danian) Agatdal Fm (and/or Eqalulik Fm) of the Nuussuaq Basin originates from the Agatdalen valley, situated in the central part of the Nuussuaq Peninsula, western Greenland. Pollen was extracted from phosphoritic nodules from the Agatdal Fm found at Turritellakløft (Big section). The macrofossils are from three localities: the Agatkløft and Qaarsutjægerdal (Big section) localities, Agatdal Fm, and the Kangersooq (Qulerुarsuup isua) locality representing either the Agatdal Fm or the slightly younger Eqalulik Fm. Magnetostratigraphic and chronometric dating of overlying and interspersing volcanic strata indicate an age of

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[**] File S1 available on page http://botany.pl/images/ibwyd/acta_paleo/Acta_Paleobot_56_2_Grimsson_et_al_S1.pdf

Table 1.Continued

	P.v.	Eq.v.	Apertures	Sculpturing (SEM)	Reference
	convex triangular to circular	circular to elliptic	3-colporate	irregular rugulate	Praglowski 1982, Denk 2003
	convex triangular to circular	circular to elliptic	3-colporate	irregular rugulate	Praglowski 1982, Denk 2003
	lobate to triangular lobate	elliptic	3-colporoidate (3-colpate)	(micro)verrucate, verrucae being fused tufts and elongated	Nixon & Crepet 1989, Wang et al. 1998
	triangular	circular to elliptic	3-colporate	(micro)verrucate, verrucae being fused tufts and elongated	Wang & Chang 1988, Nixon & Crepet 1989, Wang et al. 1998
	circular to lobate	circular to elliptic	3-colporate	granulate	Nixon & Crepet 1989, Wang et al. 1998
	circular to lobate	elliptic	3-colporate	rugulate, perforate, fossulate	Praglowski 1984
	circular to lobate, convex triangular	elliptic	3-colporate	rugulate, perforate, fossulate, some with secondary striation	Praglowski 1984
	circular to lobate	elliptic	3-colporate	rugulate, perforate, fossulate	Praglowski 1984
	lobate to circular	elliptic	3-colporate	rugulate, fossulate	Praglowski 1984
	lobate to circular	elliptic	3-colporate	rugulate, fossulate	Praglowski 1984, Manos et al. 2008
	lobate to circular	elliptic to circular	3-colpate (?3-colporoidate)	microechinate, microechini being the tips of single rugulae (rodlike vertical)	Denk & Grimm 2009, Denk & Tekleva 2014
	lobate to circular	elliptic to circular	3-colpate (?3-colporoidate)	verrucate, scattered verrucae being simple tufts	Denk & Grimm 2009, Denk & Tekleva 2014
	lobate to circular	elliptic to circular	3-colpate (?3-colporoidate)	(micro)rugulate, perforate, microrugulae agglomerate and form desert-rose-like structures	Denk & Grimm 2009, Denk & Tekleva 2014
	lobate to circular	elliptic	3-colpate (?3-colporoidate)	(micro)verrucate, verrucae being slightly convex tufts (rodlike masked)	Denk & Grimm 2009, Denk & Tekleva 2014
	lobate to circular	elliptic to circular	3-colpate (?3-colporoidate)	(micro)verrucate, verrucae being single or fused tufts	Denk & Grimm 2009, Denk & Tekleva 2014
	lobate to circular	elliptic	3-colpate (?3-colporoidate)	(micro)verrucate, verrucae being single or fused tufts	Denk & Grimm 2009, Denk & Tekleva 2014

64–62 Ma for the Agatdal Fm and 62–61 Ma for the overlying Eqalulik Fm. For a detailed geological background (including maps), stratigraphic framework (including profiles), position of outcrops, age correlations, collection history, previous palaeobotanical work, origin of macrofossils and phosphoritic nodules, and laboratory treatment of palynological samples see Grímsson et al. (2016b).

In the Princeton Basin, an outcrop of the middle Eocene Allenby Fm, the upper part of the Princeton Group, is located along the east bank of the Similkameen River, ca 8.4 km south of the town of Princeton, British Columbia, Canada (49°22′N, 120°32′W; see File S1). The uppermost part of the Allenby Fm, the Ashnola Shale, comprises silicified and fossil-rich sedimentary rocks known as the Princeton Chert beds (Read 2000, Smith & Stockey 2007, Mustoe 2011). The Princeton Chert is composed of at least 49 rhythmically bedded chert beds and carbonaceous interbeds (Mustoe 2011). Our samples originate from chert-bed 43, from the uppermost quarter of the Princeton Chert unit. The age of the Princeton Chert is not fully settled (Fig. S3 in File S1), with older K-Ar dates indicating younger ages than more recent U-Pb dates for several localities of the Okanagan belt (Denk & Dillhoff 2005 for McAbee; Moss et al. 2005 for a general overview). With respect to the stratigraphic position of the Princeton Chert beds in the uppermost part of the Allenby Fm, we follow Moss et al. (2005, fig. 2) and assume an age of ca 48 Ma.

The late Lutetian-early Bartonian Hareøen Fm crops out at the Aamaruutissa locality on the island of Qeqertarsuatsiaq, western Greenland. The palynological samples originate from a resinite-rich coal bed in the lowest part of the sedimentary succession, and the macrofossils were collected in the lowest, middle and uppermost part of the succession (see fig. 5 in Grímsson et al. 2015). The sediments comprising the plant fossils are considered to be ca 42–40 Ma, based on chronometric dating of overlying lavas (38.74±0.23 Ma; Larsen et al. 2015) and the pollen/spore spectrum. For a detailed geological background, stratigraphic framework, and information on previous palaeobotanical work see (Grímsson et al. 2015).

SAMPLE PREPARATION AND THE SINGLE-GRAIN METHOD

The palynological samples were processed according to the protocols outlined in Grímsson et al. (2008; sediments), Grímsson et al. (2011; nodules), and Denk et al. (2012; nodules). All fossil pollen grains were studied by both light and electron microscopy using the single-grain method by Zetter (1989).

CONSERVATION OF FOSSIL MATERIAL

All the macrofossils figured and mentioned in this study from Agatdalen are housed in the collection of the Geological Museum in Copenhagen (MGUH) that

Table 2. Divergence ages for the Fagaceae subtree published in the last five years. Abbreviations: **FBD** – fossilised birth-death dating, **ND** – node dating, **PL** – penalised likelihood, **TE** – total evidence dating, **UC** – uncorrelated clock

Study	Taxon set	*Fagus* root age	*Fagus* crown age	Castanoideae crown age	*Quercus* root age
Sauquet et al. (2012), “safe” ingroup and outgroup constraints; PL-ND	all Fagales	82.3 (89–76.2)	[N/A]	[fixed to 43.8]	[not reported]
—; UC-ND (log-normal priors)	all Fagales	84.7 (103.6–64.2)	[N/A]	48.7 (58.1–43.8)	31.4 (interval not reported)
Xing et al. (2014); UC-ND (uniform priors)	all Fagales	83.4 (97.8–65.5)	16.2 (24–9)	46.2 (56.3–37.2)	~ 36 (interval not reported)
—; UC-ND (log-normal priors)	all Fagales	68.1 (85.5–64)	15.7 (18.5–8.42)	37.2 (38.1–37.2)	[not reported]
Xiang et al. (2014); UC-ND	all Fagales	82.8 (87.1–76.6)	17.2 (24.2–7.9)	56.4 (66.1–50.6)	[= Castanoideae crown]
Larson-Johnson (2016), TE	all Fagales	78 (88–70)	[N/A]	47 (53–44)	20 (31–9)
Hubert et al. (2014), constraint 1 (best overall fit); UC-ND	*Quercus* and sister taxa	[N/A]	[N/A]	[N/A]	54 (68–48)
Renner et al. (2016); FBD	*Fagus*	[N/A]	53 (62–43)	[N/A]	[N/A]

is part of the Natural History Museum of Denmark. The macrofossils from Qeqertarsuatsiaq are also housed in the Copenhagen museum or in the collection of the Swedish Museum of Natural History in Stockholm (S). Numbers of the Copenhagen specimens sometimes refer to a single fossil, or part and counterpart, or a block with several fossils, or part and counterpart blocks with numerous fossils. Hence, different fossil leaves figured here can have the same MGUH number when occurring on the same hand-specimen or accompanying counterpart. SEM stubs with pollen produced under this study are stored in the collection of the Department of Palaeontology, University of Vienna, Austria, under accession numbers IPUW 7513/161–208.

POLLEN AND MACROFOSSIL DESCRIPTIONS

Terminology for angiosperm leaf morphology follows mostly Hickey (1973) and Ellis et al. (2009). The pollen descriptions include diagnostic features observed under LM and SEM, with terminology following Punt et al. (2007) and Hesse et al. (2009). All measurements of polar axis and equatorial diameter were made in LM. Plates showing dispersed pollen grains exhibit the same individual pollen grain photographed with LM, usually in polar and equatorial view, and SEM, overview and close-up displaying the characteristic sculpture of the pollen surface.

SYSTEMATIC PALAEOBOTANY

The description starts with extinct genera in alphabetical order, followed by extant genera arranged according to alphabetical order of subfamilies. When present, leaves are described after the corresponding pollen. Leaf descriptions are based on all fossil specimens encountered from the particular formation(s). Synonym lists include only taxa/specimens previously described from the same localities/formations. Pollen types (PT) and leaf morphotypes (LMT) are labelled by the taxonomic rank (family, subfamily, genus) to which they can be assigned.

Family FAGACEAE Dumort.

Genus ***Eotrigonobalanus***
Walther & Kvaček (extinct)

Eotrigonobalanus PT

Pl. 1, figs 4–6; Pl. 3, figs 1–6; Pl. 12, figs 4–6

Description. Pollen, monad, prolate, circular to lobate in polar view, elliptic in equatorial view; polar axis 17–23 µm long, equatorial diameter 12–16 µm; tricolporate, colpi long, pori elongated rectangular (lalongate), nexine slightly thickened around pori (LM); exine 0.8–1.2 µm thick, nexine slightly thinner than sexine; tectate; sculpture scabrate in LM, microrugulate, perforate in SEM, microrugulae twisted and interwoven, microrugulae 0.3–1.1 µm long, 80–170 nm wide, microrugulae fused forming larger rope-like rugulae (SEM).

Localities/age. Elk Basin, Wyoming (82–81 Ma); Turritellakløft (Big section; Agatdalen), western Greenland (64–62 Ma); Princeton Chert, British Columbia (ca 48 Ma); Qeqertarsuatsiaq, western Greenland (42–40 Ma; Grímsson et al. 2015, figs 6a–f).

Remarks. Very similar to identical dispersed fossil pollen grains have been documented from the Paleocene/Eocene boundary of Salzburg, Austria (Hofmann 2010, Hofmann et al. 2011), the early Oligocene of Cospuden, Germany, as *E. eiszmannii* Walther & Kvaček (Denk et al. 2012), and from middle Miocene sediments of Poland (Kohlman-Adamska & Ziembińska-Tworzydło 2000, Stuchlik et al. 2007). The same type of pollen has also been described from clumps attached to fossil leaves of *Eotrigonobalanus furcinervis* from the Oligocene of Witznitz, Germany, hence its generic association (Walther & Zetter 1993). The pollen grains presented here represent the oldest reports of *Eotrigonobalanus* so far.

Pollen found in-situ in catkins described as *Amentoplexipollenites catahoulaensis* Crepet & Nixon from the middle to late Oligocene of Texas (Crepet & Nixon 1989) is indistinguishable from pollen of *Eotrigonobalanus* regarding its size, form, and sculpture. *Amentoplexipollenites catahoulaensis* mainly differs from *Eotrigonobalanus* PT by its much thicker nexine. The inflorescence has been related to the modern genus *Trigonobalanopsis*.

Eotrigonobalanus leaf morphotype

Pl. 4, figs 1–6; Pl. 5, figs 1–9

1963 *Quercophyllum furcinervis americana* (Rossm.) Knowlton – Koch: p. 37, pl. 6, figs 4–6, pl. 7, figs 1–3.

1963 *Cupuliferites angmartusuticus* Koch – p. 40, pl. 8, fig. 4, pl. 9, fig. 1, pl. 10, figs 1, 2.

1963 *Quercus drymeia* Unger – Koch: p. 94, pl. 51, figs 2, 3.

Material. Specimens MGUH 10376, MGUH 10377, MGUH 10378, MGUH 10379, MGUH 10380, MGUH 10383, MGUH 10384, MGUH 10385, MGUH 10386, MGUH 10388, MGUH 10461, MGUH 10461, MGUH 10462, MGUH 10462.

Description. Leaves petiolate, petiole up to 27 mm long, lamina simple, 45 to 160 mm long, 14 to 62 mm wide, length/width ratio 2.4 to 6.2, widest in second and third quartile of lamina; lamina narrow ovate, narrow elliptic, to oblanceolate, apex acute, base acute to decurrent, margin partially or entirely toothed; teeth dentate to serrate, small to large, basal side much longer than apical side, basal side mostly convex, apical side mostly concave or straight, tooth apex simple to spinose, sinuses between teeth wide and rounded, teeth served by secondary veins, one tooth per secondary vein; primary venation pinnate, moderate in thickness, rarely stout, straight to gently curved; secondary venation craspedodromous, secondary veins moderate in thickness, straight to gently curved upwards, occasionally curving outwards when entering teeth, 7 to 12 pairs diverging from midvein at intervals of 9 to 18 mm in middle part of lamina, arising at angles of 30° to 50° from midvein, occasionally more acute on one side of lamina, usually alternate, occasionally subopposite at leaf base.

Localities/age. Agatkløft (Agatdalen), western Greenland (64–62 Ma); Kangersooq (Qulerarsuup isua, Agatdalen), western Greenland (64–62 or 62–61 Ma); Qaarsutjægerdal (Big section, Agatdalen), western Greenland (64–62 Ma).

Remarks. *Eotrigonobalanus* is a well-known extinct genus comprising extremely heterogeneous leaf forms occurring mostly in middle Eocene to early Oligocene sediments of Europe (e.g. Kvaček & Walther 1989, Palamarev & Mai 1998) and extending to the Miocene (e.g. Velitzelos et al. 2014). The leaves from the Agatdalen area show the same morphological variability as observed in European Paleogene floras and are among the earliest records of this genus.

Genus ***Fagopsiphyllum*** Manchester (extinct)

Fagopsiphyllum groenlandicum (Heer) Manchester

Pl. 6, figs 1–8; Pl. 7, figs 1–8; Pl. 14, fig. 3; Pl. 15, figs 1–6

1883 *Quercus grönlandica* Heer – p. 89, pl. 89, figs 4, 8; pl. 91, fig. 1.

1963 *Quercophyllum groenlandicus* (Heer) Koch – p. 34, pl. 5, figs 1–4; pl. 6, figs 1–3.

Material. Specimens MGUH 6538, MGUH 6542, MGUH 10369, MGUH 10370, MGUH 10371, MGUH 10372, MGUH 10373, MGUH 10374, MGUH 10375, MGUH 10397, MGUH 10411, MGUH 10428, MGUH 10437.

Description. Leaves petiolate, petiole short, up to 5 mm long, lamina simple, 40 to 130 mm long, 21 to 96 mm wide, length/width ratio 1.9 to 2.1, lamina elliptic, apex acute, base decurrent to obtuse, margin toothed, teeth dentate to serrate, large, teeth of similar size and shape, basal side equal to twice as long as apical side, basal side convex to straight, apical side straight to convex, tooth apex simple with nonglandular, nonspinose apices, sinuses between teeth narrow to wide angular, teeth occurring at regular intervals, served by secondary veins, one tooth per secondary vein; primary venation strictly regularly pinnate, midvein moderate in thickness, straight to gently curved; secondary venation craspedodromous, secondary veins of moderate thickness, evenly spaced, parallel, mostly straight, occasionally slightly recurved at base, sometimes curving upwards when entering teeth, 12 to 18 pairs diverging from midvein at intervals of 3.5 to 12 mm in middle of lamina, arising at angles of 40° to 65° from midvein, sometimes more acute on one side of the lamina, opposite to alternate, each secondary vein terminating in a marginal tooth; pair of narrow basal veins (opadial veins) running along base margin, not serving teeth; tertiary venation percurrent, veins mostly simple, sometimes branched, straight to sinuous, 5 to 7 tertiary veins per 1 cm secondary vein in large leaves, originating at right angles from both the admedial and exmedial side of secondary veins.

Note. The most typical leaf fossils of this type are allegedly from Qeqertarsuatsiaq (old name: Hareøen; Pl. 15, figs 1–5) and were first described by Heer (1883, pl. 89, figs 4 [MGUH 6538], 8 [MGUH 6542]). Inspection by FG of all museum specimens from the Cainozoic of western Greenland (housed in Copenhagen, Dublin, London, Stockholm) suggests that these specimens are not from Qeqertarsuatsiaq: the sediment in which these fossils are preserved does not correspond to any material with a genuine "Hareøen" (Danish for Qeqertarsuatsiaq) locality/collecting label, but looks identical to that known from the Upper Atanikerluk A locality (Quikavsak Fm; same age as Agatdal Fm) situated on the south coast of Nuussuaq. The MGUH 6542 specimen has an original Atanikerluk locality/collecting label that somehow must have been missed by Heer; the MGUH 6538 specimen has no locality/collecting label. Genuine "Hareøen" specimens in the Copenhagen collection described by Heer (1883) are all from the same collector (Knud Johannes Vogelius Steenstrup) and have a corresponding locality/collecting label signed with the initials KJVS. Specimen MGUH 6534 from Qeqertarsuatsiaq identified as *Quercus grönlandica* by Heer (1883, pl. 89, fig. 1a) has no margin or apex preserved and is of uncertain affinity, and is not included in our synonym list for this locality. The only convincing *Fagopsiphyllum* leaf fossil from Qeqertarsuatsiaq is specimen MGUH 6550 (see Pl. 14, fig. 3; Pl. 15, fig. 6; also pl. 91, fig. 1 in Heer 1883). Additional large-leaved Fagales/Fagaceae also occur in Qeqertarsuatsiaq (or Upper Atanikerluk A), but their venation and dentition differs from those of *Fagopsiphyllum*: some have rounded sinuses between teeth (Pl. 14, figs 1, 2), others also have secondary teeth present (Pl. 14, fig. 4; Pl. 15, fig. 7).

Localities/age. Kangersooq (Qulerarsuup isua, Agatdalen), western Greenland (64–62 or 62–61 Ma); Upper Atanikerluk A (south coast of Nuussuaq), western Greenland (64–62 Ma); Qeqertarsuatsiaq, western Greenland (42–40 Ma).

Remarks. The leaf fossils from Agatdalen were originally described as *Quercophyllum groenlandicus* by Koch (1963). The form of the leaves and their venation is strikingly similar to fossil leaves originally assigned to the extinct genus *Fagopsis* described from the late Eocene of Colorado, USA (e.g. Manchester & Crane 1983). As a result, the Agatdalen material was included into *Fagopsis* by Boulter & Kvaček (1989) along with material from the Paleocene of the Isle of Mull. Manchester later excluded Paleocene leaves of this type from high arctic areas from *Fagopsis* and placed them within their own genus, *Fagopsiphyllum* (Manchester 1999), based on the observation that the distinctive fruits of *Fagopsis* have never been found in any of the Paleocene high arctic material (Heer 1868, Brown 1962, Koch 1963, Manchester & Crane 1983, Boulter & Kvaček 1989) from North America, Greenland, and the British Isles. Recently, Bouchal et al. (2014) described the characteristic pollen, both in situ from staminate inflorescenses and dispersed, of *Fagopsis* from its type locality using SEM, a pollen type not found in the Paleocene of Agatdalen. The lack of the diagnostic fruits and pollen of *Fagopsis* in the Greenland material provides further support for Manchester's (1999) opinion that these leaves belong to a different taxon.

Genus ***Paraquercus*** gen. nov. (extinct)

Diagnosis. Fagaceae pollen; rugulate with distinctive verrucate suprasculpture; verrucae composed of very narrow, rod-like, regularly arranged rugulae, giving the pollen surface the appearance of a finely braided clew of yarn; rugulae in groups, not or rarely intertwining, parallel to radially arranged (oriented).

Etymology. Referring to the basic similarity of the pollen ornamentation with that of the putatively ancestral (plesiomorphic) pollen type of *Quercus*, pollen of *Quercus* Group Ilex, while not being produced by an oak.

Type species. *Paraquercus campania* sp. nov.

General remarks. Originally (Grímsson et al. 2015), we considered the pollen found in the Eocene Hareøen Fm (*Quercus* sp. 5, included here in the new species *Paraquercus eocaena*) to represent a relatively ancestral, extinct lineage of oaks, as it shares the basic organisation of pollen of *Quercus* Group Ilex, which represents the ancestral (plesiomorphic) oak pollen type (Denk & Grimm 2009b), and lacks the characteristics of pollen of *Eotrigonobalanus* (Tab. 1). The latter is the Fagaceae genus which, regarding pollen morphology, is most similar to pollen of oaks. Because the new pollen from the Campanian Eagle Fm and the Lutetian (middle Eocene) Princeton Chert clearly belongs to the same lineage as the pollen grain reported earlier from Qeqertarsuatsiaq, Greenland, an association of this pollen type with *Quercus* appears highly unlikely (discussed below). We regard the differences from pollen of *Eotrigonobalanus* sufficient to erect a new genus, but do not exclude the possibility that both extinct genera belong to the same evolutionary lineage. Furthermore, pollen of the extinct Fagaceae genera *Eotrigonobalanus*, *Fagopsis*, and *Trigonobalanopsis*, among others, have been linked to macrofossils, which at this point is not possible for *Paraquercus*.

Paraquercus campania sp. nov.

Pl. 1, figs 1–3

Diagnosis. Space between (micro)rugulae partly obscured by sporopollenin; from the Cretaceous.

Holotype. IPUW 7513/161 (Pl. 1, figs 1–3).

Type locality. Elk Basin, Wyoming, boundary to Montana; ca 44° 59′ N, 108° 52′ W.

Stratigraphy. Upper Eagle beds, Eagle Fm (File S1)

Age. 82–81 Ma

Species epithet. After the time period of the pollen-bearing sedimentary rocks.

Description. Pollen, monad, prolate, lobate in polar view, elliptic in equatorial view; polar axis 20–21 µm long, equatorial diameter 15–16 µm; tricolporate, colpi long, pori lalongate, nexine slightly thickened around pori (LM); exine 0.9–1.0 µm thick, nexine thinner or as thick as sexine (LM); tectate; sculpture scabrate to verrucate in LM, verrucate, (micro)rugulate, perforate in SEM, verrucae composed of very narrow rod-like (micro)rugulae, (micro)rugulae 0.5–1.3 µm long, 80–110 nm wide, (micro)rugulae in groups, parallel to radially arranged (SEM).

Remarks. *Paraquercus campania* represents one of the earliest reports of Fagaceae. It differs from its 30–40 Ma younger counterparts (*P. eocaena*) by showing a less delicate pollen surface (rugulae less distinct in general, fewer perforations). *Paraquercus* pollen is very similar to pollen of *Eotrigonobalanus* but differs mainly in the sculpture type. The (micro) rugulae are usually much longer in *Paraquercus* and they are arranged into large verrucate units, but form narrower/oblong rope-like rugulate units in *Eotrigonobalanus* (SEM).

Paraquercus eocaena sp. nov.

Pl. 12, figs 1–3

2015 *Quercus* sp. 5 – Grímsson et al.: p. 827, figs 15a–c.

Diagnosis. Space between (micro)rugulae not obscured by sporopollenin; from the Paleogene.

Holotype. IPUW 7513/197 (Pl. 12, figs 1–3).

Type locality. Princeton Chert, Princeton Basin, British Columbia, Canada; ca 49°22′N, 120°33′W.

Stratigraphy. Princeton Chert bed 43, Ashnola Shale (informal), Allenby Fm, Princeton Group (File S1).

Age. ca 48 Ma.

Species epithet. After the time period of the pollen-bearing sedimentary rocks.

Description. Pollen, monad, prolate, lobate in polar view, elliptic in equatorial view; polar axis 17–25 µm long, equatorial diameter 15–19 µm; tricolporate, colpi long, pori lalongate, nexine slightly thickened around pori (LM); exine 1.0–1.6 µm thick, nexine thinner or as thick as sexine (LM); tectate; sculpture scabrate to verrucate in LM, verrucate, (micro) rugulate, perforate in SEM, verrucae composed of very narrow rodlike (micro)rugulae, (micro) rugulae 0.5–2.1 µm long, 90–140 nm wide, rugulae in groups, parallel to radially arranged (SEM).

Remarks. In the Princeton Chert specimens the characteristic pollen surface is more distinct than in its older relative, *Paraquercus campania*, a feature we consider to be an original difference of the grains and not caused by taphonomic processes during fossilization. Also, the rugulae can be much longer in *P. eocaena*, up to 2.1 µm vs 1.3 µm in *P. campania*). This pollen type is also known from slightly younger (42–40 Ma) sediments of Qeqertarsuatsiaq, western Greenland (see figs 15a–c in Grímsson et al. 2015).

Genus ***Trigonobalanopsis*** Kvaček et H.Walther (extinct)

Trigonobalanopsis PT

Pl. 12, figs 7–13

Description. Pollen, monad, prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 18–22 µm long, equatorial diameter 13–16 µm; tricolporate, colpi long, pori small and circular, nexine slightly thickened around pori; exine 0.8–1.0 µm thick, nexine as thick or slightly thicker than sexine (LM); tectate; sculpture psilate in LM, rugulate to microrugulate, perforate in SEM, rugulae irregularly arranged or parallel in small groups, rugulae 0.5–1.5 µm long, 80–140 nm wide, rugulae conspicuously segmented (SEM).

Locality/age. Princeton Chert, British Columbia (ca 48 Ma).

Remarks. Numerous fossil leaves and cupules/fruits of *Trigonobalanopsis* have been documented from Europe and the western part of Russia from late Eocene to Pliocene sediments (summarised in Kvaček & Walther 1988, 1989, Palamarev & Mai 1998). The pollen type belonging to this extinct genus was first described by Walther & Zetter (1993) using pollen clumps adhering to the laminar surface of a *Trigonobalanopsis* leaf. Dispersed *Trigonobalanopsis* pollen grains have been reported from the early Oligocene of Germany (Denk et al. 2012), the early and late Miocene of Austria (Meller et al. 1999, Grímsson et al. 2016a) and the late Miocene of Iceland (Denk et al. 2011). The pollen grains presented here are the first and only reports of *Trigonobalanopsis* from North America, and the earliest pollen record of this genus worldwide. However, the same pollen type can also be found in latest Cretaceous (Timerdyakh Fm; latest Campanian to earliest Maastrichtian; Hofmann & Zetter 2007, 2010) Siberian sediments outcropping at the Tyung River of the Vilui Basin (C.-C. Hofmann, pers. comm., 2016).

Subfamily CASTANEOIDEAE Oerst.

Genus **indet**.

Castaneoideae PT 1

Pl. 1, figs 7–9

Description. Pollen, monad, prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 14–15 µm long, equatorial diameter 10–11 µm; tricolporate; colpi long, pori small and lolongate; exine 0.9–1.1 µm thick (LM), nexine thinner than sexine; tectate; sculpture psilate in LM, rugulate, fossulate, perforate in SEM; rugulae densely packed, irregularly arranged, 100–230 nm wide, stout, sinuous and often branched (bifurcating), with the branches running parallel, rugulae equally developed across entire pollen grain (SEM).

Locality/age. Elk Basin, Wyoming (82–81 Ma).

Remarks. Recent Castaneoideae pollen grains have been studied using LM, SEM, and TEM by e.g. Praglowski (1984) and Wang & Pu (2004). Although the pollen grains of PT 1 fall within the general type of Castaneoideae pollen, its particular sculpture pattern distinguishes it from its modern counterparts. Pollen of extant Castaneoideae can vary substantially in the arrangement and length of rugulae and the distinctness of fossulae separating these. In Castaneoideae PT 1, unusually stout and markedly sinuous rugulae lead to a unique pattern not documented so far for any modern species.

Castaneoideae PT 2

Pl. 1, figs 10–12; Pl. 3, figs 13–15; Pl. 8, figs 1–15; Pl. 12, figs 14–16

Description. Pollen, monad, prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 13–20 µm long, equatorial diameter 9–12 µm; tricolporate, colpi long, pori lalongate, nexine slightly thickened around pori (LM); exine 0.7–0.9 µm thick (LM), nexine thinner than sexine; tectate; sculpture psilate in LM, rugulate, fossulate, perforate in SEM; rugulae densely packed, irregularly arranged or aligned, 130–320 nm wide, stout, sometimes branching (bifurcating), rugulae and fossulae less distinct in polar regions, rugulae fusing along colpi and in central polar area (SEM).

Localities/age. Elk Basin, Wyoming (82–81 Ma); Turritellakløft (Big section; Agatdalen), western Greenland (64–62 Ma); Qeqertarsuatsiaq, western Greenland (42–40 Ma; Grímsson et al. 2015a, figs 8a–l).

Remarks. Differs from Castaneoideae PT 4 and Castaneoideae PT 5 in size and form. Castaneoideae PT 2 can have much longer rugulae than Castaneoideae PT 9; the rugulae are generally broader, such as those in Castaneoideae PT 4. Castaneoideae PT 2 differs from Castaneoideae PT 4 also by more elongated pori. Pollen grains of most extant Castaneoideae species studied so far (Praglowski 1984; comprising all five genera) would fall within Castaneoideae PT 2 as recognised here.

Castaneoideae PT 3

Pl. 9, figs 7–15

Description. Pollen, monad, prolate to spheroidal, outline lobate in polar view, elliptic to circular in equatorial view; polar axis 8–11 µm long, equatorial diameter 5–10 µm; tricolporate, colpi long, pori small (LM); exine 0.7–0.9 µm thick (LM), nexine thinner than sexine; tectate; sculpture psilate in LM, rugulate, fossulate, perforate in SEM; rugulae densely packed, irregularly arranged or aligned, 160–330 nm wide, stout, sometimes branching (bifurcating), rugulae and fossulae less distinct in polar regions, rugulae fusing along colpi and in central polar area (SEM).

Locality/age. Turritellakløft (Big section; Agatdalen), western Greenland (64–62 Ma).

Remarks. This morphotype is very similar to Castaneoideae PT 2, but the pollen grains are much smaller and more spheroidal.

Castaneoideae PT 4 (aff. *Lithocarpus*)

Pl. 10, figs 1–15

Description. Pollen, monad, prolate to spheroidal, outline lobate in polar view, elliptic in equatorial view; polar axis 14–17 µm long, equatorial diameter 12–15 µm; tricolporate, colpi long, pori circular (LM); exine 0.9–1.1 µm thick (LM), nexine thinner than sexine; tectate; sculpture psilate in LM, rugulate, fossulate, perforate in SEM; rugulae densely packed, irregularly arranged, 220–670 nm wide, stout, branching (bifurcating), rugulae fusing along colpi and in central polar area, running in parallel along colpi (SEM).

Locality/age. Turritellakløft (Big section; Agatdalen), western Greenland (64–62 Ma).

Remarks. Differs from Castaneoideae PT 9 in size and form and in sculpture; Castaneoideae PT 4 has much fewer and broader rugulae. Castaneoideae PT 4 pollen has so far only been found in members of the genus *Lithocarpus* (Praglowski 1984).

Castaneoideae PT 5

Pl. 11, figs 1–3

Description. Pollen, monad, prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 19–20 µm long, equatorial diameter 14–15 µm; tricolporate, colpi long, pori small and lolongate, nexine slightly thickened around pori (LM); exine 0.8–1.0 µm thick (LM), nexine thinner than sexine; tectate; sculpture psilate in LM, microrugulate to rugulate, fossulate, perforate in SEM; rugulae densely packed, irregularly arranged, 140–330 nm wide, stout, sinuous and often bifurcating, equally developed across entire pollen grain (SEM).

Locality/age. Turritellakløft (Big section; Agatdalen), western Greenland (64–62 Ma).

Remarks. Like Castaneoideae PT 2–4 and 6, Castaneoideae PT 5 differs from Castaneoideae PT 7–9 in being strictly rugulate with thin/indistinct fossulae. This is a feature also exhibited by all extant members of the Castaneoideae.

Castaneoideae PT 6

Pl. 11, figs 4–6

Description. Pollen, monad, prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 17–18 µm long, equatorial diameter 12–13 µm; tricolporate, colpi long, pori small and lolongate, nexine slightly thickened around pori (LM); exine 0.9–1.0 µm thick

(LM), nexine thinner than sexine; tectate; sculpture psilate in LM, rugulate, fossulate, perforate in SEM, rugulae elongated, 230–410 nm wide, irregularly arranged or aligned, sculpture prominently developed in polar and equatorial regions.

Locality/age. Turritellakløft (Big section; Agatdalen), western Greenland (64–62 Ma).

Remarks. This pollen type is similar to Castaneoideae PT 2 but has lolongate pori, is slightly broader, has wider sculpture elements, and the sculpture is also prominently developed in the polar regions.

Castaneoideae PT 7

Pl. 11, figs 7–9

Description. Pollen, monad, prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 15–16 µm long, equatorial diameter 10–11 µm; tricolporate, colpi long, pori small and lolongate, nexine slightly thickened around pori (LM); exine 0.8–0.9 µm thick (LM), nexine thinner than sexine; tectate; sculpture psilate in LM, intermediate between rugulate, fossulate/highly perforate, and (micro)striato-reticulate in SEM, fossulae composed of series of perforations, rugulae/striae 160–330 nm wide, sculpture prominently developed in polar and equatorial regions.

Locality/age. Turritellakløft (Big section; Agatdalen), western Greenland (64–62 Ma).

Remarks. Castaneoideae PT 7–PT 9 are very similar in LM. In SEM, Castaneoidea PT 7 is structurally intermediate between Castaneoidea PT 6 and Castaneoideae PT 8 and PT 9. Castaneoideae PT 7–PT 9 differ from Castaneoideae PT 1–PT 5 by their partly (micro) striato-reticulate sculpture, and in some case also the outline of the pori.

Castaneoideae PT 8

Pl. 11, figs 10–12

Description. Pollen, monad, prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 18–19 µm long, equatorial diameter 10–11 µm; tricolporate, colpi long, pori small and lolongate, nexine slightly thickened around pori (LM); exine 0.7–0.8 µm thick (LM), nexine thinner than sexine; tectate; sculpture psilate in LM, intermediate between rugulate, highly perforate, partly fossulate, and (micro) striato-reticulate in SEM, rugulae/striae 270–450 nm wide, sculpture prominently developed in polar and equatorial regions.

Locality/age. Turritellakløft (Big section; Agatdalen), western Greenland (64–62 Ma).

Remarks. See remarks for Castaneoideae PT 7.

Castaneoideae PT 9

Pl. 11, figs 13–15

Description. Pollen, monad, prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 19–21 µm long, equatorial diameter 10–11 µm; tricolporate, colpi long, pori small (LM); exine 0.6–0.8 µm thick (LM), nexine thinner than sexine; tectate; sculpture psilate in LM, (micro)striato-reticulate in SEM, striae/muri 200–500 nm wide, sculpture prominently developed in polar and equatorial regions, (micro)striato-reticulum fusing along colpi (SEM).

Locality/age. Turritellakløft (Big section; Agatdalen), western Greenland (64–62 Ma).

Remarks. A (micro)striate-reticulate sculpture identical to that observed in the fossil Castaneoidea PT 9 pollen has not been documented for any extant Castaneoideae species so far. Overall, the pollen represents a more open form of the typical Castaneoideae pollen, in which the usually thin, often minute, rarer indistinct fossulae are widened into small (< 1 µm in diameter) lumina, particularly in the area of the mesocolpium. This is a feature not seen in any fossil and modern Castaneoideae studied so far; thus, the Castaneoideae PT 9 may represent an extinct lineage of castaneoid Fagaceae.

Subfamily FAGOIDEAE K.Koch

Genus **indet**.

Fagoideae PT 1

Pl. 1, figs 13–15; Pl. 2, figs 1–16

Description. Pollen, monad, oblate to spheroidal, outline convex-triangular to circular in polar view, circular to elliptic in equatorial view; polar axis 14–24 µm long, equatorial diameter 15–23 µm wide; tricolporate, colpi long to medium in length, pori elongated rectangular (lalongate), nexine thickened around pori (LM); exine markedly thick (1.3–1.8 µm), nexine slightly thinner than sexine (LM); tectate; sculpture scabrate in LM, rugulate, some grains minutely fossulate in SEM, rugulae short or long, up to 2.5 µm long, 230–360 nm wide, usually sinuous, often multi-branched and intertwined, tips of rugulae not protruding (SEM).

Locality/age. Elk Basin, Wyoming (82–81 Ma).

Remarks. This pollen type shows a considerable size range and arrangement of sculptural elements seen under SEM. The sculpture can be quite open (high relief), with the rugulae at different levels (Pl. 1, fig. 15) as in modern *Fagus*, or more closed, with the rugulae at the same level separated by minute fossulae throughout (Pl. 2, fig. 3), a feature shared with Fagoideae PT 2. The rugulae can be covered by sporopollenin to a limited degree (Pl. 2, fig. 14). Comparable variation in sculpture has been observed in pollen from the same modern or extinct species (Denk 2003) and within the dispersed *Fagus* pollen assemblages of Qeqertarsuatsiaq (middle Eocene; Grímsson et al. 2015) and Lavanttal (Grímsson et al. 2016a). Fagoideae PT 1 grains differ from those of extinct and extant *Fagus* by being smaller and the occurrence of elongated rugulae, the tips of which are never protruding; furthermore, rugulae in the Wyoming pollen are often sinuous and multi-branched but usually straight (rod-like) and bifurcating in *Fagus*. The pori in *Fagus* are mostly circular or lolongate and rarely lalongate, but clearly lalongate in these fossil pollen. The nexine thickening around the pori is also more prominent than in pollen of *Fagus*. A very conspicuous difference between this pollen and extinct and extant pollen of *Fagus* is the conspicuously thick pollen wall (nexine) encountered in the fossil pollen (type 1 foot layer according to Denk & Tekleva 2014). Denk and Tekleva (2014) suggested this to be a primitive, ancestral state in many Fagaceae.

Fagoideae PT 2

Pl. 13, figs 1–3

Description. Pollen, monad, prolate to spheroidal, outline convex-triangular to circular in polar view, elliptic to circular in equatorial view; polar axis 26–27 µm long, equatorial diameter 24–25 µm; tricolporate, colpi long, pori elliptic (lolongate), nexine slightly thickened around pori (LM); exine 1.4–1.6 µm thick (LM), nexine thinner than sexine; tectate; sculpture scabrate in LM, rugulate, minutely fossulate in SEM, rugulae short (stout) to very long (rod-like), up to 4.5 µm long, 400–500 nm wide, straight or curved, occasionally bifurcating, tips of rugulae not protruding (SEM).

Locality/age. Princeton Chert, British Columbia (ca 48 Ma).

Remarks. PT 2 differs from PT 1 in the form and arrangement of sculpture elements. The rugulae are often much longer in PT 2, bifurcating (not multi-branched), and are all occurring in the same level. In LM the pollen matches that of *Fagus* (pollen size, wall thickness, outline of pori). The thickening around the pori is also similar to what can be observed in *Fagus*. The very long rugulae and minute fossulae are not characteristic of modern or fossil *Fagus,* and the fossil pollen does not have the protruding ends of rugulae observed in pollen of all modern *Fagus*. The nexine most likely corresponds to a weakly developed type 1 foot layer, hence our treatment as Fagoideae PT.

Genus ***Fagus*** L.

Fagus PT 1

Pl. 3, figs 7–12

Description. Pollen, monad, spheroidal, outline convex-triangular in polar view, circular in equatorial view; polar axis 22–24 µm long, equatorial diameter 21–25 µm; tricolporate, colpi long, pori circular, nexine thickened around pori (LM); exine 1.0–1.2 µm thick, nexine thinner than sexine (LM); tectate; sculpture scabrate in LM, microrugulate in SEM, rugulae very short, 0.4–1.0 µm long, 220–320 nm wide, partly branched or fused and protruding (SEM).

Locality/age. Turritellakløft (Big section; Agatdalen), western Greenland (64–62 Ma).

Remarks. Pollen of the small genus *Fagus* (ca nine species) has been studied comprehensively using LM, SEM, and TEM (Praglowski 1982, Denk 2003). Pollen grains of extant *Fagus* are generally similar in sculpture and outline (± spheroidal). Pollen of species of ‘Subgenus

Engleriana' according to Shen (1992), *F. engleriana*, *F. japonica*, and *F. okamotoi*, with a polar and equatorial axis ranging from 26 to 34 µm (Praglowski 1982, tab. 1; Denk 2003, tab. 2), are typically smaller than those of 'Subgenus Fagus' (of Shen 1992), but still bigger than pollen from Agatdalen. The long colpi seen in *Fagus* PT 1 are known from pollen of 'Subgenus Engleriana', but also *F. grandifolia* (the only North American species) and occasionally *F. longipetiolata* of 'Subgenus Fagus'. The oldest species of *Fagus*, *F. langevinii* Manchester & Dillhoff (leaves, fruit, and pollen) known from the early Eocene of British Columbia, western Canada, has very small to small pollen grains with long colpi (Manchester & Dillhoff 2004) very similar to the fossil grains described here. In contrast, *Fagus* pollen from the 20 Ma younger Hareøen Fm is medium-large, and fits best with pollen of *F. grandifolia* and *F. longipetiolata* ('Subgenus Fagus'). The fossil record of *Fagus* (pollen, cupules, nuts, leaves) has been summarised by Manchester & Dillhoff (2004), Denk & Grimm (2009a), and Grímsson et al. (2015). The Agatdalen pollen grains represent the oldest fossils of *Fagus* currently known. The main distinguishing feature between Fagoideae pollen closely resembling *Fagus* from the Cretaceous of Wyoming and this pollen type is the derived type 2 foot layer (see Denk & Tekleva 2014) in the Paleocene pollen.

Fagus PT 2

Pl. 13, figs 4–6

Description. Pollen, monad, spheroidal, outline convex-triangular to circular in polar view, circular in equatorial view; polar axis 22–23 µm long, equatorial diameter 21–22 µm; tricolporate, colpi long, pori small, circular, nexine slightly thickened around pori (LM); exine 1.2–1.4 µm thick (LM), nexine thinner than sexine; tectate; sculpture scabrate in LM, microrugulate to rugulate, minutely fossulate in SEM, rugulae short, 0.4–1.5 µm long, 180–360 nm wide, straight or curved, bifurcations rare, tips of rugulae can be protruding (SEM).

Locality/age. Princeton Chert, British Columbia (ca 48 Ma).

Remarks. Regarding its sculpture, *Fagus* PT 2 is intermediate between Fagoideae PT 2 and *Fagus* PT 3 from the same locality. Similarly short, rarely unbranching microrugulae are reminiscent of the sculpture of pollen included in Fagoideae PT 1 from Wyoming (Pl. 2, fig. 3), but it differs markedly in pollen shape and porus outline. It is treated as *Fagus* because of the occasionally protruding rugula tips and its type 2 footlayer.

Fagus PT 3

Pl. 13, figs 7–10

Description. Pollen, monad, spheroidal to oblate, outline circular to convex-triangular in polar view, circular in equatorial view; polar axis 21–22 µm long, equatorial diameter 23–24 µm; tricolporate, colpi long, pori elliptic (lolongate), nexine slightly thickened around pori (LM); exine 1.0–1.3 µm thick (LM), nexine thinner than sexine; tectate; sculpture scabrate in LM, microrugulate in SEM, rugulae short, rod-like, sometimes a bit curved, 0.3–1.1 µm long, 200–300 nm wide, rarely branched, tips of rugulae often protruding (SEM).

Locality/age. Princeton Chert, British Columbia (ca 48 Ma).

Remarks. This pollen type shows all the diagnostic features of modern *Fagus* pollen observed both in LM and SEM; it is only slightly smaller. Like *Fagus* PT 1 it is most similar in size to pollen of 'Subgenus Engleriana', but also shares the sculpture and colpi form/length with *F. grandifolia*. This pollen type differs from *Fagus* PT 1 in being more circular in polar view, having lalongate pori and a less conspicuous thickening of the nexine around the pori. The rugulae are longer and rarely fused.

Fagus cordifolia Heer (leaf morphotype 1)

Pl. 16, figs 1, 2

1883 *Fagus cordifolia* Heer – p. 83, pl. 92, fig. 1.

Description. Leaves, petiole not preserved, lamina simple, 50 mm long, 32 mm wide, length/width ratio 1.6, widest in the middle to lower part of the lamina, lamina ovate, apex bluntly acute, base slightly cordate, margin crenulated to dentate, when present teeth are simple and very small; primary venation pinnate, primary vein moderate in thickness, straight and becoming zigzag in apex region; secondary venation pseudo- and semicraspedodromous to craspedodromous, secondary veins moderate in thickness, straight, 12 pairs diverging from midvein at intervals of 3 to 5 mm in middle of lamina, arising at angles of 40° to 50° from midvein, usually alternate.

Locality/age. Qeqertarsuatsiaq, western Greenland (42–40 Ma).

Remarks. This leaf resembles both Betulaceae and Fagaceae in having abmedial and/or pectinal veins originating from the basalmost secondary veins. While this is typical of Betulaceae, it is also seen in a number of extant ('Subgenus Engleriana') and extinct species (e.g. *Fagus evenensis*, *F. pacifica*). The leaf margin, pseudocraspedodromous to craspedodromous, is typical of *Fagus*.

Fagus leaf morphotype 2

Pl. 16, figs 3–5; Pl. 17, figs. 1–5

Description. Leaves, petiole not preserved, lamina simple, up to 110 mm long (extrapolated), 62 mm wide, length/width ratio 1.7–1.8, widest in middle part of lamina, lamina elliptic to wide elliptic, apex not preserved, base obtuse, margin dentate, teeth simple and very small, teeth with acute apex, basal side longer than apical side, margin between two teeth straight or sigmoid; primary venation pinnate, primary vein moderate in thickness, straight; secondary venation semicraspedodromous to craspedodromous, secondary veins moderate in thickness, straight to gently curved, 11 to 13 pairs (extrapolated) diverging from midvein at intervals of 10 to 15 mm in middle of lamina, arising at angles of 40° to 50° from midvein, usually alternate above base; tertiary venation percurrent, veins simple or branched, convex, ca 5 tertiary veins per 1 cm secondary vein, originating at acute angles from both the admedial and the exmedial side of the secondary veins, alternately arranged; quaternary venation orthogonal, forming large areoles; areoles well developed, oriented, quadrangular to polygonal; veinlets branched; marginal ultimate venation looped.

Locality/age. Qeqertarsuatsiaq, western Greenland (42–40 Ma).

Remarks. The *Fagus* LMT 2 leaves differ from *Fagus cordifolia* in form of the lamina and base. The teeth in *Fagus* LMT 2 are also more prominent and more regular. Teeth are rare in *Fagus cordifolia*. It is entirely possible that the few unambiguous leaves of *Fagus* encountered from Qeqertarsuatsiaq were produced by the same species.

Subfamily QUERCOIDEAE Oerst.

Genus ***Quercus***

Quercus PT 1

aff. Group Lobatae; Pl. 13, figs 11–13

Description. Pollen, monad, prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 17–18 µm long, equatorial diameter 13–14 µm; tricolporate, colpi long, pori small (LM); exine 0.9–1.1 µm thick (LM), nexine thinner or as thick as sexine; tectate; sculpture scabrate in LM, (micro)verrucate, fossulate, perforate in SEM, (micro)verrucae with a microechinate suprasculpture, microechini poorly developed, irregularly distributed (SEM).

Localities/age. Princeton Chert, British Columbia (ca 48 Ma); Qeqertarsuatsiaq, western Greenland (42–40 Ma; Grímsson et al. 2015, fig. 11)

Remarks. *Quercus* PT 1 falls within the morphological variability of several species of *Quercus* Group Lobatae of North America (Solomon 1983a).

Quercus PT 2
(ancestral type with Group Ilex morphology)

Pl. 13, figs 14–19

Description. Pollen, monad, prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 17–24 µm long, equatorial diameter 12–14 µm; tricolporate, colpi long, pori small (LM); exine 0.8–1.0 µm thick (LM), nexine thinner than sexine; tectate; sculpture scabrate in LM, microrugulate, perforate in SEM, rugulae short and narrow, 0.3–1.1 µm long, 100–200 nm wide, irregularly arranged (SEM).

Localities/age. Princeton Chert, British Columbia (ca 48 Ma); Qeqertarsuatsiaq, western Greenland (42–40; Grímsson et al. 2015, fig. 14)

Remarks. *Quercus* PT 2 differs from other PTs of *Quercus*, and pollen formalised here as *Paraquercus eocaena* from the same locality, by the lack of a verrucate suprasculpture composed of conspicuously oriented or fused (micro)rugulae. Among the modern species, only the members of *Quercus* Group Ilex (and *Fagus*) show unmasked, irregular-oriented and intertwining rugulae, a situation that is likely ancestral within genus *Quercus* (Denk & Grimm 2009b). Further main distinguishing features between the co-occurring *Paraquercus eocaena* and *Quercus* PT 2 are the lalongate endopori of *Paraquercus*, which are small to indistinct in *Quercus* PT 2 as in other fossil and extant pollen of genus *Quercus*. The rugulae can be double as long in *Quercus* PT 2 compared to *Paraquercus eocaena*. The ends of the rugulae are frequently protruding from the pollen surface (partly erect) in *Quercus* PT 2, but never so in *Paraquercus eocaena*; the latter can be observed in extant members of *Quercus* Group Ilex (Denk & Tekleva 2014).

USING FAGACEAE POLLEN TO TRACE ANCESTRAL, EXTINCT AND MODERN (EXTANT) LINEAGES

The diagnostic value of pollen morphology in Fagaceae at various hierarchical levels is well and long established (Praglowski 1982, 1984, Solomon 1983a, b, Denk 2003, Denk & Grimm 2009b). Figure 2 shows the position of the here-described fossils against the backdrop of the current evolutionary synopsis of the family. Based on their stratigraphic distribution and extant taxonomic sorting, the Castaneoideae-type pollen appears to represent the most ancestral morphology of Fagaceae pollen, from which the other pollen types were subsequently derived (Fagoideae, *Eotrigonobalanus*/*Paraquercus* in the late Cretaceous; Trigonobalanoideae, *Trigonobalanopsis*, Quercoideae in the Paleogene). The basic and most common Castaneoideae pollen type (PT 2), still found in extant Castaneoideae species (Praglowski 1984, Wang & Pu 2004, Miyoshi et al. 2011) of genera that are more or less distantly related (*Chrysolepis* + *Lithocarpus*; *Castanea* + *Castanopsis*; *Notholithocarpus*, the genetically closest relative of *Quercus* among the Castaneoideae; Manos et al. 2008, Denk & Grimm 2010, Hubert et al. 2014) can be traced back to the Campanian of Wyoming. One of the oldest known Fagaceae, *Archaefagacea* from the early Coniacian of Japan (Takahashi et al. 2008, no LM micrograph shown), has a castaneoid pollen with a sculpture equal to that of Castaneoideae PT 2 (and PTs 3, 5, 6), whereas pollen of the slightly younger (Santonian) *Antiquacupula* (Sims et al. 1998) apparently has a different sculpture. The pollen of *Antiquacupula* is perforate and does not have the narrow and oblong rugulae that are characteristic for Castaneoideae-type pollen (see figs 13, 30–32 in Sims et al. 1998). Castaneoid pollen predates the so-far-known and here-reported first occurrences of *Fagus* (Fagoideae; Manchester & Dillhoff 2004: 50 Ma; this study: 62–64 Ma) and *Quercus* (Quercoideae; Hofmann 2010: Paleocene-Eocene boundary, ca 55 Ma). Thus, using pollen evidence, it is impossible to pinpoint the origin of modern (extant) genera of the Castaneoideae.

INITIAL SPLIT INTO TWO MAIN CLADES

The first split in the modern Fagaceae was between a lineage leading to *Fagus* (Fagoideae) and the rest of the family (trigonobalanoids, Castaneoideae, Quercoideae). From the branch-lengths in molecular phylograms (Fig. 1) it is obvious that this split must have happened long before the diversification of the remainder of the family, which – based on fossil evidence – was accomplished by the end of the Eocene (Fig. 2). The *Fagus*/Fagoideae root age, which is equivalent to the Fagaceae crown age, is one of the few estimates unanimously recovered by all dating approaches because of the used constraints, which are densely packed around the Fagaceae crown node. Independent of the data set and approach used (node dating or total evidence dating; Tab. 2), the estimates range around ca 80 Ma (Campanian), ± 20 Ma when the 95% confidence intervals are considered (= Upper Cretaceous, 100.5–66 Ma; Cohen et al. 2013, updated). Node dating (Sauquet et al. 2012, Xiang et al. 2014, Xing et al. 2014) infers minimum ages for most recent common ancestors (MRCA), hence, the molecular estimates indicate that the Fagoideae lineage was diverged by the middle Upper Cretaceous (see File S2 for issues with the total evidence dating used by Larson-Johnson 2016). This is reflected by the Campanian Fagaceae assemblage of Wyoming. In addition to two extinct Fagaceae lineages of unknown relationship to the modern two main clades (*Eotrigonobalanus*, *Paraquercus*, discussed below), we find pollen showing diagnostic features shared with

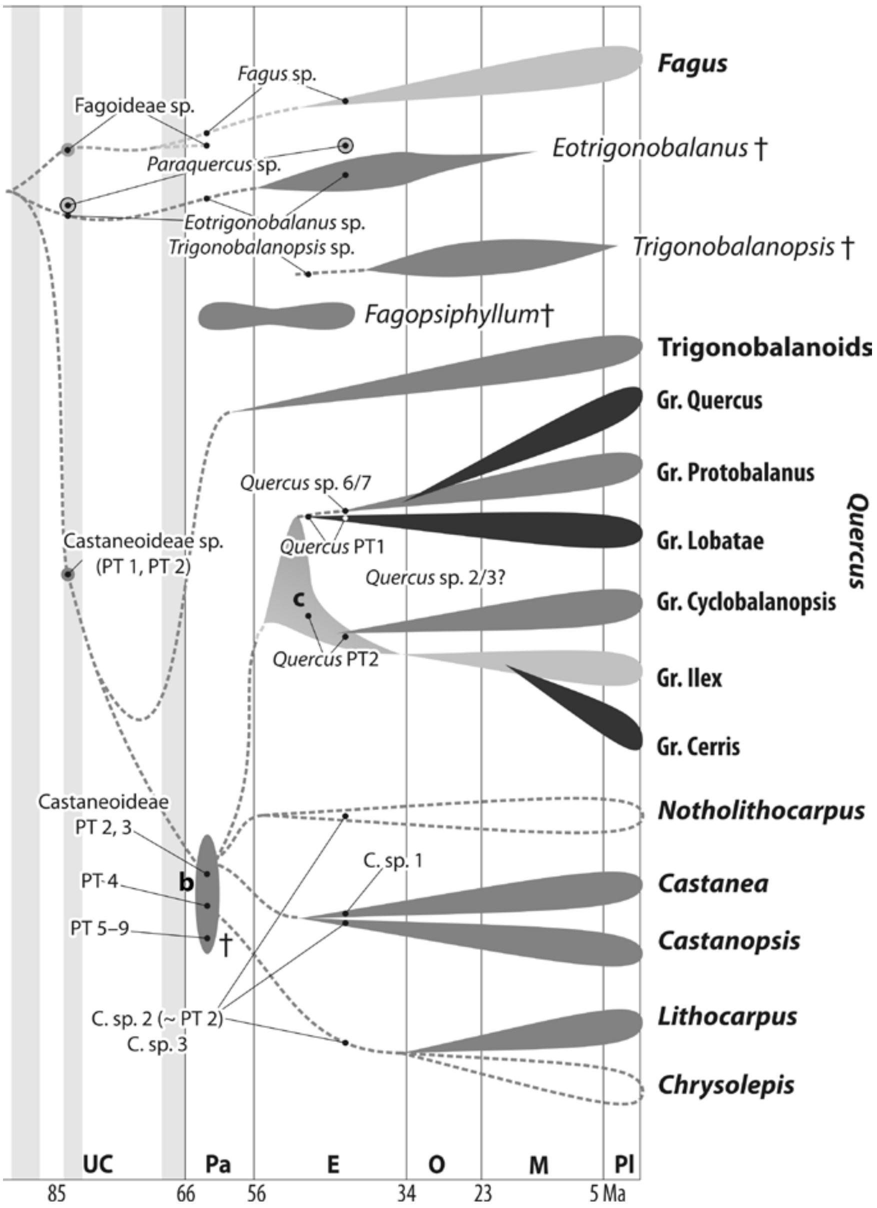

Fig. 2. Plot of the Fagaceae fossils on a phylogenetic scheme (modified after Grímsson et al. 2015), which represents the synopsis of undated and dated molecular phylogenies (Manos et al. 2008, Oh & Manos 2008, Denk & Grimm 2010, Hubert et al. 2014, Renner et al. 2016) and the fossil record. The age of the root node follows the consensus of all-Fagales-dated trees (Tab. 2)

the later (Danian) and modern *Fagus* pollen, in addition to sculptural elements reminiscent of the primitive (plesiomorphic) Castaneoideae pollen from which it putatively evolved, when the two main modern Fagaceae lineages diverged (Fig. 3).

FAGUS CROWN AGE:
FORMATION OF MODERN LINEAGES

Miocene crown estimates (24–8 Ma) for *Fagus* in the Fagales chronograms by Xiang et al. (2014) and Xing et al. (2014) are too young because the plastid data these studies relied on (exclusively or partly) fail to capture and resolve phylogenetic relationships in this genus (details provided in File S2). Precursors of all modern species/species complexes were widespread already by the Miocene (Denk 2004, Denk & Grimm 2009a). Species of 'Subgenus Engleriana', a lineage that can be traced back at least 15 Ma (Denk & Grimm 2009a), share highly similar to identical plastid sequences with sympatric but distant relatives of 'Subgenus Fagus' across their range, in addition to unique haplotypes (Fujii et al. 2002, Zhang et al. 2013; see also Simeone et al. 2016a). For this reason, Renner et al. (2016) used only two nuclear gene regions that are able to infer sensible interspecies relationships in *Fagus* (2nd intron of the LEAFY gene and individual-consensus ITS sequences) for

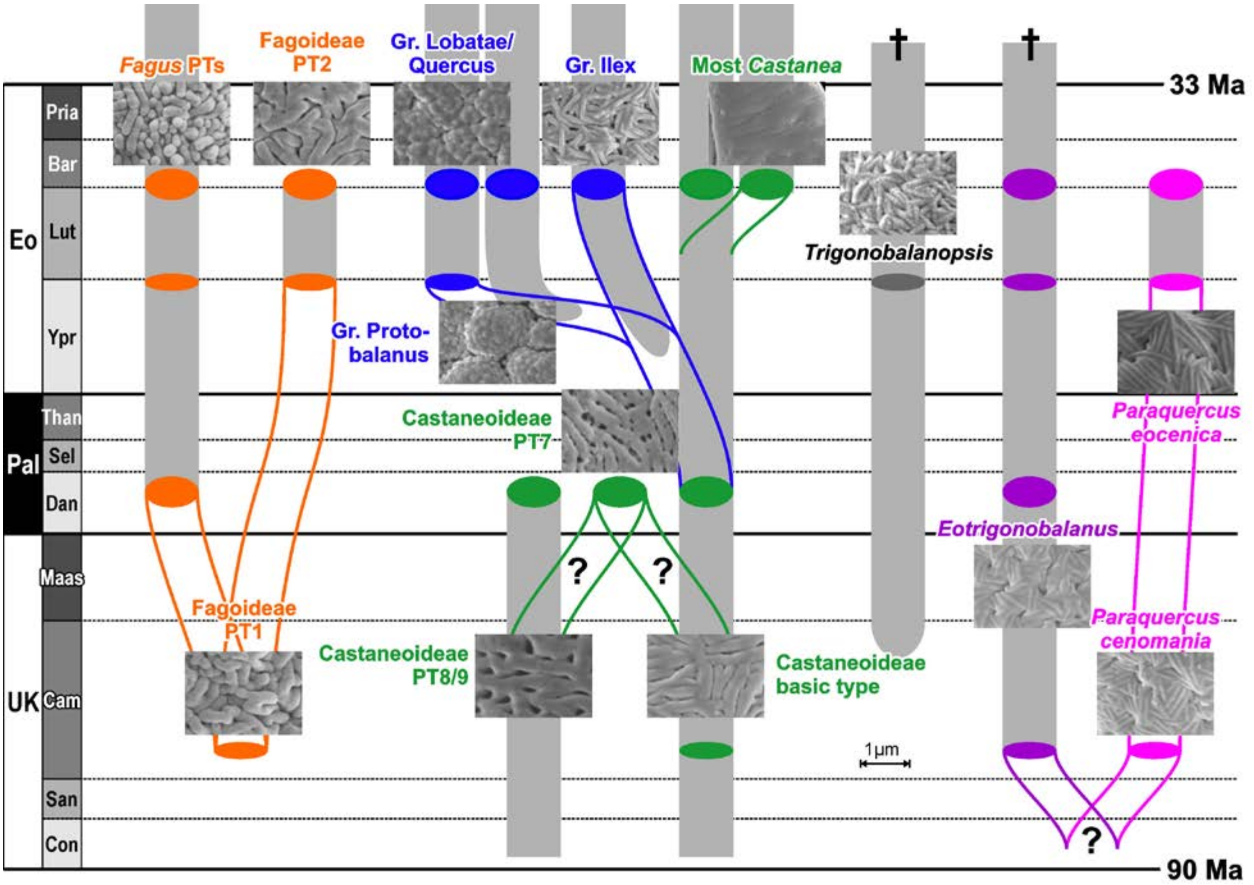

Fig. 3. Temporal distribution of early Fagaceae pollen. Grey bars show the general time range of pollen types covered in this study; coloured discs reflect the actual occurrence in one of the four studied localities. Six of these old pollen types (PT) persist until today (*Fagus*, oaks [blue signatures], Castaneoideae basic type and *Castanea*-unique type); two (*Trigonobalanopsis*, *Eotrigonobalanus*) went extinct throughout the Neogene (†); the remainder (Fagoideae PTs, extinct Castaneoideae PTs, *Paraquercus*) have so far not been observed in younger time slices

their fossilised-birth-death (FBD) dating of the genus. In contrast to node dating, where oldest fossil(s) of a lineage are used to constrain minimum root ages for that lineage, FBD dating recruits the entire fossil record to inform the temporal distribution of a lineage (Heath et al. 2014). For the FBD dating of *Fagus* more than 50 fossils informed the temporal distribution of *Fagus* lineages (leading to the nine modern species) and placed the divergence between 'Subgenus Engleriana' and 'Subgenus Fagus', i.e. the *Fagus* crown age, into the Paleocene to early Eocene (62–43 Ma; Tab. 2; Fig. 4). The split between the North American (leading to *F. grandifolia*) and Eurasian clades of 'Subgenus Fagus' (remainder of the genus; see also Denk & Grimm 2009a) was estimated to be of Eocene age (51–39 Ma). In line with these estimates (Fig. 4), the Danian *Fagus* pollen shares the long colpi seen in 'Subgenus Engleriana' and *F. grandifolia*, which apparently represents the ancestral situation in the genus. A highly similar pollen has also been described for the ca 50 Ma old *F. langevinii* (Manchester & Dillhoff 2004), which so far has been the earliest record of the genus and subsequently has been used in recent node dating to constrain the *Fagus* root age (Fig. S1 in File S2). Pollen with ancestral traits (small, long colpi) are still present in the Princeton Chert beds. On the other hand, the younger pollen grains from Qeqertarsuatsiaq, western Greenland, (42–40 Ma) match in size, form, and sculpture that of modern members of 'Subgenus Fagus', in striking agreement with the recent molecular dating (Fig. 4).

EVOLUTION AND RADIATION OF THE CORE FAGACEAE

Although the primitive (plesiomorphic) Castaneoideae pollen in general cannot be taken as evidence for the presence of the modern genera or their precursors, there are some subtypes (Castaneoideae PT 4 and Castaneoideae sp. 1 in Grímsson et al. 2015) which seem to be restricted to a single extant genus (*Lithocarpus* and *Castanea*, respectively). These could be evidence that these genera (or the lineages leading to them) were already established in the Paleocene and Eocene. While plastid data are highly ambiguous regarding intergeneric relationships in the core Fagaceae (modern Castaneoideae + *Quercus*), nuclear data (*CRC*, ITS) suggest a divergence scenario in which *Lithocarpus* (+ *Chrysolepis*) was isolated from the remainder (*Quercus*, *Notholithocarpus*, *Castanea* + *Castanopsis*) before *Quercus* diversified, radiated, and separated from the remaining Castaneoideae (Oh & Manos 2008, Denk & Grimm 2010). Such a scenario would be in agreement with the pollen record (Danian PT4 vs middle Eocene Castaneoideae sp. 1). Relying exclusively or partly on plastid data, all-Fagales dated trees failed to recognise a single oak clade in studies using more than a single accession to represent the oaks (Xiang et al. 2014, Xing et al. 2014) and differ in the placement of *Lithocarpus* and the other castaneoids (File S2). Nevertheless, since these studies rely on the same fossil priors to constrain the primary divergences in the Fagaceae, and intergeneric relationships within the core Fagaceae relate to very short branches (Fig. 1), they all estimated a Paleogene (Paleocene to Eocene) crown age for the core Fagaceae (Tab. 2).

The lack of oak pollen in the Danian of western Greenland, compared to significant diversity 20 Ma later in the same area, lends further credibility to the hypothesis that oaks evolved and started to radiate in the late Paleocene/early Eocene, as estimated by Hubert et al. (2014), i.e. more than 20 Ma earlier than estimated by all-Fagales chronograms using a single placeholder per genus (Tab. 2; Sauquet et al. 2012, Larson-Johnson 2016). Hubert et al.'s (2014) preferred chronogram – which used the oldest unambiguous record of *Quercus* Group Cyclobalanopsis as minimum age constraint for the most recent common ancestor (MRCA) of the 'Old World' clade (Hubert et al. 2014, fig. 5) – points to an early Eocene *Quercus* crown age; the latter is defined by the divergence of the 'New World' or high-latitude

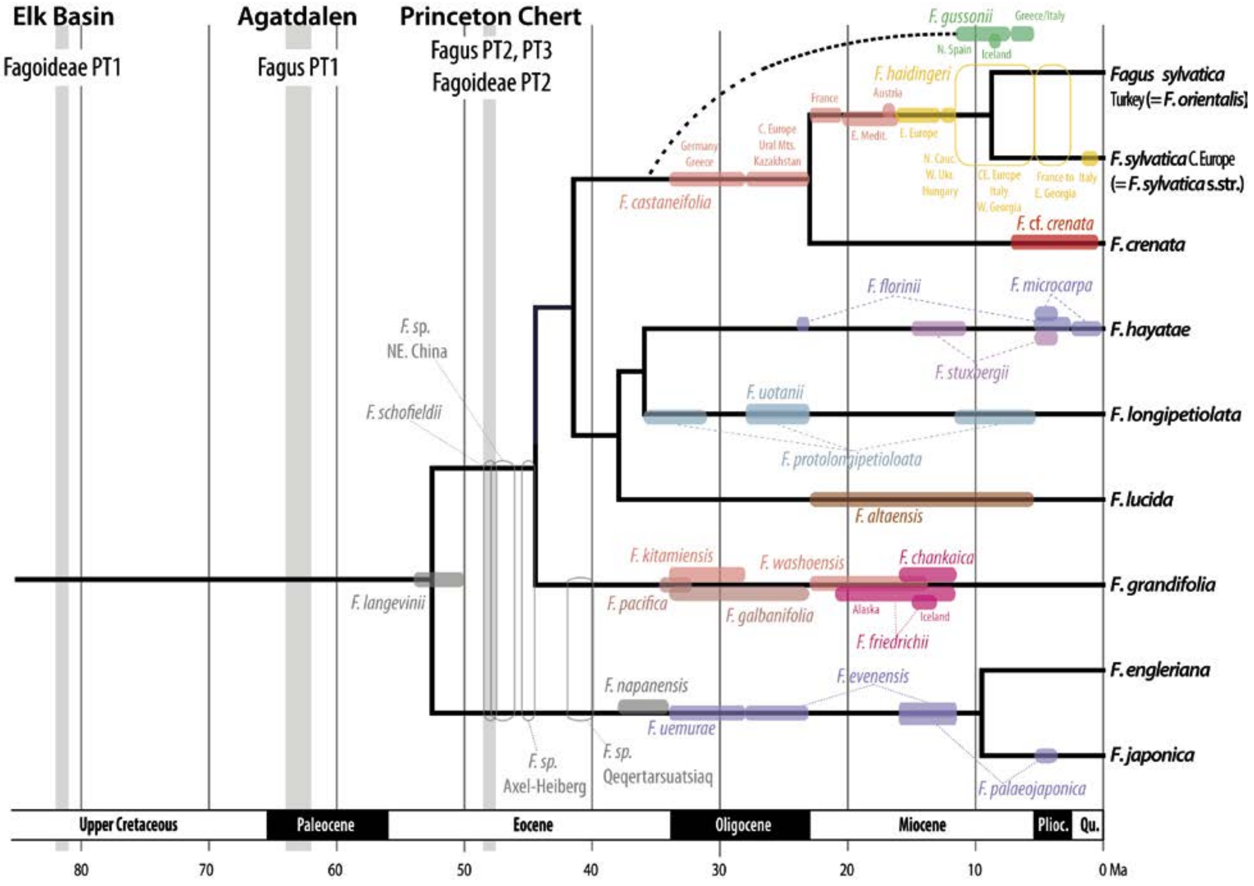

Fig. 4. Paleogene pollen records of *Fagus* compared to a recent dated tree of the genus inferred using fossilised-birth-death (FBD) dating and a set of over 50 beech micro-, meso-, and macrofossils (modified from Renner et al. 2016). Fossil taxa included for the FBD dating were placed along branches based on direct (as inferred; cf. Denk & Grimm 2009a) and indirect (personal expertise; provenance) evidence. The stratigraphic position of newly found *Fagus* pollen is indicated

clade (*Quercus* Groups Lobatae, Protobalanus, and Quercus) and the 'Old World' clade or mid-latitude clade (Groups Cyclobalanopsis, Ilex, and Cerris). Crown-group radiation within the high-latitude clade of oaks, the divergence between the red oak lineage (Group Lobatae) and the golden cup-white oak lineage (Groups Protobalanus, Quercus), was completed by the middle Eocene. This is evidenced by pollen found in the Princeton Chert (this study) and on the island of Qeqertarsuatsiaq (Grímsson et al. 2015), finds that are in good agreement with Hubert et al.'s preferred chronogram indicating an absolute minimum age (upper boundary of the 95% confidence interval) for the MRCA of the high-latitude clade of ca 35 Ma (i.e. Eocene-Oligocene boundary).

FAGOPSIPHYLLUM AND *PARAQUERCUS* – OAK-LIKE FOLIAGE AND OAK-LIKE POLLEN BUT NOT OAKS

Grímsson et al. (2015) speculated that the more primitive, extinct oak pollen types found in the 42–40 Ma Hareøn Fm come from the same plant/plant group that produced the *Fagopsiphyllum* foliage (Pl. 6, 7; Pl. 14). Indeed, there is a general similarity between *Fagopsiphyllum* and leaves of two modern, highly disjunct relict white oak species, *Quercus pontica* from north-eastern Turkey and south-western Georgia and *Q. sadleriana* from north-western California, two relicts originating from an initial radiation within the high-latitude oak clade (Hubert et al. 2014, Hipp et al. 2015; formal publication is currently under preparation; A. Hipp, pers. comm., 2016). The occurrence of potentially ancestral oak-like foliage and pollen types that show an ornamentation as would be expected for an ancestral oak (Denk & Grimm 2009b) in the right time scale (cf. Hubert et al. 2014) is puzzling. However, the Wyoming pollen described here as *Paraquercus campania* is much too old to be produced by an ancient oak lineage and shows the same unique basic ornamentation as the pollen from the Hareøn Fm that Grímsson et al. (2015) addressed as '*Quercus* sp. 5'. For this reason, the latter is moved to the new genus *Paraquercus*. *Fagopsiphyllum* foliage is much more abundant in the Agatdal Fm than in the younger Hareøen Fm (Heer 1868–1883). However, we found no evidence of oak pollen in the older Agatdal Fm. The preservation of the foliage in both formations indicates that the plants producing and shedding the *Fagopsiphyllum* foliage lived close to the depositional area; hence, it would be expected that their pollen can also be found if the foliage comes from an oak, as oaks are strictly wind-pollinated. Thus, the earlier ancient-oak-hypothesis for *Fagopsiphyllum* must be rejected. Three scenarios remain: (1) *Fagopsiphyllum* is the foliage from an extinct Fagales member, not a Fagaceae, and producing non-Fagaceae-like pollen grains; (2) *Fagopsiphyllum* is the foliage from an extinct Fagaceae lineage producing (very) few pollen grains, which are not captured in the dispersed pollen record; (3) *Fagopsiphllyum* is the foliage produced by plants with Castaneoideae-like or *Fagus*-like pollen. Scenario 1 is unlikely given the temporal and spatial restriction of *Fagopsiphyllum* during the Paleogene of the Arctic region, a time and area renowned for a vegetation including the earliest reliable records of deciduous, large-leaved Fagaceae (Heer 1868, 1883, Manchester & Dillhoff 2004, Dillhoff et al. 2005). If such leaves evolved independently in other Fagales lineages, they should be more common and widespread in the fossil record and even persisting in other extant families of the Fagales. Scenario 2 remains possible. Analysing pollen found in situ on fossil Eocene bees, Grímsson et al. (2016c) recently showed that only a fraction of insect-pollinated taxa can be retrieved from the dispersed pollen record. The newly recognised *Paraquercus* is notably rare in both the Wyoming and Qeqertarsuatsiaq localities. In both cases a single grain was found. *Fagopsiphyllum* foliage has recently been described from the latest Cretaceous of the Russian Far East (Gnilovskaya & Golovneva 2016). So it may be that the *Paraquercus* pollen and *Fagopsiphyllum* leaves come from the same plant, but the currently available association evidence is weak. Hence, we prefer to coin a new genus for the pollen. If scenario 3 applies, the common Castaneoideae PT 2 would be the likeliest candidate for pollen of the *Fagopsiphyllum* plant, as it is a type shared by several genetically distinct extant genera (species of *Castanea-Castanopsis* as well as *Lithocarpus*) and an early Fagaceae, *Archaeofagaceae* (Takahashi et al. 2008), and has been found in both formations (Tab. 2; Grímsson et al. 2015: "Castaneoideae sp. 2"; this study).

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PLATES

Plate 1

Fagaceae pollen grains from the Cretaceous Eagle Formation, Elk Basin, Wyoming, USA

1. *Paraquercus campania*, LM equatorial view. Holotype, IPUW 7513/161. Scale bar: 10 µm
2. *Paraquercus campania*, SEM equatorial view, same grain as in 1. Holotype, IPUW 7513/161. Scale bar: 1 µm
3. *Paraquercus campania*, SEM, close-up of 2, showing parallel to radially arranged (micro)rugulae in groups. Holotype, IPUW 7513/161. Scale bar: 1 µm
4. *Eotrigonobalanus* PT, LM equatorial view. IPUW 7513/162. Scale bar: 10 µm
5. *Eotrigonobalanus* PT, SEM equatorial view, same grain as in 4. IPUW 7513/162. Scale bar: 1 µm
6. *Eotrigonobalanus* PT, SEM, close-up of 5, showing twisted and interwoven microrugulae. IPUW 7513/162. Scale bar: 1 µm
7. Castaneoideae PT 1, LM equatorial view. IPUW 7513/163. Scale bar: 10 µm
8. Castaneoideae PT 1, SEM equatorial view, same grain as in 7. IPUW 7513/163. Scale bar: 1 µm
9. Castaneoideae PT 1, SEM, close-up of 8, showing rugulate, fossulate, perforate sculpture. IPUW 7513/163. Scale bar: 1 µm
10. Castaneoideae PT 2, LM equatorial view. IPUW 7513/164. Scale bar: 10 µm
11. Castaneoideae PT 2, SEM equatorial view, same grain as in 10. IPUW 7513/164. Scale bar: 1 µm
12. Castaneoideae PT 2, SEM, close-up of 11, showing rugulate, fossulate, perforate sculpture. IPUW 7513/164. Scale bar: 1 µm
13. Fagoideae PT 1, LM equatorial view. IPUW 7513/165. Scale bar: 10 µm
14. Fagoideae PT 1, SEM polar view, same grain as in 13. IPUW 7513/165. Scale bar: 1 µm
15. Fagoideae PT 1, SEM, close-up of 14, showing sinuous, multi-branched and intertwined rugulae. IPUW 7513/165. Scale bar: 1 µm


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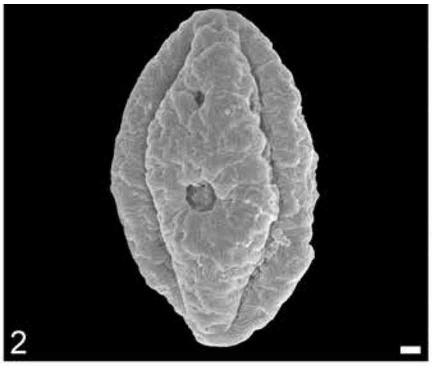
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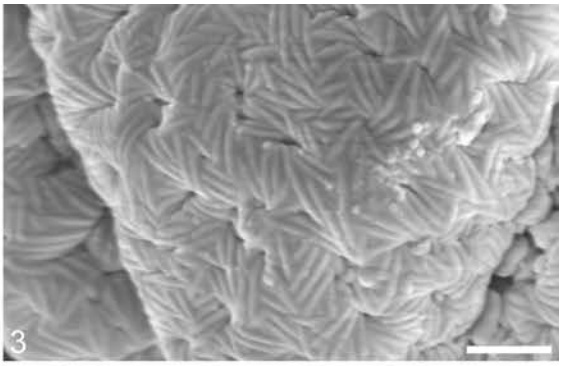
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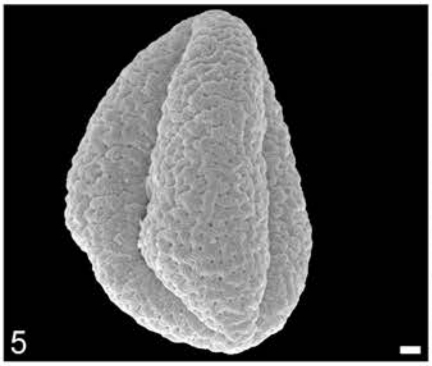
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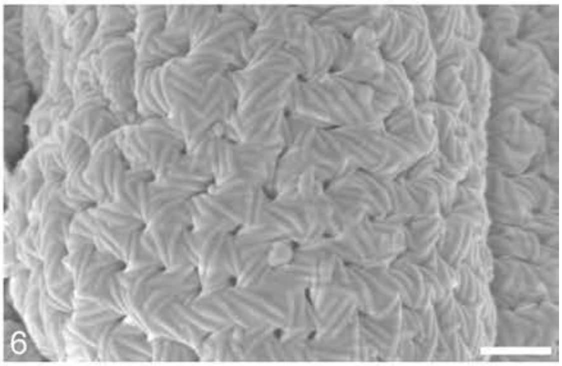
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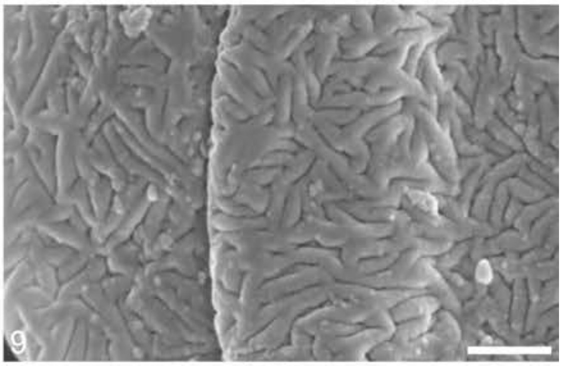
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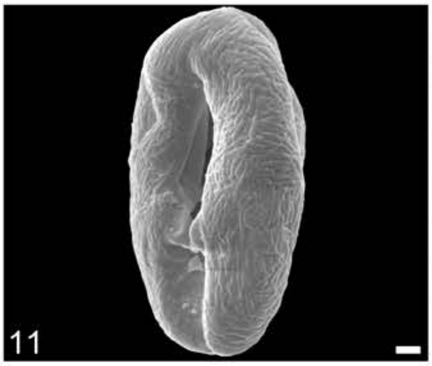
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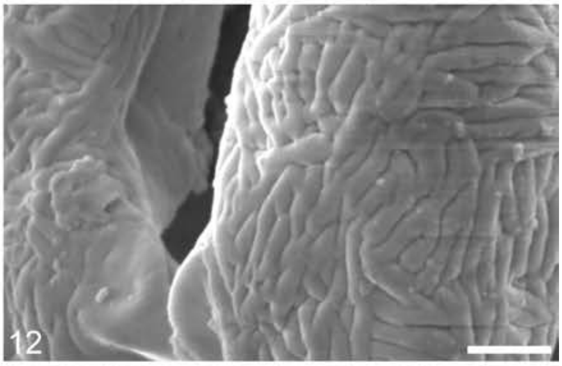
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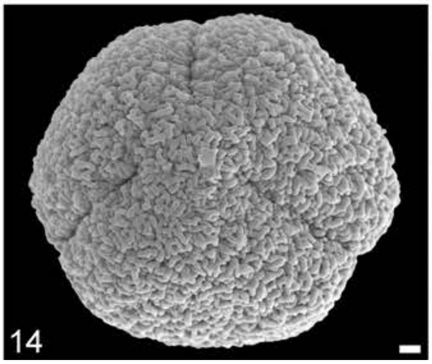
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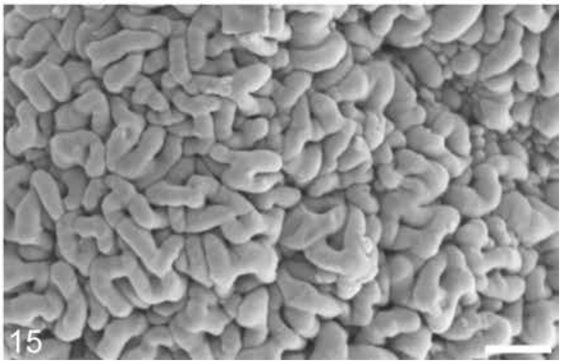
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Plate 2

Fagaceae pollen grains from the Cretaceous Eagle Formation, Elk Basin, Wyoming, USA

1. Fagoideae PT 1, LM equatorial view. IPUW 7513/166. Scale bar: 10 µm
2. Fagoideae PT 1, SEM polar view, same grain as in 1. IPUW 7513/166. Scale bar: 1 µm
3. Fagoideae PT 1, SEM, close-up of 2, showing sinuous and multi-branched rugulae. IPUW 7513/166. Scale bar: 1 µm
4. Fagoideae PT 1, LM equatorial view (upper), polar view (lower). IPUW 7513/167. Scale bar: 10 µm
5. Fagoideae PT 1, SEM polar view, same grain as in 4. IPUW 7513/167. Scale bar: 1 µm
6. Fagoideae PT 1, SEM, close-up of 5, showing sinuous and multi-branched rugulae. IPUW 7513/167. Scale bar: 1 µm
7. Fagoideae PT 1, LM equatorial view. IPUW 7513/168. Scale bar: 10 µm
8. Fagoideae PT 1, SEM equatorial view, same grain as in 7. IPUW 7513/168. Scale bar: 10 µm
9. Fagoideae PT 1, SEM, close-up of 8, showing sculpture along colpi. IPUW 7513/168. Scale bar: 1 µm
10. Fagoideae PT 1, LM equatorial view (upper), polar view (lower). IPUW 7513/169. Scale bar: 10 µm
11. Fagoideae PT 1, SEM equatorial view, same grain as in 10. IPUW 7513/169. Scale bar: 1 µm
12. Fagoideae PT 1, SEM, close-up of 11, showing sculpture along colpi. IPUW 7513/169. Scale bar: 1 µm
13. Fagoideae PT 1, SEM equatorial view. IPUW 7513/170. Scale bar: 1 µm
14. Fagoideae PT 1, SEM, close-up of 13, showing sculpture partly obscured by sporopollenin. IPUW 7513/170. Scale bar: 1 µm
15. Fagoideae PT 1, SEM polar view. IPUW 7513/171. Scale bar: 1 µm
16. Fagoideae PT 1, SEM, close-up of 15, showing sculpture in polar area. IPUW 7513/171. Scale bar: 1 µm


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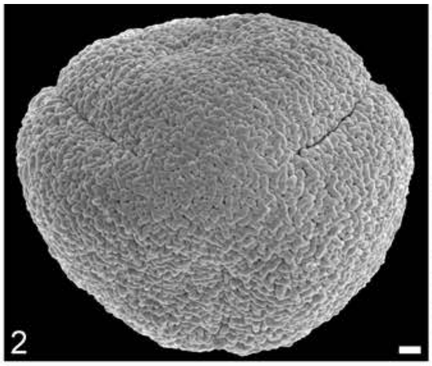
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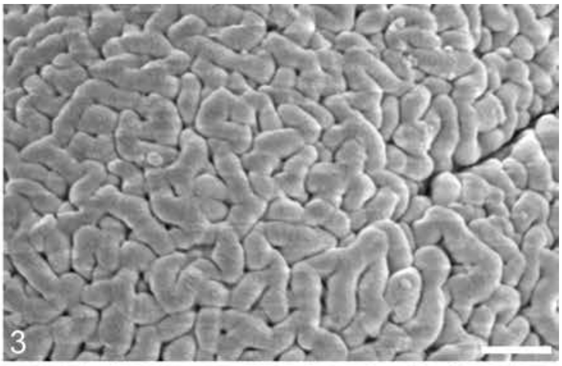
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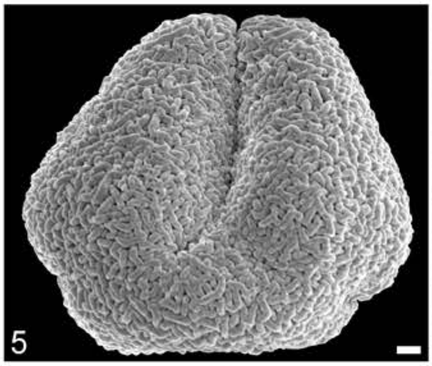
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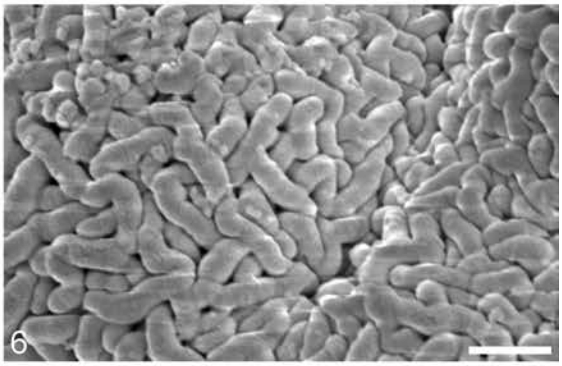
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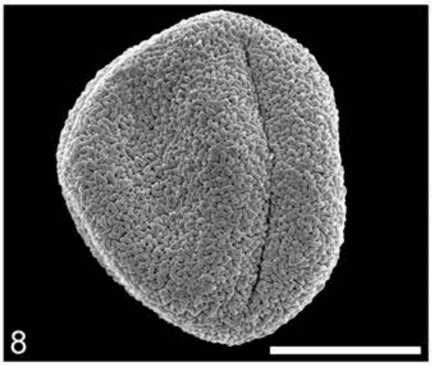
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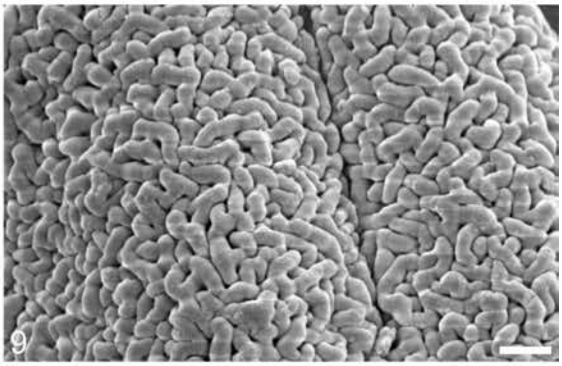
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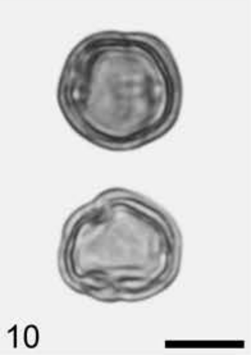
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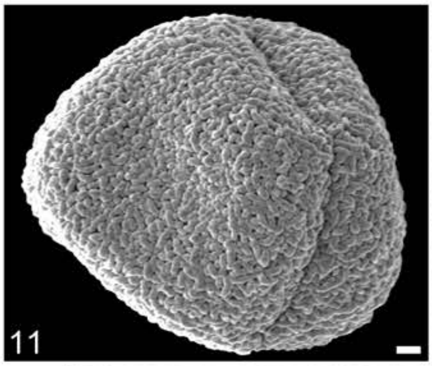
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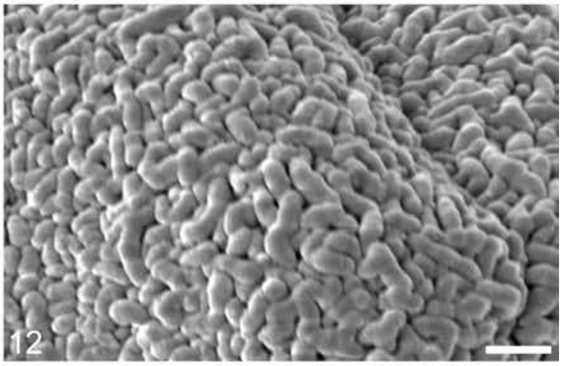
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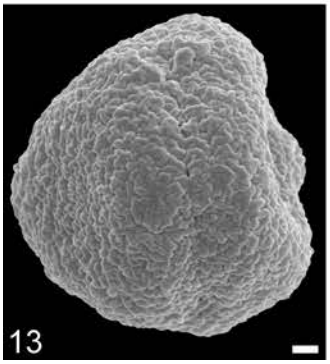
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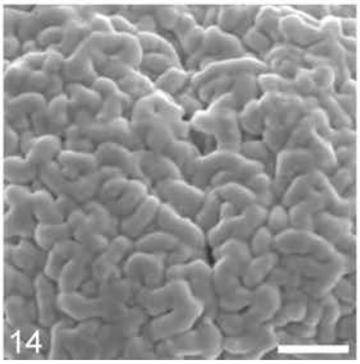
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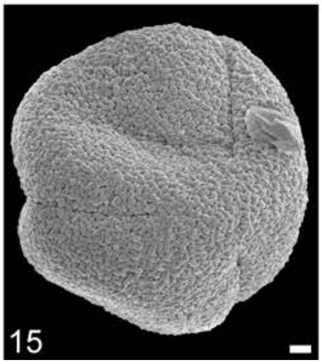
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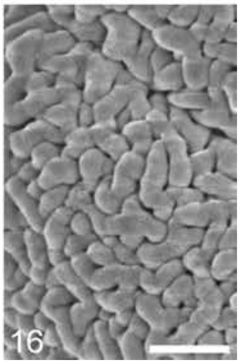
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Plate 3

Fagaceae pollen grains from the Paleocene Agatdal Formation, Turritellakløft (Big section) locality, Agatdalen valley, western Greenland

1. *Eotrigonobalanus* PT, LM equatorial view (upper) and polar view (lower). IPUW 7513/172. Scale bar: 10 µm
2. *Eotrigonobalanus* PT, SEM equatorial view, same grain as in 1. IPUW 7513/172. Scale bar: 10 µm
3. *Eotrigonobalanus* PT, SEM, close-up of 2, showing rugulate and perforate sculpture, rugulae twisted and interwoven. IPUW 7513/172. Scale bar: 1 µm
4. *Eotrigonobalanus* PT, LM equatorial view (upper) and polar view (lower). IPUW 7513/173. Scale bar: 10 µm
5. *Eotrigonobalanus* PT, SEM equatorial view, same grain as in 4. IPUW 7513/173. Scale bar: 10 µm
6. *Eotrigonobalanus* PT, SEM, close-up of 5, showing rugulate and perforate sculpture, rugulae twisted and interwoven. IPUW 7513/173. Scale bar: 1 µm
7. *Fagus* PT 1, LM equatorial view (upper) and polar view (lower). IPUW 7513/174. Scale bar: 10 µm
8. *Fagus* PT 1, SEM oblique polar view, same grain as in 7. IPUW 7513/174. Scale bar: 10 µm
9. *Fagus* PT 1, SEM, close-up of 8, showing rugulate sculpture, rugulae sometimes clustered and often diverging and protruding. IPUW 7513/174. Scale bar: 1 µm
10. *Fagus* PT 1, LM equatorial view (upper) and polar view (lower). IPUW 7513/175. Scale bar: 10 µm
11. *Fagus* PT 1, SEM oblique equatorial view, same grain as in 10. IPUW 7513/175. Scale bar: 1 µm
12. *Fagus* PT 1, SEM, close-up of 11, showing rugulate sculpture, rugulae sometimes clustered and often diverging and protruding. IPUW 7513/175. Scale bar: 1 µm
13. Castaneoideae PT 2, LM equatorial view (upper) and polar view (lower). IPUW 7513/176. Scale bar: 10 µm
14. Castaneoideae PT 2, SEM equatorial view, same gain as in 13. IPUW 7513/176. Scale bar: 1 µm
15. Castaneoideae PT 2, SEM, close-up of 14, showing rugulate sculpture, rugulae long. IPUW 7513/176. Scale bar: 1 µm


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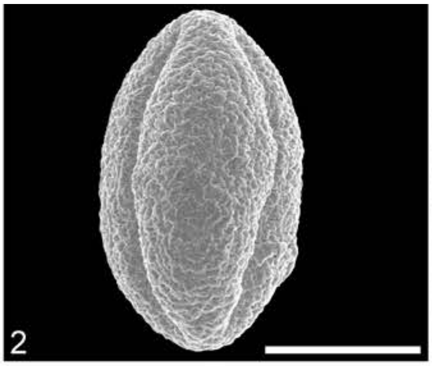
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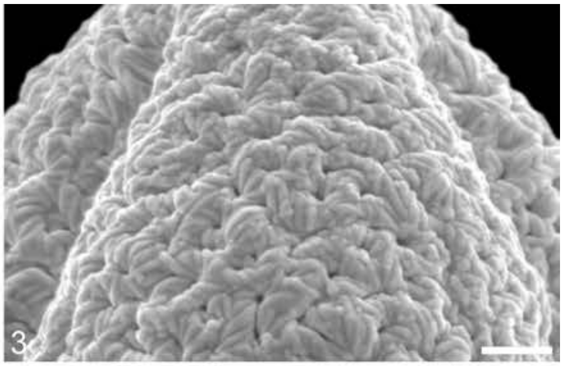
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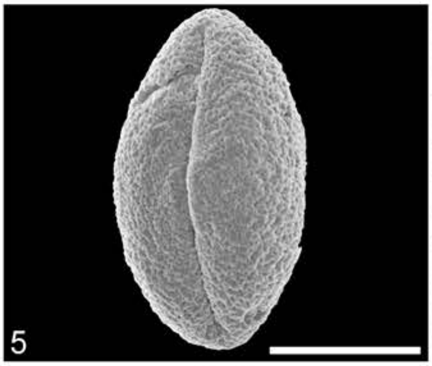
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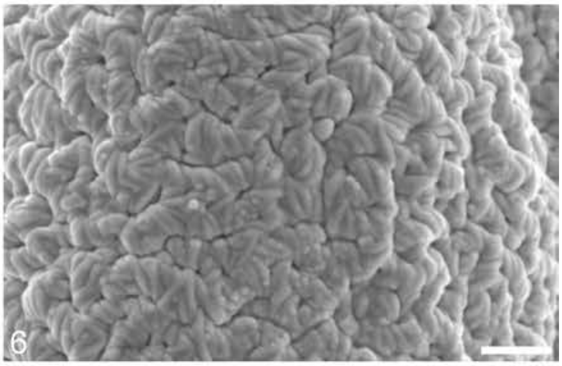
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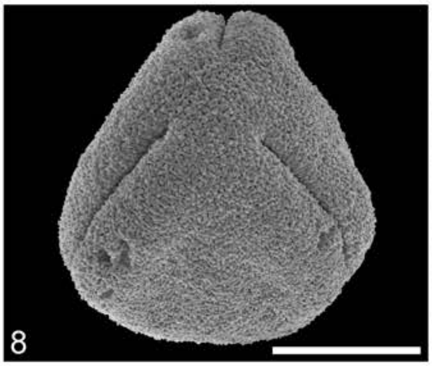
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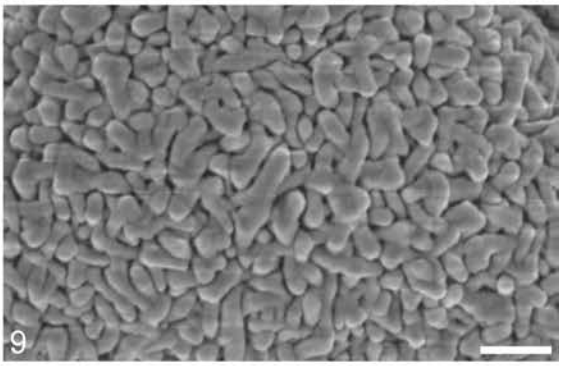
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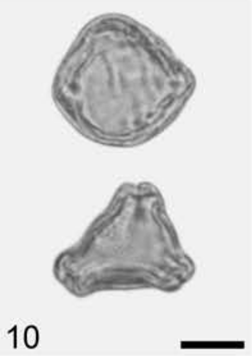
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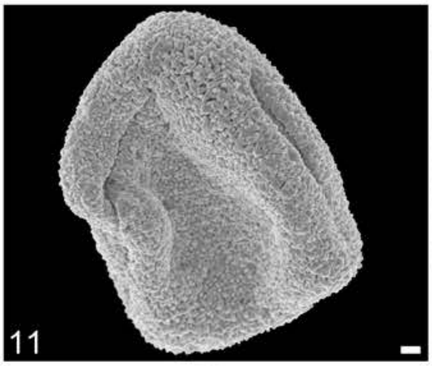
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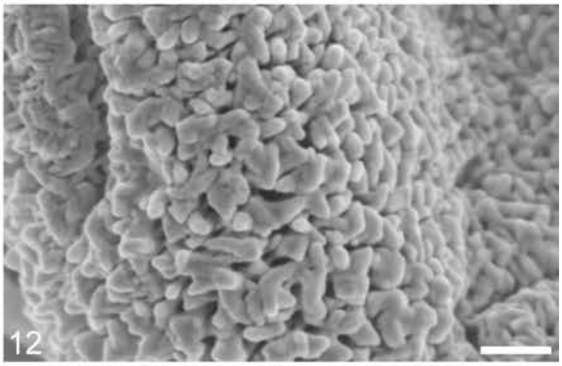
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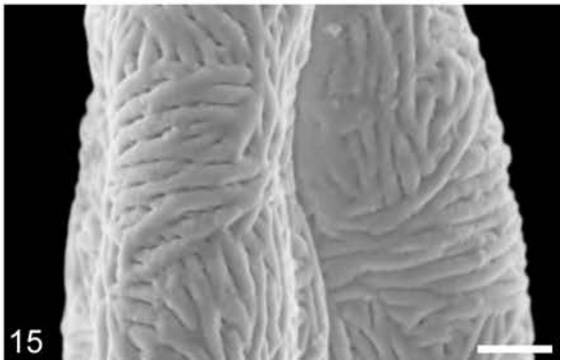
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Plate 4

Fagaceae leaves from the Paleocene of Agatdalen, western Greenland

1. *Eotrigonobalanus* leaf morphotype, with decurrent base and petiole preserved, MGUH 10385. Agatkløft, Agatdal Fm. Scale bar: 1 cm
2. *Eotrigonobalanus* leaf morphotype, base missing, MGUH 10384. Agatkløft, Agatdal Fm. Scale bar: 1 cm
3. *Eotrigonobalanus* leaf morphotype, complete lamina, petiole missing, MGUH 10383. Agatkløft, Agatdal Fm. Scale bar: 1 cm
4. *Eotrigonobalanus* leaf morphotype, counterpart to 3, MGUH 10383. Agatkløft, Agatdal Fm. Scale bar: 1 cm
5. *Eotrigonobalanus* leaf morphotype, complete lamina, petiole missing, MGUH 10386. Agatkløft, Agatdal Fm. Scale bar: 1 cm
6. *Eotrigonobalanus* leaf morphotype, lamina with few small teeth, MGUH 10462. Qaarsutjægerdal (Big section), Agatdal Fm. Scale bar: 1 cm

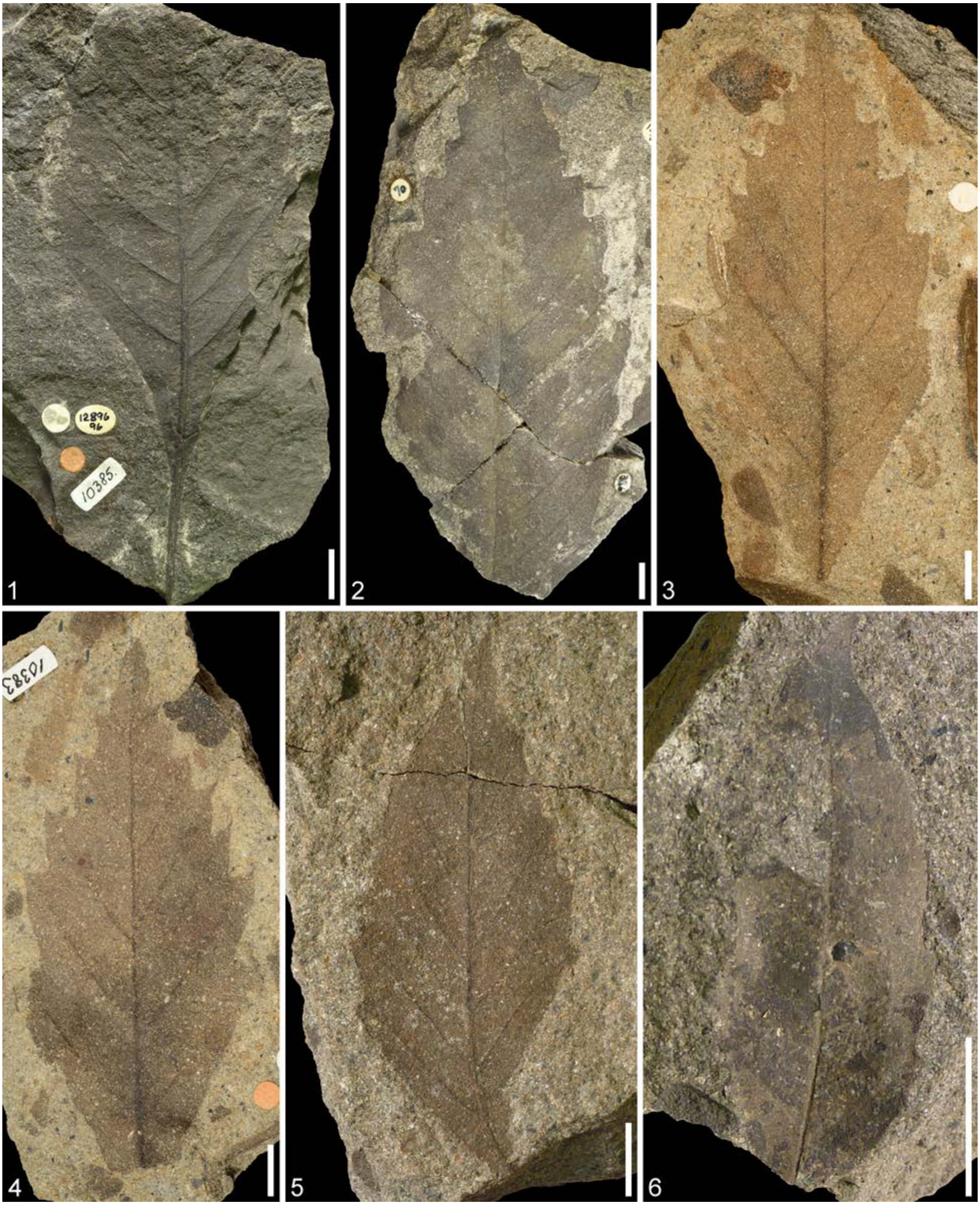
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Plate 5

Fagaceae leaves from the Paleocene of Agatdalen, western Greenland

1. *Eotrigonobalanus* leaf morphotype, narrow lamina, MGUH 10376. Qaarsutjægerdal (Big section), Agatdal Fm. Scale bar: 1 cm
2. *Eotrigonobalanus* leaf morphotype, narrow lamina, base missing, MGUH 10379. Agatkløft, Agatdal Fm Scale bar: 1 cm
3. *Eotrigonobalanus* leaf morphotype, lower half of lamina with entire margin, MGUH 10380. Agatkløft, Agatdal Fm. Scale bar: 1 cm
4. *Eotrigonobalanus* leaf morphotype, teeth in upper third of lamina, MGUH 10377. Agatkløft, Agatdal Fm. Scale bar: 1 cm
5. *Eotrigonobalanus* leaf morphotype, short elliptic lamina, MGUH 10461. Kangersooq (Quleruarsuup isua), Agatdal Fm or Eqalulik Fm. Scale bar: 1 cm
6. *Eotrigonobalanus* leaf morphotype, close-up of counterpart to 1, showing secondary venation and teeth in central part of lamina, MGUH 10376. Qaarsutjægerdal (Big section), Agatdal Fm. Scale bar: 1 cm
7. *Eotrigonobalanus* leaf morphotype, close-up of 2, showing secondary venation and marginal features, MGUH 10379. Agatkløft, Agatdal Fm. Scale bar: 1 cm
8. *Eotrigonobalanus* leaf morphotype, close-up of Pl. 4, fig. 3, showing apex and teeth in apical region, MGUH 10383. Agatkløft, Agatdal Fm. Scale bar: 1 cm
9. *Eotrigonobalanus* leaf morphotype, close-up of Pl. 4, fig. 2, showing teeth in upper part of lamina, MGUH 10384. Agatkløft, Agatdal Fm. Scale bar: 1 cm


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Plate 6

Fagaceae leaves from the Paleocene of Agatdalen, western Greenland

1. *Fagopsiphyllum groenlandicum*, small elliptic lamina, MGUH 10369. Kangersooq (Quleruarsuup isua), Agatdal Fm or Eqalulik Fm. Scale bar: 1 cm
2. *Fagopsiphyllum groenlandicum*, showing zig-zag central vein in apical region, counterpart to 1, MGUH 10369. Kangersooq (Quleruarsuup isua), Agatdal Fm or Eqalulik Fm. Scale bar: 1 cm
3. *Fagopsiphyllum groenlandicum*, medium sized elliptic lamina, central vein curved, MGUH 10372. Kangersooq (Quleruarsuup isua), Agatdal Fm or Eqalulik Fm. Scale bar: 1 cm.
4. *Fagopsiphyllum groenlandicum*, part of large lamina, MGUH 10370. Kangersooq (Quleruarsuup isua), Agatdal Fm or Eqalulik Fm. Scale bar: 1 cm
5. *Fagopsiphyllum groenlandicum*, lower half of large lamina, MGUH 10371. Kangersooq (Quleruarsuup isua), Agatdal Fm or Eqalulik Fm. Scale bar: 1 cm
6. *Fagopsiphyllum groenlandicum*, base form and venation, MGUH 10411. Kangersooq (Quleruarsuup isua), Agatdal Fm or Eqalulik Fm. Scale bar: 1 cm
7. *Fagopsiphyllum groenlandicum*, base form and venation, MGUH 10437. Kangersooq (Quleruarsuup isua), Agatdal Fm or Eqalulik Fm. Scale bar: 1 cm
8. *Fagopsiphyllum groenlandicum*, tertiary venation, MGUH 10411. Kangersooq (Quleruarsuup isua), Agatdal Fm or Eqalulik Fm. Scale bar: 1 cm


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Plate 7

Fagaceae leaves from the Paleocene of Agatdalen, western Greenland

1. *Fagopsiphyllum groenlandicum*, close-up of Pl. 6, fig. 3, showing basal part, MGUH 10372. Kangersooq (Quleruarsuup isua), Agatdal Fm or Eqalulik Fm. Scale bar: 1 cm
2. *Fagopsiphyllum groenlandicum*, close-up of Pl. 6, fig. 3, showing secondary veins ending in teeth, central vein zig-zag in apical part, MGUH 10372. Kangersooq (Quleruarsuup isua), Agatdal Fm or Eqalulik Fm. Scale bar: 1 cm
3. *Fagopsiphyllum groenlandicum*, close-up of 8, showing secondary veins ending in central part of tooth apex, MGUH 10411. Kangersooq (Quleruarsuup isua), Agatdal Fm or Eqalulik Fm. Scale bar: 1 cm
4. *Fagopsiphyllum groenlandicum*, lower to middle part of lamina, petiole preserved, MGUH 10373. Kangersooq (Quleruarsuup isua), Agatdal Fm or Eqalulik Fm. Scale bar: 1 cm
5. *Fagopsiphyllum groenlandicum*, lower part of big broadly based leaf, MGUH 10374. Kangersooq (Quleruarsuup isua), Agatdal Fm or Eqalulik Fm. Scale bar: 1 cm
6. *Fagopsiphyllum groenlandicum*, upper lateral section of lamina, MGUH 10375. Kangersooq (Quleruarsuup isua), Agatdal Fm or Eqalulik Fm. Scale bar: 1 cm
7. *Fagopsiphyllum groenlandicum*, part of elliptic lamina, numerous secondary veins, MGUH 10428. Kangersooq (Quleruarsuup isua), Agatdal Fm or Eqalulik Fm. Scale bar: 1 cm
8. *Fagopsiphyllum groenlandicum*, part of large lamina, MGUH 10411. Kangersooq (Quleruarsuup isua), Agatdal Fm or Eqalulik Fm. Scale bar: 1 cm


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Plate 8

Fagaceae pollen grains from the Paleocene Agatdal Formation, Turritellakløft (Big section) locality, Agatdalen valley, western Greenland

1. Castaneoideae PT 2, LM equatorial view. IPUW 7513/177. Scale bar: 10 µm
2. Castaneoideae PT 2, SEM equatorial view, same grain as in 1. IPUW 7513/177. Scale bar: 1 µm
3. Castaneoideae PT 2, SEM close-up of 2 showing rugulate, fossulate, perforate sculpture. IPUW 7513/177. Scale bar: 1 µm
4. Castaneoideae PT 2, LM equatorial view (upper) and polar view (lower). IPUW 7513/178. Scale bar: 10 µm
5. Castaneoideae PT 2, SEM equatorial view, same grain as in 4. IPUW 7513/178. Scale bar: 1 µm
6. Castaneoideae PT 2, SEM, close-up of 5 showing rugulate, fossulate, perforate sculpture. IPUW 7513/178. Scale bar: 1 µm
7. Castaneoideae PT 2, LM equatorial view (upper) and polar view (lower). IPUW 7513/179. Scale bar: 10 µm
8. Castaneoideae PT 2, SEM equatorial view, same grain as in 7. IPUW 7513/179. Scale bar: 1 µm
9. Castaneoideae PT 2, SEM, close-up of 8 showing rugulate, fossulate, perforate sculpture. IPUW 7513/179. Scale bar: 1 µm
10. Castaneoideae PT 2, LM equatorial view. IPUW 7513/180. Scale bar: 10 µm
11. Castaneoideae PT 2, SEM equatorial view, same grain as in 10. IPUW 7513/180. Scale bar: 1 µm
12. Castaneoideae PT 2, SEM, close-up of 11 showing rugulate, fossulate, perforate sculpture. IPUW 7513/180. Scale bar: 1 µm.
13. Castaneoideae PT 2, LM equatorial view. IPUW 7513/181. Scale bar: 10 µm
14. Castaneoideae PT 2, SEM equatorial view, same grain as in 13. IPUW 7513/181. Scale bar: 1 µm
15. Castaneoideae PT 2, SEM, close-up of 14 showing rugulate, fossulate, perforate sculpture. IPUW 7513/181. Scale bar: 1 µm

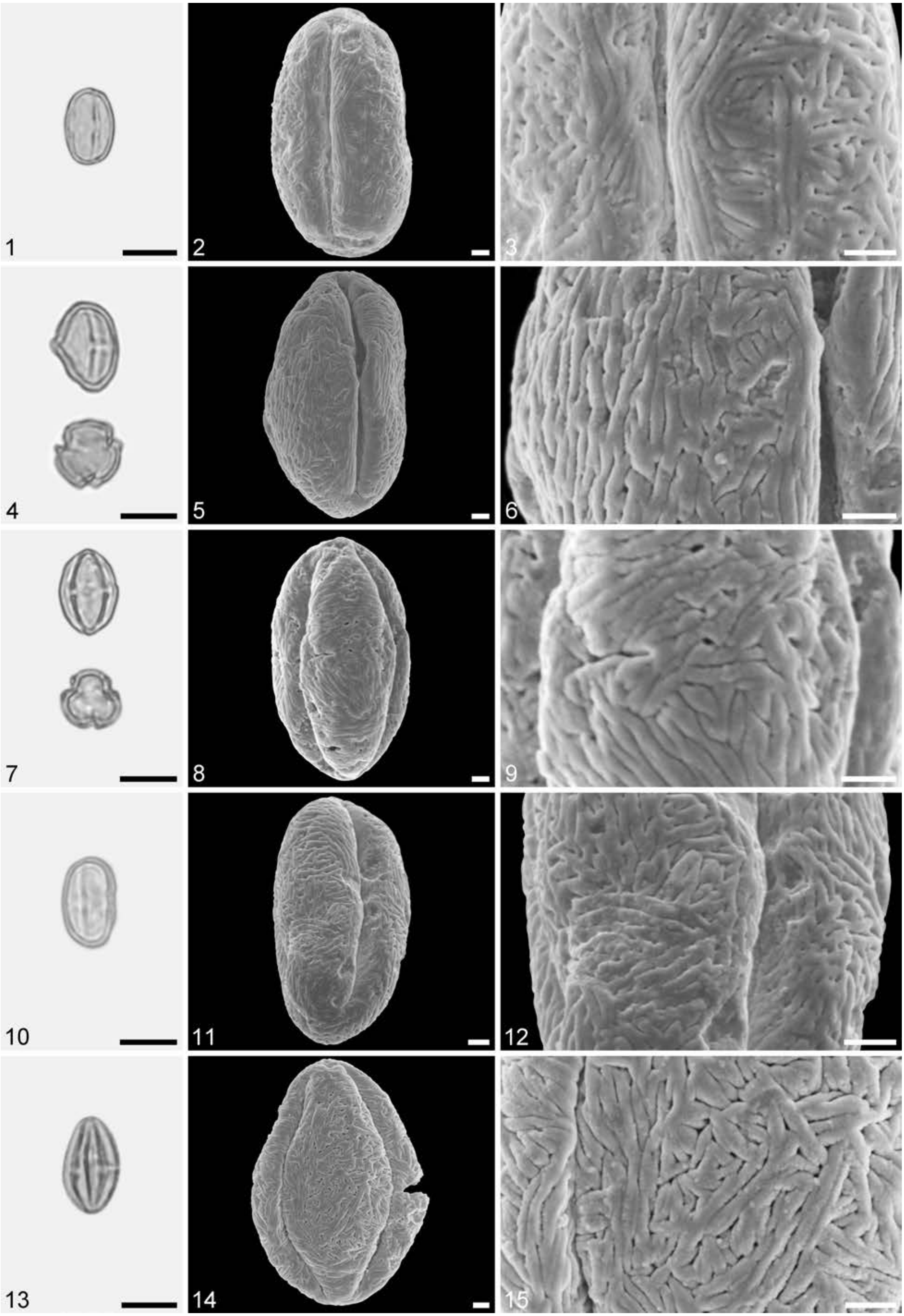
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Plate 9

Fagaceae pollen grains from the Paleocene Agatdal Formation, Turritellakløft (Big section) locality, Agatdalen valley, western Greenland

1. Castaneoideae PT 2, LM equatorial view (upper) and polar view (lower). IPUW 7513/182. Scale bar: 10 µm
2. Castaneoideae PT 2, SEM equatorial view, same grain as in 1. IPUW 7513/182. Scale bar: 1 µm
3. Castaneoideae PT 2, SEM, close-up of 2 showing rugulate, fossulate, perforate sculpture. IPUW 7513/182. Scale bar: 1 µm
4. Castaneoideae PT 2, LM equatorial view (upper) and polar view (lower). IPUW 7513/183. Scale bar: 10 µm
5. Castaneoideae PT 2, SEM equatorial view, same grain as in 4. IPUW 7513/183. Scale bar: 1 µm
6. Castaneoideae PT 2, SEM, close-up of 5 showing rugulate, fossulate, perforate sculpture. IPUW 7513/183. Scale bar: 1 µm
7. Castaneoideae PT 3, LM equatorial view (upper) and polar view (lower). IPUW 7513/184. Scale bar: 10 µm
8. Castaneoideae PT 3, SEM equatorial view, same grain as in 7. IPUW 7513/184. Scale bar: 1 µm
9. Castaneoideae PT 3, SEM, close-up of 8 showing rugulate, fossulate, perforate sculpture. IPUW 7513/184. Scale bar: 1 µm
10. Castaneoideae PT 3, LM equatorial view (upper) and polar view (lower). IPUW 7513/185. Scale bar: 10 µm
11. Castaneoideae PT 3, SEM equatorial view, same grain as in 10. IPUW 7513/185. Scale bar: 1 µm
12. Castaneoideae PT 3, SEM, close-up of 11 showing rugulate, fossulate, perforate sculpture. IPUW 7513/185. Scale bar: 1 µm
13. Castaneoideae PT 3, LM equatorial view (upper) and polar view (lower). IPUW 7513/186. Scale bar: 10 µm
14. Castaneoideae PT 3, SEM equatorial view, same grain as in 13. IPUW 7513/186. Scale bar: 1 µm
15. Castaneoideae PT 3, SEM, close-up of 14 showing rugulate, fossulate, perforate sculpture. IPUW 7513/186. Scale bar: 1 µm


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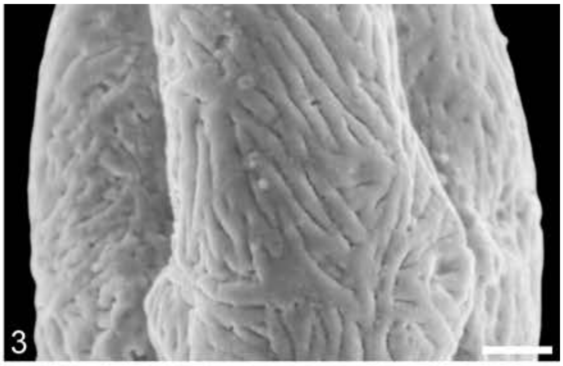
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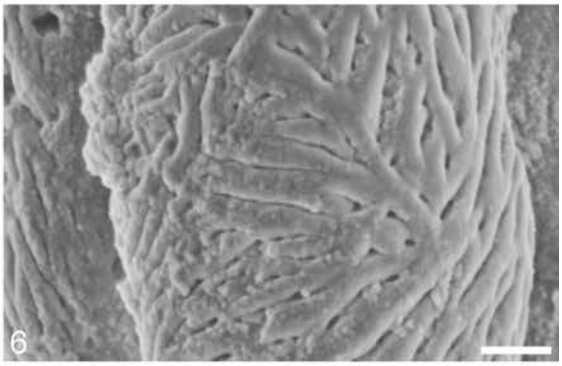
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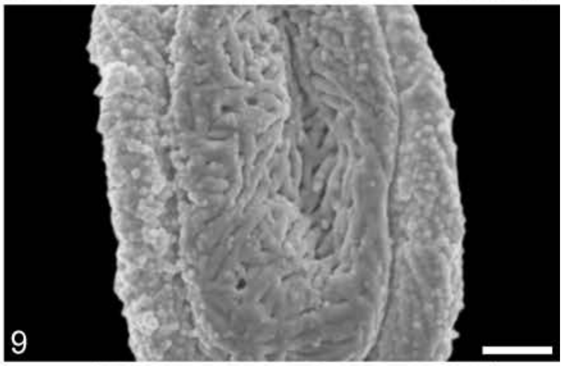
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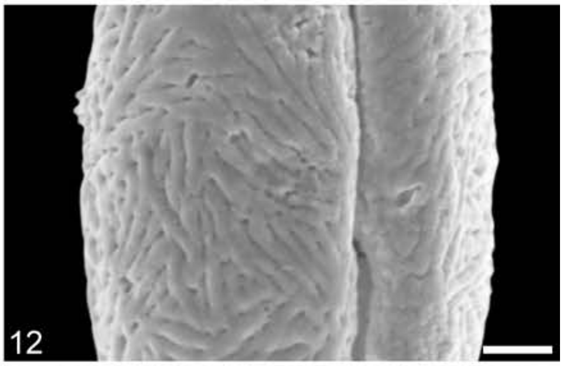
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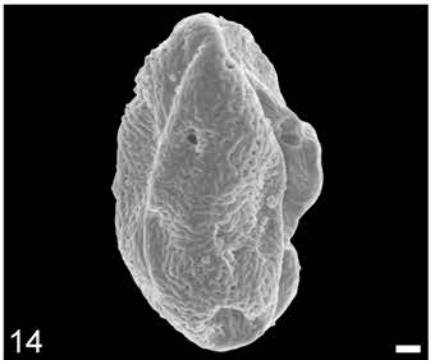
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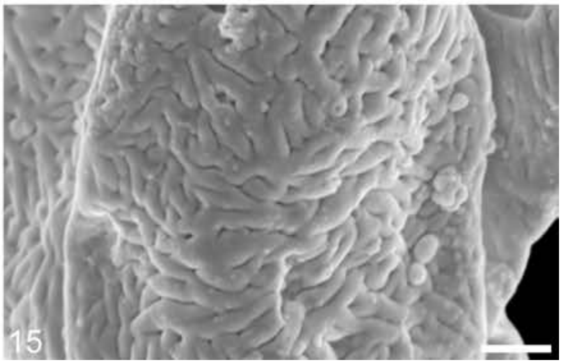
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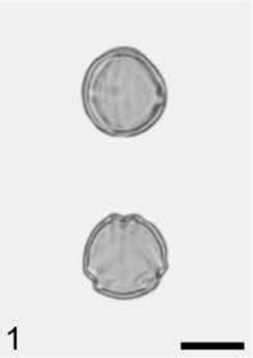
Plate 10

Fagaceae pollen grains from the Paleocene Agatdal Formation, Turritellakløft (Big section) locality, Agatdalen valley, western Greenland

1. Castaneoideae PT 4 (aff. *Lithocarpus*), LM equatorial view (upper) and polar view (lower). IPUW 7513/187. Scale bar: 10 µm
2. Castaneoideae PT 4 (aff. *Lithocarpus*), SEM equatorial view, same grain as in 1. IPUW 7513/187. Scale bar: 1 µm
3. Castaneoideae PT 4 (aff. *Lithocarpus*), SEM, close-up of 2 showing rugulate, fossulate, perforate sculpture. IPUW 7513/187. Scale bar: 1 µm
4. Castaneoideae PT 4 (aff. *Lithocarpus*), LM equatorial view. IPUW 7513/188. Scale bar: 10 µm
5. Castaneoideae PT 4 (aff. *Lithocarpus*), SEM equatorial view, same grain as in 4. IPUW 7513/188. Scale bar: 1 µm
6. Castaneoideae PT 4 (aff. *Lithocarpus*), SEM, close-up of 5 showing rugulate, fossulate, perforate sculpture. IPUW 7513/188. Scale bar: 1 µm
7. Castaneoideae PT 4 (aff. *Lithocarpus*), LM equatorial view (upper) and polar view (lower). IPUW 7513/189. Scale bar: 10 µm
8. Castaneoideae PT 4 (aff. *Lithocarpus*), SEM equatorial view, same grain as in 7. IPUW 7513/189. Scale bar: 1 µm
9. Castaneoideae PT 4 (aff. *Lithocarpus*), SEM, close-up of 8 showing rugulate, fossulate, perforate sculpture. IPUW 7513/189. Scale bar: 1 µm
10. Castaneoideae PT 4 (aff. *Lithocarpus*), LM equatorial view. IPUW 7513/190. Scale bar: 10 µm
11. Castaneoideae PT 4 (aff. *Lithocarpus*), SEM equatorial view, same grain as in 10. IPUW 7513/190. Scale bar: 1 µm
12. Castaneoideae PT 4 (aff. *Lithocarpus*), SEM close-up of 11 showing rugulate, fossulate, perforate sculpture. IPUW 7513/190. Scale bar: 1 µm
13. Castaneoideae PT 4 (aff. *Lithocarpus*), LM equatorial view (upper) and polar view (lower). IPUW 7513/191. Scale bar: 10 µm
14. Castaneoideae PT 4 (aff. *Lithocarpus*), SEM equatorial view, same grain as in 13. IPUW 7513/191. Scale bar: 1 µm
15. Castaneoideae PT 4 (aff. *Lithocarpus*), SEM, close-up of 14 showing rugulate, fossulate, perforate sculpture. IPUW 7513/191. Scale bar: 1 µm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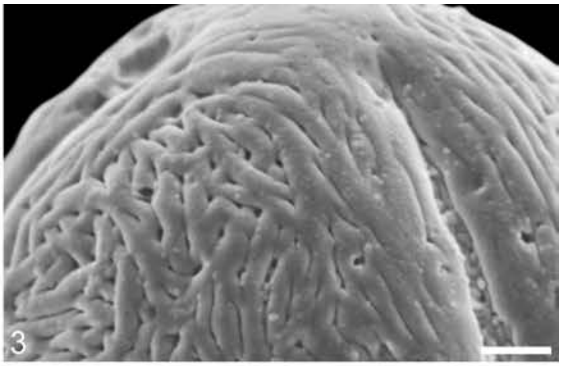
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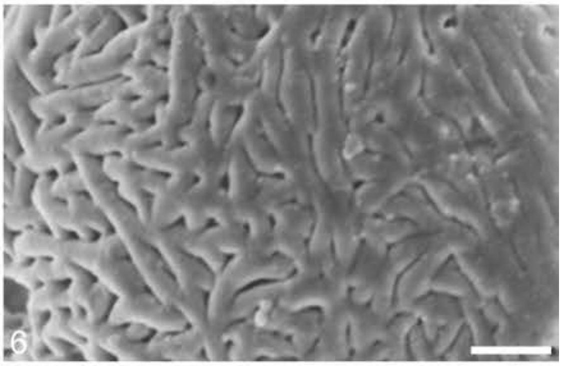
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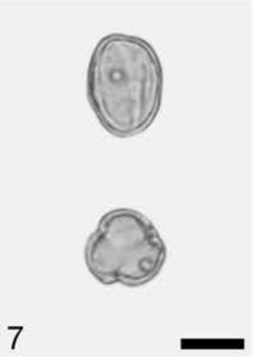
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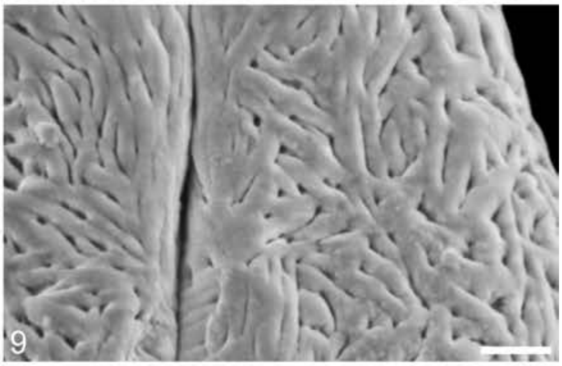
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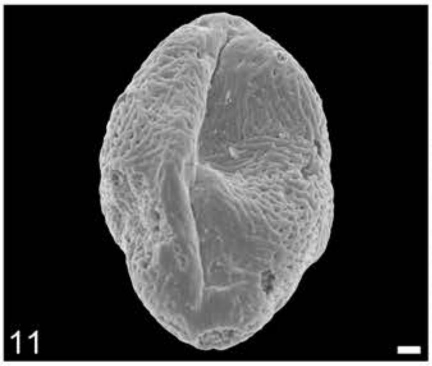
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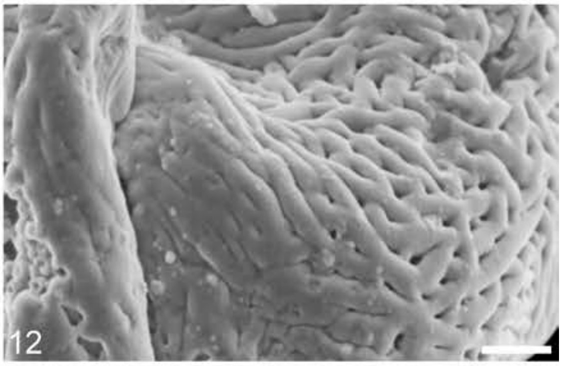
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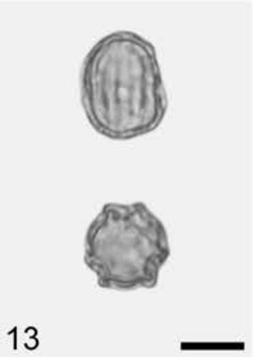
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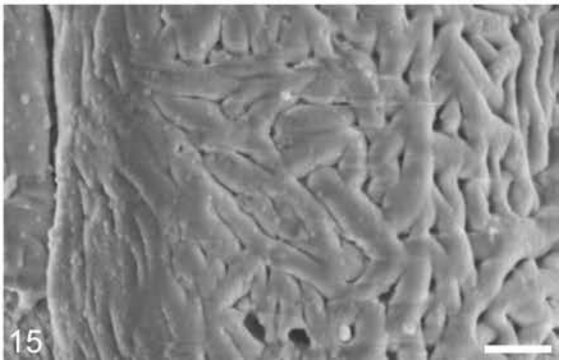
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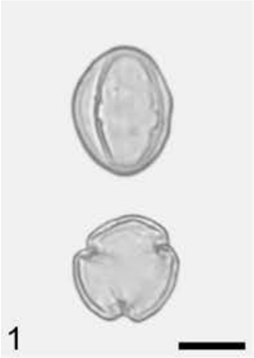
Plate 11

Fagaceae pollen grains from the Paleocene Agatdal Formation, Turritellakløft (Big section) locality, Agatdalen valley, western Greenland

1. Castaneoideae PT 5, LM equatorial view (upper) and polar view (lower). IPUW 7513/192. Scale bar: 10 µm
2. Castaneoideae PT 5, SEM equatorial view, same grain as in 1. IPUW 7513/192. Scale bar: 10 µm
3. Castaneoideae PT 5, SEM, close-up of 2 showing rugulate, fossulate, perforate sculpture. IPUW 7513/192. Scale bar: 1 µm
4. Castaneoideae PT 6, LM equatorial view (upper) and polar view (lower). IPUW 7513/193. Scale bar: 10 µm
5. Castaneoideae PT 6, SEM equatorial view, same grain as in 4. IPUW 7513/193. Scale bar: 1 µm
6. Castaneoideae PT 6, SEM, close-up of 5 showing rugulate, fossulate, perforate sculpture. IPUW 7513/193. Scale bar: 1 µm
7. Castaneoideae PT 7, LM equatorial view (upper) and polar view (lower). IPUW 7513/194. Scale bar: 10 µm
8. Castaneoideae PT 7, SEM equatorial view, same grain as in 7. IPUW 7513/194. Scale bar: 1 µm
9. Castaneoideae PT 7, SEM, close-up of 8 showing rugulate, fossulate, perforate sculpture. IPUW 7513/194. Scale bar: 1 µm
10. Castaneoideae PT 8, LM equatorial view (upper) and polar view (lower). IPUW 7513/195. Scale bar: 10 µm
11. Castaneoideae PT 8, SEM equatorial view, same grain as in 10. IPUW 7513/195. Scale bar: 1 µm
12. Castaneoideae PT 8, SEM, close-up of 11 showing rugulate, fossulate, perforate sculpture. IPUW 7513/195. Scale bar: 1 µm
13. Castaneoideae PT 9, LM equatorial view. IPUW 7513/196. Scale bar: 10 µm
14. Castaneoideae PT 9, SEM equatorial view, same grain as in 13. IPUW 7513/196. Scale bar: 1 µm
15. Castaneoideae PT 9, SEM, close-up of 14 showing (micro)striato-reticulate sculpture. IPUW 7513/196. Scale bar: 1 µm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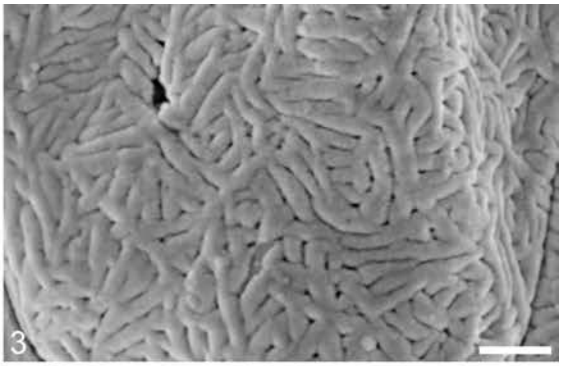
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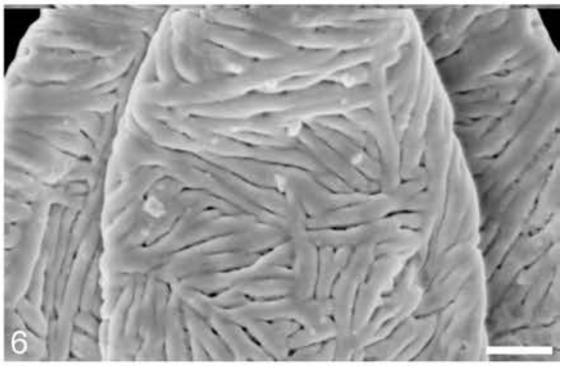
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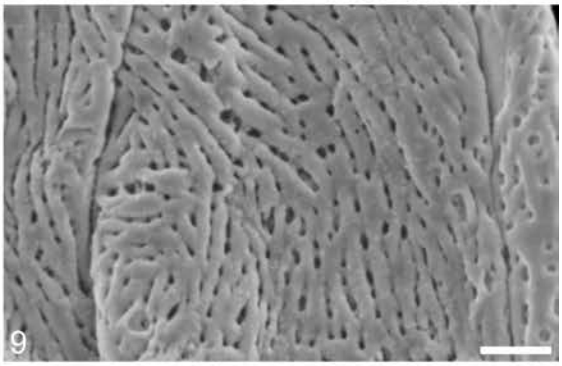
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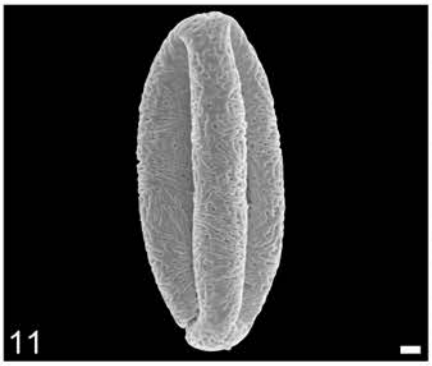
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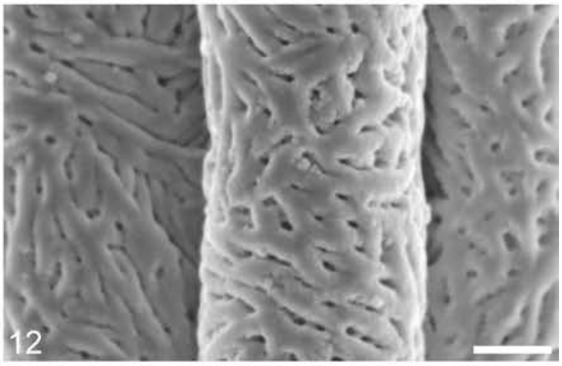
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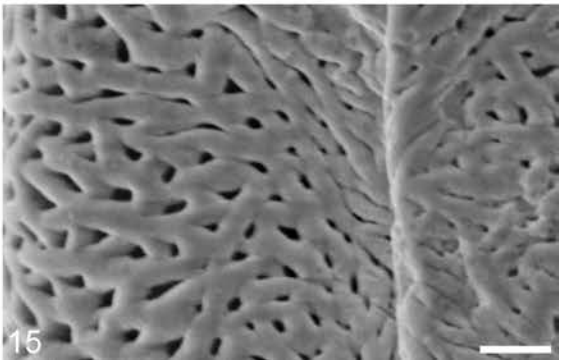
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Plate 12

Fagaceae pollen grains from the Eocene Princeton Chert beds, Allenby Formation,
British Columbia, Canada

1. *Paraquercus eocaena*, LM equatorial view. Holotype, IPUW 7513/197. Scale bar: 10 µm
2. *Paraquercus eocaena*, SEM equatorial view, same grain as in 1. Holotype, IPUW 7513/197. Scale bar: 10 µm
3. *Paraquercus eocaena*, SEM, close-up of 2, showing parallel to radially arranged (micro)rugulae in groups. Holotype, IPUW 7513/197. Scale bar: 1 µm
4. *Eotrigonobalanus* PT, LM equatorial view. IPUW 7513/198. Scale bar: 10 µm
5. *Eotrigonobalanus* PT, SEM equatorial view, same grain as in 4. IPUW 7513/198. Scale bar: 1 µm
6. *Eotrigonobalanus* PT, SEM, close-up of 5, showing twisted and interwoven microrugulae. IPUW 7513/198. Scale bar: 1 µm
7. *Trigonobalanopsis* PT, LM equatorial view. IPUW 7513/199. Scale bar: 10 µm
8. *Trigonobalanopsis* PT, SEM equatorial view, same grain as in 7. IPUW 7513/199. Scale bar: 10 µm
9. *Trigonobalanopsis* PT, SEM, close-up of 8, showing rugulate sculpture, rugulae conspicuously segmented. IPUW 7513/199. Scale bar: 1 µm
10. *Trigonobalanopsis* PT, SEM equatorial view. IPUW 7513/200. Scale bar: 10 µm
11. *Trigonobalanopsis* PT, SEM, close-up of 10, showing rugulae irregularly arranged or parallel in small groups, rugulae conspicuously segmented. IPUW 7513/200. Scale bar: 1 µm
12. *Trigonobalanopsis* PT, SEM equatorial view. IPUW 7513/201. Scale bar: 10 µm
13. *Trigonobalanopsis* PT, SEM, close-up of 12, showing rugulae and perforate sculpture. IPUW 7513/201. Scale bar: 1 µm
14. Castaneoideae PT 2, LM equatorial view. IPUW 7513/202. Scale bar: 10 µm
15. Castaneoideae PT 2, SEM equatorial view, same grain as in 14. IPUW 7513/202. Scale bar: 10 µm
16. Castaneoideae PT 2, SEM, close-up of 15, showing rugulate sculpture around colpi. IPUW 7513/202. Scale bar: 1 µm


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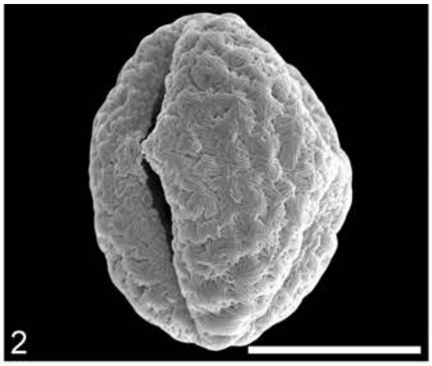
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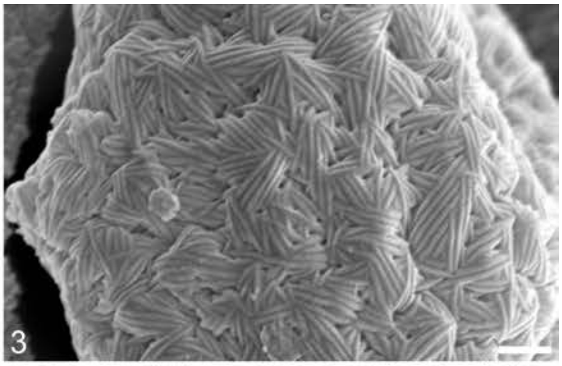
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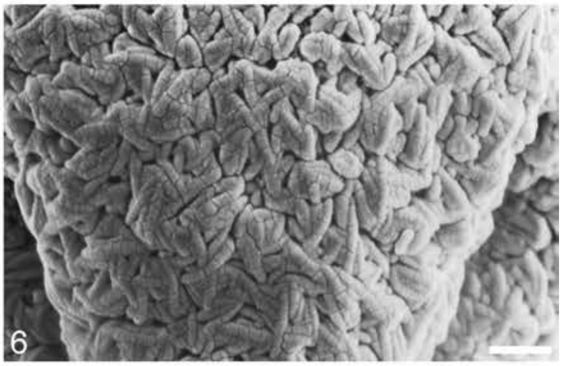
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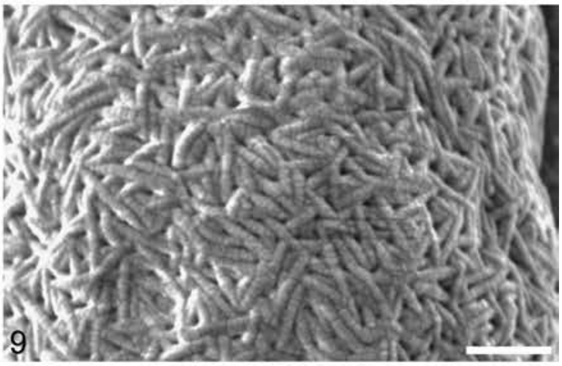
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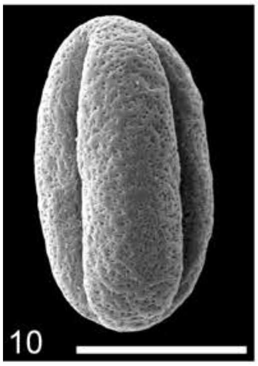
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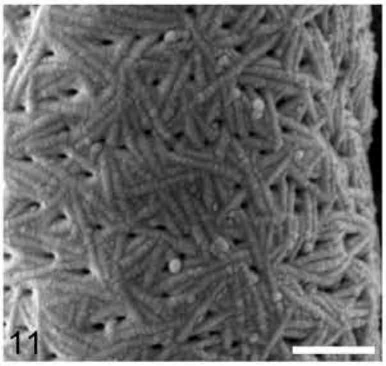
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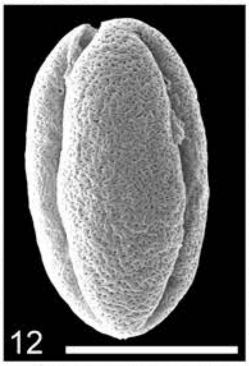
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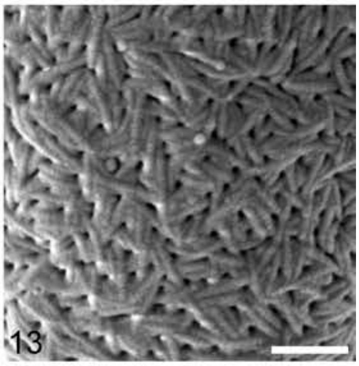
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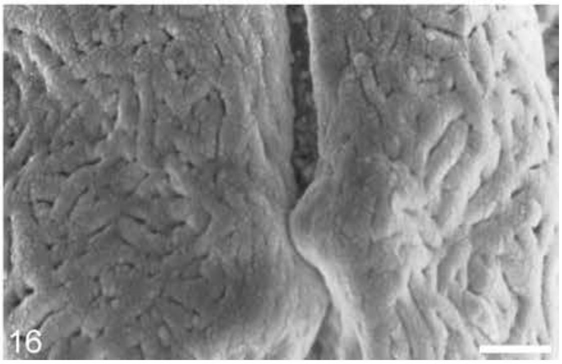
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Plate 13

Fagaceae pollen grains from the Eocene Princeton Chert beds, Allenby Formation,
British Columbia, Canada

1. Fagoideae PT 2, LM equatorial view, pori elliptic (lolongate). IPUW 7513/203. Scale bar: 10 µm
2. Fagoideae PT 2, SEM equatorial view, same grain as in 1. IPUW 7513/203. Scale bar: 10 µm
3. Fagoideae PT 2, SEM, close-up of 2, showing rugulate and minutely fossulate sculpture, rugulae not protruding. IPUW 7513/203. Scale bar: 1 µm
4. *Fagus* PT 2, LM equatorial view, pori small circular. IPUW 7513/204. Scale bar: 10 µm
5. *Fagus* PT 2, SEM equatorial view, same grain as in 4. IPUW 7513/204. Scale bar: 1 µm
6. *Fagus* PT 2, SEM, close-up of 5, showing microrugulate to rugulate and minutely fossulate sculpture, tips of rugulae sometimes protruding. IPUW 7513/204. Scale bar: 1 µm
7. *Fagus* PT 3, LM equatorial view (upper), polar view (lower), pori elliptic (lolongate). IPUW 7513/205. Scale bar: 10 µm
8. *Fagus* PT 3, SEM polar view, same grain as in 7, colpi extending from pole to pole. IPUW 7513/205. Scale bar: 10 µm
9. *Fagus* PT 3, SEM, close-up of 8, showing microrugulate sculpture. IPUW 7513/205. Scale bar: 1 µm
10. *Fagus* PT 3, SEM, close-up of 8, showing microrugulate sculpture, tips of rugulae often protruding. IPUW 7513/205. Scale bar: 1 µm
11. *Quercus* PT 1 (aff. Group Lobatae), LM equatorial view. IPUW 7513/206. Scale bar: 10 µm
12. *Quercus* PT 1 (aff. Group Lobatae), SEM equatorial view, same grain as in 11. IPUW 7513/206. Scale bar: 1 µm
13. *Quercus* PT 1 (aff. Group Lobatae), SEM, close-up of 12, showing (micro)verrucate, fossulate and perforate sculpture. IPUW 7513/206. Scale bar: 1 µm
14. *Quercus* PT 2 (ancestral type with Group Ilex morphology), LM equatorial view. IPUW 7513/207. Scale bar: 10 µm
15. *Quercus* PT 2 (ancestral type with Group Ilex morphology), SEM equatorial view, same grain as in 14. IPUW 7513/207. Scale bar: 10 µm
16. *Quercus* PT 2 (ancestral type with Group Ilex morphology), SEM, close-up of 15, showing microrugulate and perforate sculpture. IPUW 7513/207. Scale bar: 1 µm
17. *Quercus* PT 2 (ancestral type with Group Ilex morphology), LM equatorial view. IPUW 7513/208. Scale bar: 10 µm
18. *Quercus* PT 2 (ancestral type with Group Ilex morphology), SEM equatorial view, same grain as in 17. IPUW 7513/208. Scale bar: 10 µm
19. *Quercus* PT 2 (ancestral type with Group Ilex morphology), SEM, close-up of 18, showing microrugulate and perforate sculpture. IPUW 7513/208. Scale bar: 1 µm

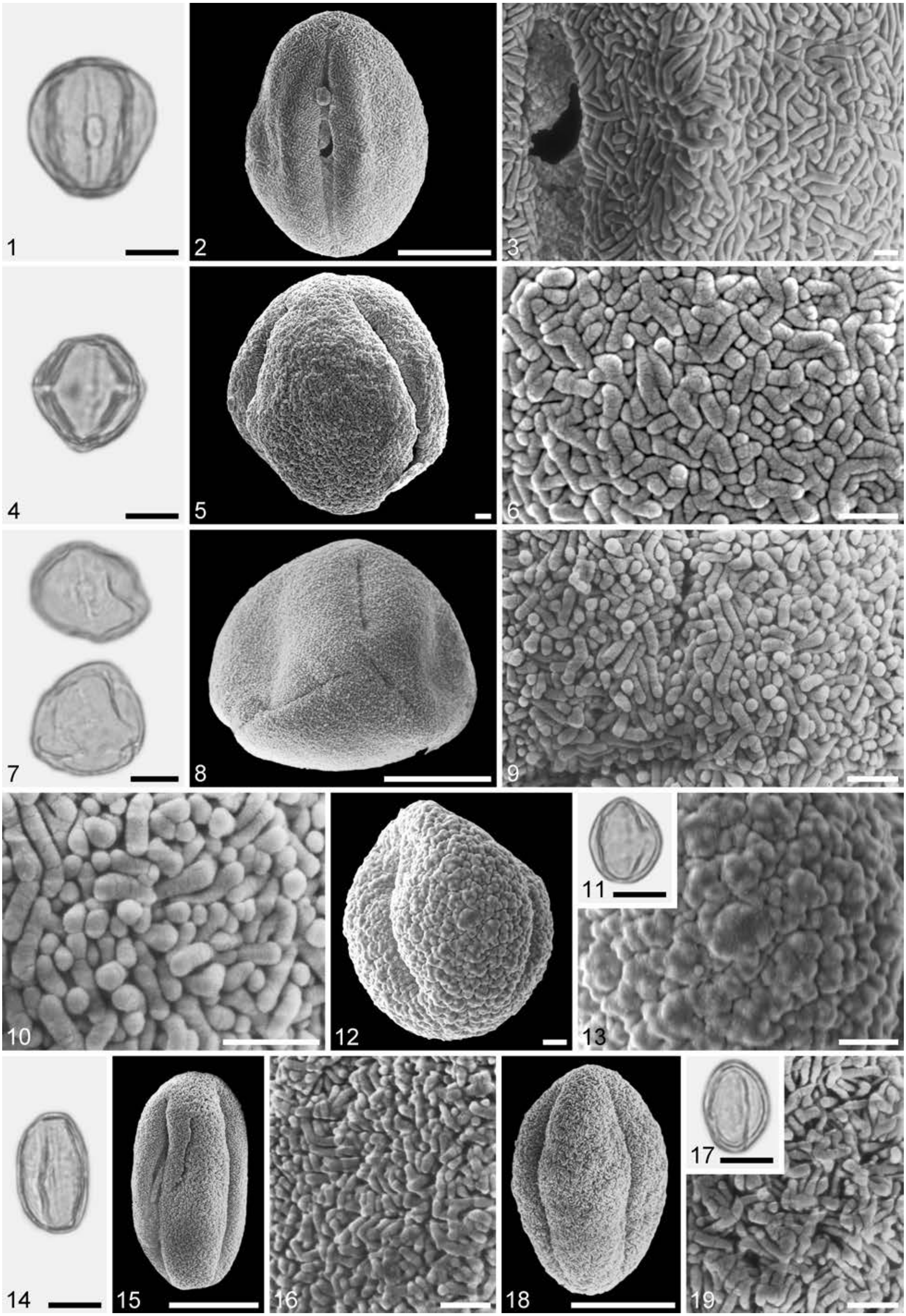
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Plate 14

Fagaceae and Fagales leaves from the Paleogene of western Greenland

1. Fagaceae indet., large lamina, MGUH 6526. Qeqertarsuatsiaq, Hareøen Fm. Scale bar: 1 cm
2. Fagaceae indet., close-up of 1, showing teeth and venation in lower half of lamina, wide rounded sinuses between teeth, MGUH 6526. Qeqertarsuatsiaq, Hareøen Fm. Scale bar: 1 cm
3. *Fagopsiphyllum groenlandicum*, part of large lamina, MGUH 6550. Qeqertarsuatsiaq, Hareøen Fm. Scale bar: 1 cm
4. Fagales indet., part of large lamina, MGUH 6552. Referred to Qeqertarsuatsiaq (Hareøen) by Heer (1883). Most likely from Upper Atanikerluk A, Quikavsak Fm. Scale bar: 1 cm

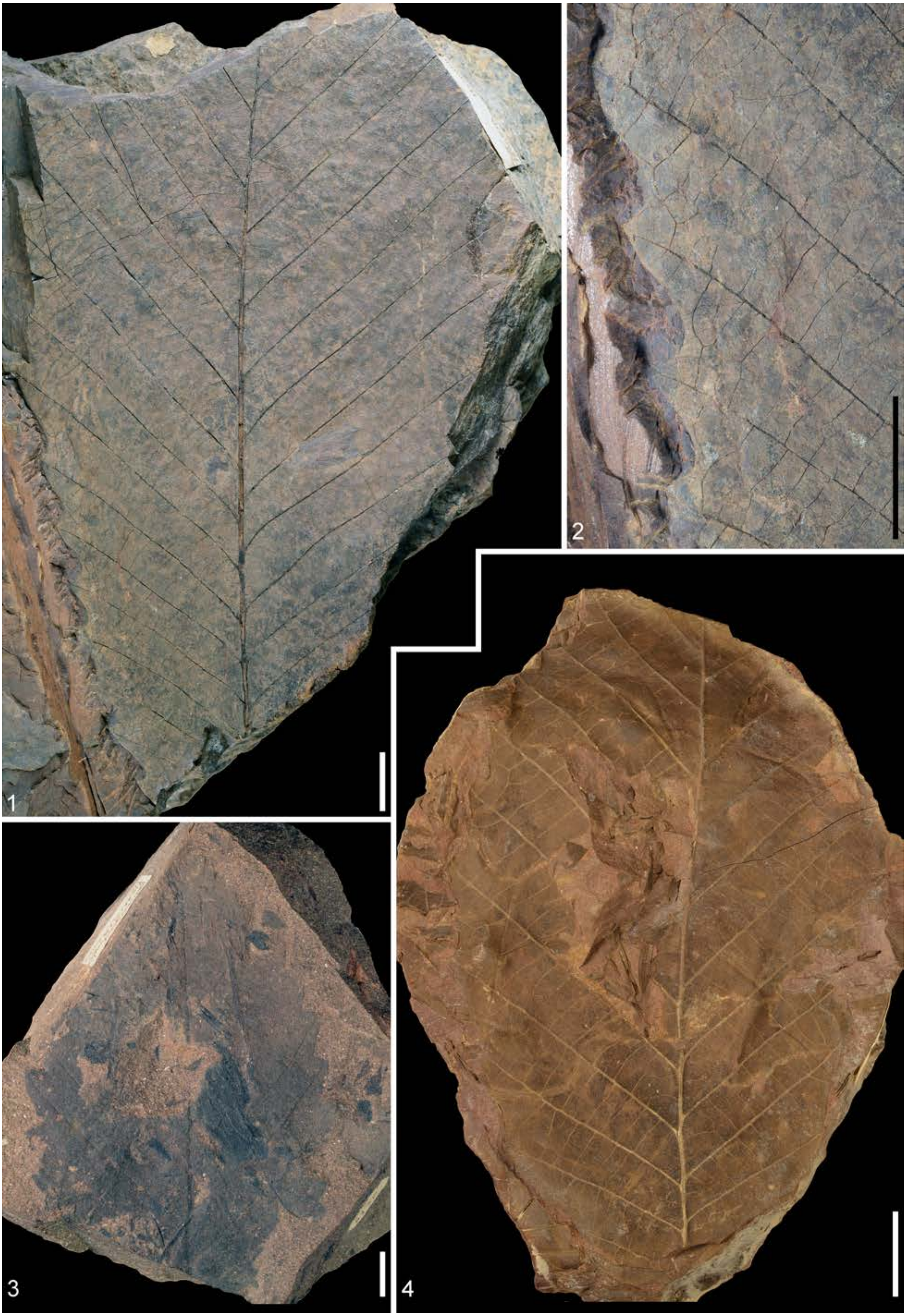
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Plate 15

Fagaceae and Fagales leaves from the Paleogene of western Greenland

1. *Fagopsiphyllum groenlandicum*, part of lamina, MGUH 6538. Referred to Qeqertarsuatsiaq (Hareøen) by Heer (1883). Most likely from Upper Atanikerluk A, Quikavsak Fm (see Note under species description). Scale bar: 1 cm
2. *Fagopsiphyllum groenlandicum*, part of lamina, counterpart to 1, MGUH 6538. Referred to Qeqertarsuatsiaq (Hareøen) by Heer (1883). Most likely from Upper Atanikerluk A, Quikavsak Fm (see Note under species description). Scale bar: 1 cm
3. *Fagopsiphyllum groenlandicum*, close-up of 1, showing teeth, MGUH 6538. Referred to Qeqertarsuatsiaq (Hareøen) by Heer (1883). Most likely from Upper Atanikerluk A, Quikavsak Fm (see Note under species description). Scale bar: 1 cm
4. *Fagopsiphyllum groenlandicum*, narrow elliptic lamina, MGUH 6542. Referred to Qeqertarsuatsiaq (Hareøen) by Heer (1883). Most likely from Upper Atanikerluk A, Quikavsak Fm (see Note under species description). Scale bar: 1 cm
5. *Fagopsiphyllum groenlandicum*, close-up of 4, showing secondary and tertiary venation and teeth along margin, MGUH 6542. Referred to Qeqertarsuatsiaq (Hareøen) by Heer (1883). Most likely from Upper Atanikerluk A, Quikavsak Fm (see Note under species description). Scale bar: 1 cm
6. *Fagopsiphyllum groenlandicum*, close-up of Pl. 14, fig. 3, showing secondary venation and teeth along margin, wide angular sinuses between teeth, MGUH 6550. Qeqertarsuatsiaq, Hareøen Fm. Scale bar: 1 cm
7. Fagales indet., close-up of Pl. 14, fig. 4, showing secondary and tertiary venation and teeth along margin, subsidiary teeth present, MGUH 6552. Referred to Qeqertarsuatsiaq (Hareøen) by Heer (1883). Most likely from Upper Atanikerluk A, Quikavsak Fm Scale bar: 1 cm

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Plate 16

Fagus leaves from the Eocene of Qeqertarsuatsiaq, Hareøen Formation, western Greenland

1. *Fagus cordifolia*, leaf, broadly based lamina, almost complete, MGUH 6558. Scale bar: 1 cm
2. *Fagus cordifolia*, leaf, close-up of 1, showing venation along margin, MGUH 6558. Scale bar: 1 cm
3. *Fagus* leaf morphotype 2, leaf, part of large lamina, S 110240. Scale bar: 1 cm
4. *Fagus* leaf morphotype 2, leaf, close-up of 3, showing base, S 110240. Scale bar: 1 cm
5. *Fagus* leaf morphotype 2, leaf, close-up of 3, showing tertiary venation and basal-most tooth above base, S 110240. Scale bar: 1 cm

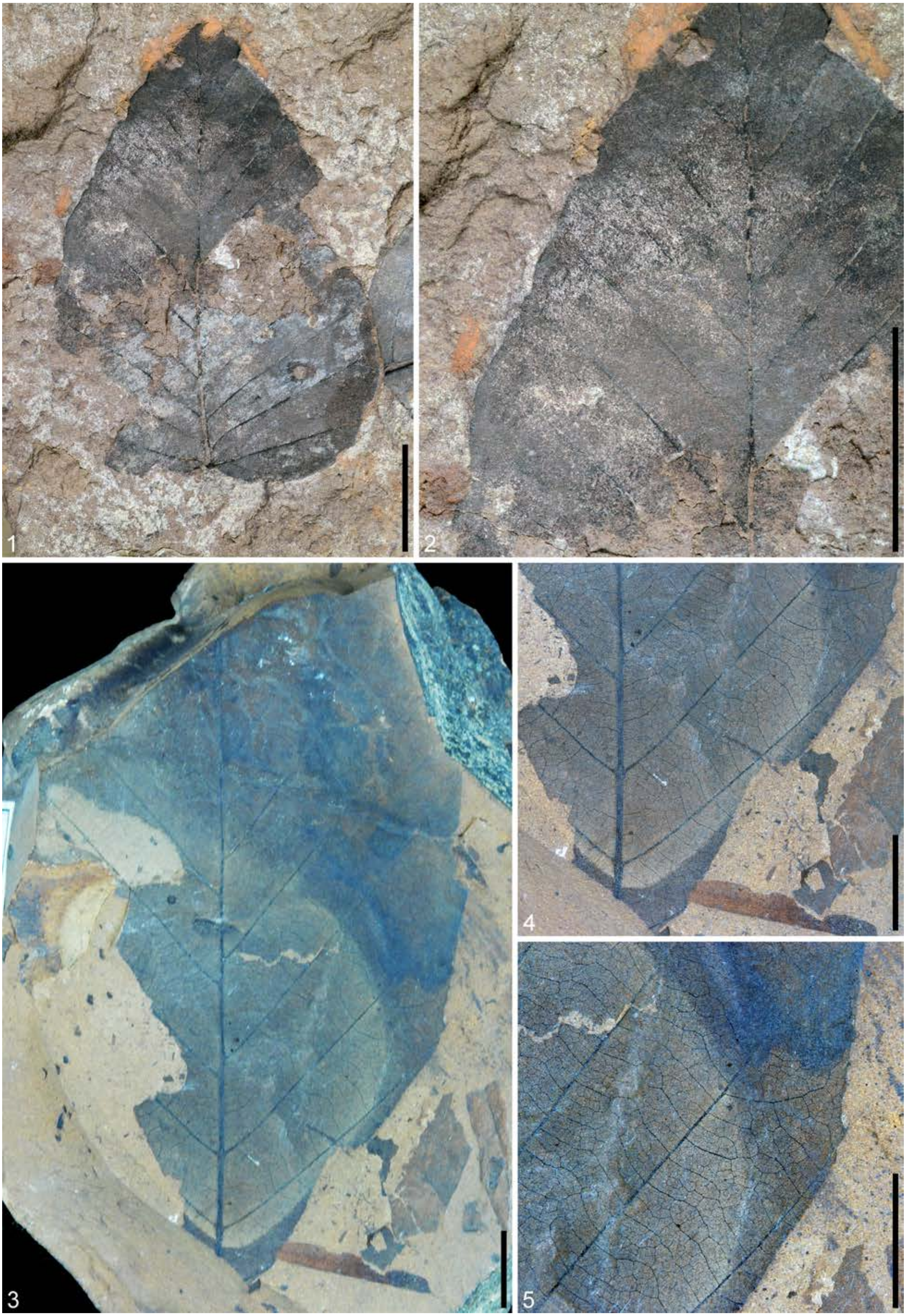
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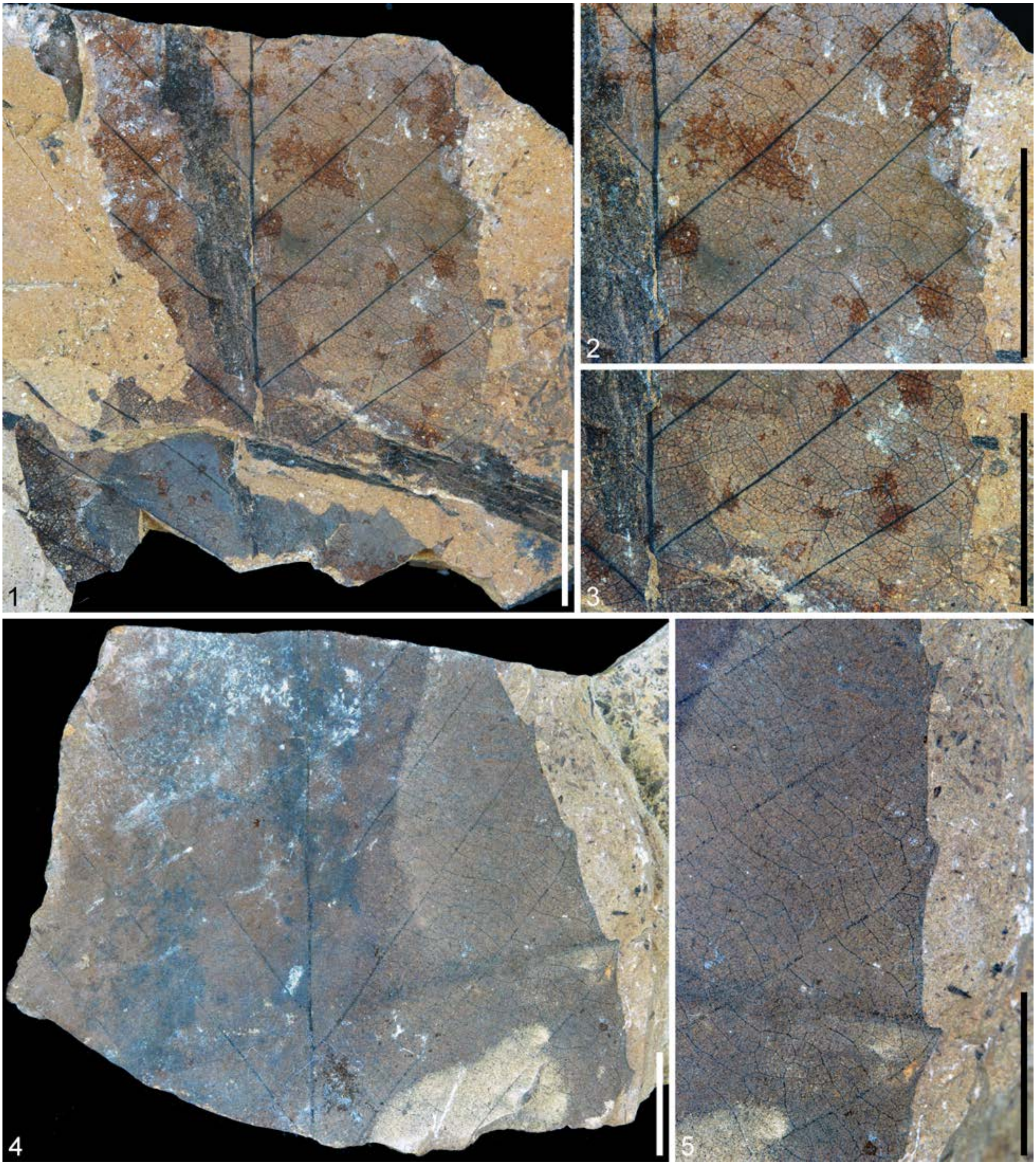
Plate 17

Fagus leaves from the Eocene of Qeqertarsuatsiaq, Hareøen Formation, western Greenland

1. *Fagus* leaf morphotype 2, leaf, part of lamina, S 109724. Scale bar: 1 cm
2. *Fagus* leaf morphotype 2, leaf, close-up of 1, showing secondary and higher-order venation and teeth in central part of lamina, S 109724. Scale bar: 1 cm
3. *Fagus* leaf morphotype 2, leaf, close-up of 1, showing secondary and higher-order venation and teeth in lower part of lamina, S 109724. Scale bar: 1 cm
4. *Fagus* leaf morphotype 2, leaf, part of large lamina, S 110238. Scale bar: 1 cm
5. *Fagus* leaf morphotype 2, leaf, close-up of 4, showing secondary and higher-order venation and teeth in central part of lamina, S 110238. Scale bar: 1 cm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