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On the origin of the Oriental plane tree (*Platanus orientalis* L.)

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Abstract: Oriental plane tree (*Platanus orientalis*) is native to the East Mediterranean region and sister to three western North American species, together forming the Pacific North American–European (PNA-E) clade. Its sister clade, comprising several eastern North American–Mexican species, has been termed the Atlantic North American (ANA) clade. The origins of *P. orientalis* and the western North American–western Eurasian disjunction in the PNA-E clade are poorly understood, with the North Atlantic and Bering land bridges being possible corridors for trans-continental migration. Molecular phylogenetic studies suggested ancient hybridization between the ANA and PNA-E clades prior to differentiation of modern species' lineages. We traced ANA- and PNA-E-specific leaf traits in the fossil record to locate areas of possible ancient hybridization. Leaf traits characteristic of the PNA-E clade occurred in western North America (late Eocene of Montana, Early Miocene of Alaska) prior to

appearing in the European fossil record. Fossil-species with mixed PNA-E–ANA leaf traits occurred in the Oligocene of Central Asia and Eocene and Miocene of western North America. In contrast, eastern North America and the Atlantic region hosted fossil-species with leaf traits characteristic of modern ANA clade members. We propose that precursors of *Platanus orientalis* migrated to Europe via Beringia and through Central Asia. Initially, these Eurasian ancestors possessed ancestral PNA-E clade leaf morphologies, which were gradually replaced by *P. orientalis*-specific traits. Treated as a single fossil-species, we document the evolution of *P. academiæ* from predominately three-lobed leaves in Miocene strata to narrowly five-lobed leaves resembling modern *P. orientalis* in younger deposits of Greece.

Key words: *Platanus*, oriental plane tree, North Atlantic land bridge, Bering land bridge, Madrean–Tethyan disjunction.

PLATANACEAE are currently represented by a single genus, *Platanus* L. (plane trees), which is found from southwestern USA to Mexico and into the eastern USA (Atlantic seaboard), the Mediterranean region into Asia Minor (*Platanus (Platanus)*); and southwestern China and Vietnam (*Platanus (Castanephyllum)*). In contrast, Platanaceae had a much wider distribution and were highly diverse during the Late Cretaceous and Palaeogene (e.g. Manchester 1986, 2014; Friis *et al.* 1988, 2011; Friis & Crane 1989; Crane *et al.* 1993; Magallón-Puebla *et al.* 1997; Kvaček *et al.* 2001; Maslova 2003; Kvaček & Manchester 2004; Golovneva 2007, 2008; Tschan *et al.* 2008; Wang *et al.* 2011; Kodrul *et al.* 2013; Mindell *et al.* 2014; Huegele & Manchester 2022; Huegele *et al.* 2022; Huegele & Wang 2023; at least 35 genera and more than 50 species).

Although the family Platanaceae dates back to the Early Cretaceous (Magallón *et al.* 2015), its modern species lineages are probably not older than Miocene in age (Feng

et al. 2005). The time-calibrated molecular phylogeny by Feng *et al.* (2005) inferred an Early Miocene crown age for the Pacific North American–European (PNA-E) clade and a Middle Miocene crown age for the Atlantic North American (ANA) clade (Fig. 1). For the split between *P. racemosa* + *P. wrightii* and *P. orientalis* an Early to Middle Miocene age was inferred. Consequently, fossil taxa of Eocene and Oligocene age belonging to *Platanus* could potentially represent extinct side lineages of either the ANA or PNA-E clade or intermediary forms showing ancestral polymorphism.

Platanus has been intensively studied morphologically (e.g. Nixon & Poole 2003; Carpenter *et al.* 2005; Denk & Tekleva 2006; Balthazar & Schönenberger 2009; Denk *et al.* 2012) and genetically (Feng *et al.* 2005; Grimm & Denk 2008, 2010; de Castro *et al.* 2013; Vargas *et al.* 2014). Modern members of *Platanus* are classified into two subgenera: *P. (Platanus)* of North America and

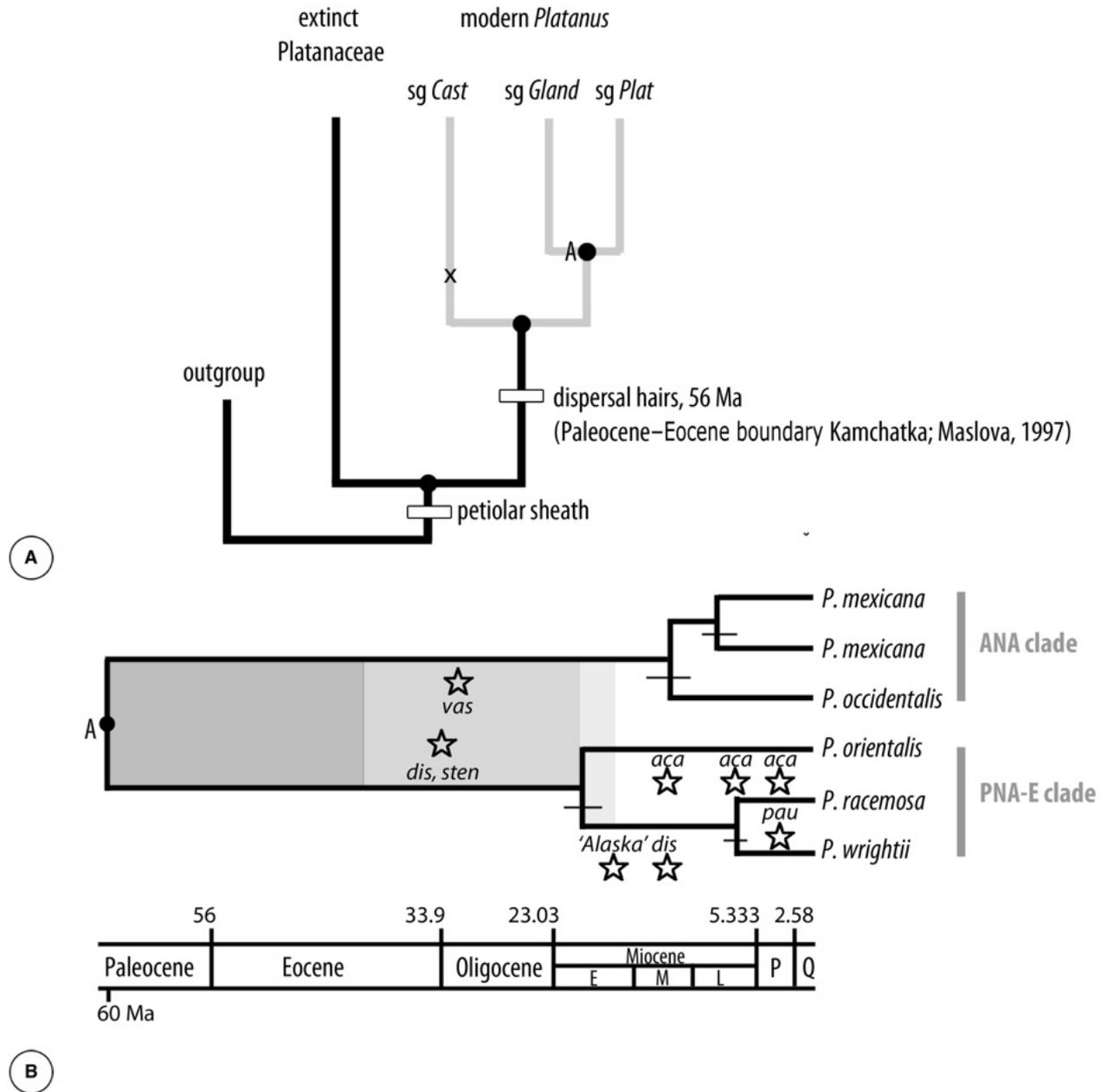


FIG. 1. Phylogenetic relationships of Platanaceae. A, relationships between two extant and one extinct subgenus in *Platanus* as discussed in Feng *et al.* (2005); empty rectangles indicate possible synapomorphies (dispersal hairs) and symplesiomorphies (petiolar sheath) used to infer the age of node A; x denotes the loss of a petiolar sheath in *P. (Castaneophyllum)*. B, time-calibrated phylogeny of *P. (Platanus)* (Feng *et al.* 2005; modified); age for ingroup node A calibrated with Paleocene fossils displaying achenes with dispersal hairs (a synapomorphy of *Platanus*); ages updated to conform to current International Chronostratigraphic Chart (Cohen *et al.* 2013; v2023/06). Grey areas indicate parts of the Palaeogene for which ancient hybridization between the Atlantic North American (ANA) and Pacific North American–European (PNA-E) lineage has been detected (Grimm & Denk 2010); fossil-species with PNA-E or mixed PNA-E and ANA characteristics are plotted on the tree. *Abbreviations:* 'Alaska', unnamed species from Alaska currently included in *P. dissecta*; *Cast*, *Platanus (Castaneophyllum)*; *dis*, *P. dissecta* Lesq.; *Gland*, *Platanus (Glandulosa)*; *pau*, *P. paucidentata* Dorf.; *Plat*, *Platanus (Platanus)*; *sg*, subgenus; *sten*, *P. stenoloba* Becker; *vas*, *P. vassiljevii* Iljinsk.

western Eurasia, and *P. (Castaneophyllum)* J.-F. Leroy of Southeast Asia (Grimm & Denk 2008). Based on fossil foliage and reproductive structures, a third, extinct

subgenus was described, *P. (Glandulosa)* Kvaček *et al.*, 2001. All modern and fossil-species considered for the present study belong to *P. (Platanus)*. The only extant

TABLE 1. Taxonomy and distribution ranges of modern *Platanus*.

Modern taxa of <i>Platanus</i> subgenus <i>Platanus</i> ^a	Distribution
Atlantic North American clade (ANA clade)	
<i>Platanus occidentalis</i> L.	Southeastern Canada, eastern USA
<i>Platanus palmeri</i> (Kuntze) ined.	USA (Texas), Mexico (Coahuila)
<i>Platanus rzedowskii</i> Nixon & J.M. Poole	Mexico (Nuevo León, Tamaulipas, ? San Luis Potosí)
<i>Platanus mexicana</i> Moric. ^b	Mexico (Hidalgo, Guanajuato, Querétaro, San Luis Potosí)
<i>Platanus lindeniana</i> M.Martens & Galeotti ^b	Guatemala, Mexico (Chiapas, Oaxaca, Puebla, Veracruz, Hidalgo)
Pacific North American–European clade (PNA-E clade)	
<i>Platanus racemosa</i> Nutt.	USA (California), Mexico (Baja California)
<i>Platanus wrightii</i> S. Watson	USA (Arizona, New Mexico), Mexico (Chihuahua)
<i>Platanus gentryi</i> Nixon & J.M. Poole	Mexico (Chihuahua, Sonora, Sinaloa)
<i>Platanus orientalis</i> L.	Southeastern Europe, southwestern Asia

Note that *Platanus mexicana* var. *interior* Nixon & J.M. Poole is a heterotypic synonym of *P. mexicana* Moric., and *Platanus mexicana* var. *mexicana* sensu Nixon & Poole (2003) corresponds to *P. lindeniana* (<https://powo.science.kew.org>).

^aBased on Nixon & Poole 2003; Grimm & Denk 2010; Denk *et al.* 2012; <https://powo.science.kew.org>.

^b*P. mexicana* sensu Denk *et al.* (2012).

western Eurasian species in this subgenus is *P. orientalis* L. with a native distribution from Italy to Iran, possibly with eastwards and westwards extensions. This broadly Mediterranean species is sister to three western North American species (variously treated as species or infraspecies taxa): *Platanus racemosa* Nutt. (California and north-western Mexico), *P. wrightii* S. Watson (Arizona, New Mexico and northern Mexico), and *P. gentryi* Nixon & J. M. Poole of the tripoint between Sonora, Chihuahua and Sinaloa (Nixon & Poole 2003; Feng *et al.* 2005; Grimm & Denk 2008, 2010). They form the PNA-E clade, which is sister to the ANA clade (Grimm & Denk 2008). The ANA clade (cf. de Castro *et al.* 2013) comprises five taxa recognized as species by us: *P. occidentalis* L. of the eastern USA and south-easternmost Canada, *P. palmeri* (Kuntze) ined. of Texas and north-eastern Mexico, *P. rzedowskii* Nixon & J. M. Poole of north-eastern Mexico (Nuevo León, Tamaulipas, San Luis Potosí), *P. mexicana* Moric. of central Mexico (Hidalgo, Querétaro into Guanajuato and San Luis Potosí), and *P. lindeniana* M. Martens & Galeotti of eastern central Mexico to Guatemala (Table 1; Nixon & Poole 2003; Denk *et al.* 2012; <https://powo.science.kew.org>). Included in *P. lindeniana* are the populations in Oaxaca (*P. oaxacana* Standl.) and Chiapas (*P. chiapensis* Standl.; <https://powo.science.kew.org>).

Despite a robust phylogenetic framework for the major infragenus groups of *Platanus*, various studies demonstrated that the origins of modern species in *Platanus* involve complex histories of ancient hybridization and secondary contact between members of the ANA and PNA-E clades in Mexico (Grimm & Denk 2008, 2010; de Castro *et al.* 2013). Moreover, the Mediterranean *P. orientalis* can still interbreed with its western North

American sister species but also with its more distant relative, the eastern North American *P. occidentalis* (the widely cultivated ‘London plane’, *P. × hispanica* Mill. ex Muenchh.; e.g. Santamour 1972), confirming that historical hybridization could confound fossil interpretations if both clades overlapped in the past.

The origin of the western North American–Mediterranean (into Iran) disjunction of the PNA-E clade remains enigmatic. This disjunction was explained with parallel adaptation to summer-dry climates in western North America and the Mediterranean region (extending into the southern foothills of the Himalayas) within widespread taxa belonging to a so-called Madrean– (or Madro-)Tethyan sclerophyll vegetation (Axelrod 1975); this would have involved a North Atlantic crossing during the Cenozoic. Kadereit & Baldwin (2012) concluded that the PNA-E disjunction in *Platanus* could be explained by parallel evolution of dry-adapted taxa from a mesophytic or northerly distributed ancestor either including the North Atlantic land bridges or the Bering land bridge. Feng *et al.* (2005) stated that there is no conclusive evidence for a North Atlantic (Madrean–Tethyan; Axelrod 1975) connection of the *P. racemosa* group and the Mediterranean *P. orientalis* and that the fossil record does not help to resolve this issue because, according to Feng *et al.* (2005), morphologies of fossils from Alaska and the Bering region are closely similar to the modern eastern North American *P. occidentalis* but not to members of the PNA-E clade. Also in Europe, the dominating Neogene *Platanus* species, *P. leucophylla* (Unger) Erw. Knobloch, has a leaf morphology distinctly similar to *P. occidentalis* of the ANA clade (e.g. Göppert 1855; Knobloch 1969). This fossil-species was widespread across Europe during the Neogene (Kovar-Eder *et al.* 1994). In

contrast, only a few records from Middle Miocene and younger strata in western Eurasia have previously been compared more closely to the modern *P. orientalis* of the PNA-E clade (Kolakovsky 1955; Kutuzkina 1958; Gaudin & Strozzi 1864).

In the present paper, we describe Late Miocene to Early Pleistocene leaf fossils from Greece with a leaf morphology similar to *P. orientalis* and investigate ancient hybridization, biogeographic origins and evolutionary history of this lineage in western North America and western Eurasia. We discuss possible ancient links between the western North American and Mediterranean populations of the PNA-E clade and propose that a North Pacific–Central Asian–western Eurasian connection is more likely than a North Atlantic (Madrean–Tethyan) link for this group of plane trees.

MATERIAL AND METHOD

Fossil material and age

The material described in the present study is mainly from the Late Miocene (Messinian) ‘Diagon valley’ leaf assemblage, Pyrgos Basin (Platana Formation; Kleinhölder 1994a). Using modern geographical names, the correct name for this locality is Tsemperoula (Τσεμπερούλα) stream (Fig. 2B, no. 1). Additional material is from the following Late Miocene to Early Pleistocene localities (Fig. 2B, nos 2–15): Pyrgos basin: Tripes abandoned opencast lignite mine, Paleochori south of Platiana, and Chrysochori (all Late Miocene); Zacharo, Kalidona and Xirochóri (all Pliocene); Sparta Basin: Skoura (Pliocene); grabens of Patra and Rio: Kaminia and Theriano (Therianón), both Early Pleistocene; Kalavryta basin: Drosato and Kalavryta–Paleochori, both Late Miocene to Early Pliocene; Corinth graben: Melíssia, Chrysanthio and Egira (Aigeira), all Early Pleistocene.

The ages of Neogene basin fillings of the Peloponnese have been established based on calcareous nannoplankton

and lithostratigraphic correlation (Velitzelos & Gregor 1990; Kleinhölder 1994a, 1994b; Trikolos & Alexouli-Livaditi 2004; van Hinsbergen *et al.* 2006). In addition, biostratigraphic correlation to well-dated localities has been established using the palynological and macrobotanical records (Velitzelos & Gregor 1990; Kleinhölder 1994a, 1994b; Liapi 2020). In general, the distinction between Late Miocene and Early Pliocene in different basins of the Peloponnese has been ambiguous because of the absence of radiometrically datable rocks (Velitzelos & Gregor 1990; Kleinhölder 1994a, 1994b; van Hinsbergen *et al.* 2006; Velitzelos *et al.* 2014; Liapi 2020). Therefore, records from the Peloponnese labelled as Late Miocene (Fig. 2) may also be of earliest Pliocene age. Nevertheless, the broad distinction between Late Miocene – Early Pliocene and Pliocene and Early Pleistocene deposits corresponds with the occurrence of distinct morphotypes of the fossil-species *P. academiae* investigated in the present study.

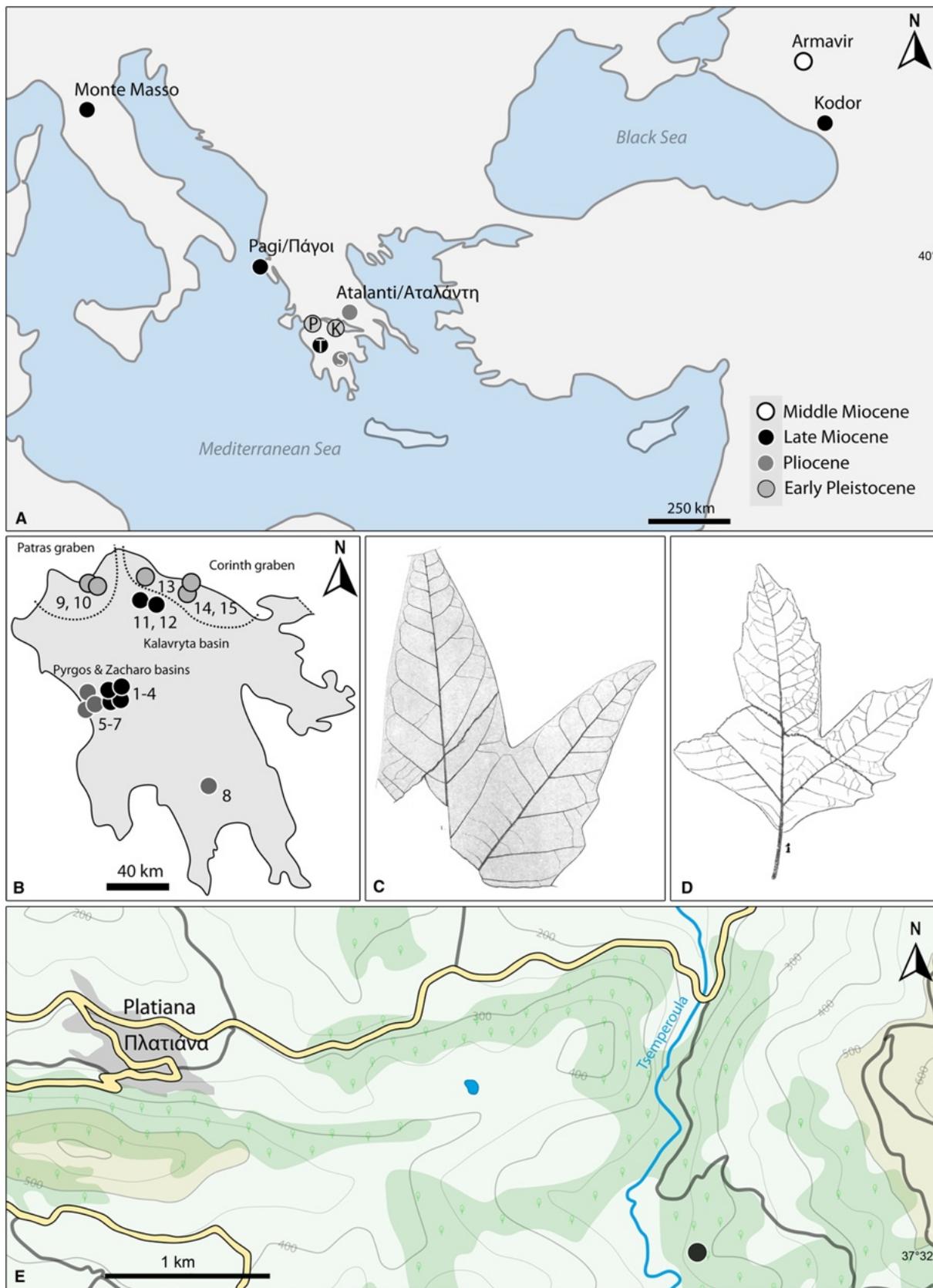
The fossil plant material was collected in the late 1980s and early 1990s by Klaus Kleinhölder. It is stored in the palaeobotanical collections of the Swedish Museum of Natural History (S).

Terminology of leaf morphology follows Ellis *et al.* (2009), Dilcher (1974) and Huegele *et al.* (2020).

Clade age inference from time calibrated phylogeny

The time-calibrated phylogeny of Feng *et al.* (2005) considered two alternative calibration points or fossils for their dating (Fig. 1A). They used the presence of dispersal hairs on the achenes as a possible synapomorphy of *Platanus* (Manchester 1994; Maslova 1997; Kvaček *et al.* 2001). Given that such hairs occur in Eocene fossils of *Platanus* (*Glandulosa*) (Mai & Walther 1985; Kvaček *et al.* 2001) and the fossil-species *P. hirticarpa* Manchester, but are absent in other early Cenozoic and Cretaceous fossil taxa of Platanaceae, Feng *et al.* (2005) used this as

FIG. 2. A, known *Platanus orientalis*-like macrofossil records in the Neogene of western Eurasia; abbreviations: K, Kalavryta basin; P, grabens of Patras and Corinth; S, Skoura; T, Tsemperoula stream (old name Diagon river) and adjacent localities. B, *Platanus* leaf fossil sites on the Peloponnese: 1, Tsemperoula (Τσεμπερούλα) stream locality (old name Diagon river, 37°32'5.68", 21°47'9.15"), Late Miocene; 2, Tripes abandoned opencast lignite mine (37°31'38.96", 21°47'41.31"), Late Miocene; 3, Paleochori (Παλαιοχώρι) south of Platiana (37°32'14.51", 21°44'56.46"), Late Miocene; 4, Chrysochori (Χρυσοχώρι) (37°31'17.34", 21°44'56.02"), Late Miocene; 5, Zacharo (Ζαχάρω) (37°28'48.59", 21°39'6.18"), Pliocene; 6, Kalidona (Καλιδόνα) (37°28'10.45", 21°42'6.87"), Pliocene; 7, Xirochóri (Ξηροχώρι(ον)) (37°31'7.18", 21°39'40.24"), Pliocene; 8, Skoura (Σκούρα) (37°0'59.68", 22°29'27.89"), Pliocene; 9, Kaminia (Καμίνια) (38°8'39.49", 21°37'17.88") only *Platanus leucophylla*, Early Pleistocene; 10, Theriano (Therianón, Θεριανό) (38°8'40.11", 21°37'40.33") only *Platanus leucophylla*, Early Pleistocene; 11, Drosato (Δροσάτο) (38°4'1.00", 22°2'7.00"), Late Miocene to Early Pliocene; 12, Kalavryta–Paleochori (Καλάβρυτα) (38°1'58.97", 22°6'46.67"), Late Miocene to Early Pliocene; 13, Melíssia (Μελίσσια) (38°11'5.08", 22°3'44.00") only *Platanus leucophylla*, Early Pleistocene; 14, Chrysanthio (Χρυσάνθιο) (38°7'2.68", 22°20'2.21"), Early Pleistocene; 15, Egira (Αιγείρα) (38°7'37.77", 22°20'40.65"), Early Pleistocene. C, type specimen of *Platanus academiae* C.T. Gaudin from ‘Monte Masso’ (= Montemassi), Tuscany, Italy, Late Miocene (Gaudin & Strozzi 1864). D, type specimen of *P. lineariloba* Kolak. from Kodor, Abkhazia, Georgia (Kolakovsky 1955). E, site map of Tsemperoula (‘Diagon valley’) flora.



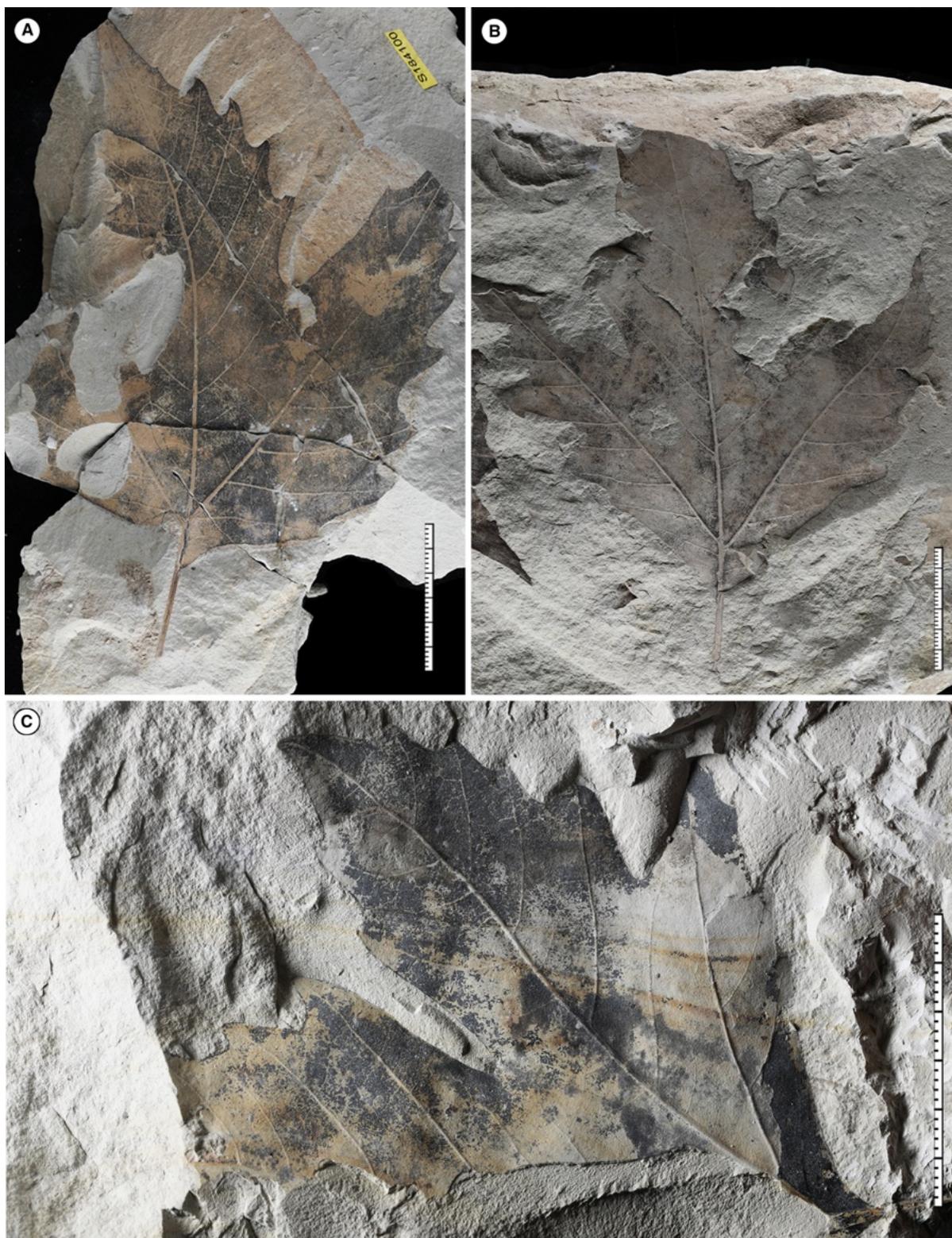


FIG. 3. Typical leaves of *Platanus academiae*, from Tsemperoula, Peloponnese, Late Miocene. A, trilobed leaf with coarse, hook-shaped teeth, central lobe triangular to rhombic, S184100. B, trilobed leaf with narrower lamina and coarse, hook-shaped teeth, central lobe rhombic, S184106. C, lateral lobe and half of the central lobe, with coarse, hook-shaped teeth, S184089. Scale bars represent 3 cm.

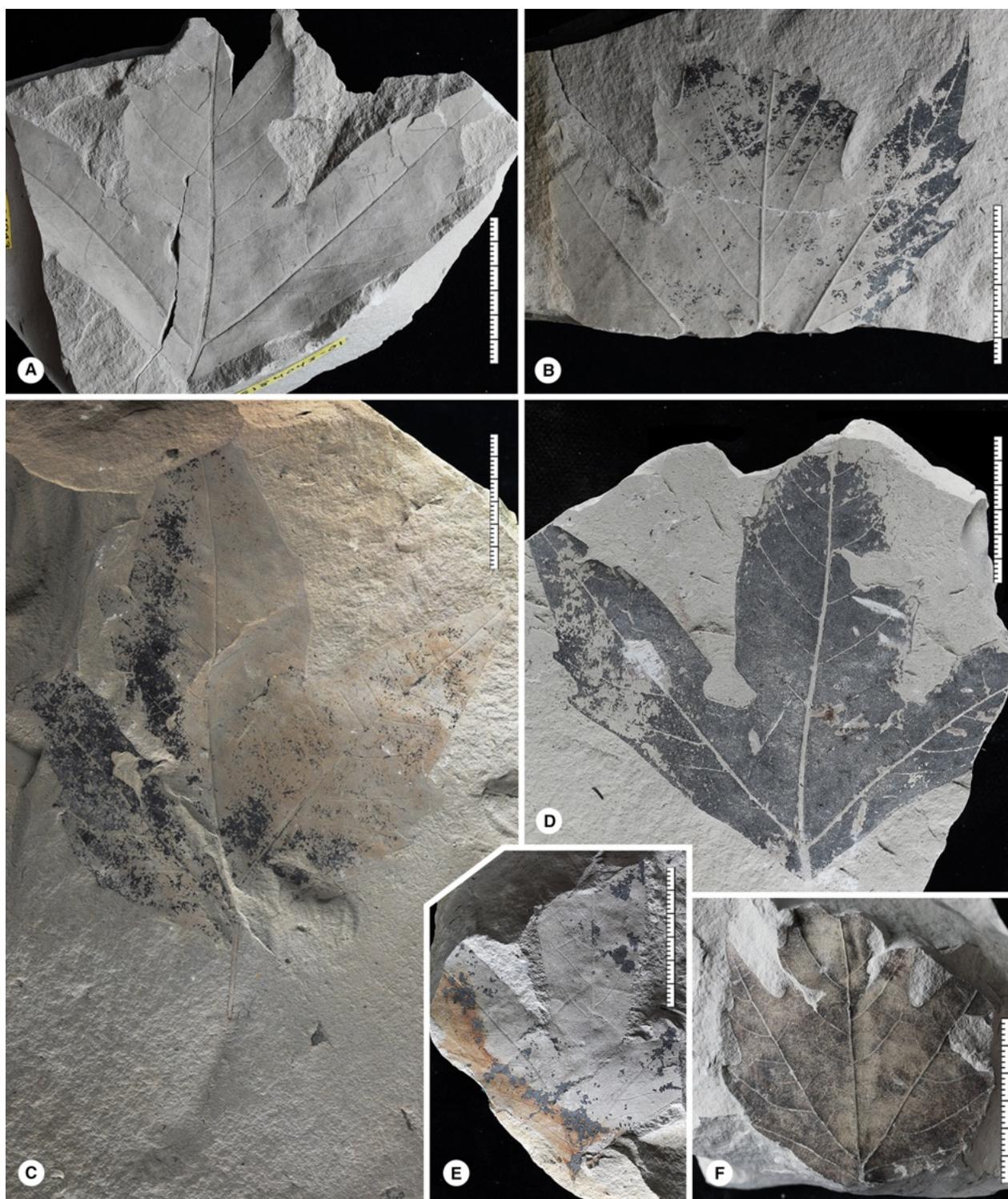


FIG. 4. *Platanus academiae* from Tsemperoula, Peloponnese, Late Miocene. Overviews of leaves matching the leaf morphological variability of modern *Platanus orientalis*. A, wide trilobed leaf, deeply lobed, with coarse teeth, S184043. B, trilobed leaf with coarse, hook-shaped teeth and delicate appearance, S184047. C, trilobed leaf with rhombic central lobe and coarse, hook-shaped teeth on lateral lobe, S184090. D, wide trilobed leaf, deeply lobed, with coarse, hook-shaped teeth on lateral lobe, S184103. E, wide trilobed leaf, deeply lobed, with triangular central lobe, S184067. F, trilobed lamina, shallowly lobed, with coarse, hook-shaped teeth, S184094. Scale bars represent 3 cm.

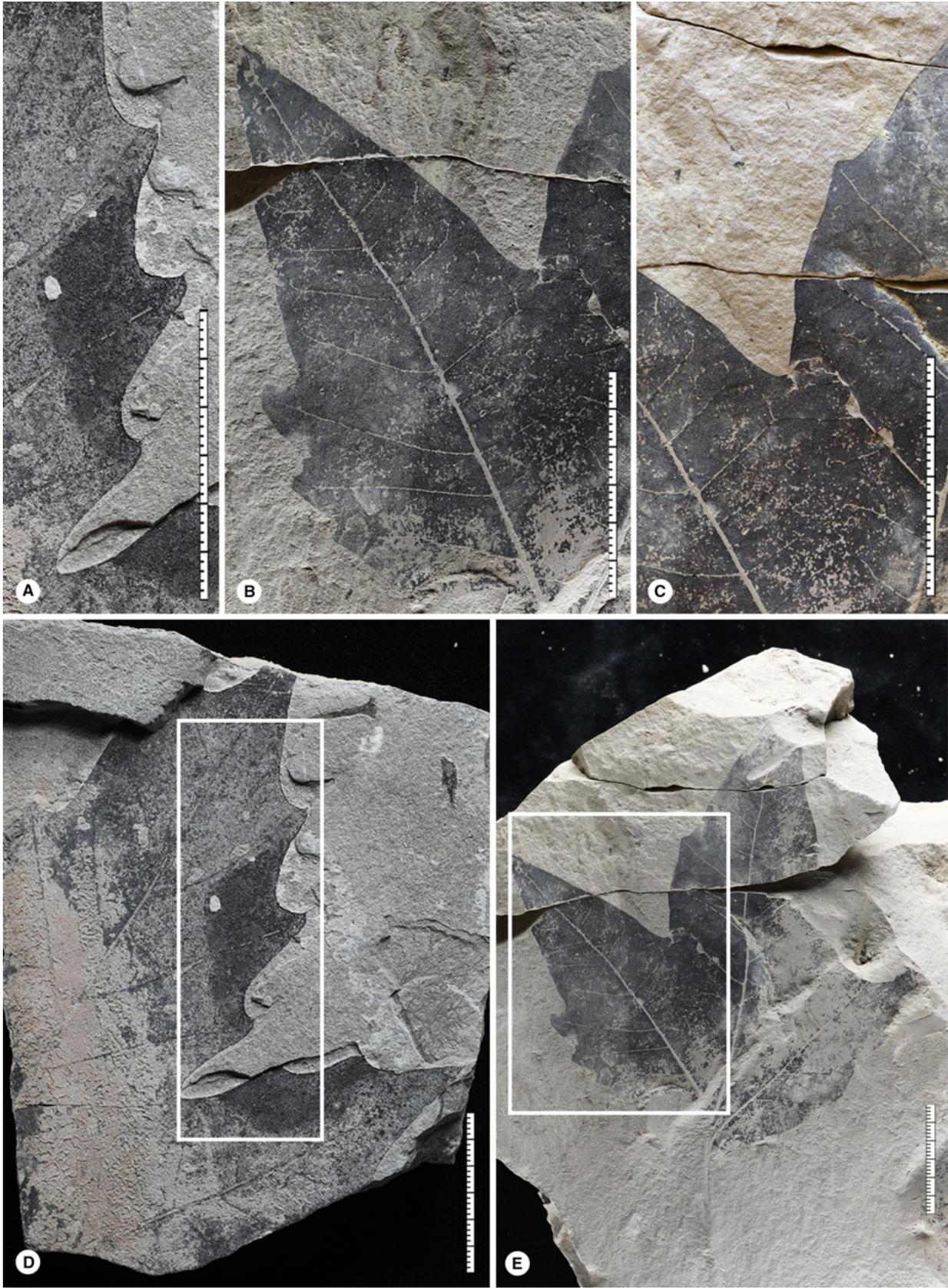


FIG. 5. Typical leaves of *Platanus academiae*, from Tsemperoula, Peloponnese, Late Miocene. A–C, margin details: A, leaf margin with coarse, hook-shaped teeth, S184035; B, lateral lobe with basal coarse, hook-shaped teeth, S184102; C, leaf margin detail with one blunt tooth on central lobe, S184102. D–E, overviews: D, central and lateral lobe, S18403; E, trilobed lamina with rhombic central lobe, S184102. Scale bars represent 3 cm.

evidence that the stem age of *Platanus* (*Platanus*) is not older than 45 myr. In fact, dispersal hairs on achenes are also known from Paleocene achenes from the Far East (Maslova 1997; Tkaprovayam Formation, uppermost Paleocene to lower Eocene; western Kamchatka), *c.* 56 myr in age. The middle Eocene *P. hirticarpa* most likely belongs to the extinct Platanaceae *Tanyoplatanus* (Indah Huegele, pers. comm. 2023), which differs from *Platanus* by its elongate infructescence and fewer achenes per floret (Manchester 1994). Another character, the petiolar sheath enclosing the bud (Nixon & Poole 2003), occurs in *Platanus* (*Platanus*) and *P. (Glandulosa)* but is lacking in *P. (Castaneophyllum)*. Fossils belonging to *Platanus* showing this character can be dated back at least to the Paleocene, *c.* 60 Ma, and hence Feng *et al.* (2005) used this age as alternative calibration for the age of *Platanus* (*Platanus*) (Fig. 1A). Given that this character is also found in many extinct genera of Platanaceae, it should not be used as a stem age for *P. (Platanus)*. The lack of this character in *P. (Castaneophyllum)* appears to be the result of a character loss in this subgenus. Therefore we used the 60 myr age estimate for *P. (Platanus)* from Feng *et al.* (2005) based on the presence of achenes with dispersal hairs in late Paleocene strata (Fig. 1B).

We are aware of a previous study (Tschan *et al.* 2008) describing *Platanus s.s.* from Cretaceous strata of Germany. Although all characters from reproductive and vegetative structures of *P. quedlinburgensis* Pacltová emend. fit with modern *Platanus*, these authors were not able to demonstrate the presence of dispersal hairs on the achenes. In a subsequent study investigating the ultrastructure of *in situ* pollen from this fossil-species, Tekleva & Denk (2012) showed that the relative thickness of the foot layer is larger in the fossil-species than in modern *Platanus*. This is a typical feature of extinct Cretaceous members of Platanaceae (e.g. Friis *et al.* 1988).

Modern plant material

Modern material was collected in the wild (stored at the Swedish Museum of Natural History) and includes all modern members of the PNA-E and ANA clades (see Grimm & Denk 2008, 2010 and Denk *et al.* 2012 for voucher numbers). Additional herbarium vouchers for comparison with the fossil material were studied from the herbaria E (Royal Botanic Garden Edinburgh), P (Muséum national d'Histoire

naturelle), ISTO (Istanbul University-Cerrahpaşa), and US (William and Lynda Steere Herbarium, New York Botanical Garden). Abbreviations follow the Index Herbariorum (<https://sweetgum.nybg.org/science/ih/>).

Leaf traits

To assess how leaf traits are distributed across modern clades and species of *Platanus* we studied extensive herbarium material and used the morphological investigations by Maslova (2003), Nixon & Poole (2003), Denk (2006), Maslova *et al.* (2008) and Denk *et al.* (2012), and the molecular phylogenetic studies by Feng *et al.* (2005) and Grimm & Denk (2008, 2010). According to Nixon & Poole (2003, p. 111), ‘leaf characters are among the most useful in *Platanus*’, and ‘all the taxa . . . can be reliably and consistently differentiated on the basis of the combination of leaf shape, number of lobes, shape of lobes, [and the] degree of secondary toothing’. The modern hybrid *P. × hispanica* (*P. orientalis* × *P. occidentalis*; e.g. Maslova *et al.* 2008) expresses a mosaic of leaf morphologies from *P. orientalis* and *P. occidentalis*, together with infructescences with a single, large fruiting head as typical of *P. occidentalis* or multiple, smaller heads as found in *P. orientalis*. Hence, the modern hybrid might be useful for comparative purposes and when examining fossilized material for evidence of ancient hybridization.

SYSTEMATIC PALAEOLOGY

Order PROTEALES Juss. ex Bercht. & J. Presl

Family PLATANACEAE T. Lestib.

Genus *Platanus* L.

Subgenus *Platanus* (*Platanus*)

Lineage PNA-E clade

†*Platanus academiae* C.T. Gaudin in Gaudin & Strozzi 1864

Figures 3–10

- 1864 *Platanus academiae* Gaudin in Gaudin & Strozzi, pp. 14–15, pl. 3, fig. 1 [here reproduced as Fig. 2C].
- 1955 *Platanus lineariloba* Kolakovsky, p. 264, pl. 15, fig. 1 [here reproduced as Fig. 2D; holotype: Sukhumi Botanical Garden, Sukhumi, Abkhasia, Georgia].
- 1958 *Platanus lineariloba* Kolak.; Kutuzkina, pl. 1, figs 1–4, pl. 2, figs 1–5, pl. 3, figs 3–5, pl. 4, figs 1–4.

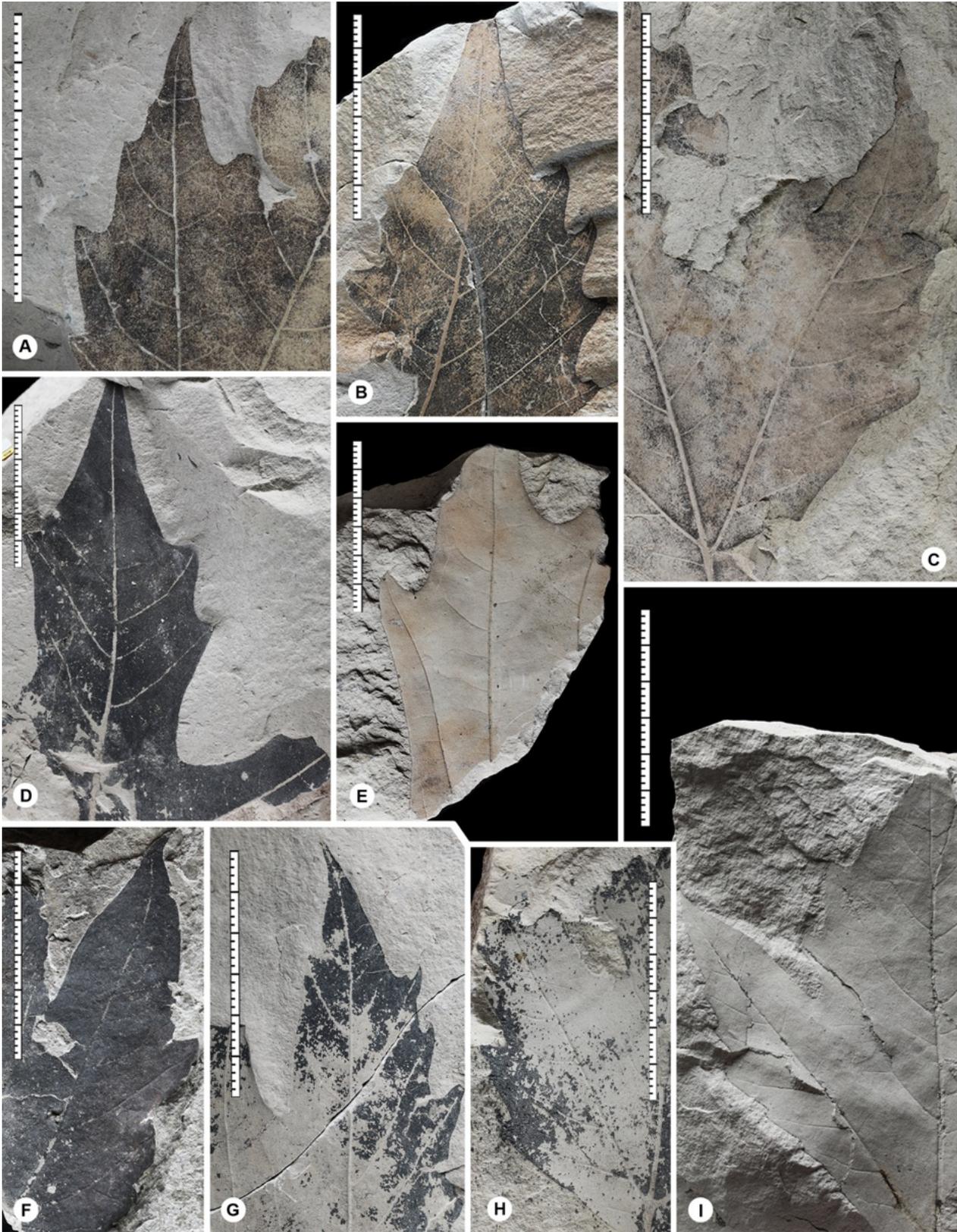


FIG. 6. Margin details of typical leaves of *Platanus academiae*, from Tsemperoula, Peloponnese, Late Miocene. A, lateral lobe with coarse, hook-shaped teeth, S184094. B, central lobe with coarse, hook-shaped teeth, S184100. C, leaf lamina with coarse, hook-shaped teeth, S184106. D, central lobe with narrow triangular shape and coarse teeth, S184092. E, margin detail with coarse, hook-shaped teeth, S184084. F, lateral lobe with coarse teeth and delicate appearance, S184037. G, lateral lobe with coarse, hook-shaped teeth and delicate appearance, S184047. H, lateral lobe with coarse, hook-shaped teeth, S184075. I, leaf with narrower lamina, triangular central lobe and coarse, hook-shaped teeth, S184081. Scale bars represent 3 cm.

- 1964 *Platanus lineariloba* Kolak.; Kolakovsky, p. 125, pl. 49, figs 3, 4.
 1964 *Platanus lineariloba* Kolak.; Kutuzkina, p. 208, pl. 10, figs 1, 4, 13, pl. 18, figs 1–8.
 1974 *Platanus lineariloba* Kolak.; Kutuzkina, p. 142, text-fig. 90, 4, pl. 60, fig. 4, pl. 62, fig. 2, pl. 65, fig. 1, pl. 70, fig. 2, pl. 71, fig. 5, pl. 74, fig. 4, pl. 77, figs 4, 6.
 1986 *Platanus academiae* C.T. Gaudin; Velitzelos & Knobloch, p. 23, pl. 10, fig. 1, pl. 12, figs 2, 5, 7, 8, pl. 13, figs 1, 4, 6–8.
 1994a *Platanus academiae* C.T. Gaudin; Kleinhölter, p. 56, pl. 3, fig. 2, pl. 21, figs 9, 10.
 1994b *Platanus academiae* C.T. Gaudin; Kleinhölter, text-fig. 2: 3.
 1995 *Platanus academiae* C.T. Gaudin; Kleinhölter, text-fig. 2: 5.
 2014 *Platanus academiae* C.T. Gaudin; Velitzelos *et al.*, pl. 31, figs 1–3.
 2020 *Platanus academiae* C.T. Gaudin; Liapi, p. 40, pl. 10, figs 1–8.

Studied material. Tsemperoula, S184034–S184059, S184060–S184067, S184068–S184080, S184081–S184085, S184086–S184089, S184090, S184091–S184099, S184100–S184106; Skoura, S183210, S183268, S183269; Chrysanthio, S182626–S182628, S182630, S182632, S182634–S182636, S182646–S182648; Chrysochori, S182628; Egira, S182757; Kalidona, S182867, S182892, S182897; Tripes abandoned opencast mine, S183531, S183532, S183536–S183540, S183547; Zacharo, S183573, S183575.

Emended description. **Lamina:** Leaves simple, palmately 3–5 lobed. Lamina deeply or shallowly lobed, lobe depth 1/2 to >2/3, central lobe shape triangular or rhombic, length to width (L : W) ratio of central lobe 1.6–2.3:1 or to 2.6:1 when the prominent teeth on the central lobe are not measured, lateral lobes mainly triangular, rarely rhombic. Leaf attachment petiolate, inflated petiole, commonly contributing to decurrent leaf base shape. Blade attachment marginal, laminar L : W ratio 1.2:1 (average), laminar shape elliptic (orbiculate), blade medially symmetrical and basal width mostly symmetrical, rarely asymmetrical (Fig. 4C). Margin toothed, serrate, rarely sinuous near the apex of the lobes (Fig. 6F) or the base of the lamina (Fig. 3A). Apex angle acute, apex shape straight or acuminate, with or without slight drip tip (Fig. 6A, F, G). Base angle acute or obtuse, base shape concavo-convex, concave or decurrent, seldom truncate. **Venation:** Primary venation suprabasal actinodromous or palinactinodromous, monopodial. Naked basal veins absent, three or five basal veins; simple and rarely compound agrophic veins present (Fig. 3B), secondary (2°) veins mostly craspedodromous, but also

semicraspedodromous (Fig. 4F). Other leaves combine craspedodromous and eucamptodromous venation (Figs 4C, 6D, H), with the latter being present near the base of the lamina or the apex of the lobes (Figs 3C, 4E, 6E). Lamina without teeth characterized by eucamptodromous or, rarely, brochidodromous 2° venation (Fig. 4C). The most typical case is craspedodromous venation in toothed and eucamptodromous in untoothed segments of the lamina. Interior 2° veins (synonym: epimedial veins; Ellis *et al.* 2009, p. 53, fig. 148) present, mostly arched but also straight or branched, with gauge intermediate between 2° and 3° veins. Major secondary spacing regular to gradually increasing proximally. Secondary angle smoothly decreasing proximally, although in the lobe-fusion part the angle abruptly becomes almost straight. Major secondary attachment decurrent proximal. Intersecondary veins present, perpendicular to superjacent major 2° veins. Intercostal tertiary vein fabric percurrent and reticulate, with angle inconsistent or decreasing proximally. **Teeth:** Margin coarsely toothed. Tooth spacing regular, rarely irregular near the leaf base (Fig. 5B) or the apex of lateral lobes (solitary teeth; Figs 4D, 5C, E), one order of teeth, 1 or 2 teeth per cm. Tooth sinus shape rounded, tooth shape concave and straight to concave distal flank, convex proximal flank, rarely concave/concave near leaf base. Tooth apically directed (serrate) or seldom directed perpendicular to the trend of the leaf margin (dentate; Figs 3A, 9C), apically intensified, coarse, hook shaped, usually not keen especially near leaf base. Bristle extension and mucronate teeth absent or very rarely present in reduced teeth ('wavy' margin; Fig. 9A, B). Lateral lobes sometimes untoothed (Fig. 4C, D, E), or with untoothed distal (inner) side (Fig. 5B). Central lobe seldom embellished with one pair of teeth (Fig. 8B, C, E). Principal vein present, terminating at the apex of tooth, or on the distal or proximal flank.

Atypical specimens include unlobed leaves with rhombic shape (Fig. 9C, D) and show combinations of the different types of dentition mentioned above. Also, leaves with two orders of teeth are present (Fig. 10A, B), and leaves with five basal veins are more common in the stratigraphically younger (Pliocene and Pleistocene) specimens.

Additional observations. Rare insect damage types encountered in leaves of *P. academiae* are shown in Figure S1, and identified according to the terminology of Labandeira *et al.* (2007). Damage types include skeletonization close to the primary vein (DT20; Fig. S1A), polylobate holes (DT03; Fig. S1B), small galls on secondary veins (DT32; Fig. S1C), and elongate surface abrasion (DT25; Fig. S1E).

Remarks. Such leaf remains have interchangeably been called *P. academiae* and *P. lineariloba*. We consider these fossil-species

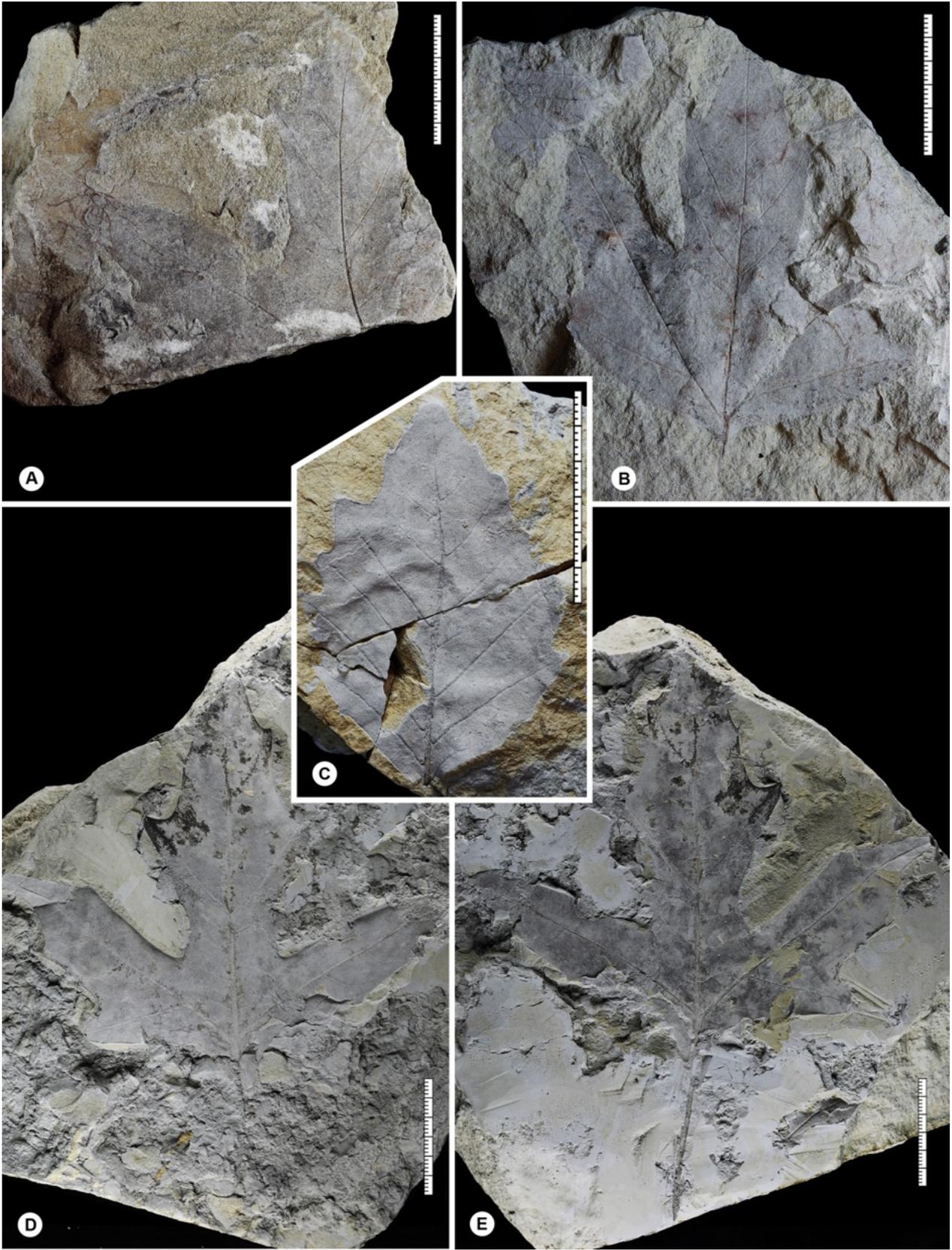


FIG. 7. Complete specimens of *Platanus academiae* leaves, markedly similar to modern *Platanus orientalis*. A–B, leaves from Chrysanthio, Peloponnese, Early Pleistocene: A, lateral lobe and triangular central lobe with coarse, hook-shaped teeth, S182630; B, trilobed leaf, lateral lobe and triangular to rhombic central lobe with coarse teeth, S182627. C–E, leaves from Skoura, Peloponnese, Pliocene: C, simple sucker-shoot leaf with serrate ‘wavy’ margin, S183210; D–E, part and counterpart specimens, deeply trilobed leaf with coarse, hook-shaped teeth, developing fourth and fifth lobes visible on part and counterpart respectively, delicate appearance (D, S183268; E, S183269). Scale bars represent 3 cm.

as synonyms and assign leaf specimens from western Eurasia with a PNA-E clade morphology to *P. academiae* due to nomenclatural priority. *Platanus academiae* was described based on a single large leaf from ‘Monte Masso’ (current name Montemassi, Grosseto Province, Tuscany; Gaudin & Strozzi 1864) associated with the *Oreopithecus*-bearing Late Miocene lignites of the Grosseto region (E. Cioppi & E. Martinetto, pers. comm. 2024). This leaf specimen has three large lobes, triangular in shape, and teeth are restricted to the outer side of the lateral lobe (Fig. 2C). In contrast, in the type specimen of *P. lineariloba* (Fig. 2D), blunt coarse teeth are also developed along the margin of the central lobe, and the lobes are more oblong to rhombic in shape. *Platanus lineariloba* was described from Late Miocene deposits of Abkhazia, Georgia (Kolakovsky 1955). Leaf specimens from coeval strata in the Tsemperoula site cover the variability represented by both *P. academiae* and *P. lineariloba* (e.g. Fig. 4D, a leaf well comparable with *P. lineariloba*; and Fig. 5B, E, a leaf highly similar to *P. academiae*). Specifically, the typical combination of craspedodromous venation in toothed and eucamptodromous to brochidodromous venation in untoothed segments of the lamina, and the deeply trilobate lamina, fit both fossil-species. From Late Miocene strata of Schossnitz (= Sośnica, district of Gmina Kąty Wrocławskie, Wrocław County, Lower Silesian Voivodeship, southwestern Poland), Göppert (1855, pl. 12, figs 1–3) described *P. cuneifolia* Göpp. Of the three figured leaves, one (fig. 1) is a deeply dissected (lobe depth >1/2), three-lobed leaf with entire margin and thus resembles the original specimen of *P. academiae*. The other two specimens are small leaves of *P. leucophylla*. Given that the leaf assemblage of Sośnica is dominated by *P. leucophylla* (described under various names: *P. aceroides* Göpp., *P. oeyhausiana* Göpp., *P. guillelmae* Göpp.), the single, incomplete leaf specimen might be an uncharacteristic leaf type occasionally encountered in modern species of *Platanus*.

Also, the leaf record of *Platanus* from Messinian deposits of Senigallia (Masalongo 1858; Massalongo & Scarabelli 1859) comprises specimens resembling *P. academiae*. Examples are *Acer heeri* v. *productum* Massal. and *A. heeri* v. *tricuspidatum* Massal. figured in Massalongo & Scarabelli (1859, pl. 17, fig. 1, pl. 18, fig. 1), and *P. aceroides* figured in Paolucci (1896, pl. 12, fig. 80). Notably, these leaves co-occur with specimens corresponding to *P. leucophylla*. Revision of this and similar floras in the northern Mediterranean region are needed to clarify the status of these specimens. It cannot be ruled out that these populations included ancient hybrids between *P. leucophylla* (ANA clade) and *P. academiae* (PNA-E clade).

Considering the number of the lobes in the fossil-species *P. academiae*, we observed a change from predominantly three-lobed, moderately dissected leaves at Middle and Late Miocene sites to 3–5-lobed, deeply dissected leaves with narrower lobes at

Pliocene and Pleistocene sites. This might reflect an evolutionary trend towards the modern species (Velitzelos & Knobloch 1986).

The *P. academiae* specimens from Pliocene and Pleistocene strata in Figures 7 and 8 show marked similarity to extant *P. orientalis* (Figs 11, 12). The lamina is deeply lobed and lateral lobes form wide angles with the central lobes. In the basal part, a shallower sinus indicates the development of additional (fourth and fifth) lobes at each side of the lamina possibly reflecting an evolutionary innovation. The shape of the central lobe is elongated and rhombic or triangular to rhombic. One or two pairs of coarse, hook-shaped teeth embellish the middle and usually also the apex of the lobe (compare Fig. 8B, C, E with Fig. 11J, K). The pair of teeth at the middle of the lobe typically exaggerate the lobe’s rhombic shape (compare with modern *P. orientalis*; Fig. 12). Despite being quite modern in appearance, the Pliocene and Pleistocene specimens of *P. academiae* differ from many modern *P. orientalis* leaves by the absence of lobate and cordate basal shapes, although these are remarkably common in modern leaves.

Leaves called ‘atypical’ might belong to basal sucker-shoots also seen in all modern-day species of *P. (Platanus)*. It is difficult to correctly classify them into a particular fossil-species. Nevertheless, sucker-shoot leaves of modern *Platanus orientalis* resemble the ones in the fossil specimens (Figs 7C, 9C, D). The mucronate reduced teeth as seen in a few specimens from the Tsemperoula assemblage (Fig. 10) are rather common in the western North American *P. gentryi* (PNA-E clade; Table 2) and in unnamed leaves from the Early Miocene of Alaska (as *P. bendirei* (Lesq.) J.A. Wolfe in Wolfe & Tanai 1980).

DISCUSSION

Leaf morphology of the Pacific North American–European lineage of Platanus

We searched for leaf morphological traits typical of the extant members of the ANA versus PNA-E clades. From the modern *P. × hispanica* Mill. ex Münchh. (London plane; including a number of heterotypic synonyms such as *Platanus × acerifolia* (Aiton) Willd., *Platanus × cuneata* Willd., and others; <https://powo.science.kew.org/>), an artificial, horticultural hybrid of *P. occidentalis* and *P. orientalis*, we know that this taxon has a wide range of leaf and infructescence morphologies approaching both typical *P. occidentalis* (ANA-clade parent) and (less so) typical *P. orientalis* morphologies (PNA-E clade parent; Maslova *et al.* 2008). However, individuals of *P. × hispanica* can be genetically quite

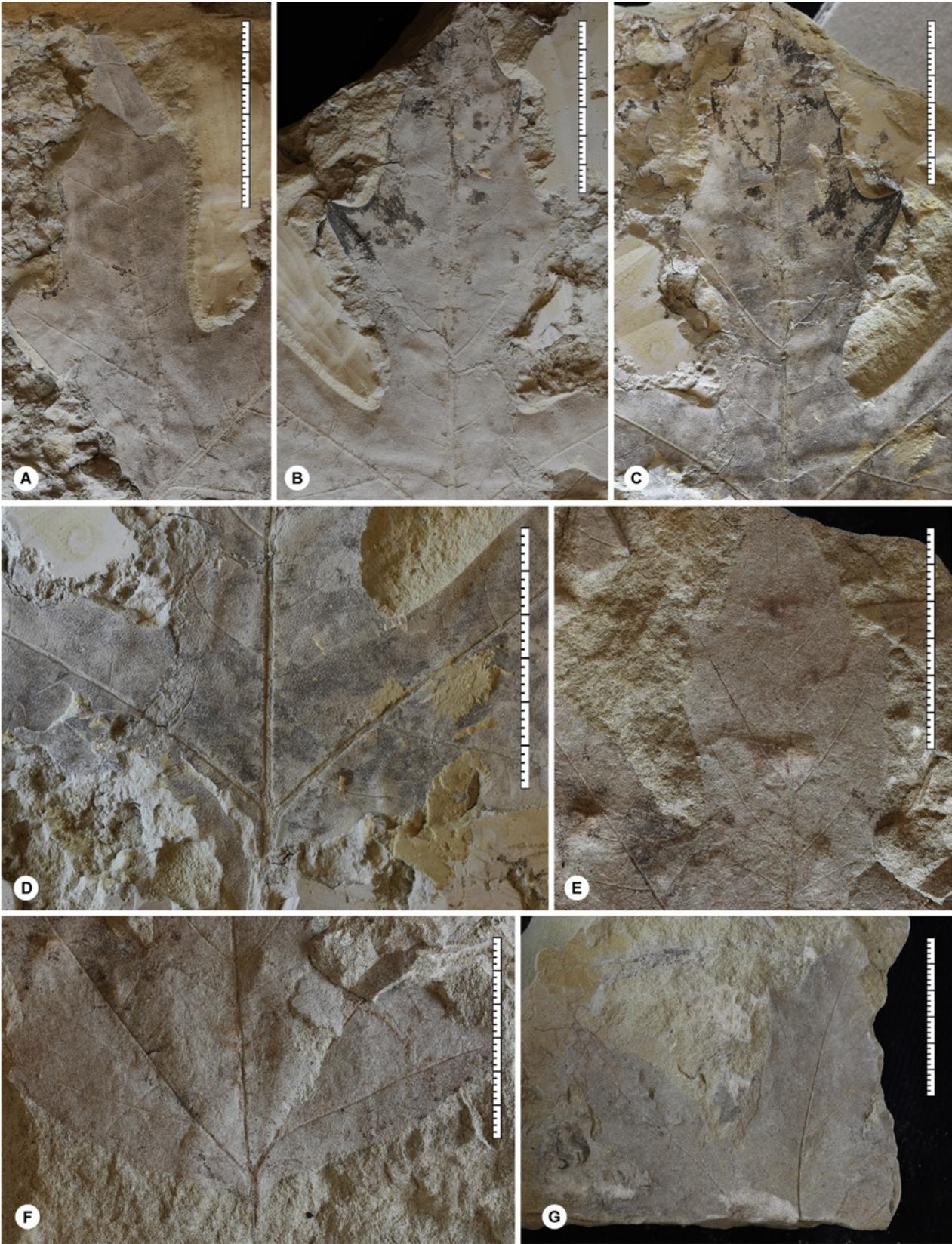


FIG. 8. Margin details of typical leaves of *Platanus academiae*, markedly similar to modern *Platanus orientalis*. A–D, leaves from Skoura, Peloponnese, Pliocene: A, detail of lateral lobe and weakly developed additional lobe, S183268; B–C, part and counterpart specimens, detail of rhombic central lobe with coarse, hook-shaped teeth and deep lobe sinuses (B, S183268; C, S183269). D, base of deeply trilobed lamina, weakly developed fourth lobe visible, S183269. E–G, leaves from Chrysanthio, Peloponnese, Early Pleistocene: E, detail of triangular to rhombic central lobe with coarse teeth, S182627; F, base of trilobed lamina, S182627; G, detail of central and lateral lobes with coarse, hook-shaped teeth, S182630. Scale bars represent 3 cm.

different, with different contributions of the parent species related to natural backcrossing (cf. Besnard *et al.* 2002; Pilotti *et al.* 2009; Grimm & Denk 2010) resulting in trees with pure and mixed leaf morphologies for the traits under study. In contrast, several morphological traits in non-hybrid modern species are well constrained (Table 2; Fig. 11).

Specifically, we found a number of combinations of leaf traits, which are highly diagnostic for modern members of the PNA-E versus ANA clades. Main leaf traits for distinguishing the two modern clades are lobe depth, shape, L : W ratio and the presence or absence of hooked teeth without a bristle-like extension (Table 2; Nixon & Poole 2003; Denk 2006; Denk *et al.* 2012; Huegele *et al.* 2020). Members of the PNA-E clade can be defined by synapomorphic character states. Other characters useful to characterize both species of the PNA-E and ANA clades are mucronate, bristle-like and fine triangular teeth. These appear to be symplesiomorphic in *Platanus* and Platanaceae. They occur both in species of the PNA-E clade (e.g. *P. gentryi*) and in ANA clade species (e.g. *P. mexicana*). *Platanus mexicana* has been suggested to be the least derived species in the ANA clade (Grimm & Denk 2008). The ancestral nature of mucronate, bristle-like and fine triangular teeth is also indicated by their common presence in Paleocene and Late Cretaceous *Platanus* and Platanaceae (e.g. Maslova 2003). In the context of evolution of the PNA-E clade, the loss of bristles in *P. orientalis* in combination with the acquisition of the conspicuous hooked teeth lacking bristles is relevant.

Our investigation of the distribution of leaf characters of the fossil-species *P. academiae* and a number of Eocene–Pliocene fossil-species, for which close affinities with the PNA-E clade have been suggested, is summarized in Table 2. If a modern (e.g. *P. × hispanica*) or a fossil-species (e.g. *P. dissecta* Lesq. (Lesquereux), *P. vassiljevii* Iljinsk., see below) combines leaf traits characteristic for the PNA-E or the ANA clade, this might indicate possible hybridization or ancestral polymorphism in fossil-species. In the modern hybrid *P. × hispanica*, leaf morphology partly tracks its hybrid origin (e.g. rather deeply lobed leaves with triangular bristle-like teeth; Table 2). In addition, *orientalis*-type (plesiomorphic) or *occidentalis*-type (apomorphic) infructescences may co-occur with different leaf types.

Hence, leaf traits investigated in the plant macrofossil record may provide information about ancient hybridization, as has been reported in molecular studies (Grimm & Denk 2008, 2010). At the same time, intermediate morphologies encountered in fossil leaves may also indicate ancestral polymorphism prior to the diversification of crown group members of the ANA and PNA-E clades, especially when combining plesiomorphic characters of parental lineages (Table 2; see below, *P. vassiljevii*). In addition, leaf traits may differ within a fossil-species across geographic and stratigraphic scales, providing important information regarding the evolution of a species: this is seen in the gradual replacement of three-lobed leaves in *P. academiae* with *P. orientalis* five-lobed forms.

Preliminary survey of insect damage types

The western Eurasian material studied here and previously published fossils belonging to the PNA-E clade showed that the large majority of our *Platanus* fossil leaves did not include insect damage. Rare cases of damage are shown in Figure S1. Comparison with leaves of the North American fossil-species *Platanus dissecta* (Wolfe 1964; Huegele *et al.* 2020), unnamed Miocene specimens of Alaska, and Pleistocene *P. racemosa* (Axelrod 1966) indicated a much greater richness of insect damage in the North American material. This damage was external; most common functional feeding groups were hole and margin feeding, which are very generalist damage types.

For a more comprehensive comparative study of plant–insect interactions between the European and the North American fossil records, a broad investigation of North American fossil leaves would be required.

*Biogeographic history of the PNA-E clade and origins of the Mediterranean *Platanus orientalis**

Morphological similarities with *P. orientalis* and western North American species of the PNA-E clade have been noted for several Palaeogene and Neogene leaf records (summarized in Figs 13, S2–S7; Tables 2, S1).

The oldest record of *Platanus* foliage possibly referable to the PNA-E clade is *Platanus stenoloba* Becker from late



FIG. 9. Leaves with atypical shapes, complete specimens, from Tsemperoula, Peloponnese, Late Miocene. A, trilobed lamina with shallow sinuses, S184075. B, narrow trilobate lamina with deep sinuses, S184093. C, obovate simple leaf with dentate margin, S184101. D, ovate simple leaf with serrate margin, S184056. Scale bars represent 3 cm.

Eocene deposits of Montana, Beaverhead Basin floras (Becker 1969; Lielke *et al.* 2012; Table 2; Figs S2, S3). *Platanus stenoloba* differs from the extinct Platanaceae *Macginitiea*, a common element of Palaeogene floras of western North America (Huegele & Correa Narvaez 2023), by the consistently suprabasal divergence of primary veins, angles between primary veins ranging from 30° to 40°, and relatively fewer, 3–5, lobes (Meyer & Manchester 1997). These leaves show the presumed apomorphies of the PNA-E clade such as great lobe depth, coarse, hooked teeth, and oblong to rhombic primary lobes with a high L : W ratio (Fig. S3). From the same deposits, Becker (1969) described *P. dissecta* Lesq. (Lesquerieux 1878), a fossil-species that is most typical of Middle Miocene strata across western North America (Huegele *et al.* 2020). These specimens (Fig. S4) are highly consistent with the Middle Miocene leaf material figured in Huegele *et al.* (2020, figs 4, 5). They show a lobe depth of *c.* 50%, and a variety of tooth types including coarse triangular ones with bristle-like extensions (possible apomorphy in the ANA clade, *P. occidentalis*) and coarse hooked teeth (possible apomorphy in the PNA-E clade, *P. gentryi*, *P. orientalis*). As such, they would qualify for an ancient hybrid between the ANA and PNA-E lineages (cf. Fig. 1). This would be in agreement with a detailed investigation of nuclear DNA markers in *Platanus* (Grimm & Denk 2010), which found evidence for ancient hybridization between the Eurasian and North American members of the PNA-E clade prior to the formation of modern species lineages (cf. Fig. 1).

A Central Asian fossil-species, *P. vassilijevii* Iljinsk. from early Oligocene deposits of Kiin-Kerish, Zajsan depression, Eastern Kazakhstan, also shows some similarity to modern PNA-E clade species (Iljinskaya 1986; Figs S5, S6). According to Iljinskaya (1986), foliage of this species matches *P. orientalis* by its leaf shape and lobe number and shape, but differs by its dentition, which resembles more closely the modern *P. mexicana s. str.* The leaf margin of *P. vassilijevii* consists of larger and smaller teeth (subsidiary teeth) with a mucronate apex, as rarely seen in modern *P. mexicana s. str.* (cf. Fig. 11E) and more commonly in *P. gentryi* (Fig. 11F, I). Hence, this leaf type comprises traits of the PNA-E clade (*P. orientalis*, *P. gentryi*) and potentially the ANA clade (*P. mexicana*). The rhombic lobe shape comparable to *P. orientalis* is observed only in a single, inconspicuously five-lobed, small leaf (Fig. S5A). The remaining specimens of *P. vassilijevii* are three lobed, with triangular lobes and

lobe depth $\leq 1/2$ (Fig. S5). They have indistinct triangular and reduced mucronate teeth, which we consider plesiomorphic in *Platanus*. Larger triangular teeth are slightly hooked as also found in *P. dissecta*. Thus, *P. vassilijevii* could represent a fossil stem lineage member of the PNA-E clade (Fig. S7A). Alternatively, it could reflect the contact zone of the early ANA and PNA-E lineages (Fig. S7B). However, the *P. vassilijevii* leaf type could also represent an ancestral leaf morphology (Fig. S7C) as also found in the most basal ANA clade member *P. mexicana* (Grimm & Denk 2008).

In the Neogene fossil record of western North America, leaf morphologies resembling modern members of the PNA-E clade are known from Early Miocene (possibly into Oligocene) to Pliocene strata. A recent revision of the widespread Middle Miocene fossil-species *P. dissecta* included another species, *P. bendirei*, as a synonym of the former species (Huegele *et al.* 2020) based on the observation that both taxa have three- and five-lobed leaves and in both taxa prominent teeth and smaller subsidiary teeth occur. We noted that leaf remains from the late Early to early Middle Miocene Seldovia Point flora of Alaska originally assigned to *P. bendirei* (Wolfe & Tanai 1980; pl. 3, fig. 4, pl. 4, figs 1, 2, 4) differ considerably from the bulk of *P. dissecta* and probably would deserve their own species name. These leaves are deeply three-lobed (lobe depth 2/3 to >3/4) and have an eroded leaf margin with an irregularly spaced coarser and finer mucronate dentition as also seen in extant leaves of *P. gentryi* from north-eastern Mexico. Hence, based on their leaf shape, lobe depth, lobe dentition and narrow rhombic lobe shape, these leaves are unambiguously referable to the PNA-E clade of modern *Platanus* (Table 2). According to Wolfe & Tanai (1980), undescribed leaves from Oligocene strata of western North America falling within the morphological variability of the Alaskan specimens differ by having several subsidiary teeth between two adjacent major teeth.

A large number of Middle Miocene leaf fossils and reproductive structures of western North America have recently been placed in the fossil-species *P. dissecta* and into the PNA-E clade (Huegele *et al.* 2020) based on lobe shape, leaf base, and leaf margin and features of the infructescence and fruiting heads. Typical leaves of *P. dissecta* resemble leaf forms encountered in the modern cultivation hybrid *P. × hispanica* (cf. Maslova *et al.* 2008, figs 2, 3) and occasionally have compound teeth with smaller teeth situated between larger teeth that terminate

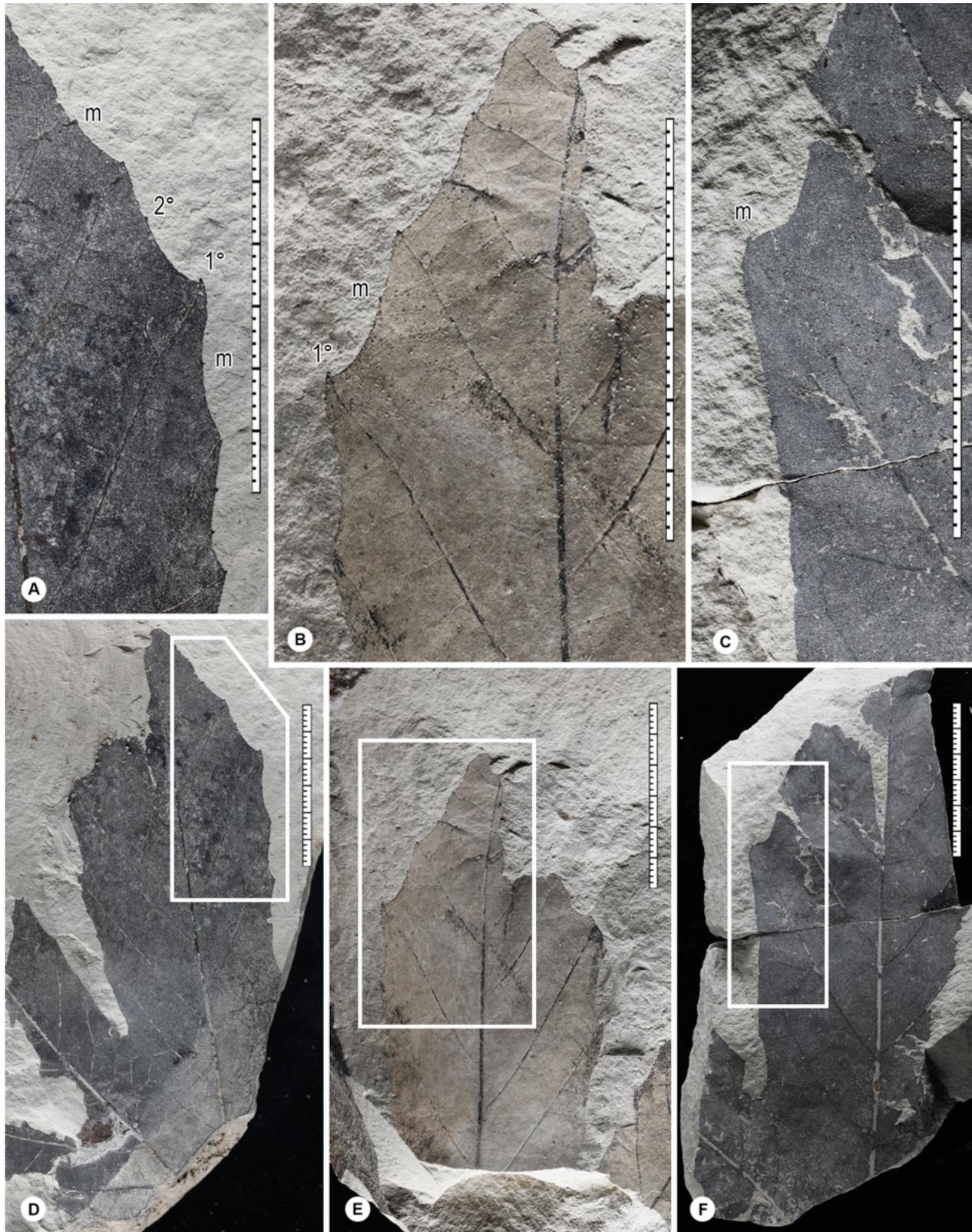


FIG. 10. Leaves with atypical dentation, from Tsemperoula, Peloponnese, Late Miocene. A–C, margin details: A, leaf with two orders of mucronate teeth, one marginal tooth of first order per secondary vein, marginal teeth of second order in between, S184105; B, leaf with two orders of mucronate teeth, S184097; C, leaf with mucronate teeth, S184048. D–F, overviews: D, S184105; E, S184097; F, S184048. *Abbreviations:* m, mucronate; 1°, primary tooth; 2°, secondary tooth. Scale bars represent 3 cm.

secondary veins (Huegele *et al.* 2020). Such compound teeth are seen in the western North American extant species *P. racemosa* and *P. gentryi* but usually not in the Mediterranean *P. orientalis* (cf. Fig. 11). In addition, such a leaf margin is occasionally observed in *P. mexicana* s.s. (Denk *et al.* 2012, fig. 5D). The intermediate leaf (and infructescence) morphology of *P. dissecta* s.s. may indicate that this fossil-species resulted from contact between PNA-E and ANA clade lineages. Grimm & Denk (2008) detected ancient hybridization between members of the PNA-E and ANA clades by the expression of pseudogenetic sequence variants (from the internal transcribed spacers, ITS1 and ITS2) of PNA-E origin but exclusively shared by *P. gentryi* and all ANA clade members except for *P. lindeniana*. Furthermore, adding data from two other non-coding nuclear regions, Grimm & Denk (2010) detected repeated lineage mixing between the western North American portion of the PNA-E clade and (parts of) the ANA clade. It is noteworthy that fossil-species with ANA clade leaf morphology were also present during the Miocene in western North America and the Midwestern USA (e.g. *P. vitifolia* MacGinitie and *P. youngii* A.K. Graham; Table S1). *Platanus vitifolia* and *P. youngii* have weakly trilobed or unlobed leaves as found in extant *P. mexicana* and *P. lindeniana*, and fine triangular and mucronate teeth; the latter may be plesiomorphic in *Platanus* (Table 2).

Younger (Pliocene and Pleistocene) records of PNA-E members in western North America include *Platanus paucidentata* Dorf from Pliocene strata of California and Oregon (Dorf 1930; Chaney 1944), and leaf remains assigned to *Platanus racemosa* from the Pleistocene Soboba flora of southern California (Axelrod 1966).

Hence, leaf traits characteristic of the PNA-E clade were present in western North America since the late Eocene, in Central Asia in the early Oligocene, and in western Eurasia since the Middle Miocene. In contrast, they are absent from the Cenozoic record of eastern North America and the North Atlantic land bridge. From the Middle Miocene (North Caucasus) onwards, the fossil-species *P. academiae* occurred in eastern and south-eastern Europe (Figs 2, 13). This fossil-species has a stratigraphic range from the Serravallian (Sarmatian regional unit of the Central Paratethys, c. 12 Ma) to the Gelasian (2.58–1.8 Ma). Stratigraphically older leaf specimens differ from younger (Pliocene and Pleistocene) ones, with the younger ones resembling modern leaves of

P. orientalis more closely and the older ones conforming to an ancestral phenotype with fewer lobes and less pronounced coarse, hooked teeth. Fossil leaves most similar to modern Oriental plane appear in the Pliocene of Skoura and younger strata on the Peloponnese peninsula of southern Greece.

Currently available data, therefore, suggest that the PNA-E lineage originated in western North America during the Eocene, possibly expanded to Central Asia via the Bering land bridge, and became widespread in western Eurasia and western North America during the Miocene. Thus, a Pacific–Central Asian connection between western Eurasian and western North American members of the PNA-E clade is favoured over a connection via the North Atlantic land bridge (Fig. 13).

Contrasting biogeographic histories of ANA and PNA-E clades and areas of potential hybridization

To compare the biogeographic histories of the ANA and PNA-E clades, we compiled available fossil records of *Platanus* (stem and crown lineages; Table S1). Platanaceous leaves from Palaeogene strata of Axel Heiberg Island (Nunavut: McIver & Basinger 1999), Greenland (Heer 1883a, 1883b) and Spitsbergen (Budantsev & Golovneva 2009) have been assigned to different fossil-species and some of them belong to extinct genera of Platanaceae. Nevertheless, these leaves and the younger ones from Miocene strata of Iceland (Grímsson *et al.* 2007) strongly resemble the modern-day *P. occidentalis* (ANA clade) by their leaf shape, lobe shape and dimensions, and dentition. From Palaeogene strata of the North Atlantic region also members of *P. (Glandulosa)* are known (Kvaček *et al.* 2001).

Palaeogene records of *Platanus* from Western Europe include *P. schimperi* (Heer) Saporta & Marion (Saporta & Marion 1878, 1885; Laurent 1912; Paleocene Menat, Gelinden floras; Kvaček & Walther 2004, Oligocene of Czech Republic), an extinct species that cannot readily be compared to any living species and perhaps represents the *Platanus* stem lineage. Andreánszky (1965) figured two leaves of *Platanus* from the early Oligocene of Hungary. The fragmentary leaf remains resemble leaves encountered in modern and fossil members of the ANA clade but cannot be assigned to a particular fossil-species. At the same time, fossil-species with ANA clade-specific leaf traits

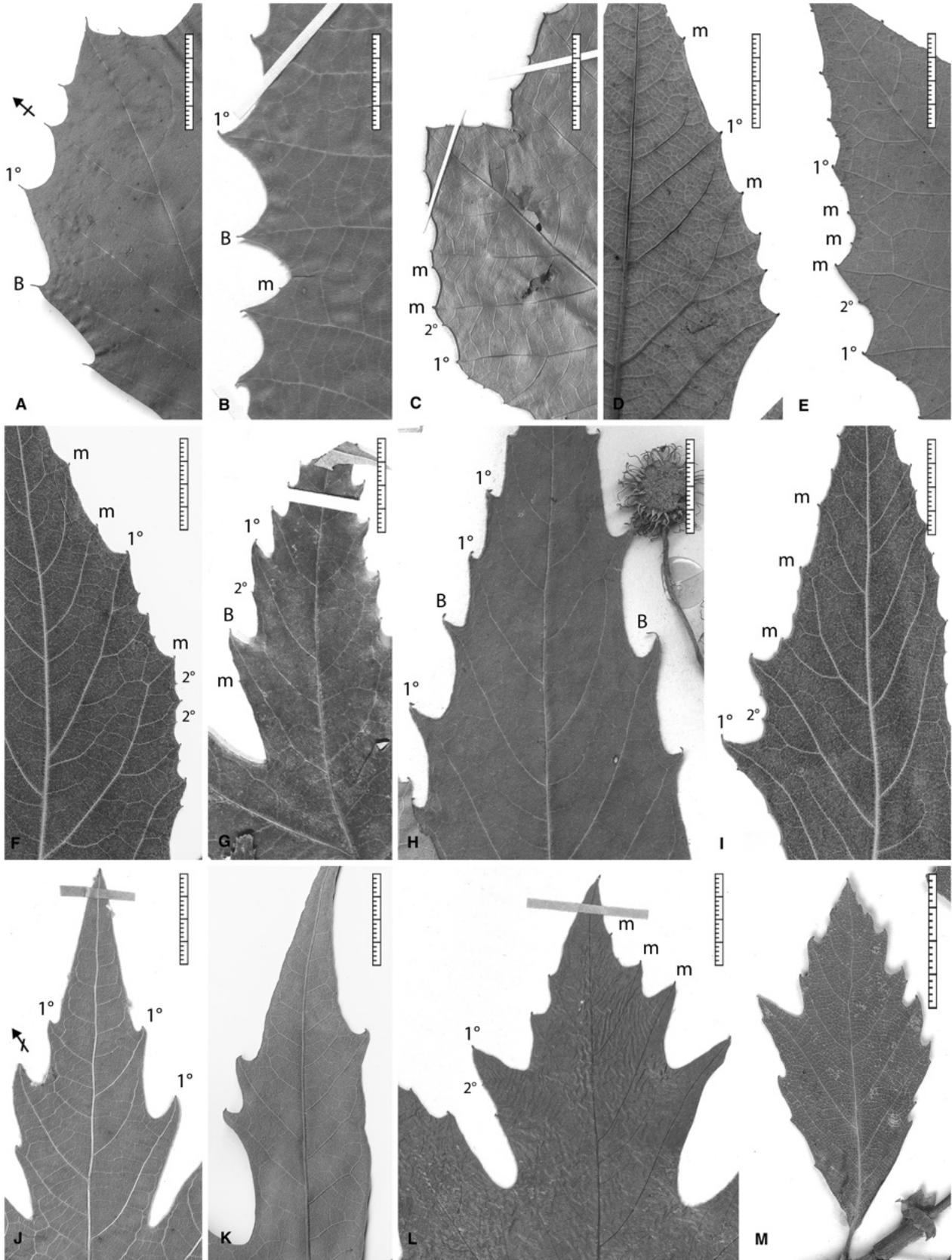


FIG. 11. Leaf margins of modern *Platanus* spp. A–E, Atlantic North American (ANA) clade members, teeth with bristle-like extensions and mucronate teeth: A, *Platanus occidentalis* Denk 2003078 (S) Salt Fork River, IL, USA; B, *P. occidentalis* US3568270 (barcode 01000201); C, *P. occidentalis* US3615523 (barcode 03664108). D, *P. mexicana* Denk 2004040 (S) Zinacantan to Ixtapa; E, *P. lindeniana* Denk 2004014 (S) Rio Misantla. F–I, western North American members of the PNA-E clade with bristle like extensions on hooked teeth and mucronate teeth: F, *P. gentryi* Denk 2004049 (S) La Vinata; G, *P. gentryi* US3706949 (barcode 03664276); H, *P. gentryi* NY 00356153; I, *P. gentryi* Denk 2004049 (S) La Vinata. J–M, western Eurasian members of the Pacific North American–European (PNA-E) clade with hooked teeth: J, *P. orientalis* E00403861; K, *P. orientalis* Denk 0405 (S) Makrilia; L, *P. orientalis* with mucronate teeth E00403824; M, *P. orientalis* E00403862. Abbreviations: B, bristle-like extension; m, mucronate; 1°, primary tooth; 2°, secondary tooth. Scale bars represent 2 cm.



FIG. 12. Modern leaves of *Platanus orientalis*. A, *Platanus orientalis* Denk 05/2002 (S) Larissa, Greece; trilobed leaf with coarse, hook-shaped teeth on primary and lateral lobes. B, *P. orientalis* Denk 2006185 (S) Coruh valley, northeast Turkey; trilobed leaf with reduced lobes. C, *P. orientalis* Denk ori0402 (S) Kavousi, Crete; five-lobed leaf with weakly expressed fourth and fifth lobes, rhombic primary and first-order lateral lobes. All scale bars represent 3 cm.

were present in the Russian Far East and Central Asia (Maslova & Fotyanova 1990, 1991; Maslova 1997; Table S1) and western North America (Manchester *et al.* 2023; Table S1). Overall, this suggests that during the Palaeogene the circumpolar region was saturated with members of extinct genera of Platanaceae, stem lineage or ANA clade members of *P.* (*Platanus*), and members of *P.* subgen. *Glandulosa*. In contrast, fossils with PNA-E clade traits are known only from western North America and their record starts much later (Fig. 13A).

During the Neogene, the North Atlantic land bridge probably continued to act as a corridor for the migration of ANA clade members from eastern North America to Europe. Grímsson *et al.* (2007) reported rare leaf remains

and pollen from Middle Miocene (*c.* 15 Ma) deposits of Iceland and referred these leaves to the widespread western Eurasian *P. leucophylla* (cf. Table S1). From coeval strata of Denmark, Friis (1985) reported infructescences, achenes and pollen of *P. (Glandulosa)*. From Middle Miocene deposits of southern Mississippi, McNair *et al.* (2019) described and figured *Platanus* leaves, which show more similarity to the modern species *P. mexicana* and *P. lindeniana* than to typical *P. occidentalis*. Younger fossils from Late Miocene and Pliocene strata of eastern North America are very similar to modern *P. occidentalis* (McCartan *et al.* 1990; Stults & Axsmith 2015; Fig. 13B). In contrast, Pliocene leaf fossils from Hidalgo, Mexico (Velasco-de León *et al.* 2010), are strikingly similar to

TABLE 2. PNA-E and ANA clade diagnostic combinations of leaf morphological traits.

Taxon	Age	Leaf organization		Teeth			Lobe shape			Reference	Taxonomy (clade)	Remarks		
		No. lobes	Lobe depth ^a	Mucronate	Bristle-like	Fine triangular	Coarse triangular with bristle	Coarse hooked without bristle	Central lobe				Central lobe L : W	Lateral lobes
<i>Platanus academiæ</i> C.T. Gaudin	† Middle Miocene to Pleistocene	3 (-5)	1/2 to >>2/3	Rare	No	No	No	Yes	Triangular to rhombic	1.6-2.3:1 (2.6:1 without measuring prominent teeth on central lobe)	Triangular to oblong	This study	PNA-E	Pliocene specimens of Skoura markedly similar to modern leaves of <i>P. orientalis</i>
<i>Platanus stenoloba</i> Becker	† Late Eocene	3 (-5)	1/2 to >2/3	Rare	No	Yes	No	Yes	Oblong to rhombic	3-4.5:1	Triangular to oblong	Becker 1969	PNA-E	Oldest fossil evidence of PNA-E lineage
<i>Platanus vassilijevii</i> Iljinsk.	† Early Oligocene	3 (-5)	≤1/2	Yes	Yes (weak)	Yes	? Yes (weak)	No	Triangular to rhombic	≤2:1	Triangular (to rhombic)	Iljinskaya 1986	Intermediate/ancestral	A single small specimen with rhombic central and lateral lobes
Unnamed species of <i>Platanus</i> (as <i>Platanus bendirei</i> (Lesq.) J.A. Wolfe (Alaska)	† Late Eocene and Miocene	3 (-5)	>2/3 to >>2/3	Yes	Yes (weak)	Yes	? Yes (weak)	No	Narrow triangular to rhombic	2.5-3:1	Narrow triangular to rhombic	Wolfe & Tanai 1980	PNA-E	Markedly similar to modern leaves of <i>P. genitryi</i>
<i>Platanus dissecta</i> Lesq.	† Late Eocene and Middle Miocene	3 (-5)	<1/2	Yes	Yes	Yes	Yes	Yes (weak)	Broad triangular to elliptic, rarely rhombic	0.6-2.2:1	Triangular	Becker 1969; Huegele et al. 2020	Intermediate	Similar to ANA clade and to <i>P. × hispanica</i>
<i>Platanus paucidentata</i> Dorf	† Pliocene	5	>2/3 to >>2/3	Very rare	Very rare	Very rare	No	No	Elliptic to narrow elliptic	1-2.75:1	Elliptic to narrow elliptic	Dorf 1930	PNA-E	Similar to modern leaves of <i>P. racemosa</i> and <i>P. wrightii</i>
<i>Platanus orientalis</i> L.	Extant	5	>1/2 to >>2/3	Rare	No	No	No	Yes	Triangular, oblong to rhombic	2-6:1	Triangular, oblong to rhombic	This study	PNA-E	-
<i>Platanus genitryi</i> Nixon & J.M. Poole	Extant	5	≥2/3 to 3/4 (to 4/5)	Yes	No	Yes	No	Yes (weak)	Narrow triangular to rhombic	2-4:1	Narrow triangular (rarely) rhombic	This study; Denk et al. 2012	PNA-E	-
<i>Platanus racemosa</i> Nutt.	Extant	5	>1/2	Rare	No	Rare	No	No	(Narrow) triangular to oblong	1 to >3:1	Triangular	This study	PNA-E	-
<i>Platanus wrightii</i> S. Watson	Extant	5	≥2/3 to 3/4	Yes	Yes	Rare	No	No	Narrow triangular, oblong, narrow elliptic	2-4:1	Triangular	This study	PNA-E	Commonly with entire margin

(continued)

TABLE 2. (Continued)

Taxon	Age	Leaf organization		Teeth				Lobe shape			Reference	Taxonomy (clade)	Remarks	
		No. lobes	Lobe depth ^a	Mucronate	Bristle-like	Fine triangular	Coarse triangular with bristle	Coarse, hooked without bristle	Central lobe	Central lobe L : W				Lateral lobes
<i>Platanus mexicana</i> Moric.	Extant	3	≤1/2 (rarely to 3/5)	Yes	Yes	Yes	No	No	Broad triangular	≤2:1	Broad triangular	This study	ANA	Typically without teeth, densely mucronate more common in vegetative shoots
<i>Platanus linderiana</i> M. Martens & Galeotti	Extant	3	≤1/2 (rarely to 3/5)	Yes	No	Yes	Sometimes (not typical)	No	Broad triangular; attenuate in tropical climate	≤2:1	Broad triangular	This study; Denk 2006; Denk et al. 2012	ANA	Typically without teeth but regional differences (populations from Chiapas frequently have teeth)
<i>Platanus rzedowskii</i> Nixon & J.M. Poole	Extant	5	≤1/2	Rare	Yes	No	Sometimes (not typical)	No	Broad triangular	≤2:1	Broad triangular	Nixon & Poole 2003; Denk 2006; Huegele et al. 2020	ANA	Typically without teeth
<i>Platanus palmeri</i> (Kuntze) ined.	Extant	5	≤1/2 (rarely to 3/5)	Rare	Yes	No	Yes	No	Broad triangular	<1:1	Broad triangular	This study; Nixon & Poole 2003	ANA	Typically without teeth
<i>Platanus occidentalis</i> L.	Extant	5	≤1/3	Yes	Yes	No	Yes	No	Broad triangular	≤1:1	Broad triangular	This study	ANA	Typically with coarse triangular teeth with distinct bristle-like extensions

All modern taxa can also have entire margined lobes. **Bold italic**, possible synapomorphy of Pacific North American–European (PNA-E) clade; **bold**, possible synapomorphy of Atlantic North American (ANA) clade. Underlined, possible symplesiomorphy, ancestral character state in subgenus *Platanus*. Mucronate teeth and triangular teeth with bristles commonly occur in Paleocene and Late Cretaceous *Platanus* and extinct Platanaceae (e.g. Maslova 2003).

[†]Fossil-species; L, length; W, width.

^aLobe length/total lamina length.

modern *P. rzedowskii* and *P. mexicana*. According to Kovar-Eder *et al.* (1994), the oldest unambiguous records of the fossil-species *P. leucophylla*, ANA clade, in western Eurasia are from Middle Miocene strata of Ukraine, suggesting that this fossil-species occurred from Iceland to Eastern Europe during the Middle Miocene. In contrast, no leaf traits matching the PNA-E clade have so far been discovered from the Atlantic and western European regions (Fig. 13B).

Summarizing the biogeographic history of the PNA-E and ANA clades (Fig. 13), it appears that an initial circumpolar distribution of the ANA clade and possibly of the extinct *P. (Glandulosa)* may have prevented the

expansion of the PNA-E clade from its initial range in western North America. During the late Palaeogene, the Beringian link of the ANA clade broke up and the PNA-E clade could migrate through the Bering land bridge and Central Asia to Europe. This scenario would be in good agreement with the dated phylogeny of Feng *et al.* (2005; Fig. 1).

CONCLUSION

We addressed the biogeographic origin of the iconic Oriental plane tree, *Platanus orientalis* and the PNA-E clade.

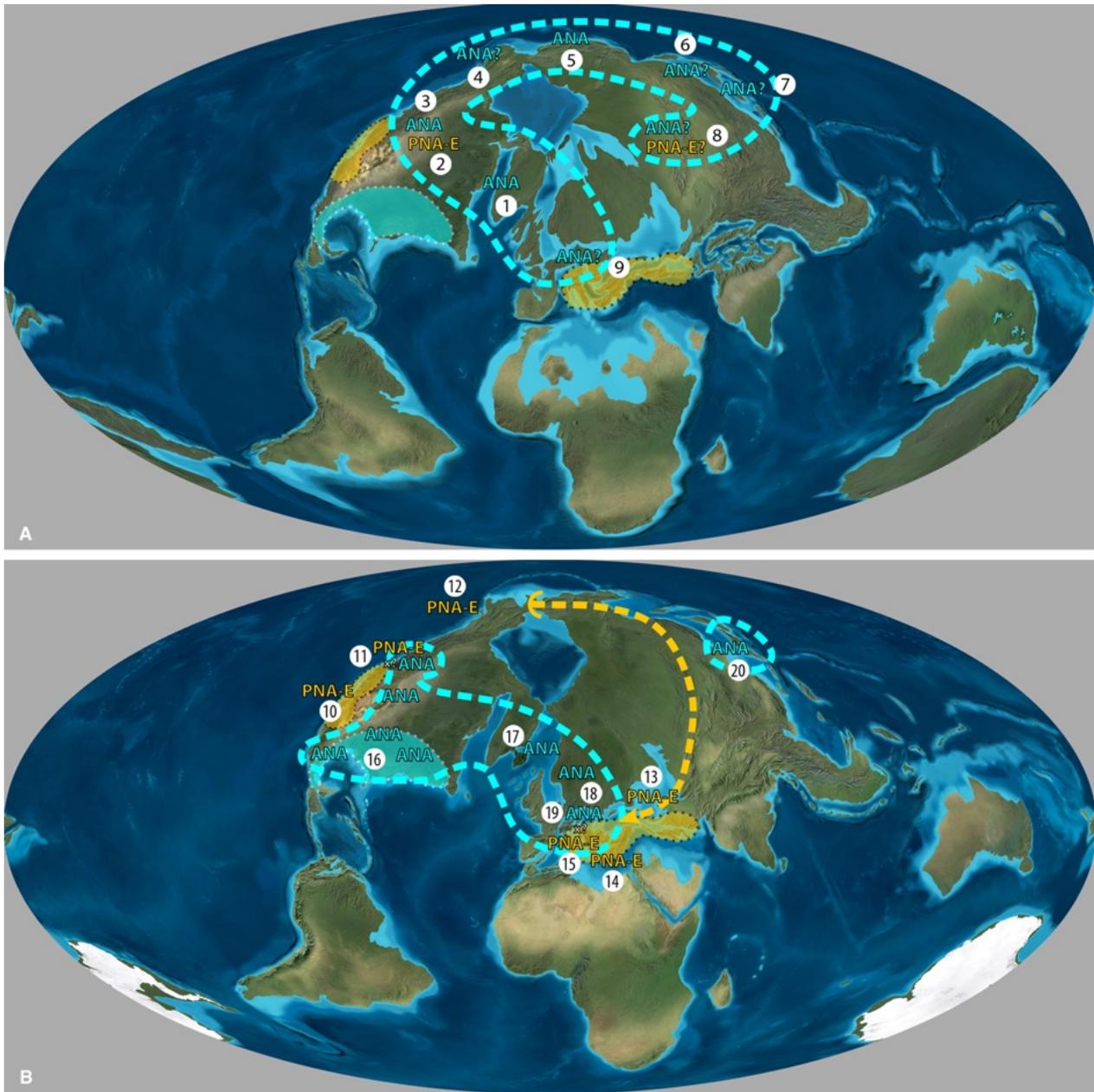


FIG. 13. Possible biogeographic and evolutionary origin of *Platanus orientalis*. Maps show the distribution of members of the Pacific North American–European (PNA-E) and Atlantic North American (ANA) clades of *Platanus* in the Palaeogene (40 Ma) (A) and Neogene (20 Ma) (B). A, two Palaeogene occurrences (2, 8) are attributable to either the PNA-E or PNA-E × ANA clade; ANA? indicates the occurrence of fossil-species representing either the ANA clade or extinct Platanaceae. B, in the Neogene, leaf occurrences with PNA-E-typical traits occur in northwestern North America and western Eurasia; note the isolated occurrences of ANA clade members in east Asia; there is evidence of ancient hybridization (×?) between ANA and PNA-E in western North America and a secondary contact between the heterozygous eastern lineage and *P. leucophylla* (ANA clade) in western Eurasia; yellow dashed arrow indicates westward-migrating members of the PNA-E clade with a tenuous connection to the North Pacific area. On both maps, the cyan-shaded area indicates the modern distribution of the ANA clade; the modern distribution of PNA-E members is shaded dark yellow. Cyan dashed outlines indicate the potentially near-circumpolar distribution of Palaeogene ANA clade members. Sources: 1, Heer (1883a, 1883b); 2, Becker (1969); 3, Meyer & Manchester (1997); 4, Hollick (1936), Mathewes *et al.* (2023); 5, Maslova (1997), Maslova & Fotyanova (1990, 1991); 6, Manchester *et al.* (2005), Pavlyutkin *et al.* (2014, 2020); 7, Oishi & Huzioka (1943); 8, Iljinskaya (1986); 9, Saporta & Marion (1878, 1885), Laurent (1912), Andreánszky (1965), Kvaček & Walther (2004), Sachse (2022); 10, Dorf (1930); 11, Lesquereux (1878, 1883), Huegele *et al.* (2020), Greenwood *et al.* (2020); 12, Wolfe & Tanai (1980); 13, Kolakovsky (1955, 1964), Kutuzkina (1958, 1964); 14, this study; 15, Gaudin & Strozzi (1864), Paolucci (1896); 16, MacGinitie (1962), Velasco-de León *et al.* (2010), McNair *et al.* (2019), Stults & Axsmith (2015); 17, Grímsson *et al.* (2007); 18, Iljinskaya (1964); 19, Göppert (1855); 20, Suzuki (1958), Tanai & Suzuki (1963). Further occurrences corresponding to the numbers used on the maps are detailed in Table S1. Palaeomaps are Mollweide views projected through the prime meridian and tilted 45°N (used with permission ©2016 Colorado Plateau Geosystems Inc.)

Previous molecular studies identified two major clades within *P. (Platanus)*, one of which (the PNA-E clade) comprises three western or Pacific North American taxa plus the Mediterranean–Near East *P. orientalis*. However, molecular phylogenetic studies were inconclusive about the origin of the disjunction in the PNA-E clade. We studied rich leaf fossil material from Miocene to Pleistocene deposits of Greece with distinct PNA-E morphologies and traced the presence of morphological traits characteristic of the PNA-E clade in the fossil record of North America and Eurasia. PNA-E clade leaf traits were present in late Eocene and Oligo-Miocene strata of western North America including Alaska, and in early Oligocene strata of Central Asia, prior to the appearance of leaf fossils with PNA-E traits in western Eurasia (collectively called *P. academiae*). In addition, western North American and possibly Central Asian leaf fossils with mixed PNA-E and ANA clade traits may indicate ancient hybridization with the ANA clade lineage as previously documented in molecular phylogenetic studies. During the Palaeogene, a circumpolar distribution of the ANA clade and *P. (Glandulosa)* may have prevented a range expansion of the PNA-E clade. Range reduction of the ANA clade during the late Palaeogene opened up the Beringian corridor for the PNA-E clade. Hence, we suggest that the modern western North American–Mediterranean disjunction in the PNA-E clade of *P. (Platanus)* is the result of a northern Pacific (Bering land bridge) to Central Asian migration into western Eurasia. This pattern does not conform to a typical Madrean–Tethyan disjunction (Axelrod 1975) as previously suggested for this group of Mediterranean-climate-type plane trees. We recognize a single fossil-species of the PNA-E clade, *P. academiae*, in

western Eurasian Middle Miocene to Pleistocene strata. We note a clear trend in leaf evolution from more general PNA-E leaf morphologies with three lobes in Miocene strata to modern *P. orientalis* morphotypes in Pliocene–Pleistocene strata. Leaf morphotypes virtually identical to the modern *P. orientalis* are common in Pliocene and Pleistocene strata of the Peloponnese peninsula of southern Greece.

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Author contributions. **Conceptualization** D Danika (DD), T Denk (TD); **Data Curation** DD, TD, D Velitzelos (DV), Ove Johansson; **Formal Analysis** B Adroit (BA); **Funding Acquisition** DD, TD; **Investigation** DD, TD, BA; **Methodology** DD, TD; **Project Administration** TD; **Resources** TD, DV; **Supervision** TD; **Visualization** DD, TD; **Writing – Original Draft Preparation** DD, TD; **Writing – Review & Editing** DD, TD, BA, DV.

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1002/spp2.1576>):

Fig. S1. Insect damage on fossil leaf specimens of *Platanus academiae* and *P. leucophylla*.

Figs S2–S4. Late Eocene *Platanus* of Montana, USA. Original specimens also figured by Becker (1969). Images courtesy of the Peabody Museum, Division of Paleobotany, Yale University; <https://peabody.yale.edu>.

Figs S5–S7. Early Oligocene *Platanus* of Kazakhstan and possible phylogenetic relationships. Specimens originally figured in Iljinskaya (1986). Specimens stored at Paleobotanical Laboratory, Komarov Botanical Garden, St Petersburg, Russia (BIN).

Table S1. A global survey of fossil-species assigned to *Platanus* ($n = 159$ spp.; Table S1 ALL) and the geographic and stratigraphic distribution of ANA and PNA-E clade leaf traits. 50 fossil-species from Cenozoic strata in the northern hemisphere are considered to belong to *Platanus* (Table S1 CENOZOIC). According to their age and geography, map numbers are assigned corresponding to those used in Figure 13.

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