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NEW EUROPEAN RECORDS AND FIRST EVIDENCE OF EPIDERMAL STRUCTURES OF *SLOANEA* L. FROM THE ITALIAN OLIGOCENE - REVISED TYPE AND ORIGINAL MATERIAL OF PRINCIPI 1916

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Key words: Northern Italy, Oligocene, *Sloanea*, Cuticle, Principi, Types, Systematic revision.

Abstract. Leaves of *Sloanea elliptica* (Andreánszky) Z. Kvaček & Hably and *S. peolai* (Principi) Hably, Tamás & Cioppi with preserved organic structures were found during the study of Principi's collection from the Oligocene flora of Santa Giustina. Fossil leaves of *Sloanea elliptica* have so far been recorded exclusively from the Palaeogene Basin of the Inner Carpathian Region, i.e. from the Lower Oligocene strata of Hungary and Slovenia, whereas *S. peolai* has been described from a single locality, Chiavon in Italy. Organic structure of *S. peolai* hitherto has not been recorded. The mass occurrence of *Sloanea elliptica* in the fossil assemblage of Santa Giustina indicates that its area was much more extensive than it was presumed. It was a characteristic element mainly of Oligocene floras, and even predominated them. This is the first record of the co-occurrence of two *Sloanea* species described on the basis of leaf remains. During the study 6 types and more than 30 illustrated specimens published in Principi's monograph were revised and identified as *S. elliptica*.

Riassunto. Durante lo studio della collezione Principi della flora oligocenica di Santa Giustina, Liguria, sono state rinvenute foglie di *Sloanea elliptica* (Andreánszky) Z. Kvaček & Hably e di *S. peolai* (Principi) Hably, Tamás & Cioppi, con strutture organiche preservate. Le foglie fossili di *Sloanea elliptica* sono state segnalate sinora solo nel Bacino paleogenico della regione interna dei Carpazi, cioè entro depositi dell'Oligocene inferiore di Ungheria e Slovenia, mentre *S. peolai* è stata descritta da una singola località in Italia settentrionale, Chiavon. Inoltre la struttura organica di *S. peolai* non è mai stata descritta sinora. La presenza massiccia di *Sloanea elliptica* nella associazione fossile di Santa Giustina indica che il suo areale di distribuzione era molto più ampio di quanto pensato. Costituiva un elemento caratteristico della flora oligocenica, talora anche dominante. Questa è la prima segnalazione della presenza concomitante delle due specie di *Sloanea*, sulla base dei resti fogliari. Durante lo studio 6 tipi e oltre 30 esemplari illustrati nella monografia di Principi sono stati revisionati ed identificati come *S. elliptica*.

Introduction

The genus *Sloanea* L. of the Elaeocarpaceae family was recorded first as fossil leaves and fruit remains from Hungary, Slovenia and the Czech Republic (Kvaček et al. 2001). *Sloanea elliptica* (Andreánszky) Kvaček & Hably described in Santa Giustina had previously been recorded from Lower Oligocene strata of Hungary and Slovenia. Remains of *Sloanea* from the Czech Republic belong to another species. The record of *Sloanea* in Palaeogene floras of Europe has also importance from a climatological point of view – the genus requiring tropical-subtropical climate – corroborates a warm climate during the Oligocene. The so far reconstructed area of *Sloanea elliptica* provides additional palaeogeographic evidence relevant for the the pre-Neogene of the Alpine-Carpathian-Dinaric region (Hably 2006; Hably & Kvaček 2006).

The fossil assemblage of Santa Giustina, Northern Italy, Liguria, was published first by Principi (1916, 1921), and later Gregor & Knobloch (2001) investigated the flora. According to present-day knowledge, the age of the fossiliferous strata is middle Stampian, whereas the age of the upper layers containing ferns is Upper Stampian (Lorenz 1969), thus Oligocene. This well corresponds to the age of strata providing the first record of *Sloanea* leaves (Kvaček et al. 2001), i.e. the Tard Clay Formation which was deposited during the Kiscellian. Its floristic composition is well-comparable to that of the Tard Clay flora. Numerous taxa are shared by the Italian and Hungarian assemblages, e.g. *Eotrigonobalanus furcinervis, Comptonia acutiloba, Comptonia schrankii, Zizyphus zizyphoides, Smilax* sp. The taxono-

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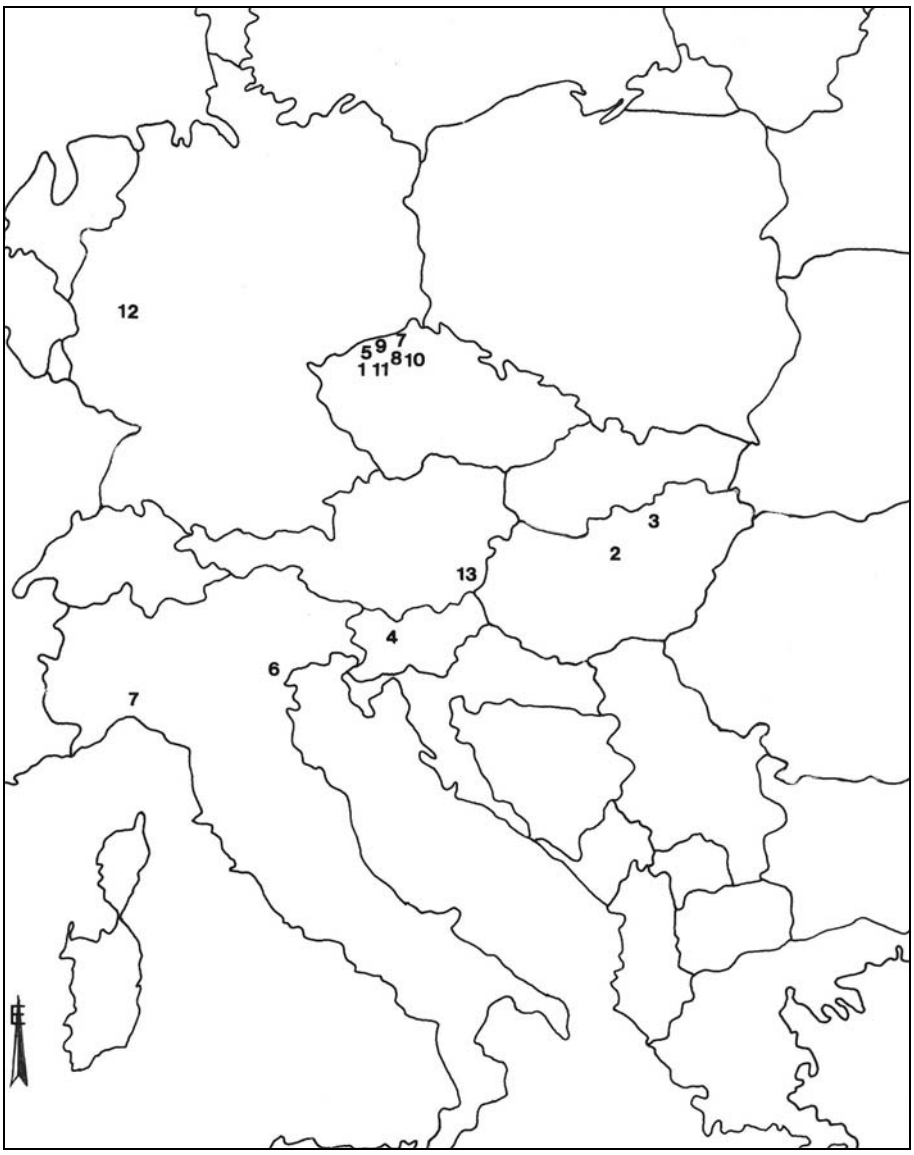


Fig. 1 - Records of *Sloanea* fossils during the Palaeogene and Neogene of Europe.

Legend:

Late Eocene:

1: **Kučlín** (Czech Republic, 50° 32' N, 13° 48' E), *Sloanea nimrodi* (Ettingshausen) Z. Kvaček & Hably (leaf) (Kvaček Z., Hably L. & Manchester S. R. 2001); *Sloanea sp.* (fruit) (Kvaček 2002).

Early Oligocene:

2: **Budapest** (Hungary, 47° 30' N, 19° 04' E), *Sloanea eocenica* (Rásky) Z. Kvaček, Hably & Manchester (fruit) (Kvaček Z., Hably L. & Manchester S. R. 2001); *Sloanea elliptica* (Andreánszky), Z. Kvaček & Hably (leaf) (Kvaček Z., Hably L. & Manchester S. R. 2001); 3: **Eger-Kiseged** (Hungary, 47° 54' N, 20° 22'E), *Sloanea elliptica* (Andreánszky), Z. Kvaček & Hably (leaf) (Kvaček Z., Hably L. & Manchester S. R. 2001); 4: **Rovte** (Slovenia, 45° 59'N, 14° 10' E), *Sloanea elliptica* (Andreánszky), Z. Kvaček & Hably (leaf) (Kvaček Z., Hably L. & Manchester S. R. 2001); 5: **Kundratice** (Czech Republic, 50° 35'N, 14° 06'E), *Sloanea artocarpites* (Ettingshausen) Z. Kvaček & Hably (leaf) as *Icaciniphyllum artocarpites* (Ettingshausen) Z. Kvaček & Bůžek (Kvaček & Walther 1998)

Early-Middle Oligocene:

6: **Chiavon** (Italy, 46° 19'N, 13° 05'E), *Sloanea peolai* (Principi) Hably, Tamás & Cioppi (leaf) (Hably L., Tamás J. & Cioppi E. 2007); 7: **Santa Giustina** (Italy, 44° 25' N, 8° 29' E), *Sloanea elliptica* (Andreánszky), Z. Kvaček & Hably (leaf); *Sloanea peolai* (Principi) Hably, Tamás & Cioppi (leaf) (Hably in this paper).

Late Oligocene:

8: **Markvartice** (Czech Republic, 50 ° 46'N, 14 ° 20'E), *Sloanea* sp. (a) (fruit) (Kvaček Z., Hably L. & Manchester S. R. 2001), *Sloanea artocarpites* (Ettingshausen) Z. Kvaček & Hably (leaf) as *Dicotylophyllum sparsidentatum* Bůžek, Holý & Kvaček (Bůžek, Holý & Kvaček 1976); 9: **Suletice-Berand** (Czech Republic, 50° 38'N, 14° 10'E), *Sloanea* sp. (a) (fruit) (Kvaček Z., Hably L. & Manchester S. R. 2001); 10: **Žichov** (Czech Republic, 50° 28'N, 13° 47'E), *Sloanea artocarpites* (Ettingshausen) Z. Kvaček & Hably (leaf) (Kvaček Z., Hably L. & Manchester S. R. 2001); 11: **Holý Kluk** (Czech Republic, 50° 22' N, 14° 03'E), *Sloanea* sp. (fruit) (Kvaček Z., Hably L. & Manchester S. R. 2001, Radoň et al. 2006), *Sloanea artocarpites* (Ettingshausen) Z. Kvaček & Hably (leaf) (Radon et al. 2006), 12: **Rott** (Germany, 50° 38'N, 7° 30'E), *Sloanea* sp. (b) (fruit) (Kvaček Z., Hably L. & Manchester S. R. 2001). *Sloanea* sp. (a) and (b) are probably different unidentified species.

Late Miocene:

13: **Mataschen** (Austria, 46° 54'N, 16° 05'E), *Sloanea sp.* (leaf) (Kovar-Eder J. & Hably L. 2006).

mical revision and the comparative study of the floras are in progress (Fig. 1).

Material and methods

Numerous original and type specimens of Principi's monograph (1916) discussing the Oligocene flora of Santa Giustina are housed in the collection of the University of Genova (DIP.TE.RIS). During the revision of this collection specimens of *Sloanea elliptica* (Andreánszky) Kvaček & Hably were recognized based on macromorphological traits due to the excellent preservation of leaves. Material: 88/1, 88/2, 88/4, 88/5, 111/1, 158/1, 158/2, 203/1, 231/2, 232/1, 232/2, 232/3b, 232/4a, 232/4b, 232/6, 232/9, 232/10, 232/11, 232/13, 232/16, 243/1, 268/1, 268/5, 268/6ab, 280/1, 307/1, 311/1, 357/2, 1349/1, SG1-SG33, and numerous specimens without inventory numbers. Cuticle preparations: SG6-20-4, SG6-20-14SG6-40-3, SG6-40-12, SC6-60-16, trichome bases: SG6-20-11. *Sloanea peolai* (Principi) Hably, Tamás & Cioppi: material: SG34 =232/14, cuticle: SG34-20-3.

Most of the leaves are fossilized in grey, heavily cemented, hard deposits whereas some remains are well-preserved with fragments of cuticles owing to the fine-grained clayey matrix. Some samples were taken to the Palaeobotanical Laboratory of the Hungarian Natural History Museum (Budapest) and studied applying fluorescence microscopy (Nikon Eclipse 600). Using this method even the comparison of *Sloanea elliptica* leaves from the Hungarian (Budapest) and Slovenian (Rovte) localities could be accomplished.

Systematic palaeontology

Sloanea elliptica (Andreánszky) Z. Kvaček & Hably

Revised type material in Santa Giustina (Principi 1916):

Ficus perseaefolia Principi, T. 32-33, f. 5.
Juglans elliptica Principi, T. 10, f. 2., T. 12-13, f. 2, 3, 4.
Pterospermites incertus Principi, T. 62, f. 1.
Rhamnus lancifolius Principi, T. 66, f. 13, T. 67, f. 7, 8?
Rhamnus peolai Principi, T. 66, f. 4.
Viburnum Sismondai Principi n. sp., T. 84, f. 1, 2.

Revised original material in Santa Giustina (Principi 1916):

Alnus nostratum Unger, T. 19, f. 8.
Artocarpidium bilinicum Ettinshausen, T. 36-37, f. 4.
Artocarpidium Desnoyersi Wat., T. 36-37, f. 2.
?*Cassia palaeo-speciosa* Staub, T. 77, f. 13.
Cinchonidium randiaefolium Etingshausen, T. 83, f. 3, 4.
Cornus Büchi Heer, T. 67, f. 12.
Cornus studeri Heer, T. 67, f. 13.
Diospyros brachysepala A. Br., T. 80, f. 1, 2, 9.
Diospyros macrophylla Principi, T. 80, f.11.
Juglans denticulata Heer, T. 10, f. 3, 4.
Juglandophyllum peramplum (Saporta) Schenk, T. 14, f. 1, 2., T. 15, f. 1.
Laurus notarisii (Massalongo) Principi, T. 45, f. 8, 9.
Laurus vetusta Saporta, T. 48, f. 7, 8.
Malpighiastrum protogaeum Staub, T. 64, f. 3.
Palaeolobium heterophyllum Unger, T. 77, f. 11.
Persea braunii Heer, T. 49, f. 4, 5.
Platanus deperdita Massalongo, T. 71, f. 1.
Populus mutabilis crenata Heer, T. 23, f. 3.
Populus mutabilis ovalis Heer, T. 21-22, f. 9.
Porana oeningensis Unger, T. 84, f. 7.
Quercus artocarpites Ettingshausen, T. 5, f. 1.
Quercus Charpentieri Heer, T. 5, f. 5, 6.
?*Quercus chlorophylla* Unger, T. 7, f. 1.
Quercus Hamadryadum Ettingshausen, T. 4, f. 7.
Rhamnus acuminatifolius Web. T. 66, f. 5.
Rhamnus acuminatus (Ettingshausen) Principi, T. 67, f. 2, 3.
?*Rhamnus deletus* Heer, T. 66, f. 11.
Rhamnus rectinervis Heer, T. 66, f. 7-10.
Rhamnus Roesleri Heer, T. 66, f. 14.
Sterculia variabilis Saporta, T. 61, f. 2.

Description. Simple leaves, rarely petiolate, petiole up to 0.8 cm. Leaves 6.5-19.0 cm long, 3.2-9.8 cm wide, mostly longer than 10 cm, and wider than 4-6 cm. Most leaves wide obovate, or occasionally elliptic. Base generally asymmetric, ranging from cuneate to rounded, apex acute. Margin subentire, irregularly undulate, widely cuneate or bluntly toothed, in the lower half of the lamina entire. Teeth irregular, generally obtuse, the basal side longer than the apical. Venation craspedodromous, or slightly transitional to semicraspedodromous. Midrib stout, continuing in a thick petiole. Secondary veins – depending on leaf dimensions – arise from the midrib at relatively great distances from each other, run steeply, sometimes join forming loops or ramify forming "y" towards the margin. In intact leaves up to 7 pairs of secondaries. The lowermost pair of secondaries considerably thinner and shorter than the other. Tertiary veins strong, clearly observable and perpendicular to secondaries.

Adaxial cuticle thick, smooth, cells polygonal, 20-30 μm in diameter, with undulate anticlinal walls. Abaxial cuticle thinner, cells polygonal, 20-30 μm with strongly undulate anticlinals. Stomata cyclocytic, aperture narrow oval, 6-8 μm long. Pairs of guard cells 6-15 μm wide, 10-16 μm long without polar thickenings. Walls of guard cells relatively thin, stomata sunken. Subsidiary cells strongly cutinized, more cutinized at the peripherial side and these walls undulate. Scattered simple trichoma bases mainly close to the veins.

Discussion. The macro- and micromorphology of leaves well correspond to *Sloanea elliptica* leaves described from the Tard Clay Formation in Budapest. However, specimens from Santa Giustina are much larger. All taxa shared by the two assemblages display this phenomenon, e.g. huge, giant specimens of *Eotrigonobalanus furcinervis* were recorded in Santa Giustina. Disparity of leafsize is similarly indicated for two Hungarian localities, i.e. specimens from the Bükk Tectonic Unit are much slender than those from the Buda Unit (Tamás & Hably 2005). Their macromorphological traits are comparable even to a lesser extent than those of the leaves from Buda and Santa Giustina.

Due to great dimensions of leaves only few are intact; either the apex or the base is fragmented. Despite the mainly coarse-grained and often strongly cemented fossiliferous matrix the tertiary veins characteristic of *Sloanea elliptica* leaves are always nicely observable. All cuticular traits correspond to those of the specimens from Budapest and Rovte. The only disparate trait is the lower density of stomata in leaves from Santa Giustina contrasting with dense stomata on leaves from Budapest and Rovte. The phenomenon that stomata are more densely arranged on smaller leaves of the same species is general.

According to the rules of nomenclature a new combination of *Sloanea elliptica* is required for eligibility. The first description of a specimen belonging to *S. elliptica* was published by Unger (1850). The description of the valid combination is in progress and its preliminary publication is to be found in a conference abstract (Hably & Kvaček 2006).

Sloanea peolai (Principi) Hably, Tamás & Cioppi

Description. Altogether one specimen represents this species from the collection. Leaf simple, petiolate. Length 10.2 cm (original length 10.5 cm), width 3.4 cm, petiole 1.3 cm. Both shape of lamina and base asymmetric. Base cuneate, on its end rounded. Apex fragmented but definitely attenuate. Margin subentire-entire. Midrib definite, continuing in long petiole. Venation semicraspedodromous-camptodromous. The distance between secondary veins from the base towards the apex: 1.1, 1.3, 1.3, 1.2, 0.8, 0.7, 0.5 cm. Secondary veins occasionally ramify forming an "Y". Tertiary veins run perpendicularly between secondaries. Secondaries quite thin thus not observable at places with thick cuticle.

Adaxial cuticle thick, smooth, composed of polygonal cells. Cells 20-30 μm in diameter, cell walls slightly undulate. Stomata anomocytic or rarely cyclocytic. The slightly cutinized guard cells of 5-8 μm in width and 8-10 μm in length smaller than those in *S. elliptica*. If there are subsidiaries they are small and more cutinized than guard cells or ordinary epidermal cells.

Discussion. *S. peolai* was described from Chiavon (Italy) according to macromorphological characters (Hably et al. 2007). This is the first time that epidermal structure of the species is described. Although the cuticle shares traits characteristic of *Sloanea* it possesses features distinctive from *S. elliptica*. The anomocytic or rarely cyclocytic stomata are smaller in *S. peolai*. If there are subsidiary cells these are smaller and more cutinized than those of *S. elliptica*. Cell walls in *S. peolai* are undulate to a lesser extent than those of the other species.

Cuticular features of *Sloanea* species recorded from the Palaeogene are quite uniform (Kvaček et al. 2001). An even greater similarity is indicated by the epidermal traits of *S. artocarpites* (Ettingshausen) Kvaček & Hably described from the Early Oligocene assemblage of Kundratice (Czech Republic). However macromorphology of the species undoubtedly separates it from other fossil members of the genus.

Palaeoenvironment and palaeoclimatology

The recent record of *Sloanea*, a member of the Elaeocarpaceae family, in the Oligocene assemblage of Santa Giustina necessitates the reevaluation of earlier estimates on the palaeoclimate of the locality. Modern members of the genus have an area in tropical-subtropical SE Asia, in the southeastern parts of China, Vietnam, Laos, Indonesia, to South America and Australia. Similarly, its fossil remains were recorded in floras of the European Palaeogene indicating subtropical climate (Kvaček et al. 2001).

Fossil leaves of *Sloanea* were described under various systematic names of species or genera mostly requiring temperate climate, e.g. *Platanus*, *Populus*, *Rhamnus*, *Juglans*, *Cornus*, deciduos *Quercus*. Consequently, due to the systematic revision of these remains, the number of thermophilous elements considerably increased.

The fossil species, *S. elliptica* must have found its climatic optimum among the tropical-subtropical climatic conditions since it was dominating in the flora. Its dominance and its relatively large leaves indicate riparian habitat. The mass occurrence of a species and the larger than average size of its leaves are frequent phenomena in riparian and other habitats with abundant water supply. Other taxa of the Santa Giustina assemblage possess also larger leaves than usual and have in other zonal associations also supported this hypothesis. It has already been observed that variation in dimension of *Sloanea* leaves in various assemblages is

PLATE 1

(abbreviations: fm – fluorescence microscope)
Sloanea elliptica (Andreánszky), Z. Kvaček & Hably.

Fig. 1 - No. (SG-6) 232/13 leaf; Fig. 2 - No. (SG-6-10-1. tif.) 232/13, cuticle, fm; Fig. 3 - No. (SG-6-20-4. tif.) 232/13, cuticle, fm; Fig. 4 - No. (SG-6-40-12. tif.) 232/13, cuticle, fm; Fig. 5 - No. 232/1 *Juglans elliptica* Principi, syntype; Fig. 6 - No (SG-6-40-3. tif.) 232/13, cuticle, fm.

PLATE 2

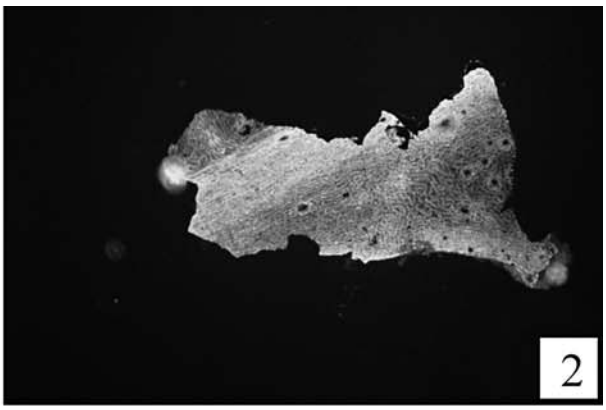
Sloanea elliptica (Andreánszky), Z. Kvaček & Hably as type and figured material of Principi 1916.

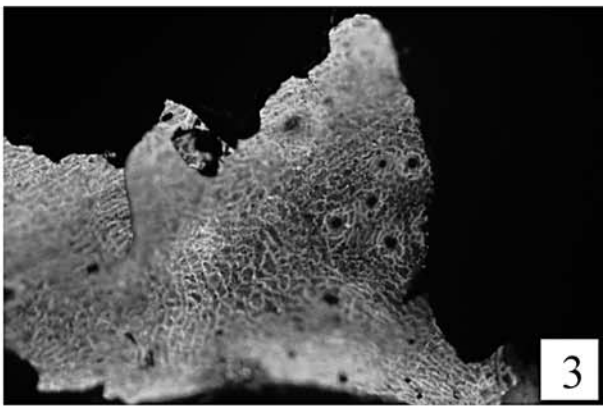
Fig. 1 - No. (SG-3) 232/6 *Juglans elliptica* Principi, syntype; Fig. 2 - No. (SG-5) 232/2 *Juglans elliptica* Principi, syntype; Fig. 3 - No. (SG-4) 232/3b *Juglans elliptica* Principi, syntype; Fig. 4 - No. (SG-7) 232/16 *Juglans elliptica* Principi, syntype; Fig. 5 - No. (SG-12) 232/4b *Juglans elliptica* Principi, syntype; Fig. 6 - No. 328/1a *Ilex longifolia* Sismonda; Fig. 7 - No. (SG-9) 233/1 *Juglans obtusifolia* Heer; Fig. 8 - No. (SG-20) 203/1 *Quercus charpentieri* Heer.

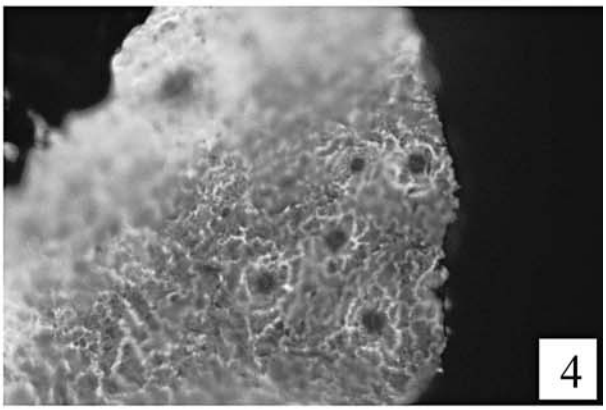
PLATE 3

Sloanea elliptica (Andreánszky), Z. Kvaček & Hably as original specimens of Principi 1916.

Fig. 1 - No. (SG-19) 216/1 *Quercus salicina* Saporta; Fig. 2 - No. (SG-10) 232/11 not figured in Principi's work, small and large leaves, dominance of the species; Fig. 3 - No. (SG-14) without inventar number, not figured in Principi's work, typical leaf morphology; Fig. 4 - *Sloanea peolai* (Principi) Hably, Tamás & Cioppi, No. SG-34 without inventar number, not figured in Principi's work, leaf; Fig. 5 - *Sloanea peolai* (Principi) Hably, Tamás & Cioppi, No. (SG-34-20-3.tif), cuticle, fm; Fig. 6 - *Sloanea elliptica* (Andreánszky), Z. Kvaček & Hably, No. (SG-21) without inventar number, not figured in Principi's work, typical leaf morphology.







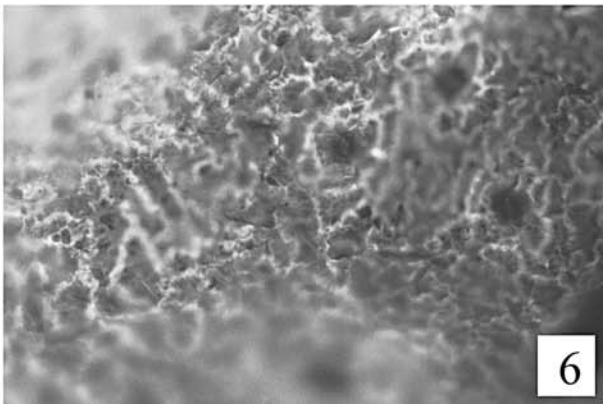


PLATE 1

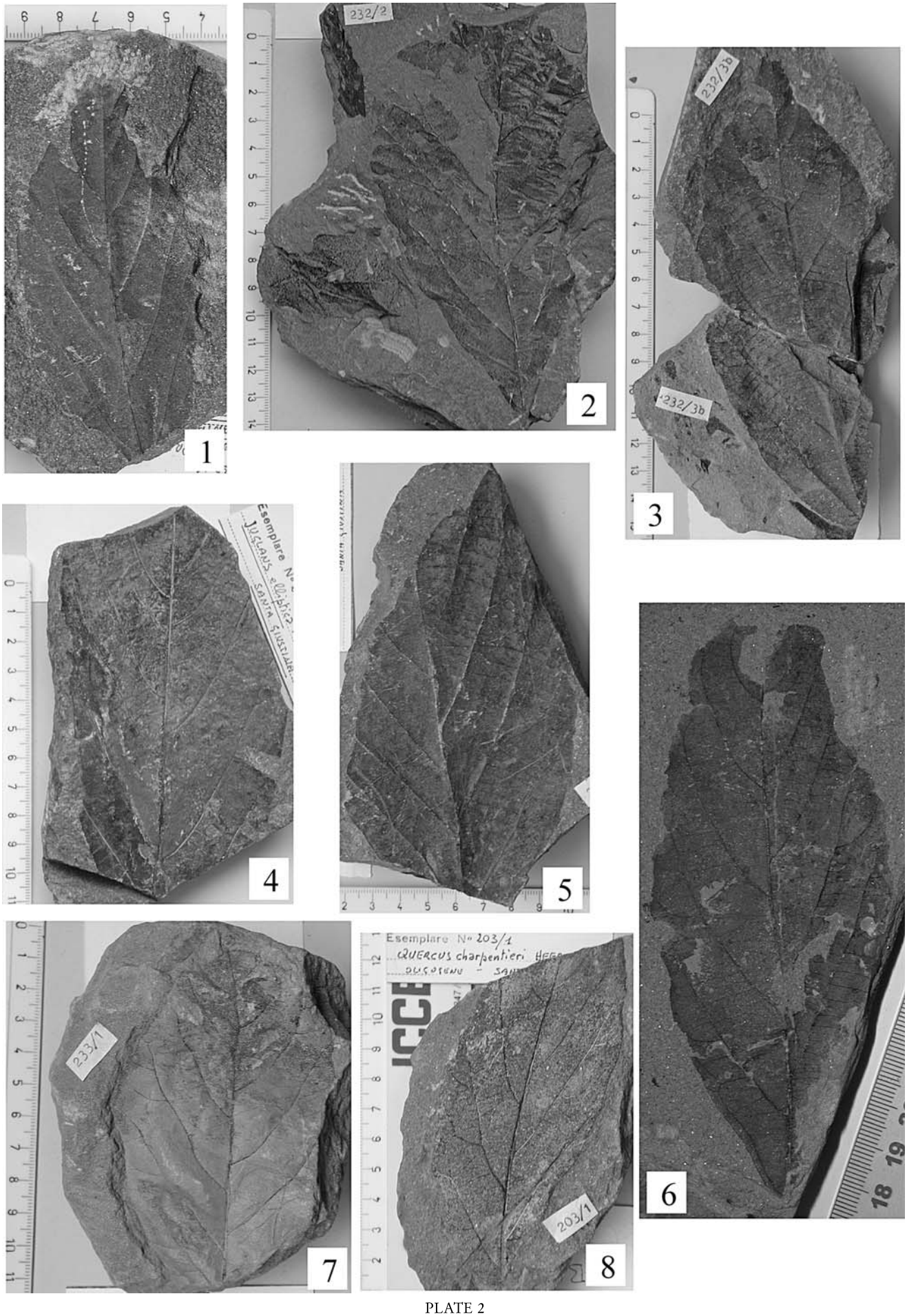


PLATE 2

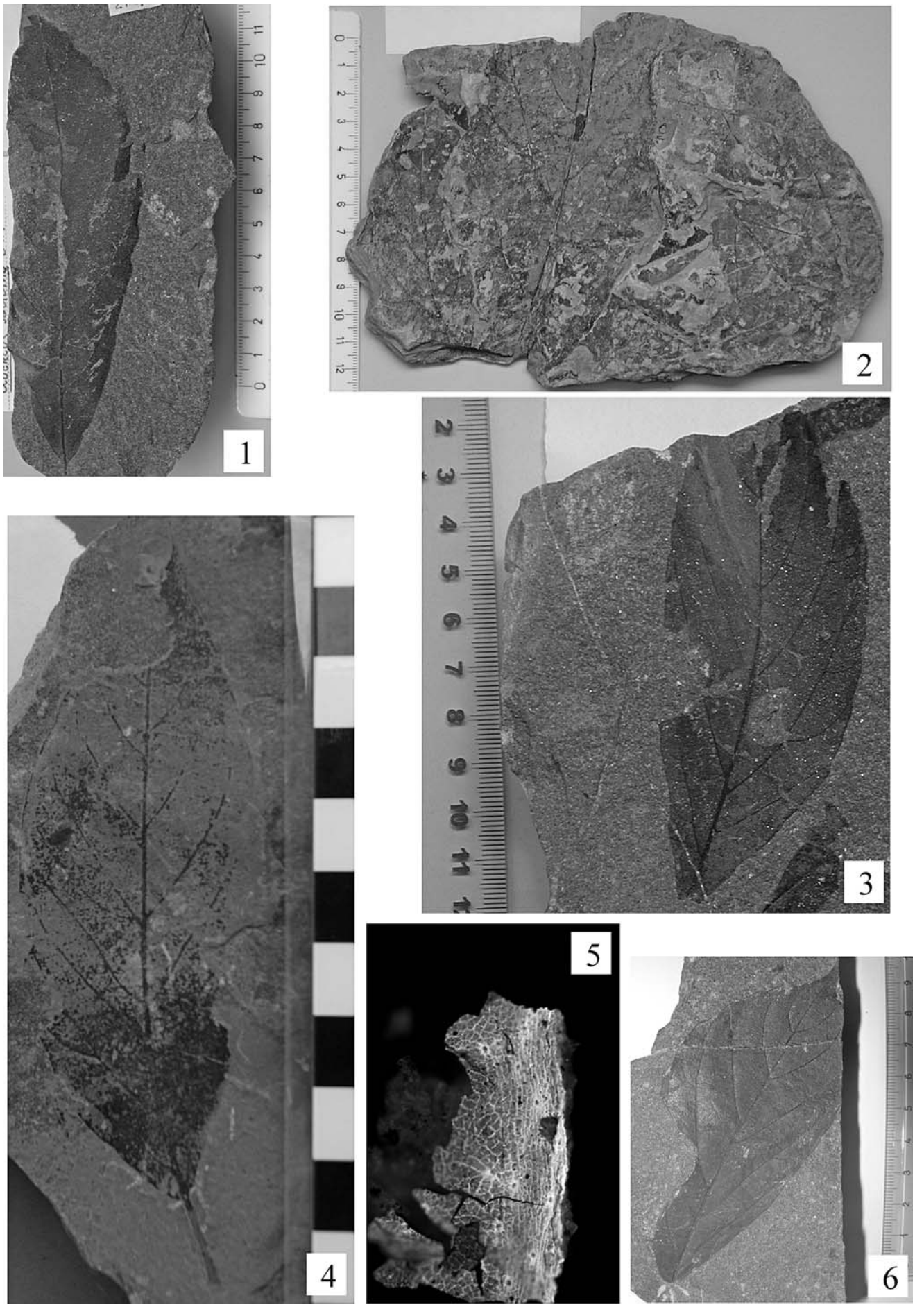


PLATE 3

closely related to climate, first of all the amount of precipitation (Tamás & Hably 2005).

Conclusions

The epidermal structures of *S. elliptica* and *S. peolai* provide unequivocal evidence that the two species existed in the Oligocene flora of Santa Giustina. *S. peolai* is a rare accessory element, whereas *S. elliptica* predominates in the flora.

The leaves of the latter species are extremely large which is also observable in the case of the leaves of other taxa in Santa Giustina. Although the taxonomic revision of the flora is in progress our studies so far corroborate warm and humid conditions or at least a habitat with abundant water supply. Riparian habitat is presumable since numerous taxa possess similarly large leaves.

With the new record of *Sloanea elliptica* the area of the species during the Oligocene greatly increased. Since it was proved to be a dominant element in the Hungarian Oligocene in both – the Buda and Bükk – Tectonic Units and has mass occurrence also in Slovenia and Italy (Santa Giustina) the species must have found its climatic optimum in this area during the Oligocene. Distribution of the species has to be interpreted in the context of palaeogeography, i.e. the Lower Oligocene strata of Hungary and Slovenia were formed in the integrated Palaeogene Basin which possessed nearly the same geographic position as Slovenia today (Kovács et al. 1996/97; Tamás & Hably 2005). Consequently, it must situated much closer to the region of Santa Giustina than today. The nearby position of the localities and the dominant character of *S. elliptica* in all fossil assemblages suggest an extensive area of the species in the middle part of Southern Europe.

Sloanea, formerly described only from Palaeogene assemblages, has previously been recorded as a relict element also in the thermophilous flora of Mataschen from the Late Miocene of Austria (Kovar-Eder & Hably 2006).

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