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Gemmatricolpites R.L. Pierce pollen from the Lower Cretaceous of the Araripe Basin (NE Brazil) - an extinct lineage of Aquifoliaceae or a product of convergent evolution?

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Abstract

Aquifoliales are an early diverging clade of asterids and its important, large woody genus *Ilex* is widespread in moist, warm to tropical habitats today. The origin and evolution of *Ilex* are still under debate because fossils assigned to *Ilex* often are seen as ambiguous and their fossil occurrence predates inferred molecular ages of the *Ilex* crown group. LM, SEM and TEM analyses of tricolpate and tricryptoaperturate *Gemmatricolpites* pollen from the Aptian Rio da Batateira Formation (Brazil) reveal an atectate, clavate to baculate ektexine with microrugulate suprasculpture. *Gemmatricolpites* has a thicker ektexine and similarly structured wall layers, but different aperture types compared to extant *Ilex* (tricolporate). Several '*Ilex*-like pollen' from Europe and South China (early Eocene to Middle Miocene) are double in size and display similar ektexine sculpture and ornamentation, but are tricolpate or tricolporate. Today, some plant genera do show variable pollen apertural conditions, so these variable apertures through time may not result solely from convergence. *Gemmatricolpites* grains from the late Early Cretaceous palaeotropics may then, in fact, represent an extinct lineage of Aquifoliales because their ektexine strongly resembles that of extant *Ilex* pollen, despite the apertural difference, whilst the double size can be interpreted as the result of whole genome duplication. After reviewing reported *Gemmatricolpites* occurrences and nearly cosmopolitan occurrence of tricolpate *Ilexpollenites* pollen and *Ilex* seeds from Upper Cretaceous strata, we suggest this would witness the origin of an ancient, now extinct lineage of Aquifoliales in North Gondwana, and its evolution and lateral migration during the Cretaceous.

Key Words

Aptian, aquifoliales, *Gemmatricolpites* pollen wall, NE Brazil, SEM and TEM

Introduction

Ilex Tourn. ex L. 1753, is a prolific pollen producer from the monotypic Aquifoliaceae (holly family) and the order Aquifoliales Senft, 1856 that includes Aquifoliaceae Bercht. & J.Presl, 1820, Helwingiaceae Decne, 1836, Phyllonomaceae Small, 1905, Cardiopteridaceae Blume, 1847, and Stemonuraceae Kårehed, 2001, families *sensu* Bremer et al. (2002) or only Aquifoliaceae, Helwingiaceae and Phyllonomaceae following Stevens (2001 onwards). We here follow the convention of the Angiosperm Phylogeny Group (Bremer et al. 2002; APG 2016). Aquifoliales are thought to be an early divergent lineage of, or sister to, the campanulids within the large asterid clade (e.g. Bremer et al. 2002, 2004; Soltis et al. 2000), whereas the campanulids are suggested to have a southern hemispheric (Gondwanan) origin (Beaulieu et al. 2013). In contrast to the species poor

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Helwingia Willd. 1806 and *Phyllonoma* Willd. 1820, *Ilex* is considered to be one of the largest genera of woody dioecious angiosperms with approximately 600 species (Manen et al. 2010).

Ilex plants today occur in tropical to warm temperate climate zones (a few outliers in the temperate realm), with centres of diversity in East Asia and South America, plus two species present in Australia, one in Africa and four in Europe (Loizeau et al. 2005). The either evergreen or deciduous *Ilex* species prefer humid habitats (Loizeau et al. 2005) and are absent under drier conditions (Martin 1977). The genus *Ilex* is easily recognized as such, but the drawback is that individual species are difficult to distinguish or separate by wood anatomy, floral morphology and leaf morphology (Baas 1973, 1975). Also, pollen morphology is not particularly useful for separating individual species (see scanning electron microscopy images of Wei et al. (2013) and Miyoshi et al. (2011).

Of the five genera of Aquifoliales, *Ilex* pollen is the only one characterized by a unique and distinctive ektexine: atectate, conspicuously clavate ektexine sculpture, often combined with baculae or gemmae (Lobreau 1969; Lobreau-Callen 1975; Martin 1977; Miyoshi et al. 2011; Muller 1981; Wei et al. 2013) using light microscopy (LM) and scanning electron microscopy (SEM). Only under SEM, however, are the ornamentation, the irregularly arranged ridges and grooves (microrugulate) on the top of the clavae and baculae visible.

This ektexine sculpture is easily recognizable using solely light microscopy and facilitates the identification of *Ilex* pollen or pollen affiliated with either Aquifoliaceae more broadly, or the fossil genera *Ilexpollenites* Thierg. in R. Potonié (1960), *Ilex* sp. (here summarized as '*Ilex*-like' pollen) or *Gemmatricolpites* R.L. Pierce (1961) in pollen assemblages extracted from sedimentary rocks. Consequently, various '*Ilex*-like' pollen have been reported from Upper Cretaceous sedimentary rocks in Antarctica, Australia, Africa, South and North America, SE Asia and Europe (e.g. Muller 1968, 1981; Lobreau-Callen 1975; Martin 1977; Kedves 1988; Askin 1990; Dettmann and Jarzen 1990; Barrón et al. 2015; Barreda et al. 2019; see also palaeogeographical distribution maps in Cuénoud et al. 2000, fig. 1; Loizeau et al. 2005, fig. 4). Additionally, Upper Cretaceous fruit and seed occurrences affiliated with modern *Ilex* (Maastrichtian *Ilex antiqua* Heer, 1882 (Knobloch and Mai 1986; Mai 1970), late Paleocene *I. gonnensis* Mai 1970 (Mai 1970, 1987, 1995) and lower Eocene *I. hercynica* Mai 1970 (Mai 1987, 1995)) have been found in Europe, but unfortunately no fossil pollen have been associated with these macrofossils. Despite these fossil occurrences, previous molecular clock dating of *Ilex* (Cuénoud et al. 2000; Manen et al. 2002, 2010) inferred that the common ancestor of the modern *Ilex* lineage is of approximately Eocene age with the crown group being of middle Miocene age, because the Upper Cretaceous presence of *Ilexpollenites* in the southern hemisphere, particularly in Australia, was doubted and so excluded (Kedves 1988; Manen et al. 2002, 2010). The reasons for this exclusion were either the lack of images or non-convincing images of '*Ilex*-like' pollen occurrences in Australia (Martin 1977) and South America but see also Loizeau et al. (2005; fig. 4). These doubts are understandable because these fossil pollen were investigated solely by LM fixed in glycerol-jelly preparations, making it impossible to turn the pollen for different views and lacking higher resolution for more detailed investigations (e.g., using SEM). However, more recent phylogenetic investigations of Aquifoliaceae by Yao et al. (2016, 2021) suggest a Late Cretaceous stem age (*c.* 84.7 Ma) and a crown group age for the early Eocene (*c.* 50.8 Ma), Additionally, Bremer et al. (2002, 2004) revealed that the diversification of asterids occurred during the Early Cretaceous with an even older stem node age for Aquifoliales of 121 Ma and a crown node age around 113 Ma; quite similar results were presented by Zhang et al. (2020) suggesting that the origin of the asterids was during the Aptian and stem age of Aquifoliaceae (including Helwingiaceae) also during the Early Cretaceous around 120 to 110 Ma. Our new data from the Aptian strata of the Araripe Basin and Eocene strata from Europe and South China corroborate the molecular studies and showcases with fossil pollen the evolution of this interesting genus.

Material and methods

Gemmatricolpites

The Araripe Basin (Fig. 1) is a fault-bounded sedimentary basin located in NE Brazil and world-famous for its exceptionally well-preserved fossil flora and fauna (Martill 2007). Studied samples were collected from the Rio da Batateira Formation (Fm), which is also referred to as a part of the Barbalha Fm (e.g., Melo et al. 2020). The dominant siliciclastic unit represents the basal part of the Post-rift Sequence I of the Araripe Basin (Coimbra and Freire 2021) and is overlain by the laminated limestones of the Crato Fm featuring abundant insect, fish, reptile and plant fossils. Stratigraphic age assignment of the Araripe sedimentary succession is a long-standing matter of debate (Arai and Assine 2020; Heimhofer and Hochuli 2010; Ponte and Appi 1990) and the ages of the Rio da Batateira and Crato Formations considered to span the Late Aptian to Early Albian (*c.* 118.5 to 110 Ma). New biostratigraphic evidence based on planktonic foraminifera and carbon isotope chemostratigraphy supports previous findings and places the position of the Aptian-Albian boundary into the lowermost Romualdo Fm of the Santana Group (Bom et al. 2023; Melo et al. 2020). A significantly older Barremian age of 123.5 ± 3.5 Ma based on Re-Os dating of black shales from the Ipubi Fm (Lúcio et al. 2020) is in marked contrast with existing biostratigraphic evidence for the Post-rift Sequence I basin fill and therefore heavily disputed (Coimbra and Freire 2021).

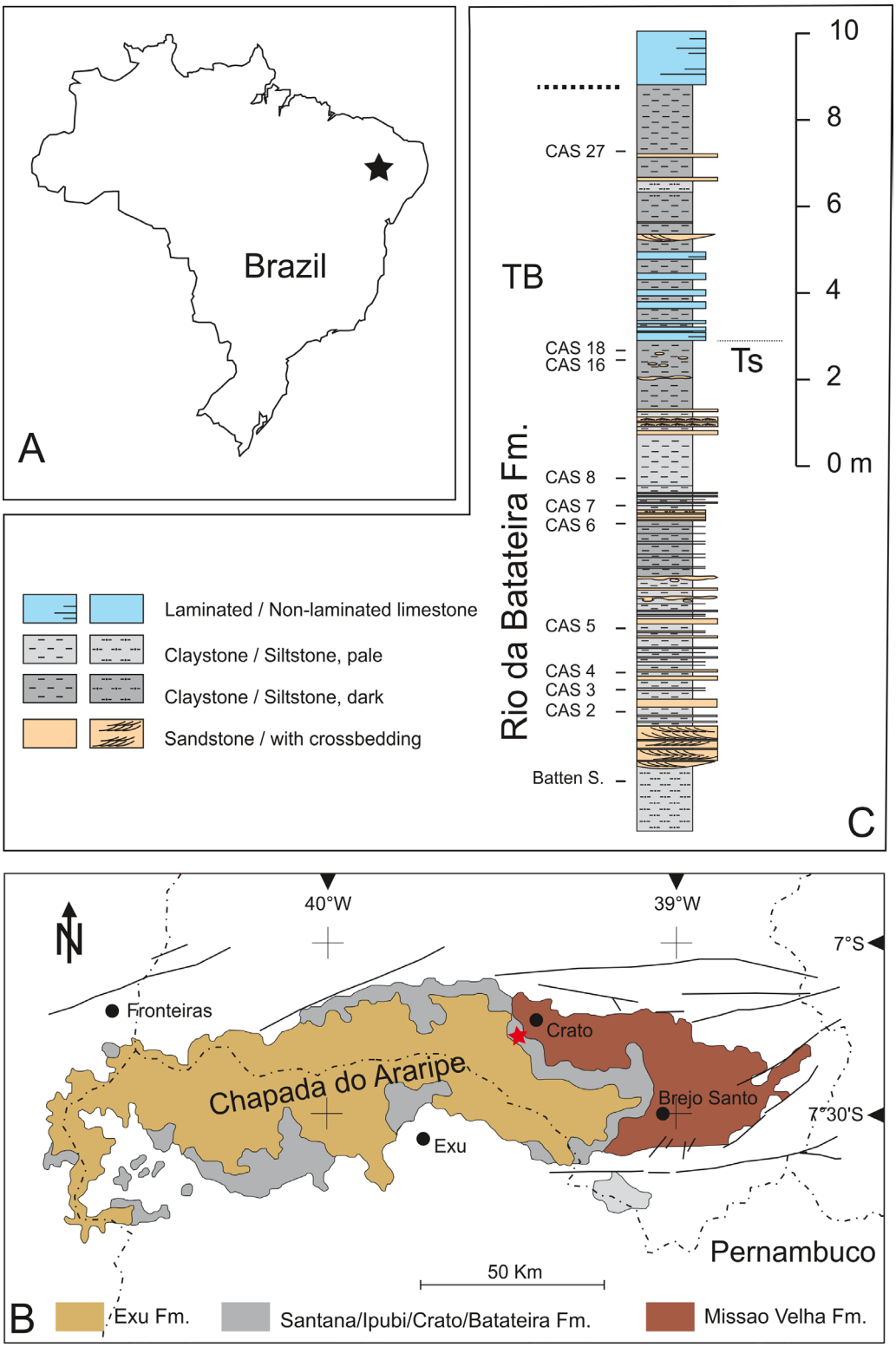

Figure 1. A. Map of the investigated locality in NE Brazil. **A.** Location of the Araripe Basin in NE Brazil. **B.** Geological map of the Araripe Basin showing the outcrops of the Santana Group. The sampling locality near Crato town indicated with an asterisk. **C.** Lithostratigraphic section of the Rio da Batateira Formation at Cascata do Crato with stratigraphic distribution of samples. TB = transition beds (lower Crato Formation), Ts = transgressive surface following Varejao et al. (2021).

In the study area, the Rio da Batateira Fm is composed of fine- to coarse-grained sandstones showing planar or trough cross stratification with interbedded grey to reddish claystones. In the upper part, several thin (up to 0.5 m) laminated limestones beds can be distinguished, which mark the transition to the overlying Crato Fm. A recently published sedimentological study of the Araripe Post-rift Sequence I interprets the strata forming the Rio

da Batateira (lower part of the Barbalha) Fm to represent the transition from a fluvial floodplain depositional environment via a bayhead delta into a setting dominated by ephemeral hypersaline lakes (Varejao et al. 2021).

Terrestrial plant remains include both larger, sometimes woody, debris as well as pollen and spores that were either blown or drifted in by flood events and ephemeral rivers (Kunzmann et al. 2009). All samples investigated here are light brown to slightly darker brown mudstones and slightly silty mudstones of fluvial origin that are lacking meso- and macrofossils (code CAS) and come from a river outcrop cutting the flanks of the Chapada do Araripe (Fig. 1) near Cascata. The samples were collected under permit by Ulrich Heimhofer (Leibniz University Hannover) in 2004. This river section comprises the Rio da Batateira Fm and the unit informally entitled "Transition Beds" (now lower Crato Fm, see Heimhofer and Hochuli 2010)).

'*Ilex*-like' pollen

The stratigraphically younger '*Ilex*-like' pollen presented here are from the following localities (from oldest to youngest):

(1) The lithological short section at St. Pankraz (Salzburg, Austria), which has not been affiliated with any formation consists of *c.* eight m thick grey claystone and marly claystone with intercalations of thin siltstone layers exposed along a hiking trail. The claystone is overlain by a few meters of pure quartz sandstone followed by calcareous arenites and the outcrop is interpreted to expose a general transgressive succession covering the Paleocene-Eocene Thermal Maximum (PETM, Hofmann et al. (2011)).

(2) In the Krappfeld area (Carinthia, Austria) the Ypresian Holzer Fm unconformably overlies Upper Campanian marlstones (marine Pemberger Fm.) and comprises ca. eight to 10 m thick, soft kaolinitic green and red clays incorporating small coal lenses and is characterized by a relatively rich terrestrial palynoflora (Hofmann et al. 2015a; Hofmann and Zetter 2001; Zetter and Hofmann 2001). The top of the clay can be assigned to the lower part of shallow benthic zone SBZ10, which has been correlated with calcareous nannoplankon zone NP12 and suggests that the claystone was deposited during the Early Eocene Climate Optimum (=EECO, Hofmann et al. (2012)).

(3) The lower Bartonian sample material comes from a former underground mine in the "Borken brown coal field" of the Borken Fm at Stolzenbach, south of Kassel, Hessen, Germany (Hofmann and Gregor 2018; Oschkinis and Gregor 2005, 1992; Ritzkowski 2005).

(4) The middle Eocene Changchang Fm in the Chanchang Basin on Hainan Island (SE China) comprises lacustrine and fluvial mudstones, siltstones and sandstones with regularly intercalated coaly horizons. The sediments display a high diversity of megafossils (leaves and diaspores, see references in Spicer et al. (2014)) and palynomorphs (Hofmann 2018; Hofmann et al. 2019; Yao et al. 2009), and are considered to be of Lutetian to Bartonian age.

(5) Sedimentary rocks from the Bayerhof Maar, which is located near the Bohemian Massif between Bayreuth in the NW and Oberweiden in the south (Bavaria, Germany) of presumably latest Oligocene to earliest Miocene age have been investigated in a pilot study previously (Sachse and Hofmann 2021) using LM and SEM. The age K/Ar age is between 23.3 and 21.7 Ma (Rohrmüller and Horn 2003).

(6) Middle Miocene sedimentary rocks of the Mühldorf Fm. at the Schasbach locality (Carinthia, Austria) are a mixture of freshwater and brackish to marine beds deposited between ca. 17 to ca. 11 Ma (Beck-Mannagetta 1952; Meller et al. 2015; Reischenbacher and Sachsenhofer 2013) and are relatively rich in palynomorphs (Hofmann and Lichtenwagner 2020).

All samples were washed, dried and crushed in a mortar with a pestle, treated with HCl and HF with subsequent acetolysis to reduce organic material such as wood and other palynodebris, and to deepen the colour of the palynomorphs. The remaining organic extracts were mixed with glycerol and stored in small glass vials. For light-microscope investigation small drops of palynomorph extract were smeared on glass-slides omitting cover-slips to be able to turn and remove pollen grains of interest with a micro-manipulator (hair mounted on a needle). Counting of the CAS samples was done using two to four slides per sample with × 600 magnification, depending on the abundance of pollen (Table 1; counts from 52-670). Pollen grains in question were re-mounted with a micro-manipulator to a clean drop of glycerine onto another slide and photographed with a Nikon Eclipse Optiphot 80 and ProgRes digital camera. After imaging, pollen grains were again transferred with a micro-manipulator onto SEM stubs, washed with alcohol and sputtered with gold. SEM investigations were done with a FEI Inspect S 5001 and Tescan Vega. The stubs and glycerol sample vials are housed in the University of Vienna, Department of Palaeontology under the inventory numbers IPUW 7841 Schasb 4_1-10; 7836 Hai gen 1-10; 7837aEoc 1-10, 7837bEoc1-10. 7842_Crato 11_1-10. The TEM was done with a Zeiss EM 900 following the protocol by Ulrich and Grímsson (2020) and Grímsson et al. (2021) with specimens additionally collected from sample CAS 6. The TEM sections are housed in the University of Vienna, Department of Botany and Biodiversity Research.

Table 1. Percentage distributions of various spores, and pollen of gymnosperms, angiosperms* (without *Gemmatricolpites*) and *Gemmatricolpites* pollen from the samples of the Cascata section in the Araripe Basin.

%	Batten	CAS2	CAS3	CAS4	CAS5	CAS6	CAS7	CAS8	CAS16	CAS18	CAS27
spores	28.2	29.6	36.7	31.9	29.5	15.2	26.9	36.9	9.7	17.2	34
gymnosperms	48.2	62.4	59.6	51.9	55.2	57.7	66.1	57.8	86.5	79	51.7
angiosperms*	23.6	8	3.7	7.7	13.7	3.3	6	4.8	3.8	3.8	14.3
Gemmatricolpites	0	0	0	8.5	1.6	23.8	1	0.3	0	0	0

Results

Numerical abundance of *Gemmatricolpites* pollen in the Rio da Batateira Fm

The percentages of spores (ferns and mosses), gymnosperms (including Araucariaceae (e.g., Hofmann et al. 2026b), cf. Podocarpaceae, Cycadales and Ginkgoaceae, Cheirolepidiaceae, Gnetales (e.g., Hofmann et al. 2022), Erdtmanithecales (e.g., Hofmann et al. 2026a)), angiosperms (all apart from *Gemmatricolpites*) and *Gemmatricolpites* are shown in Table 1. The *Gemmatricolpites* pollen do occur in five out of 11 samples from the Rio da Batateira Fm (Fig. 1) with percentages ranging from 0.3–8.5% (CAS samples 8, 7, 5 and 4) to a maximum of 23.8% in CAS 6). Sample CAS 6 also contained mixed clumps of *Gemmatricolpites* and an unknown sulcate taxon (see below). It should be pointed out that for this study the sample material was not sieved through a 10 µm sieve. As a consequence, very small pollen grains, including *Gemmatricolpites*, are recorded, in contrast to previous palynological investigations of the Rio da Batateira Fm (Heimhofer and Hochuli 2010).

Short circumdescription of extant *Ilex* pollen

Aquifoliaceae pollen seem to have not changed much in shape through time (compare Figs 2–4). Today, *Ilex* pollen is of small to medium size (polar axes range from 17.9–38.8 µm and equatorial axes from 16–35.7 µm: extracted from Wei et al. 2013, N = 51), has a tricolporate aperture (elongate ectoaperture = colpus in the ektexine and circular endoaperture = porus in the endexine), is prolate to subspheroidal in shape, has in polar view a circular to trilobate outline and in equatorial view an elliptical to circular outline. The ektexine sculpture is atectate, clavate to baculate, with clavae and interspersed baculae or gemmae in various sizes that are often decrease in size towards the colpi. SEM shows that the top of the clavae and baculae are ornamented with irregularly arranged microrugulae (Fig. 2A–D: *Ilex aquifolium*). Depending on the species these microrugulae can be either relatively faint or very conspicuous, either arranged in a dense or a very loose pattern (Fig. 4A–J).

Fossil '*Ilex*-like' pollen and *Gemmatricolpites*

Here we present the pollen morphology of various fossil '*Ilex*-like' pollen (including the taxa *Ilexpollenites* and *Ilex*) from sedimentary rocks of Eocene to Miocene age (Europe and China) and *Gemmatricolpites* pollen of Aptian age (Araripe Basin, NE Brazil) (Figs 3–6).

'*Ilex*-like' pollen from the Paleogene to Miocene

Fossil pollen affiliated with (= likely equivalent to) *Ilex* are known by various fossil genera or morphotypes in the palaeo-palynological literature (e.g., *Tricolporopollenites iliaceus* R. Potonié, *T. margaritatus* R., Potonié both later transferred to *Ilexpollenites* Thiergart ex R. Potonié 1960 or just called *Ilex* L.) and are well known worldwide since the Neogene. Here we present occurrences from the Paleocene-Eocene boundary of St. Pancraz (PETM, Austria, N = 1), the lower Eocene of Krappfeld (EECO, Austria, N = 5), the middle Eocene of Hainan (China, N = 4) and of Borken (Germany, N = 3), the Oligocene to Lower Miocene of Bavaria (Germany, N = 1) and Middle Miocene of Schaßbach (Austria, N = 2) that were investigated using LM (Fig. 4) and SEM (Figs 3, 5). All *'Ilex*-like' pollen show comparable sizes (polar axes ranging from 20.8–31.5 µm and equatorial axes ranging from 19.1–26.1 µm), are prolate to spheroidal in shape with a circular to trilobate outline in polar view and elliptical to circular outline in equatorial view. Many of them have tricolporate apertures (like extant *Ilex* pollen and Fig. 2A, C), however, endopori in the endexine are not always discernible on all the Eocene specimens from the St. Pankraz (N = 1), Krappfeld (N = 2), Borken (N = 1) and Hainan (N = 1) localities under LM and SEM (in Figs 3, 4 indicated with small asterisks), therefore some are considered tricolpate (= endoaperture in the endexine is elongate parallel to the polar axis like the ectoaperture). The ektexine is atectate and displays clavate (mushroom-like structures) to baculate and gemmate sculptural elements with clavae and baculae often decreasing in size towards the colpi. The clavae have generally circular heads but can be oval in the mesocolpium and polar areas and larger than the circular ones. Depending on the species under SEM the clavae ornamentation can display irregularly distributed faint or conspicuous ridges (microrugulae suprasculpture) that can be either loosely or densely arranged (Fig. 5A–E).

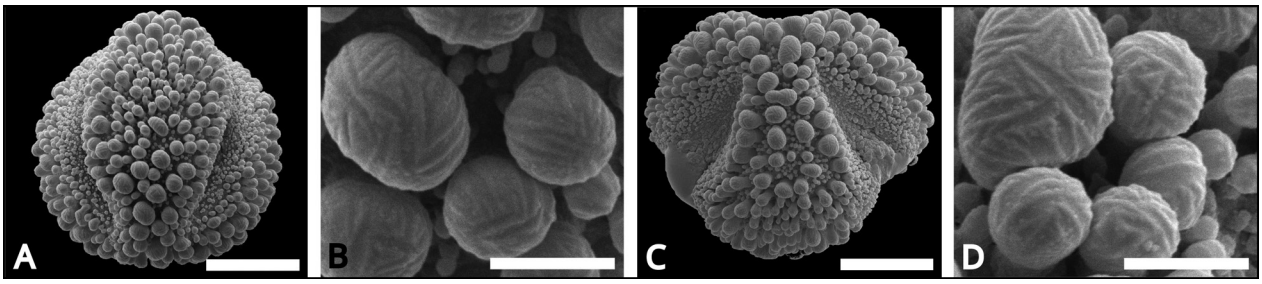

Figure 2. Extant pollen *Ilex aquifolium*, SEM overviews (**A, C**) of the atetate clavate ektexine and the size decrease of clavae towards the margo; and SEM; details (**B, D**) showing the surfaces of clavae with typical ridge and grove ornamentation and interspersed minute gemmae/baculae. Colleted by Hofmann in June 2025 in the Botanical Garden Bratislava; comparative pollen Herbarium Hofmann, Department of Palaeontology, University of Vienna. Scale bars: 10 µm in overviews, 2 µm in details.

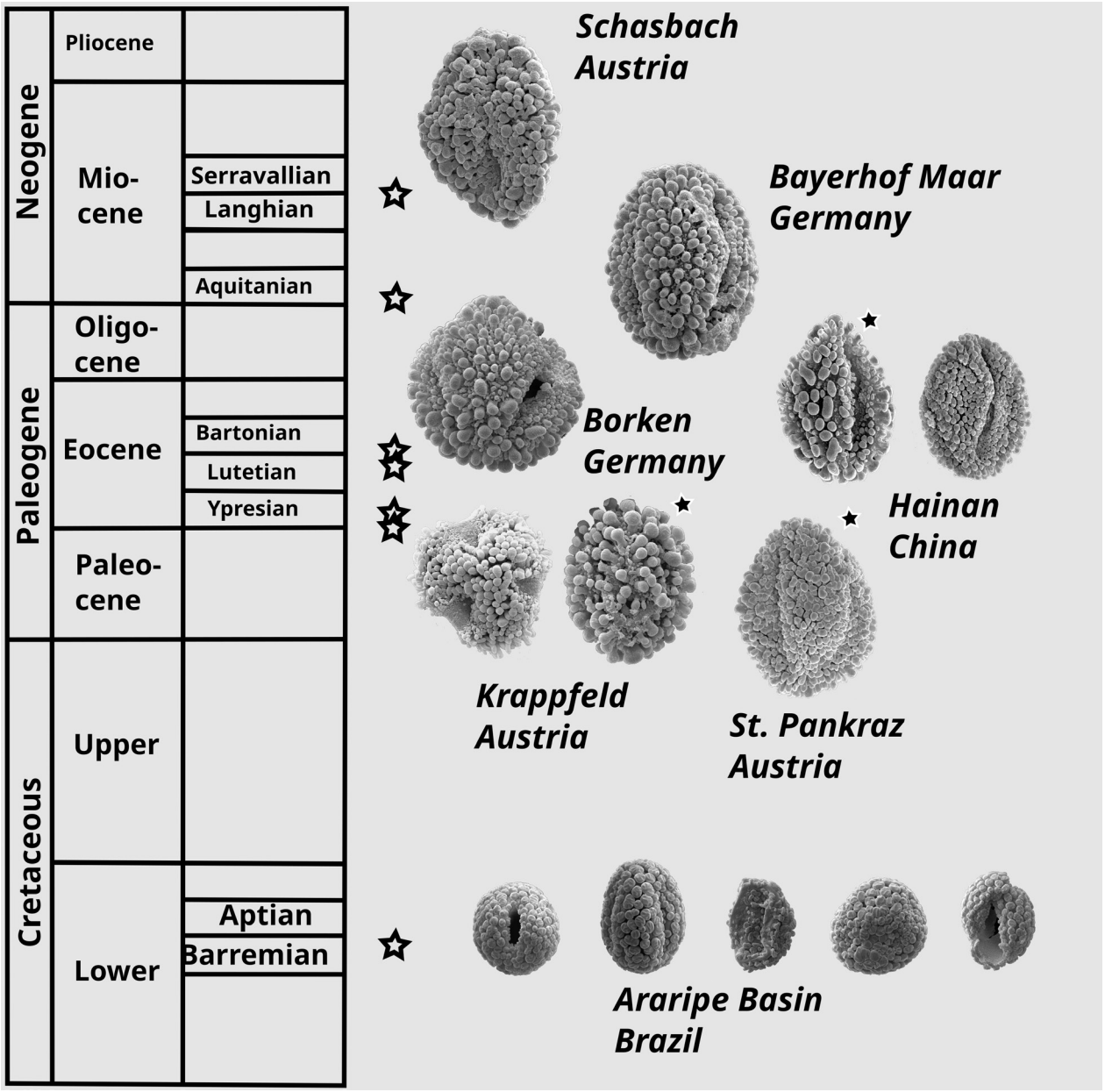

Figure 3. Distribution of "*Ilex*-like pollen" ranging from Eocene to Miocene and *Gemmatricolpites* pollen grains of the Aptian Rio da Batateira Formation from the Cascata section, Araripe Basin (left to right CAS 4, CAS 6, CAS 6, CAS 4, CAS 7, respectively); large asterisks points at the age, small asterisks indicate tricolpate specimens of the Paleogene. All magnifications × 1000.

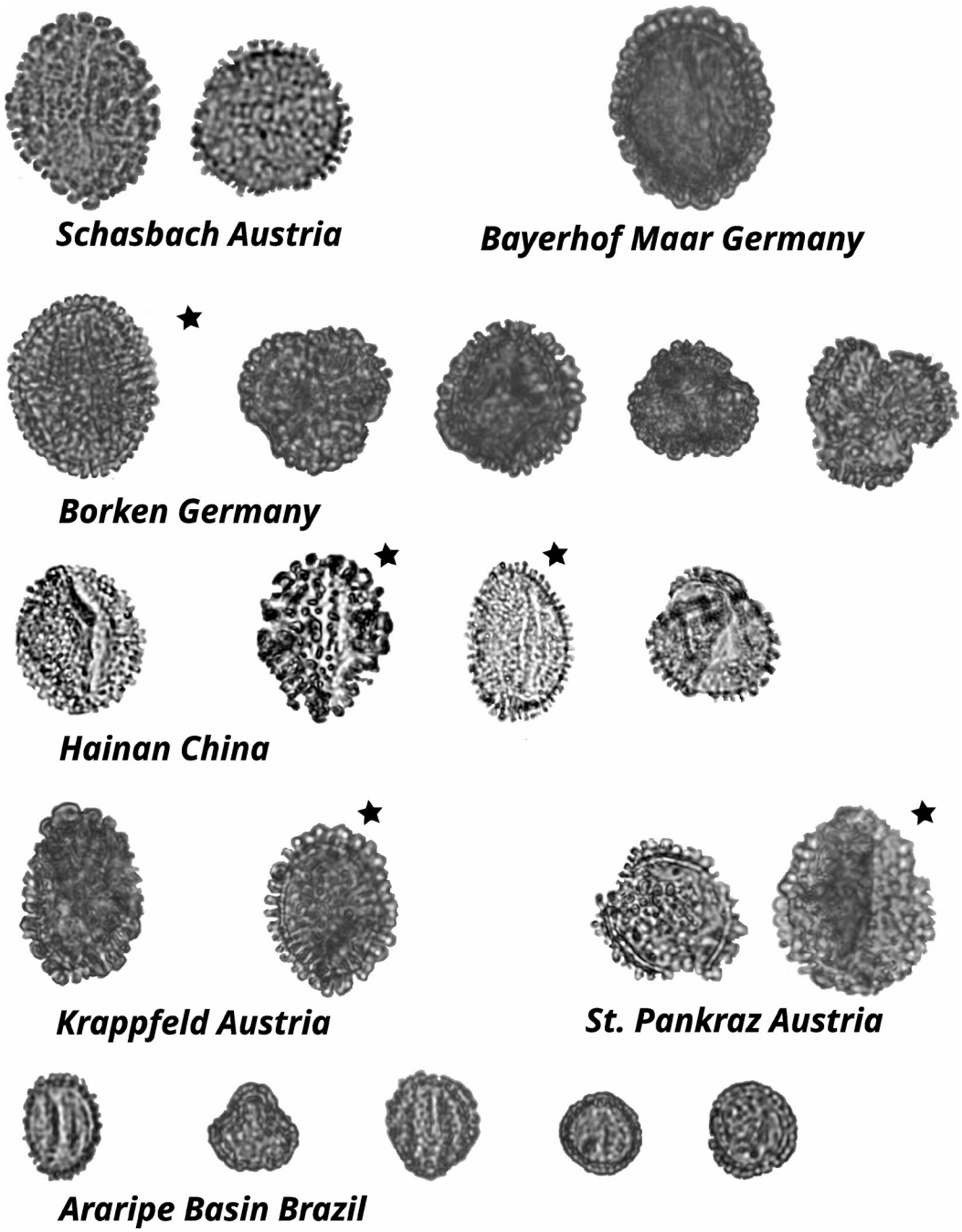

Figure 4. LM images of "*Ilex*-like pollen" from the Neogene and Paleocene, and *Gemmatricolpites* of the Aptian Rio da Batateira Formation from the Cascata section, Araripe Basin (left to right: CAS 6, CAS 6, CAS 6, CAS 4, CAS 7, respectively) in equatorial and polar views partly from Fig. 3. Asterisks indicate the tricolpate pollen from the Paleogene. All magnification × 1000.

Gemmatricolpites pollen from the Araripe Basin

Gemmatricolpites pollen from the Araripe Basin can be quite abundant (Table1) and preserved in mixed pollen clumps. Small-sized (polar axes range from 11.8–16.2 µm and equatorial axes range from 8.7–13.7 µm, N = 19, measured SEM images), prolate to spheroidal in shape, with circular to trilobate outline in polar view and elliptical to circular outline in equatorial view (Figs 3, 4, 5A, C, E, G). Apertures are tricolpate (N = 15) to (tri) cryptoaperturate (N = 4); the colpus lengths in the tricolpate pollen grains range from one third to three quarters of the polar axis; colpi can be either gaping or display enrolled colpus margins (Fig. 5A). In cryptoaperturate grains (= ectoaperture in the ektexine is inconspicuous) the areas of the equatorial apertures are indicated by smaller clavae or baculae on the footlayer (Fig. 5F, H). Under LM the clavate sculpturing is not always easily visible and can look like a reticulum because of the small size (Fig. 4); even the tricolpate nature also is not always obvious (can

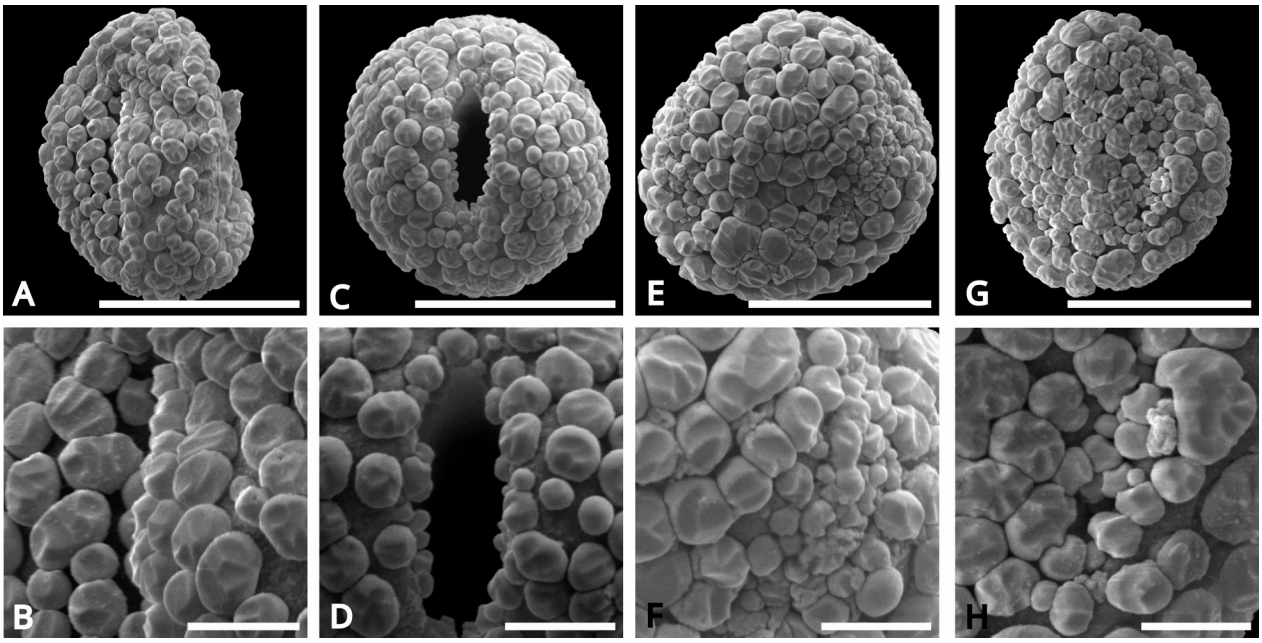

Figure 5. SEM images of various *Gemmatricolpites* grains of the Rio da Batateira Formation from different horizons of the Cascata section displaying the apertural conditions. **A–D.** Tricolpate apertural condition, note the smaller gemmae at the margo. **A, B.** From CAS 6, **C, D.** From CAS 4; E-H. Cryptoparturate condition, **E, F.** From CAS 6, **G, H.** From CAS 6. Scale bars: 10 μm (**A, C, E, G**); 2 μm (**B, D, F, H**).

be confused for tiny *Pennipollis* Friis, Pedersen & Crane, 2000 specimens). The exine is clavate (mushroom-like structures in Fig. 5B, D, F, H, 6G–L) to baculate, clavae and baculae are in various sizes, sometimes with interspersed gemmae and often decrease in size towards the colpi; under SEM the clavae and baculae are ornamented with irregularly, loosely arranged conspicuous ridges (microrugulate surprasculpture, Fig. 5B, D, F, H, 6G–L).

Several *Gemmatricolpites* specimens from sample CAS 6 were additionally investigated with TEM: The pollen wall comprises a thick ektexine (1.43–1.54 μm) with semitectum (0.57–0.75 μm), columellate infratectum (0.28–0.5 μm) and a remarkably thick, continuous foot layer (0.46–0.86 μm). With potassium permanganate the endexine stains electron dense. The endexine is bilayered, with a thin compact-continuous ektendexine and a spongy endexine. In the interapertural area the endexine is thin (0.1–0.15 μm) and thickens towards the aperture (0.65–0.85 μm).

Discussion

It can be stated that the *Gemmatricolpites*-producing plant was (at least in samples CAS 4 to CAS 6, see Table 1) a relatively important element of the spore and pollen flora and/or a prolific pollen producer. Locally, the plants bearing *Gemmatricolpites* pollen in the Araripe basin must have been quite abundant (23% of the pollen sum in CAS 6) and visited regularly by either pollen-eating florivores (flower eaters), pollinivores (pollen eaters) or pollinators, because of the presence of mixed pollen clumps (including pollen of *Gemmatricolpites* and unidentified monosulcate grains) that can be interpreted as either collecting corbiculae from pollinators or frass from florivores or pollivores (Fig. 6M).

Comparison of pollen morphologies of Aquifoliales, '*Ilex*-like' pollen and *Gemmatricolpites*

According to Schori and Furness (2014, Table 1), the characteristics of pollen in various Aquifoliales genera (using LM and SEM) can be summarized as follow: small to medium-sized, tricolporate, triporate (to occasionally stefanoporate and stefanocolporate) or tricryptoaperturate pollen, displaying a great variability in shapes (oblate, suboblate, spheroidal, spheroidal to prolate) and exine patterns (tectate to semitectate perforate, foveolate, micro-reticulate, reticulate, micro-echinate, striate, verrucate) and only *Ilex* is atectate clavate and baculate. Within Aquifoliales and all angiosperms the pollen morphology of the extant entomophilous *Ilex*, with its atectate sexine, heterogeneously arranged and sized clavae and baculae, is unique (see SEM images of extant *Ilex aquifolium* Fig. 2A–D, further Lobreau (1969), Lobreau-Callen (1975); Martin (1977); Muller (1981)), despite the superficial resemblance with the tetrad-forming *Podophyllum hexandrum* Royle, 1834 (Berberidaceae Juss. 1789) of the tectate Ranunculales. The exine sculpture of *P. hexandrum* (tectate with supratectal verrucae) and ornamentation (parallel arranged ridges and grooves on the supratectal verrucae) are very different (see Nowicke and Skvarla (1981), SEM figs 82–84 and TEM figs 198–199). The atectate condition or the reduced or absent ektexine

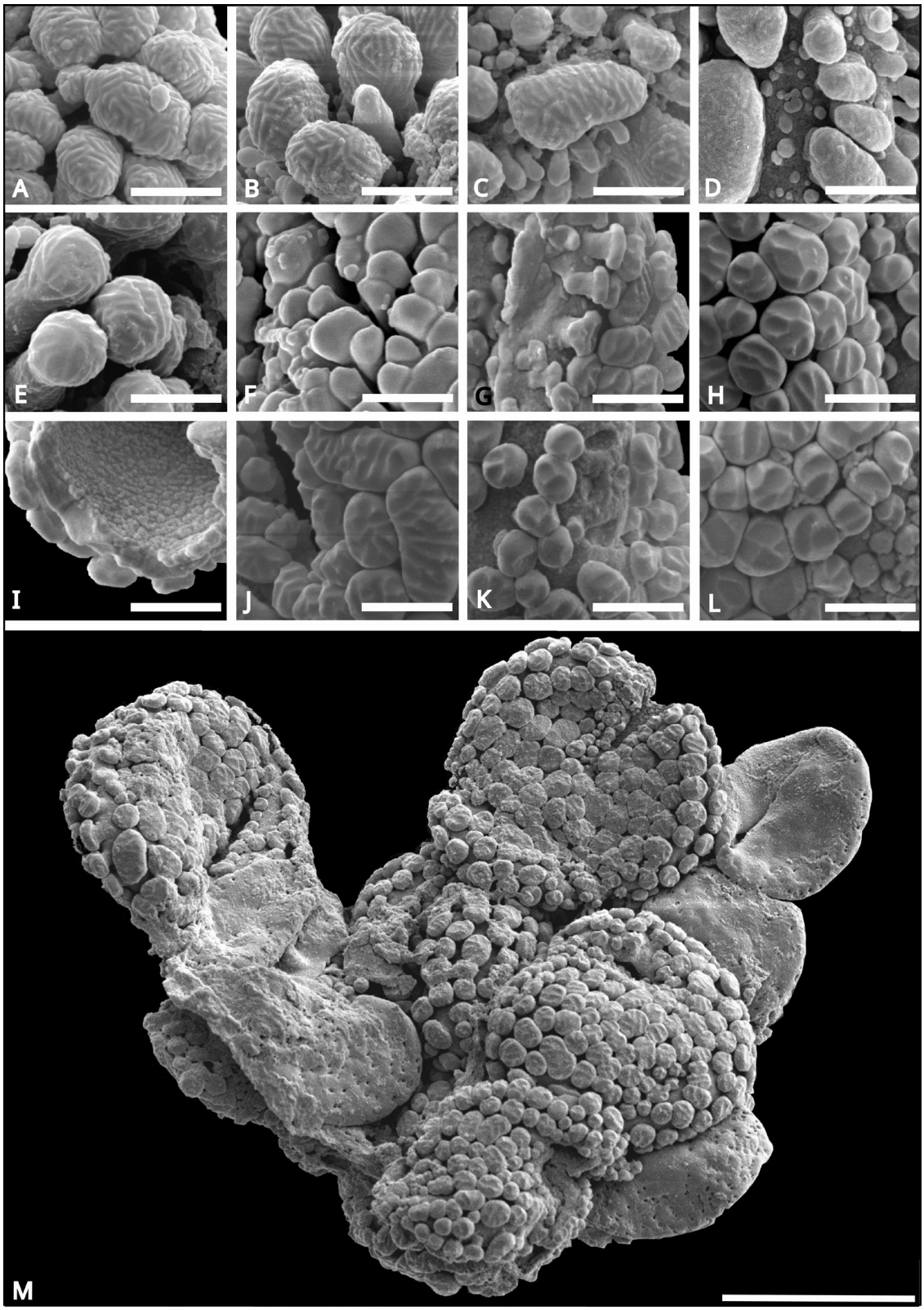

Figure 6. SEM detail images of fossil *Ilex*-like /*Ilexpollenites* pollen grains and *Gemmatricolpites* displaying the shapes and sizes of clavae and baculae and microrugulate ornamentation of clavae. **A.** Middle Miocene from Schaßbach (Austria), **B.** Oligocene to Lower Miocene from Bayerhof Maar (Germany), **C.** Bartonian from Borken (Germany), **D.** Lutetian–Bartonian from Hainan (China), **E.** Lower Eocene from Krappfeld (Austria), **F.** Lowermost Eocene from St. Pankraz (Austria) unfortunately covered with remains of glycerol from preparation, **G–M.** Aptian *Gemmatricolpites* pollen from Cascata section of the Rio da Batateira Formation, Araripe basin (Brazil): **G.** From CAS 4, **H.** From CAS 6, **I.** From CAS 7, **J.** From CAS 4, **K.** From CAS 6, **L.** From CAS 7., **M.** Mixed clump (pollen corbiculae or frass) of *Gemmatricolpites* and sulcate grains from CAS 6. Scale bar: 10 µm in overview images; 2 µm in detail images.

in pollen occurs in some other angiosperms (e.g. mostly in the orders Alismatales, Laurales and Zingiberales) and has been interpreted to be an advantage in pollination ecology in humid to wet environments by Pacini and Hesse (2012).

Ultrastructural studies on *Ilex paraguariensis* A.St.-Hil.1822 pollen (Santos and Mariath 1999, 2003a, 2003b; Santos et al. 2003, 2005) show striking similarities with the pollen wall of *Gemmatricolpites*: the pollen wall of *Ilex paraguariensis* has a thick ektexine with semitectum, columellate infratectum, moderate continuous foot layer and a bilayered endexine that increases in thickness towards the aperture. Compared to recent pollen of *I. paraguariensis*, in *Gemmatricolpites* all wall layers are thicker, especially the foot layer and the sculpture elements are smaller (e.g. in Santos and Mariath 1999, figs 13–15, or in Santos et al. 2003, fig. 16); also, the smaller-sized baculae are less abundant in *Gemmatricolpites*. The clavae and baculae of *Ilex* decrease in size towards the aperture, forming a margo, as in many of the *Gemmatricolpites* pollen (Fig. 5D, F, H, 6G, L).

Convergence or representative of an ancient extinct lineage?

The question we ask is the following: Is this just convergence of pollen morphology or is this evidence of an extinct Aquifoliales lineage? Our Aptian *Gemmatricolpites* pollen can be only distinguished from the Eocene to recent '*Ilex*-like' pollen presented here by:

(1) The generally smaller size, whereas the maximum length of the polar axes of *Gemmatricolpites* is within the range of the shortest polar axes of extant *Ilex*. This double increase in size of fossil '*Ilex*-like' pollen from the Eocene onwards demonstrated here (see Figs 3, 4) and Upper Cretaceous to Neogene from the literature (polar axes ranging 22 to 45 µm, e.g., Chmura 1973; McIntyre 1968; Muller 1968) might be interpreted as the result of whole genome duplication (WGD) that occurred in Aquifoliaceae during the Late Cretaceous according to Zhang et al. (2020, fig. 8a) after an event of environmental upheaval around the mid-Cretaceous after Chen et al. (2026). However, if a considerable increase of pollen size can be used as a trait for larger genome size (e.g., after duplication) is not equivocal (see discussion in Jardine et al. 2025).

(2) The generally tricolpate condition, where the ectoapertures in the ektexine and the endoapertures in the endexine are elongated parallel to the polar axis. This is a feature that has not been observed in extant Aquifoliales (endoapertures are circular to elongate). The same also applies to the tricryptoaperturate condition (ca. one quarter of the grains investigated), which is occasionally present in extant *Gonocaryum* Miq.1861 **(**Helwingiaceae) and *Cardiopteris* Wall. ex Royle, 1834 (Cardiopteridaceae), but not in *Ilex* (Schori and Furness 2014).

(3) Further, the presented early and middle Eocene co-occurrence of '*Ilex*-like' pollen with either tricolpate or tricolporate apertures (absence of an endoporus in some Eocene specimens indicated by small asterisks in Figs 3, 4) should be noted, whereas the '*Ilex*-like' pollen from the Oligocene/Miocene onwards tend to be tricolporate like the extant *Ilex.* The tricolpate nature of older '*Ilex*-like' pollen described here is supported by few *Ilexpollenites* taxa mentioned in the literature, which specifically were described as tricolpate: *Ilexpollenites clifdenensis* McIntyre 1968 from Santonian to Maastrichtian sedimentary rocks of Antarctica in Barreda et al. (2019, fig. 5o, LM image) and from Upper Cretaceous sedimentary rocks in New Zealand (Vajda and Raine 2003, Fig. 7A, B). The original species descriptions of *I. clifdenensis* (from the Miocene of New Zealand) and *I. megagemmatus* McIntyre 1968 (middle Eocene) by McIntyre ((1968), page 182 and figs 9–11 and 7–8 from New Zealand) are definitely stating the tricolpate aperture condition in both taxa. The same is true for *Ilexpollenites* sp. encountered in Upper Cretaceous strata of California by Chmura (1973, page 122, plate 25 figs 18–20).

The combined data (summarised in Table 2, Fig. 8) now demonstrate the discrepancy between (1) the widespread 'ancient tricolpate members' consisting of Aptian *Gemmatricolpites* (Araripe Basin) and Albian *Gemmatricolpites* (Spain, Barrón et al. (2015)), Upper Cretaceous *Gemmatricolpites*, *Ilexpollenites*, and Eocene '*Ilex*-like' pollen, and (2) the more 'modern tricolporate members' ('*Ilex*-like' pollen from Oligocene/Miocene to now). This variation of apertures in an evolutionary line is puzzling, but not uncommon. Examples from plant families in which the apertural condition within one genus (or even species) is not always fixed are: Krameriaceae Dumort. (eurosids 1) investigated by Pozhidaev (2003, Fig. 2) who demonstrated peculiar aberrant apertural conditions and exine layer variations in between and within several extant species of 16 *Krameria* Loefl. ranging from acolpate with endoapertures, cryptoaperturate, colporate, colpate to sulcate. These polymorphous *Krameria* pollen were compared with similar occurring constellations of other dicot families (compare also Pozhidaev 1998), and so the structure and positioning of the apertures of ektexine and endexine therefore were interpreted as non-homologous structures (Pozhidaev 2003). The same applies to Icacinaceae Miers (e.g., tricolporate *Icacina* and tricolpate *Apodytes*, Dahl, 1952) and Arecaceae Bercht. & J.Presl, which display also a wide variation in pollen apertures: next to the morphological very common monosulcate condition, palm pollen can be

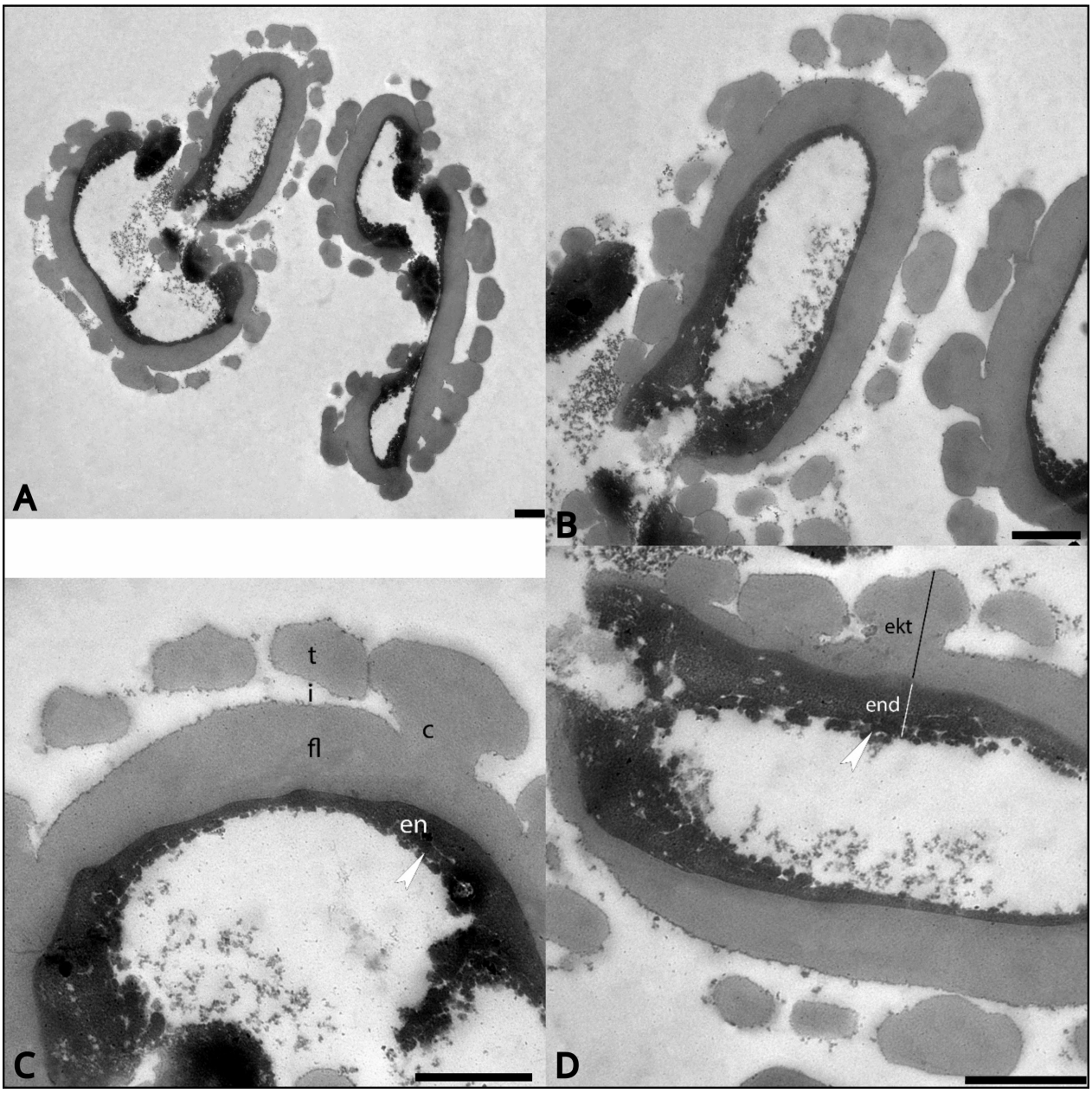

Figure 7. Transmission electron microscopy (TEM) micrographs of fossil *Gemmatricolpites* pollen from CAS 6 stained with potassium permanganate ($KMnO_4$). **A.** Pollen grains in polar view (left) and equatorial view (right). **B.** Close-up of pollen wall in aperture region. **C.** Close-up of pollen wall in interapertural area. **D.** Close-up of pollen wall in aperture region. Ektexine (ekt, black arrow) with semitectum (t), infratectum (i) columellate (c), thick continuous foot layer (fl), bilayered endexine (en, white arrow) with compact-continuous ektendexine and spongy endendexine (arrowhead). The endexine stains electron dense with $KMnO_4$ and thickens towards the aperture. Scale bars: 1 µm (**A–D**).

disulcate, trichotomosulcate, zonosulcate, diporate, triporate and inaperturate (Harley and Baker 2001; Table 1). All these aberrant, hypervariable apertural conditions in extant palm pollen also have been found in Eocene strata (LM and SEM images in e.g., Hofmann and Zetter (2001); Zetter and Hofmann (2001); Hofmann et al. (2015b)).

Combining all the above information together, we suggest a possible explanation with the following scenario: the tricryptoaperturate and tricolpate aperture conditions might have been ancestral in Aquifoliales, the tricryptoapertural condition has been observed only on *Gemmatricolpites* from the Araripe Basin (but application of SEM is necessary to observe this!). Notably, the occasional tricryptoapertural condition is still preserved in some other extant Aquifoliales (Schori and Furness 2014). Both 'ancient tricolpate' and modern tricolporate '*Ilex*-like' pollen were present during the middle Eocene in Europe and South China (and probably the USA and former Gondwana areas), whilst the 'ancient tricolpate condition' disappeared during the late Eocene and the 'modern tricolporate condition' took over. From the Oligocene onwards all '*Ilex*-like' pollen were probably tricolporate only (but see the exception of *Ilexpollenites clifdenensis* from the Miocene of New Zealand, McIntyre (1968)).

The question here arises as to which morphological trait weighs more in the circumscription of fossil versus extant *Ilex*/Aquifoliaceae pollen: does the modern tricolporate aperture condition overrule the 'older' tricolpate (and tricryptoaperturate) aperture conditions, or is the similar ultrastructure of the exine enough? All *Gemmatricolpites* and tricolpate and tricolporate '*Ilex*-like' pollen treated here share many characters with extant *Ilex*: an atectate ektexine with clavae and baculae, interspersed with gemmae whilst the clavae and baculae are ornamented with irregularly oriented microrugulate ornamentation ('ridges' only visible under SEM). This consistency in exine sculpture, ornamentation and ultrastructure might be interpreted as a long-term morphological stasis of the pollen wall. *Ilex* today is entomophilous and a prolific pollen producer; we could assume the same for the *Gemmatricolpites* plants based on the presence of mixed pollen clumps (resultant from either corbiculae or insect frass, Fig. 6).

Can all *Gemmatricolpites* grains be related to an 'extinct Aquifoliaceae lineage'?

The original description of the fossil species *Gemmatricolpites gemmatus* R. L. Pierce 1961 (a later heterotypic synonym is from van Hoeken-Klinkenberg 1964) from the Upper Cretaceous of Minnesota (US) was accompanied by two LM images (Pierce 1961, plate 3 figs 96, 97) and later by Brenner (1967, plate 3 fig. 13, not so much plate 2 fig. 9 a, b) from subsurface samples of the Raritan Fm of probable Cenomanian age. These fossil pollen might be affiliated with ancient Aquifoliaceae considering their shape, size (polar axes ca. 16 to 20 µm long) and 'gemmate' sculpturing. The same can be assumed for *Gemmatricolpites pergemmatus* Muller, 1969 (Muller 1968, plate 4 fig. 12, LM image) from the Late Cretaceous of Sarawak (Borneo, Malaysia), which looks quite similar to *Gemmatricolpites gemmatus* Pierce. Not surprisingly, this fossil species already has been associated with *Ilex* by Muller (1968: '*Gemmatricolpites gemmatus* may be a forerunner of the true *Ilex* pollen type which occurs regularly in the remainder of the Tertiary.'). Similar *Gemmatricolpites* finds come from the Albian of Spain (Barrón et al. (2015), fig. 9 AA, AB) and western USA (Brenner 1967); a quite comparable 'clavate *Tricolpites*' type has been reported from Aptian sedimentary rocks of Gabon (Doyle et al. (1977), plate 2, fig. 17). These four records might be closely related to our *Gemmatricolpites* specimens from the Araripe Basin, but unfortunately none of the LM images are sufficient enough to demonstrate that the clavae and baculae are ornamented with irregularly arranged ridges, which can be only observed under SEM.

On the other hand, other recorded *Gemmatricolpites* pollen from Albian-Cenomanian, Maastrichtian and Paleocene sedimentary rocks (e.g., *G. scabratus*, *G. gemmatus*) are far more ambiguous: either there are no images at all, or the specimens are poorly preserved or insufficiently photographed, or that the pollen sculpture is not at all comparable with Aquifoliaceae, despite the use of SEM (see Table 2; e.g. Ibrahim 1996; Zavada 2004; Vallati 2006; Volkheimer et al. 2006; Fowe Kwetche et al. 2018; Wagner and Silva 2018; Llorens et al. 2022).

Table 2. Occurrences of *Gemmatricolpites*, tricolpate *Ilexpollenites* and '*Ilex*' and 'clavate *Tricolpites* pollen' from literature and their possible affiliation to the Aquifoliaceae.

Taxon	LM	SEM	Yes	Ambi	No	Reference	Figure	Age	Locality
Gemmatricolpites sp.	x				x	Fowe Kwetche et al. 2018	figs 8, 16, 17	Paleocene	Cameroon
Gemmatricolpites sp.	x				x	Vallati 2006	fig. 6 D	Albian-Cennoman	Argentina
G. gemmatus	x		x			Pierce 1961	pl. 3 figs 96, 97	Cennoman	Minnesota
G. gemmatus	x		x			Brenner 1967	pl. 3 fig. 13	Cenomanian	Delaware
G. scabratus	x				x	Van Hoeken-Klinkenberg 1964	pl. 3 fig. 8a, b	Late Cretaceous	Nigeria
G. subsphaericus	x				x	Archangelski 1973	pl. 6 figs 6–9	Palaeocene	Argentina
G. pergemmatus	x		x			Muller 1968	pl. 4 fig. 12	Late Cretaceous	Malaysia
G. subsphaericus	x				x	Llorens et al. 2022	fig. 4F, g	Maastrichtian	Argentina
G. pergemmatus		x			x	Llorens et al. 2022	fig. 4H	Maastrichtian	Argentina
G. scabratus		x		x		Zavada 2004	figs 20, 21	Albian	S-Africa
G. gemmatus	x		x			Barrón et al. 2015	fig. 9 AA, AB	Albian	Spain
G. subsphaericus	x				x	Volkheimer et al. 2006	fig. 10H	Danian	Argentina
G. gemmatus	x			x		Ibrahim 1996	pl. 3 fig. 9	Turonian	Egypt
G. subsphaericus	x				x	Narváez 2009	pl. 22, figs 2, 6	Late Cretac/Palaeoc	Argentina
Ilexpollenites sp.	x		x			Chmura 1973	pl. 25, figs 18–20	Camp-Maastrichtian	California
I. clifdenensis	x		x			Barreda et al. 2019	fig. 5O	Santon-Maastrian	Antarctica
I. clifdenensis	x		x			McIntyre 1968	figs 9–11	middle Eocene	New Zealand
I. clifdenensis	x		x			Vajda and Raine 2003	fig. 7A, b	Late Cretac/Palaeoc	New Zealand
I. megagemmatus	x		x			McIntyre 1968	figs. 7, 8	Miocene	New Zealand
I. anguloclavatus	x		x			McIntyre 1968	figs 12, 13	Oligocene	New Zealand
I. anguloclavatus	x		x			Dettmann and Jarzen 1990	fig. 2 h, I	?Turon	Australia
I. chmurae	x		x			Boltenhagen 1976	pl. 4, figs 1–4	Late Cretaceous	Gabon
"Ilex" arnhemensis	x		x			Dettmann and Jarzen 1990	fig. 2 h, k	?Turon	Australia

Consequently, it can be stated that not all *Gemmatricolpites* pollen described and depicted in the literature can be related to the grains found in the Araripe Basin and therefore to a probable 'ancient lineage of Aquifoliaceae'. There are enough occurrences (*Gemmatricolpites*, *Ilexpollenites*, *Ilex* seeds, 'clavate *Tricolpites* type) in Lower and Upper Cretaceous strata however, to envisage an old centre of evolution in northern Gondwana, around Brazil (Barremian–Aptian) and probably Gabon (Aptian). In particular, in the Araripe Basin the pollen occurred in high numbers, and the plant must have been a common element in these floras and played an important role in the ecosystem (evidence of mixed pollen clumps). Later, lateral migrations out of the tropics to today's Spain and further distributions to North America, Europe, Antarctica, New Zealand, and Malaysia all happened before the Late Cretaceous (Fig. 8). This supports the analyses of Beaulieu et al. (2013), that the campanulids and its early diverging Aquifoliales clade probably are of Gondwanan origin.

How does it fit with the molecular dating of *Ilex*?

Phylogenetic molecular dating of asterids (Bremer et al. 2002, 2004) revealed an Early Cretaceous diversification of asterids with a stem node age for Aquifoliales of 121 Ma and 113 Ma for the crown node age, which are in congruence with an Aptian age (121.4–113.2 Ma) assigned to the Rio da Batateira Fm and the occurrence of our *Gemmatricolpites* pollen. Younger ages were presented by Magallón and Castillo (2009) with 99.7 Ma for the stem group, or 92 Ma by Magallón et al. (2015), which would be considerably younger than the *Gemmatricolpites* occurrences in the Araripe Basin, but discrepancies between fossils ages and ages inferred from molecular phylogenies are very common (see Coiro et al. 2019). Within Aquifoliales, *Ilex* and its presumable closest relatives *Helwingia* (tricolporate to hexacolporate) and *Phyllonoma* (tricolporate) are separated by a relatively large genetic distance (Soltis et al. 2000, see also Zhang et al. 2020: Aquifoliales I and Aquifoliales II), which makes the rooting of this genus within the family difficult (see Manen et al. 2002). Additionally, molecular dating of *Ilex* by Cuénoud et al. (2000) and Manen et al. (2002, 2010) suggests that the common ancestor of the 'modern *Ilex* lineage' is of approximately Eocene age, which is the time when both tricolpate and tricolporate forms of '*Ilex*-like' pollen occurred in Europe and South China (see Figs 3, 4), whereas the crown group is of middle Miocene age (all tricolporate grains Figs 3, 4). The ages inferred by Cuénoud et al. (2000) and Manen et al. (2002, 2010) were based on the assumption that either all the basal lineages of Aquifoliaceae went extinct or the affiliation of the Cretaceous fossils with *Ilex* were wrong (see discussion in Manen et al. 2002). Consequently,

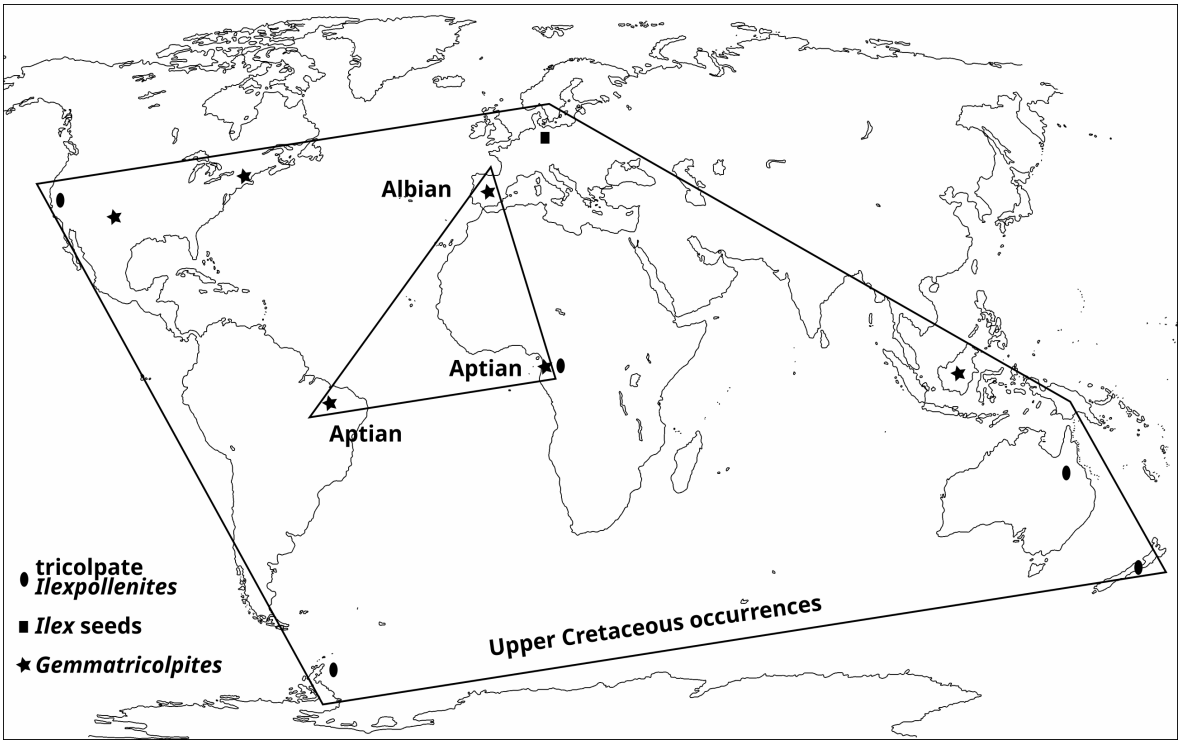

Figure 8. Earliest occurrences of *Gemmatricolpites* in northern Gondwana and adjacent areas (this paper: NE Brazil, Araripe Basin, Aptian) and 'clavate *Tricolpites*' = *Gemmatricolpites* (Doyle et al. 1977, Gabon Basin Cocobeach System, Aptian), and *Gemmatricolpites* sp. (Barrón et al. 2015, Spain, Basque-Cantabrian Basin, Albian) within the triangle; Upper Cretaceous, nearly cosmopolitical occurrences of *Gemmatricolpites* (Muller, 1968: Sarawak Malaysia; Pierce 1961: Minnesota, USA) and tricolpate *Ilexpollenites* (Barreda et al. 2019: Antarctica; Vajda and Raine 2003: New Zealand; Dettmann and Jarzen 1990: NE Australia; Chmura 1973: California, USA), and *Ilex* seeds (Knobloch and Mai 1986; Germany)(data taken from Table 2) that are related to Aquifoliaceae.

this interpretation means that all tricolpate '*Ilex*-like' pollen (mentioned above) and seeds such as the Upper Cretaceous seeds that have been affiliated with modern *Ilex* (Knobloch and Mai 1986; Mai 1970, 1987) predating the Eocene can be seen as an extinct lineage from the molecular side.

Recent phylogenetic dating by Yao et al. (2016, 2021) comprising more Chinese *Ilex* species than in previous studies suggests a Late Cretaceous stem age (*c.* 84.7 Ma) and fixed the crown group age in the lower Eocene (*c.* 50.8 Ma). The latter result would fit with the first occurrence of modern tricolporate '*Ilex*-like' pollen co-occurring with ancient tricolpate '*Ilex-like* pollen' from Europe and China during the Eocene (see Figs 2, 3). On the other hand, the stem age at *c.* 84.7 Ma is witnessed by the widespread occurrence of the 'ancient' tricolpate *Gemmatricolpites*, '*Ilex*-like' pollen and *Ilex* seeds during the Late Cretaceous.

Conclusions

The evolutionary history of Aquifoliales from the fossil record and time-calibrated phylogenies has been difficult to reconcile as older (pre-Oligocene) pollen fossils were deemed either too poorly characterised to be certain of the placement, or that despite the striking similarities in the shape and sculpture of the ektexine and the layering, the differences in the apertural condition suggested merely a convergent morphology barring their placement within Aquifoliales. Reinvestigation of fossil pollen genera potentially associated with Aquifoliales and pollen of extant plants allows us to show that differences in apertural condition can occur within genera, so the pollen morphology of *Gemmatricolpites* and some *'Ilex*-like' pollen does not have to result solely from convergence, meaning that we suggest *Gemmatricolpites* as a probable extinct lineage of Aquifoliales. The double size of '*Ilex*-like' pollen occurring in post Cretaceous strata can be interpreted to be the result of a whole genome duplication event in Aquifoliaceae during the Late Cretaceous. We evaluated and traced the likely history of this group from its initiation: late Early Cretaceous *Gemmatricolpites* pollen from the North Gondwanan Araripe Basin (and probably also from Gabon) is followed by Albian *Gemmatricolpites* pollen described from Spain. With the onset of the Late Cretaceous, *Gemmatricolpites* spread widely, reaching a cosmopolitan distribution during Late Cretaceous to Eocene times comprising *Gemmatricolpites* and tricolpate '*Ilex*-like' pollen, and various apertural conditions are known. After a period of co-occurrence of the 'ancient tricolpate lineage' and the 'modern tricolporate lineage' during the ?early to middle Eocene in Europe and South China, the modern lineage comprising only tricolporate '*Ilex*-like' pollen took over as they existed from the Oligocene up to now. This is in agreement with most molecular datings. The pollen of the ancient and modern *Ilex* are characterized by their unique atectate, clavate to baculate sculpture elements, where clavae and baculae are ornamented by irregularly arranged microrugulae seen only under SEM. This demonstrates a probable morphological stasis of the ektexine of the pollen wall, even though the oldest *Gemmatricolpites* pollen had a marginally thicker ektexine than the extant *Ilex paraguariensis*.

Acknowledgements

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
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Data availability

All of the data that support the findings of this study are available in the main text.