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Abstract

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The recently described *Platanus mexicana* var. *interior* of Nixon & J. M. Poole is critically evaluated. We show that the type of the name *P. mexicana,* collected by Berlandier in 1827, is virtually identical to morphotypes typically found within the range of *P. mexicana* var. *interior*. The reason for the taxonomic confusion is twofold: the variability of the abaxial leaf tomentum across the distribution range of *P. mexicana* and uncertainties concerning the type locality of *P. mexicana*. Field observations at the type locality of *P. mexicana* var. *interior* and throughout the range of *P. mexicana* show that the morphotype represented by the holotype is rarely found in the main distribution range of *P. mexicana* in Veracruz, Puebla, Oaxaca and Chiapas. Our findings are corroborated by the historical evidence: in his "Journey to Mexico", Berlandier, travelling from Tampico to Mexico City, did not reach the distribution area of *P. mexicana* var. *mexicana* in the sense of Nixon & J. M. Poole. This suggests that the holotype of *P. mexicana* and *P. mexicana* var. *interior* originate from the same area (northern Querétaro, northern Hidalgo) and hence, that the latter name is superfluous. The relevance of infraspecific taxa within *P. mexicana* and their delimitation against closely related taxa to the north is discussed in the light of morphological and recently published genetic evidence from original stands.

Additional key words: *Platanus mexicana* var. *interior, Platanus lindeniana,* interpopulation variability, intrapopulation variability, species boundaries, hybrid zone

"After a sojourn of four months on the Gulf Coast of Mexico, seeing the pestilential season rapidly approaching, I decided to leave for the interior." (Jean-Louis Berlandier, Journey to Mexico during the years 1826 to 1834, chapter 4: The route from Tampico de Tamaulipas to Mexico City, cited after Ohlendorf & al. 1980).

Introduction

In the most recent taxonomic account on *Platanus,* Nixon & Poole (2003: 126) proposed a new variety of *P. mexicana* Moric., *P. mexicana* var. *interior* Nixon & J. M. Poole, which shows a "distinctive suite of character-states within the general pattern of *P. mexicana*", and its "varietal epithet was chosen to reflect the distribution … in the interior highlands of Mexico." (Nixon & Poole 2003: 126). The holotype of *P. mexicana* is a specimen collected by Berlandier, probably in 1827, kept in the herbarium of the Conservatoire et Jardin botaniques de la Ville de Genève (G), unnumbered and without precise collection data given (Fig. 1A). The locality is indicated as "Circa [or Cerca?] Mexico". A number of specimens from the same gathering are kept in the herbarium of the Muséum National d'Histoire Naturelle, Paris (P). Moricand (1837: 39–40) described Berlandier's specimen as having trilobed leaves that are densely whitish tomentose on the abaxial leaf surface. The abaxial tomentum is persistent according to his description: "… à la face inférieure qui est couverte d'un duvet blanchâtre, épais, qui ne parâit point caduc." The second important character for the taxonomic assignment of Berlandier's speci-

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men in the light of Nixon & Poole's systematic treatment is the number of capitula of the female infructescence, which is two according to Moricand's description "Les chatons femelles … au nombre de deux, sessile et distants sur un pédoncule glabre …" Moricand (1837: 40).

Nixon & Poole (2003: 126) noted a significant difference between the central Mexican ("interior") and other specimens of *P. mexicana* in the herbaria: "The typical variety [var. *mexicana*] differs from the following variety [var. *interior*] by its denser and more persistent abaxial leaf vestiture, its narrower leaves often with narrower lobes, and in a tendency to have three or more capitula per carpellate inflorescence as opposed to 1 to 3" and "This variety [var. *interior*] differs from var. *mexicana* … by generally long achenes." The number of capitula in the original description of the species is, however, explicitly stated as two (Moricand 1837: 40). Following Nixon & Poole's (2003) descriptions of the two varieties, it is noteworthy that except for the density and persistence of the abaxial indumentum, Moricand's holotype would match var. *interior* rather than var. *mexicana*. Nixon & Poole (2003), not considering the low number of capitula or the colour of the indumentum as characteristic features of the holotype of *P. mexicana,* recognised the central Mexican specimens with less persistent and less dense indumentum and few capitula as the new *P. mexicana* var. *interior*. For the holotype, they chose a specimen collected by Rzedowski from El Trapiche, located in the central Mexican federal state of Querétaro de Arteaga (abbreviated Querétaro in the following).

Taxonomic concepts and morphological trends in *Platanus* are strongly linked to the provenance of the specimens (Nixon & Poole 2003; see quotations above). Nixon & Poole's newly recognised variety *interior* occurs at the northernmost range of *P. mexicana* south of the range of *P. rzedowskii* Nixon & J. M. Poole (Nixon & Poole 2003: fig. 3). According to Nixon & Poole (2003), both varieties of *P. mexicana* do not occur sympatrically with any other taxon of *Platanus*.

Importantly, Berlandier and/or Moricand did not specify the exact locality of the holotype (Fig. 1A–C). The Frenchman Berlandier travelled to Mexico in 1826 to join an expedition that led from Mexico City towards Texas (1827–28), at that time part of Mexico. He left a journal manuscript, "Voyage au Mexique par Louis Berlandier pendant les années 1826 à 1834", kept in the Library of Congress, which acquired it (among other things) from his wife after his death in 1851 (Muller in Ohlendorf & al. 1980). The manuscript has been made available and translated into English by Ohlendorf & al. (1980). According to this report, Berlandier started collecting plants in December 1826 immediately after his arrival in Pánuco, near Tampico, in the uppermost north of Veracruz. On 3 May 1827, his expedition left Tampico for Mexico City crossing the Huasteca, a region comprising lowlands and mountainous areas with ample precipitation during the entire year; basically the lands adjacent to the Río Panuco and its tributaries. It is notable that the closest occurrence of *Platanus mexicana* var. *mexicana* according to Nixon & Poole (2003; San Bartolo Tutotepec, easternmost Hidalgo), which also represents the northernmost occurrence of this variety, is at least 50–55 km (airline distance) southeast of Berlandier's route and separated by a major mountain range (≥ 2100 m) from the populations Berlandier must have passed (Fig. S1, see Appendix). In contrast, Berlandier's route crossed the range of *P. mexicana* var. *interior* according to Nixon & Poole (2003; Tianguistengo and Molango de Escamilla, northern Hidalgo). Thus, the question arises, which populations represent the typical *P. mexicana*.

If Berlandier's specimen stems from an interior population, Nixon & Poole's variety *interior* would be superfluous. Furthermore, *Platanus lindeniana* M. Mertens & Galeotti (Fig. 2) used by local taxonomists for the *Platanus* populations to the south, would then need to be recognised as a variety of *P. mexicana,* if two varieties should be distinguished. In order to address this question, we traced Berlandier's route and specimens and carried out a comprehensive morphological analysis of newly collected material from the type localities of *P. mexicana* var. *interior, P. lindeniana* and *P. chiapensis* Standl. In combination with recently published molecular analyses, character combinations of the interior and the southern and southeastern populations of *P. mexicana* and its northern neighbours, *P. rzedowskii* and *P. occidentalis* var. *palmeri* (Kuntze) Geerinck are discussed. An emended diagnosis for *P. mexicana* is provided.

Material and methods

The material investigated for the present study was collected in May and June 2004 by the first author and is stored in the herbarium of the Swedish Museum of Natural History (S). Parts of the material were used for comprehensive molecular analyses (Grimm & Denk 2008, 2010). In addition, specimens from the herbarium of the Universidad Nacional Autónoma de México (MEXU) were used to estimate the geographic range of different morphotypes (species, varieties). Type and other herbarium material deposited in the herbaria of the Conservatoire et Jardin botaniques de la Ville de Genève (G) and the Biology Department of Ghent University (GENT) were studied using high resolution digital images provided by these herbaria; type material in the herbarium of the Muséum National d'Histoire Naturelle, Paris (P) was studied during a visit to this institution.

The morphological terminology followed Hickey (1973). In addition, general descriptive terms were used in some cases; e.g. kite-shaped for leaf shape.

For the present account, the following morphological characters were screened: width-length ratio of lamina, length of petiole, leaf shape (for terminology used see

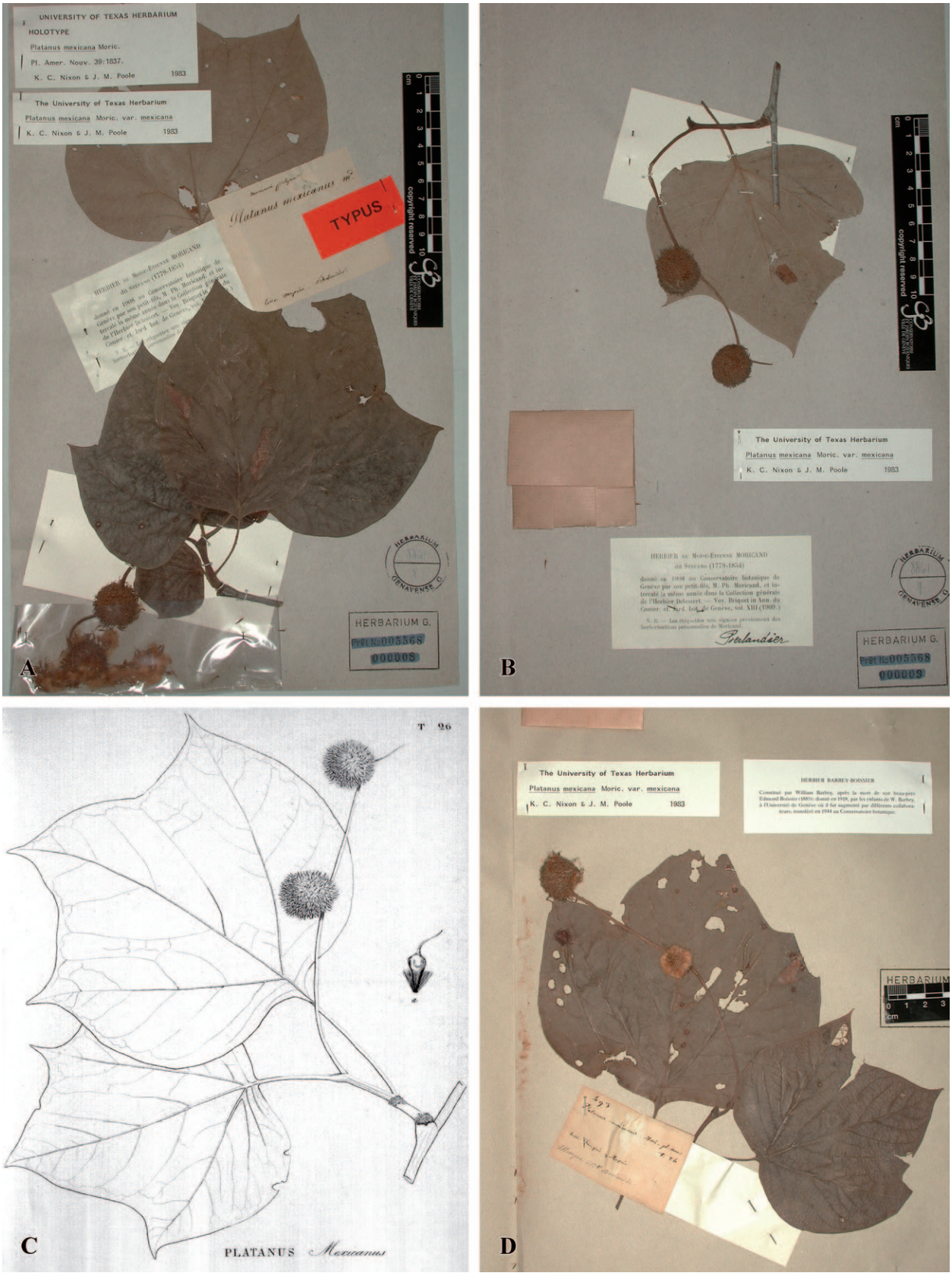

Fig. 1. A–B: holoype of *Platanus mexicana* Moric.; *Berlandier s.n.,* "Circa [cerca?] Mexico", at G, sheets 1/2 and 2/2; C: *P. mexicana,* original drawing in Moricand (1837: t. 26); D: specimen collected between Tampico and Mexico City ("entre Tampico y Mexico"); *Berlandier 493* at G.

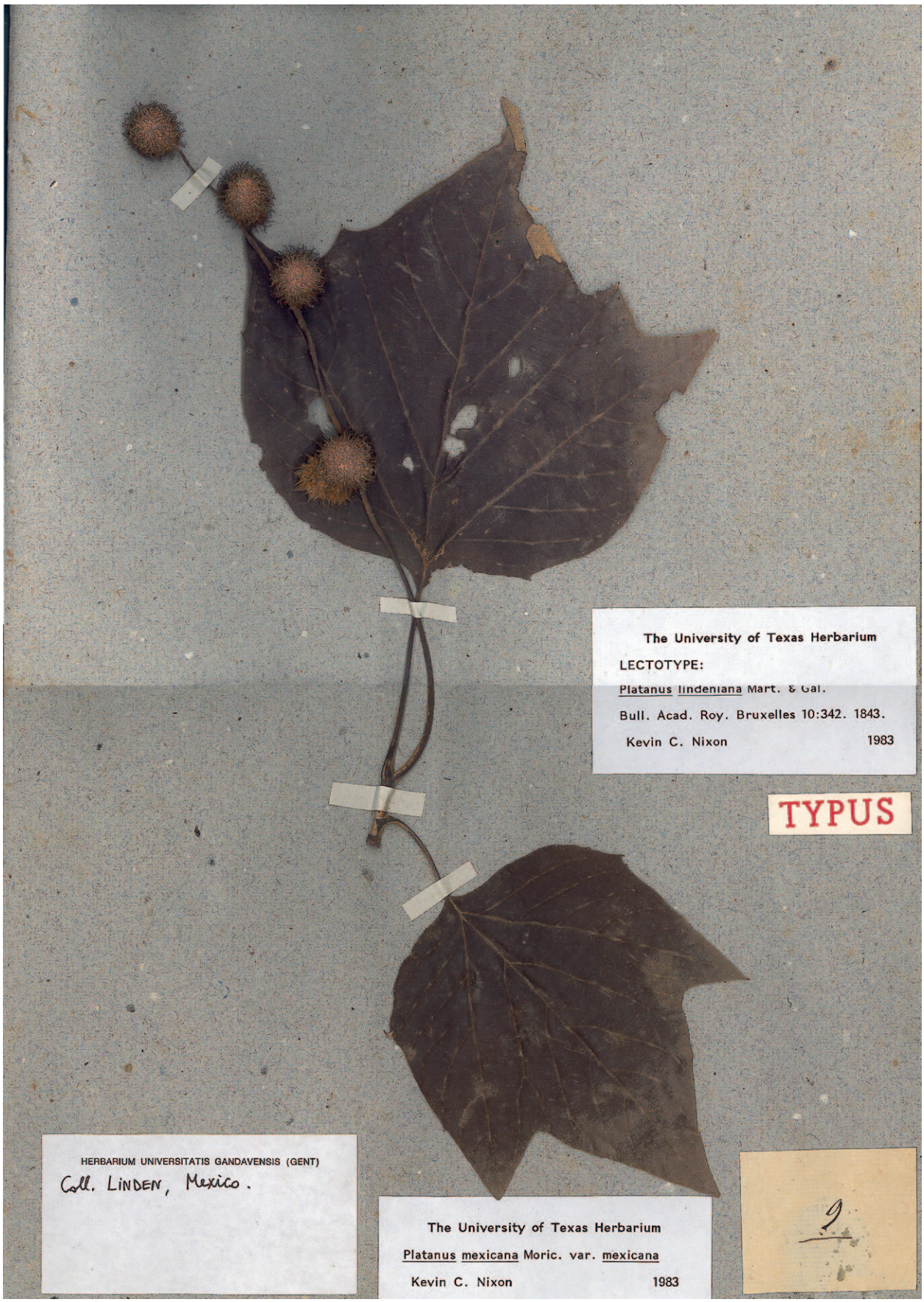

Fig. 2. Lectotype of *Platanus lindeniana* M. Martens & Galeotti – near Xalapa, Veracruz ("près de Jalapa"), *Linden 9* at GENT.

Table S1, see supplements to the online edition), number of lobes (0–5), lobe shape (elliptic, narrow pentagonal, triangular, triangular-oblong), shape of leaf base (acute, concave, cordate, cuneate, obtuse, peltate, truncate, and various intermediary types), shape of lobe apex (leaf apex if leaf unlobed; acute, acuminate, attenuate, round), type of leaf margin (entire, dentate, few teeth, glandular bristles, lobed), tooth type(s) (coarse, glandular, coarse and glandular, triangular), first and higher order venation (actinodromous, palinactinodromous, pinnate; brochidodromous, semicraspedodromous, craspedodromous, and intermediate forms), leaf pubescence (glabrous, trichomes along veins, glabrescent, trichomes easily removable, persistent/not whitish, white-tomentose), length of infructescence axis, heads (capitula) sessile or stalked (length of stalk), diameter and number of heads, length and shape of apex of achenes (acute, knobby, roundish; ± hairy).

Results

The morphological variability of *Platanus mexicana* was assessed based on detailed field observations and morphological analyses of 47 individuals of selected populations within the range of *P. mexicana* var. *mexicana* according to Nixon & Poole (2003) plus 19 individuals within the range of *P. mexicana* var. *interior,* the latter including 13 individuals from the type locality of *P. mexicana* var. *interior* (Table S1, S2, see supplements to the online edition). In order to document leaf variability of individual trees, leaves of one to several twigs were measured (in total 1177 leaves). For comparison and discussion, morphological data of ten individuals of *P. rzedowskii* and 12 collections of *P. occidentalis* var. *palmeri* (provisionally recognised as species *P. palmeri;* see Grimm & Denk 2010) were included (Table S1, S2, see supplements to the online edition).

Specimens collected in Querétaro — Three populations in the state of Querétaro, along the valley of the Arroyo Jalpan, were visited; one located between El Llano and San Pedro, a second near Ahuacatlán and the population of the holotype of *Platanus mexicana* var. *interior* between Jalpan and El Trapiche (Fig. 5–6; Fig. S1, see Appendix). Fruiting twigs of the collected specimens have one to three capitula (Fig. 3). At the two locations west of the type locality, the individuals predominantly show nearly glabrous or glabrescent leaves (Fig. 4, 6C–D) as expected for *P. mexicana* var. *interior* and leaves with a persistent (greenish), ± loosely dense tomentum (Fig. 6A). At the type locality of var. *interior,* a significant proportion of specimens have leaves with a persistent, very dense white tomentum (Fig. 4, 5A–B, 7A–B). This is considered a typical feature of *P. mexicana* var. *mexicana* and is also found on the holotype and further material collected by Berlandier during the same trip and kept in G and P (Fig. 1). The three populations in Querétaro are distinct from the remainder of *P. mexicana* by their low number of capitula on the female infructescences (Fig. 3), whereas the abaxial leaf indumentum is highly variable (Fig. 5, 6, 7A–C). Notably, numerous individuals can be found at the type locality of *P. mexicana* var. *interior* that exactly match the holotype of the name *P. mexicana:* showing two capitula and wide-lobed leaves with a dense, persistent abaxial indumentum, literally a "duvet blanchâtre" as described in the original publication (Fig. 5A, 6A). Thus, a number of specimens from the type locality of *P. mexicana* var. *interior* exactly fit Moricand's description of *P. mexicana.*

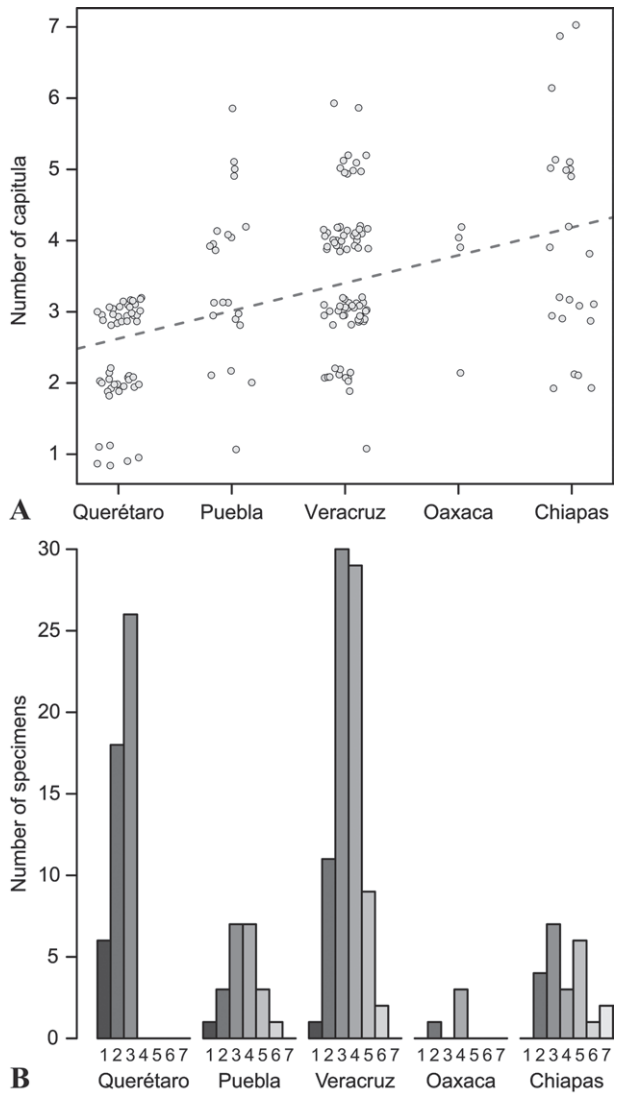

Fig. 3. Number of capitula per fertile axis from major geographic provenances. – Populations of Querétaro, i.e. *Platanus mexicana* var. *interior* according to Nixon & Poole (2003), differ from other *P. mexicana* in their tendency to reduced numbers of capitula. Data include specimens from our own field collection and material housed in MEXU. Note that the holotype of *P. mexicana* has two capitula.

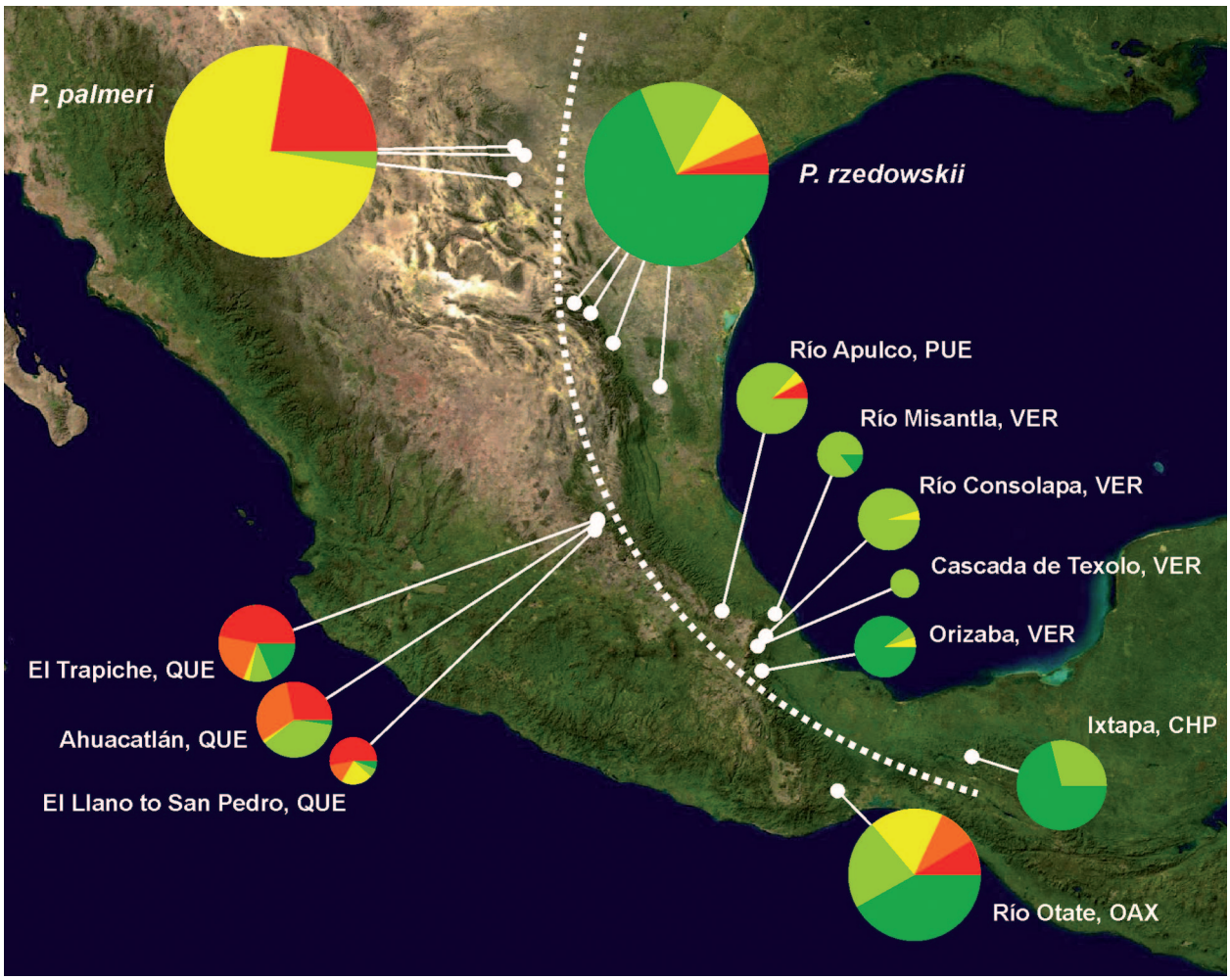

Fig. 4. Geographic plot of abaxial leaf indumentum types in *Platanus mexicana* (newly collected material). – Leaves with persistent indumentum: dark green = abaxial leaf surface whitish tomentose as in the holotype of *P. mexicana* ("duvet blanchâtre"); light green = greenish or brownish indumentum of variable density. Leaf with non-persistent indumentum: yellow = indumentum of variable density easily removable; orange = glabrescent leaves; red = (nearly) glabrous leaves. The situation in *P. palmeri* (always glabrous or glabrescent) and *P. rzedwoskii* (indumentum always persistent according to Nixon & Poole 2003) is shown for comparison.

Specimens collected in Puebla — Specimens of *Platanus mexicana* were collected in Puebla along the Río Apulco, between Apulco and Atzalán (in total 17 individuals included in the survey). Six were fruiting, one fertile axis was found with only two capitula; all other showed three to five capitula (Fig. 3). Most leaves show a persistent abaxial indumentum, typically brownish in colour (Fig. 7D, 8A); six out of 75 recorded leaves were glabrous (Fig. 4). The leaves of the branch with a 2-capitulate infructescence axis show a well-developed and persistent abaxial tomentum, which is brownish and not whitish tomentose as in Berlandier's specimens. In addition, leaves are kite-shaped and dentate as in the type of *P. lindeniana* from Veracruz. From the same tree, twigs with 4 and 5 capitula per infructescence axis were collected (Table S1, see supplements to the online edition).

Specimens of other provenances — Populations of *Platanus mexicana* from various stands in Veracruz (collected along Río Consolapa, between Coatepec to Jalapa; Río Misantla, Yecuatla to Misantla; Cascada de Texolo, Xico; Orizaba) consistently show a relatively dense abaxial tomentum (Fig. 7E–I, 8B–D); it could easily be removed in only six leaves out of 233 analysed (Fig. 4; Table S1, see supplements to the online edition). As in the Puebla population, the few 2-capitulate twigs have leaves that are very similar to the type of *P. lindeniana*. Only in Orizaba, the southernmost population visited, many leaves were creamish-whitish below (Fig. 7E); the remainder shows a type of indumentum as found in the type of *P. lindeniana*.

All individuals from Chiapas (Ixtapa to Zinacatán) have persistently tomentose leaves (Fig. 7L, 9C–D). The number of capitula ranges from 2 to 7, but 2-capitulate infructescence axes are extremely rare among the specimens investigated (Tables S1, S2, see supplements to the online edition). Samples from the isolated population visited at the Río Otate, southern Oaxaca (Fig. S1, see Appendix), do not include fruiting material. During the

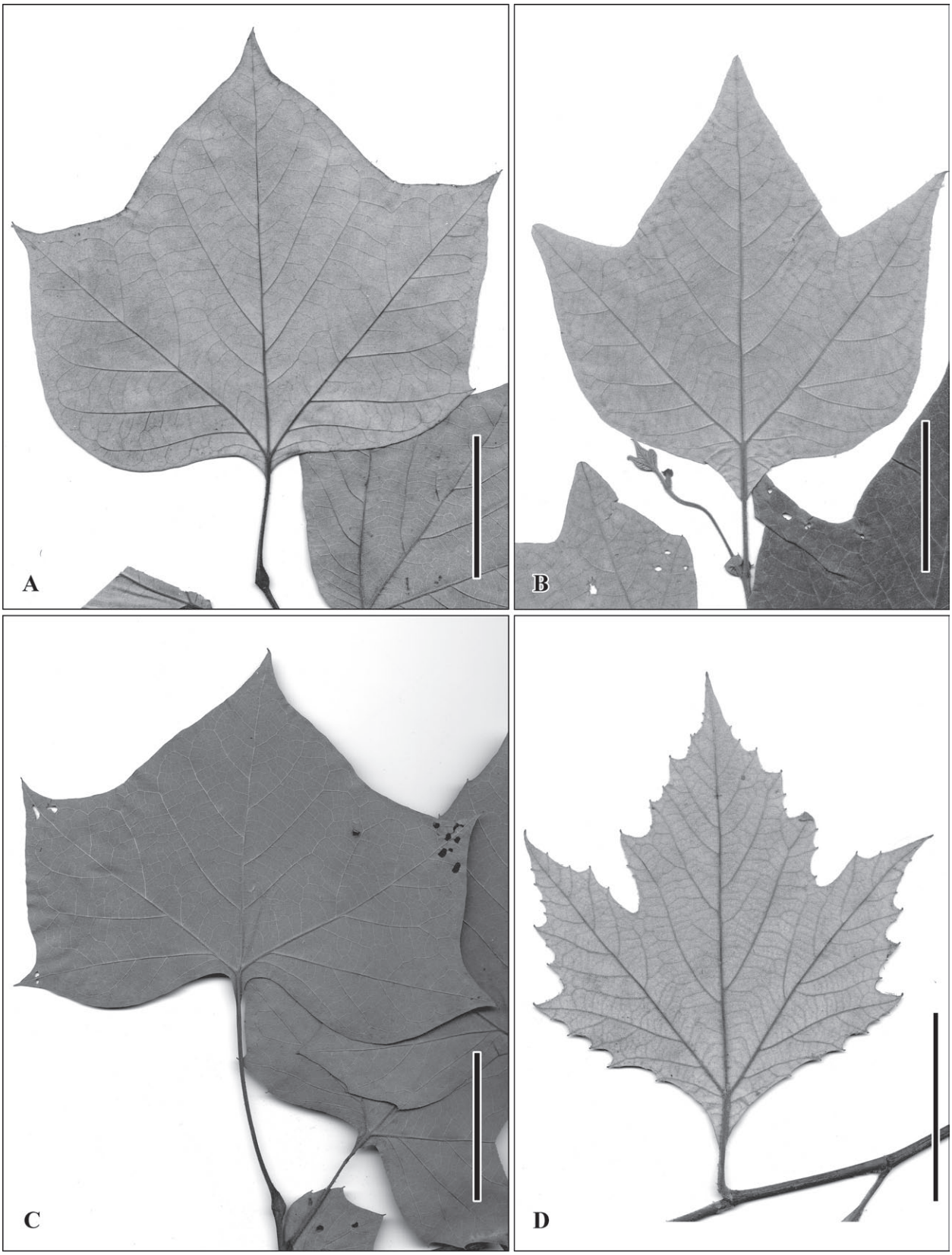

Fig. 5. Leaf variability in *Platanus mexicana,* Jalpan to El Trapiche, Querétaro; type locality of *P. mexicana* var. *interior* – A: leaf whitish tomentose underneath; morphotype virtually identical to the holotype of *P. mexicana, Denk 2004083,* S; B: leaf whitish tomentose underneath, *Denk 2004077,* S; C: leaf glabrous underneath; morphotype very similar to *P. palmeri, Denk 2004081,* S; D: distinctly dentate leaf, whitish pubescent underneath, *Denk 2004074-1,* S. – Scale bar = 5 cm.

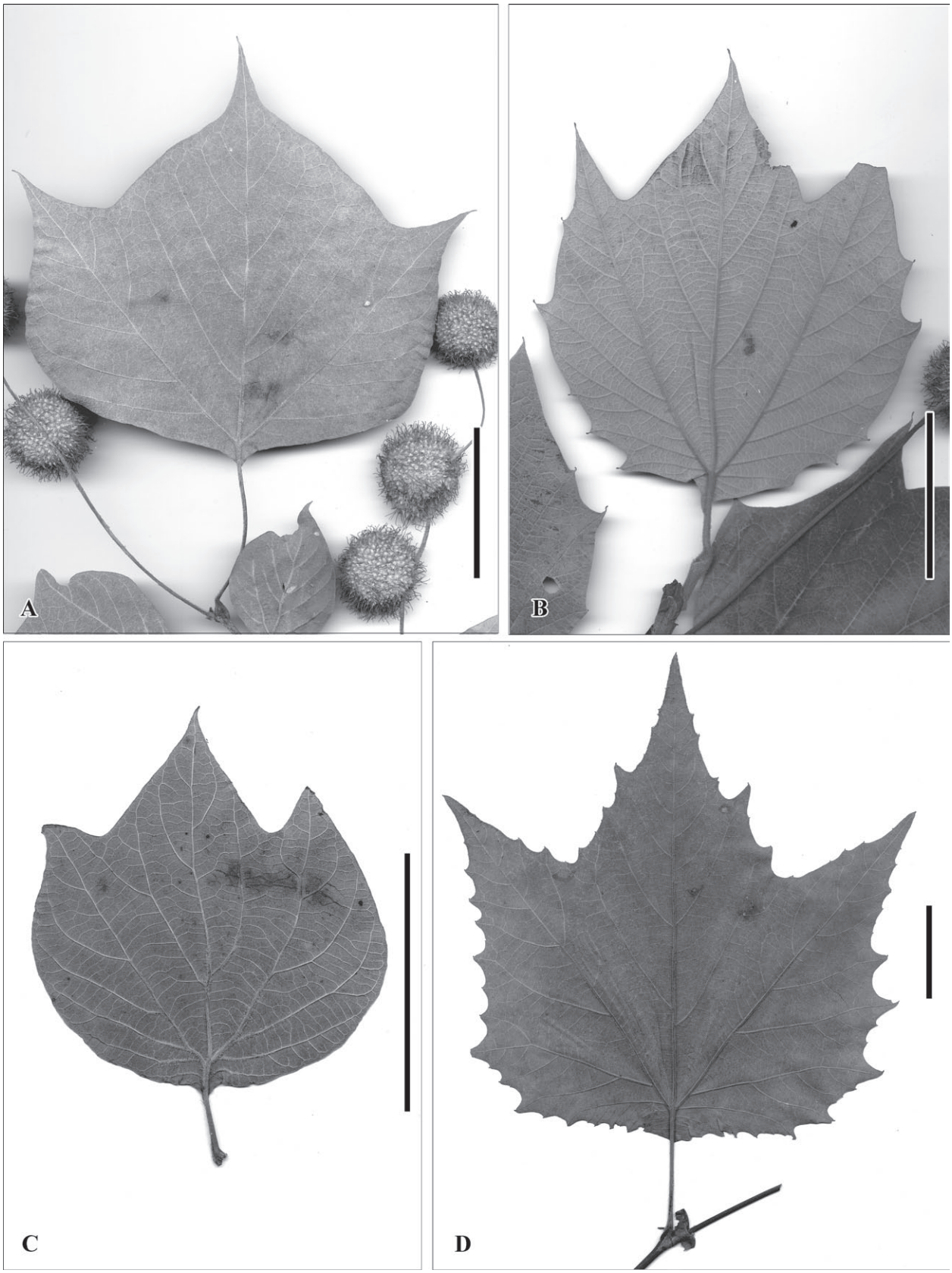

Fig. 6. Leaf variability in *Platanus mexicana,* Ahuacatlán to El Llano, Querétaro, west of the type locality of *P. mexicana* var. *interior* – A: leaf light greenish pubescent underneath, *Denk 2004073-5,* S; B: leaf brownish pubescent underneath, *Denk 2004072-3,* S; C: leaf with non-persistent indumentum underneath, *Denk 2004069-5,* S; D: distinctly dentate leaf, from the same tree as C, *Denk 2004069-2,* S. – Scale bars = 5 cm.

Fig. 7. Indumentum types in *Platanus mexicana* (A–L) and *P. rzedowskii* (M–O) – A–C: most common types in Querétaro, whitish tomentose and light greenish: Jalpan, *Denk 2004074,* S (A); El Trapiche, *Denk 2004083,* S (B); El Trapiche, *Denk 2004078-1,* S (C); D: brownish, densely tomentose type frequently found along the Río Apulco, Puebla, *Denk 2004026-5,* S; E–I: variation of indumentum types found in Veracruz: Texolo cascades, brownish tomentum similar to D, *Denk 2004002,* S (E): Coatepec, near Xalapa, *Denk 2004008-2,* S (F); Misantla, *Denk 2004014-6,* S (G); leaf from the same tree as G, but with light greenish indumentum, *Denk 2004014-1,* S (H); Orizaba; creamish brown dense tomentum, *Denk 2004025,* S (I); J–K: Río Otate, Oaxaca, whitish greenish light indumentum co-occurring with glabrescent leaves: *Denk 2004032-2,* S (J), *Denk 2004032-3,* S (K, same tree as J); L: Zinacantán to Ixtapa, Chiapas; withish tomentose; type locality of *P. chiapensis, Denk 2004039-4,* S; M–O: indumentum types of *P. rzedowskii,* ranging from densely whitish tomentose (M, N) to sparsely green and glabrescent (O): Nuevo Léon, El Ebanito to Las Crucitas, *Denk 2004097-3,* S (M), *Denk 2004097-2,* S (N), *Denk 2004094-4,* S (O). – Scale bar = 4 mm; all images are of the same scale.

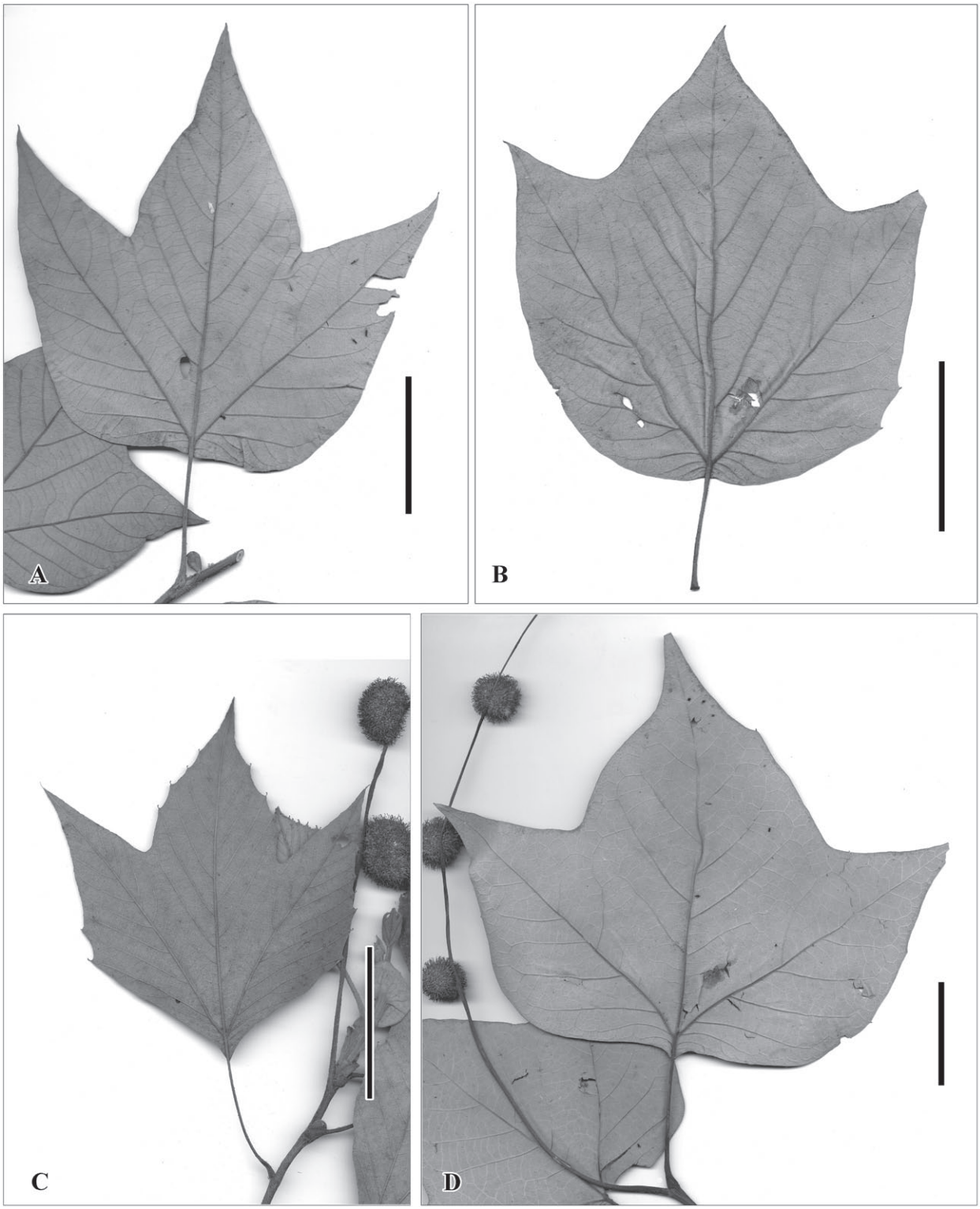

Fig. 8. Leaf variability in populations referred to as *Platanus mexicana* var. *mexicana* by Nixon & Poole (2003) and *P. lindeniana* by Standley (1922); Puebla (A), Veracruz (B–D) – A: leaf with brownish tomentum; Río Apulco, *Denk 2004026-1,* S; B: leaf with light brownish tomentum; Texolo cascades, *Denk 2004026-1,* S; C: leaf with greenish-greyish, less dense tomentum; Coatepec, near Xalapa, *Denk 2004004,* S; D: leaf with creamish-brownish tomentum; Río Misantla, *Denk 2004014-6,* S. – Scale bars = 5 cm.

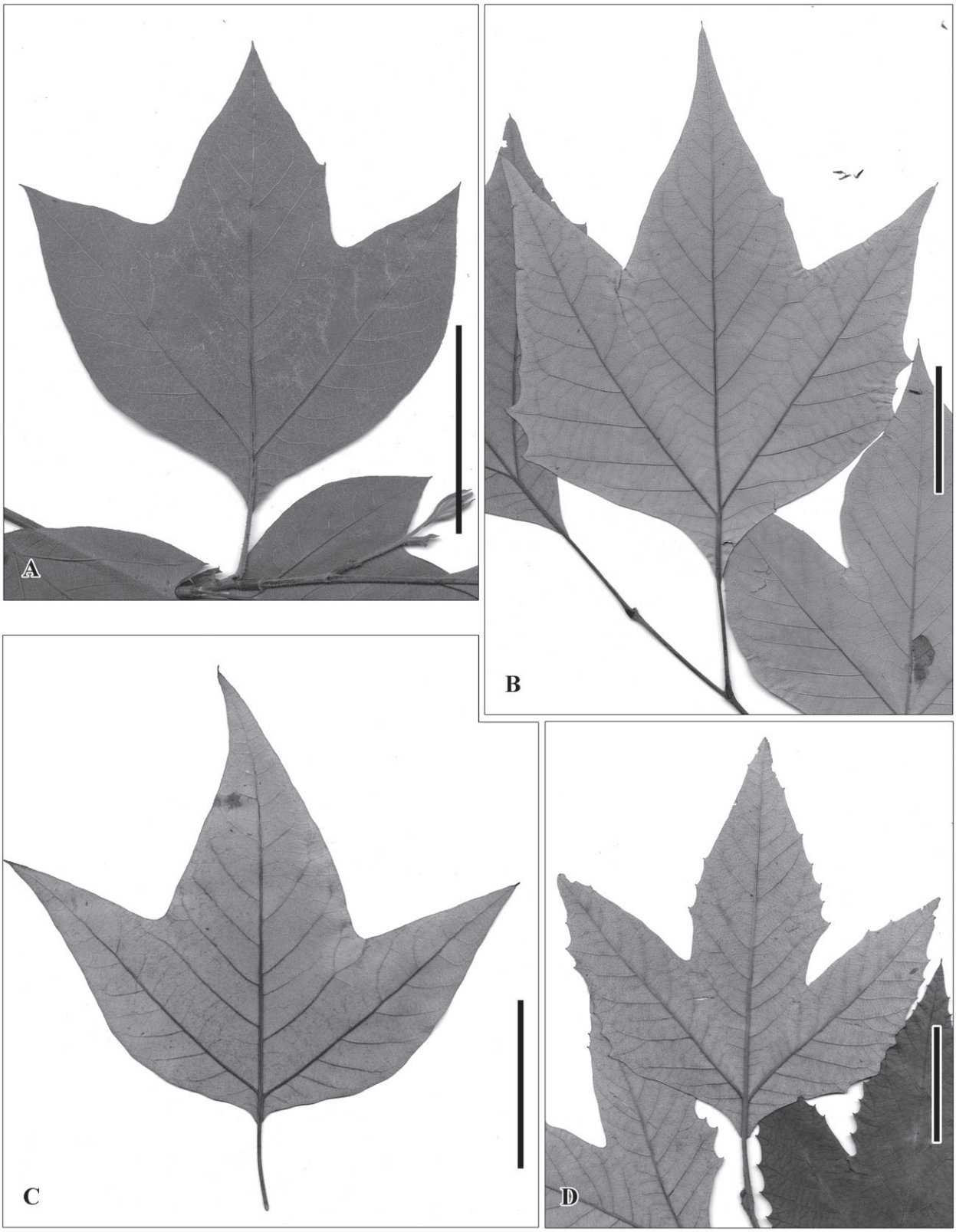

Fig. 9. Leaf variability in populations addressed as *Platanus mexicana* var. *mexicana* by Nixon & Poole (2003) – A–B: Río Otate, Oaxaca: leaf with non-persistent indumentum, glabrescent, *Denk 2004034-1,* S (A); leaf greenish-whitish underneath, *Denk 2004032-2,* S (B); C–D: Zinacantán (type locality of *P. chiapensis*) to Ixtapa, Chiapas; leaves whitish tomentose underneath, *Denk 2004042-4,* S (C), *Denk 2004040-1,* S (D). – Scale bars = 5 cm.

time of field work, none of the c. 300 individuals that compose this disjunct and restricted population along the Río Otate was fruiting. Also, mature fruits could not be found in the litter around the trees in this area. Among the specimens kept in MEXU, one from the Río Otate area has a 2-capitulate infructescence axis, while a number of specimens from farther north are 4-capitulate. The leaves (139 analysed) are predominantly persistently tomentose, but apparently this character is becoming increasingly unstable: in 25 leaves, the trichomes are easily removable, and another 25 leaves are glabrescent, including 12 leaves that are more or less glabrous (Fig. 7 J–K, 9A–B). This resembles the observation made for the population at El Trapiche, Quéretaro (cf. Fig. 6).

Specimens kept in MEXU — About 300 vouchers of Mexican species of *Platanus* are kept in MEXU. Many are labelled as *"P. mexicana"* and represent fruiting twigs. We included these data to be able to better estimate the distribution range of distinct morphotypes of *P. mexicana,* in particular with respect to regions that are close to the distribution area of *P. palmeri* and *P. rzedowskii,* and to obtain better census data on the number of capitula per infructescences. In total, 154 of the c. 300 vouchers represent *P. mexicana;* included are 25 vouchers from localities of the interior (federal states of San Luis Potosí, Querétaro, Guanajuato and Hidalgo). Those from Guanajuato (*Platanus* is only found in the northeast) are peculiar; the investigated specimens show characteristics of *P. palmeri, P. rzedowskii* or *P. mexicana*.

Discussion

Origin of the holotype of *Platanus mexicana,* a historical and geographic excurse

Noting the importance of the geographic setting for the definition of var. *interior* and var. *mexicana* in Nixon & Poole (2003), it is astonishing that these authors did not try to trace the provenance of the type specimen of *P. mexicana.* They refer to the holotype as "circa Mexico" following Moricand's description (1837: 39–40) and did not further elaborate on the meaning of this inscription. Instead of "circa" (Latin meaning: around, in the vicinity), the first word on the original label of the holotype specimen could also read "Cerca" (Spanish meaning: close, nearby). According to Ohlendorf & al. (1980: appendix B), Berlandier used a mixture of Spanish and French to address localities. More importantly, it is common practice in Mexico to refer to Mexico City (Spanish: Ciudad de México) as 'México'; the French name is 'Mexico'. In Berlandier's lists of collected specimens ("Expéditions"; Ohlendorf & al. 1980, provided a summary of numbers and associated localities), all references of Mexico refer to the city of Mexico. The correct translation of the original label attached to the holotype of *P. mexicana* should therefore be "in the vicinity of Mexico [City]". Did Berlandier collect this specimen in the (relative) vicinity of Mexico City, hence, in the interior highlands?

To address this question, another collection of Berlandier with the number *493* (collected in the Huasteca, according to the "Expéditions") that could be located in the herbaria G and P, is of importance. The specimens are virtually identical to the holotype of *Platanus mexicana* (see Fig. 1). The collection consists of several herbarium sheets all having the same number but slightly different information about the origin of the specimens. One specimen kept in Geneva is labelled as "entre Tampico y Mexico"; it was collected on Berlandier's trip from Tampico to Mexico City, covered by chapter 4 in first volume of his journal manuscript (Berlandier 1826–34, cited after Ohlendorf & al. 1980: 60–92). The Spanish inscription appears to be in the same handwriting as "circa/cerca Mexico". The northernmost population of the typical variety according to Nixon & Poole (2003: 127) is located in easternmost Hidalgo: "Hidalgo: Río [Cueva los Caliches], San Bartolo Tutotepec, 3.6.1972, *Leyva 648* [ARIZ, CAS, ENCB, MICH]"; see Fig. S1, Appendix). San Bartolo Tutotepec is situated northeast of a water divide (at an altitude of 2100–2800 m) that marks the eastern border of the Sierra Madre Oriental, and hence, outside the interior highlands and Berlandier's route.

Another two specimens with the same number *493* are kept in Paris, one labelled as "Environs de Mexico", and the other with a relatively precise description of the locality and a date; it was collected on the way to Real del Monte ("Real[?] de Tampico a Real delmonte, mai 1827"). Real del Monte (officially re-named Mineral del Monte in 1824) is a city in the Sierra Madre Oriental, above 2700 m, and a waypoint on Berlandier's journey outlined in chapter 4 of his journal, the crossing of the Huasteca. The rivers in this area drain northwards towards the Lago Metztitlán (1250 m) not eastwards like those of the San Bartolo Tutotepec population behind the water divide. Several specimens kept in MEXU originate exactly from stands north (and south) of the Lago Metztitlán. According to Nixon & Poole's (2003) concept these specimens would fit better with *P. mexicana* var. *interior*. These populations are in penultimate vicinity to the route, Berlandier took from Tampico to Real del Monte and Mexico City following an, at that time, abandoned trading route leading from the coast into the interior highlands of the Sierra Madre Oriental. Two thirds of this route goes through "mountainous country" (Berlandier 1826–34: 61 cited after Ohlendorf & al. 1980). The tributaries of the Río Pánuco, for instance the Río Moctezuma and Río Tempoal, originate in the same area of the Sierra Madre Oriental from which Berlandier had collected *Platanus* for the first time at a grove comprising plentiful "*Salix viridis*" (possibly *S. nigra*) and sycamores (*"P. occidentalis"*) along the banks of the Río Moctezuma on 9 May 1827, and noted "…. an

extremely abundant plant collection made here." (cited after Ohlendorf & al. 1980).

Although Nixon & Poole (2003) do not explicitly comment on these specimens, they indicated the presence of *Platanus mexicana* var. *interior* in northern Hidalgo, the region of the Huasteca crossed by Berlandier (Nixon & Poole 2003: fig. 4; no vouchers given). There can be little doubt that the specimens with the number *493* were collected in the area north or south of the Lago Metztitlán on the way from Tampico to Mexico City, and before the expedition had reached the central (and higher) parts of the Sierra Madre Oriental, possibly at the aforementioned sycamore grove along the Río Moctezuma.

Berlandier used "Mexico" to refer to Mexico City and not the country of Mexico, indicating that the holotype of *Platanus mexicana* originated from central Mexico. Unfortunately, the holotype is unnumbered but may have been collected even closer to Mexico City than the numbered specimens (collection *493*). Thus, Berlandier's holotype came from an interior population. Even if the inconsistencies between Berlandier's numbering and the localities listed in his "Expéditions" are taken into account, there can be no doubt that all specimens of *P. mexicana* obtained from Berlandier were collected in May 1827 on his trip from Tampico to Mexico City, and most likely were included in the shipment of 89 parcels to Geneva from 8 November 1827 (see Ohlendorf & al. 1980: appendix) and, hence, represent populations of the interior. Berlandier never travelled into the distribution area of the typical variety in the sense of Nixon & Poole (2003).

In the light of Berlandier's specimens, which have leaves with whitish tomentose abaxial face and 1–2 capitula per infructescence, and Moricand's (1843) original description, Standley (1922) was entirely correct at his time to use the name *Platanus mexicana* for the populations of *P. rzedowskii*. In the above mentioned two character states, plants of *P. rzedwoskii* are identical to Berlandier's specimens, whereas *P. chiapensis* Standl., *P. lindeniana* M. Martens & Galleotti and *P. oaxacana*

Table 1. Character state combinations encountered in individuals of *Platanus mexicana* (material collected by us and kept in MEXU), and resulting taxa following the classifications of Standley (1922) and Nixon & Poole (2003).

Taxonomically important character states	**Standley's (1922)**	**Nixon & Poole (2003)**
Leaves whitish tomentose; 1–3 capitula[1]	*P. mexicana* Moric.	Provenance-dependent, either var. *mexicana* (holotype only!), var. *interior* Nixon & J. M. Poole, or *P. rzedwoksii* Nixon & J. M. Poole
Leaves brownish, creamish, greenish or whitish tomentose; 3–7 capitula	*P. lindeniana* M. Martens & Galeotti *P. chiapensis* Standl.	*P. mexicana* var. *mexicana*
Leaves glabrescent, 1–3 capitula	*P. glabrata* Fernald	*P. mexicana* var. *interior* ?hybrids of var. *interior* and *P. rzedowskii* *P. occidentalis* var. *palmeri* (Kuntze) Geerinck
Leaves sparsely tomentose, not whitish	*P. oaxacana* Standl.	*P. mexicana* var. *mexicana*

[1]This character state combination is encountered in Berlandier's specimens, including the holotype of *P. mexicana*.

Table 2. Scheme for a varietal subdivision of *Platanus mexicana* taking into account the central Mexican population.

Taxon	***P. mexicana* var. *mexicana***	***P. mexicana* var. *lindeniana***
Synonyms (only newly described taxa and originally described species)	*P. mexicana* var. *interior* Nixon & Poole *?P. mexicana* × *rzedowskii* fide Nixon & Poole	*P. lindeniana* M. Martens & Galeotti *P. chiapensis* Standl. *?P. oaxacana* Standl.
Occurrence	Central Mexico: Querétaro, and adjacent parts of San Luis Potosí, Guanajuato, Hidalgo	Southeastern Mexico: Veracruz (incl. [S]E Hidalgo) to Guatemala
Abaxial leaf surface	Densely tomentose to glabrous	Densely tomentose, rarely glabrous, in particular in southernmost populations (Oaxaca)
Number of capitula on the female infructescence axis	1–3	(2–)3–5(–7)

Standl. differ by having 3–6(–7) capitula and a tomentum that only in a few cases is whitish (Fig. 4, 7; cf. Martens & Galeotti 1843; Standley 1922). Moreover, Standley's concept of *P. glabrata* includes all Mexican specimens with 1–2(–3) capitula and glabrescent leaves; it comprises specimens referred by Nixon & Poole (2003) to *P. mexicana* var. *interior, P. mexicana* var. *interior* × *P. rzedowskii* and *P. occidentalis* var. *palmeri* (Table 1). In this context, a footnote added by the botanical advisors involved in the translation of Berlandier's journal, requires attention. On p. 72 of Ohlendorf & al.'s (1980) translation, where Berlandier described the sycamore grove along the banks of Río Moctezuma, they note that Berlandier's *'P. occidentalis'* is likely referring to *P. mexicana* Moric. and/or *P. occidentalis* var. *glabrata*.

Necessary changes in the diagnosis of *Platanus mexicana*

Nixon & Poole (2003: 127ff) introduced a new variety *interior* for the interior populations of *Platanus mexicana* because of their "distinctive suite of character-states": glabrescent, broadly-lobed leaves on fertile axes, with two or three capitula (rarely one or four). However, individuals identical to Moricand's holotype (whitish tomentose, (1–)2(–3] capitula; see Fig. 1, 5, 6) are relatively abundant within the assumed range of *P. mexicana* var. *interior* (Querétaro and adjacent parts of Guanajuato, Hidalgo and San Luis Potosí), most notably also at the type locality of var. *interior.* By contrast, they are rare or entirely absent in populations farther south. Following the 'distinctive suite' argument of Nixon & Poole (2003), such individuals of the interior would hence represent var. *mexicana* and not var. *interior*. Distinguishing a variety *interior*, or, in general, two varieties, is then pointless because both alleged varieties occur sympatrically (following Nixon & Poole 2003). Consequently, the diagnosis of *P. mexicana* needs to be emended to fully accommodate all individuals assigned to *P. mexicana*: female infructescences with (1–)2–5(–7) capitula, with a trend towards increased numbers of capitula to the south (Fig. 3); leaves with persistent abaxial indumentum or glabrescent, in particular at stands close to the margin of the distribution area (Querétaro and adjacent areas, Oaxaca) with moderate precipitation (Fig. 4, 7; Table 2).

Main features distinguishing northern ('interior') and central to southern populations of *Platanus mexicana* are indeed the number of capitula and the diversity of leaf types (Fig. 1–3; 5–6, Tables S1, S2, see supplements to the online edition) encountered in single populations (e.g. the population at the type locality of *P. mexicana* "var. *interior*" close to El Trapiche, cf. Fig. 5). This includes morphotypes otherwise restricted to *P. palmeri* (e.g. Fig. 6C), which are completely absent in populations farther south (traditionally referred to as *P. lindeniana, P. oaxacana* and *P. chiapensis*). The northern populations (including Berlandier's specimens) differ from the remainder of *P. mexicana* by consistently having 1–3 capitula instead of 3–5(–7), rarely 1–2 (Fig. 3), found farther south. Moricand's holotype and the vouchers with Berlandier's collection no. *493*, displaying the same morphology as the type, fit perfectly within the variability of the 'interior' populations thriving in Querétaro and adjacent areas. In Querétaro (own data; specimens kept at MEXU) and northern Hidalgo (MEXU), specimens that match the holotype in every detail are rather frequently met (see Fig. 5A, 6A). Hence, if two (geographical) varieties are distinguished, all central Mexican populations, var. *interior* according to Nixon & Poole, must instead be referred to as *P. mexicana* var. *mexicana* according to Art. 26.1 of the Vienna Code (McNeill & al. 2006). The name of the second variety would then be *P. mexicana* var. *lindeniana* (Puebla, Veracruz, Oaxaca, Chiapas, Guatemala). At the rank of variety, *lindeniana* has priority over other epithets (Vienna Code, Art. 11.4; see Nixon & Poole 2003 for synonyms of *P. mexicana* Moric.).

Emended diagnosis for *Platanus mexicana* Moric. (incl. *P. lindeniana* M. Martens & Galeotti, *P. chiapensis* Standl. and *P. oaxacana* Standl.) **—** Leaves with three to five lobes; if more than three lobes, basal ones inconspicuous; leaves unlobed at the first position of annual shoots; abaxial leaf surface glabrous to densely tomentose; number of capitula on female infructescence axis (1–)2–5(–7). Nuclear encoded DNA sequences: 5S rDNA intergenic spacer of *Platanus mexicana-occidentalis* type; ITS1 and ITS2 diagnostic at species level; second intron of the *LEAFY* gene of general ANA type (Grimm & Denk 2010). For a varietal subdivision, see Table 2.

An intriguing alternative hypothesis

Nixon & Poole (2003) reported morphologically ambiguous specimens from a region where the ranges of *Platanus mexicana* "var. *interior*" and *P. rzedowskii* overlap (Ríoverde, San Luis Potosí). They considered these specimens as "intermediates" between *P. mexicana* and *P. rzedowskii* (Fig. 10), the northeastern neighbour of *P. mexicana* and referred to them as potential hybrids between *P. mexicana* "var. *interior*" and *P. rzedowskii.* They distinguished two major groups: (1) specimens with *P. rzedowskii* leaves and *P. mexicana* inflorescences and achenes, and (2) those with *P. mexicana* "var. *interior*" leaves (i.e. glabrescent *P. mexicana*) but *P. rzedwoskii*-like single massive capitula (note that this latter character combination is also found in *P. palmeri*).

Molecular analyses have demonstrated that individuals of *Platanus rzedowskii* are significantly distinct from *P. mexicana* and closely related to *P. palmeri* (Grimm & Denk 2008, 2010). Like *P. rzedowskii, P. palmeri* typically has 1 to 2 capitula. Molecular data also showed evidence of occasional lateral gene flow between *P. mexicana* and *P. palmeri/rzedowskii* in central Mexico. *P.*

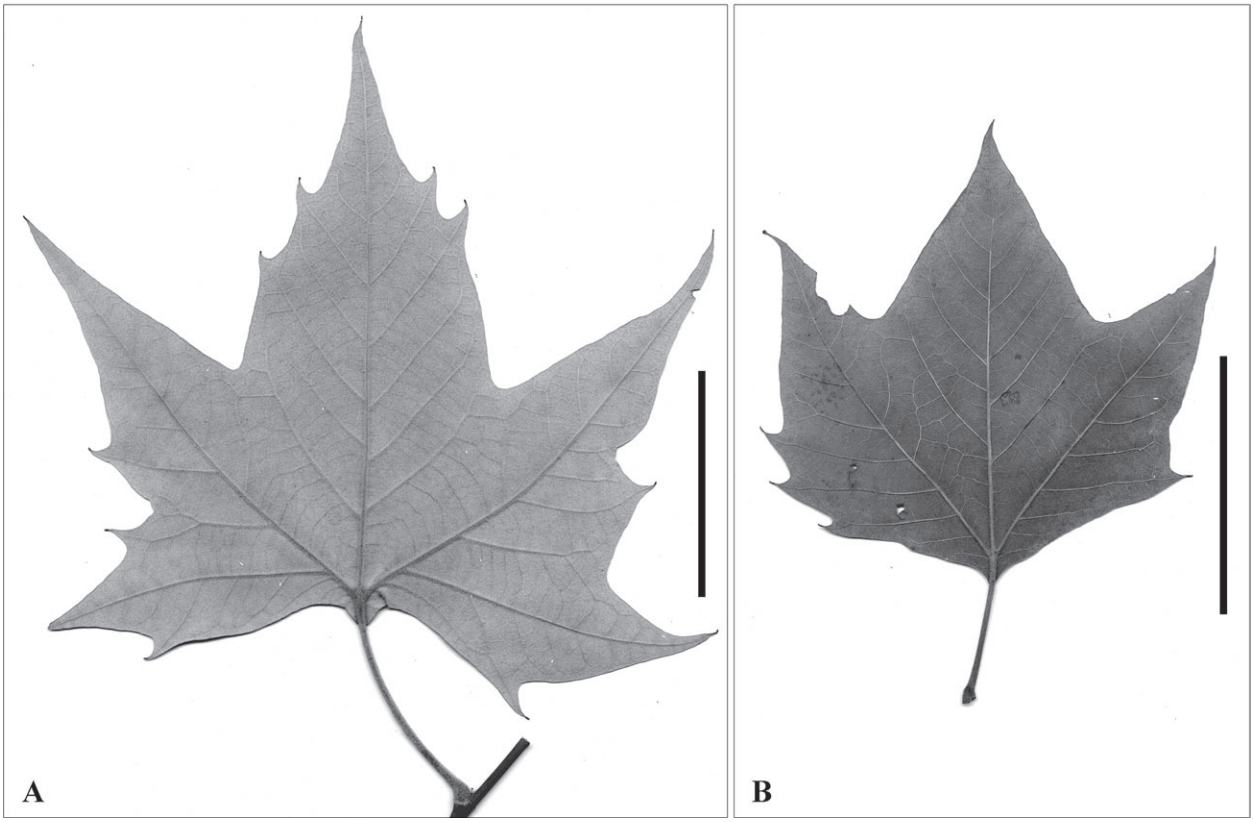

Fig. 10. Typical leaf morphotypes of *Platanus rzedowskii;* El Ebanito to Las Crucitas, Nuevo Léon – A: leaf whitish-tomentose underneath, *Denk 2004097-1,* S; B: leaf sparsely greenish-tomentose underneath; *Denk 2004096-4,* S. – Scale bars = 5 cm.

mexicana type individuals showing genetic introgression from *P. palmeri/rzedowskii* originate from the Querétaro populations and fully fit within the morphological diagnosis given in Table 2 for the emended *P. mexicana* var. *mexicana*. Noting the geographic setting (Fig. 4; see also Nixon & Poole 2003: fig. 4), it appears reasonable that the northern populations of *P. mexicana* (var. *mexicana* in Table 2) are to some extent distinct from the remainder because they represent the contact zone between *P. mexicana* var. *lindeniana* to the south and *P. palmeri/rzedowskii* to the north. The reduced number of capitula and increased leaf variability in the northern populations of *P. mexicana* may morphologically reflect this introgression. In this context, it makes sense that the northernmost populations of *P. mexicana* in San Luis Potosí show characteristics of *P. palmeri/rzedowskii* such as the single massive capitula that have not been reported from Querétaro and northern Hidalgo, and *P. mexicana* in general. Notably, a specimen from eastern San Luis Potosí (*F. Medellín L. 621*, MEXU), more than 500 km airline south of the southernmost populations of *P. palmeri* according to Nixon & Poole (2003: fig. 4), represents a fruiting twig matching perfectly *P. palmeri*.

The Querétaro populations are genetically largely of the *Platanus mexicana* type (Grimm & Denk 2008, 2010). This can be explained by more frequent or more recent backcrossing with the southern *P. mexicana* (var. *lindeniana*) rather than with the northern *P. palmeri/rzedowskii.* The superficial incongruence between genetic (no or little introgression) and morphological (introgression) evidence can be understood using the hybrid 'London plane' *P.* × *hispanica (P. orientalis* × *P. occidentalis)* as an example. In this case, the genetic signature of *P. occidentalis* may not be detected despite strong morphological evidence of the hybrid origin of individuals (Besnard & al. 2002; Grimm & Denk 2008, 2010; but see Pilotti & al. 2009). In this context it would be prospective to screen genetically all populations of *P. mexicana* intermediate to *P. rzedowskii* in Guanajuato, San Luis Potosí and northern Hidalgo. Mapping the potential hybrid or contact zone is the necessary next step to define the species boundaries and diagnostic characters of *P. mexicana* (ranging from central Mexico to Guatemala) against *P. palmeri/rzedowskii* (north, northeast and central Mexico). If the 'interior' populations of *P. mexicana* including Berlandier's holotype (*P. mexicana* var. *mexicana* in Table 2) are actually representing introgrades or hybrids between *P. palmeri/rzedowskii* and the eastern and southern populations of *P. mexicana* (*P. mexicana* var. *lindeniana* in Table 2), further taxonomic revision is needed. From the currently available data, a distinct species *P. lindeniana* (incl. *P. chiapensis* and *P. oaxacana;* but excluding the 'interior' populations of *P. mexicana*) would be morphologically (this study; Nixon & Poole

2003) and genetically (Grimm & Denk 2008, 2010) sufficiently different from *P. palmeri/rzedowskii*. Thus, *P. mexicana* s.str. would represent *P. palmeri/rzedowskii* × *lindeniana.*

Conclusions

In the light of the apparent northern ('interior') provenance and the morphological attributes of the holotype of *Platanus mexicana*, we propose to discard a varietal subdivision of *P. mexicana.* Instead, we emended the original diagnosis of *P. mexicana* so that this species covers all morphotypes traditionally recognised as *P. mexicana* (excluding *P. rzedowskii*), *P. glabrata* p.p. (central Mexico), *P. lindeniana, P. oaxacana* and *P. chiapensis*; morphotypes encountered in individuals that share a unique genetic signature clearly distinct to other species of *Platanus*. Considering the situation in Querétaro and adjacent areas, Nixon & Poole's (2003) concept of a variety *interior* has no foundation and demonstrates the pitfalls of taxonomic revisions based largely on herbarium material. Morphotypes identical to Moricand's holotype and exactly matching his original description are frequently met within the interior Mexican mountains but appear to be underrepresented in herbarium collections. Specimens with few capitula and whitish tomentose abaxial leaf surfaces are not rare mutants but more or less common in central Mexico, co-occurring with glabrescent types.

As long as genetic data are missing for all central Mexican populations, *Platanus mexicana* Moric. can be used as the (provisional) correct name also for the eastern and southern Mexican and Guatemalan populations (traditionally referred to as *P. lindeniana, P. oaxacana* and *P. chiapensis*) as suggested by Nixon & Poole (2003). However, the diagnosis of *P. mexicana* needs to be emended in order to accommodate both the central Mexican *P. mexicana* individuals with increasingly glabrescent leaves and those individuals with a distinct brownish, or light greenish tomentum and numerous capitula in eastern and southern Mexico and Guatemala. If further genetic evidence will prove the hybrid (or introgressive) nature of the central Mexican ('interior') *P. mexicana,* and hence the holotype collected by Berlandier, this species will need to be split into *P. lindeniana* and *P.* × *mexicana* (= *P. lindeniana* × *P. palmeri/rzedowskii*).

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Note: The electronic supplements are available at http://www.bgbm.org/willdenowia/ElectronicSupplements.htm

Appendix

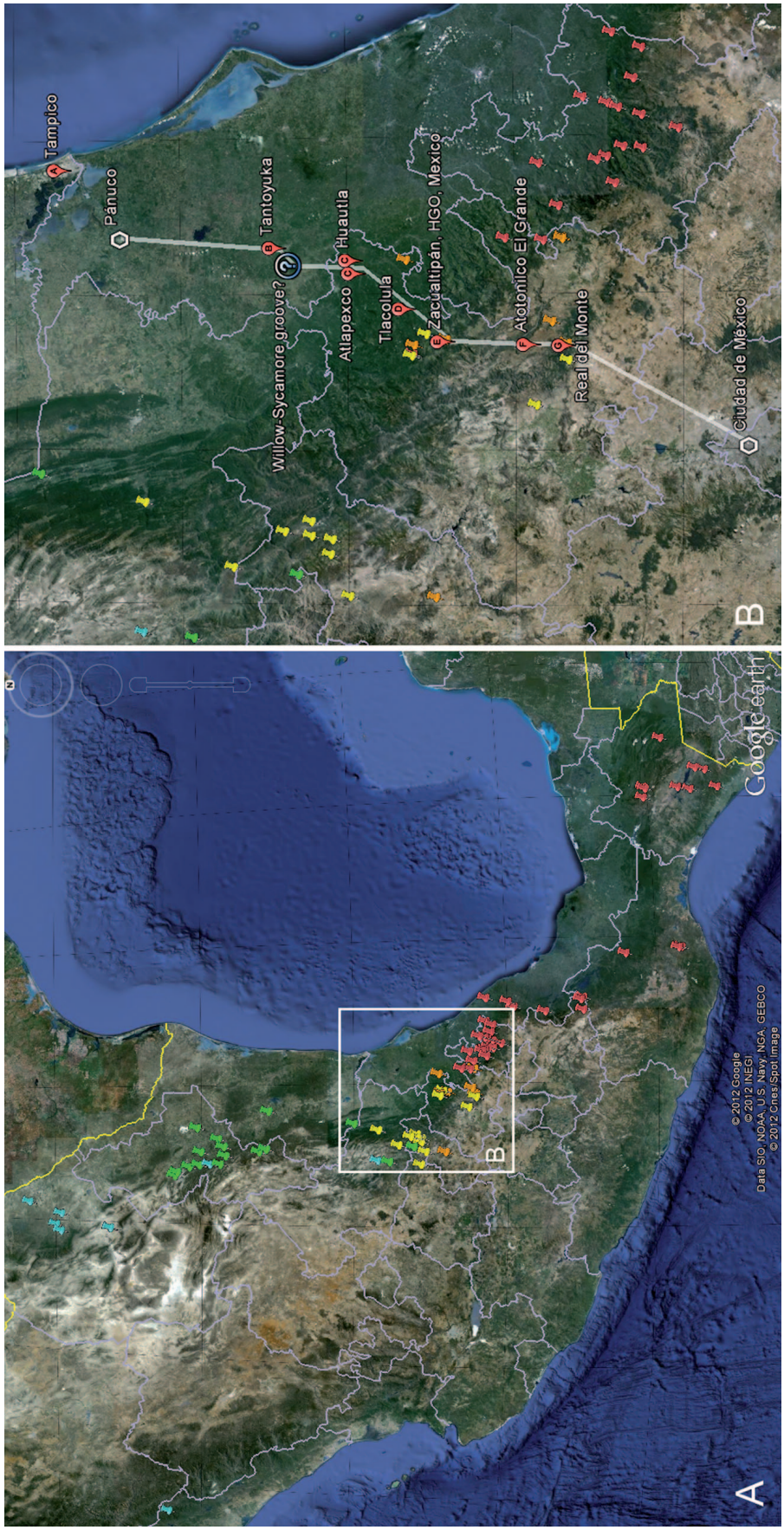

Fig. S1. A: Distribution of members of the ANA clade of *Platanus* in Mexiko based on vouchers stored in MEXU and field observations. – Cyan = *P. palmeri;* green = *P. rzedowskii;* yellow = *P. mexicana* var. *mexicana;* red = *P. mexicana* var. *lindeniana;* orange = ambiguous individuals of *P. mexicana.* – B: Enlarged section as indicated by the rectangle in A showing Berlandier's route. – Based on Google Earth. An interactive version of this map is provided as a supplement to the online edition; opening the Google Earth kmz file Denk+al_Fig_S1.kmz will start Google Earth, for explanation click on 'File S1' and 'Berlandier's route'.