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THE EARLY OLIGOCENE FLORA OF SANTA GIUSTINA (LIGURIA, ITALY) - REVISION AND COMPARISON WITH THE FLORA OF THE TARD CLAY FORMATION

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Abstract. Based on palaeobotanical material preserved at the University of Genoa, Italy (DIP.TE.RIS.), a revision of the Early Oligocene flora of Santa Giustina, as well as the 1916 monograph of Principi, was undertaken. It is shown that apart from members of the Lauraceae family, *Eotrigonobalanus furcinervis* and *Sloanea olmediaefolia* were dominant in the flora, which was mainly composed of warmth-demanding species. The site is primarily characterized by remnants of the vegetation developed under warm and moist climate and abundant water supply. A few additional plants from the neighboring zonal vegetation are also present. The flora is quite reminiscent of that of the Tard Clay Formation, part of the Inner Carpathian Region, providing a proven link to the floristic relationships of these areas. Up to the Pre-Neogene, the Inner Carpathian Region and the surrounding Alpine-Carpathian-Dinaric Region was composed of a composite terrane that 1) existed independently from Stable Europe, and, 2) had a much more southerly position than today. This terrane collage was sharply bordered from all directions except west, as is supported by new evidences of the floristic affinities with the Santa Giustina flora.

Riassunto. Viene presentata la revisione della flora di età Eo-Oligocenica di Santa Giustina sulla base del materiale conservato all'Università di Genova (DIP.TE.RIS.), così come sulla monografia di Principi del 1916. Si dimostra che a parte forme della famiglia Lauriaceae, le forme *Eotrigonobalanus furcinervis* e *Sloanea olmediaefolia* furono dominanti nella flora, composta da specie di clima caldo. La località è caratterizzata soprattutto da resti di una vegetazione sviluppatasi in clima caldo umido e con abbondante disponibilità di acqua. Si aggiungono a questa flora poche piante provenienti da associazioni vegetali dei dintorni. La flora ricorda strettamente quella della Tard Clay Formation, nei Carpazi interni, dimostrando con questo un legame floristico tra le due aree. Prima del Neogene, i Carpazi interni e la regione Alpino-Dinarica erano formati da un insieme di *terrane* che erano indipendenti dall'Europa stabile ed occupavano una posizione decisamente più meridionale dell'Attuale. Questo insieme di *terrane* aveva bordi ben definiti in tutte le direzioni, tranne che verso ovest come indicano le nuove evidenze di affinità floristiche con la flora di Santa Giustina.

Introduction

The flora of the Santa Giustina site (Liguria, northern Italy) was first published by Principi (1916, 1921); recently, the site was further researched and new results were communicated by Gregor & Knobloch (2001). Most of the material studied by Principi (1916) is deposited in the palaeontological collection of the Genoa University (DIP.TE.RIS.), and that collection served as the basis for the present revision of the Santa Giustina flora.

The monograph of Principi, published more than 90 years ago, contains excellent illustrations and is not only an important reference, but, is also great support material in regards to the lost specimens. Revisionary work is leading to a reevaluation of the originally published taxa. Recently, the genus *Sloanea* was published (Hably 2007), in which cuticular evidences were presented in support of the presence of this important genus. In the current revision, all well-preserved specimens that allowed safe identification based on current taxonomic procedures will be discussed.

The layers containing most of the plant remnants are in the middle Stampian strata, while those containing the ferns are of upper Stampian position (Lorenz 1969), that is, Oligocene. Our revisions have revealed many taxa in common with those of the Early Oligocene flora of the Inner Carpathians, in spite of the rather great distance between them. At the same time, it is

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known that the Inner Carpathian region and the surrounding Alpine-Carpathian-Dinaric terrane collage, which existed independently from Stable Europe even in the Early Oligocene, was, on one hand, positioned much more southerly, and, on the other hand, was bordered by the sea from all directions but west, with which it could have had a floristic interaction (Hably 2006; Hably & Tamás 2006).

Materials and methods

The current revision is based on the same material that had been used originally by Principi for his monograph (1916) and preserved at Genoa (see above). This also includes a fairly large additional amount of previously unidentified material of the same collection that did not appear amongst the illustrations of Principi's work. In the present synonym list we added the corresponding plate and figure numbers, and when available, also the inventory numbers in parentheses. Given that only very few cuticle samples were available, and most of those were in rather poor condition, making preparation practically impossible, identifications were based on macromorphology. The 1916 edition of the Principi monograph only covers Angiosperms, while in the 1921 edition he included Gymnospermns. In the present study we excluded ferns, and only partially dealt with Gymnosperms as this latter group contains some characteristic elements that deserved inclusion.

The revised flora of Santa Giustina was compared with that of the Tard Clay Formation found in the Inner Carpathian Region, most of which was previously revised and published (Hably 1979, 1992; Manchester & Hably 1997; Hably & Fernandez Marrón 1998; Kvaček & Hably 1998; Hably & Manchester 2000; Hably & Thiébaut 2002). For the comparative revision the following materials were used: the Santa Giustina material preserved at the palaeobotanical collection of the University of Genoa (DIP.TE.RIS.); several thousand specimens from the Budapest and Eger-Kiseged sites, preserved in the palaeobotanical collections of the Hungarian Natural History Museum (BP); and the Eger-Wind Factory lower flora preserved at the Mátra Museum in Gyöngyös. Most of the revisions were based on macromorphology, since cuticles were rarely available in the Santa Giustina samples. However, when cuticle samples were available, they were analyzed under Nikon Eclipse 600 fluorescent microscope in the palaeobotanical laboratory of the Hungarian Natural History Museum.

Revision of the Oligocene flora of Santa Giustina (revision of the 1916 monograph of Principi)

Currently accepted names from the 1916 monograph by Principi are accompanied by the corresponding synonyms, and plate and figure numbers used in the original monograph. Whenever it was possible to link the figure with the specimen, we also provide the corresponding inventory number of the original collection.

Doliostrobus taxiformis (Sternberg) Z. Kvaček

2002 *Doliostrobus taxiformis* (Sternberg) Z. Kvaček emend. Kunzmann; Z. Kvaček, p. 51, pl. 1. figs. 1-3.

1921 *Cryptomeria Sternbergii* (Göppert) Gardn., Principi, pl. 16, fig. 6.

1921 *Glyptostrobus Europaeus* Brongniart, Principi, pl. 16, fig. 7.

Remarks. This extinct genus is one of the most characteristic Gymnosperms of the flora, widely distributed in the Early Oligocene of Europe, but missing from the Late Oligocene.

Pinus sp.

Pl. 5, fig. 3

Remarks. This is a pine cone, confirming the existence of this genus as an accessory element.

Daphnogene sp.

Pl. 1, figs 1, 2

1916 *Litsaea magnifica* Saporta, Principi, pl. 50, fig. 9

1916 *Cinnamomum Rossmässleri* Heer, Principi, pl. 51, fig. 3, pl. 55, fig. 4

1916 *Cinnamomum polymorphum* Heer, Principi, pl. 51, figs. 4, 5, pl. 53, figs. 1, 8

1916 *Cinnamomum grandifolium* (Heer) Schimper, Principi, pl. 51, fig. 6, pl. 52, fig. 1, pl. 53, fig. 4

1916 *Cinnamomum Scheuchzeri* Heer, Principi, pl. 51, fig. 7, pl. 53, figs. 2, 5, 9, pl. 54, figs. 1, 2

1916 *Cinnamomum Paoluccii* Principi, Principi, pl. 52, fig. 2

1916 *Cinnamomum spectabile* Heer, Principi, pl. 52, figs. 3, 4, pl. 53, fig. 7

1916 *Cinnamomum lanceolatum* Heer, Principi, pl. 52, fig. 5, pl. 53, fig. 6

1916 *Cinnamomum Buchi* Heer, Principi, pl. 52, fig. 6

1916 *Cinnamomum transversum* Heer, Principi, pl. 53, fig. 3

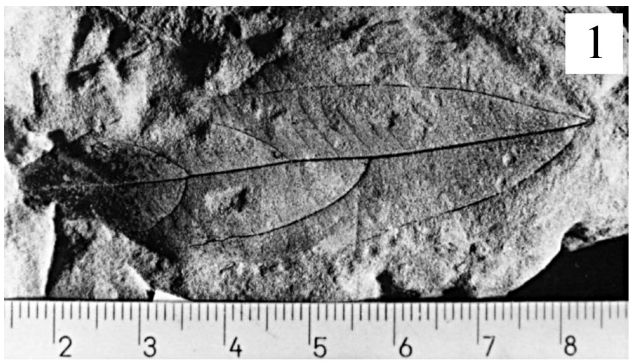
1916 *Daphnogene Gastaldii* Sismonda, Principi, pl. 54, figs. 5, 6

1916 *Daphnogene Raincourli* Saporta, Principi, pl. 55, figs 2, 3

Remarks. Remnants of the genus *Daphnogene* are easily recognized macromorphologically. Although common in the flora, they are not really abundant, similar to the situation in the Lower Oligocene sites in Hungary (where they become much more frequent by the Upper Oligocene).

PLATE 1

Fig. 1 - *Daphnogene* sp. (Previously treated as *Cinnamomum buchi*, DIP.TE.RIS, No 78/1); Fig. 2 - *Daphnogene* sp. (Previously treated as *Cinnamomum lanceolatum*, DIP.TE.RIS, No 80/6); Fig. 3 - Lauraceae sp. (Previously treated as *Terminalia pannonica*, DIP.TE.RIS, No 326/1); Fig. 4 - Lauraceae sp. (Previously treated as *Ficus lanceolata*, DIP.TE.RIS, No 259/1); Fig. 5 - Lauraceae sp. (Previously treated as *Ficus lanceolata*, DIP.TE.RIS, No 259/2); Fig. 6 - Lauraceae sp. (Previously treated as *Ficus arcinervis*, DIP.TE.RIS, No 247/1); Fig. 7 - *Platanus fraxinifolia* (Previously treated as *Pterocarya denticulata*, DIP.TE.RIS, No 224/1); Fig. 8 - *Eotrigonobalanus furcinervis* (Previously treated as *Castanea recognita*, DIP.TE.RIS, No 194/3); Fig. 9 - *Eotrigonobalanus furcinervis* (Previously treated as *Castanea sezanensis*, DIP.TE.RIS, No 195/1); Fig. 10 - *Eotrigonobalanus furcinervis* (Previously treated as *Quercus furcinervis*, DIP.TE.RIS, No 208/4); Fig. 11 - *Eotrigonobalanus furcinervis* (Previously treated as *Quercus furcinervis*, DIP.TE.RIS, No 208/5)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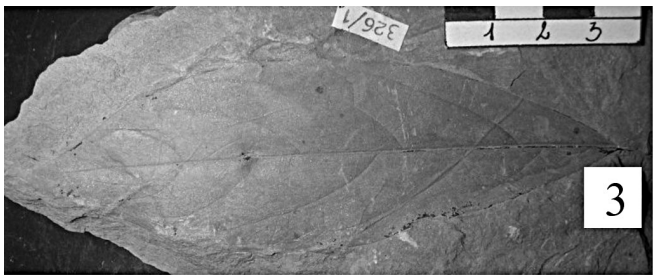
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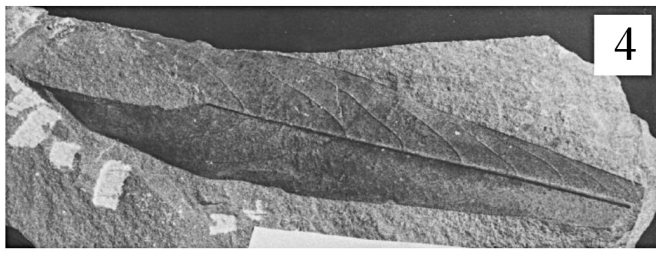
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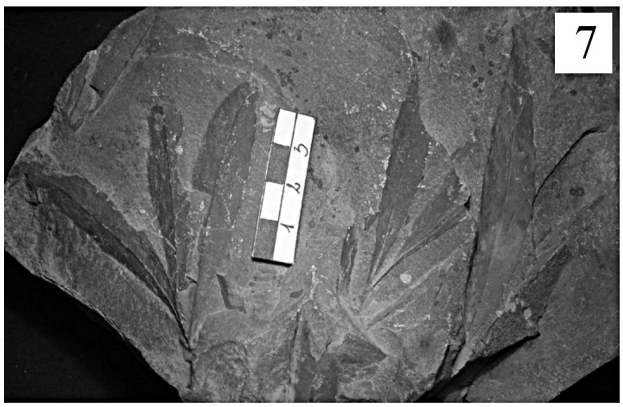
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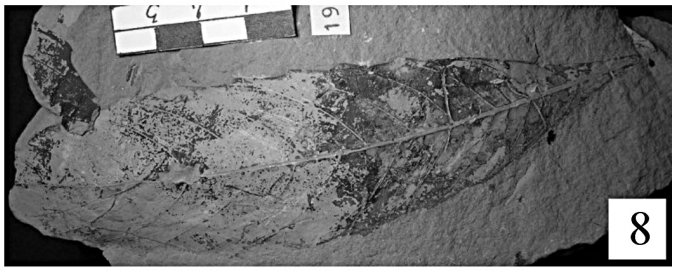
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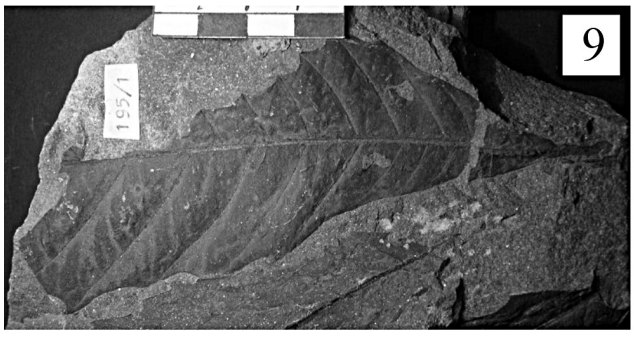
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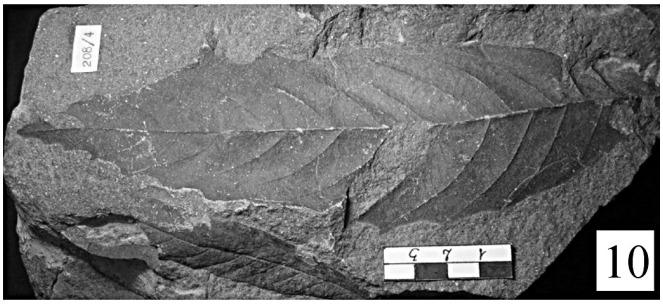
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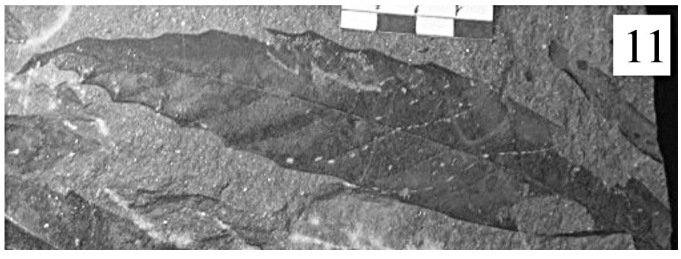
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Lauraceae gen. et. sp.

Pl. 1, figs 3-6

1916 *Ficus ligustrica* Principi, Principi, pl. 26, fig. 5, pl. 31, fig. 3
1916 *Ficus lanceolata* Heer, Principi, pl. 27, fig. 1(No. 259/1), fig. 3(No. 259/2), figs. 5, 6
1916 *Ficus coriacea* Principi, Principi, pl. 29, figs. 2
1916 *Ficus daphnogenes* Ettingshausen, Principi, pl. 30, fig. 3
1916 *Ficus arcinervis* Heer, Principi, pl. 30, fig. 6 (No. 247/1)
1916 *Ficus uranii* Ettingshausen, Principi, pl. 31, fig. 4
1916 *Ficus atlantidis* Ettingshausen, Principi, pl. 32-33, fig. 1
1916 *Ficus ettingshauseni* Principi, Principi, pl. 32-33, fig. 4, pl. 34-35, fig. 4
1916 *Laurus Reussi* Ettingshausen, Principi, pl. 45, figs. 4, 5, pl. 48, fig. 5
1916 *Laurus grandifolia* Ettingshausen, Principi, pl. 45, fig. 6
1916 *Laurus Fürstenbergi* A. Br., Principi, pl. 45, fig. 7
1916 *Laurus longifolia* Principi, Principi, pl. 46, fig. 2
1916 *Laurus princeps* Heer, 46:4, Principi, pl. 48, fig. 2
1916 *Laurus Zeilleri* Principi, Principi, pl. 46, fig. 5
1916 *Laurus nectandroides* Ettingshausen, Principi, pl. 46, fig. 6, pl. 48, fig. 4
1916 *Laurus ocoteaefolia* Ettingshausen, Principi, pl. 47, figs. 1, 2
1916 *Laurus primigenia* Unger, Principi, pl. 47, figs. 3, 4, 5, 6
1916 *Laurus szwoszowicziana* Unger, Principi, pl. 47, fig. 7
1916 *Laurus tetrantheroides* Ettingshausen, Principi, pl. 47, fig. 8, pl. 48, fig.10
1916 *Laurus Haueri* Ettingshausen, Principi, pl. 47, fig.9
1916 *Laurus attenuata* Wat., Principi, pl. 48, fig. 1
1916 *Laurus obovata* Weber, Principi, pl. 48, figs. 3, 9
1916 *Laurus tristaniaefolia* Web., Principi, pl. 48, fig. 6
1916 *Persea superba* Saporta, Principi, pl. 49, fig. 6
1916 *Oreodaphne Massalongoi* Paol., Principi, pl. 54, figs. 3, 4
1916 *Oreodaphne Heeri* Gaudin, Principi, pl. 54, figs. 7, 8
1916 *Bombax longifolium* Principi, Principi, pl. 62, figs. 3, 4
1916 *Bombax Procaccinii* Principi, Principi, pl. 62, fig. 5
1916 *Terminalia pannonica* Unger, Principi, pl. 72-73, figs. 3, 4 (No. 326/1ab)
1916 *Eugenia haeringiana* Unger, Principi, pl. 72-73, figs. 5, 6, 7
1916 *Eugenia aizoon* Unger, Principi, pl. 72-73, fig. 8
1916 *Daphnogene protogaea* Ettingshausen, Principi, pl. 72-73, fig. 9
1916 *Grevillea lancifolia* Heer, Principi, pl. 72-73, figs. 10, 11

Remarks. Specimens belonging to this group are abundant in the flora, well represented in the monograph by illustrations of numerous original specimens. However, since these specimens have their cuticles poorly preserved, we had to rely on macromorphology, and determinations could only be made to family rank, not below that level. It is noted here that remains belonging to this family are also abundant in the Lower Oligocene flora of Hungary.

?Platanus neptuni (Ettingshausen) Bůžek, Holý, Kvaček

1967 *Platanus neptuni* (Ettingshausen) Bůžek, Holý, Kvaček, p. 205, pl. 1. figs. 1-6, pl. 2. figs. 1-9.
1916 *Carya bilinica* Unger, Principi, pl. 14, fig.3, pl. 15, fig. 3

Remarks. In the original monograph, two figures refer to the presence in the Santa Giustina flora of the type form of the species, that is, the simple leaved form. However, no supportive voucher was found in the collection, not even among the unprocessed specimens. Thus, it is concluded that if the species was indeed present, it only had a subordinate role.

Platanus neptuni mf. **fraxinifolia** (Johnson & Gilmore) Kvaček & Manchester

Pl. 1, fig. 7

2004 *Platanus neptuni* mf. *fraxinifolia* (Johnson & Gilmore) Kvaček & Manchester, p. 11, fig. 7.
1916 *Carya denticulata* (Weber) Heer, Principi, pl. 14, figs. 5, 6, 7 (No. 224/1).

Remarks. Currently subsumed into *Platanus neptuni* as a morphoform (Kvaček & Manchester 2004), one specimen referable to this taxon was found among remnants of compound leaves in the Principi collection. As a rare accessory element, it must have played a subordinate role in the flora. In Hungary it is absent in the Lower Oligocene, but known in the Upper Oligocene.

Platanus cf. **schimperi** (Heer) Saporta & Marion

Pl. 5, fig. 9

1912 *Platanus schimperi* (Heer) Saporta et Marion; Laurent, p. 102-107, pl. 10. fig. 3, pl. 11. fig. 5., pl. 12, fig. 1.

Remarks. The collection contains a single unaccessioned specimen with venation clearly referring to *Platanus*, most probably *P. schimperi*, the only European Paleogene species that possesses morphological features of a "modern" *Platanus*. In Hungary *P. schimperi* has been recorded as a very rare accessory element of the Tard Clay Formation with only one specimen being found in Budapest (Pálfalvy 1978) and one in Eger-Kiseged (Andreánszky 1965). The Paleogene has basically been characterized by *P. neptuni*; the "modern" lobed-leaf species of *Platanus* only appear much later in Europe, in the Upper Miocene (Pannon), quite often abundantly represented by *P. leucophylla*.

Eotrigonobalanus furcinervis (Rossmässler) Walther & Kvaček

Pl. 1, figs 8-11

1989 *Eotrigonobalanus furcinervis* (Rossmässler) Walther & Kvaček, p. 583, pl. 33, figs. 1-6, pl. 38, fig. 3, pl. 39, fig. 1., pl. 40, figs. 1-5, pl. 41. figs. 1-4, pl. 42. figs. 1-4, pl. 43. figs. 1-6, text.-figs. 3-5.
1916 *Dryophyllum Dewallquei* Sapora et Marion, Principi, pl. 1, fig. 14, pl. 2, figs. 1, 2, 8
1916 *Castanea recognita* Schimper, Principi, pl. 2, fig. 5 (No. 194/3)

1916 *Castanea Perrandoi* Principi, Principi, pl. 2, fig. 7, pl. 3, fig. 2
1916 *Castanea sezannensis* Wat., Principi, pl. 3, fig. 1 (No. 195/1)
1916 *Castanea nervosa* Principi, Principi, pl. 3, fig. 4
1916 *Quercus furcinervis* Heer, Principi, pl. 3, fig. 7, pl. 4, figs. 1 (No. 208/4), 2, 3 (No. 208/5), 4
1916 *Quercus pseudolonchitis* Ettingshausen, Principi, pl. 5, fig. 8
1916 *Quercus Cyri* Unger, Principi, pl. 6, figs. 1, 9
1916 *Quercus drymeja* Unger, Principi, pl. 6, figs. 2, 3
1916 *Quercus mediterranea*, Principi, pl. 6, figs. 4,5
1916 *Quercus urophylla* Unger, Principi, pl. 6, fig. 7
1916 *Quercus De Visianii* Principi, Principi, pl. 6, fig. 8
1916 *Quercus lonchitis* Unger, Principi, pl. 6, figs. 10, 13, pl. 7, fig. 2
1916 *Quercus etymodrys* Unger, Principi, pl. 6, fig. 12
1916 *Quercus proteifolia* Paol., Principi, pl. 7, fig. 3
1916 *Myrica aemula* Schimper, Principi, pl. 17, figs. 1, 2, 3, 4, 5, 6, 7
1916 *Myrica longifolia* Unger, Principi, pl. 18, fig. 3
1916 *Myrica dentata* Principi, Principi, pl. 18, fig. 11
1916 *Myrica longifolia* Unger, Principi, pl. 18, fig. 5
1916 *Sapindus undulatus* A. Br., Principi, pl. 63, fig. 13
1916 *Ilex studeri* De la Harpe, Principi, pl. 65, fig. 3

Remarks. This is a dominant element of the flora, extremely well represented in both the monograph and the collection. Due to the variability that hindered recognition of various forms to belonging to the same species, it is not surprising that *Eotrigonobalanus furcinervis* appears under many different names in the monograph. The Santa Giustina flora contains explicitly large leaved specimens; new collections preserved at DIP.TE.RIS also contain very large leaved specimens, proving its dominance and that it flourished at its optimum. *Eotrigonobalanus furcinervis* is among the most characteristic and widely distributed species of the Lower Oligocene. Since in the southern parts of Central Europe it is confined to the Lower Oligocene, it also aids in age determination (Selmeczi & Hably 2010).

Quercus lonchitis Unger

Pl. 2, fig. 1

1850 *Quercus Lonchitis* Unger; Unger p. 33, pl. 9. figs. 3-8.

Material: Santa Giustina No. 164/1

Remarks. This species is neither mentioned nor illustrated in the Principi monograph, even though it is present on one of the original specimens also containing *Populus mutabilis crenata* Heer (which was described and depicted from that particular specimen). Since it occurs only in one specimen, it was probably a rare accessory element in the Santa Giustina flora. The species is locally frequent in the floras of the Tard Clay Formation, e.g. at Budapest-Óbuda (Hungary), and Socka (Slovenia).

Comptonia difformis (Sternberg) Berry

Pl. 2, fig. 2

1906 *Comptonia difformis* (Sternberg) Berry, p. 495
2004 *Comptonia difformis* (Sternberg) Berry; J. Kvaček, p. 548-549.
1916 *Comptonia Berryi* Principi, Principi, pl. 17, fig. 11. Material: Santa Giustina, No. 186/1
1916 *Comptonia elegans* Ettingshausen, Principi, pl. 17, figs. 12, 13

Remarks. *Comptonia difformis* morphologically is a very variable species and a rare accessory element in the flora of Santa Giustina, similarly, in the Oligocene flora of Hungary.

Comptonia schrankii (Sternberg) Berry

Pl. 2, fig. 6

1906 *Comptonia schrankii* (Sternberg) Berry, p. 514.
2009 *Comptonia schrankii* (Sternberg) Berry; Erdei & Rákosi, p. 49, figs. 4. 7, 8, 9.
1916 *Comptonia Schranki* Sternberg, Principi, pl. 17, figs. 14, 15, 16?, 17.

Material: Santa Giustina, No. 187/1

Remarks. Characteristic of the older Paleogene, this species has small lobes than those presented above; it occurs in the flora as a rare accessory element.

Engelhardia orsbergensis (Wessel et Weber) Jähnichen, Mai & Walther

Pl. 5, fig.1

1977 *Engelhardia orsbergensis* (Wessel et Weber) Jähnichen, Mai & Walther; Jähnichen et al. p. 323, pl. 9. fig. 4.
1916 *Sapindus cassoides* Ett, Principi, pl. 63, figs. 6, 7, 8
1916 *Sapindus Pythii* Unger, Principi, pl. 63, fig. 9

Material: 285/1a

Remarks. In addition to the illustrated specimens, the original collections contain some unpublished fragments which were nor depicted in the monograph, but with high probability belong to this species. The small number of specimens (leaflets) implies that it was a rare accessory element, which in comparison with other similar floras appears to be rather unusual, as in the Oligocene it normally occurs in great abundance.

Sloanea olmediaefolia (Unger) Z. Kvaček & Hably

Pl. 2, figs 3-5, 7-9; Pl. 3, figs 1, 4, 7

2008 *Sloanea olmediaefolia* (Unger) Z. Kvaček & Hably, Hably & Z. Kvaček, p. 140, fig. 1. 1-5.
1916 *Quercus Hamadryadum* Ettingshausen, Principi, pl. 4, fig. 7
1916 *Quercus artocarpites* Ettingshausen, Principi, pl. 5, fig. 1

1916 *Quercus Charpentieri* Heer, Principi, pl. 5, figs. 5 (No. 203/1), 6

1916?*Quercus chlorophylla* Unger, Principi, pl. 7, fig. 1

1916 *Juglans elliptica* Principi, Principi, pl. 10, fig. 2 (No. 232/1 Holotype), pl. 12-13, figs. 2, 3, 4

1916 *Juglans denticulata* Heer, Principi, pl. 10, figs. 3, 4

1916 *Juglandophyllum peramplum* (Saporta) Principi, Principi, pl. 14, figs. 1,2, pl. 15, fig. 1

1916 *Alnus nostratum* Unger, Principi, pl. 19, fig. 8

1916 *Populus mutabilis ovalis* Heer, Principi, pl. 21-22, fig. 9

1916 *Populus mutabilis crenata* Heer, Principi, pl. 23, fig. 3

1916 *Ficus perseaefolia* Principi, Principi, pl. 32-33, fig. 5 (No. 268/1)

1916 *Artocarpidium Desnoyersi* Wat., Principi, pl. 36-37, fig. 2

1916 *Artocarpidium bilinicum* Ettingshausen, Principi, pl. 36-37, fig. 4 (No. 280/1)

1916 *Laurus Notarisii* (Massalongo) Principi, Principi, pl. 45, figs. 8, 9

1916 *Laurus vetusta* Saporta, Principi, pl. 48, figs. 7 (No. 120/1), 8 (No. 120/2)

1916 *Persea Brauni* Heer, Principi, pl. 49, figs. 4, 5 (No. 88/4) there are toothed margin, which is not visible on the figure at Principi

1916 *Sterculia variabilis* Saporta, Principi, pl. 61, fig. 2 (No. 307/1)

1916 *Pterospermites incertus* Principi, Principi, pl. 62, fig. 1 (No. 311/1 Holotype)

1916 *Malpighiastrum protogaeum* Staub, Principi, pl. 64, fig. 3 (No. 316/1)

1916 *Ilex longifolia* Sismonda, Principi, pl. 65, fig. 1 (no 328/1a)

1916 *Rhamnus peolai* Principi, Principi, pl. 66, fig. 4

1916 *Rhamnus acuminatifolius* Weber, Principi, pl. 66, fig. 5

1916?*Rhamnus rectinervis* Heer, Principi, pl. 66, figs. 7, 8, 9, 10

1916?*Rhamnus deletus* Heer, Principi, pl. 66, fig. 11

1916 *Rhamnus lancifolius* Principi, Principi, pl. 66, fig. 13, pl. 67, figs. 7, 8(?)

1916 *Rhamnus Roesleri* Heer, Principi, pl. 66, fig. 14

1916 *Rhamnus acuminatus* Ettingshausen, Principi, pl. 67, figs. 2, 3

1916 *Cornus Büchi* Heer, Principi, pl. 67, fig. 12

1916 *Cornus studeri* Heer, Principi, pl. 67, fig. 13

1916 *Platanus deperdita* Massalongo, Principi, pl. 71, fig. 1

1916 *Palaeolobium heterophyllum* Unger, Principi, pl. 77, fig. 11

1916?*Cassia palaeo-speciosa* Staub, Principi, pl. 77, fig. 13

1916 *Diospyros brachysepala* A. Br., Principi, pl. 80, figs. 1 (No. 357/2 teeth are well visible on the original material), 2, 9

1916 *Diospyros macrophylla* Principi, Principi, pl. 80, fig. 11 (No. 360/1 Holotype)

1916 *Cinchonidium randiaefolium* Etingshausen, Principi, pl. 83, figs. 3, 4

1916 *Viburnum sismondai* Principi, Principi, pl. 84, fig. 1(No. 158/1), 2 (158/2)

1916 *Porana oeningensis* Unger, Principi, pl. 84, fig. 7

Remarks. *Sloanea* is one of the dominant species of the flora with leaves occurring in great numbers within the monograph as well as among the unpublished specimens. Its presence is clearly proven by our cuticle analyses, which also resulted in the synonymization under *Sloanea olmediaefolia* of several taxa published by Principi (Hably 2007; Hably & Kvaček 2006, 2008).

Leguminosae gen et sp.

1916 *Cassia berenices* Unger, Principi, pl. 76, figs. 1, 2, 3, 4, 5, 6, 7

1916 *Cassia phaseolites* Unger, Principi, pl. 76, figs. 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18

1916 *Cassia Fischeri* Heer, Principi, pl. 76, figs. 19, 20, 21, 22

1916 *Cassia Zephyri* Unger, Principi, pl. 67, figs. 23, 24

1916 *Cassia vulcanica* Ettingshausen, Principi, pl. 67, figs. 25, 26, pl. 77, figs. 4, 5

1916 *Cassia lignitum* Unger, Principi, pl. 77, figs. 1, 2, 3

Remarks. Both the monograph (with its illustrations) and the original collection contain many leaflet fragments, which probably belong to a legume. Similar specimens frequently occur in the European Oligocene.

Acherniaephyllum hydrarchos (Unger) Hably n. comb.

Pl. 5, figs 2, 4-8

1850 *Ficus hydrarchos* Unger, p. 165 (35), 33 (12): 2.

1960 *Acherniaephyllum kraeuseli* Rásky, p. 427, 1: 2, 3.

1960 *Passifloriaephyllum kraeuseli* Rásky, p. 433, 4: 16.

1916 *Cinnamomum rotundifolium* Principi, p. 119, 51: 8 (No. 84/2),

1916 *Dombeyopsis dubia* Principi, 61: 7.

1916 *Ficus populina* Heer, Principi, p. 75, 30: 5. (No. 270/1)

1916 *Magnolia ovalifolia*, Principi, p. 125, 55: 1 (No. 73/1)

1916 *Sterculia variabilis* Saporta, Principi, p. 128, 61: 1, 2. (No. 307/1)

Lectotype designated herein: **Socka** GBA 1851/03/21 (Type of *Ficus hydrarchos* Unger, Taf. 13, fig. 2).

Additional material: **Santa Giustina**: unpublished, No. 95/2; **Trbovlje:** unpublished material, GBA 2006/84/1157; **Budapest – Nagybátony-Újlak** brickyard: BP 60.33.1., 60.34.2. = 60.35.1. (counterpart), 60.36.1. = 60.37.1. (counterpart), 60.38.1., 2006.131.2., 2007.216.2., 2007.217.2., 2007.575.2., 2007.576.1., 2007.577.1., 2007.578.1., 2007.579.1., 2007.580.1., 2007.581.2., 2007.582.1., 2007.583.1., 2007.584.1., 2007.585.1.; **Eger-Kiseged**: BP 83.296.1., 2007.570.2., BP 2007.571.1., 2007.572.1., 2007.573.2., 2007.574.1.

PLATE 2

Fig. 1 - *Quercus lonchitis* (not figured in the Principi's coll., DIP.-TE.RIS, No164/1); Fig. 2 - *Comptonia acutiloba* var. *serrata* (Previously treated as *Comptonia elegans*, DIP.TE.RIS, No. 186/1); Fig. 3 - *Sloanea olmediaefolia* (Previously treated as *Artocarpidium bilinicum*, DIP.TE.RIS, No 280/1); Fig. 4 - *Sloanea olmediaefolia* (Previously treated as *Quercus charpentieri*, DIP.TE.RIS, No 203/1); Fig. 5 - *Sloanea olmediaefolia* (Previously treated as *Ficus perseaefoli*, DIP.TE.RIS, No 268/1); Fig. 6 - *Comptonia schrankii* (Previously treated as *Comptonia schrankii*, DIP.TE.RIS, No. 187/1); Fig. 7 - *Sloanea olmediaefolia* (Previously treated as *Sterculia variabilis*, DIP.-TE.RIS, No 307/1); Fig. 8 - *Sloanea olmediaefolia* (Previously treated as *Persea braunii*, DIP.TE.RIS, No 88/4); Fig. 9 - *Sloanea olmediaefolia* (Previously treated as *Pterospermites incertus*, holotype, DIP.-TE.RIS, No 311/1).


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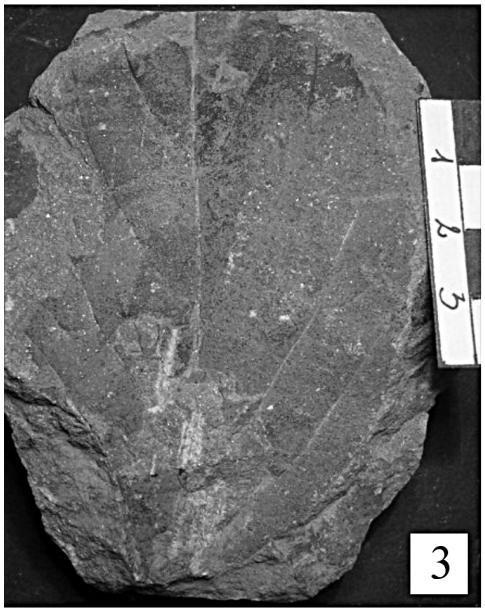
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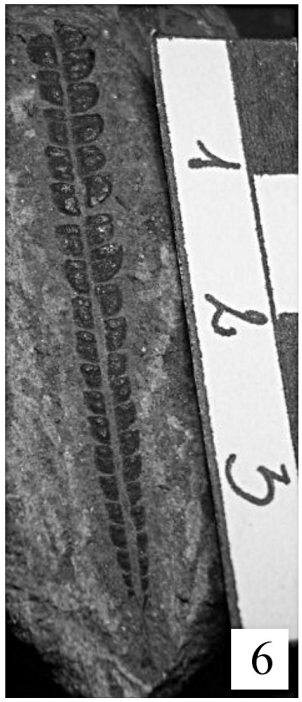
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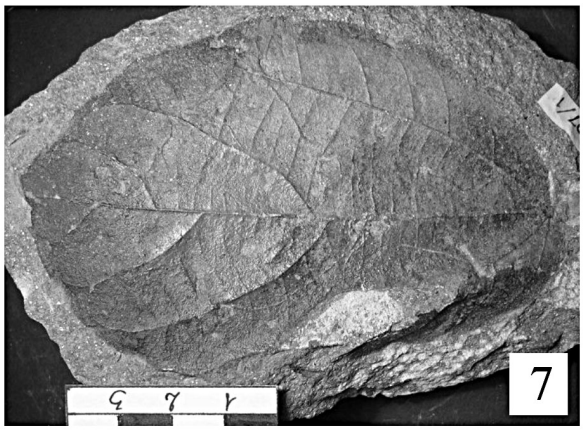
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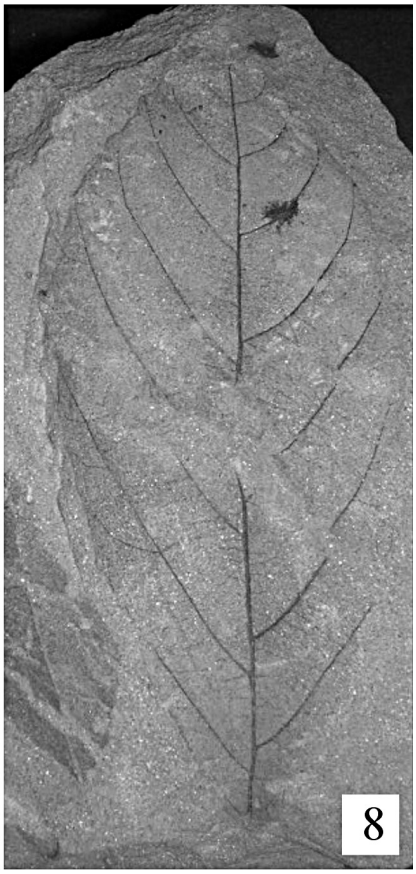
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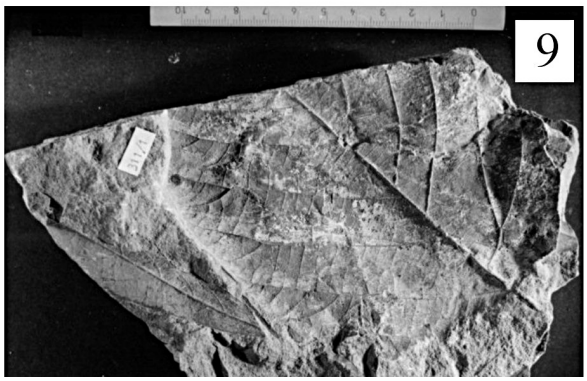
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Description. Leaves simple with petiole 0.3-2.5 cm long; usually elliptic, rarely ovate or obviate, 4.8-12 long by 4-8 cm wide. Basal part of leaf blade slightly asymmetrical, varies from rounded to acute, leaf apex usually attenuate, sometimes acute. Leaf margin entire up to the middle or two-third of blade, serration only occurs in the upper third or upper half. Teeth sparse, irregular, sometimes only a single tooth found (e.g. BP 2007.575.2., Principia 61: 7), occasionally with a miniature tooth below it (BP 2007.217.2); or leaf sometimes with 3 to 4 large, blunt, low-angle teeth on the margin (BP 60.34.2., Unger 33: 2). Since teeth are sparsely spaced, in many leaf fragments these are absent. Primary vein strong, with prominent secondary basal veins on each side; from these, occasionally thin additional third-order basal veins depart. In case of leaves with acute and slightly asymmetrical bases these additional thin basal veins may only appear on one side (BP 2007.575.2.), occasionally departing from the strong secondary basal vein instead of the basal part of the leaf base (BP 2007.570.2). Secondary veins 2 to 4, these are only found in the upper half or upper third of the blade. The strong basal veins are somewhat curving, more or less parallel with the margin. Veins usually do not terminate in teeth but recurve (with a brochidodromous character) (BP 2007.575.2.), or may end in a small teeth (BP 2007.217.2). The first pair of secondary veins terminates in a large tooth (BP 2007.217.2, BP 2007.575.2.). Venation between the basal veins and leaf margin shows a dense loop-like system, while the blade area between the principal vein and basal veins contains a dense third-order venation with horizontal or upside-down-V pattern.

Discussion. Due to their wide range of variability and that they usually occur in small numbers per site, these fragments have been discussed in the literature under various names. Only the comprehensive study of Early Oligocene floras has revealed the fact that it is a widely distributed but rare or accessory element of the Early Oligocene. It has been recorded from Budapest and Eger-Kiseged (Hungary), Socka and Trbovlje (Slovenia), and Santa Giustina (Italy), that is, it lived in the paleogene basin of the Alpine-Carpathian-Dinaric Region, and even in areas adjacent from the west.

Kydia kraeuseli (Rásky) Hably n. comb.

Pl. 4, figs 1-8

1943 *Ficus kräuseli* Rásky, p. 516, 17: 1
1943 *Cercis parvifolia* Lesquereux, Rásky, p. 527, 24:1
1943 *Cercis hungarica* Rásky, p. 528, 24: 2, 4)
1956 *Kydia palaeocalycina* Rásky, p. 176, 31: 1,2)
1966 *Ficus latsonoides* Andreánszky, p. 79, f. 71,72
1916 *Ficus tiliaefolia* A. Br., Principi, 29:4 (No. 277/9), 30: 4
1916 *Cercis virgilianum* Massalongo, Principi, 77: 6-8
1916 *Populus leuce* Unger, Principi, p. 65, 21-23: 1 (No. 163/4), 21-23: 3 (No. 163/1)

Additional material: **Santa Giustina**: No. 163/1, No. 277/2, 277/3ab, 277/5ab; **Budapest-Nagybátony-Újlak** brickyard: BP: 56.138.1.= 56.139.1. (Holotype of *Kydia palaeocalycina* Rásky with counterpart), 56.140.1., 56.141.1., 56.142.1., 56.143.1., 56.143.1., 60.31.1., 60.32.1., 63.1052.1., 63.1054.1., 64.414.1.= 64.415.1. (counterpart), 2004.440.1., 2004.439.1., 2004.448.1., 2006.96.2., 2006.97.2., 2006.98.2., 2006.99.1., 2006.100.2., 2006.101.1., 2006.102.2., 2006.103.2., 2006.104.1., 2006.105.1., 2006.106.1., 2006.107.2., 2006.108.1., 2006.109.1., 2006.110.1., 2006.111.1., 2006.112.1., 2006.113.1., 2006.114.1., 2006.115.2., 2006.116.1., 2006.117.2., 2006.118.2., 2006.119.1., 2006.120.1., 2006.121.2., 2006.122.1., 2006.123.1., 2006.124.1., 2006.125.1., 2006.16.2., 2006.127.2., 2006.128.1., 2006.129.1; **Budapest-Csillaghegy** brickyard: BP: 61.22.1., 61.23.1., 61.24.1. (Holotype of *Cercis hungarica* Rásky), Budapest-Szépvölgy brickyard: BP: 61.16.1.= 61.17.1., (Holotype of *Ficus kräuseli* Rásky with counterpart); **Trbovlje**: GBA 2006-84-15, 2006-84-402, 2006-84-712, 2006- 84-717, 2006- 84-1153, 2006- 84-1154, 2006-84-1155, 2006- 84-1156, 2006- 84-1158, 2006- 84-1159, 2006- 84-1160, 2006- 84-1162, 2006- 84-1163, 2006- 84-1164, 2006- 84-1165, 2006- 84-1166; **Eger-Wind** brickyard, lower flora: MM 61.821.1., 62.645.1., 62.646.1., 64.88.2., 64.132.2.

Description. Leaves simple, petioled. Intact petiole 4.0-7.0 cm long, but larger leaves may have petioles longer than 7 cm. Petiole may be as thick as 0.5 cm in diameter. Leaf blade very wide ovate, 3.5-17.5 cm long and 3.5-17 cm wide. Basal part cordate to truncate, apex rounded to acute. Leaf margin entire, sometimes with low-angle and blunt teeth, in which case the leaf blade exhibits a somewhat undulate character. Primary vein strong, with 2 basal veins starting at the very base of the blade. First pair of basal veins is rather weak and more or less parallel with the margin near the basal area. Second pair of basal veins strong, straight, and perpendicular to primary; approaching the margin the secondaries become thinner and connected with smaller veins in a loop-like pattern. Tertiary veins departing from the secondaries approaching the margin, these also forming

PLATE 3

Fig. 1 - *Sloanea olmediaefolia* (Previously treated as *Diospyros brachisepala*, DIP.TE.RIS, No 357/2); Fig. 2 - *Acherniaephyllum hydrarchos* (Previously treated as *Cinnamomum rotundifolium*, DIP.-TE.RIS, No 84/2); Fig. 3 - *Acherniaephyllum hydrarchos* (Previously treated as *Ficus populina*, DIP.TE.RIS, No 270/1); Fig. 4 - *Sloanea olmediaefolia* (Previously treated as *Diospyros macrophylla*, holotype, DIP.TE.RIS, No. 360/1); Fig. 5 - *Kydia kräuseli* (Previously treated as *Populus leuce*, DIP.TE.RIS, No 163/4); Fig. 6 - *Acherniaephyllum hydrarchos* (Previously treated as *Magnolia ovalifolia*, DIP.TE.RIS, No 73/1); Fig. 7 - *Sloanea olmediaefolia* (Previously treated as *Viburnim sismondai*, DIP.TE.RIS, No 158/1); Fig. 8 - *Kydia kräuseli* (Previously treated as *Populus leuce*, DIP.TE.RIS, No 163/1); Fig. 9 - *Kydia kräuseli* (Previously treated as *Ficus tiliaefolia*, DIP.TE.RIS, No. 277/9).


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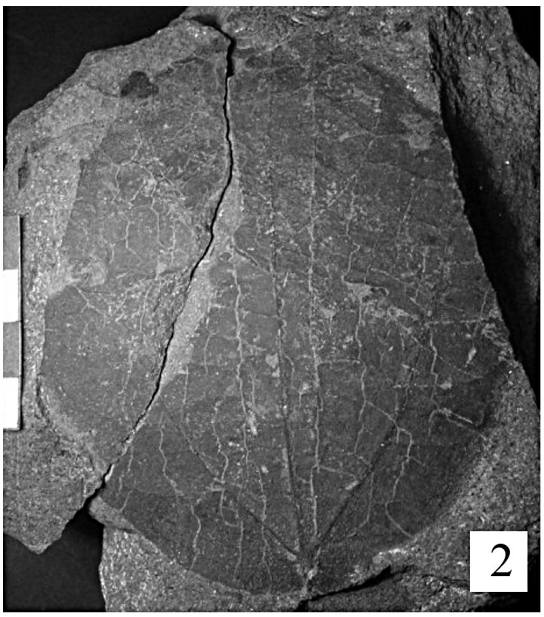
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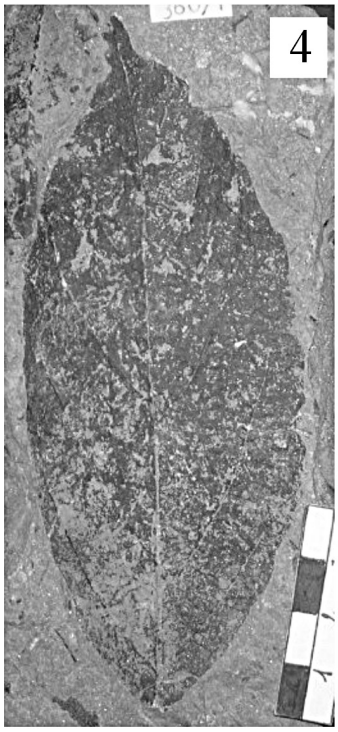
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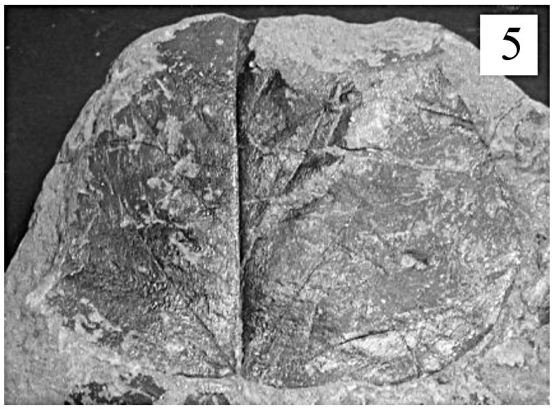
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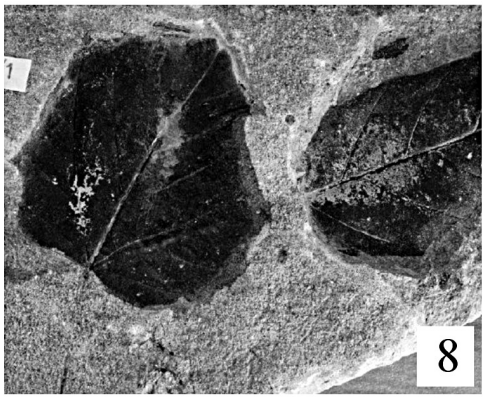
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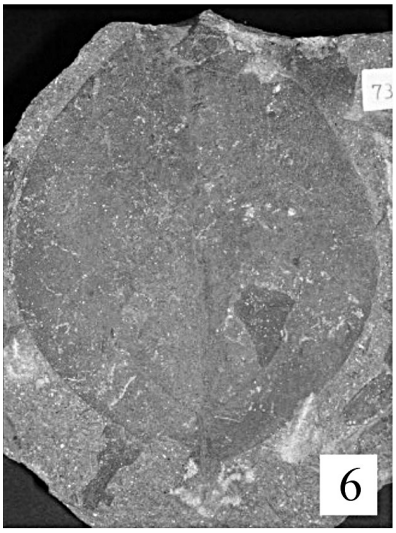
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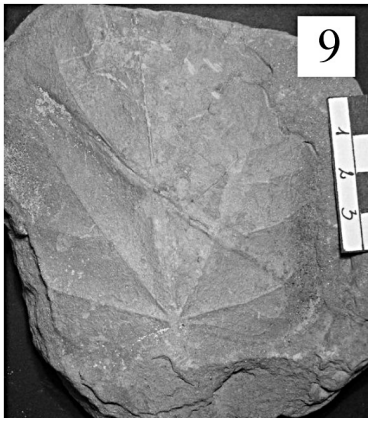
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a loop-like system of low-ranked veins. Additional secondary veins depart in a widely spaced manner from both the base and from each other; perpendicular to the primary vein. Besides the basal pair of veins, the departing of three or four additional pairs of secondary veins is observed.

Discussion. Even from the same formation, the species has been described under different names. Based on unpublished specimens in the collections at BP it can be concluded that it was an important accessory element in some sites of the Tard Clay Formation, and rare in other places. Its Early Oligocene occurrence are known from Hungary, Slovenia, and northern Italy. In Hungary, it was found in the so-called lower flora at the Eger-Wind Factory. Since this site has been (improperly) discussed as a single unit, it needs to be emphasized that the compositions of the lower and upper floras are markedly different. The lower flora should be regarded as Middle Oligocene, while the upper flora has its position above the Eger layer, thus possibly transitioning into the Miocene. Many species that are characteristic of the lower flora and that of the Tard Clay Formation, are absent in the Upper Oligocene.

Zizyphus zizyphoides (Unger) Weyland

1916 *Zizyphus ungeri* Heer, Principi, pl. 66, figs 1, 2

Remarks. A characteristic species of the Early Paleogene of southern Europe, it is known from the Eocene and Lower Oligocene. It is one of the dominant elements of the Tard Clay Formation, being common in both the Budapest and Eger-Kiseged sites. The northern boundary of its distribution is Kučlin (Czech Republic). It is regarded as a subxerophilous plant, in part supported by the fact that in the Santa Giustina flora it is a very rare accessory element.

Reconstruction of the flora, vegetation, and climate of the Oligocene of Santa Giustina

The flora revision presented here encompasses 18 taxa which obviously cannot represent a full record of the flora. This is due to the fact that many specimens were rather poorly preserved, precluding their identification; furthermore, ferns and palms (although present) were not the subject of this revision. However, after most of the Dicotyledones have been identified, we now have a good picture of the flora. It can be safely stated that there are 3 dominant taxa: *Sloanea olmediaefolia, Eotrigonobalanus furcinervis*, and members of the family Lauraceae. Also, many remains belonging to Leguminosae are present, as well as those of numerous species of palmate-leaved palms and ferns.

The special character to this flora is lent by *Sloanea olmediaefolia*, as well as those species that occur here as rare or maybe more-or-less frequent accessory elements, and known to occur only in some of the European Oligocene floras. Such species include *Quercus lonchitis*, *Kydia kraeuseli, Acherniaephyllum hydrarchos*, and even we can list here *Zizyphus zizyphoides*, a species whose range of distribution also has a well confined area. A number of accessory species, which often dominated the vegetation of certain European paleogene floras, have a subordinate role here, such as *Platanus neptuni,* or *Engelhardia orsbergensis*. The genus *Comptonia* is represented here by several species characteristic of the Paleogene.

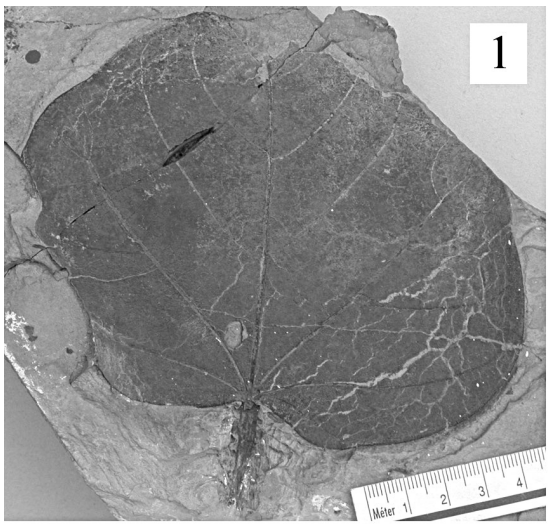
Based on the floristic composition it is assumed that the site was once a habitat with good water supply, perhaps positioned near a water body or found in an inundated area which only contained a small number of species of the nearby zonal vegetation. The vegetation must have been a multilayered stand with abundant and diverse fern populations (Principi 1921), as well as lianas; the composition of woody plants included both shrubby and arboreal dicotyledonous plants.

The presence of warmth-demanding plants in the flora indicates the climate must have been warm and subtropical. All taxa recorded here are thermophyllous, warm subtropical elements while there is a clear absence of temperate-zone species or genera. The dominant *Sloanea olmediaefolia* and members of the family Lauraceae are all warmth-demanding, as well as the accessory elements, *Kydia kraeuseli, Acherniaephyllum hydrarchos*, *Zizyphus zizyphoides, Platanus neptuni,* and *Engelhardia orsbergensis.* The presence of *Comptonia* refers to a wet(land) habitat although this simple fact cannot be used for climate identification. The generally large leaf size (Hably 2007) also refers to abundant water supply; it is observed that species recorded here have leaves much larger than those of the same species found in other European floras. The subordinate occurrence of xerophilous-subxerophilous species is also supportive to the above statements. For example, *Zizyphus zizyphoides,* which belongs in this category, is

PLATE 4

Kydia kräuseli

Fig. 1 - Budapest-Óbuda, No. BP 56.138.1. (paratype of *Kydia paleocalycina* Rásky); Fig. 2 - Santa Giustina, DIP.TE.RIS, No. 277/2 (Previously treated as *Ficus tiliaefolia*); Fig. 3 - Eger, Wind-bickyard, No. MM 62.645.1. (Previously treated as *Ficus latsonoides* Andreánszky); Fig. 4 - Trbovlje, No. GBA 2006/84/402; Fig. 5 - Budapest-Óbuda, No. BP 2006.117.2.; Fig. 6 - Santa Giustina, DIP.TE.RIS No. 163/1 (Previously treated as *Populus leuce*); Fig. 7 - Budapest-Óbuda, No. BP. 61.22.1.; Fig. 8 - Santa Giustina, DIP.TE.RIS No. 277/3 (Previously treated as *Ficus tiliaefolia*)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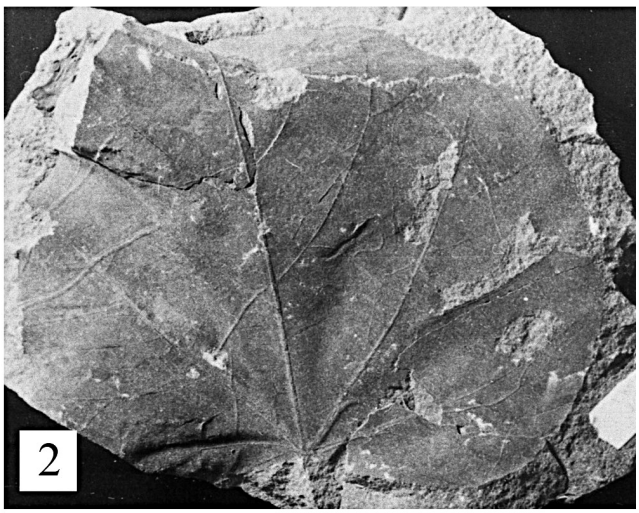
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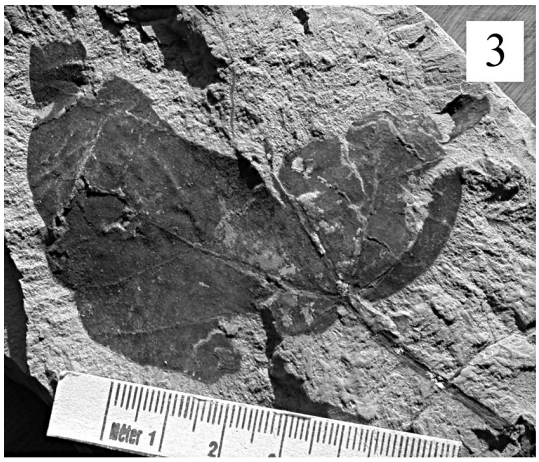
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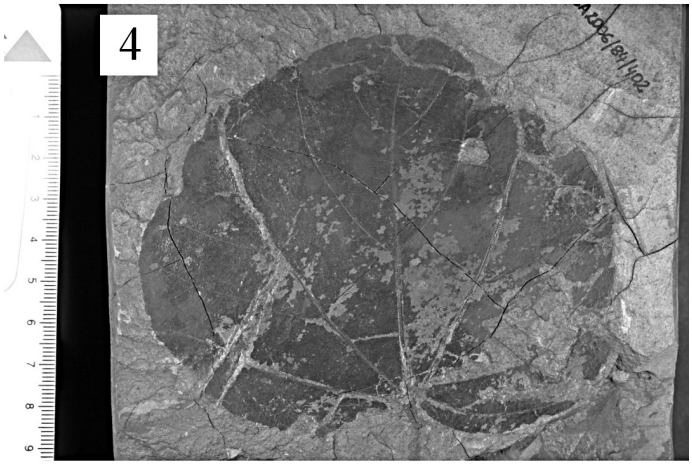
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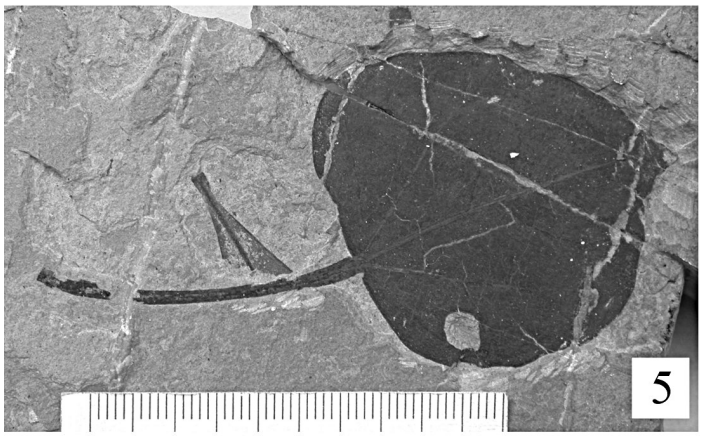
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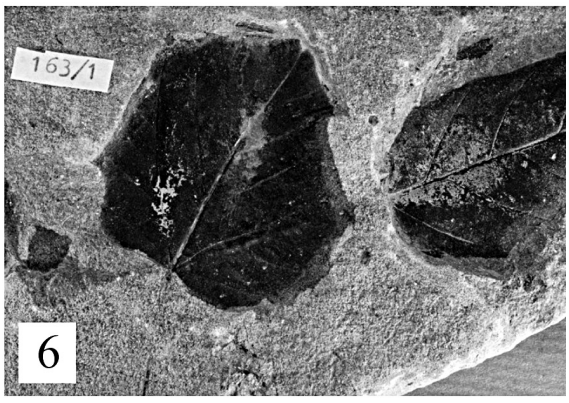
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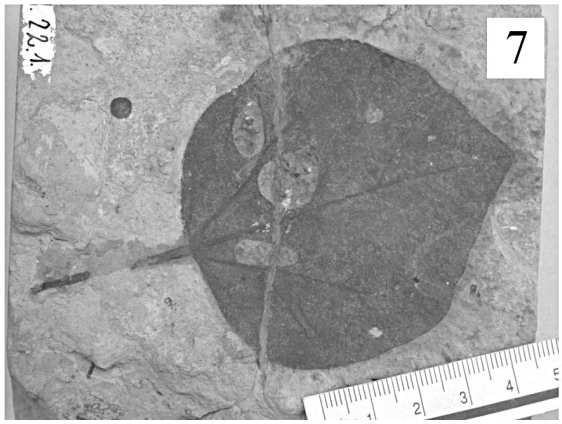
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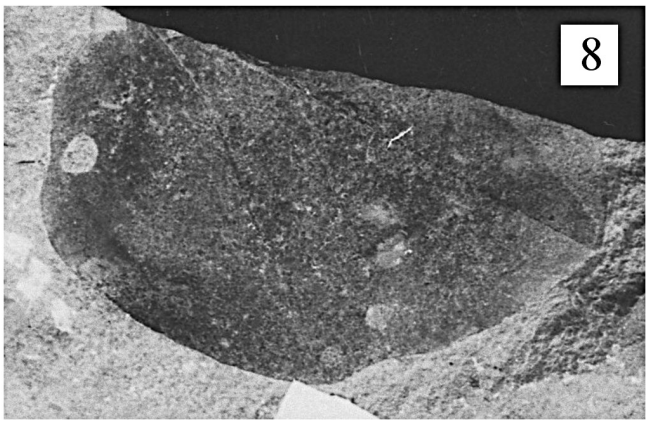
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known only from a very few specimens that were found at this site.

Flora of the Tard Clay Formation

The well-preserved flora of the Tard Clay, which includes some taxa of exotic character, has long been one of the more thoroughly researched floras (Andreánszky & Novák 1957; Andreánszky 1956, 1959, 1963ab, 1967; Hably 1979, 1986, 1992; Rásky 1943, 1956, 1960), with several species that have undergone revisions in the last decade (Manchester & Hably 1997; Kvaček & Hably 1998; Hably & Manchester 2000; Hably 2001; Hably & Thiébaut 2002). Dominant taxa include *Doliostrobus taxiformis, Eotrigonobalanus furcinervis, Zizyphus zizyphoides, Sloanea olmediaefolia, Engelhardia orsbergensis,* and several species of Lauraceae. Other characteristic species of this flora are *Raskya vetusta, Tetrapterys harpyiarum, Ailanthus tardensis, Kydia kraeuseli, Acherniaephyllum hydrarchos,* and *Sloanea eocenica*. Up to recent times, several species of the flora thought to have been endemic to the Inner Carpathian Region, namely *Tetrapterys harpyiarum*, *Ailanthus tardensis, Kydia palaeocalycina, Acherniaephyllum hydrarchos,* and *Sloanea eocenica*, have been found, most remarkably, in the Santa Giustina flora.

Along leaf remnants, many winged fruits have been recovered in great quantities, and several taxa have only been found as fruit samples; quite often, fruits are better preserved in the flora, than the leaves of the same taxon. This phenomenon can easily lead to the supposition of a "semipersistant" vegetation (Hably & Erdei 1999). This multilayered tropical-subtropical forest may have contained a rich array of lianas (e.g., *Smilax*) and climbing palms (Palmae). All species are considered warmth-demanding, mostly frost-intolerant, and the flora includes members of such tropical families as Elaeocarpaceae and Malpighiaceae.

Comparison of the Santa Giustina flora to that of the Tard Clay Formation

Shared elements: *Blechnum dentatum; Acrostichum lanzaeanum; Antrophytes egedensis; Pronephrium stiriacum; "Sequoia langsdorfii"; Doliostrobus taxiformis; Pinus* sp.*; Daphnogene* sp.*; Laurophyllum* sp.; Lauraceae gen. et sp.; *Acherniaephyllum hydrarchos; Comptonia schrankii; Myrica (Comptonia) acutiloba; Myrica (Comptonia) acutiloba* var. *dentata; Engelhardia orsbergensis; Eotrigonobalanus furcinervis; Platanus neptuni; Platanus schimperi; Quercus lonchitis; Sloanea olmediaefolia; Dalbergia bella;* Leguminosae gen. et sp.; *Kydia kraeuseli; Zizyphus zizyphoides; Sabal major.*

The Tard Clay flora comes from the upper layers of the formation, and since it has been recorded from the NP 23 nannoplancton zone (Nagymarosy & Báldi-Beke 1988), its age has been identified as the end of the Early Oligocene. In Hungary, this flora had been found in two tectonic units, namely the Buda and Bükk. In the Early Oligocene these areas had a more southwesterly position (in the territory of present-day Slovenia) as part of a unified Paleogene basin. During the pre-Neogene this area existed as an independent terrane, sharply separated from Stable Europe from the north, east and south, with some connection only to the west. The tectonic movements had a western-northeastern direction (Nagymarosy 1990; Csontos et al. 1992; Kovács et al. 1996/97). The Tard Clay Formation has a warmth-demanding flora, which includes some exotic elements, but has no traces of temperate-zone, arctotertiary plants. With respect to its present geographical and longitudinal position, this Thermophyllic aspect appears to be rather unusual, since in the relatively nearby floras found in Germany and Bohemia the temperate elements have had a significant role. The terrane theory has clearly proved that the Inner Carpathian and the surrounding Alpine-Carpathian-Dinaric were made of a terrane collage up to the pre-Neogene, which had a position of more southerly than today.

Our revision has revealed a number of elements common between the Santa Giustina flora and that of the Tard Clay Formation as part of the Inner Carpathian Region, with an overlap of taxa of 44%, which is considered rather high. The common elements include such specific taxa as *Kydia kraeuseli* or *Acherniaephyllum hydrarchos*, which are only known from these areas. The above outlined affinities are proofs of floristic connections between the respective areas leading back as far as the early Oligocene.

PLATE 5

Fig. 1 - *Engelhardia orsbergensis* DIP.TE.RIS No. 285/1, Santa Giustina; Fig. 2 - *Acherniaephyllum hydrarchos* DIP.TE.RIS No. 95/2, Santa Giustina; Fig. 3 - *Pinus* sp. DIP.TE.RIS No. 65/1, Santa Giustina; Fig. 4 - *Acherniaephyllum hydrarchos* DIP.TE.RIS No. 270/1 (Previously treated as *Ficus populina*); Fig. 5 - *Acherniaephyllum hydrarchos* No. GBA 1851/03/21, lectotype, and holotype of *Ficus hydrarchos* Unger, Socka; Fig. 6 - *Acherniaephyllum hydrarchos* No. BP 60.34.2., Budapest-Óbuda, (holotype of *Acherniaephyllum kraeuseli* Rásky); Fig. 7 - *Acherniaephyllum hydrarchos* No. BP 2007.217.2., Budapest-Óbuda; Fig. 8 - *Acherniaephyllum hydrarchos* No.BP 83.296.1., Eger-Kiseged; Fig. 9 - *Platanus* cf. *schimperi*, DIP.TE.RIS without number, Santa Giustina.

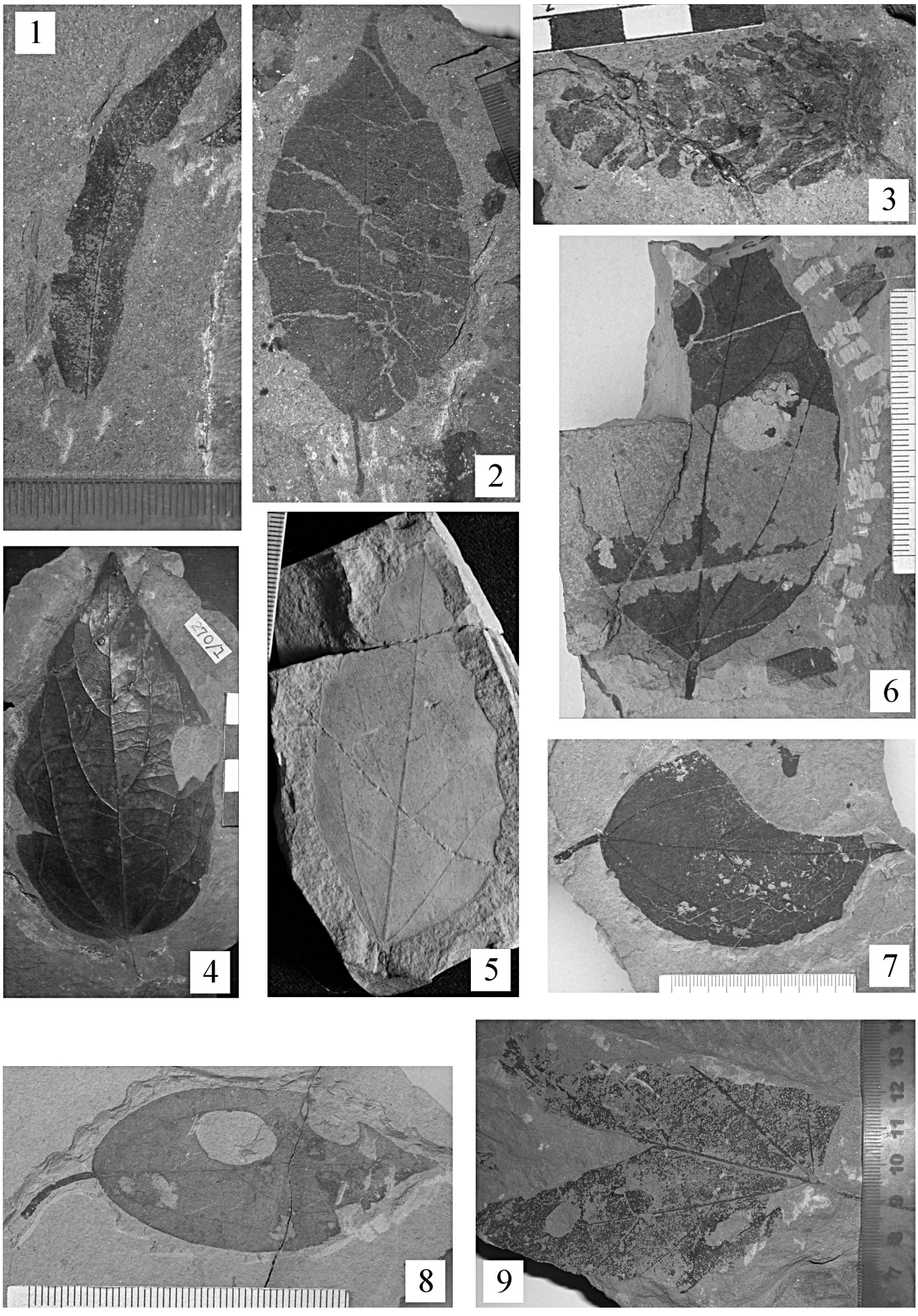
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Fig. 1 - Plant elements of the flora of Santa Giustina.
Comptonia schrankii, *Sloanea olmediaefolia*, *Acherniaephyllum hydrarchos*, *Platanus* cf. *schimperi*, *Engelhardia orsberigensis, Quercus lonchitis, Zizyphus zizyphoides*, *Platanus neptuni* mf. *fraxinifolia*, *Kydia kraeuseli*, *Eotriginobalanus furcinervis* (narrow form), Lauraceae gen. et sp., *Daphnogene* sp., *Eotriginobalanus furcinervis* (wide form), *Pinus* sp.

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