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Plant diversity at the final stage of the Miocene Climate Optimum – Revision of the flora of Leoben, Styria, Austria

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ABSTRACT. The floras of Leoben and Parschlug (Styria, Austria) derive from nearby basins along the Mur/Mürz fault system, representing the drowning stages of the mires in these basins. They are regarded as being similar in age. Based on its revision, the flora of Parschlug is interpreted to reflect the vegetation in the close lake surroundings and the hinterland of the respective basin. Subhumid sclerophyllous forest is concluded to be the most likely major vegetation type in the hinterland, which developed under seasonally dry climate. These results raised the question of a potential signal provided by the Leoben flora. A comparison of both floras, however, turned out to be impossible based solely on the monographical studies by Ettingshausen (1869a, 1888) and would require a comprehensive taxonomic revision, which is presented here. The Leoben flora is dated to the Middle Miocene (Langhian/Badenian, 14.9/ ±0.7 Ma). It comprises mainly leaves, but also remains of flowers, inflorescences and fructifications, mostly preserved as strongly compressed impressions. The present revision reduces the number of taxa from 382 (in Ettingshausen, 1888, excluding fungi) to ~175 or to ~150 when different organs of probably one biological fossil-species are fused. Although the taxonomic resolution is limited especially for entire-margined taxa due to the lack of cuticles, the floristic diversity is high. Spore-producing plants are generally rare. Conifers are diverse although their remains are not abundant except for *Glyptostrobus* and *Pinus*. Angiosperms include more than 30 families of which Betulaceae, Fagaceae, Lauraceae and Sapindaceae are most diverse. Two fossil-species are described for the first time and 8 new combinations of angiosperms are introduced.

Phytosociologically the flora represents plants of a floating-leaf plant zone, ferns, reeds and sedges from the lake margin and of swampy habitats, as well as woody taxa from swampy forests, along streams and in the closer surroundings of the lake segueing into mesophytic hinterland forests.

The Integrated Plant Record (IPR) vegetation analysis is applied to assess the most likely major vegetation type (zonal vegetation), and the Similarity Approach (application of Drudges) predicts the most likely modern vegetation proxies for the Leoben assemblage. Palaeoclimate proxies are assessed by the Climate Leaf Analysis Multivariate Program (CLAMP), and the Leoben flora is compared to floras in the Paratethys region and surroundings that are of similar age, namely Oberdorf, Parschlug (Styria), Mecsek Mts. (Hungary) and the Cypris Formation (northern Bohemia).

KEYWORDS: taxonomy, vegetation reconstruction, modern vegetation proxies, palaeoclimate

INTRODUCTION

The Leoben Basin is situated N of the town Leoben and about 20 km SW of the Parschlug Basin in Styria (Austria) (Fig. 1). Both basins are situated along the Mur/Mürz fault system in the Eastern Alps and are known for their rich late Early/early Middle Miocene plant assemblages. Based on the revision of the flora of Parschlug, the vegetation and climate were reconstructed in the surroundings of the Parschlug lake (Kovar-Eder et al., 2004, 2022). These results indicate sclerophyllous subhumid forest (sensu Kovar-Eder and Kvaček,

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2007; Teodoridis et al., 2011a, 2011–2021) as the most likely zonal vegetation type, whereby thermophilous mixed deciduous broadleaved forests distributed today in southern and southeastern Europe (sensu Bohn et al., 2004), are the most similar modern vegetation. The climate signal of Parschlug indicates distinct seasonality both in precipitation and temperature. These results are outstanding among the Early/Middle Miocene Central European records because this is the time interval of the Miocene Climate Optimum (~16.9–14.7 Ma, MCO) or the subsequent Middle Miocene Transition (MMCT) (e.g. Steinthorsdottir et al., 2020). For the MCO a greenhouse climate is assumed, whereas cooling and a less favourable climate related to the expansion of the Antarctic ice sheet are proposed for the MMCT (Shevenell et al., 2004, 2008; Lear et al., 2010). The age estimation of the Parschlug flora is based on radiometric data from the adjacent basins along the Mur/Mürz fault system (Sachsenhofer et al., 2010) because no such data are available from the Parschlug Basin.

In the light of the results for Parschlug, the Leoben flora, which was studied monographically by Ettingshausen (1869a, 1888), became a focus and it became evident that an interpretation of the vegetation and climate of this assemblage first requires a taxonomic revision. In addition to Ettingshausen's monographs, selected taxa served for further morphological studies (Ettingshausen 1878a, 1882, 1887, 1893, 1894). Later, this flora attracted little attention in palaeobotanical research, possibly because Ettingshausen had figured relatively few taxa compared to the high number of described ones. Hofmann (1933) provided mainly a summary of Ettingshausen's results. Thereafter only few taxa from the Leoben

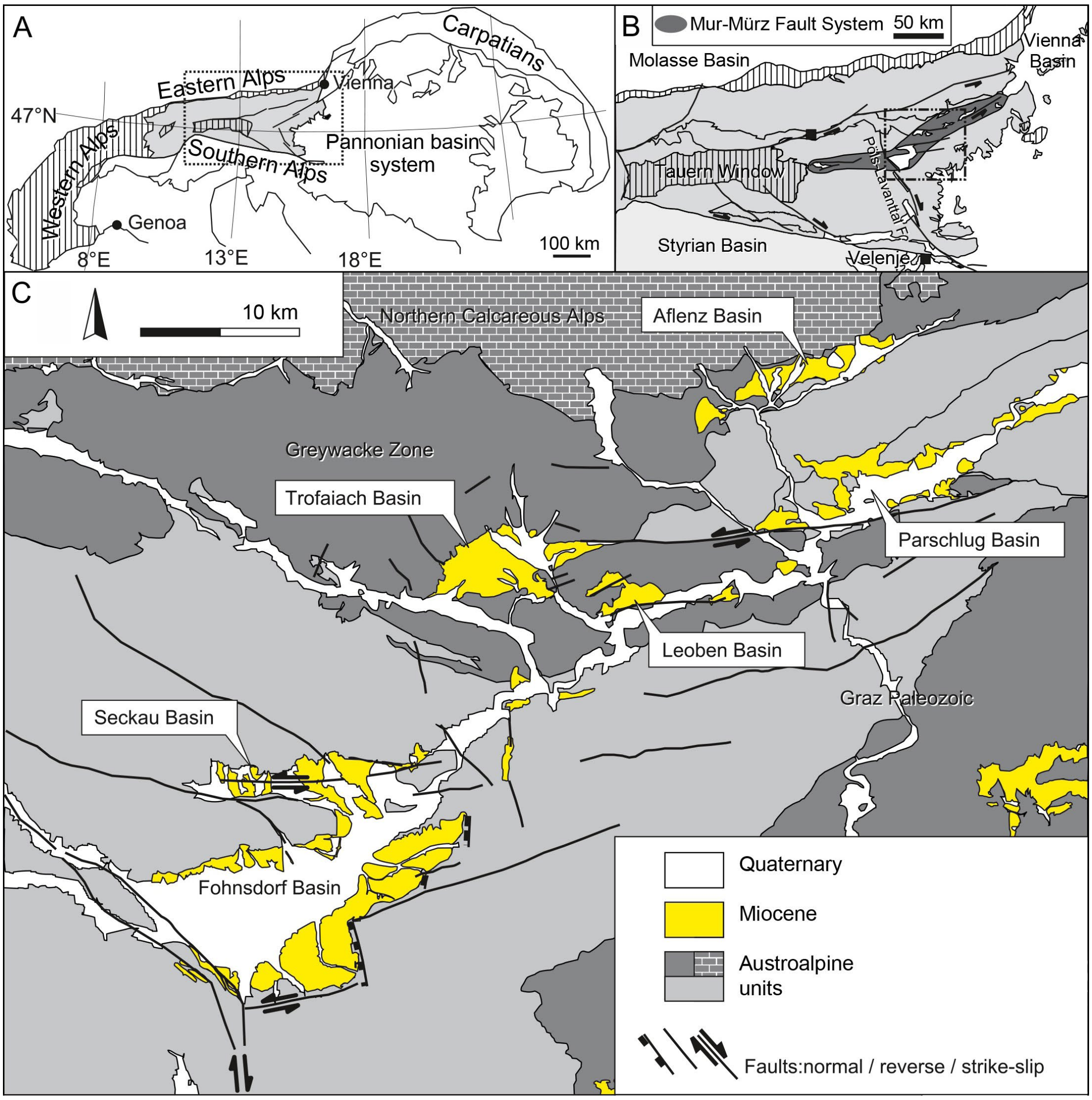

Figure 1. Location of the Leoben Basin and geological sketch map (modified from Gruber et al., 2012)

flora were included in plant taxonomic investigations (Jähnichen et al., 1984; Klaus, 1984, 1985; Kvaček and Walther, 1981; Mai, 1994; Hably and Thiébaut, 2002). Kvaček (2004) proved the correct assignment of *Ceratozamia hofmannii* Ettingsh. to the cycads based on cuticular analysis. Finally, the Leoben flora served Mai (1995) for the definition of the "Florenkomplex Langenau-Leoben".

GEOLOGY AND STRATIGRAPHY

During the Miocene, orogen-parallel extension and eastward lateral extrusion caused the development of small, fault-bounded intramontane basins in the Eastern Alps (Ratschbacher et al., 1991; Decker and Peresson, 1996; Gruber et al., 2012). Along the Mur-Mürz fault system such basins are the Fohnsdorf, Leoben, Trofaiach, and Parschlug Basins, which formed between left-stepping ENE-striking faults (Sachsenhofer et al., 2000, 2003; Strauss et al., 2001). Although the sediment thickness of the basin fills varies considerably, the general stratigraphic sequence is similar in these basins: alluvial sediments developed at the base, followed by usually one coal seam which is overlain by lacustrine fine-grained sediments. This sequence is often followed by coarsening upward and fluvial gravels on top (Sachsenhofer et al., 2002).

The Leoben Basin, situated N of the town of Leoben, is subdivided by a basement high into the Seegraben and the Tollinggraben subbasins. The basin formation started as a halfgraben in a general strike-slip setting, and further N-S shortening caused deformation and reverse faulting along the southern margin of the basin (Neubauer et al., 2000; Sachsenhofer et al., 2010; Gruber et al., 2012). The sedimentation started with coarse-grained clastic sediments and thin coaly layers (Lackenschweiger, 1937). Coal formation commenced in a low-lying mire, followed by the phase of an ombrotrophic raised mire, yielding an up to 16-m-thick coal seam overlying the alluvial sediments but usually developed directly on the Palaeozoic basement. The coal formation in a raised mire is indicated by the high quality of the coal, poor in ash and sulphur (Gruber and Sachsenhofer, 2001). The coal is intercalated by four tuff interseams altered into kaolinite (Gruber et al., 2012). This coal seam is overlain by sapropelic shales ("Brandschiefer") up to 18 m thick that were deposited during the drowning stage of the raised mire caused by high subsidence rates (Gruber and Sachsenhofer, 2001). These shales yield the very rich flora described first by Ettingshausen (1869a, 1888) and which is the subject of the here presented revision. These lake sediments also bear fish remains first described by Weiler in Krejci-Graf et al. (1930). They were revised to a single freshwater fossil-species, *Palaeoleuciscus etilius* (Rückert-Ukümen), by Gaudant (1993). At the base of the shales a tuff layer has been dated by the single zircon crystal fission track method to an age of 14.9 ± 0.7 Ma (Sachsenhofer et al., 2010), i.e. Middle Miocene, Langhian/early to middle Badenian age (Cohen et al., 2013, updated, International Chronostratigraphic Chart, 2023/04; Neubauer et al., 2015). Upwards, the sapropelic shales grade into marls and sandstones (Lackenschweiger, 1937). Southwards, this sequence reaches a thickness of 140 m. Conglomerates up to 60 m thick unconformably overlie this mainly lacustrine sequence, extending also on the basement. A mammal fauna (sites Seegraben, Münzenberg) is known from sandstones ~240 m above the coal seam (Zdarsky, 1909; Mottl, 1970). It is assigned to Mammal Neogene zone MN 5 (Van der Made et al., 2007). The differences in the composition of taxa between Seegraben and Münzenberg are a matter of discussion (Zdarsky, 1909; Mottl, 1970). Van der Made (1989) described from this fauna a new bovid genus and species, *Pseudoeotragus seegrabensis* Van der Made. Furthermore, terrestrial and freshwater gastropods have been reported by Zdarsky (1909). The top of the Miocene sequence is formed by marly sandstones and conglomerates (Gruber et al., 2012).

Ettingshausen (1869a) distinguished four sites in the southern part of the Seegraben subbasin: Seegraben next to Walpurga well (also spelled Walpurgis), Seegraben near Unter-Buchwieser (also spelled Unterbuchwieser), Münzenberg, and Moskenberg. He described the plant-bearing layers there in different vertical position to the seam as follows: (1) Moskenberg: plant-bearing sediments at ~8.2 m above the seam, light brownish-grey shale, difficult to split, rich in well-preserved fossils; (2) Münzenberg: ~2.75 m above the seam, light-grey, well fissile shale, plant-bearing sediment ~26 cm thick, plant remains very well preserved; (3) Seegraben near Unter-Buchwieser close to

Seegraben next Walpurgis well: ~1.8 m above the coal seam, reddish-grey, poorly fissile shale; (4) Seegraben next to Walpurgis well: directly above the coal seam, 5.2 to 7.9 cm thick, sandy, endurated sandstone, clay (the original text in German is not clear: "… aus einem sandigen oft zu einem feinkörnigen Sandsteine erhärteten Thone …"). This latter description may refer to tuffs and/or tuffitic sediments because the volcanogenic origin was not recognised by authors in the 19th and early 20th centuries; (pers. comm. L. Kunzmann). Possibly the radiometric date (14.9 ± 0.7 Ma; Sachsenhofer et al., 2010) derives from this layer which is superimposed by grey-black bituminous shale that rarely bears plant remains (Table 1). Figure 2 provides a N–S section through the Seegraben subbasin.

MATERIAL

This study is based on the Miocene plant collections from Leoben of the following institutions: (1) Natural History Museum Vienna (NHMW), (2) Institute of Biology (formerly Institute of Botany), Karl-Franzens-University, Graz (IBUG), (3) Universalmuseum Joanneum, Graz (LMJ), (4) former Geologische Bundesanstalt Wien now integrated in Bundesanstalt für Meteorologie, Geophysik und Geologie, GeoSphere Austria (GBA), all in Austria, and (5) NATURALIS, Leiden, Netherlands (Table 2a). Unpublished Leoben material distributed to other institutions in Austria and abroad is not included in this study. The material primarily comprises leaves and to a lesser degree fruits, seeds and floral remains. This here presented revision deals with the plant remains, while the fungi described by Ettingshausen (1869a, 1888) are not included. The collection of the NHMW, which Ettingshausen (1888) already mentioned as being the largest one, was the primary source for this study. It also includes a few specimens labelled as "coll. Hofmann" (Adolf Hofmann, 1853–1913, geologist, palaeontologist, study at Montanuniversity Leoben; Österreichiches Biographisches Lexikon 1815–1950, acc. November 2023), which also served Ettingshausen (1888) for his monograph. The palaeobotanical Leoben collection NHMW comprises almost 1500 slabs. Ettingshausen (1869a) mentioned that he collected material over 6 weeks from Moskenberg and that he had sent ~1000 slabs to Vienna. This material probably went to the NHMW and possibly also GBA collections. The IBUG, LMJ, GBA and NATURALIS collections served to complete the taxonomic spectrum, the morphological variability of taxa and to locate type specimens. The IBUG collection, which is the second richest (more than 1000 slabs), was transferred to the NHMW in 2019. Both in the NHMW and IBUG collections all specimens are labelled on the backside indicating the specimen number and, in the NHMW collection, also the locality where it was found. While the NHMW collection further includes the NHMW labels, such labels are missing in the IBUG collection. At both, NHMW and IBUG, handwritten historical inventories provide additional information. Thanks to the inventory at IBUG and due to the numbers sticking on the backside of the specimens of this collection, Ettingshausen's assignments are evident. The Leoben monograph by Ettingshausen (1869a) was mainly based on the NHMW collection, but during this study a few specimens were also detected in the GBA collection. The NHMW and parts of the IBUG collection were the main sources for the monograph Ettingshausen (1888) on the Leoben flora. These collections served further for several publications by Ettingshausen (1878a, 1882, 1893, 1894).

The collection in the LMJ in Graz comprises less than 300 slabs, supposedly including historical material from the collection Glowacki (Prof. Julius Glowacki, 1846–1915; botanist mosses and lichens, study in Vienna and Graz; Österreichisches Biographisches Lexikon 1815–1950, acc. November 2023) also mentioned by Ettingshausen (1888), as well as material collected later. The specimens possibly deriving from the Glowacki collection lack labels and are of variable lithology, so that the original localities of the slabs may be equivocal. In the LMJ collection no original specimen from Ettingshausen (1888) has been identified.

Ettingshausen (1888) mentioned further the collection of GBA (formerly Geologische Reichsanstalt Wien). Today this collection comprises ~400 specimens,

Table 1. Sites of the Leoben flora as designated in Ettingshausen (1869a, 1888) and in the here presented revision, the position of the plant-bearing layers in relation to the coal seam, and the systematics of Ettingshausen's collection numbers in relation to the NHMW collection file numbers. Note that some specimens at the NHMW collection bear different collection file numbers. Such specimens were either (1) not part of Ettingshausen's collection, (2) not numbered by Ettingshausen, e.g. specimens from the collection Hofmann, or (3) the original collection file number was lost

Site (Ettingshausen, 1869a, 1888)	Site as cited in this paper	Position of plant-bearing layers above coal seam (Ettingshausen, 1869a)	Site acronym (Ettingshausen, 1888)	NHMW collection file no.	Ettingshausen collection no. (Ett.)
Moskenberg	Moskenberg	8.2 m	Leoben I	1878/6/3504–4216	1501–2213
Münzenberg	Münzenberg	2.75 m	Leoben II	1878/6/4217–4411	2214–2408
Seegraben beim Unter-Buchwieser	Seegraben Unter-Buchwieser	1.8 m	Leoben III	1878/6/4412–4435	2409–2432
Seegraben Walpurgis-Schacht	Seegraben Walpurgis-Schacht	directly above seam	Leoben IV	1878/6/4436–4477	2433–2474
Further numbering not consecutive according to sites	–	–	–	1878/6/>4477	>2474

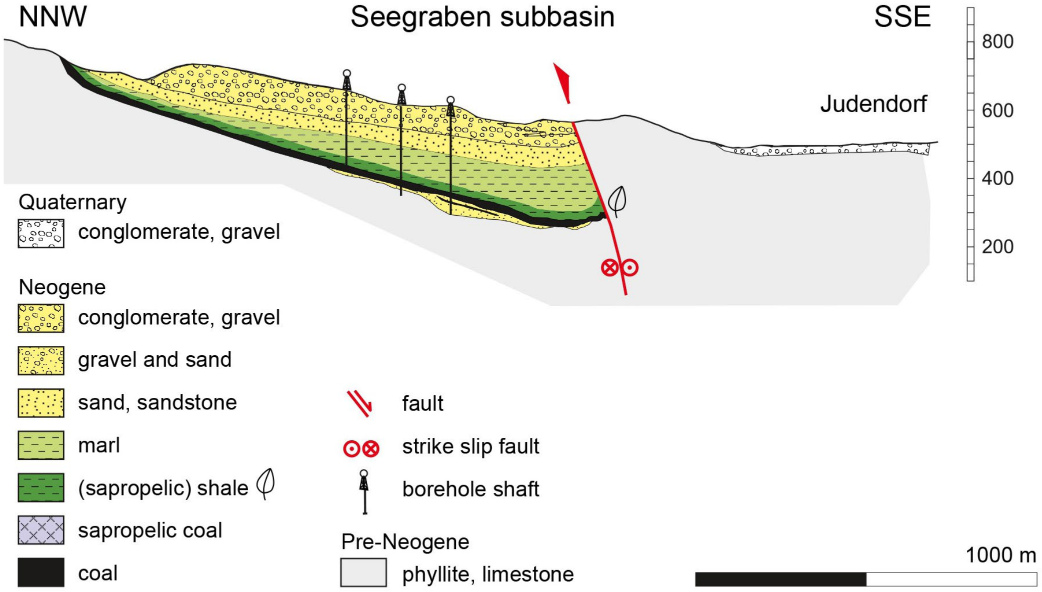

Figure 2. N–S section through the Seegraben subbasin of the Leoben Basin. The Leoben flora derives from sites in the southern part of the Seegraben subbasin (Moskenberg, Münzenberg, Seegraben Unter-Buchwieser and Seegraben Walpurgis-Schacht) (Modified from Gruber et al., 2012)

some of them labelled, others not. There is only a single historical handwritten label explaining acronyms for the collecting sites Moskenberg, Münzenberg and Seegraben. Only the latter two sites are indicated on the respective specimens, while this is not the case for slabs from Moskenberg. This is probably because most of the material derived from Moskenberg and that it was economical to label only the specimens from the other sites. It is unclear whether this explanatory note refers to all specimens of the GBA's Leoben collection because this collection received specimens from different sources at different times. Therefore, specimens lacking the exact locality (Moskenberg, Münzenberg, Seegraben) are listed simply as "Leoben" in the here presented study.

The Leoben collection of NATURALIS, Leiden, comprises nearly 100 slabs, at least some of them from the Hofmann collection mentioned by Ettingshausen (1888) as, e.g. *Ceratozamia hofmannii* (Kvaček, 2004). Images of specimens that potentially could be originals of Ettingshausen (1888) were provided by NATURALIS and, as far as relevant, are included here.

Commonly, more than one plant remain is preserved on one slab. Overall, more than 4000 plant remains were studied for the here presented revision.

In the inventories of the NHMW and IBUG collections different fossil taxa on single slabs are occasionally (but not consistently) indicated in addition to the collection file numbers by lowercase letters (a, b, c, etc.). In exceptional cases, the respective fossil remains are labelled on the slabs themselves. Furthermore, Ettingshausen (1888) quoted his own collection numbers for the specimens of the NHMW collection without the differentiation by lowercase letters; otherwise he mentioned only the respective collection without providing numbers. In such cases, it cannot be definitively determined which specimens of the IBUG, LMJ, GBA and NATURALIS collections served, in fact as original material unless such specimens were figured. Finally, in the NHMW collection it was not always possible to unambiguously identify which letter refers to which fossil remain. On many slabs with several fossil remains, Ettingshausen referred only to one of them. In such cases, different remains were labelled by capital letters (A, B, C, etc.) in the course of the here presented study. Note that Ettingshausen never indicated part and counterpart. Often such specimens were found scattered across the collections with numbers far apart, sometimes even with different systematic assignments, and occasionally part and counterpart were distributed to different collections, e.g. NHMW and IBUG or NHMW and GBA. Specimens with part and counterpart were brought together within each of the collections (NHMW, IBUG, GBA), but no specimen was moved from one collection to the other. In some cases, even different localities were indicated for part and counterpart. Such discrepancies could not be resolved.

In the paragraphs "Material" in the systematic part the specimens are listed for every here described taxon. Firstly, specimens characteristic of a taxon and specimens relevant in the context of this revision regarding taxonomy and nomenclature are provided. Slabs with more than one remain are listed in Supplementary File 1[1]. Supplementray File 2[2] lists the

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[1] Supplementary File 1. List of slabs (collection file numbers and taxonomic assignments) that yield more than one fossil-taxon. In the column Ettingshausen no., lowercase letters indicate the designation of remains by Ettingshausen, whereas capital letters have been assigned in the course of the current study. Not all remains of abundant taxa are included in the Systematic Part in the paragraphs Material

[2] Supplementary File 2. List of specimens incertae sedis or undeterminable remains. Included are first of all remains which served Ettingshausen for the description of new fossil-species or which were figured in one of his publications (Ettingshausen, 1869a, 1888, 1878a). H – holotype, S – syntype, AO – figured spcimen, BM – specimen listed for a taxon in one of Ettingshausen's publications, Pb number – number in type catalogue (Kovar-Eder, 1990) and OETYP database

Table 2a, **b**. List of acronyms for (**a**) institutions and collections and (**b**) acronyms used in the applied evaluation techniques: Integrated Plant Record (IPR) vegetation analysis (Kovar-Eder and Kvaček, 2007; Teodoridis et al., 2011a, 2011–2021), Similarity Approach (Drudges) (Teodoridis et al., 2020; Kovar-Eder et al., 2021) and Climate Leaf Analysis Multivariate Program (CLAMP) (Wolfe, 1993; Spicer, 2011–2021)

a.

	Acronym this paper	Institution/designition	Collection acronym (Ettingshausen, 1888)	Remarks
Institutions/collections	NHMW	Natural History Museum Vienna	K.k. N.H.M.	
	IBUG	Institute of Biology at the Karl-Franzens-University, Graz	N. Coll. Ett.	former Institute of Botany
	LMJ	Universalmuseum Joanneum, Graz		former Landesmuseum Joanneum
	GBA	Bundesanstalt für Meteorologie, Geophysik und Geologie, GeoSphere Austria	K.k. G. R. A.	former Geologische Bundesanstalt
	NATURALIS	NATURALIS, Leiden		
		Collection of Prof. Dr. Julius Glowacki	Coll. Glow.	parts now in LMJ
		Collection of Adolf Hofmann	Coll. Hofm.	parts now in NHMW and NATURALIS

b.

Technique	Acronym	Designation
Integrated Plant Record (IPR) vegetation analysis	BLD	Broad-leaved deciduous component
	BLE	Broad-leaved evergreen component
	SCL + LEG	Sclerophyllous and legume-like components
	DRY and MESO HERBS	Dry and mesophytic herb components
		Broad-leaved deciduous forest
		Mixed mesophytic forest
		Broad-leaved evergreen forest
		Subhumid sclerophyllous forest
Similarity Approach (Drudges)	BLEF China, Japan	Broad-leaved Evergreen Forest China, Japan
	MMF China	Mixed Mesophytic Forest Lower Yangtze Provinces
	BLDF Upper Yangtze, Honshu	Broad-leaved Deciduous Forests Upper Yangtze Provinces, Mt. Emei and Honshu
	BLDF N and NE Provinces	Broad-leaved Deciduous Forests of the Northern and Northeastern Provinces, China
	MCF China, Japan	Montane Coniferous Forests China, Honshu, Yakushima
	Formation F (Europe)	Mesophytic broadleaved deciduous and mixed broad-leaved/conifer forests
	Formation D (Europe)	Mesophytic and hygromesophytic coniferous and mixed broad-leaved-coniferous forests
	Formation C (Europe)	Subarctic, boreal and nemoral-montane open woodlands as well as subalpine and oro-Mediterranean vegetation
Climate Leaf Analysis Multivariate Program (CLAMP)	MAT	Mean Annual Temperature
	WMMT	Warmest Month Mean Temperature
	CMMT	Coldest Month Mean Temperature
	GROWSEAS	Length of the Growing Season
	GSP	Growing Season Precipitation
	MMGSP	Mean Monthly Growing Season Precipitation
	3_WET	Precipitation Mean during 3 Consecutive Wettest Months
	3_DRY	Precipitation Mean during 3 Consecutive Driest Months
	RH	Relative Humidity
	SH	Specific Humidity
	ENTHAL	Enthalpy

specimens that may represent one or the other of the here described taxa and those specimens regarded as indeterminable. Note that neither all specimens of abundant taxa nor poorly preserved ones lacking diagnostically relevant features are included.

The systematics of the paragraphs "Material" (in the systematic part) is as follows: collection acronym and collection file no., e.g. NHMW: 1878/6/XX. For specimens of the NHMW collection, Ettingshausen's collection nos, e.g. (Ett. XX), and the type database number of the NHMW according to OETYP and Kovar-Eder (1990) follow, Pb XX, to the extent that they exist. Note that not all specimens of Ettingshausen (1869a, 1888) are included in this database. Part and counterpart are indicated by "+". Moreover, Ettingshausen's taxonomic assignments are provided in italics and brackets. If the specimens are not evidently included in Ettingshausen's publications, the assignments are designated with "in sched.", i.e. in schedule. In the IBUG collection, Ettingshausen's taxonomic assignments are based on the inventory of the collection in which they are listed. In a few cases, numbers were found to exist twice, which is indicated by “bis”. Finally, the binomina of fossil-species described here for the first time and new combinations of genera and species names have been registered in the Plant Fossil Names Registry (Kvaček, J., 2024).

PRESERVATION

The plant-bearing fine-grained shales are well bedded, and plant remains are densely packed and often superimposed, comprising mainly impressions of leaves devoid of organic material but also of flowers and inflorescences, impressions or casts of seeds, fruits and infructescences (Fig. 3a, b). Multiple fractures of the plant material, especially of the leaf material, point towards diagenetic pressure causing induration of the sediment and syndiagenetic distraction of the fossil leaf material (e.g. Figs 7.11, 8.4) (see also paragraph Taphonomy).

SOURCES OF UNCERTAINTY

The Leoben flora comprises material collected mostly in the 19th century. Ettingshausen (1869a) provided some details on the collecting sites Moskenberg, Münzenberg, Seegraben Walpurgis well and Seegraben Unter-Buchwieser, but no detailed profiles of the historical sites are available (except for the rough description in Ettingshausen (1869a), see Geology and Stratigraphy). The material was collected by different collectors and over long time-spans, which may have compensated for the focus of individuals. Nevertheless, sampling was not performed in a stratified manner. Although the fossil-bearing strata represent lake sediments, differences in the composition of taxa in different layers cannot be excluded. The presence of accumulated plant debris on the surface of some slabs (Fig. 3b) indicates at least some variation in the sedimentation regime. Only in the GBA collection are some leaf specimens preserved organically although strongly compressed. This may indicate that such material was more common but more difficult to conserve, making it less attractive for early collectors. Impressions of pine cones bear traces of pyritisation, pointing to destruction of the organic material. The abundance of pine needles, seeds and male catkins indicates that cones were more common and are underrepresented in the collections. By far the most material derives from Moskenberg followed by Münzenberg, whereas the very small quantities deriving from Seegraben Unter-Buchwieser and Seegraben Walpurgis well hamper a comparison of the sites. Finally, the latter two sites are distinguished only in the NHMW and IBUG collections.

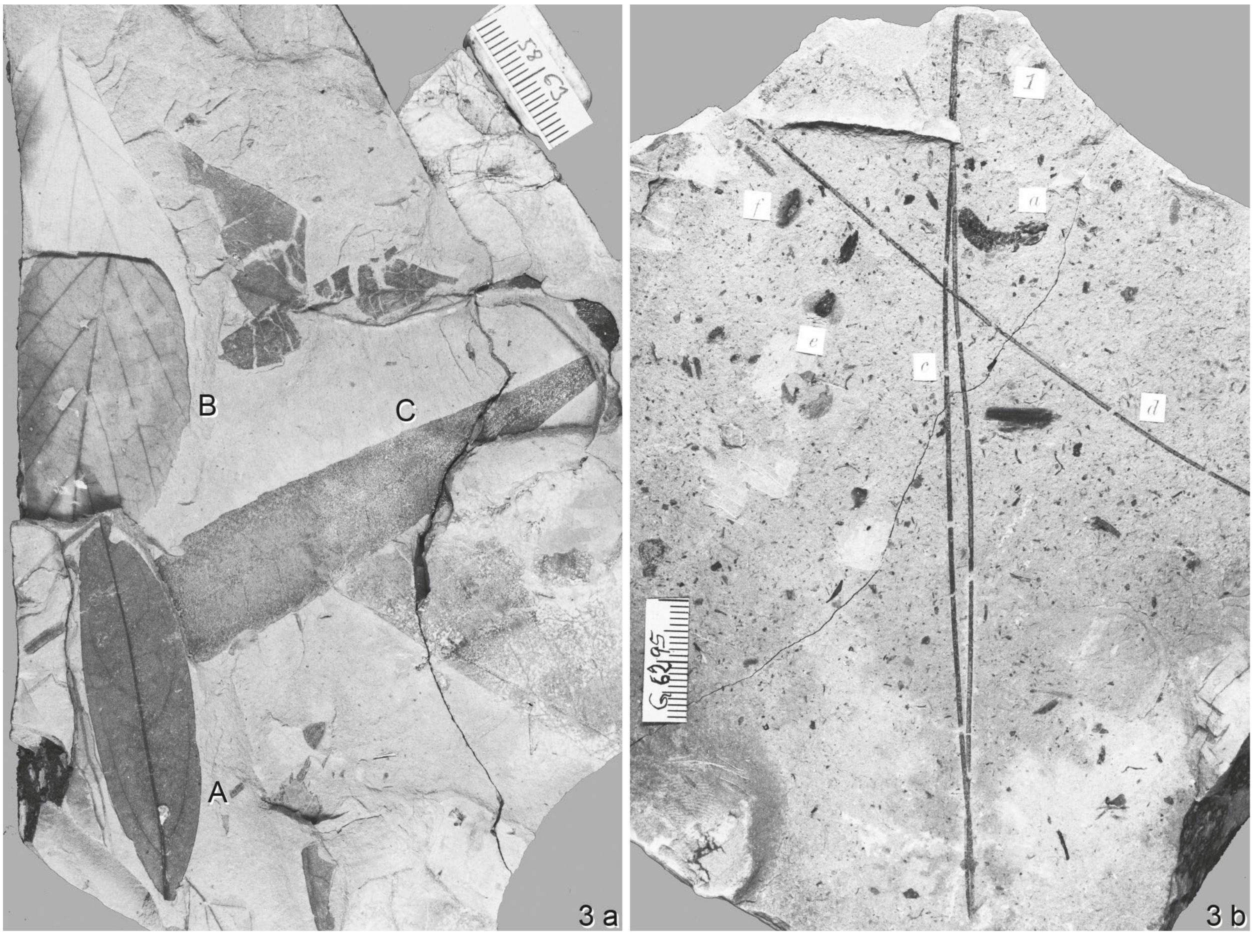

Figure 3a, **b**. **3a**. Slab showing several, partly superimposed leaf remains. A. *Laurophyllum* cf. *pseudoprinceps*, B. *Alnus julianiformis*, C. *Myrica joannis*; NHMW 1878/6/7866 (Ett. 5863); **3b**. Sediment surface with different plant organs and debris. a. *Pinus* sp. – male catkin, c, d. *Pinus* sp. – two-needled fascicles, e. *Tetraclinis salicornioides* winged seed, f. (?) *Sequoia abietina* seed, IBUG Ett. 6295, Ettingshausen (1878a: pl. 8, fig. 1)

METHODS

Beyond standard methods (magnifying glass, binocular) photographs were made using a Nikon D600 digital camera, Micro-Nikkor-P 1:3.5, 55 mm with reflected light. Selected catkins were studied using first an epifluorescence microscope and SEM (National Museum, Prague) for the potential preservation of pollen and then were treated based on the standard technique using Schulze's reagents. A Micro-CT scanner YXLON FF35 CT (FXE Direct Beam, PerkinElmer Y Panel 4343 CT) (NHMW) was used to scan selected infructescences with a voltage of 100 kV and 300 µA producing scans with 3600 projections at 1 s each, voxel size resolution 35.6 µm. The preservational state of the fossil material hampered cuticular and pollen analysis, and the endurated sediment biased the attempts to perform micro-CT scans. These preservational characteristics reduce the taxonomic resolution of this revision (see also paragraph Preservation). The CT scan images were processed using VG studio max and Avizo (courtesy of S. Manchester).

The terminology of the leaf morphological descriptions follows Ellis et al. (2009). In the diagnoses, length (l) and width (w) of the lamina are provided as l × w and the ratio l/w is calculated. Most leaves are incompletely preserved. Such remains were mentally reconstructed and this size estimation is indicated. Therefore, measurements are indicated by "~". Angles of secondary veins are provided as narrow (prevailingly <45°), moderate (prevailingly 30–60°) or wide (prevailingly >50°). In addition to the features defined by Ellis et al. (2009) for teeth of the leaf margin, the tooth height is provided as the distance from the tangent of the theoretically entire margin to the most distant point of teeth. In this respect three categories are distinguished: <1 mm, >1 and <5 mm, and >5 mm. Descriptions are restricted to characters present: unpreserved features are not mentioned as not preserved unless they are relevant in the context.

Systematics of conifers follows Christenhusz et al. (2011), while the systematics of angiosperms follows the Angiosperm Phylogeny Website (Stevens, 2001 onwards).

For the binomina of the described taxa the position of "(?)" is used as follows: behind the genus name – referring to uncertainty in the genus name, behind the species name – referring to uncertainty in the species name, in front of the genus name – referring to uncertainty in the taxon as such.

Regarding the taxa described from Leoben, the synonymies are restricted to taxa/specimens that can be assigned unambiguously to Ettingshausen's publications, especially his monographs (Ettingshausen, 1869a, 1888). Therefore, taxa that were described only in Ettingshausen (1869a) but remained unfigured are not included in the synonymies. Furthermore, synonymies are restricted to the first description of the respective taxon, to records from basins along the Mur/Mürz fault system (Parschlug Basin, Tamsweg Basin), the Styrian Basin (Oberdorf), and to selected floras similar in age from the Paratethys surroundings: Cypris Formation (northern Bohemia; Bůžek et al., 1996) and the Mecsek area (Hungary; Hably, 2020); otherwise they include only the most relevant taxonomic monographs.

Finally, the following online resources were used: Angiosperm Phylogeny Website (Stevens 2001 onwards), IPNI (2023), JACQ, OETYP, NMNS Cleared Leaf Database, POWO, Trees and Shrubs online, WFO, Wilf et al., (2021).

INTEGRATED PLANT RECORD (IPR) VEGETATION ANALYSIS

The IPR vegetation analysis is a semiquantitative method based on foliar physiognomy and the autecology of taxa to assess major zonal vegetation types for Paleogene and Neogene floras (Kovar-Eder and Kvaček, 2003; 2007; Kovar-Eder et al., 2008; Teodoridis et al., 2011a). This approach differentiates between presumably zonal and azonal taxa and enables taking specific factors into account by variegating the taxa's scoring. Such factors may, for example, include uncertainties regarding autecology. The differentiation between zonal and azonal taxa is essential to determine the zonal vegetation type of a fossil assemblage. The zonal vegetation types are defined by their proportions of the following major (key) components: BLD (broad-leaved deciduous), BLE (broad-leaved evergreen), SCL + LEG (sclerophyllous and legume-like), DRY and MESO HERBS (dry and mesophytic herbs). The major (zonal) vegetation types distinguished are: broad-leaved deciduous forests, mixed mesophytic forests, broad-leaved evergreen forests, subhumid sclerophyllous forests, xeric open woodlands and xeric grasslands or steppe (sensu Teodoridis et al., 2011a). The most recent descriptions of all components and major vegetation types are accessible at http://www.iprdatabase.eu/components-character (Teodoridis et al., 2011–2021). For acronyms see Table 2b.

SIMILARITY APPROACH (TOOLS DRUDGE 1 AND 2)

This approach has been developed to assess the most similar modern vegetation proxies for Paleogene and Neogene plant assemblages out of a set of currently 503 modern vegetation units of vegetation types from Asia and vegetation formations from Europe largely based on Wang (1961), Bohn et al. (2004) and Teodoridis et al. (2011a) (Teodoridis et al., 2020: appendix 7). The similarity approaches are executed by the tools Drudge 1 and 2, which have been described in detail by Teodoridis et al. (2020, 2021). Based on the IPR vegetation analysis, Drudges 1 and 2 automatically calculate (a) the IPR Similarity, which is the similarity of the proportions of major zonal angiosperm components and (b) the Taxonomical Similarity (TS) at the genus level by cluster analysis (Ward's method, Euclidian distance) between a given fossil assemblage and the reference set of modern vegetation and (c) the Results Mix, in which the major zonal angiosperm components of the IPR Similarity and the TS results are weighted equally. The results display the similarity hits for the given fossil plant assemblage. The five best fits of modern vegetation proxies of the IPR Similarity, the TS and the Results Mix are regarded as being the most likely modern vegetation proxies. Drudge 1 calculates the highest level of correspondence of the proportions of the zonal woody angiosperm components (BLD, BLE, SCL+LEG). Drudge 2 further includes DRY and MESO HERBS to better distinguish more open vegetation types from closed ones. In the course of applying the Similarity Approach to a wide range of representative Paleogene and Neogene floras of Europe, Turkey and Armenia, Kovar-Eder et al. (2021) rendered the East Asian vegetation types more precisely (ibidem, table 3). This scheme is applied here, and the following East Asian vegetation types relevant for the here presented study are distinguished: Broad-leaved Evergreen Forests, China, Japan (BLEF China, Japan); Mixed Mesophytic Forests Lower Yangtze Provinces (MMF China); Broad-leaved Deciduous Forests Upper Yangtze Provinces, Mt. Emei and Honshu (BLDF Upper Yangtze, Honshu); Broad-leaved Deciduous Forests of the Northern and Northeastern Provinces, China (BLDF N and NE Provinces); Montane Coniferous Forests, China, Honshu, Yakushima (MCF China, Japan) (Table 2b). The European vegetation formations relevant for the Leoben flora are: Formation C – Subarctic, boreal and nemoral-montane open woodlands, as well as subalpine and oro-Mediterranean vegetation, Formation D – Mesophytic and hygromesophytic coniferous and mixed broad-leaved-coniferous forests, Formation F – Mesophytic broadleaved deciduous and mixed broadleaved/conifer forests (sensu Bohn et al., 2004; Teodoridis et al., 2020, Kovar-Eder et al., 2021) (Table 2b). The results of the IPR vegetation analysis for Leoben serve as the basis for the similarity approaches in the here presented study.

CLIMATE LEAF ANALYSIS MULTIVARIATE PROGRAM (CLAMP)

CLAMP is a multivariate statistical technique based on the relationship between leaf physiognomy of woody dicotyledoneous angiosperms and climate to assess palaeoclimatic parameters for fossil floras. Since its introduction by Wolfe (1993) this technique has been refined (Wolfe and Spicer, 1999; Spicer, 2000, 2007; Spicer et al., 2004) and new CLAMP calibration data have been integrated, including gridded meteorological data (Spicer et al., 2009, 2020; Jacques et al., 2011; Khan et al., 2014; Yang et al., 2015). Further methodological modifications were introduced by Teodoridis et al. (2011b, 2012), Yang et al. (2011, 2015), Teodoridis, and Mazouch (2017) and Zolina et al. (2020).

CLAMP employs the Canonical Correspondence Analysis (Ter Braak, 1986) to estimate the following climatic parameters: MAT (Mean Annual Temperature), WMMT (Warmest Month Mean Temperature), CMMT (Coldest Month Mean Temperature), GROWSEAS (length of the Growing Season), GSP (Growing Season Precipitation), MMGSP (Mean Monthly Growing Season Precipitation), 3-WET (Precipitation Mean during 3 Consecutive Wettest Months), 3-DRY (Precipitation Mean during 3 Consecutive Driest Months), RH (Relative Humidity), SH (Specific Humidity) and ENTHAL (Enthalpy) (For acronyms see Table 2b).

CLAMP may produce different results depending on which modern calibration data set is used. A statistical tool (Teodoridis et al., 2011b, 2012) helps to determine the most appropriate calibration data set. This tool is based on the similarities (i.e. minimum difference MIN DIFFi) of the fossil (studied) and modern (calibration) leaf physiognomic characteristics from the Physg3br (144), Physg3ar (173) and PhysgAsia1 (189) modern calibration sets (from Spicer et al., 2009; Jacques et al., 2011). An updated version of this tool was presented in Kovar-Eder et al. (2022: appendix 4), including additional calibration data sets, namely PhysgAsia2 (177) (Khan et al., 2014) and PhysgGlobal (378) (Yang et al., 2015). Nonetheless, no comparison of the techniques to determine the best-fitted calibration (a) as proposed on the CLAMP website (Spicer, R.A., 2011–2021) and (b) the recent update of the tool published in Kovar-Eder et al. (2022) has been performed.

The CLAMP analysis of the Leoben flora was performed on the CLAMP website (Spicer 2011–2021) using various calibration data sets available there. The best suited calibration data set was determined as proposed there and by the updated tool published in Kovar-Eder et al. (2022).

Mean Annual Precipitation (MAP) cannot be simply estimated by CLAMP, although it is an important climatic parameter. Based on original CLAMP estimations, MAP was calculated for the flora of Parschlug as follows: 3-WET + 3-DRY + (MMGSP × 6) and 3-WET + 3-DRY + [(GSP – 3-WET)/5.3] × 6 (Kovar-Eder et al., 2022). This formula was also applied to estimate MAP for Leoben.

For the Leoben flora, CLAMP was performed with the following calibration data sets: Physg3brcAZ_GRIDMet3brcAZ comprising 144 sites predominantly in the Northern Hemisphere; Physg3arcAZ_GRIDMet3arcAZ, which includes the former sites plus sites with pronounced cold winter (together 173 sites); PhysgAsia1_GRIDMetAsia1 (189 sites) including the Physg3brcAZ calibration plus 45 data sets from China; PhysgAsia2_HiResGRIDMetAsia2 yielding the Physg3brcAZ calibration plus sites from southern China, India and Thailand; and finally PhysgGlobal_HiResGRIDMetGlobal378, which yields 378 sites from all continents except Antarctica (see Spicer, 2011–2021).

SYSTEMATIC PART

Class BRYOPSIDA Rothm.

Order incertae sedis

Genus **Muscites** Brongn.

***Muscites* sp.**

Fig. 4.1

1888 *Muscites savinensis* Ettingsh.; Ettingshausen, p. 270.

Material. Moskenberg: IBUG: Ett. 5368, (*Muscites savinensis*).

Description. Multiply branched, mat-like, foliated axes; leaves linear-shaped, up to 3 mm long, with central costa, broad base attached to axis, apex rounded.


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34b
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a
25
26
27
28
29
33
23
30
1mm
31
1mm
32
34a

Remarks. Ettingshausen (1888) referred to a single specimen from the collection IBUG, which is very likely the specimen at hand. A further assignment is not possible because diagnostically relevant features are lacking.

Class POLYPODIOPSIDA
Cronq., Takht. et W. Zimm.

Order EQUISETALES Dumort.

Family EQUISETACEAE Rich.

Genus ***Equisetum*** L.

Equisetum parlatorii (Heer) Schimp.

Fig. 4.2

1855 *Physagenia parlatorii* Heer; Heer, p. 109, pl. 42, figs 2–17.
1869–1874 *Equisetum parlatorii* (Heer) Schimp.; Schimper, p. 261.

Material. Seegraben Walpurgis-Schacht: IBUG: Ett. 6272 + 6273, (*Carpolithes speciosus* sp. n., in sched.).

Description. Fragment of a (?) rhizome consisting of three bulbs originating from a centre, one bulb almost complete, l × w ~18 × 10 mm, surface with few longitudinally running veins.

Remarks. This remain strongly resembles the rhizome bulbs of horsetails as reported from numerous sites, e.g. Monod, Switzerland (Heer, 1855), Schrotzburg, Germany (Heer, 1859), Moravska Nová Ves, Moravia, Czech Republic (Knobloch, 1969), Wörth near Kirchberg/Raab, Styria, Austria (Kovar-Eder and Krainer, 1990).

Order OSMUNDALES Link

Family OSMUNDACEAE
Bercht. et C. Presl

Genus ***Osmunda*** L.

Osmunda parschlugiana
(Unger) Andr.

Fig. 4.3–4.6

1847 *Pteris parschlugiana* Unger; Unger, p. 122, pl. 36, fig. 6.
1888 *Pteris parschlugiana* Unger; Ettingshausen, p. 271, pl. 9, fig. 35.
1959 *Osmunda parschlugiana* (Unger) Andr.; Andreánszky, p. 45, pl. 7, fig. 4, text-fig. 2.
1999 *Osmunda parschlugiana* (Unger) Andr.; Ströbitzer, p. 93, pl. 1, fig. 1, pl. 7, fig. 18.
2001 *Osmunda parschlugiana* (Unger) Andr.; Kovar-Eder and Meller, p. 70.
2003 *Osmunda parschlugiana* (Unger) Andr.; Kovar-Eder and Meller, p. 285, pl. 1, figs 15–17.
2004 *Osmunda parschlugiana* (Unger) Andr.; Kovar-Eder et. al., p. 52, pl. 1, figs 1, 2.

Material. Moskenberg: NHMW: 1878/6/3948 (Ett. 1945), B; 1878/6/6796 (4793), Pb 1857, (*Pteris parschlugiana*). IBUG: Ett. 5369,

◄

Figure 4. **1**. *Muscites* sp., IBUG Ett. 5368; **2**. *Equisetum parlatorii* (Heer) Schimp., IBUG Ett. 6272; **3–6**. *Osmunda parschlugiana* (Unger) Andr., **3**. IBUG Ett. 5372, (*Pteris parschlugiana*), **4**. IBUG 6302, (*Pteris parschlugiana*), **5**. IBUG Ett. 5369, (*Pteris parschlugiana*), **6**. NHMW 1878/6/6796 (Ett. 4793), Pb 1857; **7**. *Pronephrium stiriacum* (Unger) Erw. Knobloch et Kvaček, IBUG Ett. 5374, (*Phegopteris stiriaca*); **8**, **9**. Pteridophyta gen. et sp., **8**. NHMW 1878/6/6798 (Ett. 4795), Pb 1876, (*Pteris moskenbergensis*), Ettingshausen (1869a: pl. 1, fig. 11, holotype), **9**. NHMW 2023/0072/0003 (Ett. 4793 bis); **10**, **11**. *Pinus* sp. – two-needled fascicles, **10**. IBUG Ett. 6295, c, (*Pinus hepios*), Ettingshausen (1878a: pl. 8, fig. 1), **11**. NHMW 1878/6/9693 (Ett. 7690), (transition *P. palaeo-laricio* to *P. hepios*), Ettingshausen (1878a: pl. 8, fig. 3); **12**. *Pinus* sp. – 4 (?) 5-needled fascicle, NHMW 1878/6/9772 (Ett. 7769), (*P. palaeo-cembra*), Ettingshausen (1878a: pl. 2, fig. 6); **13**. *Pinus* sp. – cluster of needles, NHMW 2023/0072/0012; **14**, **15**. *Pinus* sp. – cones, **14**. NHMW 1878/6/9712 (Ett. 7709), a, (*P. laricio*), Ettingshausen (1878a: pl. 10, fig. 2a), **15**. NHMW 1871/38/36, (*P. laricio*), Pb 2154; **16–18**. *Pinus* sp. – male catkins, **16**. NHMW 1878/6/9701 (Ett. 7698), (*P. hepios*), Ettingshausen (1878a: pl. 10, fig. 6), **17**. NHMW 1878/6/9734 (Ett. 7731), Pb 1891, (*P. prae-silvestris*), Ettingshausen (1878a: pl. 10, fig. 7), **18**. IBUG Ett. 6295, a, (*P. hepios*), Ettingshausen (1878a: pl. 8, fig. 1); **19–23**. *Pinus* sp. – winged seeds, isolated wings, **19**. NHMW 1878/6/3889 (Ett. 1886), (*P. prae-silvestris*), **20**. NHMW 1878/6/9713 (Ett. 7710), (*P. laricio*), Ettingshausen (1878a: pl. 7, fig. 1), **21**. NHMW 1878/6/9715 (Ett. 7712), A, Pb 1885, (*P. laricio*), Ettingshausen (1878a: pl. 7, fig. 10), **22**. NHMW 1878/6/9710 (Ett. 7707), (*P. laricio*), Ettingshausen (1878a: pl. 7, fig. 7), **23**. NHMW 1878/6/9735 (Ett. 7732), Pb 1889, (*P. prae-silvestris*), Ettingshausen (1878a: pl. 7, fig. 17); **24**. *Amentotaxus* sp., NHMW 1878/6/4473 (Ett. 2470), A, (*Cyperites binervis*), Ettingshausen (1888: pl. 2, fig. 25, syntype); **25**, **26**. *Taiwania* cf. *paracryptomerioides* Kilpper, **25**. NHMW 1878/6/3609 (Ett. 1606), (*Sequoia couttsiae*), **26**. NHMW 1878/6/7046 (Ett. 5043), A, (*S. couttsiae*); **27**. *Calocedrus suleticensis* (Brabenec) Kvaček, NHMW 1878/6/6989 (Ett. 4886), (*Libocedrus salicornioides*); **28–31**. *Tetraclinis salicornioides* (Unger) Kvaček, **28**. GBA 2024/0001/0021 (*Libocedrites haidingeri* in sched.), twig fragment, **29**. IBUG 5378, (*Libocedrus salicornioides*), twig fragment, **30**. NHMW 1878/6/4068 (Ett. 2065), (*L. salicornioides*), twig fragment, **31**. NHMW 1878/6/3595 (Ett. 1592), (*Callitris brongnartii*), winged seed; **32**. (?) *Sequoia abietina* (Brongn.) Erw. Knobloch, IBUG Ett. 6295, f, (*S. langsdorfii*), seed; **33**. *Taxus* vel *Cephalotaxus* sp., NHMW 1878/6/4203 (Ett. 2200), B; **34a**, **b**. *Cephalotaxus* vel *Torreya* sp., IBUG Ett. 5574 + 5576, A, (*Abies* sp. in sched.), part and counterpart, 34a with twig fragment of *Sequoia abietina* on top. For all photographs the scale at bottom right of the figure is 10 mm except for photographs with embedded scale in which the scale is also 10 mm

(*P. parschlugiana*), Ettingshausen (1888: pl. 9, fig. 35) + GBA 2024/0001/0004; IBUG: Ett. 5370 + 5371, (*P. parschlugiana*); Ett. 5372, (*P. parschlugiana*); Ett. 6302, a, (*P. parschlugiana*).

Description. Fragments of isolated pinnulae, the longest fragment 51 mm long, 13 mm wide; pinnulae parallel-sided; base not preserved; apex bluntly acute; margin finely crenulate; midvein distinct; secondary veins densely and regularly spaced, angle of origin moderate to narrow, then turning, running almost perpendicular to midvein towards margin; secondaries forking once closely to midvein, each branch forking again about half way towards margin; branches ending in sinuses of crenation.

Remarks. The remains of this fern are few and fragmentarily preserved. In the course of this revision a further fragment was detected on slab NHMW 1878/6/3948 (Ett. 1945, B) associated with *Ulmus* sp. Although Ettingshausen indicated also Münzenberg as locality, all remains at hand are labelled as deriving from Moskenberg. *O. parschlugiana* is characteristic of swamp environments.

Order POLYPODIALES
R.M. Tryon et A.F. Tryon

Family THELYPTERIDACEAE
Pic. Serm.

Genus ***Pronephrium*** C. Presl

Pronephrium stiriacum
(Unger) Erw. Knobloch et Kvaček

Fig. 4.7

1847 *Polypodites stiriacus* Unger; Unger, p. 121, pl. 36, figs 1–5.
1888 *Phegopteris stiriaca* Unger; Ettingshausen, p. 272.
1976 *Pronephrium stiriacum* (Unger) Erw. Knobloch et Kvaček; Knobloch and Kvaček, p. 12, pl. 1, fig. 1.
2004 *Pronephrium stiriacum* (Unger) Erw. Knobloch et Kvaček; Kovar-Eder et al., p. 52, pl. 1, fig. 3.

Material. Moskenberg: IBUG: Ett. 5374, (*Phegopteris stiriaca* in sched.).

Description. Fragment of a pinna lacking base and apex; almost 80 mm long, 17 mm wide; consisting of largely fused pinnulae except the lowermost one which is fused only about half its length with adjacent pinnula; apices of pinnulae free, forming a dentate-crenate margin; pinna with one strong central vein; venation of pinnulae delicate; each pinnula with midvein and several veins originating from it on both sides, diverging towards margin.

Remarks. This is the only remain of this fern in the studied collection but is not the specimen listed by Ettingshausen (1888) because that author indicated the locality Münzenberg and collection Hofmann. *P. stiriacum* is characteristic for swampy facies, where it may occur in masses, e.g. in Murnerweiher (near Wackersdorf, Bavaria, Lower/Middle Miocene; Knobloch and Kvaček, 1976). From Styria it is known among others from Wörth near Kirchberg/Raab (Tortonian / Pannonian, Central Paratethys stage) (Kovar-Eder and Krainer, 1990). Its extremely rare occurrence in the Leoben assemblage indicates that it was either not common or was transported from the growth site.

Pteridophyta gen. et **sp**.

Fig. 4.8, 4.9

1869a *Pteris moskenbergensis* Ettingsh. sp. n.; Ettingshausen, p. 37, pl. 1, fig. 11.
1888 *Pteris moskenbergensis* Ettingsh.; Ettingshausen, p. 271.

Material. Moskenberg: NHMW: 1878/6/6798 (Ett. 4795), Pb 1876, (*Pteris moskenbergensis*), Ettingshausen (1869a: pl. 1, fig. 11, holotype). Leoben: NHMW: 1878/6/6799 (Ett. 4796), (*Pteris radobojensis* in sched.) + counterpart IBUG: Ett. 5373, (*Pteris oeningensis* in sched.), labelled as Moskenberg and Münzenberg; NHMW: 2023/0072/0003 (Ett. 4793 bis).

Description. Small and poorly preserved apical frond fragments; pinnulae very small <2–7 mm long, up to 2 mm wide; attached with broad base to rhachis, shape triangular to oblong, apex acute or rounded; margin entire; midvein present, straight or curved; details of further venation not visible.

Remarks. These remains lack details for a more precise taxonomic assignment. They do not necessarily belong to a single fossil-species. Specimen NHMW 1878/6/6798 (Ett. 4795) represents the type specimen of *Pteris moskenbergensis*. The best-preserved specimen (Ett. 4793 bis) is the fragment of a frond apex including the terminal pinnula (Fig. 4.9).

GYMNOSPERMAE

Order CYCADALES
Pers. ex Bercht. et J. Presl

Family ZAMIACEAE Horan.

Genus ***Ceratozamia*** Brongn.

Ceratozamia hofmannii Ettingsh.

See Kvaček (2004). No other remain has been detected in the here studied collection material.

Order PINALES Gorozh.

Family PINACEAE Spreng. ex F. Rudolphi

Genus ***Pinus*** L.

Ettingshausen (1888) differentiated 14 fossil-species, assigning both sterile and fertile organs to most of them. The binomina *Pinus palaeo-laricio*, *P. prae-silvestris* and *P. palaeo-cembra* were introduced first by Ettingshausen (1878a) based partially on material from Leoben. The descriptions of *Pinus palaeo-laricio* and *P. palaeo-cembra* followed later in Ettingshausen (1888).

***Pinus* sp.** – two-needled fascicles

Fig. 4.10, 4.11

1878a *Pinus palaeo-laricio* Ettingsh. nomen nudum; Ettingshausen, p. 68, 73, pl. 2, fig. 2.
1878a *Pinus hepios* Unger; Ettingshausen, p.73, pl. 8, figs 1c, d, 2a.
1878a Übergangsglied *Pinus palaeo-laricio* Ettingsh. und *P. hepios* Unger; Ettingshausen, p. 68, 73, pl. 8, fig. 3.
1878a *Pinus laricio* Poir.; Ettingshausen, p. 68, 73, pl. 8, figs 4a, 5a, pl. 9, figs 11, 12.
1888 *Pinus rigios* Unger; Ettingsh., p. 305.
1888 *Pinus palaeo-laricio* Ettingsh.; Ettingshausen, p. 275.
1888 *Pinus hepios* Unger, p.p.; Ettingshausen, p. 276.
1888 *Pinus laricio* Poir., p.p.; Ettingshausen, p. 276, non pl. 2, figs 6, 7.
1999 Pinus sp. 1; Ströbitzer, p. 93, pl. 1, figs 2, 3, pl. 7, figs 1, 3.
2004 *Pinus* sp. div. p.p.; Kovar-Eder et al., p. 53, only pl. 1, fig. 7.

Material. Moskenberg: NHMW: 1878/6/3589 (Ett. 1586), (*Pinus laricio*); 1878/6/3590 + 9697 (1587, A + 7694, A), (*P. palaeo-laricio*), Ettingshausen (1878a: pl. 2, fig. 2, syntype); 1878/6/3753 (1750), (*P. laricio* in sched.); 1878/6/3774 (1771), (*P. laricio*); 1878/6/3775 (1772), (*P. laricio*); 1878/6/3868 (1865), (*P. hepios* in sched.); 1878/6/3891 (1888), (*P. hepios* in sched.); 1878/6/4040 (2037), b, (*P. hepios* in sched.); 1878/6/4063 (2060), (*P. laricio* in sched.); 1878/6/4065 (2062), (*P. hepios* in sched.); 1878/6/4185 (2182), b, (*P. hepios* in sched.); 1878/6/7095 + 7096 (5092 + 5093), (*P. hepios*); 1878/6/7796 (5793), B; 1878/6/9700 (7697), a, (*P. hepios*), Ettingshausen (1878a: pl. 8, fig. 2); 1878/6/9717 (7714), (*P. laricio*), Ettingshausen (1878a: pl. 8, fig. 4a); 1871/38/43. IBUG: Ett. 6295, c, d, (*P. hepios*), Ettingshausen (1878a: pl. 8, fig. 1). Münzenberg: NHMW: 1878/6/9708 (Ett. 7705) (*P. laricio*). Seegraben Walpurgis-Schacht: NHMW: 1878/6/7094 (Ett. 5091), Pb 2376, (*P. palaeo-laricio*); 1878/6/9693 (7690), (Übergang *P. palaeo-laricio* zu *P. hepios*), Ettingshausen (1878a: pl. 8, fig. 3). Seegraben Unter-Buchwieser: NHMW: 1878/6/4425 (Ett. 2422), Pb 2349, (*P. rigios*). Seegraben: NHMW: 1871/38/61 (*P. rigios* in sched.). IBUG: Ett. 5499 + 5500, (*P. hepios*).

Description. Two-needled fascicles; brachyblast indistinct, ~7 mm long (NHMW 1871/38/61) ; needle length (including brachyblast) up to at least 100 mm, width 0.5–1.5 mm, margin entire, needle apex acute (IBUG Ett. 5499); some specimens with lines running parallel to needle length, indicating vein, resin channels or position of stomatal bands.

Remarks. Most of the recovered fascicles still joined with the brachyblast bear two needles. All specimens except one are incomplete in length and the degree to which the needle length differed remains open, which could indicate more than one fossil-species. The variation in needle width potentially suggest two fossil-species. Very slender needles could derive from the same pine as the cone of *P. cortesii* Al. Brongn., which is closely related to the modern *P. halepensis* (see below). Note, however, that the needle margin is finely serrate in the latter species, which has not been observed in the fossil remains. Specimen NHMW 1878/6/9708 is a slab with numerous needles but lacking their bases. The subparallel and slightly diverging arrangement of some needles also suggests a pine with two needles per fascicle.

***Pinus* sp.** – 4 (?) 5-needled fascicles

Fig. 4.12

1878a *Pinus palaeo-cembra* Ettingsh. nomen nudum; Ettingshausen, p. 69, 77, pl. 2, figs 6, 7 (part + counterpart).

1888 *Pinus palaeo-strobus* Ettingsh., p.p.; Ettingshausen, p. 275.

1888 *Pinus palaeo-cembra* Ettingsh., p.p.; Ettingshausen, p. 275.

1893 *Pinus taedaeformis* Unger; Ettingshausen, p. 342, pl. 2, fig. 7.

Material. Seegraben Walpurgis-Schacht: NHMW: 1878/6/7081 (Ett. 5078), Pb 2341, (*Pinus palaeo-strobus*); 1878/6/7082 (5079), Pb 2343, (*P. palaeo-strobus*); 1878/6/7085 (5082), Pb 2342, (*P. palaeo-strobus*); 1878/6/7086 (5083), Pb 2339, (*P. palaeo-strobus*); 1878/6/9772 + 9773 (Ett. 7769 + 7770), (*P. palaeo-cembra*), Ettingshausen (1878a: pl. 2, figs 6, 7, holotype). Münzenberg: IBUG: Ett. 5569, (*P. taedaeformis*), Ettingshausen (1893: pl. 2, fig. 7).

Description. Fascicles with 4 to (?) 5 needles; brachyblast short (only one specimen), needle length up to 96 mm (all incomplete), width 0.5–0.7 mm, margin entire.

Remarks. All specimens are incomplete in length, and 4 needles are definite but a fifth one is uncertain in several specimens. These pine remains likely underwent some transport before deposition.

***Pinus* sp.** – clusters of needles

Fig. 4.13

1878a *Pinus palaeo-strobus* Ettingsh.; Ettingshausen, p. 73, pl. 2, fig.1.

Material. Seegraben Walpurgis-Schacht: NHMW: 1878/6/9771 (Ett. 7768), (*Pinus palaeo-strobus*), Ettingshausen (1878a: pl. 2, fig. 1). Leoben: NHMW: 2023/0072/0012.

Description. Clusters of entire-margined needles lacking bases and apices; needle length >70 mm and >130 mm.

Remarks. These specimens indicate the deposition of foliated branches. The bases and brachyblasts are not preserved. The number of needles per fascicle, therefore, remains ambiguous.

***Pinus* sp.** – male catkins

Fig. 4.16–4.18

1878a *Pinus prae-silvestris* Ettingsh. nomen nudum, p.p.; Ettingshausen, p. 69, 76, pl. 10, figs 7, 8.

1878a *Pinus laricio* Poir., p.p.; Ettingshausen, p. 75, pl. 10, fig. 5.

1878a *Pinus hepios* Unger; Ettingshausen, p. 75, pl. 10, fig. 6.

1888 *Pinus goethana* Unger, p.p.; Ettingshausen, p. 275.

1888 *Pinus laricio* Poir., p.p.; Ettingshausen, p. 276, non pl. 2, figs 6, 7.

1888 *Pinus hepios* Unger, p.p.; Ettingshausen, p. 276.

1888 *Pinus prae-silvestris* Ettingsh., p.p.; Ettingshausen, p. 277.

2004 *Pinus* sp. div. sp.; Kovar-Eder et al., p. 53, pl. 1, figs 9, 10, only figs 6, 7.

Material. Moskenberg: NHMW: 1878/6/4075 (Ett. 2072), (*Pinus goethana*); 1878/6/4076 (2073), (*P. hepios* in sched.); 1878/6/4077 (2074), (*P. hepios* in sched.); 1878/6/7098 (5095), (*P. hepios*); 1878/6/7104 (5101), (*P. prae-silvestris*); 1878/6/9701 (7698), (*P. hepios*), Ettingshausen (1878a: pl. 10, fig. 6); 1878/6/9711 (7708), (*P. laricio*), Ettingshausen (1878a: pl. 10, fig. 5); 1878/6/9733 (7730), Pb 1890, (*P. prae-silvestris*), Ettingshausen (1878a: pl. 10, fig. 8, syntype); 1878/6/9734 (7731), Pb 1891, (*P. prae-silvestris*), Ettingshausen (1878a: pl. 10, fig. 7, syntype). IBUG: Ett. 6295, a, (*P. hepios*), Ettingshausen (1878a: pl. 8, fig. 1).

Description. Compressed (fragmentary) catkins, originally probably cylindrical; specimens NHMW 1878/6/9701 and NHMW 1878/6/9734 complete, with basal bracts, length (including bracts) × width 18 × 3 mm and 15 × 2.5 mm, bent; other catkins length incomplete, width 2.5–5.5 mm; stamina densely spaced.

Remarks. Details of the basal scales and stamina are not discernible. Thicker and more slender catkins may represent different fossil-species.

***Pinus* sp.** – winged seeds, isolated wings

Fig. 4.19–4.23

1869a *Pinus stenoptera* Ettingsh. sp. n., p.p.; Ettingshausen, p. 41, pl. 1, figs 17, 18, non 19.

1869a *Pinus pachyptera* Ettingsh. sp. n., p.p.; Ettingshausen, p. 42, pl. 1, fig. 21.

1878a *Pinus palaeo-laricio* Ettingsh., nomen nudum, p.p.; Ettingshausen, p. 68, 74, pl. 1, figs 13, 17, 18.

1878a *Pinus laricio* Poir., p.p.; Ettingshausen, p. 68, 75, pl. 7, figs 1–3, 7, 10.

1878a *Pinus prae-silvestris* Ettingsh. nomen nudum, p.p.; Ettingshausen, p. 69, 75, pl. 7, figs 17, 18.

1888 *Pinus palaeo-laricio* Ettingsh., p.p.; Ettingshausen, p. 275.

1888 *Pinus laricio* Poir., p.p.; Ettingshausen, p. 276, pl. 2, fig. 6.

1888 *Pinus prae-silvestris* Ettingsh., p.p.; Ettingshausen, p. 277.

Material. Moskenberg: NHMW: 1878/6/3588 (Ett. 1585), (*Pinus laricio* in sched.); 1878/6/3593 + 3594 (1590 + 1591), Pb 1874, 1875, (*P. stenoptera*), type, Ettingshausen (1869a: pl. 1, fig. 18, (?) 17; 1878/6/3889 (1886), (*P. prae-silvestris*); 1878/6/4072 (2069), (*P. laricio* in sched.); 1878/6/9713 (7710), (*P. laricio*), Ettingshausen (1878a: pl. 7, fig. 1); 1878/6/9714 (7711), Pb 1884, (*P. laricio*), Ettingshausen (1878a: pl. 7, fig. 2); 1878/6/9715 (7712), A, Pb 1885, (*P. laricio*), Ettingshausen (1878a: pl. 7, fig. 10); 1878/6/9716 (7713), Pb 1886, (*P. laricio*), Ettingshausen (1878a: pl. 7, fig. 3); 1878/6/9735 (7732), Pb 1889, (*P. prae-silvestris*), Ettingshausen (1878a: pl. 7, fig. 17); 1878/6/9736 (7733), Pb 1888, (*P. prae-silvestris*), Ettingshausen (1878a: pl. 7, fig. 18). IBUG: Ett. 5531, A, (*P. laricio*). Münzenberg: NHMW: 1878/6/9710 (Ett. 7707), (*P. laricio*), Ettingshausen (1878a: pl. 7, fig. 7).

Description. Winged seeds, isolated wings, seeds partly fully developed, partly unripe or abortive; developed seeds ~7 mm long and 4 mm wide; shape variable, elliptic to elongated, proximally narrowed; shape of not fully developed or abortive seeds very variable, round to elliptic, much smaller; wing membranaceous, elongated, adnate to seed, dorsal line rather straight to somewhat convex, slightly thickened close to seedbody, ventral line straight to convex; wing sometimes with striae paralleling its long axis; wing enclosing about one third of seedbody of fully developed seeds; in not fully developed/abortive seeds enclosing it more comprehensively.

Remarks. The remains of winged seeds are very variable. Zidianakis et al. (2016) demonstrated that the intra-specific variability of winged seeds is wide when unripe or abortive seeds are taken into account.

***Pinus* sp.** – cones

Fig. 4.14, 4.15

1878a *Pinus laricio* Poir., p.p.; Ettingshausen, p. 76, pl. 10, fig. 2a.

1888 *Pinus laricio* Poir., p.p.; Ettingshausen, p. 276, pl. 2, fig. 7, non fig. 6.

1984 *Pinus halepensis* Mill.; Klaus, p. 48.

Material. Moskenberg: NHMW: 1878/6/3534 (Ett. 1531), (*Pinus laricio*); 1878/6/9712 (7709), a, (*P. laricio*), Ettingshausen (1878a: pl. 10, fig. 2a). Münzenberg: NHMW: 1871/38/36, (*P. laricio*), Pb 2154. Note that this specimen is not the counterpart of the specimen figured by Ettingshausen (1878a: pl. 10, fig. 2a) as indicated in OETYP and by Kovar-Eder (1990).

Description. Woody female cones, strongly compressed, shape conical, length × widest width 43–45 × 17–19 mm, tapering towards apex; apophyses helically arranged, shape rhomboidal, relatively flat with radial striae (NHMW 1878/6/3534, Ett. 1531), transversal keel only occasionally visible, no longitudinal keel visible; umbo in central position, shape deltoidal, mucro small, probably also in central position.

Remarks. Neither the cone figured by Ettingshausen (1888: pl. 2, fig. 7) nor isolated pine cone scales have been detected among the collection material. In specimen NHMW 1878/6/3534 (Ett. 1531), the transversal keel is well visible on a single apophysis. On this specimen, the fine radiating striae appear somewhat damaged by secondary scratches (possibly caused by a brush). Possibly due to preservation (compression), the transversal keel is only occasionally faintly visible and striae are not preserved in specimen NHMW 1878/6/9712 (Ett. 7709) (Fig. 4.14). The assignment by Ettingshausen (1878a, 1888) to *P. laricio* Poir., which is a synonym of the modern *P. nigra* Aiton, indicates the morphological resemblance to that pine.

Section *Halepensis* Loudon

Pinus cortesii Al. Brongn.

1822a *Pinus cortesii* Al. Brongn.; Brongniart, p. 324, pl. 17, fig. 7.

1984 *Pinus halepensis* Mill.; Klaus, p. 48.

1985 *Pinus halepensis* Mill. ssp. *styriacus* Klaus ssp. n.; Klaus, p. 116, pl. 1, figs 1–5, pl. 2, fig. 1.

Material. Seegraben: NHMW: 1886, Pb 515, (*Pinus halepensis*), Klaus (1984, 1985) cone 6.

Description. See Klaus (1984, 1985).

Remarks. Mai (1994) noted phylogenetic problems of applying the binomen *Pinus halepensis* (a modern species) creating a subspecies for fossil specimens. Instead, Mai proposed *Pinus cortesii* for fossil cones closely resembling *P. halepensis*, which is the oldest mention of such a cone.

Order CUPRESSALES Link

Family CUPRESSACEAE Gray sensu Farjon (2005)

Subfamily CUPRESSOIDEAE Sweet

Genus ***Calocedrus*** Kurz

Calocedrus suleticensis (Brabenec) Kvaček

Fig. 4.27

1888 *Libocedrus salicornioides* Endl., p.p.; Ettingshausen, p. 273.
1909 *Libocedrus suleticensis* Brabenec; Brabenec, p. 60, text-fig. 42.
1999 *Calocedrus suleticensis* (Brabenec) Kvaček; Kvaček, p. 194, figs 1–6, 16–26.

Material. Moskenberg: NHMW: 1878/6/6989 (Ett. 4886), (*Libocedrus salicornioides*); cf. 1878/6/6990 (4887), (*L. salicornioides*). Seegraben Walpurgis-Schacht: IBUG: cf. Ett. 5577, (Coniferae sp. (Abietinae) in sched.).

Description. Restricted to specimen NHMW 1878/6/6989 (Ett. 4886): Fragment of a multiply branched, flattened spray; leaves decussate in pseudowhorls of four leaves, two facial and two lateral ones, adpressed to the axis but likely not adnate; facial leaves triangular, apically covering base of next whorl, with distinct midrib; lateral ones duplicate, falcate, apical part free, apex bluntly acute; size of leaves and pseudowhorls variable depending on position on the spray, twig branching unilateral alternate to opposite.

Remarks. While the assignment of specimen NHMW 1878/6/6989 (Ett. 4886) is unambiguous, it remains ambiguous for the more poorly preserved specimens in which the presumable pseudowhorls and their leaves are less distinct.

Although Kvaček (1999) described *Calocedrus suleticensis* from Oligocene deposits of Bohemia (Suletice-Berand and Holý Kluk) and Hungary (Kiseged), the specimen from Leoben closely resembles it. Unfortunately, neither cone nor seed of *Calocedrus* have been detected in the Leoben flora. Miocene records of this conifer are still scarce, deriving from Asia (South China; Zhang et al., 2015; He and Wang, 2021), North America (Middle Miocene, Clarkia flora; Kvaček and Rember, 2007), Greece (Lower Miocene, Kimi; Kvaček, 1999) and Turkey (Lower Miocene, Güvem; Denk et al., 2017b).

Genus ***Tetraclinis*** Mast.

Tetraclinis salicornioides (Unger) Kvaček

Fig. 4.28–4.31

1847 *Thuites salicornioides* Unger; Unger, p. 11, pl. 2, figs 1–4.
1869a *Callitris brongniartii* Endl.; Ettingshausen, p. 39, pl. 1, fig. 23.
1989 *Tetraclinis salicornioides* (Unger) Kvaček; Kvaček, p. 48, pl. 1, fig. 11, pl. 2, figs 2–14, pl. 3, figs 1–4, text-fig. 1.
1999 *Tetraclinis salicornioides* (Unger) Kvaček; Meller et al., p. 129, pl. 1, fig. 1, pl. 3 figs 9, 10.
1999 *Tetraclinis salicornioides* (Unger) Kvaček; Ströbitzer, p. 95, pl. 1, figs 19, (?) 20, pl. 7, figs 19, (?) 20.
2001 *Tetraclinis salicornioides* (Unger) Kvaček; Kovar-Eder and Meller, p. 72.

Material. Moskenberg: NHMW: 1878/6/3595 (Ett. 1592), Pb 1873, (*Callitris brongnartii*), Ettingshausen (1869a: pl. 1, fig. 23), winged seed; 1878/6/4068 (2065), (*Libocedrus salicornioides* in sched.), twig fragment; 1878/6/4085 (2082), D. IBUG: Ett. 5375 + 5376, (*L. salicornioides* in sched.), twig fragment; Ett. 6295, e, (*Callitris brongniartii*), winged seed, Ettingshausen (1878a: pl. 8, fig. 1 e); note that Ettingshausen (1878a) did not quote this seed. Münzenberg: IBUG: Ett. 5377, (*Libocedrus salicornioides* in sched.); Ett. 5378, (*Libocedrus salicornioides* in sched.), twig fragment. Leoben: GBA: 2024/0001/0010, (*Callitris brongniartii*), seed; 2024/0001/0021 (*Libocedrites haidingeri*), twig fragment.

Description. Twig fragments consisting of several segments, each made of two facial and two duplicate lateral leaves fused along most of their length, forming phylloclade-like whorls; surface view three-veined; segments up to 6–7 mm long and ~2 mm wide, base rounded.

Imprint of symmetrical, two-winged seeds; shape reniform, overall l × w ~5.8 × 9.3 and ~5.3 × 7 mm; wings as wide as seed body but longer; l × w of seed body ~4.8 × 3.5 and ~4.3 × 2.3 mm, seed body ovate, base rounded, apex acute.

Remarks. While the specimens listed by Ettingshausen (1888) for *Libocedrus salicornioides* represent *Calocedrus suleticensis* (see that section), some twig fragments which remained unmentioned by him clearly document the occurrence of *T. salicornioides*. On specimen NHMW 1878/6/3595 (Ett. 1592) one wing of the seed is damaged, and on none of the specimens is the vascularisation on the seed body visible. Beyond the European occurrences, the co-occurrence of foliated twigs, cones and seeds of *T. salicornioides* is documented from sites in western North America (Kvaček et al., 2000).

Subfamily SEQUOIOIDEAE Saxton

Genus **Sequoia** Endl.

Sequoia abietina (Brongn.) Erw. Knobloch

Figs 4.32, 5.1–5.3

1822a *Phyllites abietina* Brongn.; Brongniart, p. 362, pl. 11, fig. 13.
1869a *Sequoia hardtii* Endl., p.p.; Ettingshausen, p. 40, pl. 1, fig. 27, non 28.
1888 *Sequoia tournalii* (Brongn.), p.p.; Ettingshausen, p. 274.
1888 *Sequoia langsdorfii* Brongn.; Ettingshausen, p. 274, pl. 2, fig. 2.
1964 *Sequoia abietina* (Brongn. in Cuvier) Erw. Knobloch; Knobloch, p. 601.
1999 *Sequoia abietina* (Brongn.) Erw. Knobloch; Meller et al., p. 130, pl. 1, fig. 2.
1999 *Sequoia abietina* (Brongn.) Erw. Knobloch; Ströbitzer, p. 94, pl. 1, fig. 9, pl. 7, fig. 8.
2001 *Sequoia abietina* (Brongn.) Erw. Knobloch et/vel *Glyptostrobus europaeus* (Brongn.) Unger, p.p.; Kovar-Eder and Meller, p. 71.
2003 *Sequoia abietina* (Brongn.) Erw. Knobloch; Kovar-Eder and Meller, p. 285, pl. 1, figs 1–4, 13.

Material. Moskenberg: NHMW: 1878/6/3538 (Ett. 1535), twig + cone, (*Sequoia langsdorfii* in sched.); 1878/6/3606 (1603), (*S. langsdorfii* in sched.), twig; 1878/6/3607 (1604), (*S. langsdorfii* in sched.), cone; (?) 1878/6/3744 (1741), (*S. langsdorfii* in sched.), twig; 1878/6/4137 (2134), B, twig; 1878/6/7030 (5027), (*S. langsdorfii* in sched.), twig; 1878/6/9165 + 9166 (7162 + 7163), (*S. langsdorfii*), cone. IBUG: Ett. 5465, (*S. langsdorfii*); Ett. 5466, (*S. langsdorfii*); Ett. 5469, (*S. langsdorfii*); Ett. 5471, (*S. langsdorfii*), twigs; (?) Ett. 6295, f (*S. langsdorfii*), seed, Ettingshausen (1878a: pl. 8, fig. 1f). Seegraben Walpurgis-Schacht: IBUG: Ett. 5472, (*S. langsdorfii*), multiply branched twig. Leoben: GBA: 2024/0001/0018, cones.

Description. Twigs with spirally arranged either taxodioid or cryptomerioid/cupressoid leaves; at base of twigs with taxodioid leaves, clusters of scale-like cupressoid leaves; taxodioid leaves spread distichously in one plane, rigid, one-veined, basally twisted, up to 20 mm long, ~1 mm wide, apex shortly pointed; cones ~10 mm in diameter.

Remarks. *Sequoia abietina* is well documented by both taxodioid and cupressoid/cryptomerioid foliated twigs, as well as cones. Compared to *Glyptostrobus europaeus*, in *S. abietina* the taxodioid needles appear to be stiffer and usually slightly broader. The base of such twigs of *S. abietina* bears densely clustered, small, scale-like cupressoid leaves. Nevertheless, an unambiguous assignment is not always possible (see below). Specimen IBUG Ett. 6295 f is the only one possibly representing a seed of *S. abietina* (refigured here on Fig. 4.32).

Subfamily TAIWANIOIDEAE L.Chu Li

Genus **Taiwania** Hayata

Taiwania cf. ***paracryptomerioides*** Kilpper

Fig. 4.25, 4.26

1888 Sequoia couttsiae Heer, p.p.; Ettingshausen, p. 274.

Material. Moskenberg: NHMW: 1878/6/3609 (Ett. 1606), (*Sequoia couttsiae*); 1878/6/7046 (5043), A, (*S. couttsiae* in sched.). Münzenberg: IBUG: Ett. 5434, (*S. couttsiae*). Leoben: GBA: 2024/0001/0003.

Description. Twig fragments, longest 33 mm long, leaves solid, helically arranged, attached to axis by broad decurrent base, free part triangular, somewhat sickle-shaped, proximal flank keeled, 2–7 mm long and 1–3 mm wide at base of free part; apex (bluntly) acute; one thick central vein parallel to leaf length.

Remarks. Grossmorphologically these remains closely resemble the short shoots described from Eschweiler, Lower Rhine Embayment, Upper Miocene (Kilpper, 1968) and the shoot reported from Witznitz, Saxony (Mai and Walther, 1991). At the former site, strobili of *Taiwania* were also associated.

Subfamily TAXODIOIDEAE Endl. ex K. Koch

Genus ***Glyptostrobus*** Endl.

Glyptostrobus europaeus (Brongn.) Unger

Fig. 5.4–5.7

1833 *Taxodium europaeum* Brongn.; Brongniart, p. 168.
1850b *Glyptostrobus europaeus* (Brongn.) Unger; Unger, p. 434.
1858 *Widdringtonia ungeri* Endl.; Ettingshausen, p. 742; pl. 1, fig. 1.
1869a *Glyptostrobus europaeus* Unger; Ettingshausen, p. 40.
1869a *Sequoia hardtii* Endl., p.p.; Ettingshausen, p. 40, pl. 1, fig. 28, non 27.
1888 *Widdringtonia ungeri* Endl., p.p.; Ettingshausen, p. 273.
1888 *Glyptostrobus europaeus* Brongn.; Ettingshausen, p. 273, pl. 2 figs 3–5.
1888 *Glyptostrobus ungeri* Heer, p.p.; Ettingshausen, p. 274.
1888 *Sequoia tournalii* Brongn., p.p.; Ettingshausen, p. 274.
1996 *Glyptostrobus europaeus* (Brongn.) Unger; Kovar-Eder, p. 149, pl. 1, figs 7–13, pl. 2, figs 1–3.
1999 *Glyptostrobus europaeus* (Brongn.) Unger and *Sequoia abietina* (Brongn.) Erw. Knobloch, p.p.; Meller et al., p. 130.
1999 *Glyptostrobus europaeus* (Brongn.) Unger; Ströbitzer, p. 94, pl. 1, figs 10–12, (?) 13, pl. 7, figs 9, 10.
2001 *Sequoia abietina* (Brongn.) Erw. Knobloch et/vel *Glyptostrobus europaeus* (Brongn.) Unger, p.p.; Kovar-Eder and Meller, p. 71.
2004 *Glyptostrobus europaeus* (Brongn.) Unger; Kovar-Eder et al., p. 54, pl. 1, figs 14–15.

Material. Moskenberg: NHMW: 1878/6/3601 (Ett. 1598), (*Glyptostrobus europaeus* in sched.), cone; 1878/6/3604 (1601), (*G. europaeus* in sched.), twig; 1878/6/3638 (1635), Pb 1864, (*G. europaeus*), seed, Ettingshausen (1888: pl. 2, fig. 5); 1878/6/3641 (1638), (*G. europaeus* in sched.), twig; 1878/6/3643 (1640), (*G. europaeus* in sched.), seed; 1878/6/3646 (1643), Pb 1865, (*G. europaeus*), seed, Ettingshausen (1888: pl. 2, fig. 3); 1878/6/3901 (1898), (*Sequoia couttsiae* in sched.), twig; 1878/6/3909 (1906), (*S. couttsiae* in sched.), twig with cone; 1878/6/8979 (6976), (*Glyptostrobus europaeus*), cone; 1878/6/8980 (6977), Pb 1866, (*G. europaeus*), cone; 1878/6/9067 (7064), A, (*Sequoia tournalii*), as (*Sequoia hardtii*) in Ettingshausen (1869a: pl. 1, fig. 28), twig; and many more specimens not listed by Ettingshausen (1888). IBUG: Ett. 5401–5403, (*Glyptostrobus europaeus*), seeds. Münzenberg: NHMW: 1878/6/4267 (Ett. 2264), Pb 2153, (*Widdringtonia ungeri*), twig; 1878/6/6941 (4938), (*Glyptostrobus europaeus* in sched.), twig with cone; 1878/6/7008 + 7009 (5005 + 5006), (*G. ungeri* in sched.); 1878/6/9902 (7899), Pb 2152, (*G. europaeus*), Ettingshausen (1888: pl. 2, fig. 4), seed. IBUG: Ett. 5404, (*G. europaeus*), seed.

Description. (Branched) twigs with cupressoid/cryptomerioid or taxodioid foliage; leaves helically arranged, taxodioid ones irregularly spread, <10 mm long, cupressoid/cryptomerioid leaves triangular, base closely adpressed to axis, apical part either also adpressed to axis or free and outspread, partly sickle-shaped; cones: l × w ~18–20 × 14–15 mm; winged seeds: ~10 mm long, seed and wing almost of same length, wing often incomplete.

Remarks. Remains of *Glyptostrobus europaeus* (twigs, cones, seeds) are much more numerous in the collection than the material listed by Ettingshausen (1888) would let expect. In fact, *G. europaeus* is the most common conifer in this assemblage aside from pine remains. The branched twig figured as *Sequoia hardtii* (Ettingshausen, 1869a: pl. 1, fig. 28; NHMW 1878/6/9067, Ett. 7064) and later transferred to *S. tournalii* (Ettingshausen, 1888) represents *G. europaeus*. The taxodioid needles of this specimen appear soft, so that the assignment to *Sequoia* is very unlikely. For the assignment of the cone that Ettingshausen (1869a, 1888) also assigned to *S. hardtii* and *S. tournalii*, respectively, see section *Sequoia abietina*.

Family TAXACEAE Gray

Genus ***Amentotaxus*** Pilg.

***Amentotaxus* sp.**

Fig. 4.24

1888 *Cyperites binervis* Ettingsh. sp. n.; Ettingshausen, p. 278, pl. 2, figs 24, 25.

Material. Seegraben Walpurgis-Schacht: NHMW: 1878/6/4472 + 4473 (Ett. 2469 + 2470, A), Pb 2330, (*Cyperites binervis*), Ettingshausen (1888: pl. 2, fig. 24, 25, holotype).

Description. Needle fragment 75 mm long (incomplete), maximal width 3.5 mm; lacking base and apex, tapering along length; margin entire; with two bands paralleling needle length.

Remarks. Neither it is possible to estimate the complete length of this specimen nor to determine the proximal (base) and distal end (apex). The parallel bands may represent the stoma bands indicating that the abaxial surface is preserved, thus explaining that the midvein is not visible. The considerable length and the presumable stoma bands point towards *Amentotaxus* (Ferguson et al., 1978). Needles of *Cathaya* may also reach considerable length but are narrower and do not tapper along their length.

Genus ***Cephalotaxus*** Siebold et Zucc. ex Endl. vel ***Torreya*** Arn.

Cephalotaxus vel ***Torreya*** **sp.**

Fig. 4.34

Material. Seegraben Walpurgis-Schacht: IBUG: Ett. 5574 + 5576, A, (*Abies* sp. in sched.).

Description. Part and counterpart of branched, foliated twig fragment, 35 mm long; needles up to at least 20 mm long and ~1–1.3 mm wide, straight to slightly sickle-shaped, at base twisted and decurrent on main axis, needle apex (?) acute, margin entire.

Remarks. In the Leoben material this specimen is unique by its long, slightly sickle-shaped needles which are twisted at the base and further decurrent along the main axis. The twig fragment appears to be branched but the physical connection to the side branch is not preserved. The twig fragment at the top of this slab represents *Sequoia abietina* (Fig. 4.34a).

Genus ***Taxus*** L. vel ***Cephalotaxus*** Siebold et Zucc. ex Endl.

Taxus vel ***Cephalotaxus*** **sp.**

Fig. 4.33

Material. Seegraben Walpurgis-Schacht: NHMW: 1878/6/4203 (Ett. 2200), B.

Description. Needle lacking apex, l × w ~17 (incomplete) × 2 mm, base obtuse, shortly petiolate, petiole bent, margin entire, needle tapering slightly along its length, one central vein parallel needle length.

Remarks. The slightly tapering needle suggests that it was not very long. The obtuse base, the short petiole, the width and the limited length indicate either *Taxus* or *Cephalotaxus*. Needles of *Torreya* are also shortly petiolate but wider and reach considerable length (LePage, 2011). In *Pseudotsuga* the needles are revolute, which is not the case in this specimen. Needles of *Cephalotaxus* were recorded based on gross morphology and cuticles at the main seam parting of Oberdorf, N Voitsberg (Styria) (Kovar-Eder and Meller, 2003).

ANGIOSPERMAE

Order NYMPHAEALES Dumortier vel PROTEALES Bercht. et J. Presl

Family NYMPHAEACEAE Salisb. vel NELUMBONACEAE A. Richard

“***Nelumbium***” ***buchii*** Ettingsh.

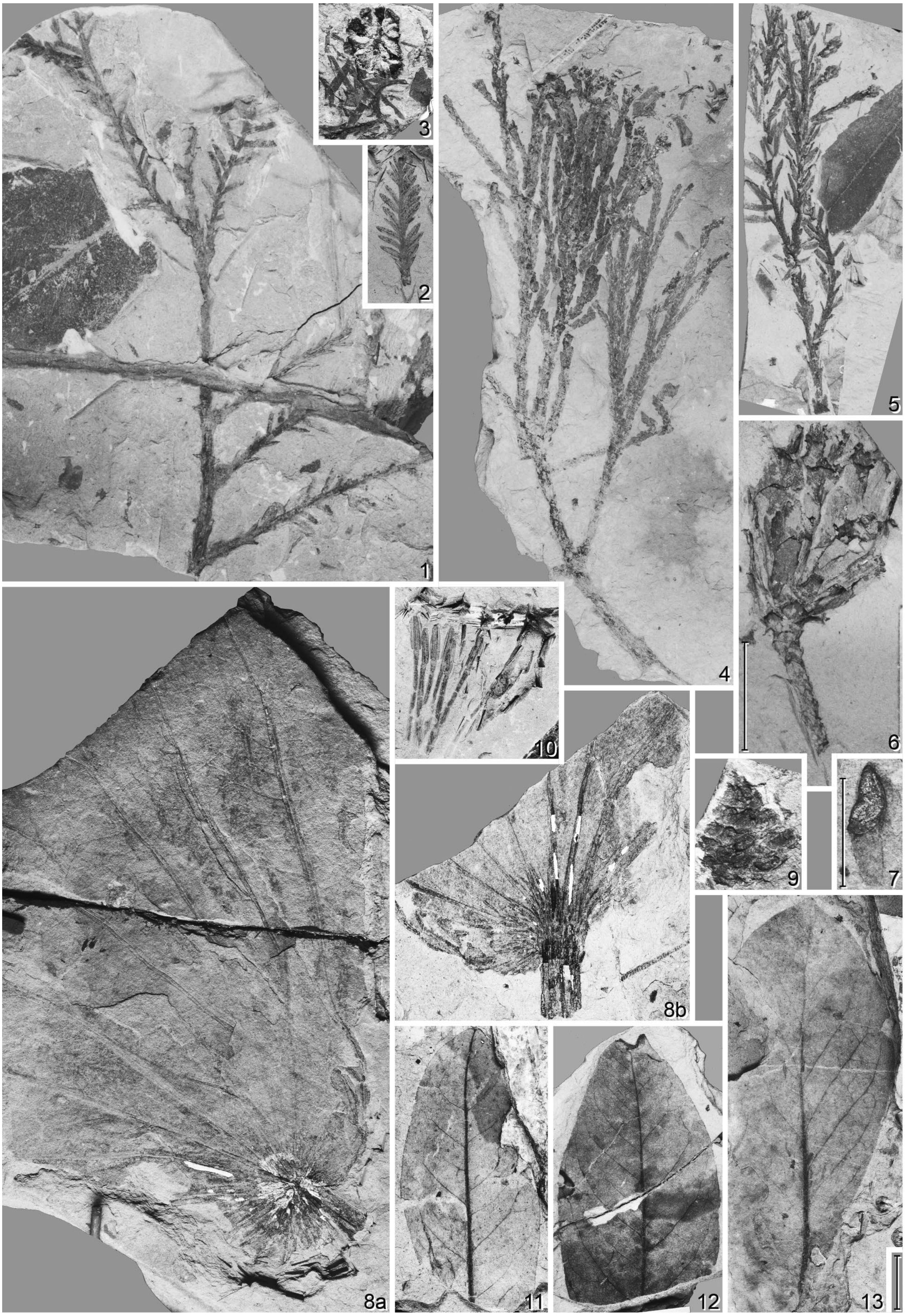
Fig. 5.8

1869a *Anoectomeria brongniartii* Saporta; Ettingshausen, p. 77, pl. 4, fig. 18.
1888 *Nelumbium buchii* Ettingsh.; Ettingshausen, p. 335, pl. 7, fig. 13.

Material. Moskenberg: NHMW: 1878/6/3525 + 3526 (Ett. 1522 + 1523), (*Nelumbium buchii*); 1878/6/3527 (1524), (*N. buchii*), Ettingshausen (1888: (?) pl. 7, fig. 13); 1878/6/3528 (1525), (*N. buchii*). Münzenberg: NHMW: 1878/6/4403 (2400), A, Pb 2217, (*N. buchii*). Leoben: LMJ: 201.064, 201.065.

Description. Fragments of petiolate, probably floating leaves; petiole 10 mm long (incomplete), up to 10 mm wide; petiole attachment marginal or minimally peltate excentric; lamina shape (?) roundish; margin (?); venation actinodromous with >10 thick veins, diverging rapidly, dichotomising distally; veins connecting primaries delicate, (forked)percurrent, sinuate; white strands at leaf base and along main veins near base.

Remarks. Except for the here figured specimen (NHMW 1878/6/3525 + 3526, Ett. 1522 + 1523), the others are less well preserved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fragments. Only this specimen shows sinuate (forked)percurrent veins connecting the main veins. This specimen shows also white strands at the leaf base and along the main veins. These strands possibly represent laticifers or latex. Specimen NHM 1878/6/3527 (Ett. 1524) may be the specimen figured by Ettingshausen (1888: pl. 7, fig. 13) mirror-inverted, or it is its counterpart.

In modern Nelumbonaceae (1 genus, 2 species), the petiole attachment is peltate central, contrary to the here described fossils. The strands along main veins and near the base of the fossils (possibly representing laticifers or latex) would, however, point towards Nelumbonaceae. Among modern Nymphaeaceae, the leaves of *Nymphaea* L., *Nuphar* Sm. and *Barclaya* Wall. differ from the fossils by having a midvein and reticulate connecting veins. In *Euryale ferox* Salisb. the petiole attachment is central and the surface is spiny, thus differing from the fossil remains. In *Victoria* R.H. Schomb. the petiole attachment is central and its natural geographical occurrence in South America makes a close relationship more unlikely.

Nymphaeaceae vel **Nelumbonaceae gen.** et **sp.** – rhizome fragment and diaphragmas

Fig. 5.9

1869a *Anoectomeria brongniartii* Saporta; Ettingshausen, p. 77, pl. 4, figs 16, 17.

1888 *Castanea atavia* Unger, p.p.; Ettingshausen, p. 292.

Material. Moskenberg NHMW: 1878/6/7503 (Ett. 5500), (*Castanea atavia*). Münzenberg: NHMW: 1878/6/4329 (Ett. 2326), Pb 2224, (*Anoectomeria brongniartii*); 1878/6/4372 (2369), B.

Description. Isolated diaphragmas and a rhizome fragment with several closely spaced diaphragmas; diameter of single diaphragmas up to 5 mm.

Remarks. In the studied material, only a single rhizome fragment has been encountered (Fig. 5.9), and isolated diaphragmas have been observed only very rarely.

Nymphaeaceae (?) vel **Nelumbonaceae** (?) **gen.** et **sp.** – stamina

Fig. 5.10

1888 *Echitonium microspermum* Unger, p.p.; Ettingshausen, p. 326, pl. 5, fig. 15.

Material. Moskenberg: NHMW: 1878/6/6825 (Ett. 4822), (*Schizaea neogenica* in sched.); 1878/6/7163 (5160), B. IBUG: Ett. 6107, (*Echitonium microspermum*), Ettingshausen (1888: pl. 5, fig. 15).

Description. Cluster of 6 stamina, isolated stamen and anther; filaments up to 18 mm long, 0.8–0.9 mm wide, anthers ~6–7 mm long and 1.3–1.7 mm wide.

Remarks. The considerable size of these stamina along with the presence of leaves, rhizomes and isolated diaphragmas of Nymphaeaceae vel Nelumbonaceae point towards the water lily or lotus family. The development of anthers was studied for *Nelumbo lutea* (Willd.) Pers. (Kreunen and Osborn, 1999). Accordingly, the size of the anthers measures up to 7 mm in an early stage (sporogenous tissue stage) and reaches up to 34–38 mm at maturity. The attempt to extract pollen from a theca of the fossil specimen NHMW 1878/6/6825 (Ett. 4822) was unsuccessful (pers. comm. R. Zetter). In case these stamina derive from Nelumbonaceae, they may represent an early stage in which pollen was not yet developed.

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Figure 5. **1–3**. *Sequoia abietina* (Brongn.) Erw. Knobloch; **1**. IBUG Ett. 5472, (*S. langsdorfii*), twig, **2**. NHMW 1878/6/3606 (Ett. 1603), (*S. langsdorfii*), twig, **3**. NHMW 1878/6/3607 (Ett. 1604), (*S. langsdorfii*), cone; **4–7**. *Glyptostrobus europaeus* (Brongn.) Unger, **4**. NHMW 1878/6/3641 (Ett. 1638), (*G. europaeus*), twig, **5**. NHMW 1878/6/9067 (Ett. 7064), A, (*Sequoia tournalii*), as (*Sequoia hardtii*) in Ettingshausen (1869a: pl. 1, fig. 28), twig, **6**. NHMW 1878/6/8979 (Ett. 6976), (*G. europaeus*), cone, **7**. NHMW 1878/6/3643 (Ett. 1640), (*G. europaeus*), seed; **8a**, **b**. *"Nelumbium" buchii* Ettingsh., NHMW 1878/6/3525 + 3526 (Ett. 1522 + 1523), (*N. buchii*); **9**. Nymphaeaceae vel Nelumbonaceae gen. et sp. – rhizome fragment and diaphragmas, NHMW 1878/6/7503 (Ett. 5500), (*Castanea atavia*); **10**. Nymphaeaceae (?) vel Nelumbonaceae (?) gen. et sp. – Stamina, NHMW 1878/6/6825 (Ett. 4822), (*Schizaea neogenica* in sched.); **11–13**. *Magnolia* cf. *liblarensis* (Kräusel et Weyland) Kvaček, **11**. NHMW 1878/6/9197 (Ett. 7194), B, **12**. NHMW 1878/6/6917 (Ett. 4914), C, **13**. NHMW 1878/6/3881 (Ett. 1878), b, (*Daphne palaeo-laureola*), counterpart to NHMW 1878/6/3919 (Ett. 1916), (*Daphne palaeo-mezereum*), Pb 1964, Ettingshausen (1888: pl. 4, figs 1, 1a, syntype). For all photographs the scale at bottom right of the figure is 10 mm except for photographs with embedded scale in which the scale is also 10 mm

Order MAGNOLIALES Bromhead

Family MAGNOLIACEAE Juss.

Genus ***Magnolia*** L.

Magnolia cf. ***liblarensis*** (Kräusel et Weyland) Kvaček

Figs 5.11–5.13, 23.1

1888 *Ficus jynx* Unger, p.p.; Ettingshausen, p. 297.
1888 *Daphne radobojana* Unger, p.p.; Ettingshausen, p. 311.
1888 *Daphne palaeo-laureola* Ettingsh.; Ettingshausen, p. 312.
1888 *Daphne palaeo-mezereum* Ettingsh. sp. n.; Ettingshausen, p. 312, pl. 4, figs 1, 1a.
(?) 1888 *Protea europaea* Ettingsh. sp. n., p.p.; Ettingshausen, p. 313, pl. 4, fig. 14, (non figs 12, 13).
1888 *Diospyros brachysepala* A. Braun, p.p.; Ettingshausen, p. 329, non pl. 4, fig. 9.
cf. 1959 *Papilionaceophyllum liblarense* Kräusel et Weyland; Kräusel and Weyland, p. 111, pl. 24, figs 37–41, pl. 25, figs 42–47, pl. 26, fig. 48.
cf. 1979 *Magnolia liblarensis* (Kräusel et Weyland) Kvaček; Kvaček, p. 172, pl. 37, figs 2–5.

Material. Moskenberg: NHMW: 1878/6/3875 (Ett. 1872), A, (*Diospyros brachysepala*); 1878/6/3881 + 3919 (1878, b + 1916), Ett. 1878, b (*Daphne palaeo-laureola*), Ett. 1916 (*Daphne palaeo-mezereum*), Pb 1964, Ettingshausen (1888: pl. 4, figs 1, 1a, syntype); 1878/6/3973 + 3974 (1970 + 1971), (*Laurus* sp. in sched.); 1878/6/4007 (2004), B; 1878/6/9197, B + 9198, B (7194, B + 7195, B). Münzenberg: NHMW: 1878/6/4316 (Ett. 2313), Pb 2173, (*Ficus jynx*); 1878/6/6917 (4914), C, (on backside). IBUG: Ett. 6058, (*Daphne radobojana*). Leoben: GBA: 2024/0001/0005.

Description. Simple leaves, petiole not preserved; laminar shape obovate to (broad) elliptic, l × w ~(52) 60–71 (100) × 24–35 mm, ratio l/w ~1.2–2.3 (3.5); base angle acute, base shape straight, cuneate; apex angle obtuse to wide acute, apex shape straight to slightly convex, bluntly acute to shortly bluntly acuminate; margin entire; midvein thick, straight, secondaries already delicate, brochidodromous, widely spaced, up to 18 mm in middle part of lamina; 2° veins arising under moderate angle, ascending at first usually rather straight, then in wide curves, forking in marginal third of distance between midvein and margin, branches of adjacent secondaries looping; exmedial veinlets forming further smaller loops along margin; intersecondaries occasionally developed, reaching about half the distance between midvein and margin; tertiaries delicate, partly percurrent, partly reticulate, not dense; higher-order veins reticulate, areoles polygonal.

Remarks. Ettingshausen (1888) assigned part and counterpart of specimen NHMW 1878/6/3881 + 3919 (Ett. 1878, b + 1916) to different fossil-species (*Daphne palaeo-laureola*, *Daphne palaeo-mezereum*. *Protea europaea* (Ettingshausen, 1888: pl. 4, fig. 14) may also represent *Magnolia*, but this specimen was not detected in the collection material. The gross-morphological features of these leaves point towards *Magnolia*. The unequivocal specific assignment depends, however, on the cuticular morphology, which is not available from the Leoben material. Usually the leaves of *M. liblarensis* are preserved fragmentarily only, e.g. South Bohemian Basin (Knobloch and Kvaček, 1996), Mataschen, Styria, Austria (Kovar-Eder and Hably, 2006), Arjuzanx, France (Kvaček et al., 2011), Frankfurt am Main, Germany (Kvaček et al., 2020). Insofar, the record from Leoben is remarkable. Leaves of *M. kristinae* Knobloch et Kvaček tend to be more slender (lanceolate), e.g. Knobloch and Kvaček (1976), Mai and Walther (1991). *M. liblarensis* is commonly known from swamp facies of Miocene deposits and even may occur in masses (Schneider, 2007; Kvaček et al., 2011).

Order LAURALES Bercht. et Presl

Family LAURACEAE Jussieu

Putative leaves of Lauraceae occur quite frequently in the Leoben assemblage. Leaf morphological studies of modern Lauraceae from Teneriffa (*Apollonias barbujana* (Cav.) A. Braun, *Laurus azorica* (Seub.) Franco, *Ocotea foetens* (Aiton) Baill. and *Persea indica* (L.) Spreng.) showed that ultimate veinlets in the areoles are either absent or unbranched (Rasche and Kovar-Eder, 2009). Under favourable preservation, this feature may be useful to differentiate fossil Lauraceae leaves from other entire-margined taxa. However, morphotypes beyond the family level distinguished solely by gross morphology must remain tentative because only cuticular characters allow robust differentiation.

Genus ***Daphnogene*** Unger

Daphnogene polymorpha (A. Braun) Ettingsh.

Figs 6.1–6.4, 23.2

1845 *Ceanothus polymorphus* A. Braun; A. Braun, p. 171.

1851 *Daphnogene polymorpha* Ettingsh.; Ettingshausen, p. 16, pl. 2, figs 23–25.

1888 *Cinnamomum rossmaessleri* Heer, p.p.; Ettingshausen, p. 308.

1888 *Cinnamomum scheuchzeri* Heer, p.p.; Ettingshausen, p. 308.

1888 *Cinnamomum lanceolatum* Unger, p.p.; Ettingshausen, p. 308.

1888 *Cinnamomum polymorphum* A. Braun, p.p.; Ettingshausen, p. 309, non pl. 4, fig. 20.

1888 *Vaccinium acheronticum* Unger; Ettingshausen, p. 331.

1888 *Loranthus palaeo-eucalypti* Ettingsh., p.p.; Ettingshausen, p. 334, pl. 7, fig. 9.

1999 *Daphnogene polymorpha* (A. Braun) Ettingsh.; Meller et al., p. 132, pl. 2, fig. 4, pl. 3, figs 5–7.

1999 *Daphnogene* typus *bilinica* (Unger) Kvaček et Knobloch vel *D. polymorpha* (A. Braun) Ettingsh.; Ströbitzer, p. 96, pl. 1, figs 21, 22, pl. 7, figs 24, 25.

2001a *Daphnogene polymorpha* (A. Braun) Ettingsh.; Kovar-Eder et al., p. 73.

2004 *Daphnogene polymorpha* (A. Braun) Ettingsh.; Kovar-Eder et al., p. 55, pl. 2, fig. 8.

2022 *Daphnogene polymorpha* (A. Braun) Ettingsh.; Kovar-Eder et al., p. 88, pl. 1, fig. 13.

Material. Moskenberg: NHMW: 1878/6/3539 (Ett. 1536), (*Cinnamomum scheuchzeri*); 1878/6/3573 (1570), (*C. lanceolatum*); 1878/6/3574 (1571), (*C. lanceolatum*); 1878/6/3734 (1731), (*C. polymorphum*); 1878/6/3735 (1732), (*C. polymorphum*); 1878/6/3807 + 3808, (1804 + 1805), Pb 1971, Pb 1972, (*C. polymorphum*); 1878/6/3856 (1853), (*C. lanceolatum*), counterpart 1878/6/4460 (2457), Pb 2336, see Seegraben Walpurgis-Schacht; 1878/6/3938 (1935), (*C. polymorphum*); 1878/6/4046 (2043), (*C. polymorphum*); 1878/6/4059 (2056), A, (*C. lanceolatum*); 1878/6/4060 (2057), (C. *lanceolatum*); 1878/6/4198 (2195), (*C. scheuchzeri*); 1878/6/4199 (2196), Pb 2122, (*Loranthus palaeo-eucalypti*), Ettingshausen (1888: pl. 7, fig. 9), number listed also for (*Cinnamomum scheuchzeri*) in Ettingshausen (1888); 1878/6/7798 (5795), B; 1878/6/7878 (5875), (*C. scheuchzeri*); 1878/6/7882 (5879), (*C. lanceolatum*). Münzenberg: NHMW: 1878/6/4259 (Ett. 2256), Pb 2207, (*C. polymorphum*); 1878/6/4363 (2360), Pb 2214, (*Vaccinium acheronticum*); 1878/6/7905 (5902), Pb 2209, (*Cinnamomum polymorphum*); 1878/6/9006 (7003), (*C. polymorphum*). IBUG: Ett. 6210, B + 6211, B; it is not possible to assign Ettingshausen's identifications (*Celastrus europaea* in sched.) and (*Sapindus dubius* in sched.) to the leaves on this slab. Seegraben Walpurgis-Schacht: NHMW: 1878/6/4460 (Ett. 2457), Pb 2336, (*Cinnamomum lanceolatum*); counterpart NHMW 1878/6/3856 (1853), (*C. lanceolatum*), see Moskenberg.

Description. Petiolate leaves, petiole up to at least 8 mm long, lamina ovate, elliptic, oblong to slightly obovate, l × w ~(27) 30 to ≥ 100 × 7–22 mm, ratio l/w ~2.7–6.1; base angle (narrow) acute, base shape almost straight to slightly convex, occasionally slightly concave; apex angle (narrow) acute, apex shape concave, i.e. apex (long) acuminate to acute; margin entire; venation suprabasal acrodromous, basal secondaries originating staggered, running widely curved towards margin, reaching mostly into apical third of lamina, looping there indistinctly with next pair of secondaries; further secondaries few, widely spaced, eucamptodromous; tertiaries vaguely visible, (forked-)percurrent, originating from midvein under wide angle, originating exmedially from basal pair of secondaries under moderate angles, course of 3° veins sinuous; higher-order veins rarely preserved, forming very regular, mainly 4-sided small meshes, no ultimate veinlets.

Remarks. *Daphnogene polymorpha* is represented both by the *polymorpha* and *bilinica* physiognomy (shade and sun leaves) (Kvaček and Walther, 1974) but its remains are not very abundant in the Leoben flora. Specimens NHMW 1878/6/3856 (Ett. 1853) and NHMW 1878/6/4460 (Ett. 2457) unequivocally represent part and counterpart of one leaf. Ettingshausen indicated on the former Leoben I, i.e. Moskenberg, while on the latter Leoben IV, i.e. Seegraben Walpurgis-Schacht. This discrepancy remains unresolved. The assignment of these leaves to *Daphnogene* instead of *Cinnamomum* Schaeff. appears more suitable because no cupules or fruits of *Cinnamomum* were detected among the collection material. For further details regarding *C. polymorphum* (A. Braun) Heer plexus see Holý et al. (2012).


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Genus ***Ocotea*** Aubl.

***Ocotea* sp.**

Figs 6.5–6.7, 23.3

1869a *Echitonium macrospermum* Ettingsh. sp. n., p.p.; Ettingshausen, p. 71, pl. 4, fig. 3, non 4.
1888 *Olea stiriaca* Ettingsh., p.p.; Ettingshausen, p. 306.
1888 *Cinnamomum polymorphum* A. Braun, p.p.; Ettingshausen, p. 309.
1888 *Echitonium macrospermum* Ettingsh., p.p.; Ettingshausen, p. 326.

Material. Moskenberg: NHMW: 1878/6/3597 (Ett. 1594), (*Echitonium macrospermum*), Ettingshausen (1869a: pl. 4, fig. 3, syntype); 1878/6/3983 + 4012, (1980 + 2009), (*Cinnamomum polymorphum*); 1878/6/7867 (5864), B, Pb 1982; 1878/6/8138 (6135), Pb 1955, (*Olea stiriaca*). Seegraben: GBA: 2024/0001/0011, (*Daphnogene polymorpha*).

Description. Petiolate leaves; petiole up to 9 mm long; lamina oblong, elliptic to somewhat obovate, l × w ~37–58 × 12–20 mm, ratio l/w ~2.5–3.4; base angle (narrow) acute, base shape straight to somewhat convex; apex angle (narrow) acute, apex shape straight to concave, i.e. apex probably acuminate; margin entire to somewhat undulate; midvein straight or bent, moderately strong, secondaries brochidodromous to eucamptodromous, widely spaced, basal pair of secondaries more or less prominent, originating under steeper angles and often ascending further up than following secondaries; tertiaries partly percurrent, partly reticulate, further venation reticulate; pocket-like domatia in axils between midvein and basal secondaries.

Remarks. More prominent basal secondaries along with domatia in the axils between primary vein and primarily basalmost secondaries have been reported for *Ocotea hradekensis* (Kvaček et Bůžek) Kvaček (Bůžek et al., 1996; Holý et al., 2012). These authors interpreted the domatia as axillary glands. In modern Lauraceae, domatia (pits, pockets or hair tufts) are common traits known from several genera (Watson and Dallwitz, 1992 onwards). In *Ocotea foetens* (Aiton) Baill., which is regarded as the nearest living relative of *O. hradekensis*, domatia are pockets covered by hairs (Nickol, 1998 and own observations). The specimens from Leoben exhibit such pit- or pocket-like structures. Most distinct are such domatia in the specimens NHMW 1878/6/3983 + 4012 (Ett. 1980 + 2009), NHM 1878/6/7867 (Ett. 5864) and NHMW 1878/6/8138 (Ett. 6135) (Figs 6.5, 6.7, 23.3). In the latter specimen the basal secondaries resemble the following secondaries in length and thickness.

Genus ***Sassafras*** J. Presl

cf. *Sassafras* sp.

Fig. 6.8

1869a *Daphnogene laurifolia* Ettingsh. sp. n.; Ettingshausen, p. 63, pl. 3, fig. 14.
1888 *Daphnogene laurifolia* Ettingsh.; Ettingshausen, p. 309.

Material. Moskenberg: NHMW: 1878/6/7918 (Ett. 5915), Pb 1981, (*Daphnogene laurifolia*), Ettingshausen (1869a: pl. 3, fig. 14, holotype).

Description. Simple leaf, lacking petiole and apex; laminar shape elliptic, l × w ~100 × 39 mm, ratio l/w ~2.6; base angle acute, base shape

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Figure 6. **1–4**. *Daphnogene polymorpha* (A. Braun) Ettingsh., **1**. NHMW 1878/6/4046 (Ett. 2043), (*Cinnamomum polymorphum*), **2**. NHMW 1878/6/3574 (Ett. 1571), (*C. lanceolatum*), **3**. NHMW 1878/6/3807, (Ett. 1804), Pb 1971, (*C. polymorphum*), **4**. NHMW 1878/6/7878 (Ett. 5875), (*C. scheuchzeri*); **5–7**. *Ocotea* sp., see domatia in axils of basal secondaries, **5**. NHMW 1878/6/3983, (Ett. 1980), (*Cinnamomum polymorphum*), **6**. NHMW 1878/6/3597 (Ett. 1594), (*Echitonium macrospermum*), Ettingshausen (1869a: pl. 4, fig. 3, syntype), **7**. NHMW 1878/6/7867 (Ett. 5864), B, Pb 1982, see also holes in lamina indicating feeding traces; **8**. cf. *Sassafras* sp., NHMW 1878/6/7918 (Ett. 5915), Pb 1981, (*Daphnogene laurifolia*), Ettingshausen (1869a: pl. 3, fig. 14, holotype); **9–11**. *Laurophyllum* cf. *pseudoprinceps* Weyland et Kilpper, **9**. NHMW 1878/6/4161 (Ett. 2158), b, **10**. NHMW 1878/6/4161 (Ett. 2158), a, **11**. NHMW 1878/6/3761 (Ett. 1758), Pb 1913, (*Laurus tetrantheroides*); **12a**, **b**, **13**. *Laurophyllum* sp. 1, see domatia at the origin of several secondaries, **12a**, **b**. NHMW 1878/6/7871 + 7872, (Ett. 5868 + 5869), Pb 1983, (*Litsaea miocenica*), Ettingshausen (1869a: pl. 3 fig. 6, syntype), **13**. NHMW 1878/6/4150 (Ett. 2147), B, Pb 2044; **14a**, **b**, **15**. *Laurophyllum* sp. 2, **14a**. NHMW 1878/6/9085 (Ett. 7082), Pb 1923, (*Laurus primigenia*), Ettingshausen (1869a, pl. 3, fig. 11, 11 a), **14b**. counterpart NHMW 1878/6/9086 (Ett. 7083), (*Laurus ocoteaefolia*), **15**. NHMW 1878/6/7873 (Ett. 5870), Pb 1974, (*Litsaea miocenica*); **16–18**. *Laurophyllum* sp. 3, **16**. NHMW 1878/6/4142 (Ett. 2139), Pb 1918, (*Laurus princeps*), **17**. NHMW 1878/6/3743 (Ett. 1740), (*L. nectandroides*), **18**. NHMW 1878/6/3706 (Ett. 1703), Pb 1917, (*L. princeps*); **19**, **20**. *Laurophyllum* sp. 4, **19**. NHMW 1878/6/3797 (Ett. 1794), Pb 1967, (*Oreodaphne stiriaca*), Ettingshausen (1888: pl. 4, fig. 21), **20**. NHMW 1878/6/7867 (Ett. 5864), A, Pb 1982, (*O. stiriaca*), Ettingshausen (1869a: pl. 3, fig. 12, syntype); **21**. Araceae (?) gen. et sp., IBUG Ett. 5531, leaves B, C, F superimposed close to axis, D, E fragmentary leaves. Their orientation indicates that they may derive from the same specimen; **22**. *Potamogeton* sp., NHMW 1878/6/7210 (Ett. 5207) Pb 1862, (*Najadopsis trinervia*), (?) Ettingshausen (1869a: pl. 1, fig. 13, (?) holotype). For all photographs the scale at bottom right of the figure is 10 mm except for photographs with embedded scale in which the scale is also 10 mm

somewhat convex, on one side concave near very base; margin entire; midvein straight, slender; secondaries eucamptodromous, lowermost pair suboppositely positioned, as delicate as further secondaries, angle of origin of secondaries moderate, course straight to moderately curved near margin; distance between lowermost pair of secondaries and next secondaries wider (18 and 19 mm) than between further secondaries (max. 12 mm); tertiaries percurrent, undulate, widely spaced, tertiaries connecting secondaries and midvein horizontally, angle of tertiaries connecting secondaries obtuse towards midvein; agrophilic veins developed along lowermost pair of secondaries, looping along margin.

Remarks. This leaf differs from *Daphnogene polymorpha* in that all secondaries are almost equally thick, although the lowermost pair is positioned further away from the next secondaries than are all other secondaries. Moreover, the basal secondaries are shorter and the number of secondaries is higher than in *D. polymorpha*. The midvein is slender and the appearance of the blade implies a chartaceous rather than a coriaceous texture. Unlobed fossil leaves of *Sassafras* have been reported by Kvaček et al. (2011) from Arjuzanx (France, Middle to early Late Miocene).

Genus ***Laurophyllum*** Goepp.

Laurophyllum cf. ***pseudoprinceps*** Weyland et Kilpper

Fig. 6.9–6.11

1888 *Ficus lobkowitzii* Ettingsh., p.p.; Ettingshausen, p. 297.

1888 *Laurus agathophyllum* Unger, p.p.; Ettingshausen, p. 305.

1888 *Laurus tetrantheroides* Ettingsh., p.p.; Ettingshausen, p. 305.

1888 *Nectandra arcinervia* Ettingsh., p.p.; Ettingshausen, p. 306, pl. 2, figs 27, 27a.

1888 *Apocynophyllum haeringianum* Ettingsh., p.p.; Ettingshausen, p. 324.

cf. 1963 *Laurophyllum pseudoprinceps* Weyland et Kilpper; Weyland and Kilpper, p. 100, text-fig. 6, pl. 23, figs 14–19.

Material. Moskenberg: NHMW: 1878/6/3761 + 3762 (Ett. 1758 + 1759), Pb 1913 + Pb 1914, (*Laurus tetrantheroides*); 1878/6/4161 (2158), a, b, (*Apocynophyllum haeringianum*/ *Cinnamomum scheuchzeri*, assignment of taxa to leaves unclear) + 1878/6/7866 (5863), A, (*Nectandra arcinervia*), Pb 1970; 1878/6/7682 (5679), (*Ficus lobkowitzii*). Münzenberg: NHMW: 1878/6/4250 (Ett. 2247), Pb 2190, (*Laurus agathophyllum*); 1878/6/4257 + 4258 (2254 + 2255), Pb 2181, (*Nectandra arcinervia*); Ettingshausen (1888: pl. 2, figs 27, 27a).

Description. Petiolate leaves, petiole very fragmentarily preserved; laminar shape oblong, elliptic to somewhat obovate, l × w ~ (32) 38– >100 × (11) 14–27 mm, ratio l/w ~(2.4) 3–4; base angle acute, base shape slightly convex, straight, somewhat decurrent; apex angle (narrow) acute, apex shape straight and convex at utmost apex to concave, i.e. bluntly acute to acuminate; margin entire; midvein usually straight, secondaries brochidodromous to eucamptodromous, arising at moderate angles (at narrow angles in small leaves), position subopposite to alternate, widely spaced, at variable distances within one leaf, course curved; secondaries providing a not very regular appearance; intersecondaries present depending on distance between secondaries; length of intersecondaries variable, from very short to reaching more than half way towards margin; tertiaries forming large, more or less distinct meshes, reticulate; 4° veins and higher-order ones regularly reticulate; areoles commonly 4- to 5-sided, veinlets (?) absent.

Remarks. Apart from *Daphnogene polymorpha*, *Laurophyllum pseudoprinceps* is the most common Lauraceae in the Neogene European record. Unambiguous assignments to *L. pseudoprinceps* are based on cuticular features. Based on these traits, detailed grossmorphological documentation of *L. pseudoprinceps* was provided, e.g. by Knobloch and Kvaček (1976) and Kovar-Eder and Hably (2006). Leaves are differently sized, variable in laminar shape, and the 2° and 3° venation does not appear very regular. Domatia-like structures are absent. *L.* cf. *pseudoprinceps* is very probably more common among the lauroid leaves from Leoben than those listed under “Material” but an unambiguous assignment is not possible.

Laurophyllum **sp. 1**

Figs 6.12, 6.13, 23.4

1869a *Litsea miocenica* Ettingsh. sp. n., p.p.; Ettingshausen, p. 61, pl. 3 fig. 6.

1888 *Laurus phoeboides* Ettingsh.; Ettingshausen, p. 303.

1888 *Laurus swoszowiciana* Unger; Ettingshausen, p. 305.

1888 *Oreodaphne stiriaca* Ettingsh., p.p.; Ettingshausen, p. 306.

1888 *Olea stiriaca* Ettingsh., p.p.; Ettingshausen, p. 322.

Material. Moskenberg: NHMW: 1878/6/3803 (Ett. 1800), Pb 1951, (*Olea stiriaca*); 1878/6/4150 (2147), B, Pb 2044, (on backside); 1878/6/7868 (5865), Pb 1968, (*Oreodaphne stiriaca*); 1878/6/7871 + 7872, (5868 + 5869), Pb 1983, (*Litsaea miocenica*), Ettingshausen (1869a: pl. 3, fig. 6, syntype). Münzenberg: NHMW: 1878/6/4251 (Ett. 2248), Pb 2211, (*Laurus swoszowiciana*); 1878/6/4374 (2371), Pb 2189, (*Laurus phoeboides*). LMJ: 79.029. Leoben: GBA: 2024/0001/0006, (*Litsea miocenica*); 2024/0001/0017, (*Laurus nectandroides*).

Description. Simple leaves; petiole (fragmentary, one specimen) 3 mm long, straight; laminar shape elliptic to somewhat obovate to oblong, l × w ~(32) 50–100 × (8) 11–37 mm; ratio l/w ~1.8–4.7 (6.25); base angle (narrow) acute, base shape straight to slightly convex; apex angle (narrow) acute, apex shape straight to slightly acuminate, utmost apex not preserved; margin entire; midvein straight, only exceptionally curved; secondaries brochidodromous (to eucamptodromous), widely spaced, subopposite to alternate, angle of origin moderate to acute (in narrow specimens), course curved, unbranched, looping near margin, loops more or less well visible; in some axils of midvein and secondaries patches or pocket-like structures indicating domatia; tertiaries (forked-)percurrent, angle between midvein and tertiaries wide obtuse; numerous short veinlets arising from midvein, angle of origin about 90°; 4° veins reticulate, higher-order venation quadrangular to hexagonal, ultimate veinlets largely absent (?).

Remarks. Specimen NHMW 1878/6/7872 (Ett. 5869) shows pocket-like structures in several axils of midvein and secondaries, whereas on its counterpart NHMW 1878/6/7871 (Ett. 5868) weak dark patches are recognisable in these positions (Fig. 6.12a, b). The other leaves also show more or less distinct dark patches in such axils indicating domatia (see also section *Ocotea* sp.). The venation details, which are best preserved in specimen NHMW 1878/6/4150 (Ett. 2147, B), indicate an areolation probably largely lacking ultimate veinlets (Fig. 23.4). The domatia and areolation may point towards *Laurus*. Pocket-like domatia covered by hairs are recorded for, e.g. *Laurus azorica* (Seub.) Franco (Nickol, 1998). Domatia do occur also in *L. nobilis* L. Contrary to *Ocotea* sp., in *Laurophyllum* sp. 1 the basal secondaries do not differ from the following secondaries and domatia are not restricted to the basalmost pair of secondaries.

***Laurophyllum* sp. 2**

Figs 6.14, 6.15, 23.5

1869a *Laurus primigenia* Unger, p.p.; Ettingshausen, p. 58, pl. 3, figs 11, 11b.

1888 *Laurus ocoteaefolia* Ettingsh., p.p.; Ettingshausen, p. 304.

1888 *Laurus tetrantheroides* Ettingsh., p.p.; Ettingshausen, p. 305.

1888 *Nectandra arcinervia* Ettingsh., p.p.; Ettingshausen, p. 306, non pl. 2, figs 27, 27a.

1888 *Litsea miocenica* Ettingsh., p.p.; Ettingshausen, p. 308.

Material. Moskenberg: NHMW: 1878/6/7840 (Ett. 5837), Pb 1911, (*Laurus tetrantheroides*); 1878/6/7873 (5870), Pb 1974, (*Litsea miocenica*); 1878/6/9085 (7082), Pb 1923, (*Laurus primigenia*), Ettingshausen (1869a: pl. 3, figs 11, 11 a) + 1878/6/9086 (7083), (*Laurus ocoteaefolia*); Münzenberg: NHMW: 1878/6/4328, B + 4336, A (Ett. 2325 + 2333), Ett. 2333 Pb 2196, (*Nectandra arcinervia*); 1878/6/4343 (2340), B, Pb 2304, backside.

Description. Narrow leaves, petiole up to 6 mm long (fragmentary); lamina slender oblong, sickle-shaped, l × w ~50–116 × 10–22 mm, ratio l/w ~5–5.9; base angle narrow acute, base shape straight, decurrent tapering into petiole; apex angle narrow acute, apex shape straight to slightly convex on one and concave on other side, long acute; margin entire, (?) thickened; midvein moderately strong, considerably bent or sinuate; secondaries delicate, brochidodromous (to eucamptodromous), widely spaced, originating at narrow angle, course curved; intersecondaries present, tertiaries delicate, indistinct, already almost as delicate as higher-order veins; tertiaries percurrent to reticulate, widely spaced; higher-order veins reticulate, areoles often 4-sided, ultimate veinlets (?) lacking.

Remarks. Ettingshausen (1869a: pl. 3, figs 11, 11a) assigned specimen NHMW 1878/6/9085 (Ett. 7082) to *Laurus primigenia*. Later he listed this specimen and its counterpart as *L. ocoteaefolia* (Ettingshausen 1888: p. 304).

These leaves are characterised by their very slender shape with a decurrent base and long acute apex with steeply ascending secondaries. The 2° venation is already delicate although their marginal loops are well discernible. The tertiaries are already indistinct.

Laurophyllum sp. 3

Figs 6.16–6.18, 23.6

1888 *Laurus princeps* Heer; Ettingshausen, p. 304.
1888 *Laurus nectandroides* Ettingsh., p.p.; Ettingshausen, p. 305.

Material. Moskenberg: NHMW: 1878/6/3706 (Ett. 1703), Pb 1917, (*Laurus princeps*); 1878/6/3742 (1739), (*L. nectandroides* in sched.); 1878/6/3743 (1740), (*L. nectandroides*); 1878/6/4142 (2139), Pb 1918, (*L. princeps*); 1878/6/7837 (5834), Pb 1920, (*L. nectandroides*).

Description. Large, simple leaves; petiole not preserved; laminar shape slender elliptic to slightly obovate, l × w ~>100–130 × 26–31 mm, ratio l/w ~3.6–4.3; base angle acute, base shape mainly straight to slightly convex; apex angle acute, apex shape straight to slightly acuminate (rarely preserved); margin entire; midvein straight; secondaries eucamptodromous, widely spaced, subopposite to alternate, originating at moderate angle, curved upwards, tapering, connecting distally to superimposed secondaries by loops of minor gauge; intersecondaries present, 0–2 between adjacent secondaries, reaching about half the distance between midvein and margin; tertiaries percurrent, forked-percurrent to reticulate towards leaf apex, percurrent tertiaries straight to sinuate, widely spaced, 3–4 per cm, forming large meshes; higher-order veins reticulate, areoles vague, often 4-sided.

Remarks. Among Lauraceae foliage from Leoben, these leaves are distinct by their considerable size and eucamptodromous venation. Although some leaves appear more chartaceous than others, the preservation state as leaf imprints does not allow a robust interpretation of the lamina texture.

Laurophyllum sp. 4

Figs 6.19, 6.20, 23.7

1869a *Oreodaphne stiriaca* Ettingsh. sp. n.; Ettingshausen, p. 61, pl. 3, fig. 12.
1888 *Laurus nectandroides* Ettingsh., p.p.; Ettingshausen, p. 305.
1888 *Oreodaphne stiriaca* Ettingsh., p.p.; Ettingshausen, p. 306, pl. 4, fig. 21.

Material. Moskenberg: NHMW: 1878/6/3797 (Ett. 1794), Pb 1967, (*Oreodaphne stiriaca*), Ettingshausen (1888: pl. 4, fig. 21), note that Ettingshausen (1888: p. 306) listed number Ett. 1974 instead (presumably a printing error); 1878/6/3802 (1799), Pb 1969, (*Oreodaphne stiriaca*); 1878/6/7836 (5833), Pb 1921, (*Laurus nectandroides*); 1878/6/7867 (5864), A, Pb 1982, (*Oreodaphne stiriaca*), Ettingshausen (1869a: pl. 3, fig. 12).

Description. Simple leaves, petiole not preserved; laminar shape (slender) elliptic, base angle acute, base shape straight, cuneate; apex angle acute, apex shape straight to slightly concave, i.e. acute to slightly acuminate; l × w ~60–80 × 15–25 mm, ratio l/w ~3–4.2; margin entire, midvein straight to minimally bent; secondaries eucamptodromous to brochidodromous, alternate to subopposite, widely spaced, 10–15 (20) mm in middle part of lamina; angle of origin moderate, narrower near base, course of secondaries curved, tapering towards margin, forming loops mainly of minor gauge; intersecondaries delicate, if present at all; tertiaries percurrent, sinuate to reticulate, delicate; areoles 4- to 5-sided, lacking ultimate veinlets.

Remarks. These leaves differ from *Laurophyllum* sp. 3 by their smaller size and somewhat lower length/width ratio, as well as by less numerous and less prominent intersecondaries. The regular pattern of secondaries distinguishes them from *Laurophyllum* cf. *pseudoprinceps*. Basal secondaries not differing from the following ones and the absence of domatia are differential features towards *Ocotea* sp. and *Laurophyllum* sp. 1.

Order ALISMATALES
Dumortier

Family ARACEAE Juss.

Araceae (?) **gen**. et **sp**.

Figs 6.21, 23.8

Material. Moskenberg: IBUG: Ett. 5531, B–F.

Description. Two types of leaves along an (?) axis of ~2 mm width with a central vascular strand, leaves without physical connection to axis; leaves B, C, F clustered, leaf fragments D and E isolated; B, C, F: Leaf cluster of three or (?) four oval to almost orbicular to slightly reniform, short-petiolate leaves partly superimposing each other; uppermost complete, other ones partly covered by superimposing ones; complete leaf with 2-mm-long petiole broadening towards base, l × w ~25 × 16 mm; other leaves probably similar in size; base angle ~180°, base shape rounded to almost truncate; apex (visible only in uppermost leaf): angle acute, shape (?) acuminate; margin serrate with tiny, narrow, regularly spaced teeth to (?) entire; venation campylodromous, uppermost leaf 6 veins, number of veins in other leaves uncertain; faint cross veins connecting main veins obliquely visible near margin of uppermost leaf. Leaves D, E: Fragments of apical leaf parts, l × w ~43 × 29 mm and 18 × 12 mm (length and width incomplete); laminar shape (?); apex angle acute, apex shape straight to acuminate; margin simple serrate, teeth spine-like, hook-shaped, up to 1 mm high; at least 3 main veins running into leaf apex.

Remarks. Surprisingly Ettingshausen paid attention only to the pine seed on this slab (A). The position of the leaf cluster (B, C, F) and leaves D and E in relation to the axis imply that they derive from a single plant specimen. This presumption is supported by the fact that no other resembling leaf has been detected among the several thousand specimens studied from Leoben. The major venation of the leaves points towards a monocotyledonean relationship and the leaf cluster may indicate floating leaves of an aquatic plant reminiscent of *Limnobiophyllum* Krassilov, of which *L. expansum* (Heer) Kvaček and *L. scutatum* (Dawson) Krassilov are known (e.g. Kvaček, 1995; Stockey et al., 1997). The axis at the base of the leaf cluster resembles stolons of *Limnobiophyllum* (Kvaček, 1995) but its true nature remains open because of the lack of a physical connection to the leaf cluster. No roots attached to the leaf cluster are preserved.

Differences towards *Limnobiophyllum* are the morphological variability of the leaves, the serration of at least parts of the margin, the absence of interprimaries, and the acuminate (?)/acute apex. Currently the author is unaware of any other fossil-taxon resembling the here described specimen.

Family POTAMOGETONACEAE Bercht. et J. Presl

Genus ***Potamogeton*** Walter

***Potamogeton* sp.**

Fig. 6.22

(?) 1869a *Najadopsis trinervia* Ettingsh. sp. n.; Ettingshausen, p. 38, pl. 1, fig. 13.

1888 *Najadopsis trinervia* Ettingsh., p.p.; Ettingshausen, p. 281.

Material. Moskenberg: NHMW: 1878/6/7210 (Ett. 5207) Pb 1862, (*Najadopsis trinervia*), (?) Ettingshausen (1869a: pl. 1, fig. 13, (?) holotype).

Description. Cluster of slender elongate and delicate leaves, l × w at least up to 33 × 7 mm (both length and width incomplete); margin probably entire; central main vein accompanied by further lateral longitudinal veins; transversal veins perpendicular to longitudinal ones regularly spaced.

Remarks. It is difficult to decide whether the specimen at hand represents the holotype figured by Ettingshausen (1869a: pl. 1, fig. 13) because the drawing is very faint. The leaves are not complete. There is no evidence for marginal teeth that might indicate *Najas* L. The probably entire margin and the venation paralleling the leaf margin with interconnecting transversal veins segmenting the leaf in rectangular fields point towards *Potamogeton*.

Order LILIALES Perleb

Family SMILACACEAE Vent.

Genus ***Smilax*** L.

Smilax sphenophylla
(Unger) Kovar-Eder comb. nov.

PFNR Unique Identifier: PFN003317.

Fig. 7.21

1847 *Quercus aspera* Unger; Unger, p. 108, pl. 30, figs 1–3, pl. 31, figs 1, 3.

1847 *Ilex sphenophylla* Unger; Unger, p. 148, pl. 50, fig. 9.

1888 *Rhamnus aizoides* Unger; Ettingshausen, p. 350.

2004 *Mahonia* (?) *aspera* (Unger) Kovar-Eder et Kvaček; Kovar-Eder et al., p. 57, pl. 13, figs 1–8.

2015 *Smilax miohavanensis*, Denk, D. Velitzelos, T. Güner et Ferrufino-Acosta; Denk et al., p. 426, figs 4–7.


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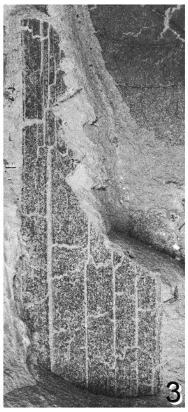
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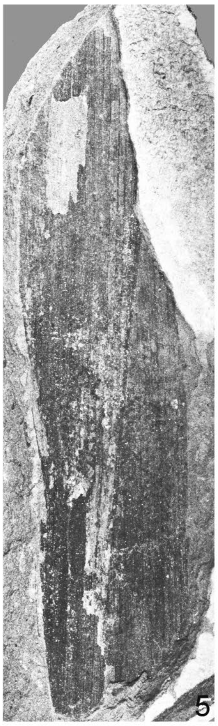
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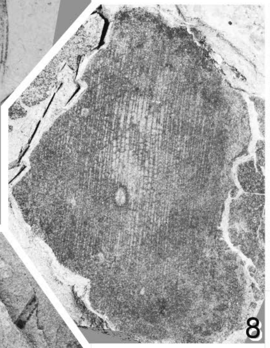
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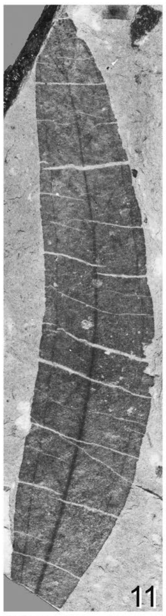
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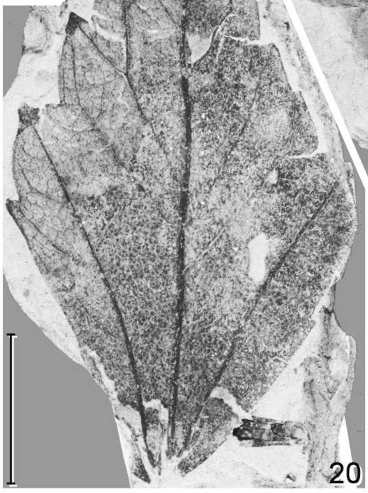
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2018 *Mahonia* (?) *sphenophylla* (Unger) Doweld; Doweld, p. 74.

2022 *Mahonia* (?) *sphenophylla* (Unger) Doweld; Kovar-Eder et al., p. 97, pl. 7, figs 12–16.

Lectotype designated here. *Ilex sphenophylla* Unger (1847: p. 148, pl. 50, fig. 9 lower left), LMJ 76.515, Parschlug. Note, that the lectotype *Quercus aspera* Unger (1847: p. 108, pl. 30, fig. 2 top right), LMJ 76.529 designated by Kovar-Eder et al. (2004: p. 57, pl. 13, fig. 3) from Parschlug, is obsolete.

Basionym. *Quercus aspera* Unger (1847: p. 108).

Locus typicus. Parschlug, Styria, Austria.

Material. Moskenberg: NHMW: 1878/6/4141 (Ett. 2138), (*Rhamnus aizoides*).

Description. Small leaf, sessile or subsessile; laminar shape elliptic to slightly obovate, slightly asymmetrical, l × w ~19 × 12 mm, ratio l/w ~1.5; base angle obtuse, base shape convex, asymmetrical; apex incomplete, apex angle probably wide obtuse, apex shape convex; margin entire except for few isolated, tiny, spine-like teeth; venation almost basal acrodromous, midvein strong, basal pair of secondaries and next pair steeply ascending into the apical third of lamina, (?) looping.

Remarks. Denk et al. (2015) moved this fossil-taxon to the genus *Smilax* and proposed the species epitethon *miohavanensis* because the epitethon *aspera* in connection with *Smilax* woud be a younger homonym of the recent species *S. aspera* L. These authors overlooked that Heer (1856) already recognised this fact and it was further repeated by Doweld (2018). (Nevertheless, the leaves figured by Heer (1856: pl. 77, figs 7, 8) do not represent the here discussed fossil-species.) Denk et al. (2015) hesitated to regard *Ilex sphenophylla* Unger (1847: pl. 50, fig. 9) as being synonymous, which was the next available species name published by Unger (1847). These authors argued that the 3 fossils shown on that figure are not on the same slab but on individual ones. In this respect, Denk et al. (2015) failed to take into account that Unger used to assemble fossil remains from individual slabs on a single artificial one. Furthermore, at least specimen LMJ 76.515 definitely represents the original figured by Unger (1847: pl. 50, fig. 9 lower left). Therefore, the species epitethon *sphenophylla* has priority over *miohavanensis* and must be retained. Consequently LMJ 76.515 is designated as lectotype here. Instead, Denk et al. (2015) selected a holotype from the Turkish locality Kasapligil (which is not the type locality) of the here discussed fossil-species although they designated Parschlug material including Unger's type material of *Quercus aspera* (LMJ 76.529 and LMJ 76.532) as paratypes (!) for *S. miohavanensis*. Doubtlessly, these authors regard the material from Turkey as being conspecific with former *Q. aspera* (Unger, 1847). Consequently, *Smilax miohavanensis* Denk et al. (2015) must be regarded as a nomen superfluum. In accordance with the International Code of Nomenclature for algae, fungi and plants (Shenzhen Code; Turland et al., 2018), the designation of a holotype was superfluous because Article 7.4 reads: "A replacement name is typified by the type of the replaced synonym …".

Contrary to Parschlug, where *Smilax sphenophylla* is quite common, there is only a single specimen available from the Leoben flora.

◄———

Figure 7. **1**, **2**. "*Typha*" *latissima* A. Braun, **1**. NHMW 1878/6/3533 (Ett. 1530), B; **2**. 1878/6/7291 (5288), (*T. latissima*); **3**. Poales gen. et sp. 1, NHMW 1878/6/4111 (Ett. 2208), a, (*Typha latissima*); **4**. Poales gen. et sp. 2, NHMW 1878/6/4313 (Ett. 2310), Pb 2160, (*Arundo goepperti*); **5**. Poales gen. et sp. 3, NHMW 1878/6/4312 (Ett. 2309), Pb 2155, (*Phragmites oeningensis*); **6**. Poales gen. et sp. 4, NHMW 1878/6/4001 (Ett. 1998), (*Panicum rostratum*); **7**. Poales gen. et sp. 5, NHMW 1878/6/3896 (Ett. 1893), (*Phragmites oeningensis*); **8**. Poales gen. et sp. 6, NHMW 1878/6/4186 (Ett. 2183), B, Pb 2098; **9–11**. *Smilax* sp., **9**. IBUG Ett. 5720, B, **10**. IBUG Ett. 6239, (*Coriaria stiriaca*), Ettingshausen (1888: pl. 9, fig. 16, holotype), **11**. NHMW 1878/6/8750 (Ett. 6747), Pb 2093, (*Eucalyptus persidis*), Ettingshausen (1888: pl. 9, fig. 33, holotype); see syndiagenetic distraction; **12**. *Berberis mahonioides* Kovar-Eder sp. n., IBUG Ett. 6147, holotype, (*Nymphaeophyllum denticulatum* sp. n. in sched.), see feeding traces; **13–16**. *Berberis* cf. *teutonica* (Unger) Kovar-Eder et Kvaček, **13**. NHMW 1878/6/8509 (Ett. 6506), Pb 2018, (*Maytenus submarginata*), Ettingshausen (1869a: pl. 5, fig. 17, holotype), **14**. NHMW 1878/6/3612 (Ett. 1609), (*Celastrus europaeus*), **15**. 1878/6/4375 (Ett. 2372), Pb 2179, (*Daphne protogaea*), Ettingshausen, (1888: pl. 4, fig. 3), **16**. NHMW 1878/6/4322 (Ett. 2319), Pb 2303, (*Pterocelastrus elaenus*); **17–19**. (?) *Platanus neptuni* (Ettingsh.) Bůžek, Holý et Kvaček, **17**. NHMW 1878/6/4364 (Ett. 2361), Pb 2222, (*Diospyros brachysepala*), **18**. NHMW 1878/6/4461 (Ett. 2458), (*Euonymus* sp.), **19**. NHMW 1878/6/4217 (Ett. 2214), Pb 2279, (*Carya bilinica*); **20**. *Parthenocissus rhombifolia* (Ettingsh.) Kovar-Eder comb. nov., NHMW 1878/6/4049 (Ett. 2046), Pb 2105, lectotype, (*Acer rhombifolium* Ettingsh., sp. n.), Ettingshausen (1869a: pl. 5, fig. 5, syntype); **21**. *Smilax sphenophylla* (Unger) Kovar-Eder comb. nov., NHMW 1878/6/4141 (Ett. 2138), (*Rhamnus aizoides*). For all photographs the scale at bottom right of the figure is 10 mm except for photographs with embedded scale in which the scale is also 10 mm

Its small size, laminar shape, leaf margin and the acrodromous venation are characteristics unambiguously pointing towards this fossil-taxon. Based on the molecular phylogenetic framework and leaf morphology, *S. sphenophylla* is placed in the Caribbean Havanensis group of the "New World Clade" of *Smilax* (Denk et al., 2015).

Smilax **sp.**

Fig. 7.9–7.11

non 1869a *Smilax moskenbergensis* Ettingsh. sp. n.; Ettingshausen, p. 38, pl. 1, fig. 14.

(?) 1888 *Smilax ovata* P. Wessel; Ettingshausen, p. 279.

non 1888 *Smilax moskenbergensis* Ettingsh.; Ettingshausen, p. 280, pl. 3, fig. 6.

1888 *Hakea plurinervia* Ettingsh., p.p.; Ettingshausen, p. 314, non pl. 4, figs 24, 25.

1888 *Coriaria stiriaca* Ettingsh. sp. n.; Ettingshausen, p. 357, pl. 9, fig. 16.

1888 *Eucalyptus persidis* Ettingsh. sp. n.; Ettingshausen, p. 358, pl. 9, fig. 33.

Material. Moskenberg: NHMW: 1878/6/8750 + 8751 (Ett. 6747 + 6748), Pb 2093, (*Eucalyptus persidis*), Ettingshausen (1888: pl. 9, fig. 33, holotype). IBUG: Ett. 6037, (*Cinnamomum rossmaessleri* in sched.). Münzenberg: NHMW: 1878/6/4382 (Ett. 2379), Pb 2182, (*Hakea plurinervia*). IBUG: Ett. 6239, (*Coriaria stiriaca*), Ettingshausen (1888: pl. 9, fig. 16, holotype). Seegraben Walpurgis-Schacht: IBUG: Ett. 5720, B.

Description. Simple leaves; laminar shape variable, ovate, oblong, l × w ~43–85 × 16–17 mm, ratio l/w ~2.5–5.3; base angle ranging from (narrow) acute to ~90°, base shape convex or straight, apex angle narrow acute, apex shape straight to acuminate; margin entire, venation basal acrodromous with at least 3 to (?) 5 major veins running in leaf apex; midvein thin, nearly straight to bent, lateral main veins more delicate than midvein; secondaries widely spaced, arising from midvein at moderate to acute angle, angle decreasing near apex, course smoothly curved to nearly straight, fusing with lateral main veins.

Remarks. This type of venation in entire-margined leaves occurs in *Smilax* but also, e.g. in *Saururus* L. (Piperales). The description of *Smilax ovata* P. Wessel (Ettingshausen, 1888) may indicate that this remain could have been conspecific with the here described leaves, but this original was not among the studied collection material. Moreover, the specimens of *S. moskenbergensis* Ettingsh. (Ettingshausen, 1869a: pl. 1, fig. 14; Ettingshausen, 1888: pl. 3, fig. 6) were not detected in the studied material and probably must be excluded because, according to Ettingshausen, the lateral veins do not reach the leaf apex. Leaf IBUG Ett. 6239 resembles *Smilax* sp. from Arjuzanx (Kvaček et al., 2011: pl. 3, fig. 1). The leaf NHMW 1878/6/4382 (Ett. 2379) is more fragmentary and the number of major veins is equivocal (probably 5). The slender leaf described by Ettingshausen (1888) as *Eucalyptus persidis* (Fig. 7.11) may be reminiscent of Lythraceae J.St.-Hil. (*Decodon* J.F. Gmel.), but in this specimen the secondaries are far less dense and ascend more steeply than in Lythraceae. *S. ovata* (Wessel and Weber, 1856) was based on specimens from Orsberg (Upper Oligocene), but these specimens were unavailable for the revision of this flora by Winterscheid and Kvaček (2014). Therefore, only the generic affiliation is listed here.

Rather variable leaf shape occurs in, e.g. *Smilax elegans* Wall. ex Kunth (N-Pakistan to Central China) but the major veins of this species are more than three. The laminar shape and major venation (3 main veins) of specimen NHMW 1878/6/8750 + 8751 (Ett. 6747 + 6748) (Fig. 7.11) resembles *S. glabra* Roxb. (Assam to Taiwan, Indo-China) (JACQ, POWO accessed August, 2023).

Order POALES Small

Leaf fragments of Poales are rather rare in the Leoben assemblage and no specimen showed a leaf base or apex. Venation details are often only vaguely preserved. No slab with mass occurrence has been detected among the collection specimens. Seven types can be distinguished, indicating the diversity of probably Cyperaceae Jussieu, Typhaceae Jussieu or Poaceae Barnhart. Except for "*Typha*" *latissima* A. Braun, all are documented by single specimens only.

Genus incertae sedis

"***Typha***" ***latissima*** A. Braun

Fig. 7.1, 7.2

1851 *Typha latissima* A. Braun; A. Braun in Stizenberger, p. 75.

1855 *Typha latissima* A. Braun; Heer, p. 98, pl. 43, 44.

1888 *Typha latissima* A. Braun, p.p.; Ettingshausen, p. 282.

1888 *Sparganium acheronticum* Unger; Ettingshausen, p. 282.

Material. Moskenberg: NHMW: 1878/6/3533 (Ett. 1530), B; 1878/6/4054 (2051), b, Pb 1883, (*Sparganium* sp. in sched.); 1878/6/7288 (5285), (*Typha latissima*); 1878/6/7291 (5288), (*T. latissima*); 1878/6/7307 (5304), (*Sparganium acheronticum*). Leoben: GBA: 2024/0001/0015.

Description. Fragments of parallel-sided leaves, longest fragment 94 mm (incomplete), width ~4–22 mm, entire-margined; 6– (?)15 1° veins; venation parallelodromous, veins at distances of ~0.5 mm; single to few finer parallel 2° veins interspaced; transversal veins connecting 1° veins, mostly straight, more rarely bent, perpendicular to oblique to longitudinal veins, at distances of 1–4 (5) mm.

Remarks. Such remains with 1° and 2° veins and cross veins connecting 1° ones are usually assigned to *Typha latissima*. The true generic affinity is undecided, however, because the venation features of such fossil remains are not restricted to the genus *Typha*.

Poales gen. et **sp. 1**

Fig. 7.3

Material. Moskenberg: NHMW: 1878/6/4111 (Ett. 2208), a, (*Typha latissima* in sched.).

Description. Parallel-sided leaf fragment, 50 mm long (incomplete), 20 mm wide, entire-margined; venation parallelodromous, four 1° veins at distances of 3–4 mm, 2–3 (or more) delicate 2° veins between adjacent major veins; transversal veins present, straight, bent, moderately oblique at distances of 2–4 (5) mm connecting 2° veins and 2° to 1° veins.

Remarks. This specimen differs from "*Typha*" *latissima* by the broader lamina, considerably wider spaced major veins and transversal veins connecting the 2° order ones.

Poales gen. et **sp. 2**

Fig. 7.4

1888 *Arundo goepperti* Heer; Ettingshausen, p. 277.

Material. Münzenberg: NHMW: 1878/6/4313 (Ett. 2310), Pb 2160, (*Arundo goepperti*).

Description. Fragment of a parallel-sided, entire-margined leaf, 58 mm long (incomplete), 25 mm wide with numerous, very densely spaced, uniform, parallel, faint (?) veins.

Remarks. This specimen is an impression implying a chartaceous texture indicative of a leaf, contrary to Ettingshausen's (1888) assumption of an axis.

Poales gen. et **sp. 3**

Fig. 7.5

1888 *Phragmites oeningensis* A. Braun, p.p.; Ettingshausen, p. 278.

Material. Münzenberg: NHMW: 1878/6/4312 (Ett. 2309), Pb 2155, (*Phragmites oeningensis*).

Description. Leaf fragment, parallel-sided, 88 mm long (incomplete), 19–21 mm wide; margin (?) entire; venation parallelodromous; 1° vein distinct, dividing the lamina into two halves, ~10 or more 2° veins on both sides in distances <1 mm; (?) ~2–3 3° veins in between two adjacent 2° ones; transversal veins inconspicuous, connecting anastomoses indistinct, closely spaced.

Remarks. This leaf differs from all others by the presence of a central vein. The preservation of the specimen at hand merely allows estimating the number of 2° and 3° parallel veins and the probable presence of transversal veins interconnecting the longitudinal ones.

"*Bambusa*" *lugdunensis* Saporta described from Europe, e.g. Worobiec (2003), Worobiec and Worobiec (2005), *Bambusium angustifolium* L. Wang et Z.K. Zhou and *Bambusium latifolia* L. Wang et Z.K. Zhou from China (Wang et al., 2013) resemble this specimen by a strong midvein and the presence of 2° and 3° parallel longitudinal veins. The fewer parallel 2° and higher number of 3° veins and the serrate margin distinguish these fossil-species from the specimen at hand.

Poales gen. et **sp. 4**

Fig. 7.6

1888 *Panicum rostratum* Heer; Ettingshausen, p. 278.

Material. Moskenberg: NHMW: 1878/6/4001 (Ett. 1998), (*Panicum rostratum*).

Description. Fragment of a parallel-sided leaf or axis, 30 mm long (incomplete), 7 mm wide; margin entire; texture probably coriaceous, 1° order veins >10, intervals not very regularly spaced, alternating with 2° order veins, no transversal veins.

Remarks. The coriaceous texture and the absence of transversal veins characterise this specimen.

Poales gen. et **sp**. **5**

Fig. 7.7

1888 *Phragmites oeningensis* A. Braun, p.p., Ettingshausen, p. 278.

Material. Moskenberg: NHMW: 1878/6/3896 (Ett. 1893), (*Phragmites oeningensis*).

Description. Fragment of a parallel-sided, entire-margined leaf, 35 mm long (incomplete), 20 mm wide, 16–17 1° veins paralleling leaf length, in distances of ~1 mm, (?) 2–4 2° order veins between adjacent 1° veins; transversal veins horizontal to oblique in distances of ~1–2 mm, connecting 1° veins.

Remarks. This specimen differs from "*Typha*" latissima by more widely spaced 1° veins and more densely spaced transversal veins. It differs from Poales gen. et sp. 3 by the absence of a prominent central vein.

Poales gen. et **sp**. **6**

Fig. 7.8

Material. Moskenberg: NHMW: 1878/6/4186 (Ett. 2183), B, Pb 2098.

Description. Fragment of a parallel-sided leaf, 51 mm long (incomplete), 34 mm wide (? complete); numerous and dense, equally delicate veins paralleling leaf length, ~4–10 per 2 mm, in central part of lamina wider spaced than along the margins; transversal veins present, spacing up to 1 mm.

Remarks. Distinctive features of this specimen are the width along with the very numerous and densely spaced uniform veins which are interconnected by transversal veins.

Order RANUNCULALES
Bercht. et J. Presl

Family RANUNCULACEAE Juss.

Genus ***Clematis*** L.

Clematis oligoneure
(Ettingsh.) Kovar-Eder comb. nov.

PFNR Unique Identifier: PFN003320

Figs 22.4, 23.11

1869a *Elaeodendron oligoneure* Ettingsh. sp. n.; Ettingshausen, p. 85, pl. 6, fig. 2.

1888 *Elaeodendron stiriacum* Ettingsh., p.p.; Ettingshausen, p. 346.

Holotype designated here. NHMW 1878/6/8549 (Ett. 6546), Pb 2130, (*Elaeodendron oligoneure*), Ettingshausen (1869a: pl. 6, fig. 2, holotype); (*Elaeodendron stiriacum*), Ettingshausen (1888), refigured on Figs 22.4, 23.11.

Basionym. *Elaeodendron oligoneure* Ettingsh., Ettingshausen (1869a: p. 85).

Derivatio nominis. Referring to the low number of secondaries.

Locus typicus. Historical locality Moskenberg near Leoben, Leoben Basin, Styria (Ettingshausen, 1869a).

Stratum typicum. Shales ~8.2 m above the coal seam (Ettingshausen, 1869a), 14.9 ± 0.7 Ma (a tuff layer near the base of the shales overlying the coal seam, Sachsenhofer et al., 2010).

Material. Moskenberg: NHMW: 1878/6/8549 (Ett. 6546), Pb 2130, (*Elaeodendron oligoneure*), Ettingshausen (1869a: pl. 6, fig. 2, holotype); (*Elaeodendron stiriacum*), Ettingshausen (1888).

Emended diagnosis. Long-petiolulate leaflet; laminar shape slightly (?) obovate and asymmetrical; base angle wide acute, shape slightly convex, apex (?) acute; margin with few teeth, height ~1 mm; distal and proximal flanks straight, sinus acute, apex bluntly acute; secondaries semicraspedodromous, widely spaced, looping in marginal quarter of lamina, exmedial veinlets running into tooth sinus or (?) apex; tertiaries widely spaced, percurrent to reticulate.

Description. Long-petiolulate leaflet; petiolule at least 6 mm long, laminar shape slightly (?) obovate, slightly asymmetrical, l × w ~42 × 20 mm, ratio l/w ~2.1; base incomplete, angle wide acute, base shape slightly convex, apex angle acute, apex shape (?) straight; margin coarsely simple serrate with few teeth, tooth height around 1 mm, distal and proximal flanks straight, sinus acute, apex bluntly acute; midvein straight; secondaries semicraspedodromous, widely spaced, 4–5 on each side, angle of origin acute to moderate, course curved, secondaries looping in marginal quarter of lamina, exmedial veinlets running into tooth sinus or (?) apex; tertiaries delicate, widely spaced, percurrent to reticulate.

Remarks. Ettingshausen (1869a) described this leaf first as *Elaeodendron oligoneure*

(Celastraceae R. Br.) and later transferred it to *E. stiriacum* (Ettingshausen, 1888), in which he fused several morphologically very different specimens. Due to the coarsely serrate margin, widely spaced secondaries and tertiaries and the venation course near the margin, this specimen is comparable to leaflets of *Clematis*. The here described leaf may also be reminiscent of *Celtis* or Vitaceae. But in *Celtis*, teeth are more numerous and the tertiaries are percurrent. In Vitaceae the secondaries serve the tooth apices, which is ambiguous in the specimen at hand. Recently, Hably (2020) described *C. csabae* from Magyaregregy which differs by size, absence of petiolule, more widely spaced secondaries in the basal part of the lamina and distinctly more prominent 3° order venation. *C. oligoneure* differs from *Parthenocissus rhombifolia* by the semicraspedodromous secondaries (see that section).

Family BERBERIDACEAE Juss.

Subfamily BERBERIDOIDEAE Kostel.

Genus **Berberis** L.

Berberis mahonioides
Kovar-Eder sp. n.

PFNR Unique Identifier: PFN003339

Figs 7.12, 23.9

Holotype designated here. IBUG Ett. 6147.

Derivatio nominis. Referring to the former genus *Mahonia*, which is now included in the genus *Berberis*.

Locus typicus. Historical locality Münzenberg near Leoben, Leoben Basin, Styria (Ettingshausen, 1869a).

Stratum typicum. Shales ~2.75 m above the coal seam (Ettingshausen, 1869a), 14.9 ± 0.7 Ma (a tuff layer near the base of the shales overlying the coal seam, Sachsenhofer et al., 2010).

Material. Münzenberg: IBUG: Ett. 6147, (*Nymphaeophyllum denticulatum* sp. n. in sched.).

Diagnosis. Sessile leaflet, asymmetrical; base cordate; margin serrate, teeth tiny, narrow, distantly spaced; midvein thick, secondaries slender, festooned brochidodromous, arising at wide angle from midvein, forming elongate, angular loops well within lamina; tertiaries irregular reticulate; veinlets arising from marginal loops probably ending in tooth apices.

Description. Leaflet lacking apical part, sessile, asymmetrical; laminar shape probably elliptic, l × w (?)~100 × 35 mm; base angle obtuse, base shape cordate; margin finely serrate, teeth narrow, <1 mm high, at distances of 3–6 mm, proximal flank very short, distal flank straight, slightly concave, sinus angular or rounded, apex acute or blunt; midvein thick, secondaries festooned brochidodromous, slender, arising at wide angle on broader side of midvein, at (?) moderate angle on the narrower side, distances of 3–7 mm, straight to slightly curved, forming differently sized, angular loops at variable distances from leaf margin; tertiaries irregularly reticulate to percurrent; veinlets arising from marginal loops probably ending in tooth apices.

Remarks. This remain, especially its base and the 2° veins forming differently sized angular loops, is strongly reminiscent of a leaflet of *Berberis* (former *Mahonia*). The teeth are, however, tiny and do not appear to be spine-like. According to Güner and Denk (2012), pinnate secondary venation pattern would point towards the Group Occidentales rather than Orientales.

Berberis mahonioides differs by the absence of prominent basal secondaries and tiny, more numerous, teeth that are not spine-like from *Mahonia bilinica* (Unger) Kvaček et Bůžek (Bílina, northern Bohemia; Kvaček and Bůžek, 1994), *M. pseudosimplex* Kvaček et Walther (Bechlejovice, northern Bohemia, Early Oligocene; Kvaček and Walther, 2004), *M. exulata* (Unger) Kvaček et Teodoridis (several Miocene sites in Europe; Kvaček and Teodoridis, 2019), and *M. mangbangensis* D. Tang et J. Wu (Tang D. et al., 2023). *M.* cf. *pseudosimplex* (La Cerdanya, Spain, Late Miocene; Barrón et al., 2014) lacks prominent basal secondaries as in the Leoben specimen but the teeth are spiny and less numerous and the lamina is smaller than in the latter specimen. More similar is *M. heterophylla* Kolak. from Kodor (Abkhazia, Pliocene; Kolakovskii, 1964), resembling in size and serration *B. mahonioides*, but in *M. heterophylla* the angle between midvein and secondaries is narrower and the loops therefore ascend more steeply. *B. mahonioides* differs further from *M. somaensis* T. Güner et Denk (Turkey, Middle Miocene; Güner and Denk, 2012) by less steeply ascending loops of secondaries and more numerous and tinier teeth.

Berberis* cf. *teutonica
(Unger) Kovar-Eder et Kvaček

Figs 7.13–7.16, 23.10

cf. 1850a *Clethra teutonica* Unger; Unger, p. 439.

cf. 1866 *Crataegus teutonica* (Unger) Unger; Unger, p. 60, pl. 19, figs 24, 25.

1869a *Maytenus submarginata* Ettingsh. sp. n.; Ettingshausen, p. 84, pl. 5, fig. 17.

1888 *Daphne protogaea* Ettingsh., p.p.; Ettingshausen, p. 312, pl. 4, fig. 3, non figs 4, 5.

1888 *Celastrus europaeus* Unger, p.p.; Ettingshausen, p. 344.

1888 *Pterocelastrus elaenus* Unger, p.p.; Ettingshausen, p. 344.

1888 *Maytenus submarginata* Ettingsh., Ettingshausen, p. 345, pl. 9, fig. 4.

cf. 2004 *Berberis teutonica* (Unger) Kovar-Eder et Kvaček; Kovar-Eder et al., p. 56, pl. 2, figs 9, 10.

Material. Moskenberg: NHMW: 1878/6/3612 + 3613 (Ett. 1609 + 1610), (*Celastrus europaeus*); 1878/6/4110 + 4190 (2107 + 2187), (*Pterocelastrus elaenus*); 1878/6/4147 (2144), (*Celastrus europaeus*); 1878/6/8509 (6506), Pb 2018, (*Maytenus submarginata*), Ettingshausen (1869a: pl. 5, fig. 17, holotype) + 1878/6/8824 (Ett. 6821), C, Pb 2079. Münzenberg: NHMW: 1878/6/4322 (Ett. 2319), Pb 2303, (*Pterocelastrus elaenus*); 1878/6/4375 (2372), Pb 2179, (*Daphne protogaea*), Ettingshausen (1888: pl. 4, fig. 3).

Description. Simple leaves, petiole short, straight to slightly angular to midvein, stout, 3–(?) 10 mm long; laminar shape obovate to nearly elliptic, l × w ~28–63 × 12–25 mm, ratio l/w ~2.3–2.6 (3.75); base angle acute to moderate, shape mainly straight to slightly concave or convex, i.e. cuneate to decurrent; apex angle obtuse, apex shape straight to moderately rounded, utmost apex blunt; margin very finely serrate to sometimes (?) entire, teeth tiny and inconspicuous, height < 1 mm, density variable among specimens; midvein strong, straight; secondaries distinctly thinner than midvein, (?) brochidodromous, irregularly spaced, spacing narrower near base, wider higher up; angle of origin narrow; secondaries ascending steeply, sometimes branching, joining to form elongated meshes partly with tertiary veins; near margin, loops of secondaries give rise to exmedial veinlets partly joining again in tiny loops, others running into marginal teeth; tertiaries widely spaced, irregular; higher-order veins reticulate.

Remarks. The specimen with best-preserved venation and marginal serration is NHMW 1878/6/8509 (Ett. 6506) (Figs 7.13, 23.10) assigned by Ettingshausen (1869a: pl. 5, fig. 17) to *Maytenus submarginata*. In the other specimens the venation is far less well visible. *Berberis* leaves were mistaken by Ettingshausen for numerous, partly even South Hemispherian genera. The true generic affinity has been recognised by, e.g. Palamarev and Petkova (1987), Kvaček and Erdei (2001), Kottis et al. (2002), Kovar-Eder et al. (2004), and Kvaček and Teodoridis (2019).

The venation pattern with steeply ascending delicate secondaries forming elongated meshes is characteristic. *B. berberidifolia* (Heer) Palamarev et Petkov (Heer, 1859; Palamarev and Petkova, 1987), which occurs accessorily in European Miocene floras, e.g. Öningen, Germany (Heer, 1859), Bilina, Bohemia, Czech Republic (Kvaček et al., 2004a), Drenovets, Bulgaria (Palamarev and Petkova, 1987), has a similar leaf shape but differs by much more distinct teeth and less dense secondaries. *Berberis* sp. from Wischgrund (Germany, Upper Miocene; Striegler, 2017) resembles by the minute serration but teeth are spiny and the leaves are narrower. The morphological variability of *B. teutonica* is still unclear because only few specimens were available from the type locality Parschlug (Kovar-Eder et al., 2004, 2022). The laminar shape of the here described leaves appears to be more elongate than at Parschlug.

Order PROTEALES
Bercht. et J. Presl

Family PLATANACEAE T. Lestib.

Genus ***Platanus*** L.

(?) ***Platanus neptuni***
(Ettingsh.) Bůžek, Holý et Kvaček

Fig. 7.17–7.19

1888 *Diospyros brachysepala* A. Braun, p.p.; Ettingshausen, p. 329, non pl. 6, fig. 8.

1888 *Carya bilinica* Unger, p.p.; Ettingshausen, p. 353.

Material. Münzenberg: NHMW: 1878/6/4217 (Ett. 2214), Pb 2279, (*Carya bilinica*);

1878/6/4364 (2361), Pb 2222, (*Diospyros brachysepala*); 1878/6/4461 (2458), (*Euonymus* sp. in sched.).

Description. Fragments of leaves; petiole 6 mm long, slightly swelling towards base (NHMW 1878/6/4364, Ett. 2361), laminar shape oblong to slender elliptic, l × w (?)~55 to >100 × 20–40 mm, ratio l/w ~>2.5–3; margin entire near base, then regularly simple serrate to almost crenate, tooth height <1 mm, distal flank very short, straight to convex, proximal flank straight to minimally concave (NHMW 1878/6/4217, Ett. 2214), sinus rounded to angular, apex blunt; midvein straight; secondaries already hardly visible.

Remarks. Laminar shape and leaf margin are reminiscent of *Platanus neptuni*. In that fossil-species the secondaries are usually well visible. Early Middle Miocene records from Central Europe are already rare, accounting for the equivocal assignment. Although the well documented variability of *P. neptuni* mf. *fraxinifolia* (Johnson et Gilmore) Kvaček et Manchester from Janda (Serbia, Oligocene; Djordjević-Milutinović and Dulić, 2009) is very wide, the leaves from Leoben are larger and broader and the petiole of specimen NHMW 1878/6/4364 (Ett. 2361) indicates a leaf rather than a leaflet.

Order VITALES Reveal

Family VITACEAE Jussieu

Genus **Parthenocissus** Planch.

Parthenocissus rhombifolia
(Ettingsh.) Kovar-Eder comb. nov.

PFNR Unique Identifier: PFN003322

Figs 7.20, 23.12

1869a *Acer rhombifolium* Ettingsh. sp. n., p.p.; Ettingshausen, p. 80, pl. 5, fig. 5, (non 4).

1888 *Acer rhombifolium* Ettingsh., p.p.; Ettingshausen, p. 340, (non pl. 8, fig. 6).

Lectotype designated here. NHMW 1878/6/4049 (Ett. 2046), Pb 2105, *Acer rhombifolium* Ettingsh., sp. n., Ettingshausen (1869a: p. 80, pl. 5, fig. 5, syntype), refigured on Fig. 7.20 and Fig. 23.12.

Basionym. *Acer rhombifolium* Ettingsh., Ettingshausen (1869a: p. 80).

Derivation nominis. Referring to the laminar shape.

Locus typicus. Historical locality Moskenberg near Leoben, Leoben Basin, Styria (Ettingshausen, 1869a).

Stratum typicum. Shales ~8.2 m above the coal seam (Ettingshausen, 1869a), 14.9 ± 0.7 Ma (a tuff layer near the base of the shales overlying the coal seam, Sachsenhofer et al., 2010).

Material. Moskenberg: NHMW: 1878/6/4049 (Ett. 2046), Pb 2105, (*Acer rhombifolium*), Ettingshausen (1869a: p. 80, pl. 5, fig. 5, syntype).

Emended diagnosis. Elliptic to obovate, somewhat asymmetrical (?) leaflet, base acute; margin entire near base, then asymmetrically simple serrate with few, big teeth; teeth bigger on one side than on the other; tooth shape variable, sinus angular, apex bluntly acute, (?) glandular; venation basal acrodromous with 3 major veins, near margin a further, more delicate vein developed; angle between major veins 25–30°; central main vein running into leaf apex, lateral main veins running into tooth apices; secondaries irregularly, widely spaced, angle of origin moderate, course straight to slightly curved, ending in tooth apices; branches of two adjacent secondaries may run into one tooth, merging in its apex; exmedial veinlets arising from lateral major veins and secondaries or their branches looping along margin; further venation reticulate.

Description. (?) leaflet; laminar shape elliptic to minimally obovate, somewhat asymmetrical, l × w ~42 × 24 mm; base incomplete, base angle acute, base shape straight; apex missing, (?) acute; margin entire in basal third of lamina, then asymmetrically simple serrate; teeth big, size variable, height >1 and <5 mm, few, ~3 (–? 5) on each side, bigger on left side; distal flank straight, concave, proximal flank convex, flexuous, straight, sinus angular, apex bluntly acute, (?) glandular; venation basal acrodromous with 3 major veins; on one side near margin a further, more delicate vein developed, other side damaged; angle between main veins 25–30°; central main vein running into leaf apex, lateral main veins running into tooth apices; secondaries irregularly, widely spaced, arising at moderate angles, running straight to slightly curved into tooth apices; some secondaries forking once; branches of two adjacent secondaries may run into same tooth, merging in its apex; exmedial veinlets arising from lateral major veins and secondaries or their branches looping along margin; tertiaries and higher-order venation reticulate.

Remarks. This remain probably represents a leaflet because of its slightly asymmetrical shape, asymmetrical dentation and acute, entire-margined base. It remains disputable whether the teeth on the left side are glandular because those on the right side are not. The tertiaries are not percurrent as usually in *Acer* L. An affinity to Vitaceae appears more likely. The vein pattern of secondaries and higher-order veins of this fossil resembles that of, e.g. *Parthenocissus quinquefolia* (L.) Planch., whereas three prominent main veins arising at the base account for some uncertainty in the generic assignment.

Genus **Vitis** L.

Vitis stricta (Goepp.) Erw. Knobloch

Fig. 8.1

1855 *Acer stricta* Goepp.; Goeppert, p. 35, pl. 23, figs 1–3, (?) 4, 5.
1869a *Vitis teutonica* A. Braun; Ettingshausen, p. 76, pl. 4, fig. 15.
1888 *Vitis teutonica* A. Braun, p.p.; Ettingshausen, p. 351.
1969 *Vitis stricta* (Goepp.) Knobloch; Knobloch, p. 125, text-fig. 269, pl. 64, fig. 9.

Material. Moskenberg: IBUG: Ett. 6224, (*Vitis teutonica*), Ettingshausen (1869a: pl. 4, fig. 15).

Description. Simple, (?) palmately 5-lobed leaf lacking petiole and distal part of lamina; laminar shape (?) orbiculate, l × w ~80–84 × 89 mm, ratio l/w ~0.9; base angle reflex, base shape cordate or lobate; margin sharply serrate, teeth ~5 mm high, regularly spaced, distal flank convex, straight, proximal flank concave, sinus angular, apex narrow, sharply pointed; venation palmate, 5 main veins arising at base, central one straight, lateral ones curved, angle between main veins ~40–50°, minor secondaries arising from lateral main veins simple craspedodromous, compound agrophic, angle of origin moderate to moderately wide, course curved, running into tooth apices; inner tertiaries percurrent, spacing ~3–5 mm, angle wide obtuse towards central vein, angle increasing exmedially and proximally; further veins reticulate.

Remarks. Only this specimen clearly represents *Vitis stricta* because specimen NHMW 1878/6/3596 (Ett. 1593) listed by Ettingshausen (1888) must be assigned to *Acer* (see Supplementary File 2) and no further specimens were detected. This type of foliage usually occurs accessorily only in fossil assemblages, e.g. Bockwitz near Borna, Germany (Mai and Walther, 1991), northern Bohemia (Kvaček et al., 2004a), Moravská Nová Ves, Moravia (Knobloch, 1969). Mai and Walther (1991) described the cuticle and completed the synonymy provided by Knobloch (1969). The latter author confirmed further the grossmorphological similarity to the modern *Vitis vulpina* (synonym *V. cordifolia* Michx). from eastern North America. Mai and Walther (1991) also stated similarities to modern *Vitis* species of the Atlantic North America, mentioning among others *V. vulpina* L.

Order OXIDALES Heintze

Family ELAEOCARPACEAE Juss.

Genus **Sloanea** L.

Sloanea serratifolia
(Ettingsh.) Kovar-Eder comb. nov.

PFNR Unique Identifier: PFN003326

Figs 8.4–8.7, 23.13–23.14

1869a *Artocarpidium serratifolium* Ettingsh. sp. n.; Ettingshausen, p. 55, pl. 3, figs 1, 2.
1869a *Euonymus moskenbergense* Ettingsh. sp. n.; Ettingshausen, p. 83, pl. 6, fig. 3, non 4.
1869a *Hippocratea crenulata* Ettingsh. sp. n.; Ettingshausen, p. 86, pl. 6, fig. 5.
1888 *Ficus lanceolata* Heer with *Xylomites ficicolus* Ettingsh. sp. n.; Ettingshausen, p. 269, pl. 1, fig. 15.
1888 *Ficus lanceolata* Heer, p.p.; Ettingshausen, p. 296.
1888 *Artocarpidium serratifolium* Ettingsh., p.p.; Ettingshausen, p. 299.
1888 *Persea heeri* Ettingsh.; Ettingshausen, p. 307.
1888 *Persea hapalophylla* Ettingsh. sp. n.; Ettingshausen, p. 307, pl. 4, figs 7, 8.
1888 *Apocynophyllum lanceolatum* Unger, p.p.; Ettingshausen, p. 323.
1888 *Euonymus herthae* Ettingsh. sp. n.; Ettingshausen, p. 346, pl. 8, fig. 17.
1888 *Hippocratea crenulata* Ettingsh.; Ettingshausen, p. 347.
1888 *Photinia eratonis* Ettingsh. sp. n.; Ettingshausen, p. 359, pl. 9, fig. 34.

Lectotype designated here. NHMW 1878/6/7710 (Ett. 5707), Pb 1977, *Artocarpidium serratifolium* Ettingsh. sp. n., Ettingshausen (1869a: p. 55, pl. 3, fig. 2, syntype), refigured on Fig. 8.5, Fig. 23.13.

Paratypes. NHMW: 1878/6/3738 + 3750 (Ett. 1735 + 1747), (*Persea heeri*), Ett. 1747 figured on Fig. 8.7, Fig. 23.14; 1878/6/4191 (2188), (*Euonymus* sp. in sched.); 1878/6/7658 (5655), (*Ficus lanceolata*) figured on Fig. 8.4; 1878/6/7864 (5861), Pb 2198, (*Persea hapalopyhlla*), Ettingshausen (1888: pl. 4, fig. 8).

Basionym. *Artocarpidium serratifolium* Ettingsh., Ettingshausen (1869a: p. 55).

Derivatio nominis. Referring to the minutely serrate margin.

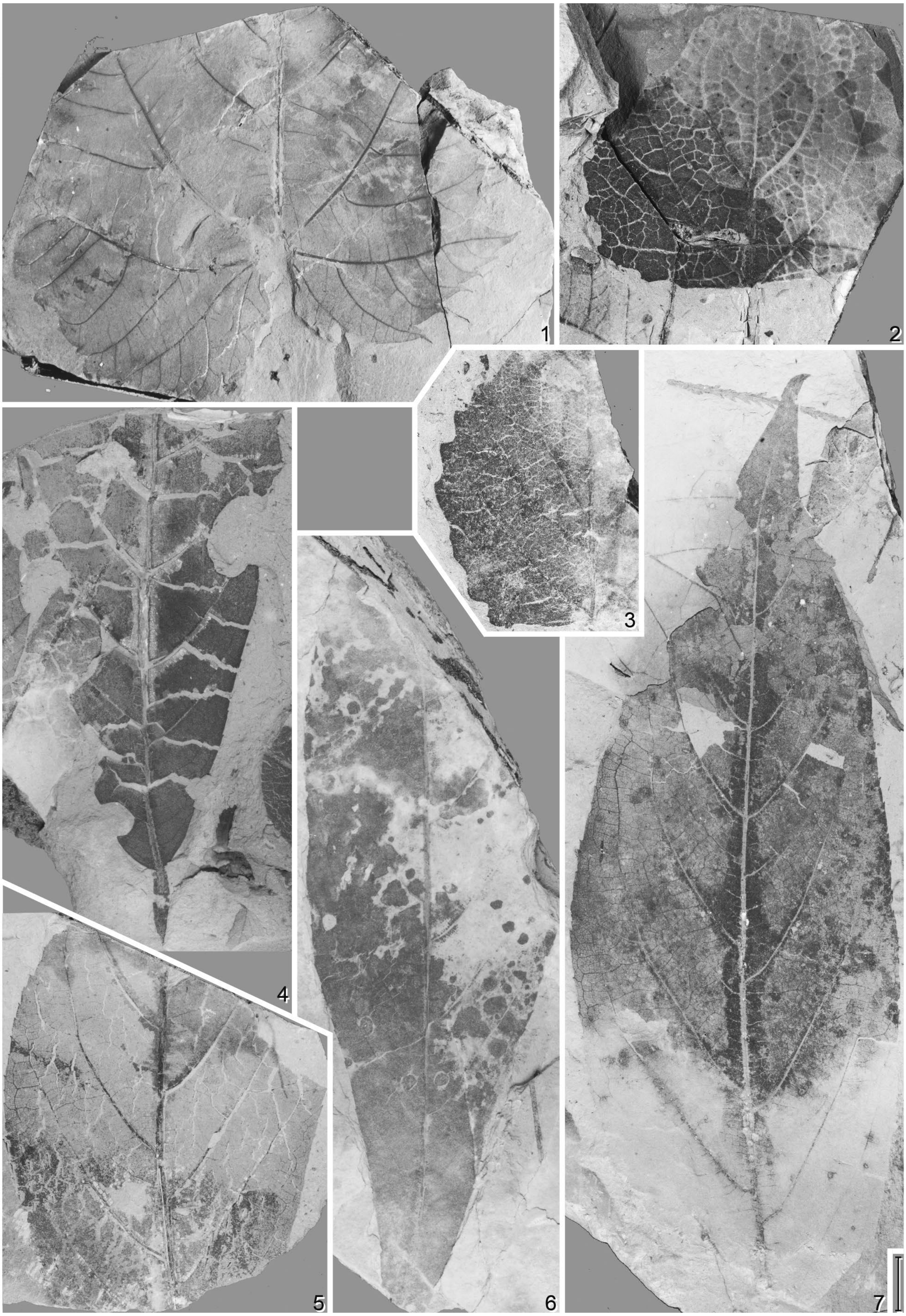
Locus typicus. Historical locality Moskenberg near Leoben, Leoben Basin, Styria (Ettingshausen, 1869a).

Stratum typicum. Shales ~8.2 m above the coal seam (Ettingshausen, 1869a), 14.9 ± 0.7 Ma (a tuff layer near the base of the shales overlying the coal seam, Sachsenhofer et al., 2010).

Material. Moskenberg: NHMW: 1878/6/3509 + 3510 (Ett. 1506 + 1507), (*Euonymus herthae*), Ettingshausen (1888: pl. 8, fig. 17); 1878/6/3644 (1641), B; 1878/6/3695 (1692), B; 1878/6/3737 (1734) (*Persea heeri*); 1878/6/3738 + 3750 (1735 + 1747), (*P. heeri* + *P.* sp. in sched.); 1878/6/3751 + 3752 (1748 + 1749), Pb 1975, (*P. hapalophylla*), Ettingshausen (1888: pl. 4, fig. 7, syntype); 1878/6/3831 (1828) (*Xylomites ficicolus* on *Ficus lanceolata*), Ettingshausen (1888: pl. 1, fig. 15); 1878/6/3892 (1889), Pb 1929, (*Artocarpidium serratifolium*); 1878/6/3893 (1890), Pb 1930, (*A. serratifolium*); 1878/6/4028 (2025), (*Juglans* sp. in sched.); 1878/6/4052 (2049), C; 1878/6/4055 + 4213 (2052 + 2210), Pb 2089, Pb 2090, (*Terminalia miocenica*); 1878/6/4122 (2119), Pb 1991, (*Apocynophyllum lanceolatum*); 1878/6/4131 (2128), (*Artocarpidium* sp. in sched.); 1878/6/4191 (2188), (*Euonymus* sp. in sched.); 1878/6/7658 (5655), (*Ficus lanceolata*); cf. 1878/6/7659 (5656), (*F. lanceolata*); 1878/6/7710 (5707), Pb 1977, (*Artocarpidium serratifolium*), Ettingshausen (1869a, pl. 3, fig. 2, syntype); 1878/6/8553 (6550), Pb 2009, (*Hippocratea crenulata*), Ettingshausen (1869a: pl. 6, fig. 5, holotype); 1878/6/9217 + sine no. (7214 + sine no.). Münzenberg: NHMW: 1878/6/4227 (Ett. 2324), (*Euonymus muenzenbergensis* in sched.); 1878/6/7864 (5861), Pb 2198, (*Persea hapalopyhlla*), Ettingshausen (1888: pl. 4, fig. 8, syntype); 1878/6/8202 (6199), (*Codia leobensis* in sched.). IBUG: Ett. 5997, (*Ficus lanceolata*). Seegraben Unter-Buchwieser: NHMW: 1878/6/4415 (Ett. 2412), a, Pb 2355, (*Photinia eratonis*), Ettingshausen (1888: pl. 9, fig. 34, holotype). Seegraben Walpurgis-Schacht: NHMW: 1878/6/4476 (Ett. 2473), b, (*Hippocratea crenulata*). Leoben: LMJ: 201.011.

Emended diagnosis. Petiolate, very large-sized leaves, lamina obovate (to elliptic), mostly slightly asymmetrical, l × w up to 210 × 70 mm, base cuneate, at utmost base sometimes obtuse, apex acute/acuminate; margin mostly entire near base, then serrate with tiny, widely spaced teeth to more rarely entire; midvein strong, often bent; secondaries thin, eucamptodromous to semicraspedodromous, widely spaced, at moderate to narrow angles, curved, occasionally branched; exmedial veinlets of secondaries or their branches looping near margin, further veinlets running into teeth; single long intersecondaries interspacing with secondaries, tertiaries (forked-)percurrent, almost perpendicular to secondaries, obtuse towards midvein; higher-order veins reticulate.

Description. Petiolate, very large, leaves, petiole rarely preserved, incomplete, l up to 13 mm; laminar shape slightly obovate, more rarely elliptic, somewhat asymmetrical, more rarely symmetrical, l × w ~90–210 × (20) 30–60 (70) mm, ratio l/w ~(2.3) 2.8–4 (4.5); base angle (narrow) acute, base shape straight, i.e. cuneate, in case of bent midvein slightly concave on one side and slightly convex on the other, utmost base (near midvein) occasionally obtuse; apex (rarely preserved) acute/acuminate; margin mostly entire near base, higher up minutely serrate to rarely entire; teeth tiny, height <1 mm, often widely, not very regularly spaced, distal flank very short, proximal flank very long, straight to apically concave, apex (bluntly) acute, sinus angular, occasionally rounded; midvein strong, somewhat bent to straight; secondaries distinctly thinner, eucamptodromous to semicraspedodromous, secondaries widely, not very regularly spaced, basalmost pair often almost opposite, further pairs alternate more rarely subopposite; secondaries arising at moderate to narrow angle, angle narrow especially in smaller parts of lamina, course curved, sometimes branching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in marginal part of lamina; in marginal third of lamina numerous exmedial veinlets branching off from 2° veins or their branches, veinlets looping, giving rise to further veinlets; ultimate veinlets running into teeth; single intersecondaries interspacing with secondaries, reaching more than half distance between midvein and margin; several short, thin veins arising from midvein almost perpendicularly, corresponding in thickness to tertiaries; tertiaries distinctly weaker than secondaries, (forked-)percurrent, curved to sinuate, almost perpendicular to secondaries, obtuse towards midvein; higher order venation reticulate, mostly 4- to 5-sided.

Remarks. Evidently, Ettingshausen (1888) did not recognise the tiny teeth of the leaf margin in several specimens (e.g. *Ficus lanceolata*, pl. 1, fig. 15, *Persea hapalophylla*, pl. 4, figs 7, 8). The petiole is preserved very rarely and only fragmentarily.

These leaves correspond largely to those recognised as Elaeocarpaceae from the European Paleogene (Kvaček et al., 2001; Hably, 2007; Hably et al., 2007). More specifically, they closely resemble *Sloanea artocarpites* (Ettingsh.) Kvaček et Hably because of their big size and the tiny marginal serration (Kvaček et al., 2001, 2018; Walther and Kvaček, 2007). The morphology of the abaxial cuticle, which could further support the generic assignment, is unfortunately not available. So far, records of *Sloanea* were restricted to the Paleogene, the youngest record of *S. artocarpites* deriving from Matrý near Sebuzín (České středohoří Mts., Czech Republic, 30.8–24.7 Ma; Kvaček et al., 2018). Thus, the rich occurrence in the Leoben assemblage is very extraordinary. Due to the stratigraphic gap of at least 10 Ma between the Paleogene occurrences and the Leoben flora, the new fossil-species *S. serratifolia* is introduced here.

From Parschlug *Dicotylophyllum* sp. S (Kovar-Eder et al., 2022: pl. 5, figs 13, 14) resembles by leaf shape and minute marginal dentition. It differs, however, by the stout and straight midvein, broader base, convex base shape and secondaries arising at wider angle from the midvein.

Order MALPIGHIALES Martius

Family SALICACEAE Mirbel

Genus ***Populus*** L.

Populus latior A. Braun

Fig. 8.2–8.3

1822b	*Phyllites populina* Brongn.; Brongniart, p. 237, pl. 14, fig. 4.
1845	*Populus latior* A. Braun; A. Braun, p. 169.
1856	*Populus latior* A. Braun; Heer, p. 11, pl. 53, figs 1, 6–8, 10, pl. 54, figs 2, 3, 5, pls 55, 56, pl. 57, figs 2, 3, 6, 7, pl. 95, fig. 15.
1869a	*Urtica miocenica* Ettingsh. sp. n.; Ettingshausen, p. 55, pl. 2, fig. 21.
1888	*Urtica miocenica* Ettingsh.; Ettingshausen, p. 299.
1888	*Populus latior* A. Braun, p.p.; Ettingshausen, p. 300, non pl. 3, fig. 21.
1999	*Populus* cf. *populina* (Brongn.) Erw. Knobloch; Ströbitzer, p. 107, pl. 4, fig. 16, pl. 12, figs 5, 6.
2004	*Populus populina* (Brongn.) Erw. Knobloch; Kovar-Eder et al., p. 70, pl. 8, figs 19–21.
2022	*Populus latior* A. Braun; Kovar-Eder et al., p. 98, pl. 8, figs 16, 17.

Material. Moskenberg: NHMW: 1878/6/3618 + 7760 (Ett. 1615 + 5757), (*Populus latior*); 1878/6/4210+4211(2207+2208,D); 1878/6/7761, 2002B0001/0001 (Ett. 5758), A, Pb 5704, (*Urtica miocenica*), Ettingshausen (1869a: pl. 2, fig. 21, holotype), this specimen is listed as Ett. 7857 in Ettingshausen (1888) but according to the NHMW inventory it must be Ett. 5758 instead. IBUG: Ett. 6002, A + 6003, (*Populus latior*, in sched.). Münzenberg: NHMW: 1878/6/4282 (Ett. 2279), (*Populus latior*).

Description. Long-petiolate leaves, mostly fragmentarily preserved, petiole >10 mm long, laminar shape orbiculate, l × w ~55–64 × 60–64 mm, ratio l/w ~0.9–1.1; base truncate, apex (?); margin simple serrate, tooth height >1 mm and <5 mm, regularly spaced, distal and proximal flank convex, sinus and apex rounded; midvein straight; secondaries semicraspedodromous (?), first pair of secondaries arising directly at base, secondaries

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Figure 8. **1**. *Vitis stricta* (Goepp.) Knobloch, IBUG Ett. 6224 (*Vitis teutonica*), Ettingshausen (1869a: pl. 4, fig. 15); **2**, **3**. *Populus latior* A. Braun, **2**. NHMW 1878/6/7761, 2002B0001/0001 (Ett. 5758), A, Pb 5704, (*Urtica miocenica*), Ettingshausen (1869a: pl. 2, fig. 21, holotype), **3**. NHMW 1878/6/3618 (Ett. 1615), (*Populus latior*); **4–7**. *Sloanea serratifolia* (Ettingsh.) Kovar-Eder comb. nov., **4**. NHMW 1878/6/7658 (Ett. 5655), (*Ficus lanceolata*), paratype, see also syndiagenetic distraction, **5**. NHMW 1878/6/7710 (Ett. 5707), Pb 1977, lectotype, (*Artocarpidium serratifolium*), Ettingshausen (1869a: pl. 3, fig. 2, syntype), **6**. NHMW 1878/6/3831 (Ett. 1828) (*Ficus lanceolata* with *Xylomites ficicolus*), **7**. NHMW 1878/6/3750 (Ett. 1747), (*Persea* sp.), paratype. For all photographs the scale at bottom right of the figure is 10 mm

widely spaced, angle of origin moderate, course curved; secondaries forking once or giving rise to exmedial veinlets; branches of secondaries and veinlets either looping or running into teeth; in the case of loops, further veinlets run into teeth; tertiaries percurrent to reticulate.

Remarks. The "Drüsenborsten" mentioned and figured by Ettingshausen (1869a: pl. 2, fig. 21) more likely represent fungal remains (Fig. 8.2). Ettingshausen (1888) included also male catkins in *P. latior*. In 2002, an attempt was undertaken to retrieve pollen grains from specimen NHMW 1878/6/3615 (Ett. 1612), which appeared suitable. The obtained grains were pentaporate, pointing towards Betulaceae (Fig. 22.38, see section Betulaceae gen. et sp. – catkins). An unambiguous assignment of the male catkin figured by Ettingshausen (1888: pl. 3, fig. 21) to a collection specimen was not possible.

Genus ***Salix*** L.

Salix varians Goepp.

Figs 9.1–9.3, 23.15

1855 *Salix varians* Goepp.; Goeppert, p. 27, pl. 20, fig. 1.
1888 *Salix varians* Goepp.; Ettingshausen, p. 301.
1888 *Salix subrepens* Ettingsh. sp. n.; Ettingshausen, p. 302, pl. 2, fig. 28, pl. 3, fig 20.
2001 *Salix varians* Goepp.; Kovar-Eder and Meller, p. 83.
2003 *Salix varians* Goepp.; Kovar-Eder and Meller, p. 291, pl. 2, figs 1–3, pl. 4, figs 4–8.

Material. Moskenberg: NHMW: 1878/6/3815 + 3816 (Ett. 1812 + 1813, a), (*Salix subrepens*), Ettingshausen, (1888: pl. 2, fig. 28, pl. 3, fig. 20, holotype); 1878/6/7801 + 7802 (5798 + 5799), (*Salix varians*). IBUG: Ett. 6009, (*Salix varians*).

Description. Simple leaves; laminar shape oblong, l × w up to ~180 × 33 mm, ratio l/w ~3.1–5.4; base angle acute, base shape convex; apex angle narrow acute, apex shape straight; margin indistinctly and regularly simple serrate, teeth densely spaced, tiny, height < 1 mm, distal and proximal flank convex, sinus rounded, apex rounded to acute; midvein strong, straight to apically slightly bent; secondaries semicraspedodromous, angle of origin wide, running in wide arcs towards margin (big specimen), angle moderate to narrow, running in steep arcs towards margin (smaller specimen); intersecondaries present, especially well developed where spacing of secondaries is wide; tertiaries percurrent, sinuate, angle of tertiaries towards midvein wide obtuse.

Remarks. *Salix* leaves are extremely rare in the Leoben assemblage. In specimen IBUG Ett. 6009 the secondaries ascend steeply and the tooth apices appear partly more acute than rounded. *Salix subrepens* is based only on specimen NHMW 1878/6/3815 + 3816 (Ett. 1812 + 1813, a) (Ettingshausen, 1888). It must therefore be assumed that the figures (Ettingshausen, 1888: pl. 2, fig. 28, pl. 3, fig. 20) represent part and counterpart of a single leaf. Contrary to Ettingshausen's diagnosis, this specimen is definitely not entire-margined. No remains of fruiting capsules are available and the male catkin mentioned by Ettingshausen (1888) was not among the studied material.

***Salix* sp.**

Figs 21.19, 21.20, 22.1, 23.16

1869a *Ficus fridaui* Ettingsh. sp. n.; Ettingshausen, p. 53, pl. 2, figs 5a, (?) 5b.
1888 *Ficus fridaui* Ettingsh., p.p.; Ettingshausen, p. 297.

Material. Moskenberg: NHMW: 1878/6/4054 (Ett. 2051), a, Pb 1883, (*Ficus fridaui*); 1878/6/7670 (5667), Pb 1905, (*F. fridaui*), Ettingshausen (1869a: pl. 2, fig. 5a, holotype); 1878/6/7672 (5669), Pb 1904, (*F. fridaui*); 1878/6/7673 (5670), Pb 1901, (*F. fridaui*) + 1878/6/7761, 2002B0001/01 (5758), B, Pb 5704, the label Ett. 7857 on the specimen is not correct, according to the NHMW inventory it must be Ett. 5758 instead; 1878/6/7674 (5671), Pb 1903, (*F. fridaui*); 1878/6/7675 (5672), Pb 1899, A, (*F. fridaui*). IBUG: Ett. 6000, (*F. fridaui* in sched.).

Description. Short-petiolate leaves; petiole 3 mm long, (?) complete, (in one specimen preserved); lamina elliptic, ovate, (?) slightly asymmetrical, l × w ~58–78 × 17–28 mm, ratio l/w ~2.7–3.7; base angle acute, base shape convex to almost straight, asymmetrical; apex angle acute, apex shape straight to convex on one side and concave on the other; margin entire; midvein thick, straight to slightly curved; secondaries brochidodromous, arising at wide to moderate angles, moderately spaced, curved, looping very close to margin, basal most pairs running closely along margin; usually 1–2 intersecondaries between adjacent secondaries, intersecondaries partly short, sometimes reaching about half distance between midvein and margin; tertiaries percurrent, sinuous or forming a chevron, originating from secondaries almost perpendicular or at distinctly acute angle.

Remarks. *Ficus fridaui* (Ettingshausen, 1869a) may refer to the toponym Friedau (spelled with "ie"), a legal district formerly in Styria now in Slovenia. In Ettingshausen (1888: p. 297) *Ficus fridani* was a spelling mistake. In none of these studies did Ettingshausen refer to the origin of the species epitethon.

The venation pattern, course of secondaries, intersecondaries and tertiaries, strongly recalls *Salix*. The margin is entire, which is less common in *Salix*. More material would be necessary to assess the variability.

Order FABALES Bromhead

Family FABACEAE Lindley

Genus ***Leguminosites*** Bowerbank

cf. ***Leguminosites palaeogaeus*** (Unger) Kovar-Eder et Kvaček

Fig. 9.4

1888 *Cassia feroniae* Ettingsh., p.p.; Ettingshausen, p. 364, pl. 9, fig. 22.

cf. 2004 *Leguminosites palaeogaeus* (Unger) Kovar-Eder et Kvaček; Kovar-Eder et al., p. 74, pl. 9, fig. 1.

cf. 2020 *Leguminosites palaeogaeus* (Unger) Kovar-Eder et Kvaček; Hably, p. 84, pl. 15, fig. 16.

Material. Moskenberg: NHMW: 1878/6/3564 + 3565 (Ett. 1561 + 1562), Pb 2071, (*Cassia feroniae*), Ettingshausen (1888: pl. 9, fig. 22).

Description. Fragment of a pod, l × w ~50 (incomplete) × 5 mm, with at least 7 seeds, dorsal and ventral sutures straight, no contractions; seeds rounded to oval, diameter ~3 mm, not closely spaced.

Remarks. This legume pod is the only one documented from the Leoben flora. This specimen resembles *Leguminosites palaeogaeus* (Unger) Kovar-Eder et Kvaček from Parschlug (Kovar-Eder et al., 2004) and Magyaregregy (Hably, 2020), which also lacks contractions, but it differs by smaller size and smaller, more widely spaced seeds. There is also some similarity to *Leguminocarpon* type I sensu Hably (1992), but essential features such as the prominent venation of the valves and base and apex are not preserved in the here described specimen.

Genus ***Leguminophyllum*** A. Escalup-Bassi

***Leguminophyllum* sp. 1**

Figs 9.5, 23.17

1888 *Dalbergia haeringiana* Ettingsh., p.p.; Ettingshausen, p. 362.

Material. Moskenberg: NHMW: 1878/6/8815 (Ett. 6812), Pb 2085, (*Dalbergia haeringiana*).

Description. Probably leaflet, (?) sessile; laminar shape oblong, asymmetrical, l × w ~31 × 9 mm, ratio l/w ~3.4; base angle acute, base shape convex, apex angle acute, apex shape convex, rounded; margin entire near base then minutely crenate-dentate, tooth height < 1 mm, tooth spacing ~2 mm in middle part of lamina, decreasing towards apex, distal flank very short, proximal flank straight, apically convex, sinus angular, apex blunt, occasionally (?) glandular near leaf apex; midvein bent in upper part; secondaries distinct, festooned brochidodromous, angle of origin narrow to moderate, spacing of secondaries ~3–6 mm; single intersecondaries developed in case of wide distance between secondaries; tertiaries also distinct, percurrent, partly alternate percurrent, spacing 1–2 mm, straight to sinuate; higher-order veins faint, reticulate.

Remarks. The asymmetrical shape points towards a leaflet rather than a leaf. The second specimen assigned by Ettingshausen (1888) to *Dalbergia haeringiana* differs by an entire margin and less prominent secondaries and tertiaries (see *Leguminophyllum* sp. 2).

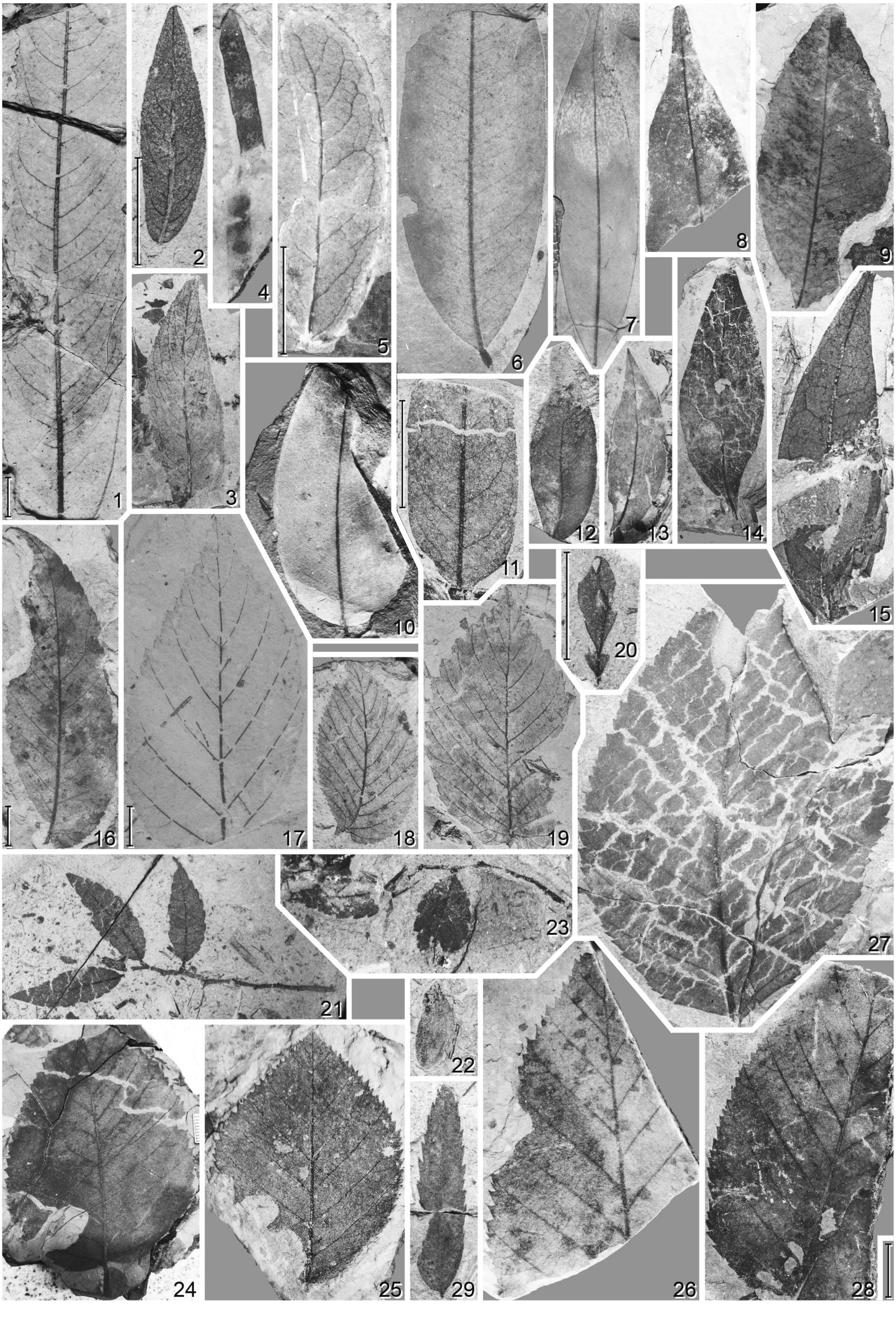
***Leguminophyllum* sp. 2**

Figs 9.11, 23.18

1888 *Dalbergia haeringiana* Ettingsh., p.p.; Ettingshausen, p. 362.

Material. Moskenberg: NHMW: 1878/6/8816 (Ett. 6813), Pb 2086, (*Dalbergia haeringiana*).

Description. Leaflet lacking apical part; laminar shape oblong, l × w ~30 × 10 mm, ratio l/w ~3; base asymmetrical, base angle ~90°, base shape straight at base then convex,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utmost base not preserved; margin entire; midvein straight, thick; secondaries brochidodromous, considerably thinner than midvein, arising at moderate angle, spacing ~8 mm, curved, interspacing with delicate interscondaries that reach exmedial half of distance between midvein and margin; tertiaries indistinct, reticulate to percurrent, further venation reticulate.

Remarks. At a first glance this specimen may be reminiscent of *Podocarpium podocarpum* (A. Braun) Herend. In that fossil-species, one of the basalmost secondaries ascends along the margin into the middle part of the lamina and the secondaries are densely spaced. Both features do not apply to the here described leaflet. For the differences from specimen NHMW 1878/6/8815 (Ett. 6812), also assigned to *Dalbergia haeringiana* by Ettingshausen (1888), see previous paragraph.

***Leguminophyllum* sp. 3**

Figs 9.10, 23.19

1869a *Dalbergia pterocarpoides* sp. n.; Ettingshausen, p. 95, pl. 6, fig. 9.

1888 *Dalbergia pterocarpoides* Ettingsh., p.p.; Ettingshausen, p. 362.

Material. Moskenberg: NHMW: 1878/6/8817 + 8818 (Ett. 6814 + 6815), Pb 2087, (*Dalbergia pterocarpoides*), Ettingshausen (1869a: pl. 6, fig. 9, holotype). Münzenberg: NHMW: 1878/6/4231 + 4404 (Ett. 2228 + 2401), Pb 2301, Pb 2300, (*Dalbergia pterocarpoides*), in Ettingshausen (1888: p. 362) number 2288 is a printing mistake, the correct number is 2228.

Description. Two subsessile leaflets lacking apex; petiolule <1 mm long; laminar shape elliptic, l × w ~54 × 24 mm and ~30 × 12 mm, respectively, ratios l/w ~2.2 and 2.4; base angle wide obtuse, base shape convex, almost rounded; margin (?) subentire; midvein strong, almost straight; secondaries eucamptodromous/brochidodromous, delicate, originating at wide angle, spacing narrow near base, further up increasing and less regular, smoothly curved, steeply ascending towards apex near margin; intersecondaries dense, of different thickness and length; further venation finely reticulate, meshes narrow, shortly elongated; veinlets near margin looping in small narrow meshes.

Remarks. The dense venation pattern characterises these specimens.

***Leguminophyllum* sp. 4**

Figs 9.6, 23.20

1888 *Cassia phaseolites* Unger, p.p.; Ettingshausen, p. 363.

Material. Moskenberg: NHMW: 1878/6/8836 + 8837 (Ett. 6833 + 6834), Pb 2066, Pb 2067, (*Cassia phaseolites*).

Description. Short-petiolulate (?) leaflet lacking apical part; petiolule 3 mm long, thick, angular towards midvein; lamina oblong to slightly elliptic, l × w (?)~80 × 27 mm, ratio l/w (?)~3; base angle wide acute, base shape somewhat convex; margin entire; midvein thick, slightly bent near base, then straight; secondaries delicate, (festooned) brochidodromous,

←

Figure 9. **1–3**. *Salix varians* Goepp., **1**. 1878/6/7801 (Ett. 5798), (*Salix varians*), **2**. NHMW 1878/6/3816 (Ett. 1813, a), (*Salix subrepens*), Ettingshausen, (1888: pl. 2, fig. 28, pl. 3, fig. 20, holotype), **3**. IBUG Ett. 6009 (*Salix varians*); **4**. cf. *Leguminosites palaeogaeus (*Unger*)* Kovar-Eder et Kvaček, NHMW 1878/6/3565 (Ett. 1562), Pb 2071, (*Cassia feroniae*), counterpart of Ettingshausen (1888: pl. 9, fig. 22); **5**. *Leguminophyllum* sp. 1, NHMW 1878/6/8815 (Ett. 6812), Pb 2085, (*Dalbergia haeringiana*); **6**. *Leguminophyllum* sp. 4, NHMW 1878/6/8836 (Ett. 6833), Pb 2066, (*Cassia phaseolites*); **7**, **8**. *Leguminophyllum* sp. 5, **7**. NHMW 1878/6/7866 (Ett. 5863), F, Pb 1970, **8**. NHMW 1878/6/8839 (Ett. 6836), Pb 2069, (*Cassia phaseolites*); **9**. *Leguminophyllum* sp. 6, IBUG Ett. 5811, B; **10**. *Leguminophyllum* sp. 3, NHMW 1878/6/8817 (Ett. 6814), Pb 2087, (*Dalbergia pterocarpoides*), Ettingshausen (1869a: pl. 6, fig. 9, holotype); **11**. *Leguminophyllum* sp. 2, NHMW 1878/6/8816 (Ett. 6813), Pb 2086, (*D. haeringiana*); **12–15**. *Leguminophyllum* sp. 7, **12**. NHMW 1878/6/7692 (Ett. 5689), Pb 2168, (*Ficus rachoyana*), Ettingshausen (1888: pl. 2, fig. 26, holotype), **13**. NHMW 1878/6/4212 (Ett. 2209), a, Pb 2131, (*Cassia memnonia*), **14**. NHMW 1878/6/4145 (Ett. 2142), Pb 2139, (*C. fischeri*), **15**. NHMW 1878/6/8894 + 8895 (Ett. 6891), Pb 2073, (*Leguminosites pachyphyllus*), Ettingshausen (1869a: pl. 6, fig. 17, holotype); **16–19**. *Ulmus pyramidalis* Goepp., **16**. NHMW 1878/6/3760 (Ett. 1757), (*Carpinus heeri*), **17**. NHMW 1878/6/3532 (Ett. 1529), A, (*Ulmus bronnii*), **18**. NHMW 1878/6/7467 (Ett. 5464), (*Ostrya atlantidis*), Ettingshausen (1869a: pl. 2, fig. 13), **19**. NHMW 1878/6/3546 (Ett. 1543), (*Ulmus bronnii*); **20**. *Ulmus* sp. – fructus, NHMW 1878/6/7599 (Ett. 5596), (*Ulmus braunii*); **21**. *Cedrelospermum ulmifolium* (Unger) Kovar-Eder et Kvaček, NHMW 1878/6/3580 (Ett. 1577), (*Planera ungeri*); **22**. *Cedrelospermum aquense* (Saporta) Saporta, NHMW 1878/6/3583 (Ett. 1580), Pb 1941, (*Embothrium stiriacum*), Ettingshausen (1888: pl. 4, fig. 32); lectotype of *Cedrelospermum stiriacum* (Ettingsh.) Kovar-Eder et Kvaček (Kovar-Eder et al., 2004); **23**. *Zelkova zelkovifolia* (Unger) Bůžek et Kotlaba, GBA 2024/0001/0030, (*Planera ungeri*); **24–28**. *Ulmus* (?) *prisca* Unger, **24**. GBA 2024/0001/0024, (*Ulmus prisca*), Ettingsh. (1869a: pl. 2, fig. 6), **25**. LMJ 201.035, **26**. NHMW 1878/6/6455 (Ett. 4452), Pb 1800, (*Phyllerium palaeo-carpini* on *Carpinus heeri*), Ettingshausen (1888: pl. 1, fig. 3), **27**. IBUG Ett. 5964, (*Ulmus bronnii*), **28**. LMJ 221.631; **29**. *Sorbus* (?) sp., NHMW 1878/6/4283 (Ett. 2280), Pb 2249, (*Rhus intermedia*), Ettingshausen (1888: pl. 9, fig. 12, syntype). For all photographs the scale at bottom right of the figure is 10 mm except for photographs with embedded scale in which the scale is also 10 mm

regularly, widely spaced, at first straight, slightly curved in marginal region of lamina; two orders of intersecondaries: longer intersecondaries almost as strong as secondaries looping along margin with secondaries; weaker and shorter intersecondaries reaching hardly half way between midvein and margin; tertiaries indistinct, (alternate) percurrent to reticulate, obtuse to midvein.

Remarks. The thick petiolule may indicate a non-deciduous physiology. Ettingshausen (1888) assembled very different leaf remains as *Cassia phaseolites*. Nonetheless, no other specimen resembles the here described one. Some are differentiated here in *Leguminophyllum* sp. 5 and *Dicotylophyllum* sp. H (see respective paragraphs), other remains are incertae sedis.

Leguminophyllum sp. 5

Fig. 9.7, 9.8

1888 *Cassia phaseolites* Unger, p.p.; Ettingshausen, p. 363.

Material. Moskenberg: NHMW: 1878/6/4000 (Ett. 1997), Pb 2063, (*Cassia phaseolites*); 1878/6/7866 (5863), F, Pb 1970; 1878/6/8839 (6836), Pb 2069, (*Cassia phaseolites*).

Description. (?) Leaflets, petiolule not preserved or (?) sessile; lamina oblong to slender elliptic, l × w ~66–106 × 15–26 mm, ratio l/w ~4–4.3; base angle acute, base shape somewhat convex; apex angle narrow acute, apex shape long acuminate; margin entire; midvein straight and thick, secondaries very delicate, only faintly visible, (?) eucamptodromous or (?) brochidodromous, angle of origin moderate to moderately wide, spacing regular, 3–5 mm in middle part, course slightly curved, interspacing with intersecondaries of similar thickness; secondaries looping with intersecondaries; further vein fabric unclear.

Remarks. These remains are characterised by their long acuminate leaf apex. The very thick midvein compared to the delicate secondaries may indicate a coriaceous texture and non-deciduous phenology. Ettingshausen (1888) referred to specimens figured in Sotzka (Unger, 1851: pl. 44, figs 1–5). These figures differ considerably by asymmetrical laminar shape, longer petiole or petiolule and blunt apex. The leaf remains summarised here differ from *Leguminophyllum* sp. 4 by more slender laminar shape, faintly visible, more steeply ascending secondaries. Essential features such as the acuminate apex of *Leguminophyllum* sp. 5 are not preserved in *Leguminophyllum* sp. 4, while the characteristic petiolule of *Leguminophyllum* sp. 4 is not preserved in *Leguminophyllum* sp. 5.

Leguminophyllum sp. 6

Figs 9.9, 24.1

Material. Münzenberg: IBUG: Ett. 5811, B.

Description. Single (?) leaflet, (?) sessile; laminar shape elliptic, l × w ~56 × 23 mm, ratio l/w ~2.4; base angle acute, base shape slightly asymmetrically, somewhat convex; apex angle acute, apex shape straight, utmost apex incomplete, (?) acuminate, (?) blunt; margin entire near base then shallow crenate; midvein almost straight; secondaries delicate, irregularly festooned brochidodromous, densely spaced, originating at moderate to wide angle, course first straight then slightly curved, occasionally forking in marginal part of lamina, looping at variable distance from margin, loops angular; intersecondaries interspaced, not always clearly distinguishable from 2° veins; intersecondaries also looping with adjacent veins; tertiaries alternate percurrent to reticulate; higher-order veins reticulate.

Remarks. *Leguminophyllum* sp. 6 differs from *Leguminophyllum* sp. 4 by smaller size, lower l/w ratio of the blade, the crenulate margin and closer spacing of secondaries.

Leguminophyllum sp. 7

Figs 9.12–9.15, 24.2

1869a *Leguminosites pachyphyllus* Ettingsh. sp. n.; Ettingshausen, p. 97, pl. 6, fig. 17.
1888 *Ficus rachoyana* Ettingsh. sp. n.; Ettingshausen, p. 298, pl. 2, fig. 26.
1888 *Cassia fischeri* Heer, p.p.; Ettingshausen, p. 364.
1888 *Cassia memnonia* Unger; Ettingshausen, p. 364.

Material. Moskenberg: NHMW: 1878/6/4145 (Ett. 2142), Pb 2139, (*Cassia fischeri*); 1878/6/4212 (2209), a, Pb 2131, (*Cassia memnonia*); 1878/6/8894 + 8895 (6891 + 6892), Pb 2073, (*Leguminosites pachyphyllus*), Ettingshausen (1869a: pl. 6, fig. 17, holotype). Münzenberg: NHMW: 1878/6/7692 + 8846 (Ett. 5689 + 6843), Pb 2168 + Pb 2141, (*Ficus rachoyana* + *Cassia fischeri*), Ettingshausen (1888: pl. 2, fig. 26, holotype of *F. rachoyana*); 1878/6/8847 (Ett. 6844), Pb 2142, (*Cassia fischeri*).

Description. Probably petiolulate leaflets; laminar shape elliptic to slightly obovate, somewhat asymmetrical, l × w ~(28) 37–68 × (10) 12–20 mm, ratio l/w ~(2.7) 3.1–3.5; base angle acute, base shape asymmetrical, one side convex, other side concave; apex angle acute, apex shape straight to somewhat convex on one side, concave on other side, long acuminate; margin entire; midvein mostly distinctly bent; secondaries brochidodromous, angle of origin moderate, spacing moderate, regular, course curved, looping at some distance from margin; tertiaries reticulate, coarsely meshed; higher-order veins finely reticulate.

Remarks. Ettingshausen (1888) described specimen NHMW 1878/6/7692 + 8846 (Ett. 5689 + 6843) as different fossil-species (*Ficus rachoyana* and *Cassia fischeri*) although they definitely represent part and counterpart of a single leaflet. The asymmetrical shape and the bent midvein of all specimens point towards leaflets rather than leaves. *Leguminophyllum* sp. 7 shares the long acuminate leaf apex with *Leguminophyllum* sp. 5 but it differs by the asymmetrical shape, smaller size and bent midvein.

Order ROSALES Perleb

Family RHAMNACEAE Juss.

Genus **Berchemia** Neck. ex DC.

Berchemia (?) **sp.**

Figs 13.1, 24.3

1888 *Dioclea protogaea* Ettingsh., p.p.; Ettingshausen, p. 362.

Material. Münzenberg: IBUG: Ett. 6251, (*Dioclea protogaea* in sched.).

Description. Simple leaf lacking petiole and apex; laminar shape broad elliptic, l × w ~70 × 56 mm, ratio l/w ~1.3; base angle obtuse, base shape convex to moderately truncate; margin entire to minimally undulate; midvein slightly bent; secondaries eucamptodromous, widely spaced, angle of origin proximally wide, decreasing, moderate towards apex, distinctly, smoothly curved; distally secondaries looping with exmedial loops of veinlets arising from the following 2° veins; intersecondaries and numerous epimedial tertiaries present especially in apical part; tertiaries very dense, (forked-)percurrent, slightly undulate, angle towards midvein almost perpendicular; 4° veins partly similar to tertiaries, partly reticulate; higher-order veins reticulate.

Remarks. Characteristics of this very well-preserved fragment are the smoothly curved and widely spaced secondaries along with very dense, sinuate, percurrent tertiaries. Ettingshausen assumed it to be a leaflet of *Dioclea* Kunth (Fabaceae) native to Mexico and tropical South America, in which the shape of the lateral leaflets is asymmetrical. Due to the incompleteness of the fossil at hand it cannot be excluded that its shape was asymmetrical. The pattern of the 3° veins resembles that of *Dioclea*.

However, Ettingshausen did not consider other genera with similar tertiary venation pattern occurring in Eurasia as *Cornus* L. or *Berchemia* Neck. Ex DC.

From Kreuzau (Germany), Ferguson (1971) described *Berchemia* resembling the specimen from Leoben. The tertiary fabric in the latter specimen is, however, less dense. Comparing cleared leaves of *Berchemia* and *Cornus* (NMNS Cleared Leaf Database, accessed June, 2023), e.g. *B. floribunda* (Wall.) Brongn. (syn. *B. racemosa* Siebold et Zucc.), reveals a resemblance to the specimen from Leoben by leaf shape, the minimally undulate margin and the course of secondaries, but the density of tertiaries is even higher and the secondaries run directly along the margin, tapering considerably. In *Cornus* the secondaries tend to run into the leaf apex and the 3° veins tend to be less dense.

Family ROSACEAE Juss.

Genus **Sorbus** L.

Sorbus (?) **sp.**

Fig. 9.29

1888 *Rhus intermedia* Ettingsh. sp. n., p.p.; Ettingshausen, p. 355, pl. 9, fig. 12.

Material. Münzenberg: NHMW: 1878/6/4283 (Ett. 2280), Pb 2249, (*Rhus intermedia*), Ettingshausen (1888: pl. 9, fig. 12, syntype).

Description. Leaflet, sessile to subsessile, laminar shape oblong, l × w ~40 × 9 mm, ratio l/w ~4.4; base angle obtuse, base shape convex, asymmetrical, apex angle narrow acute, shape straight, incomplete; margin entire near base, then sharply simple serrate, teeth regularly spaced, height >1 mm and <5 mm, distinctly inclined towards leaflet apex, distal and proximal flank ± straight, sinus angular, apex narrow acute; midvein straight; further venation details hardly discernible.

Remarks. Ettingshausen (1888) fused 3 specimens with acute teeth in *Rhus intermedia*, which represent different taxa. For differences towards specimen NHMW 1878/6/4062 + 4120 (Ett. 2059 + 2117) see *Dicotylophyllum* sp. P, and for specimen NHMW 1878/6/4148 (Ett. 2145) see paragraph *Toxicodendron melaenum*. Although the shape and serration of the here described specimen are reminiscent of *Sorbus* L., the venation details would be important for an unambiguous taxonomic assignment. For differences towards “*Rhus*” *appendiculata* see respective paragraph.

Family ULMACEAE Mirbel

Genus ***Cedrelospermum*** Saporta emend. Manchester

Cedrelospermum ulmifolium (Unger) Kovar-Eder et Kvaček

Figs 9.21, 24.4

1850a *Comptonia ulmifolia* Unger; Unger, p. 394.
1888 *Planera ungeri* Ettingsh., p.p.; Ettingshausen, p. 296.
2004 *Cedrelospermum ulmifolium* (Unger) Kovar-Eder et Kvaček; Kovar-Eder et al., p. 68, pl. 8, figs 1–5, 12.
2022 *Cedrelospermum ulmifolium* (Unger) Kovar-Eder et Kvaček; Kovar-Eder et al., p. 87, pl. 2, figs 16–18.

Material. Moskenberg: NHMW: 1878/6/3580 (Ett. 1577), (*Planera ungeri*) + GBA: 2024/0001/0002.

Description. Twig with three leaves attached; leaves almost equal in size and shape; petiole very short, 1–1.5 mm long, laminar shape oblong, slender elliptic, l × w 20–23 × 6.5–7.5 mm, ratio l/w 2.7–3.5; base slightly asymmetric, base angle wide acute to obtuse, base shape convex; apex angle acute, apex shape almost straight; margin simple serrate; teeth regular in shape and size, 7 to 8 per side, tooth height up to 1 mm, distal flank short, straight to slightly convex, proximal flank convex to slightly flexuous, sinus angular to rounded, tooth apex bluntly acute; midvein straight to slightly bent; secondaries craspedodromous, distinctly thinner than midvein, number almost corresponding to number of teeth, 2° veins originating at wide angle, slightly bent, running into tooth apices, giving rise to exmedial veinlets that run into sinus; tertiaries reticulate.

Remarks. This well-preserved twig is the only remain of *Cedrelospermum* foliage among the studied material from Leoben and it is the only specimen that Ettingshausen (1888) explicitly mentioned. Kovar-Eder et al. (2004) stated that *C. flichei* (Saporta) Hably et Thiebaut from Magyaregregy, Hungary (Hably and Thiébaut, 2002; Hably, 2020) and *C. ulmifolium* show a very close resemblance and very likely represent a single fossil-species. Therefore, the epitethon *ulmifolium* published by Unger (1850a) has priority over *flichei* (Saporta, 1891).

Cedrelospermum aquense (Saporta) Saporta

Fig. 9.22

1862 *Embothrites aquensis* Saporta; Saporta, p. 260, pl. 8, fig. 8.
1888 *Embothrium stiriacum* Ettingsh. sp. n.; Ettingshausen, p. 316, pl. 4, fig. 32.
1889 *Cedrelospermum aquense* (Saporta) Saporta; Saporta, p. 93, pl. 18, fig. 11.
1890 *Embothrium styriacum* Ettingsh., Ettingshausen, p. 110, pl. 4, figs 39, 40.
2004 *Cedrelospermum stiriacum* (Ettingsh.) Kovar-Eder et Kvaček comb. nov.; Kovar-Eder et al., p. 68, pl. 8, fig. 6.

Material. (?) Moskenberg: NHMW: 1878/6/3583 (Ett. 1580), Pb 1941, (*Embothrium stiriacum*), Ettingshausen (1888: pl. 4, fig. 32); lectotype of *Cedrelospermum stiriacum* (Kovar-Eder et al., 2004).

Description. Samaroid fruit, l × w = 16 × 7 mm; wing somewhat asymmetrical and asymmetrically positioned cleft of styles, wing with at least 5 veins nearly parallel to long axis of wing; l × w of endocarp 6.2 × 4 mm; delimitation between wing and endocarp, as well as complete number of veins unclear.

Remarks. This fruit is embedded in light grey sediment, thus differing from all other Leoben material, although it is labelled by Ettingshausen on the backside as “Leoben 1”, i.e. Moskenberg. Therefore, the true origin of this specimen is equivocal. It was chosen as lectotype (Kovar-Eder et al., 2004) because it is the only specimen listed explicitly by Ettingshausen (1888: p. 316) for this fossil-taxon. At that time, the assumption was that the samaras from Magyaregregy, Parschlug and Leoben differ by being larger than *C. aquense*. Respective studies by Hably (2020) showed, however, that the general morphology coincides largely with that of *C. aquense*.

Beyond the occurrences of *Cedrelospermum* in Europe and North America (Manchester, 1989; Magallón-Puebla and Cevallos-Ferriz, 1994), it was recently also reported from China (Jia et al., 2015, 2019), indicating the wide distribution across the northern hemisphere.

Genus ***Ulmus*** L.

Ulmus pyramidalis Goepp.

Figs 9.16–9.19, 24.5

1855 *Ulmus pyramidalis* Goepp.; Goeppert, p. 29, pl. 13, figs 10–12.
1855 *Ulmus carpinoides* Goepp.; Goeppert, p. 28, pl. 13, figs 4–9.
1869a *Ostrya atlantidis* Unger, p.p.; Ettingshausen, p. 46, pl. 2, fig. 13.
1888 *Ostrya atlantidis* Unger, p.p.; Ettingshausen, p. 294.
1888 *Carpinus heeri* Ettingsh., p.p.; Ettingshausen, p. 294.
1888 *Ulmus bronnii* Unger, p.p.; Ettingshausen, p. 295.

Material. Moskenberg: NHMW: 1878/6/3532 (Ett. 1529), A, (*Ulmus bronnii*); 1878/6/3546 (1543), (*U. bronnii*); 1878/6/3760 (1757), (*Carpinus heeri*); 1878/6/3948 (1945), A, (*U. bronnii*); 1878/6/7467 (5464), (*Ostrya atlantidis*), Ettingshausen (1869a: pl. 2, fig. 13). IBUG: Ett. 5970, (*U. bronnii* in sched.). Münzenberg: NHMW: 1878/6/4281 (Ett. 2278), Pb 2177, (*O. atlantidis*).

Description. Asymmetrical leaves, petiole not preserved, probably very short; lamina elliptic to slightly ovate, l × w = 45–90 × 18–47 mm, ratio l/w = 1.7–3.1; base distinctly asymmetrical, base angle obtuse, base shape on wider side convex, on more narrow one less convex to almost straight, slightly to distinctly cordate; apex angle acute, shape rather straight to slightly convex, utmost apex acute to acuminate; margin distinctly regularly double serrate; first-order teeth: height >1 mm and <5 mm, distal flank convex, flexuous or straight, proximal flank mainly convex or more rarely flexuous or straight; second-order teeth more variable than first-order ones, height ± 1 mm, sinus angular, apex sharp; each 1° tooth with one, two or more rarely three (NHMW 1878/6/7467) smaller teeth on proximal side; midvein straight or somewhat bent; secondaries craspedodromous, regularly, densely spaced, arising at a moderate angle near base and in the middle part of lamina, angle decreasing towards apex, near apex narrow; secondaries straight to somewhat curved, mainly unforked, only occasionally forked once, near margin giving rise to exmedial veinlets running into 2° teeth; tertiaries (forked-) percurrent, sinuate, rather dense, regularly spaced, angle towards midvein wide obtuse, 4° and higher-order veins reticulate.

Remarks. Leaves of *Ulmus* are rather rare in the Leoben assemblage. Only one leaf represents the *pyramidalis* morphotype (NHMW 1878/6/3760, Ett. 1757, Fig. 9.16), while the majority corresponds to the *carpinoides* morphotype, which is usually regarded within the variability of *U. pyramidalis* because both morphotypes cooccur at many European localities and cannot be separated satisfactorily (Hantke, 1954; Knobloch and Kvaček, 1976; Kovar-Eder, 1988). The fact that leaves of the *carpinoides* morphotype in Leoben are more numerous than those of the *pyramidalis* morphotype (the latter usually being more common than the former) could point towards two fossil-species. The low number of specimens at hand, however, does not allow further differentiation.

***Ulmus* sp.** – fructus

Fig. 9.20

1888 *Ulmus braunii* Heer; Ettingshausen, p. 295.

Material. Moskenberg: NHMW: 1878/6/7599 (Ett. 5596), (*Ulmus braunii*). Leoben. GBA: 2024/0001/0028 (*Ulmus braunii*).

Description. Samaroid fruits, shape slender elliptic, l × w ~9–11 × 3–6 mm; stalk fragmentary, with persistent perianth, ~1 mm long; stipe (between perianth and fruit base) 2–3 mm long; endocarp spindle-shaped (NHMW 1878/6/7599, Ett. 5596) to oval (GBA 2023/0001/0028), l × w ~3 × 1 mm (NHMW 1878/6/7599, Ett. 5596) and ~3.5 × 2.4 mm (GBA 2023/0001/0028); wings ~1.3–2 mm wide, with prominent marginal veins; base of wings decurrent (NHMW 1878/6/7599, Ett.

5596); GBA 2024/0001/0028 with distinct axial vein deflecting from stipe; wing apex bipartite, acute with style remnants.

Remarks. Elm samaras are very rare in the Leoben flora. Due to the differences in shape and size, it cannot be excluded that these specimens represent two different fossil-species. The Parschlug flora yielded several samaras of *Ulmus parschlugiana* (Kovar-Eder et Kvaček), which differ by broader shape of both the whole fruit and the endocarp (Kovar-Eder et al., 2004). Furthermore, in Parschlug the elm samaras cooccur with leaves of *Ulmus plurinervia* Unger, which are missing in the Leoben assemblage.

Ulmus (?) ***prisca*** Unger

Figs 9.24–9.28, 24.6

1847 *Ulmus prisca* Unger; Unger, p. 93, pl. 24, fig. 6, (non fig. 5).
1850a *Ulmus prisca* Unger; Unger, p. 410.
1859 *Ulmus prisca* Unger; Massalongo and Scarabelli, p. 212, pl. 21, fig. 8.
1869a *Ulmus bronnii* Unger; Ettingshausen, p. 52, pl. 2, fig. 6.
1888 *Phyllerium palaeo-carpini* Ettingsh. sp. n. on *Carpinus heeri* Ettingsh.; Ettingshausen, p. 264, pl. 1, fig. 3.
1888 *Ulmus bronnii* Unger, p.p.; Ettingshausen, p. 295.

Material. Moskenberg: NHMW: 1878/6/6454 + 6455 (Ett. 4451 + 4452), Pb 1800, (*Phyllerium palaeo-carpini* on *Carpinus heeri*), Ettingshausen (1888: pl. 1, figs 3, 3a, holotype of fungus). IBUG: Ett. 5964, (*Ulmus bronnii* in sched.); Ett. 5966, (*U. bronnii* in sched.); Ett. 5978, (*U. bronnii* in sched.). Münzenberg: IBUG: Ett. 5976, (*U. bronnii* in sched.). Seegraben Walpurgis-Schacht: NHMW: 1878/6/4475 (Ett. 2472), a, Pb 2373, (*U. bronnii*). Leoben: LMJ: 201.035; LMJ 221.631. GBA: 2024/0001/0008, (*U. bronnii*); 2024/0001/0020, (*U. bronnii*); 2024/0001/0022, (*U. bronnii*); 2024/0001/0023; 2024/0001/0024, (*U. prisca*), Ettingsh. (1869a: pl. 2, fig. 6); 2024/0001/0031.

Description. Simple short-petiolate leaves; petiole 10 mm long (one specimen), laminar shape (broad) elliptic to ovate, more or less asymmetrical, l × w ~42–88 × 31–65 mm, ratio l/w ~1.3–2.1; base angle (wide) obtuse, base shape convex to minimally cordate, more or less asymmetrical; apex angle acute, apex shape straight; margin regularly, densely serrate, teeth above secondaries, only slightly bigger than teeth in between, if at all; tooth height >1 mm and <5 mm, distal flank acuminate, concave, straight, proximal flank mostly acuminate, slightly convex to straight, sinus angular, apex acute, acuminate elongated, pointed; midvein straight to slightly bent; secondaries craspedodromous, terminating in tooth apices, spacing regular, moderately dense, arising at wide to moderate angle near base, angle tapering towards apex, course straight to slightly bent, abaxial minor secondaries delicate, running into tooth apices between secondaries; tertiaries distinctly more delicate than secondaries, percurrent, straight to sinuate, dense, ~7 per cm, angle towards midvein wide obtuse.

Remarks. The marginal serration of these remains indicates a separate fossil-taxon but, beyond the tertiary venation, the general venation pattern and especially its fabric near the leaf margin is poorly preserved. Based on leaf and fruit Unger (1847) described *Ulmus prisca* Unger from Radoboj figuring a single leaf specimen of which the leaf shape and margin are very similar to the here described leaves. Beyond this record, this fossil-species has been rarely recorded and these records are ambiguous, e.g. Unger (1851) or they remained unfigured (Wessel and Weber, 1856; Zwanziger, 1873, 1877). Moreover, Nagalhard (1922) argues that the leaf from Radoboj may belong to *Betula*.

Similarly shaped leaf margins may occur in *Betula*, *Carpinus* and *Ulmus*, e.g. *Betula grossa* Siebold et Zucc., *Carpinus cordata* Blume, *Ulmus* div. sp. The asymmetrical laminar shape of the most complete specimens (IBUG Ett. 5964 and GBA 2024/0001/0024) is reminiscent of *Ulmus*. While *Betula* is documented by a few and *Ulmus* by two samaroid fruits (see respective paragraphs), no samaroid fruits of *Carpinus* have been detected in the collection material, contrary to Ettingshausen (1888: pl. 3, fig. 9).

For differences towards *Alnus menzelii* and “*Corylus*” *palaeoavellana* see respective paragraphs.

Genus ***Zelkova*** Spach

Zelkova zelkovifolia
(Unger) Bůžek et Kotlaba

Fig. 9.23

1843 *Ulmus zelkovaefolia* Unger; Unger, p. 94, pl. 24, figs 7 (right), 9–13.

1963 *Zelkova zelkovaefolia* (Unger) Bůžek et Kotlaba; Kotlaba, p. 59, pl. 3, figs 7, 8.
1999 *Zelkova zelkovifolia* (Unger) Bůžek et Kotlaba; Ströbitzer, p. 103, pl. 3, fig. 15, pl. 11, fig. 3.
2004 *Zelkova zelkovifolia* (Unger) Bůžek et Kotlaba; Kovar-Eder et al., p. 69, pl. 8, figs 8–11.

Material. Moskenberg: GBA: 2024/0001/0029, (*Planera ungeri*), part + counterpart; 2024/0001/0030, (*Planera ungeri*).

Description. One twig with two leaves and a single, large leaf; leaves subsessile to petiolate, petiole 12 mm long; laminar shape ovate to elliptic, l × w ~20 × 8–10 and 92 × 47 mm; base angle acute to obtuse, base shape more or less asymmetrical, almost straight to convex; apex angle acute, apex shape acuminate; margin coarsely serrate, number of teeth corresponding number of secondaries, tooth height >1 mm and <5 mm, distal flank convex, straight, slightly flexuous, proximal flank mainly convex to flexuous, sinus angular, apex (blunt) acute; midvein straight, secondaries simple craspedodromous terminating in marginal teeth, regularly spaced, angle of origin moderate, course slightly curved; tertiaries faint, percurrent, angle obtuse to midvein, almost perpendicular to 2° veins.

Remarks. The twig (NHMW 1878/6/3580, Ett. 1577) mentioned by Ettingshausen (1888) for *Z. zelkovifolia* (former *Planera ungeri*) represents *Cedrelospermum ulmifolium* (see respective paragraph). *Zelkova zelkovifolia* is a really rare accessory element in the Leoben assembalge confined to a single twig with two leaves and a rather big leaf remain. Ettingshausen (1869a) recognised already the difference to the Parschlug flora where this fossil-species is very common.

Order FAGALES Engler

Family BETULACEAE Dumortier

Genus ***Alnus*** Miller

Alnus gaudinii

(Heer) Erw. Knobloch et Kvaček

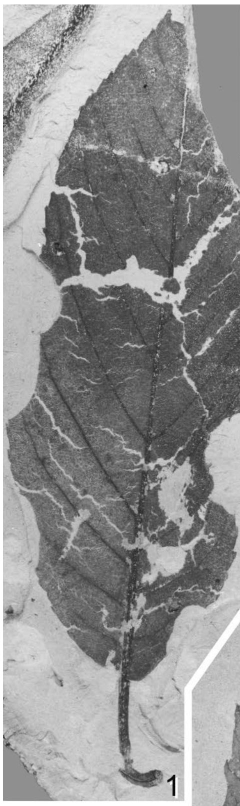
Figs 10.1–10.5, 24.7

1859 *Rhamnus gaudinii* Heer; Heer, p. 79, pl. 124, figs 4–15, pl. 125, figs 1, 7, 13.
(?) 1869a *Prunus palaeo-cerasus* Ettingsh., p.p.; Ettingshausen, p. 94, pl. 6, fig. 12, non 13.
1888 *Rhamnus gaudinii* Heer, p.p.; Ettingshausen, p. 349.
1888 *Carya bilinica* Unger, p.p.; Ettingshausen, p. 353.
(?) 1888 *Prunus palaeo-cerasus* Ettingsh., p.p.; Ettingshausen, p. 361, non pl. 7, fig. 18.
1976 *Alnus gaudinii* (Heer) Erw. Knobloch et Kvaček; Knobloch and Kvaček, p. 33, pl. 6, figs 1, 3; pl. 7, figs 1, 5; pl. 13, fig. 4; pl. 15, figs 1–4, 7, 8, 10, 11, 13, 15, 17; pl. 16, figs 1–5; pl. 19, fig. 15; pl. 20, fig. 10; text-figs 11, 12.
2004 *Alnus gaudinii* (Heer) Erw. Knobloch et Kvaček; Kovar-Eder et al., p. 60, pl. 3, fig. 5.

Material. Moskenberg: NHMW: 1878/6/3505 (Ett. 1502), A, B, Pb 2043, 2 leaves, A (*Carya bilinica*), B; 1878/6/3513 (1510), (*Rhamnus gaudinii*); 1878/6/3515 (1512), (*R. gaudinii*); 1878/6/3516 (1513), (*R. gaudinii*); (?) 1878/6/3523 (1520), A, (*Prunus palaeo-cerasus*), Ettingshausen (1869a: pl. 6, fig. 12, syntype); 1878/6/3523 (1520), B, (*P. palaeo-cerasus*); 1878/6/3557 (1554), B; 1878/6/4109 (2106), (*Ulmus bronnii* in sched.); 1878/6/4203 (2200), A, (*R. gaudinii*); 1878/6/8590 (6587), (*R. gaudinii*).

Description. Long-petiolate simple leaves; petiole up to 24 mm long, straight to bent; laminar shape slender elliptic to more rarely elliptic, mostly symmetric, l × w ~(55) 75–90 (95) × (22) 30–34 (37) mm, ratio l/w ~(1.9) 2.3–2.7 (3); base angle mostly obtuse to more rarely acute, base shape convex, occasionally asymmetrical; apex angle acute, apex shape straight to acuminate; margin simple serrate, only near very base entire; teeth tiny, height <1 mm, ± regularly spaced, variably shaped, sinus angular, tooth apex acute to rounded, occasionally gland-tipped; midvein straight, secondaries semicraspedodromous, moderately to densely spaced (up to 13 pairs), originating at moderate to acute angle, course moderately curved to nearly straight; tertiaries usually faintly visible, densely spaced, (forked-) percurrent, straight to weakly convex or sinuate, wide oblique to midvein; a veinlet occasionally visible arising from marginal-most tertiary running into tooth. NHMW 1878/6/3523 (Ett. 1520, A): abaxial branches of 2° veins (minor secondaries/tertiaries) running into teeth; ~4–5 tertiaries per cm; 4° veins (forked-)percurrent to reticulate; higher-order veins reticulate, areoles well developed, free-ending veinlets forked.

Remarks. In several specimens the long petiole is preserved and some leaves are rather complete, indicating that they were resistant and/or did not undergo longer transport. The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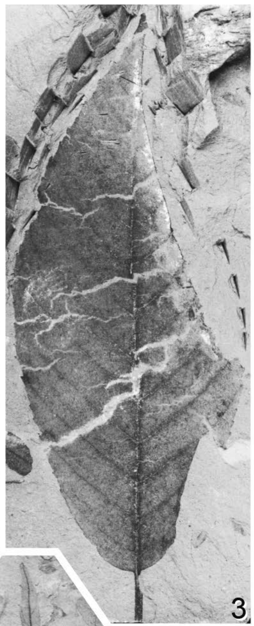
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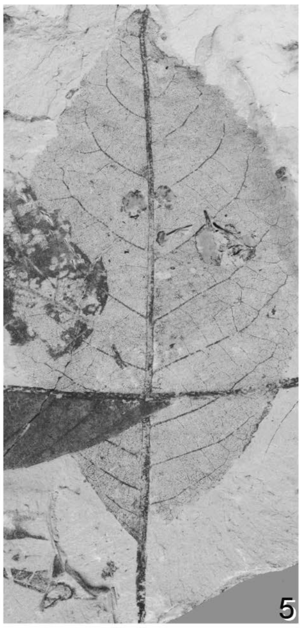
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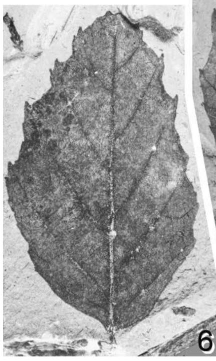
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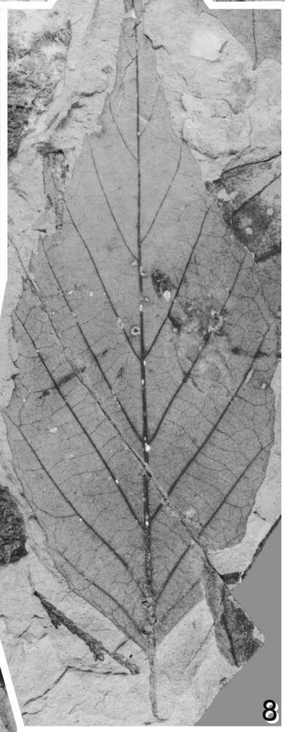
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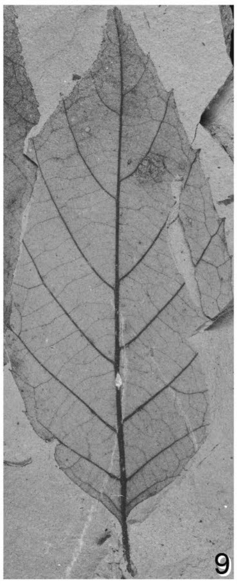
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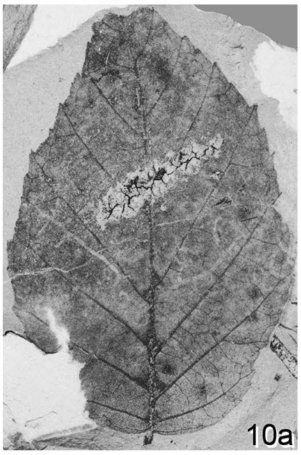
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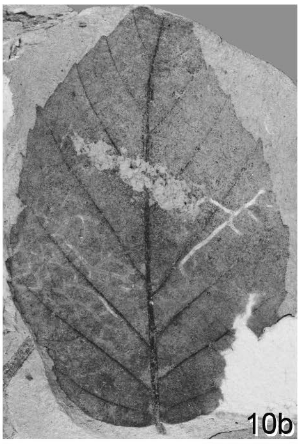
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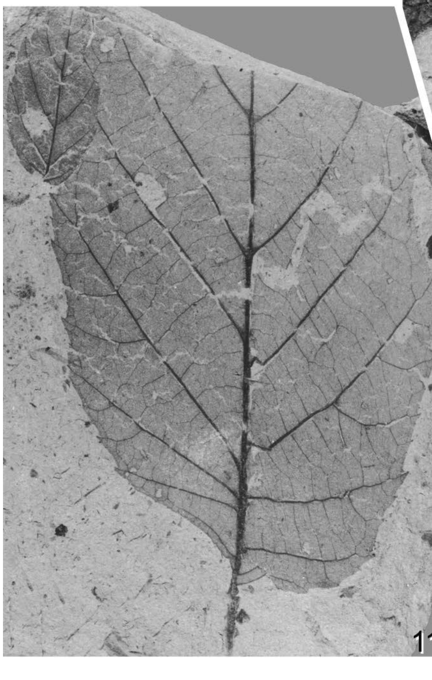
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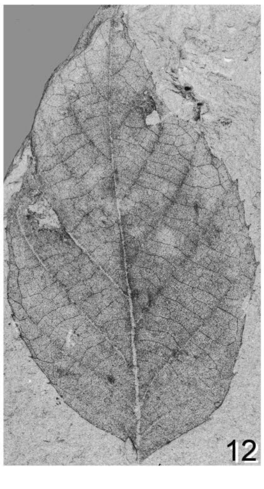
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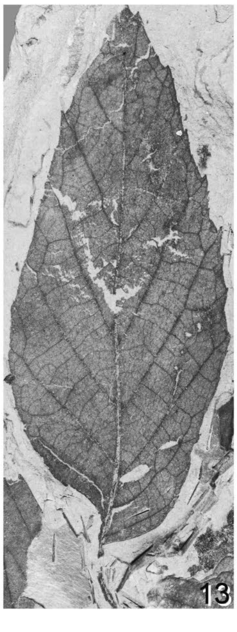
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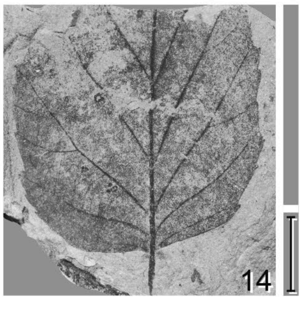

14

lamina appears more coriaceous than in the other alder species from Leoben.

In specimen NHMW 1878/6/3523, A, (Ett. 1520) the marginal serration is damaged, but the venation details are extraordinarily well preserved, which indicates a chartaceous texture and therefore accounts for some uncertainty in the assignment. *Prunus palaeo-cerasus* (Ettingshausen, 1869a: pl. 6, fig. 13, NHMW 1878/6/4455; Ett. 2452, b) probably represents a Betulaceae, but the unusually big teeth argue against an assignment to *A. gaudinii*. *P. palaeo-cerasus* (in sched., IBUG Ett. 6247 + 6294, a) differs by its marginal serration (see *Dicotylophyllum* sp. E). Finally, the specimen figured by Ettingshausen (1888: pl. 7, fig. 18) as fruit remain has not been identified in the studied material.

Based on gross morphology (laminar size, shape and serration) this alder resembles leaves of *Eucommia* Oliv. *A. gaudinii* differs by more densely spaced secondaries and tertiaries.

Based on gross morphology and cuticles, Knobloch and Kvaček (1976) stated closest similarity to the modern *Alnus nitida* (Spach) Endl. from the northwestern Himalaya region. Due to the common co-occurrence of *A. gaudinii* leaves and *A. kefersteinii* (Goepp.) Unger female cones, they may derive from the same fossil-species (Kvaček and Walther, 1998) (see section *A. kefersteinii*).

Alnus gracilis Unger

Fig. 12.6, 12.7

1847 *Alnus gracilis* Unger, p.p.; Unger, p. 116, pl. 33, figs 8, 9.
1888 *Alnus gracilis* Unger, p.p.; Ettingshausen, p. 286, pl. 2, fig. 22.

Material. Moskenberg: NHMW: 1878/6/3549 (Ett. 1546), (*Alnus gracilis*); 1878/6/3551 + 7442 (1548 + 5439), (*A. gracilis*); 1878/6/3684 (1681), (*A. gracilis*); 1878/6/7105 (5102), A; 1878/6/7432 (5429), (*A. gracilis* in sched.); 1878/6/7434 (5431); (*A. gracilis* in sched.); 1878/6/9133 (7130), Pb 5497, (*A. gracilis*), Ettingshausen (1888: pl. 2, fig. 22); 2023/0072/0005 (coll. Hofmann sine no.).

Description. Stalked woody cones in clusters of at least 3 to 4; l × w ~(5.5) 7–11 × 4.5–6 mm, ratio l/w ~(1.2) 1.7–2; cone scales filigree.

Remarks. These cones occur still attached to the stalk and in clusters, indicating that they were embedded near where they were shed. Due to the common co-occurrence with sometimes even mass-occurrences of *Alnus julianiformis* leaves, e.g. Most Basin, northern Bohemia (Kvaček et al., 2004a, b), it is widely accepted that both organs represent a single biological species (see below). The Leoben assemblage includes several fossil-species of alder leaves, but only two types of female cones can be distinguished (see section *A. kefersteinii*). The author therefore refrains from combining leaves and fruits to a single fossil-species. For differences from *A. kefersteinii* see that taxon.

Alnus julianiformis

(Sternberg) Kvaček et Holý

Figs 10.6–10.14, 24.8–9

1823 *Phyllites julianaeformis* Sternberg; Sternberg, p. 37, 39, pl. 36, fig. 2.
1869a *Fagus feroniae* Unger; Ettingshausen, p. 48.
1869a *Populus geinitzii* sp. n., p.p.; Ettingshausen, p. 57, pl. 3, fig. 10, (non fig. 9).
1869a *Maesa stiriaca* sp. n.; Ettingshausen, p. 73, pl. 4, fig. 8.
1869a *Cissus fagifolia* Ettingsh. sp. n., p.p.; Ettingshausen, p. 76, pl. 5, fig. 1.
1882 *Fagus feroniae* Unger; Ettingshausen, p. 99, pl. 17, figs 1, 3, 4, pl. 18, figs 1–6.
(?) 1888 *Betula prisca* Ettingsh., p.p.; Ettingshausen, p. 285, non pl. 2, figs 13, 14.
1888 *Betula kefersteinii* Goepp., p.p.; Ettingshausen, p. 286, non pl. 2, fig. 21.
1888 *Alnus gracilis* Unger, p.p.; Ettingshausen, p. 286, pl. 2 fig. 2 (leaf).
1888 *Fagus feroniae* Unger; Ettingshausen, p. 293.
1888 *Populus geinitzii* Ettingsh., p.p.; Ettingshausen, p. 300.

←

Figure 10. **1–5**. *Alnus gaudinii* (Heer) Erw. Knobloch et Kvaček, **1**. NHMW 1878/6/3515 (Ett. 1512), (*Rhamnus gaudinii*), **2**. NHMW 1878/6/3513 (Ett. 1510), (*R. gaudinii*), **3**. NHMW 1878/6/8590 (Ett. 6587), (*R. gaudinii*), **4**. NHMW 1878/6/3523 (Ett. 1520), B, (*Prunus palaeo-cerasus*), **5**. (?) *Alnus gaudinii* (Heer) Erw. Knobloch et Kvaček, NHMW 1878/6/3523 (Ett. 1520), A, (*P. palaeo-cerasus*), Ettingshausen (1869a: pl. 6, fig. 12, syntype); **6–14**. *Alnus julianiformis* (Sternberg) Kvaček et Holý, **6**. NHMW 1878/6/3713 (Ett. 1710), (*Fagus feroniae*), **7**. NHMW 1878/6/3723 (Ett. 1720) (*F. feroniae*), **8**. NHMW 1878/6/7471 (Ett. 5468), B, (*F. feroniae*), **9**. NHMW 1878/6/3717 (Ett. 1714), Pb 505, (*F. feroniae*), Ettingshausen (1882: pl. 17, fig. 4), **10a**, **b**. NHMW 1878/6/3623 + 7425 (Ett. 1620 + 5422), (*Alnus kefersteinii*); part and counterpart of one leaf, **10a**. (Ett. 1620) showing shade of domatia at the origin of the basal secondaries, while this is not the case in **10b**. (Ett. 5422), **11**. NHMW 1878/6/3530 (Ett. 1527), (*Carya bilinica*), **12**. NHMW 1878/6/3553 (Ett. 1550) (*A. kefersteinii*), **13**. NHMW 1878/6/8373 (Ett. 6370), Pb 2096, (*Cissus fagifolia*), Ettingshausen (1869a: pl. 5, fig. 1, syntype), **14**. NHMW 1878/6/7795 (Ett. 5792), Pb 1984, (*Populus geinitzii*), Ettingshausen (1869a: pl. 3, fig. 10, syntype). For all photographs the scale at bottom right of the figure is 10 mm

1888 *Fraxinus primigenia* Unger, p.p.; Ettingshausen, p. 323.
1888 *Maesa stiriaca* Ettingsh.; Ettingshausen, p. 327.
1888 *Cissus fagifolia* Ettingsh., p.p.; Ettingshausen, p. 352, pl. 8, fig. (?) 14.
1888 *Carya bilinica* Unger, p.p.; Ettingshausen, p. 353.
1894 *Fagus feroniae* Unger, p.p.; Ettingshausen, pl. 1, figs 2–4, non 5, 6–15, 17, 18, pl. 2, figs 1, 3–6, 8, 9, 11, non 13, non 14, 16–18, (?)19, 20–23.
1974 *Alnus julianiformis* (Sternberg) Kvaček et Holý; Kvaček and Holý, p. 368, text-fig. 1, pls I–III, pl. IV, fig. 1.
1999 *Alnus julianiformis* (Sternberg) Kvaček et Holý; Ströbitzer, p. 100, pl. 2, fig. 13, pl. 3, fig. 2, pl. 10, figs 1–3, 6.
2004 *Alnus julianiformis* (Sternberg) Kvaček et Holý; Kovar-Eder et al., p. 59, pl. 3, fig. 6.

Material. Moskenberg: NHMW: 1878/6/3529 + 3530 (Ett. 1526 + 1527), (*Carya bilinica*); 1878/6/3531 (1528), A, (*Alnus kefersteinii* in sched.); 1878/6/3553 (1550), (*A. kefersteinii* in sched.); 1878/6/3554 (1551), (*A. kefersteinii*); 1878/6/3571 (1568), B, Pb 2117; 1878/6/3621 (1618), (*A. kefersteinii* in sched.); 1878/6/3622 + 3652 (1619 + 1649), (*A. kefersteinii* in sched.); 1878/6/3623 + 7425 (1620 + 5422), (*A. kefersteinii*); 1878/6/3649 (1646), B, D, (*A. kefersteinii* in sched.); 1878/6/3660 (1657), Pb 778, (*Fagus feroniae*), Ettingshausen (1882: pl. 18, fig. 4); 1878/6/3665 (1662), B, (*Alnus kefersteinii* in sched.); 1878/6/3673 (1670), (*A. gracilis*); 1878/6/3674 (1671), (*A. gracilis*); 1878/6/3679 (1676), (*A. gracilis*); 1878/6/3685 (1682), (*A. gracilis*); 1878/6/3713 (1710), (*Fagus feroniae* in sched.); 1878/6/3717 + 4033 (1714 + 2030), Pb 505, (*F. feroniae*), Ett. 1714 Ettingshausen (1882: pl. 17, fig. 4); 1878/6/3718 (1715), (*F. feroniae*); 1878/6/3719 (1716), (*F. feroniae* in sched.); 1878/6/3721 (1718), Pb 506, (*F. feroniae*), Ettingshausen (1882: pl. 17, fig. 1); 1878/6/3722 (1719), Pb 2100, (*F. feroniae*), Ettingshausen (1882: pl. 18, fig. 6); 1878/6/3723 (1720) (*F. feroniae* in sched.); 1878/6/3873 + 3874 (1870 + 1871), (*Betula prisca*); 1878/6/3981 (1978); 1878/6/4121 + 8213 (2118 + 6210), (*Maesa stiriaca*), Ett. 6210, Ettingshausen (1869a: pl. 4, fig. 8, holotype); 1878/6/4155 (2152), Pb 1957, (*Fraxinus primigenia*); 1878/6/7410 (5407), (*Betula prisca* in sched.); 1878/6/7424 (5421), A, B, (*Alnus kefersteinii* in sched.); 1878/6/7436 (5433), (*A. gracilis* in sched.); 1878/6/7471 (5468), B, (*Fagus feroniae*); 1878/6/7472 (5469), (*F. feroniae* in sched.); 1878/6/7473 (5470), (*F. feroniae* in sched.); 1878/6/7474 (5471), (*F. feroniae* in sched.); 1878/6/7794 + 7795 (5791 + 5792), Pb 1984, (*Populus geinitzii*), Ettingshausen (1869a: pl. 3, fig. 10, syntype); 1878/6/7797 (5794), B; 1878/6/8373 + 8374 (6370 + 6371), Pb 2096, (*Cissus fagifolia*), Ettingshausen (1869a: pl. 5, fig. 1, syntype); 1878/6/9059 (7056), (*Fagus feroniae*); 1878/6/9060 (7057), (*F. feroniae*); 1878/6/9061 (7058), (*F. feroniae* in sched.); 1878/6/9147 (7144), Pb 1892, (*Betula prisca*). IBUG: Ett. 5807, (*Fagus feroniae*), Ettingshausen (1894: pl. 1, fig. 7); IBUG Ett. 5817, (*F. feroniae*), Ettingshausen (1894: pl. 1, fig. 5); Ett. 5819, (*F. feroniae*), Ettingshausen (1894: pl. 2, fig. 9); Ett. 5823, (*F. feroniae*), Ettingshausen (1894: pl. 2, fig. 1); Ett. 5830, (*F. feroniae*), Ettingshausen (1894: pl. 2, fig. 3); Ett. 5848, (*F. feroniae*), Ettingshausen (1894: pl. 1, fig. 3); Ett. 5856, (*F. feroniae*); Ett. 5867, (*F. feroniae*), Ettingshausen (1894: pl. 1, fig. 18); Ett. 5880, (*F. feroniae*), Ettingshausen (1894: pl. 1, fig. 14); Ett. 5881, (*F. feroniae*), Ettingshausen (1894: pl. 2, fig. 18); Ett. 5894, (*F. feroniae*), Ettingshausen (1894: pl. 1, fig. 6); Ett. 5928, (*F. feroniae*), Ettingshausen (1894: pl. 2, fig. 23); Ett. 5932, (*F. feroniae*), Ettingshausen (1894: pl. 2, fig. 5). Münzenberg: NHMW: 1878/6/4273 (2270), Pb 2171, (*Fagus feroniae*); 1878/6/4274 (2271), (*F. feroniae* in sched.); 1878/6/4275 (2272), Pb 1320, (*F. feroniae*); 1878/6/4280 (2277), Pb 2169, (*Alnus kefersteinii*); 1878/6/4394 (2391), e, Pb 2132, (*Fagus feroniae*); 1878/6/7427 (5424), (*Alnus kefersteinii* in sched.); 1878/6/7476 (5473), (*Fagus feroniae* in sched.); 1871/38/33, (*F. feroniae*). IBUG: Ett. 5811, A, (*F. feroniae*); Ett. 5812 + 5813, (*F. feroniae*), Ettingshausen (1894: pl. 1, fig. 2); Ett. 5824, (*F. feroniae*), Ettingshausen (1894: pl. 1, fig. 13); Ett. 5833, (*F. feroniae*), Ettingshausen (1894: pl. 2, fig. 21); Ett. 5846, (*F. feroniae*); Ett. 5860, (*F. feroniae*), Ettingshausen (1894: pl. 2, fig. 6); Ett. 5870, (*F. feroniae*), Ettingshausen (1894: pl. 1, fig. 12); Ett. 5871, (*F. feroniae*), Ettingshausen (1894: pl. 2, fig. 17); Ett. 5884, (*F. feroniae*), Ettingshausen (1894: pl. 2, fig. 22); Ett. 5888, (*F. feroniae*), Ettingshausen (1894: pl. 2, fig. 20); Ett. 5903, (*F. feroniae*), Ettingshausen (1882: pl. 18, fig. 5); Ett. 5906, (*F. feroniae*), Ettingshausen (1894: pl. 2, fig. 11); Ett. 5925, (*F. feroniae*), Ettingshausen (1894: pl. 1, fig. 10). Seegraben Walpurgis-Schacht: NHMW: 1878/6/4444 (Ett. 2441), (*Fagus feroniae* in sched.); 1878/6/4462 (2459), Pb 2333, (*Betula prisca*). IBUG: Ett. 5828 + 5829, (*Fagus feroniae*), Ettingshausen (1894: pl. 2, fig. 4); Ett.

5834, (*F. feroniae*), Ettingshausen (1894: pl. 1, fig. 17); Ett. 5843, (*F. feroniae*), Ettingshausen (1894: pl. 2, fig. 8); Ett. 5849, (*F. feroniae*), Ettingshausen (1894: pl. 1, fig. 8); Ett. 5853, (*F. feroniae*); Ett. 5657, (*Alnus kefersteinii*).

Description. Petiolate leaves; petiole up to 18 mm long, slender, straight to slightly curved; laminar shape ovate to elliptic, l × w = (27) 45–78 (86) × (12) 23–38 (42) mm, ratio l/w = (1.5) 1.8–2.6 (3.2), mostly around 2; base angle wide acute to obtuse, base shape moderately convex to sometimes nearly truncate, usually symmetrical, sometimes more or less asymmetrical; apex angle acute, apex shape almost straight to acuminate; margin (double) serrate, teeth from almost equal in size to differentiated into bigger and smaller ones (1° and 2° order); distal flank short, straight, weakly convex or weakly concave, proximal flank straight to slightly convex, sinus angular, apex acute to rounded; midvein slender, mostly straight, tapering along length; secondaries craspedodromous in 7–8 pairs, positioned suboppositely to alternate, lowermost pair usually semicraspedodromous, weaker, running along margin; secondaries arising near base under wide (to moderate) angle, higher up usually at moderate angle; angle further decreasing towards leaf apex; in basal part of lamina commonly dark patches in axils (? tufts) between midvein and secondaries; course of secondaries straight to slightly curved, running into 1° teeth; in some specimens near base of lamina secondaries initially somewhat approaching midvein; secondaries only occasionally forking near margin giving rise to exmedial branches (minor secondaries); 2° teeth served by veinlets arising exmedially from secondaries or from tertiaries and higher-order loops, respectively, more rarely served by minor secondaries; tertiaries (forked-)precurrent, more or less sinuate, at (wide) obtuse angle towards midvein; marginal tertiaries often distinct, sending veinlets into 2° teeth; 4° veins also (forked-)percurrent in larger leaves, otherwise reticulate; higher-order veins polygonal reticulate; areoles well developed; ultimate veinlets branched.

Remarks. Leaves of *Alnus julianiformis* are among the most common in Leoben. Their variability is wide, including leaves with characteristic shape, venation and minutely toothed margin (Fig. 10.10, 10.12), as well as leaves with rather big first-order teeth (Fig. 10.6) resembling for example *Quercus furcinervis* Rossm. from Bilina (Ettingshausen 1866: pl. 16, fig. 12), which Knobloch and Kvaček (1976) already regarded synonymous with *A. julianiformis*. The assignment to *Populus* of specimen NHMW 1878/6/7794 + 7795 (Ett. 5791 + 5792, Fig. 7.14), which represents part of the type material of *P. geinitzii* (Ettingshausen 1869a, 1888), must be rejected because in *Populus* the secondaries are semicraspedodromous to semibrochidodromous and the marginal serration is quite different. The craspedodromous, somewhat irregularly spaced secondaries, their course and their branches terminating in tooth apices account for the assignment to Betulaceae; the almost truncate base is observed in several specimens of *A. julianiformis* in the Leoben material. Ettingshausen (1888) even recognised the similarity of leaves assigned by him to *Cissus*. The specimen figured in Ettingshausen (1869a: pl. 5, fig.1) must definitely be assigned to *A. julianiformis* instead, while the systematic affinity of the specimen figured by that author (1888: pl. 8, fig. 14) remains ambiguous.

The wide variability of *A. julianiformis* helps explain the diverse assignments by Ettingshausen (1869a, 1888). Note, the heading *"Betula kefersteini"* (Ettingshausen, 1888: p. 286) was probably a printing error because, in the text for this taxon, Ettingshausen referred to *Alnus*.

In modern Betulaceae and especially in *Alnus*, tufts are common in vein axils. In the Leoben material of *A. julianiformis*, dark patches in the axils between midvein and secondaries occur frequently. Ettingshausen (1894) discussed their occurrence, finally arriving at the conclusion that they constitute artefacts due to fossilisation rather than domatia (tufts). The recent findings of domatia on leaf compressions of *A. julianiformis* (Worobiec and Szynkiewicz, 2007) and the fact that some specimens from Leoben are preserved as part and counterpart and show dark patches only on one of these two parts, point more towards domatia than to artefacts in the Leoben material (NHMW 1878/6/3623 + 7425, Ett. 1620 + 5422, Fig. 10.10a, b; NHMW 1878/6/3622 + 3652 (Ett. 1619 + 1649)), (see also paragraph Taphonomy).

A. julianiformis is well known from many Early Miocene to Pliocene sites, e.g. Bilina, northern Bohemia (Kvaček and Holý, 1974); Mydlovary Formation, South Bohemia

(Knobloch and Kvaček, 1976); Lower Rhine Embayment, Wackersdorf, Germany (Ferguson, 1971; Knobloch and Kvaček, 1976); Søby flora, Denmark (Christensen, 1976); Sośnica, Ruszow, Bełchatów, Poland (Hummel, 1991; Zastawniak and Walther, 1998; Worobiec and Szynkiewicz, 2007). Nonetheless, the issue of the number of fossil-species included in the wide variability is not satisfactorily resolved (Knobloch and Kvaček, 1976, 1996). Despite the richness of alder leaves studied from Leoben, a further differentiation of fossil-species was also not possible.

Kvaček and Holý (1974) stated gross-morphological similarity of *A. julianiformis* to *A. japonica* (Thunb.) Steud., and cuticular similarity to *A. trabeculosa* Hand.-Mazz. *A. japonica* thrives from southern Russian Far East to eastern China, Korea, Japan and Taiwan whereas *A. trabeculosa* occurs primarily in temperate regions of China and Japan (POWO, accessed June, 2022).

Alnus kefersteinii (Goepp.) Unger

Fig. 12.8

1836 *Alnites kefersteinii* Goepp.; Goeppert, p. 364, pl. 41, figs 1–19.
1847 *Alnus kefersteinii* (Goepp.) Unger; Unger, p. 115, pl. 33, figs 1–3.
1888 *Betula kefersteinii* (Goepp.) Heer, p.p.; Ettingshausen, p. 286.

Material. Moskenberg: NHMW: 1878/6/3555 (Ett. 1552), (*Alnus kefersteinii*); 1878/6/7423 (5420), (*A. kefersteinii* in sched.).

Description. Isolated woody female cones, l × w = 17 × 14 and 18 × 15 mm, ratio l/w = 1.2; stalk absent in one specimen, fragmentarily preserved in the other, ~3 mm long.

Remarks. Although more strongly lignified and more robust than *A. gracilis*, *A. kefersteinii* is only preserved as single cones in the Leoben assemblage. *A. kefersteinii* differs from *A. gracilis* by bigger size and lower length/width ratio. Kvaček and Walther (1998) regarded *A. kefersteinii* cones to derive from the same woody species as *A. gaudinii* leaves which was later supported by the occurrences in Seifhennersdorf (Walther and Kvaček, 2007). In the Leoben assemblage an unambiguous assignment of fruiting cones to a leaf taxon is hampered by the fact that five fossil-species of alder leaves must be distinguished (see also paragraph *A. gracilis*).

Alnus menzelii Raniecka-Bobrowska

Figs 11.1–11.5, 24.10

1888 *Xylomites alni* Ettingsh. on *Alnus gracilis* Unger; Ettingshausen, p. 268, pl. 1, fig. 14.
1888 *Carpinus heeri* Ettingsh., p.p.; Ettingshausen, p. 294, (non pl. 3, figs 7, 8).
1888 *Ulmus bronnii* Unger, p.p.; Ettingshausen, p. 295.
1954 *Alnus menzelii* Raniecka-Bobrowska; Raniecka-Bobrowska, p. 11, fig. 4, fot. 11–13.
2001 *Alnus menzelii* Raniecka-Bobrowska; Kovar-Eder and Wójcicki, p. 224, pl. 1, figs 14–18, pl. 4, figs 2–8, textfig. 3/7–9.
2007 *Alnus menzelii* Raniecka-Bobrowska; Worobiec and Szynkiewicz, p. 37, pl. 3, figs 5, 6, pl. 4, figs 1–4, pl. 5, figs 2–4.

Material. Moskenberg: NHMW: 1878/6/3507 (Ett. 1504), (*Ulmus bronnii*); 1878/6/3697 + 3832 (1694, A + 1829, a), Pb 1898, (*Carpinus heeri*); 1878/6/4085 (2082), C; 1878/6/6573 (4570), Pb 2148, (*Xylomites alni* on *Alnus gracilis*), Ettingshausen (1888: pl. 1, fig. 14); 1878/6/7450 (5447), (*Carpinus heeri*). IBUG: Ett. 5967 + 5968, (*Ulmus bronnii* in sched.).

Description. Simple leaves; petiole up to 22 mm long; laminar shape ovate to elliptic, l × w ~60–100 × 38–66 mm, ratio l/w ~1.5–1.8; base angle wide obtuse, base shape more or less cordate, symmetrical to somewhat asymmetrical; apex not preserved; margin distinctly, densely, regularly double serrate, tooth height ~1 mm, 2 to several 2° teeth between two adjacent 1° ones, distal and proximal flanks rather variable, convex, acuminate, straight or concave; sinus angular, apex acute; midvein straight to moderately bent; secondaries simple craspedodromous, regularly and moderately to densely spaced, almost straight, near base of lamina secondaries sometimes shortly approximating midvein (angle of origin narrow) before turning towards margin; otherwise angle of origin moderate; marginally secondaries producing one to several indistinct exmedial branches (resembling 3° veins); tertiaries (forked-)percurrent, distinctly more delicate than 2° veins, slightly bent to slightly sinuate, densely spaced, 6–8 per cm; angle of tertiaries to midvein wide oblique; exmedial branches of 2° veins and veinlets arising from marginal tertiaries serving 2° teeth.

Remarks. Only few and fragmentarily preserved specimens are available. The cordate base and the innervation of 2° teeth by indistinct exmedial branches of secondaries, as well as veinlets arising from marginal tertiaries point towards *A. menzelii*. Unfortunately, the areoles and ultimate veinlets are not visible: their presence could support this assignment because in *Alnus menzelii* the ultimate veinlets are (multiply) branched. In contrast, in *Carpinus grandis* the areoles are characterised by lacking or unbranched to one-branched veinlets (Worobiec and Szynkiewicz, 2007). *Alnus menzelii* differs from *Ulmus* (?) *prisca* by the cordate leaf base and differently sized 1° and 2° teeth. For differences from "*Corylus*" *palaeoavellana* see respective paragraph.

According to Raniecka-Bobrowska (1954) nearest living relatives of *A. menzelii* are *A. subcordata* C.A. Mey., and *A. serrulata* (Aiton) Willd. The former grows on river banks in the Caucasus region and Iran and the latter is a shrub occurring in east Canada and eastern to central U.S.A. (POWO, accessed May, 2022).

Alnus milleri
(Ettingsh.) Kovar-Eder comb. nov.

PFNR Unique Identifier: PFN003330

Figs 11.6–11.13, 24.11

1869a *Tilia milleri* Ettingsh. sp. n.; Ettingshausen, p. 79, pl. 5, fig. 2.
1869a *Rhamnus alnifolius* Ettingsh. sp. n.; Ettingshausen, p. 88, pl. 5, fig. 15.
1888 *Dothidea dryadum* Ettingsh. sp. n. on *Betula dryadum*; Ettingshausen, p. 267, pl. 1, fig. 9 (leaf).
1888 *Betula dryadum* Brongn., p.p.; Ettingshausen. p. 285.
1888 *Alnus gracilis* Unger, p.p.; Ettingshausen, p. 286.
1888 *Tilia milleri* Ettingsh., p.p.; Ettingshausen, p. 337.
1888 *Rhamnus alnifolius* Ettingsh., p.p.; Ettingshausen, p. 350, non pl. 9, fig. 10.
1888 *Spiraea osiris* Ettingsh., p.p.; Ettingshausen, p. 360.

Lectotype designated here. NHMW 1878/6/3572 (Ett. 1569), Pb 2110, *Tilia milleri* Ettingsh. sp. n. (Ettingshausen, 1869a: p. 79, pl. 5, fig. 2) refigured on Figs 11.6, 24.11.

Paratypes. NHMW 1878/6/3579 + 3899 (1756 + 1896), Pb 2116 + Pb 2115, (*T. milleri*), figured on Fig. 11.7; NHMW 1878/6/4174 + 4189 (2171 + 2186), (*Tilia milleri*), figured on Fig. 11.8.

Basionym. *Tilia milleri* Ettingsh., Ettingshausen (1869a: p. 79).

Derivatio nominis. Ettingshausen (1869a) devoted *Tilia milleri* to Prof. Albert v. Miller, who supported collecting at Leoben. Both men were friends.

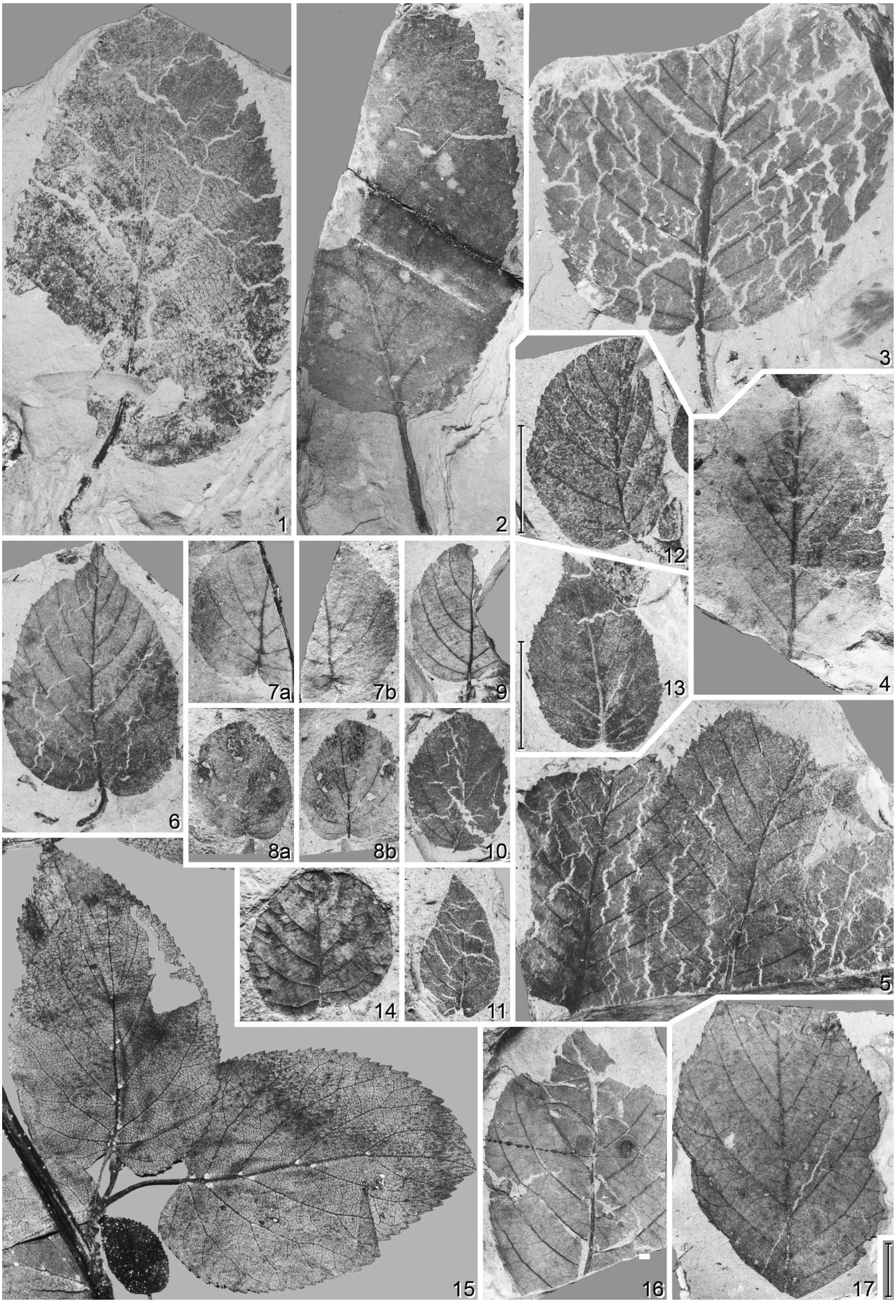
Locus typicus. Historical locality Moskenberg near Leoben, Leoben Basin, Styria (Ettingshausen, 1869a).

Stratum typicum. Shales ~8.2 m above the coal seam (Ettingshausen, 1869a), 14.9 ± 0.7 Ma (a tuff layer near the base of the shales overlying the coal seam, Sachsenhofer et al., 2010).

Material. Moskenberg: NHMW: 1878/6/3536 (Ett. 1533), B; 1878/6/3550 (1547), (*Alnus gracilis*); 2023/0072/0006 (1878/6/XXXX); 1878/6/3571 (1568), A, Pb 2117, (*Tilia milleri*); 1878/6/3572 (1569), Pb 2110, (*T. milleri*), Ettingshausen (1869a: pl. 5, fig. 2, syntype), + GBA: 2024/0001/0001; 1878/6/3579 + 3899 (1756 + 1896), Pb 2116 + Pb 2115, (*T. milleri*); 1878/6/4085 (2082), b, (*Betula dryadum* in sched.). 1878/6/4174 + 4189 (2171 + 2186), (*Tilia milleri*), note that Ettingshausen (1888: p. 267) reads *Dothidea dryadum* on *Betula dryadum* for no. Ett. 2171; however, this number is listed for *Tilia milleri* but not for *B. dryadum*. 1878/6/4189 (2186), Pb 2111, (*T. milleri*); 1878/6/4201 (Ett. 2198), Pb 2011, (*Rhamnus alnifolius*), Ettingshausen (1869a: pl. 5, fig. 15, holotype); 1878/6/4215 (2212), (*Betula dryadum*); 1878/6/7438 (5435), (*Alnus gracilis* in sched.); 1878/6/8765 (6762), Pb 2133, (*Spiraea osiris*). IBUG: Ett. 6164 + 6165, (*Tilia milleri*). Münzenberg: NHMW: 1878/6/4394 (Ett. 2391), d, Pb 2132, (*Betula dryadum* in sched.).

Emended diagnosis. Petiolate small-sized leaves; lamina up to 40 mm long, broad ovate–elliptic to orbiculate, more or less symmetrical, ratio l/w ~1–1.5; base mostly cordate; apex shape acute to acuminate; margin finely serrate, teeth narrow, (bluntly) acute, partly probably glanduliferous, almost equally sized or slightly bigger above secondary veins; up to 5 teeth in between teeth above secondaries; up to 8 pairs of secondaries, (semi-) craspedodromous, almost straight to moderately curved, diverging towards margin, one to several exmedial veinlets serving marginal teeth or joining in loops giving rise to veinlets running into teeth; tertiaries (forked-)percurrent; tufts at origin of secondaries in basal part of lamina.

Description. Petiolate small leaves, petiole curved, up to 8 mm long (preserved in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holotype NHMW 1878/6/3572, Ett. 1569, Pb 2110); laminar shape slightly broad ovate, broad elliptic to orbiculate, more or less symmetrical; l × w ~19–40 × 15–27 (33) mm, ratio l/w ~1–1.5; base angle wide obtuse, base shape mostly cordate, rarely convex, mainly symmetrical; apex angle (wide) acute to obtuse, apex shape convex to acuminate, utmost apex often blunt; margin distinctly, finely and regularly serrate, teeth tiny, narrow, (bluntly) acute, height < 1 mm, directed towards leaf apex, partly probably glandular; up to 5 teeth in between teeth above secondaries; teeth above secondaries sometimes slightly bigger than teeth in between; midvein straight, secondaries (semi-) craspedodromous, in up to 8 pairs, subopposite near base, alternate in upper part of lamina; basalmost first two pairs of secondaries often very closely spaced, arising at wide angle; towards apex angle of origin of secondaries (strongly) decreasing; additionally a pair of fine veins running along margin of cordate base; spacing of 2° veins wide in central part of lamina; course straight to moderately curved, somewhat diverging towards margin, exmedially giving rise to one to several veinlets either running into marginal teeth or joining in loops; such loops giving again rise to higher-order veins which end in teeth; tertiaries (forked-) percurrent, densely spaced, angle towards midvein wide obtuse, angle decreasing towards apex; quaternaries and higher-order veins reticulate; tufts occasionally indicated at the origin of secondaries in basal part of lamina.

Remarks. These leaves are quite distinct from all other Betulaceae morphotypes by their usually cordate base and small size. Ettingshausen's assignments of these specimens preferably to Betulaceae (different genera and species) and linden indicate his ambivalence. That author even assigned the leaf NHMW 1878/6/4174 (Ett. 2171) to *Betula dryadum* Brongn. infected by a fungus (*Dothidea dryadum* Ettingsh.) (Ettingshausen, 1888: p. 267), while he listed this specimen for *Tilia milleri* (Ettingshausen, 1888: p. 337) but not among the material for *B. dryadum*.

Figures 11.7a, b and 11.8a, b represent specimens preserved with part and counterpart. However, only Figs 11.7a and 11.8a show dark spots in the axils of the midvein and secondaries while the counterparts do not. These patches are likely remains of tufts visible only on the impression of the abaxial leaf surface (see also section *Alnus julianiformis*).

In fact, the here described leaves resemble those of *Tilia* by general laminar shape, cordate base, tufts in vein axils and occasionally gland-tipped teeth. Linden leaves differ, however, by bigger size, oblique base and asymmetrical laminar shape, and especially by actinodromous venation. The assignment to the Betulaceae is based especially on the (semi-) craspedodromous venation and serration, in which veinlets arising from tertiaries in front of the margin run into the teeth.

Alnus cycladum Unger from Kimi on Evia, Greece (Unger, 1867) was based on female strobili and leaves. The laminar shape of the leaves resembles *A. milleri*, but the leaves are larger, the leaf base is less distinctly cordate, the serration is coarser, the midvein is sometimes sinuate and the lamina appears uneven, structured by the venation, especially the tertiaries. This latter feature is characteristic because it is obvious in material from the type locality Kimi studied at the NHMW (Fig. 11.14), and such specimens have also been reported from Güvem and Soma (Turkey) (Denk et al.,

◄

Figure 11. 1–5. *Alnus menzelii* Raniecka-Bobrowska, **1**. NHMW 1878/6/3507 (Ett. 1504), (*Ulmus bronnii*), **2**. NHMW 1878/6/3832 (Ett. 1829), a, Pb 1898, (*Carpinus heeri*), **3**. IBUG Ett. 5968, (*Ulmus bronnii*), **4**. NHMW 1878/6/6573 (Ett. 4570), Pb 2148, (*Xylomites alni* on *Alnus gracilis*), Ettingshausen (1888: pl. 1, fig. 14), **5**. NHMW 1878/6/7450 (Ett. 5447), (*Carpinus heeri*); **6–13**. *Alnus milleri* (Ettingsh.) Kovar-Eder comb. nov., **6**. NHMW 1878/6/3572 (Ett. 1569), Pb 2110, lectotype, (*Tilia milleri*), Ettingshausen (1869a: pl. 5, fig. 2, syntype), **7a**, **b**. NHMW 1878/6/3579 + 3899 (Ett. 1756 + 1896), Pb 2116 + Pb 2115, paratype, (*T. milleri*), part and counterpart, **7a**. (Ett. 1756) with distinct shades of domatia in axils between midvein and secondaries, **7b**. (Ett. 1896), **8a**, **b**. NHMW 1878/6/4174 + 4189 (Ett. 2171 + 2186), paratype, (*T. milleri*), part and counterpart; **8a**. (Ett. 2186) shades of domatia in axils between midvein and secondaries near base visible, **8b**. (Ett. 2171), **9**. NHMW 1878/6/4201 (Ett. 2198), Pb 2011, (*Rhamnus alnifolius*), Ettingshausen (1869a: pl. 5, fig. 15, holotype), **10**. NHMW 2023/0072/0006, **11**. NHMW 1878/6/4215 (Ett. 2212), (*Betula dryadum*), **12**. NHMW 1878/6/8765 (Ett. 6762), Pb 2133, (*Spiraea osiris*), **13**. NHMW 1878/6/7438 (Ett. 5435), (*Alnus gracilis*); **14**. *Alnus cycladum* Unger, Kimi, Greece, NHMW; the lamina appears uneven, structured by the venation, especially the tertiaries; **15**. *Alnus cordata* Desf., Stable identifier: https://pi.jacq.org/PI031352; specimen PI 031352, stored under taxonname *Alnus cordata* (Loisel.) Duby; Note tufts (domatia) in the axils between midvein and secondaries and glandular teeth; **16**, **17**. *Alnus* cf. *oberdorfensis* Kovar-Eder, **16**. NHMW 1878/6/8591 (Ett. 6588), (*Rhamnus gaudinii*), **17**. NHMW 1878/6/3658 (Ett. 1655), (*Alnus kefersteinii*). For all photographs the scale at bottom right of the figure is 10 mm except for photographs with embedded scale in which the scale is also 10 mm

2017b, 2022). Furthermore, the records from Turkey differ also from the Leoben material by a coarser serration and different tooth shape. From Parschlug Betulaceae gen. et sp. indet. (Kovar-Eder et al., 2022: pl. 2, fig. 6) resembles by leaf shape, size and cordate base but differs by distinctly larger teeth.

Similar leaf shape with distinctly cordate base occurs today in *Betula* and *Alnus*. In *B. maximowicziana* Reg., which is native to Japan, the leaves are cordate but differ from the fossils by a distinctly larger lamina and by a sharply double-serrate margin with 1° teeth distinctly bigger than 2° ones (“*Betula maximowicziana”* on website Trees and Shrubs Online, accessed January, 2023). Among alders, *Alnus cordata* Desf., native to southern Italy and Corsica, is closely similar based on leaf shape and cordate base, serration and tufts in the axils between midvein and secondaries. Also, the leaf size of this species is relatively small compared to other alders, albeit somewhat bigger (35–100 mm long) than in *A. milleri* (Baxter and McAllister, 2021). Although gland-tipped teeth are known to occur in *Alnus*, this is not explicitly characteristic of *A. cordata*. Herbarium material shows, however, such teeth (Fig. 11.15). Based on molecular phylogeny, *A. cordata* is closely related to *A. subcordata* C.A. Mey. and *A. orientalis* Decne (Colagar et al., 2016). The former is native to Hyrcanian forests, the latter occurs in the eastern Mediterranean region. The leaves of both species differ considerably from the fossils by both laminar and base shape, as well as larger size, and *A. orientalis* differs furthermore by its irregular coarse serration.

Alnus cordata fossilis and *A. subcordata fossilis* from Kodor (Kolakovskii, 1964) differ from the leaves described here by bigger size and different shape.

Alnus aff. ***cecropiifolia*** (Ettingsh.) Berger

Figs 12.1, 12.2, 24.12

- (?) 1851 *Artocarpidium cecropiaefolium* Ettingsh. sp. n.; Ettingshausen, p. 15, pl. 2, figs 3, 4.
- (?) 1867 *Carpinus grandis* Unger; Stur, p. 157, pl. 4, fig. 3.
- 1888 *Alnus kefersteinii* Goepp., p.p.; Ettingshausen, p. 286, non pl. 2, fig. 21.
- 1888 *Quercus pseudo-alnus* Ettingsh., p.p.; Ettingshausen, p. 290.
- 1888 *Quercus charpentieri* Heer; Ettingshausen, p. 290.
- 1888 *Corylus mac quarrii* Forb., p.p.; Ettingshausen, p. 293.
- 1888 *Artocarpidium serratifolium* Ettingsh., p.p.; Ettingshausen, p. 299.
- 1888 *Diospyros brachysepala* A. Braun, p.p.; Ettingshausen, p. 329.
- 1888 *Juglans undulata* Ettingsh., p.p.; Ettingshausen, p. 353.
- (?) 1955 *Alnus cecropiifolia* (Ettingsh.) Berger comb. nov.; Berger, p. 87, fig. 30.

Material. Moskenberg: NHMW: 1878/6/3552 (Ett. 1549), (*Alnus kefersteinii* in sched.); 1878/6/3624 (1621), (*A. kefersteinii* in sched.); 1878/6/3659 (1656), (*A. kefersteinii* in sched.); 1878/6/3662 + 3770 (1659 + 1767), (*Quercus charpentieri*); 1878/6/3666 (1663), (*Alnus kefersteinii* in sched.); 1878/6/3667 (1664), (*A. kefersteinii* in sched.); 1878/6/3915 (1912), (*Diospyros brachysepala*); 1878/6/3985 + 3986 (1982 + 1983), Pb 2135, (*Juglans undulata*); 1878/6/4006 (2003), (*Corylus mac quarrii*); 1878/6/4094 (2091), Pb 1928, (*Artocarpidium serratifolium*); 1878/6/4100 (2097), (*Quercus pseudo-alnus*); 1878/6/9131 (7128), A, (*Alnus kefersteinii*). Münzenberg: NHMW: 1878/6/7426 (Ett. 5423), (*Alnus kefersteinii* in sched.). IBUG: Ett. 5951, (*Corylus palaeo-avellana* in sched.).

Description. Long-petiolate, large, simple leaves; petiole straight to slightly bent, up to 23 mm long; laminar shape elliptic to ovate, l × w ~75–100 (110) × (35) 45–60 (80) mm, ratio l/w ~(1.3) 1.5–1.8; base angle (wide) obtuse or acute, base shape convex to rounded, at lowermost base usually concave/cuneate to nearly truncate; apex not preserved; margin double serrate, 1° teeth triangular, distinctly bigger than 2° ones, distinctly directed towards leaf apex, up to at least three 2° teeth in between two adjacent 1° ones, sinus and apex acute, distal flank straight to convex, proximal flank straight, concave or convex; midvein more or less straight, slender; secondaries (semi-)craspedodromous, widely spaced, subopposite to alternate, lowermost pair weak, short, running parallel to leaf margin; following one or two pairs of secondaries usually approaching midvein near their origin, then turning towards margin, secondaries curved, running into apices of 1° teeth (craspedodromous) or veinlets arising from looping secondaries or tertiaries serving 1° teeth (semicraspedodromous); near base, secondaries arising at narrow to moderate angle in case of acute base angle and cuneate base shape, arising at wide angle in case of obtuse/rounded to truncate base; further secondaries arising at moderate angle; tertiaries (forked-) percurrent, sinuate, 3–5 per cm; marginalmost tertiaries distinct, veinlets arising from top of sinus and higher-order veinlets serving 2° teeth; quaternaries reticulate; in some specimens dark patches at origin of secondaries in basal part of lamina.

Remarks. Ettingshausen preferably assigned these leaves to *Alnus kefersteinii*. For nomenclatural reasons this binomen is reserved for female cones (see respective section). The preservation of most leaves as fragments hampers an unambiguous assignment. The preservational state is likely related to the large size of the blades but may also indicate mechanical stress due to transport (see paragraph Taphonomy). The vein pattern near the margin – with secondaries or veinlets arising from loops serving big teeth, while teeth in between are commonly supported by veinlets originating at the top of the sinus of distinct, marginalmost tertiaries – accounts for the generic assignment to *Alnus* (compare Czeczott, 1934). Differential traits from other alders from the Leoben assemblage are the larger size, lower length/width ratio and the marginal serration with 1° teeth distinctly bigger than 2° ones. The dark patches in the axils between midvein and secondaries indicate tufts on the lower leaf surface, which is supported by a specimen preserved as part and counterpart showing patches on NHMW 1878/6/3985 (Ett. 1982), while its counterpart NHMW 1878/6/3986 (Ett. 1983) does not (compare paragraphs *Alnus julianiformis* and *A. milleri*). The lack of transitional leaf forms towards *A. julianiformis* rules out that the here described specimens represent aberrant foliage of that fossil-species.

Leaf size and shape of the Leoben specimens coincide with that of *A. cecropiifolia* (Berger, 1955; Knobloch, 1969). The leaf base preserved in few specimens is, however, truncate to decurrent at the utmost base, the margin is distinctly double serrate and the secondary veins are less dense than in *A. cecropiifolia*. With respect to the leaf base and number of secondaries, the Leoben specimens closely resemble the description of *A. cecropiifolia* from Sośnica, Poland (Zastawniak and Walther, 1998). *A. cecropiifolia* is more common in the Late Miocene, often occurring in large quantities in species-poor assemblages, associated with *Glyptostrobus europaeus* and *Byttneriophyllum tiliifolium* (A. Braun) Knobloch et Kvaček, e.g. Dozmat (Hably and Kovar-Eder, 1996), Poštorná, Mähren (Knobloch, 1969), contrasting the occurrence in the Leoben assemblage.

Alnus cf. ***oberdorfensis***
Kovar-Eder

Figs 11.16, 11.17, 24.13

1888 *Betula prisca* Ettingsh., p.p.; Ettingshausen, p. 285.

1888 *Alnus kefersteinii* Goepp., p.p.; Ettingshausen, p. 286, pl. 2, fig. 21.

1888 *Alnus gracilis* Unger, p.p.; Ettingshausen, p. 286.

1888 *Rhamnus gaudinii* Heer, p.p.; Ettingshausen, p. 349.

cf. 2001 *Alnus oberdorfensis* Kovar-Eder sp. n.; Kovar-Eder and Meller, p. 75, pl. 1, figs 2–9, pl. 3, fig. 14, pl. 4, figs 1–7.

Material. Moskenberg: NHMW: 1878/6/3548 (Ett. 1545), (*Alnus gracilis*); 1878/6/3656 (1653), (*A. kefersteinii* in sched.); 1878/6/3658 (1655), (*A. kefersteinii* in sched.); 1878/6/3665 (1662), A, (*A. kefersteinii* in sched.); 1878/6/3951 (1948), (*Betula prisca*); 1878/6/8591 (6588), (*Rhamnus gaudinii*).

Description. Simple leaves; petiole not preserved; lamina shape elliptic, slightly ovate to slightly obovate; l × w ~41–68 × 26–43 mm, ratio l/w ~1.5–1.7; base angle obtuse, base shape mostly somewhat convex; apex angle acute, apex shape incomplete, (?) straight; margin double serrate, teeth narrow, height mostly up to 1 mm, rarely slightly bigger, 1° teeth only slightly bigger than 2° ones; up to 4 teeth in between 1° teeth; distal and proximal flanks variable, sinus angular, tooth apex (bluntly) acute, occasionally (?) glandulous; midvein straight, slender; secondaries (semi-) craspedodromous; secondaries regularly, moderately, alternate to suboppositely spaced, slightly curved, somewhat diverging towards margin, occasionally forking in marginal area, either looping or directly running into 1° teeth, near base angle of origin wide to moderate, angle narrowing towards apex, angle narrow apically; (?) tufts in axils of midvein and secondaries especially in basal part of lamina; tertiaries percurrent to more rarely forked-percurrent, sinuate, 4–5 per cm, angle to midvein obtuse; marginal tertiaries or higher-order loops serving 2° teeth; quaternaries polygonate reticulate; higher-order veins indistinct, reticulate.

Remarks. These leaves differ from most alder leaves from Leoben by rather regular, small and densely spaced teeth. First-order teeth resemble 2° ones in size or are only slightly bigger. Grossmorphologically, very similar are *Alnus oberdorfensis* (Kovar-Eder and Meller, 2001), *A. rostaniana* Saporta (Mai and Walther, 1991) and *A. adscendens* (Goepp.) Zastawniak et Walther in Zastawniak et al. (Zastawniak and Walther, 1998), which were typified both based on gross morphology and cuticles. Due to the lack of cuticles in the Leoben material the comparison remains restricted to gross morphology. No tufts have been reported from any of these taxa, which may reflect differences in preservation. Comparing laminar size, the Leoben material is most similar to *A. oberdorfensis*.

***Alnus* sp.** – leaves

Fig. 12.3–12.5

1869a *Spiraea acherontica* Ettingsh. sp. n.; Ettingshausen, p. 93, pl. 6, fig. 10.
1888 *Spiraea acherontica* Ettingsh.; Ettingshausen, p. 360.
1888 *Spiraea osiris* Ettingsh., p.p.; Ettingshausen, p. 360.
1888 *Rhamnus alnifolius* Ettingsh., p.p.; Ettingshausen, p. 350, pl. 9, fig. 10.

Material. Moskenberg: NHMW: 1878/6/4080 (Ett. 2077), Pb 2012, (*Rhamnus alnifolius*); Ettingshausen (1888: pl. 9, fig. 10); 1878/6/8762 (6759), Pb 2094, (*Spiraea acherontica*), Ettingshausen (1869a: pl. 6, fig. 10, holotype); 1878/6/8763 (6760), Pb 2074, (*Spiraea osiris*). Münzenberg: NHMW: 1878/6/4390 + 8766 (Ett. 2387 + 6763), Pb 2264 + Pb 2262, (*S. osiris*); 1878/6/4392, (2389), a, (*S. osiris*); 1878/6/8767 (6764), Pb 2265, (*S. osiris*).

Description. Leaves small, petiole (?) short; lamina elliptic to slightly obovate, l × w ~11–20 × 8–15 mm, ratio l/w consistantly 1.3–1.4; base somewhat asymmetrical, base shape convex to almost straight, base angle ~90°; apex incomplete, angle obtuse, shape slightly convex; margin double serrate, teeth very tiny, sinus (?) angular, apex bluntly acute, partly (?) glandular; midvein straight, thick, secondaries craspedodromous to (?) semicraspedodromous, widely spaced, arising at acute to moderate angles, ascending steeply, course straight to slightly curved, somewhat diverging, serving 1° teeth; secondaries arising near base, giving rise to exmedial veins that run into teeth between 1° ones; tertiaries percurrent, curved, angle towards midvein obtuse; in apical part of leaf, veinlets arising from marginalmost tertiaries serving teeth between 1° ones.

Remarks. Characteristic features of these leaves are the small size with somewhat asymmetrical shape, the serration, the low number of steeply ascending secondaries, percurrent tertiaries and the marginal venation serving the teeth. The assignment to *Spiraea* (Ettingshausen, 1869a, 1888) must be rejected because in *Spiraea* the tertiaries are reticulate and both tooth shape as well as the vein fabric serving the teeth are different. The asymmetrical shape and the probably short petiole could indicate leaflets instead of leaves. The double serration, with teeth served either by secondaries or their exmedial branches or by veinlets arising from marginal tertiaries, however, points towards Betulaceae affinity and more precisely towards *Alnus*. These remains probably represent early leaves of young shoots of *Alnus julianiformis* and/or of one or the other fossil-species of alder.

***Alnus* sp.** – winged seeds

Fig. 12.9, 12.10

1888 *Betula prisca* Ettingsh., p.p.; Ettingshausen, p. 285.

Material. Moskenberg: NHMW: 1878/6/9149 (Ett. 7146) (*Betula prisca* in sched.). IBUG: Ett. 5626, (*Betula prisca*).

Description. Two-winged nutlets, l × w ~2.9 × 3.5 mm and ~4.2 × 4.4 mm (measured without style remnants, including wings); nutlet roundish to oval, ~2.9 × 2.5 mm and ~4.2 × 2.5 mm, with remains of bipartite style at apex; wings narrow.

Remarks. These are the only seeds discovered among the studied collection material representing *Alnus*. This is surprising because alder leaves are among the most common components in the Leoben flora, while *Betula* foliage occurs rarely. Generally, alder nutlets have rarely been reported associated with *Alnus* foliage, e.g. in Frankfurt am Main (Mädler, 1939). Records of *Betula* are more common, e.g. Sośnica (Zastawniak and Walther, 1998), although in *Betula* the wings appear more delicate than in *Alnus*.

Genus **Betula** L.

Betula similis (?) (Goepp.) Zastawniak et Walther

Figs 12.11–12.15, 24.14

(?) 1855 *Alnus similis* Goepp.; Goeppert, p. 13, pl. 4, fig. 5.

1888 *Betula prisca* Ettingsh.; Ettingshausen, p. 285, non pl. 2, figs 13, 14.

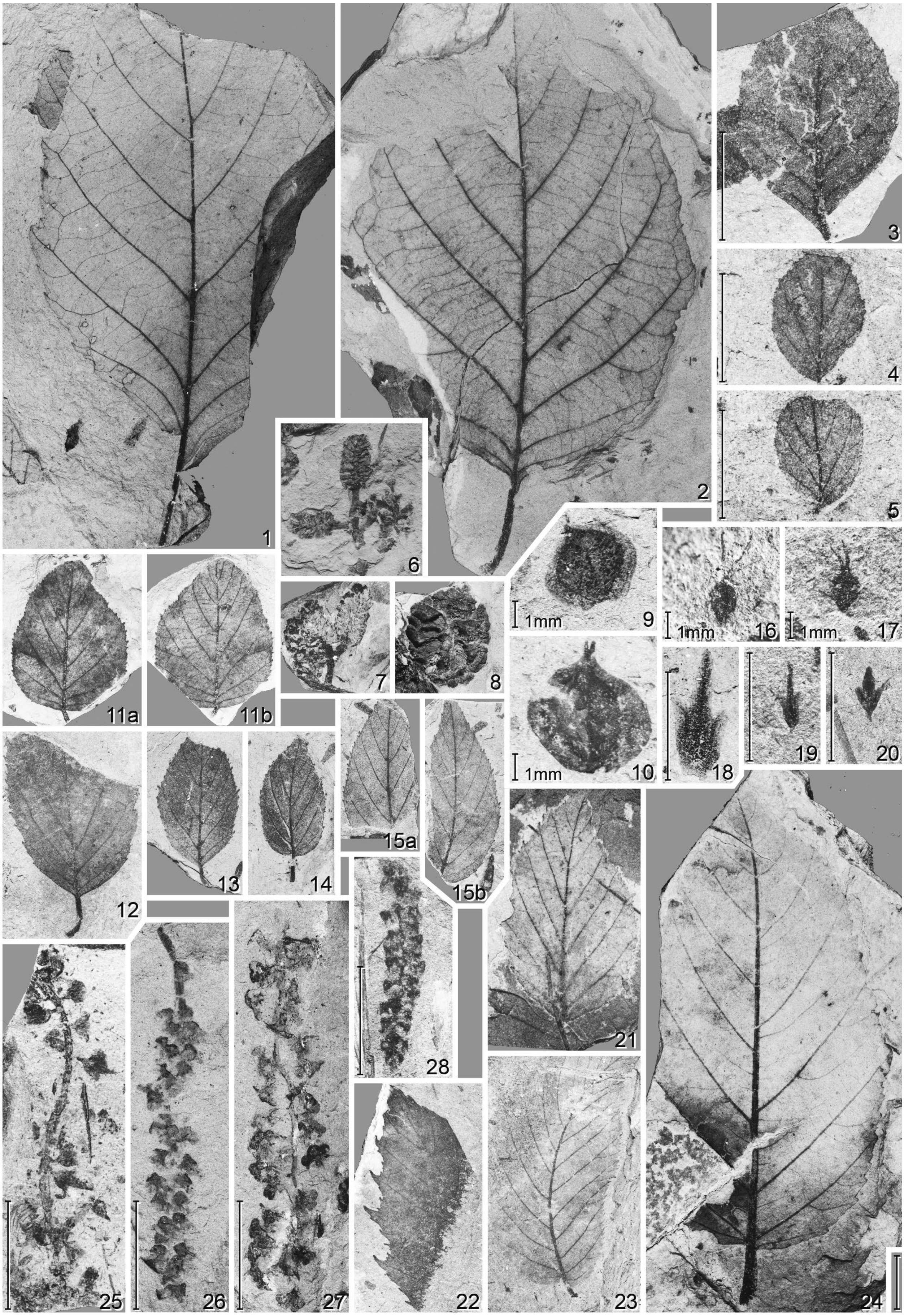
(?) 1998 *Betula similis* (Goepp.) comb. nov.; Zastawniak and Walther, p. 103, fig. 2: 8, 11, 12, fig. 3: 5, 8, fig. 10: 1–13, fig. 13: 12, 13, pl. 4, fig. 5, pl. 5, figs 1–7, pl. 6, figs 6–8.

Material. Moskenberg: NHMW: 1878/6/4015 + 4037 (2012 + 2034), (*Betula prisca* in sched.); 1878/6/7411 (5408), (*B. prisca* in sched.); 1878/6/7413 (5410), (*B. prisca* in sched.) + IBUG Ett. 5627 see locality Münzenberg. IBUG: Ett. 5632 (*B. prisca*); Ett. 6012, B. Münzenberg: NHMW: 1878/6/7415 (Ett. 5412), (*Betula prisca*). IBUG: Ett. 5627, (*B. prisca*), see locality Moskenberg.

Description. Petiolate simple leaves; petiole up to 10 mm long, straight to slightly bent; laminar shape ovate to elliptic, l × w ~23–37 × 13–21, ratio l/w ~1.4–2.5; base angle wide acute to wide obtuse, base shape nearly truncate to rounded, convex-cuneate; apex angle (narrow) acute, apex shape straight to acuminate; margin entire near base, then regularly, densely double serrate, teeth small, up to 1 mm high, above secondaries slightly larger than teeth in between, narrow, pointing towards apex, sometimes hook-shaped, sometimes curved outwards; distal and proximal flanks variable, straight, convex, concave; teeth tips often glandular; midvein straight, secondaries and their branches craspedodromous; secondaries more or less regularly spaced, angle of origin almost 90° at base in truncate leaves, angle tapering towards apex, near apex angle narrow; secondaries mainly straight; dark patches indicating domatia in axils between midvein and secondaries; tertiaries fine, dense, (forked-) percurrent, straight to somewhat sinuate, perpendicular to wide obtuse to midvein; in apical part of leaf, 2° teeth served by veinlets arising from marginal tertiaries; higher-order veins reticulate.

Remarks. Leaf shape, secondaries, and the serration account for the assignment to *Betula*. The dark patches in the axils between midvein and secondaries of several specimens indicate that the abaxial surface is preserved in these specimens and that tufts (domatia) were developed. These tufts were not only developed near the leaf base but also up into the middle or even apical part of the lamina. When part and counterpart are preserved, tufts are visible only on one slab, indicating that these represent the abaxial surface while the other slab represents the adaxial surface (NHMW 1878/6/7413, Ett. 5410 + IBUG Ett. 5627 and NHMW 1878/6/4015 + 4037, Ett. 2012 + 2034), (Fig. 12.11a, b, 12.15a, b) (compare also *Alnus julianiformis*, *A. milleri*). Glandular teeth are especially distinct in several specimens (Fig. 12.12, 12.13, 12.15). Tufts are generally common in modern *Betula*, and glandular teeth do occur but may be more prominent, e.g. *Betula maximowicziana* Regel, or indistinct, e.g. *Betula pendula* Roth. In specimen NHMW 1878/6/4015 + 4037 (Ett. 2012 + 2034), smaller teeth are primarily served by veinlets arising from marginal tertiaries instead of exmedial branches of secondaries.

Zastawniak and Walther (1998) determined *Alnus similis* (Goeppert, 1855: pl. 4, fig. 15) as lectotype for *Betula similis* from Goeppert's original material from Sośnica. This decision was based on the facts that *B. subpubescens* (Goeppert, 1855: pl. 3, fig. 9) was too fragmentarily preserved and that Goeppert's drawing did not correctly reflect the morphology of this specimen, so that it could not serve as an undisputable lectotype. They also listed this specimen in their section on problematic specimens, quoting correctly the specimen number and "pl. 3 fig. 9" in Goeppert (1855) (Zastawniak and Walther, 1998: p. 117). Worobiec and Szynkiewicz (2007: p. 45) misinterpreted "pl. 3 fig. 9" to refer to the plates in Zastawniak and Walther (1998) instead of Goeppert (1855) and thus concluded that a "mistakenly-printed" photograph was figured on pl. 3 fig. 9 of their publication. Worobiec and Szynkiewicz (2007) agree to the opinion of Zastawniak and Walther (1998) that the specimen from Sośnica figured by Goeppert (1855: pl. 3, fig. 9) is not suitable to serve as a "standard specimen" and selected an epitype for *B. subpubescens* from Bełchatow. This specimen from Bełchatow is also preserved very fragmentarily but the microstructures are well visible (Worobiec and Szynkiewicz, 2007: pl. 6, figs 2, 3a–c, pl. 7, fig 2a–e). It is therefore not evident that the holotype of *B. subpubescens* and this epitype are conspecific. Moreover, those authors did not provide a differentiation from


1
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B. similis. Therefore, following Zastawniak and Walther (1998), the binomen *B. similis* has been chosen for the here described specimens. The uncertainty in the specific assignment refers to the glandulous appearing tooth apices and the tufts at the origin of secondaries in the here described specimens. *B. similis* from Frankfurt am Main also shows tufts in the axils, but few tooth apices appear to be glandulous (Kvaček et al., 2020: fig. 8e).

***Betula* sp. 1** – leaf

Figs 12.21, 24.15

1888 *Betula brongniartii* Ettingsh., p.p.; Ettingshausen, p. 285, (?) pl. 2, fig. 11.

Material. Seegraben Walpurgis-Schacht: IBUG: Ett. 5648, A, (?) B, (*Betula brongniartii*); Ett. 5649 + 6296, a, (*Betula brongniartii*).

Description. Simple, petiolate, double-serrate leaves; petiole up to 9 mm long, (?) complete; laminar shape broad ovate, l × w ~42–45 × 25–26 mm, ratio l/w ~1.6–1.8; base angle obtuse, base shape straight (broad cuneate) at first, then convex; apex angle acute, apex shape convex on one side, concave on the other (slightly damaged), somewhat acuminate (IBUG Ett. 5649 + 6296a); margin saw-like double serrate; teeth above secondaries biggest, height ~1 mm, all teeth sharp, shape very variable, distal flank concave, straight, proximal flank straight, convex, concave, sinus angular or rounded, apex acute, occasionally (?) glandular; midvein slender, straight or slightly curved near apex; secondaries craspedodromous, slender, moderately dense, near base arising at moderate angle, angle tapering towards apex; secondaries more or less straight, subparallel, somewhat diverging towards margin, running straight into tooth apices; basal secondaries sending veinlets into marginal teeth near base; tertiaries delicate, percurrent, curved to slightly sinuous, obtuse to midvein; 2° teeth served by veinlets arising from marginalmost tertiaries or branches of secondaries; higher-order veins reticulate.

Remarks. *Betula* sp. 1 differs from *B. similis* (?) by larger blades and very differently sized 1° and 2° teeth. An assignment at the fossil-species level would require more information about the morphological variability.

***Betula* sp. 2** – leaf

Figs 12.22, 24.16

1888 *Betula brongniartii* Ettingsh., p.p.; Ettingshausen, p. 285, non pl. 2, fig. 11.

Material. Seegraben Walpurgis-Schacht: NHMW: 1878/6/4445 (Ett. 2442), Pb 2334, (*Betula brongniartii*).

Description. Apical leaf fragment with very sharply double-serrate margin; laminar shape and size (?); 1° teeth up to almost 3 mm high, distal flank concave, proximal side convex, sinus angular to rounded, apex bluntly acute, glandular; further teeth much smaller, <1 mm high, up to 6 between 1° ones, variously shaped, sinus angular, apex bluntly acute, glandular; midvein delicate, secondaries delicate, craspedodromous, running into apices of 1° teeth; tertiaries percurrent; veinlets arising from secondaries and from marginal tertiaries serving 2° teeth.

Remarks. Based on the pronounced betuloid marginal serration and the fabric of secondaries and tertiaries, this fragment is assigned to birch. The margin resembles *Betula*

◄

Figure 12. 1, 2. *Alnus* aff. *cecropiifolia* (Ettingsh.) Berger, **1**. NHMW 1878/6/7426 (Ett. 5423), (*Alnus kefersteinii*), **2**. NHMW 1878/6/9131 (Ett. 7128), A, (*A. kefersteinii*); **3–5**. *Alnus* sp. – leaves, **3**. NHMW 1878/6/8762 (Ett. 6759), Pb 2094, (*Spiraea acherontica*), Ettingshausen (1869a: pl. 6, fig. 10, holotype), **4**. NHMW 1878/6/8767 (Ett. 6764), Pb 2265, (*Spiraea osiris*), **5**. NHMW 1878/6/8766 (Ett. 6763), Pb 2262, (*S. osiris*); **6**, **7**. *Alnus gracilis* Unger, **6**. NHMW 1878/6/9133 (Ett. 7130), Pb 5497, (*Alnus gracilis*), Ettingshausen (1888: pl. 2, fig. 22), **7**. NHMW 1878/6/3684 (Ett. 1681), (*A. gracilis*); **8**. *Alnus kefersteinii* (Goepp.) Unger, NHMW 1878/6/7423 (Ett. 5420), (*A. kefersteinii*); **9**, **10**. *Alnus* sp. – winged seeds, **9**. NHMW 1878/6/9149 (Ett. 7146) (*Betula prisca*), **10**. IBUG Ett. 5626 (*B. prisca*); **11–15**. *Betula similis* (?) (Goepp.) Zastawniak et Walther, **11a**, **b**. **11a**. NHMW 1878/6/7413 (Ett. 5410) + **11b**. IBUG Ett. 5627 (*Betula prisca*), part and counterpart, **12**. IBUG Ett. 6012, B, **13**. NHMW 1878/6/7411 (Ett. 5408), (*B. prisca*), **14**. NHMW 1878/6/7415 (Ett. 5412), (*B. prisca*), **15a**, **b**. NHMW 1878/6/4015 + 4037 (Ett. 2012 + 2034), (*B. prisca*), part and counterpart, **15a.** (Ett. 2012), **15b.** (Ett. 2034); **16**, **17**. *Betula* sp. – winged seeds, while the styles are distinct, the lateral wings are faintly visible only, **16**. IBUG Ett. 6294, H, **17**. IBUG Ett. 6294, I; **18–20**. *Betula* sp. – bracts, **18**. IBUG Ett. 5624, (*Betula prisca*), **19**. NHMW 1878/6/9875 (Ett. 7872), (*B. prisca*), **20**. NHMW 1878/6/3950 (Ett. 1947), A, (*B. prisca*); **21**. *Betula* sp. 1 – leaf, IBUG 6296, a, (*Betula brongniartii*); **22**. *Betula* sp. 2 – leaf, NHMW 1878/6/4445 (Ett. 2442), Pb 2334, (*Betula brongniartii*); **23**. *Carpinus* vel *Ostrya* sp., IBUG Ett. 5959, (*Ostrya atlantidis*); **24**. *Carpinus grandis* Unger, NHMW 1878/6/3741 (Ett. 1738), (*Carpinus heeri*); **25–28**. Betulaceae gen. et sp. – catkins, **25**. NHMW 1878/6/7798 (Ett. 5795), A, (*Populus geinitzii*), **26**. NHMW 1878/6/3616 (Ett. 1613), (*P. latior*), **27**. NHMW 2023/0072/0001, **28**. NHMW 2023/0072/0002. For all photographs the scale at bottom right of the figure is 10 mm except for photographs with embedded scale. If not stated otherwise the embedded scale is also 10 mm

brongniartii Ettingsh. from Matrý (northern Bohemia, Late Oligocene; Kvaček et al., 2018). *B. brongniartii* was described from Zichov (Bohemia, Oligocene; Ettingshausen, 1866) and the original specimens were refigured by Hably et al. (2001). Neither the drawings in Ettingshausen (1866) nor the images of these specimens in Hably et al. (2001) show such a pronounced sharp serration as the specimens from Matrý and from Leoben.

***Betula* sp.** – bracts

Fig. 12.18–12.20

1869a *Betula prisca* Ettingsh., p.p.; Ettingshausen, p. 45, pl. 1, fig. 24.
1888 *Betula prisca* Ettingsh., p.p.; Ettingshausen, p. 285.

Material. Moskenberg: NHMW: 1878/6/3950 (Ett. 1947), A, (*Betula prisca*); 1878/6/9875 (7872), (*B. prisca* in sched.). Seegraben Unter-Buchwieser: NHMW: 1878/6/8010 (Ett. 6007), B. Seegraben Walpurgis-Schacht: IBUG: Ett. 5624, (*Betula prisca*).

Description. Isolated, shortly petioled 3-lobed bracts of fruits; shape and size variable, base rounded, lobes elongated diverging; width at point of separation of lobes ~1.4–3 mm, central lobe 4.4–6.2 mm long and up to 1.1 mm wide, lateral lobes distinctly shorter.

Remarks. Similar bracts are reported from different sites as *Betula longisquamosa* Mädler. Mai and Walther (1988) did not provide details on the size of the specimens from Thüringen. *B. longisquamosa* from Sośnica (Zastawniak and Walther, 1998) is larger than the specimens from Leoben. From Frankfurt am Main, *B. longisquamosa* figured by Kvaček et al. (2020: fig. 8f) would measure ~15 mm in length, which would be exceptionally long for *Betula*. According to Mädler (1939), the bracts from this site are 6–8 mm long. Mädler's measures imply that the scale may not be correct in Kvaček et al. (2020). Regardless, the remains from Leoben are smaller than those from Frankfurt am Main.

***Betula* sp.** – winged seeds

Fig. 12.16, 12.17

Material. Moskenberg: IBUG: Ett. 6294, H, I.

Description. Two-winged nutlets with two long styles; l × w ~1.3 × 3 mm and ~1.4 × 2.5 mm (measured without styles); styles up to 1.7 mm long; nutlet obovate, narrower at base than at apex, l × w ~1.3 × 0.9 and ~1.4 × 0.9 mm; wings broad, butterfly-like, membranaceous.

Remarks. These remains definitely represent *Betula* seeds. Both are preserved in a layer of plant debris on a slab that bears several leaf remains. They remained undetected by Ettingshausen.

Genus ***Carpinus*** L.

Carpinus grandis Unger

Figs 12.24, 13.4, 13.5, 24.17

1850a *Carpinus grandis* Unger, Unger, p. 408.
1852 *Carpinus grandis* Unger; Unger, p. 39, pl. 20, figs 4, 5.
1888 *Carpinus heeri* Ettingsh., p.p.; Ettingshausen, p. 294, non pl. 3, figs 7, 8.

Material. Moskenberg: NHMW: 1878/6/3741 (Ett. 1738), (*Carpinus heeri*). IBUG: Ett. 5955, (*Carpinus heeri*). Leoben: GBA: 2024/0001/0012, B; 2024/0001/0025, (*Ulmus prisca*).

Description. Petiolate, simple leaves; petiole 10 mm long (one specimen), stout; lamina slightly ovate to (slender) elliptic, l × w ~82–90 × 40–50 mm, ratio l/w ~1.7–2.1; base angle obtuse, base shape broadly rounded; apex angle acute, apex shape straight or acuminate (incomplete); margin double serrate, tooth height around 1 mm, 1° teeth slightly bigger than 2° ones, up to at least 4 2° teeth between adjacent 1° ones; distal flank straight to slightly concave, proximal flank straight, moderately convex or acuminate; sinus mostly angular, rarely rounded, apex acute; midvein straight to bent near apex, tapering from base to apex; secondaries and branches arising abaxially from secondaries simple craspedodromous; secondaries arising at moderate angle, mainly moderately spaced, course rather straight; abaxial branches of secondaries and further branches serving marginal teeth; intersecondaries between adjacent secondaries present, length variable (NHMW 1878/6/3741, Ett. 1738); tertiaries (forked-) percurrent, sinuate, 2–3 per cm, obtuse to midvein.

Remarks. Except specimen NHMW 1878/6/3741 (Ett. 1738), all specimens listed explicitely by Ettingshausen (1888) for *Carpinus heeri* are leaf remains representing other Betulaceae genera or *Ulmus*, whereas the specimens detected in the GBA collection are quite characteristic. The specimen from the NHMW collection is less characteristic due to more widely spaced secondaries and the presence of intersecondaries. Neither the samaroid fruit of *C. heeri* (Ettingshausen, 1888: pl. 3, fig. 9) nor any other hornbeam samara has been detected among the studied collection material.

Carpinus vel ***Ostrya*** **sp**.

Fig. 12.23

1888 *Ostrya atlantidis* Unger, p.p.; Ettingshausen, p. 294.

Material. Moskenberg: IBUG: Ett. 5959, (*Ostrya atlantidis*).

Description. Short-petiolate leaf; petiole ~3 mm long, (?) complete; laminar shape slender elliptic, l × w ~47 × 25 mm, ratio l/w ~1.9; base angle obtuse, base shape slightly cordate; apex angle acute, shape (?); margin sharply, densely, double serrate, teeth similar in size, up to 1 mm high, narrow, distal flank straight, concave, sometimes convex, proximal flank convex, straight, concave, sinus angular, apex narrow acute; midvein bent, secondaries craspedodromous, densely spaced, straight on one side, slightly curved on the other one; secondaries branching once to twice in marginal third of lamina, forming abaxial minor secondaries running into teeth; tertiaries delicate, percurrent, dense.

Remarks. This particular specimen definitely represents *Carpinus* or *Ostrya*, as Ettingshausen (1888) suggested, because of the densely spaced craspedodromous secondaries and minor secondaries running into the tooth apices of the characteristically sharply double-serrate, saw-like margin. The gross-morphological distinction between *Carpinus* and *Ostrya* leaves is problematic unless fruits are available even for modern material. No fruits of hornbeam are available from Leoben (see paragraph *C. grandis*) and the remains regarded as fructifications of *Ostrya* by Ettingshausen (1888) are bud scales and scales, bracts or corolla elements of uncertain taxonomic affinity (see respective paragraphs). Consequently, an unequivocal assignment of this leaf to *Carpinus* or *Ostrya* is not possible. Considering that reliable fossil records of *Ostrya* are generally very rare, *Carpinus* may be more likely. This leaf differs from *Carpinus grandis* by the densely spaced secondaries and tertiaries, the absence of intersecondaries and the saw-like margin.

Betulaceae gen. et **sp**. – catkins

Figs 12.25–12.28, 22.38

1869a *Populus geinitzii* Ettingsh. sp. n., p.p.; Ettingshausen, p. 57, pl. 3, fig. 9, non fig. 10.
1888 *Betula prisca* Ettingsh., p.p.; Ettingshausen, p. 285.
1888 *Populus latior* A. Braun, p.p.; Ettingshausen, p. 300, (?) pl. 3, fig. 21.
1888 *Populus geinitzii* Ettingsh., p.p.; Ettingsh., p. 300.

Material. Moskenberg: NHMW: 1878/6/3615 (Ett. 1612) (*Populus. latior*); 1878/6/3616 + 9866 (1613 + 7863), 1613 (*P. latior*), 7863 (*P. geinitzii* in sched.); 1878/6/3627 (1624), (*P. latior*); 1878/6/3628 (1625), (*P. latior*); 1878/6/XX (16XX), 2023/0072/0001; 1878/6/3969 (1966), (*Betula* sp. in sched.); 1878/6/7412 (5409), (*Betula prisca*); 1878/6/7798 (5795), A, (*Populus geinitzii*); 1878/6/9084 (7081), (*P. latior*). Münzenberg: NHMW: 2023/0072/0002 (coll. Hofmann sine no). Seegraben Unter-Buchwieser: NHMW: 1878/6/7417 (Ett. 5414).

Description. Catkins; l × w ~(21) 35–40 × 5–7 mm; bracts lobed to rhomboidal, partly in pre-anthesis, anthesis and post-anthesis state.

Remarks. Concluding from the abundances of leaf taxa in the Leoben assemblage, especially *Alnus* may be expected to be represented by catkins. Pollen analysis was attempted from catkins in the pre-anthesis and anthesis state but was sucessful only for specimen NHMW 1878/6/3615 (Ett. 1612). This specimen was prepared by the method usually applied to cuticles using Schulze's reagents in 2001 or 2002. It shows densely spaced pentaporate pollen indicating *Betula* or *Alnus* (Fig. 22.38). The assignment of the other catkins must remain tentative because pollen is not available. Specimens NHMW 1878/6/7412 (Ett. 5409) and NHMW 2023/0072/0002 represent catkins in transition from pre-anthesis to flowering stage, while other catkins, e.g. NHMW 1878/6/3615 (Ett. 1612), NHMW 1878/6/3616 + 9866 (Ett. 1613 + 7863), NHMW 2023/0072/0001 (Ett. 16XX), NHMW 1878/6/9084 (Ett. 7081), show anthesis to post-anthesis stage. The bracts of the specimens NHMW 2023/0072/0001 (Ett. 16XX) and NHMW 1878/6/7798 (Ett. 5795), (Fig. 12.25, 12.27), resemble those that have been found isolated (see paragraph *Betula* sp. – bracts).

Specimens NHMW 1878/6/3616 + 9866 (Ett. 1613 + 7863), representing part and counterpart of one catkin, were identified by Ettingshausen as two different species of *Populus*: *P. latior* the former (Ettingshausen, 1888) and *P. geinitzii* (in sched.) the latter. The catkins described as *Populus geinitzii* (Ettingshausen, 1869a: pl. 3, fig. 9) and *Populus latior* Ettingshausen (1888: pl. 3, fig 21) could not be identified among the studied material (see also section *P. latior*), and the leaf figured as *P. geinitzii* (Ettingshausen, 1869a: pl. 3, fig. 10) has been identified as *Alnus julianiformis* in this study (see that section). Furtheron, contrary to Ettingshausen (1869a: p. 57), no fruit remains assignable to *Populus* were detected in the studied collections. Poplar remains in the Leoben assemblage are generally restricted to few fragmentarily preserved leaves only. Therefore, findings of poplar catkins may be improbable. Regarding further possible affinity, the catkins at hand are considerably larger than those reported from *Myrica*, e.g. Kohlman-Adamska et al. (2004), Zidianakis et al. (2015).

Family FAGACEAE Dumortier

Genus ***Fagus*** L.

Fagus deucalionis Unger

Fig. 13.2, 13.3

1847 *Fagus deucalionis* Unger; Unger, p. 27, figs 1–6.

Material. Moskenberg: NHMW: 1878/6/3576 (Ett. 1573), (*Fagus feroniae* in sched.). Leoben: LMJ: 201.028.

Description. Two almost complete leaves, petiole not preserved; lamina shape elliptic to slightly obovate, l × w ~63 × 26 mm and 72 × 35 mm, ratio l/w ~2.4 and 2.1; base angle acute, base shape nearly straight (minimally convex); apex angle acute, apex shape straight to slightly concave; margin entire in lower half of lamina, simple serrate in apical part, margin undulate between adjacent secondaries; teeth narrow, tooth height up to 1 mm, somewhat S-shaped (NHMW 1878/6/3576, Ett. 1573), base rounded, apex bluntly acute, one tooth above each secondary vein; midvein slender, straight, near apex slightly undulate (NHMW 1878/6/3576, Ett. 1573); secondaries simple craspedodromous, near base (where margin undulate) eucamptodromous; secondaries moderately densely spaced (at least 10–11 pairs), straight, unforked, originating at moderate wide angle, in basal part of lamina at their utmost origin converging towards midvein, then turning exmedially; 2° veins parallel to each other, slightly diverging towards margin, running directly into marginal teeth; tertiaries delicate, hardly visible, angle of tertiaries towards midvein obtuse (?), tertiaries connecting secondaries at almost right angle (?).

Remarks. Among the rich material from Leoben, only two leaves represent *Fagus* because most specimens assigned by Ettingshausen (1888) to *F. feroniae* are Betulaceae, mainly *Alnus julianiformis* (see respective section). The simply toothed and slightly undulate course of the margin between two adjacent secondaries, the slender, straight, regularly spaced and parallel secondaries, the slightly undulate course of the midvein near the apex, along with the extremely delicate tertiaries clearly point towards the genus *Fagus*. The specific assignment follows Holý et al. (2012), who merged *F. deucalionis* and *F. menzelii* Kvaček et Walther (1991).

Genus ***Quercus*** L.

Quercus drymeja Unger

Figs 13.11–13.15, 24.18

1847 *Quercus drymeja* Unger; Unger, p. 113, pl. 32, figs 1, 2, 4, non fig. 3.

1869a *Castanea atavia* Unger; Ettingshausen, p. 48, pl. 2, fig. 16, non figs 17–20.

1869a *Quercus milleri* Ettingsh. sp. n., p.p.; Ettingshausen, p. 50, pl. 2, fig. 1, non fig. 2.

1888 *Quercus drymeja* Unger, p.p.; Ettingshausen, p. 288.

1888 *Quercus lonchitis* Unger, p.p.; Ettingshausen, p. 289.

1888 *Rhopalophyllum acuminatum* Unger, p.p.; Ettingshausen, p. 314, non pl. 4, figs 16–19.

2004 *Quercus drymeja* Unger; Kovar-Eder et al., p. 61, pl. 4, figs 1–7.

2022 *Quercus drymeja* Unger; Kovar-Eder et al., p. 99, pl. 9, figs 17–21.

Material. Moskenberg: NHMW: 1878/6/4098 (Ett. 2095), (*Quercus lonchitis*); 1878/6/4099 (2096), A, (*Q. lonchitis*); 1878/6/4102 (2099), (*Q. milleri* in sched.); 1878/6/4103 (2100), (*Q. drymeja*); 1878/6/7528 + 7529 (5525 + 5526), (*Q. milleri*); 1878/6/8103 (6100), (*Rhopalophyllum acuminatum*). Seegraben

Walpurgis-Schacht: NHMW: 1878/6/4464 (Ett. 2461), (*Sapindus* sp. in sched.).

Description. Long-petiolate leaves; petiole up to 20 mm long, slender, straight or somewhat bent; laminar shape slender elliptic to somewhat ovate, near base often somewhat asymmetrical, l × w ~36–70 (90) × 10–22 mm, ratio l/w ~(3.2)3.5–6.9 (7.6); base more or less symmetrical, base angle (narrow) acute, base shape convex to straight, apex angle narrow acute, apex shape straight; margin entire in basal part of lamina, then simple serrate; teeth widely spaced, height between 1 mm and <5 mm, sometimes hook-shaped, sinus mostly rounded, more rarely acute, apex acute or spine-like, distal flank mainly straight to concave, proximal flank straight (slightly concave or convex); midvein thick, straight to bent in basal part; secondaries distinctly thinner, eucamptodromous in basal part of lamina but simple craspedodromous in toothed part; number of secondaries corresponding to number of teeth in serrate part; secondaries arising at moderate angle, angle decreasing towards apex, course of secondaries slightly curved; tertiaries percurrent, angle towards midvein obtuse, further venation reticulate.

Remarks. Grossmorphologically, specimen NHMW 1878/6/4103 (Ett. 2100) may be mistaken for *Myrica lignitum*. *Q. drymeja* differs from *M. lignitum* by the acute to spine-like tooth shape, more widely spaced secondaries corresponding to the number of teeth, steeper angle of the secondaries and percurrent tertiaries.

Denk et al. (2017c) proposed the *Quercus drymeja* morphotype complex in which four morphotypes are distinguished. In this sense, the here described leaves represent the *Q. drymeja* Parschlug morphotype.

Quercus gigas
Goepp. emend. Walther and Kvaček (1991)

Figs 13.6–13.10, 14.1, 14.2, 24.19

1855 *Quercus gigas* Goepp.; Goeppert, p. 16, pl. 8, fig. 1.

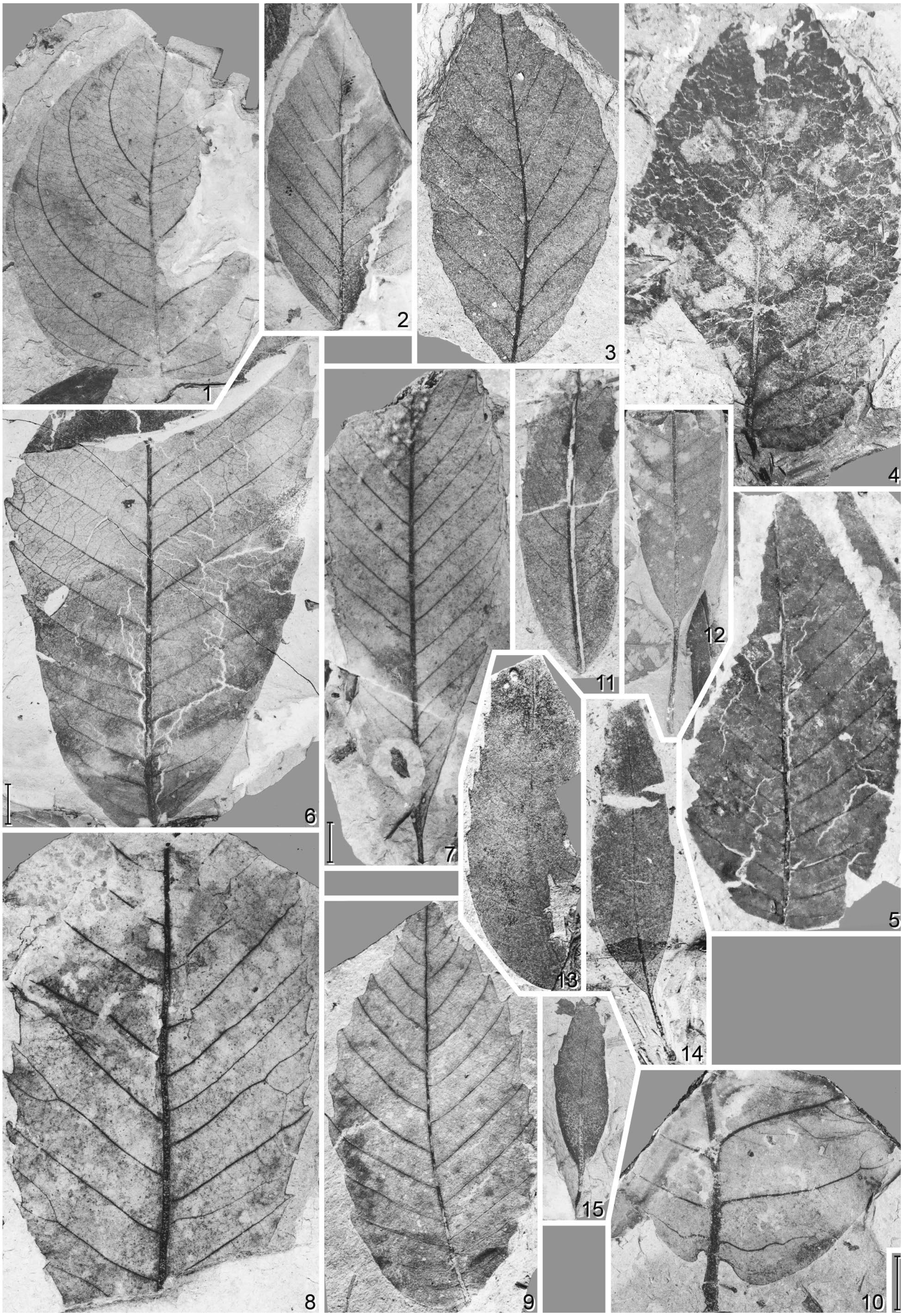
1882 *Castanea atavia* Unger; Ettingshausen, p. 97, pl. 14, figs 2–7, pl. 15, figs 1–6.

1888 *Castanea atavia* Unger, p.p.; Ettingshausen, p. 292.

1991 *Quercus gigas* Goepp. emend. nov.; Walther and Zastawniak, p. 160, pl. 4, figs 1–3, pls 5, 6, pl. 7, figs 1–3, pls 8–10; text-figs 3–7.

Material. Moskenberg: NHMW: 1878/6/3689 (Ett. 1686), Pb1897, (*Castanea atavia*), Ettingshausen (1882: pl. 14, fig. 7); 1878/6/3691 (1688), Pb 1895, (*C. atavia*), Ettingshausen (1882: pl. 15, fig. 3); 1878/6/3695 (1692), A, (*C. atavia*); 1878/6/3696 + 7484 (1693 + 5481), (*C. atavia*); 1878/6/3697 + 3832 (1694, B + 1829, b), Pb 1898, (*C. atavia*), Ettingshausen (1882: pl. 14, fig. 6); 1878/6/3698 + 3699 (1695 + 1696), (*C. atavia*); 1878/6/3700 (1697), (*C. atavia*); 1878/6/3703 (1700), (*C. atavia*); 1878/6/3833 (1830), (*C. atavia* in sched.); 1878/6/4209 (2206), b, (*C. atavia* in sched.); 1878/6/7482 (5479), (*C. atavia*); 1878/6/7485 (5482), (*C. atavia*); 1878/6/7488 (5485), (*C. atavia*); 1878/6/7490 + 7491 (5487 + 5488), (*C. atavia*); 1878/6/9141 (7138), (*C. atavia*); 1878/6/9144 (7141), (*C. atavia*); 1878/6/9146 (7143), (*C. atavia*); 1878/6/9205 (7202), (*C. atavia*); 1878/6/9210 (7207), (*C. atavia*); 1878/6/9211 (7208), (*C. atavia*); 1878/6/9212 (7209), (*C. atavia*), Ettingshausen (1882: pl. 14, fig. 4); 1878/6/9214 (7211), (*C. atavia*); 1878/6/9215 (7212), Pb 1896, (*C. atavia*), Ettingshausen (1882: pl. 14, fig. 5). Münzenberg: NHMW: 1878/6/9202 + 9203 (Ett. 7199 + 7200), Pb 2146, (*C. atavia*), Ettingshausen (1882: pl. 15, fig. 1); 1878/6/9204 (7201), (*C. atavia*); 1871/38/27, 30–32 (*C. atavia*). Seegraben Unter-Buchwieser: NHMW: 1878/6/9200 (Ett. 7197), (*C. atavia*), Ettingshausen (1882: pl. 14, fig. 1).

Description. Fragments of large petiolate leaves, base and apex rarely preserved; petiole at least up to 10 mm long, straight; laminar shape elliptic, oblong to obovate, l × w ~140–190 × 30–75 mm, ratio l/w ~2.1–3.7 (5); base angle acute to obtuse, base shape convex to straight, rarely complex, symmetrical to somewhat asymmetrical, apex angle (narrow) acute, apex shape straight to concave; margin entire near base, then simply sharply serrate, second-order teeth very rare; teeth often spine-shaped, tooth height >1 and <5 mm, shape of distal and proximal flanks variable, sinus rounded, more rarely angular, apex narrow acuminate, acute to bluntly acute; midvein mostly straight, secondaries simple craspedodromous, occasionally branching once at about 2/3 of the distance from midvein (Fig. 13.8); secondaries originating at moderate angle, steeper in the case of narrow base and apex, running into tooth apices; basal secondaries brochidodromous in the case of untoothed margin near base; secondaries more or less regularly and moderately densely spaced, near origin sometimes slightly converging to midvein,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further course rather straight, occasionally slightly curved when entering teeth; tertiaries delicate, (forked-) percurrent, undulate, rather densely spaced, angle towards midvein wide obtuse, almost rectangular to secondaries; in the case of a second-order tooth, an exmedial veinlet arises from a more distinct tertiary vein to run into the tooth apex (Fig. 13.6, 13.8); higher-order veins reticulate.

Remarks. *Quercus gigas* leaves belong to the most common taxa in the Leoben flora. The specimens figured by Ettingshausen (1869a: pl. 2, figs 17–20) for *Castanea atavia* (i.e. *Quercus gigas*) are catkins (see section *Castanea* vel *Quercus* sp. – male catkins) and the leaf specimen figured there (pl. 2, fig. 16) possibly represents *Quercus drymeja* but that particular specimen has not been identified among the studied collection material. The material of *Castanea atavia* listed in Ettingshausen (1888) further includes bud scales described there as nuts (see paragraph Bud scales) and therefore have to be excluded from this fossil-species.

Castanea atavia Unger was based on material from Socka, Slovenia (formerly Sotzka, Eocene) and morphologically differs among others by smaller size, more slender shape and fewer secondaries and teeth. Denk and Bouchal (2021) suggest the extinct genus *Castaneophyllum* for these leaves from Socka. In the Leoben material, distinct marginal tertiaries run almost parallel to the margin between two adjacent teeth. Walther and Zastawniak (1991) mentioned this feature as characteristic of *Quercus*. In the European Neogene, the presence of *Castanea* appears to be restricted to the youngest Neogene (Kvaček and Walther, 1989). Thus, Ettingshausen's assignment of these leaves to *Castanea* is corrected here.

The dilemma to differentiate macromorphologically and/or micromorphologically leaves of fossil-species within the genus *Quercus* was the subject of several studies (e.g. Czeczott, 1951; Hummel, 1983; Walther and Zastawniak, 1991) but remains unsatisfactorily resolved. Moreover, Denk et al. (2017a) also stressed the challenge to resolve modern oaks based on leaves beyond the section level.

Compared to *Quercus kubinyii* (Kováts ex Ettingsh.) Czeczott, blades of *Q. gigas* are usually larger and the ratio l/w is lower, i.e. the width is bigger.

Although numerous specimens of *Q. gigas* are available, in most of them only the middle part is preserved whereas base and apex are missing. This may be related to (1) the large size of the blades, (2) their probably chartaceous texture, (3) diagenetic fragmentation of the leaves and the sediment (see paragraph Preservation), and (4) fragmentation caused during excavation rather than by long-distance transport (see section Taphonomy).

Quercus mediterranea Unger

Fig. 14.15–14.17

1847 *Quercus mediterranea* Unger; Unger, p. 114, pl. 32, figs 1 top left, 7, 9; (?) figs 5, 6, 8.
1888 *Betula rectinervis* Ettingsh. sp. n.; Ettingshausen, p. 285, pl. 2, fig. 12.
1888 *Quercus palaeo-ilex* Ettingsh. sp. n., p.p.; Ettingshausen, p. 289.
1888 *Ulmus plurinervia* Unger, p.p.; Ettingshausen, p. 295.
2004 *Quercus mediterranea* Unger; Kovar-Eder et al., p. 62, pl. 4, figs 8–16.
2022 *Quercus mediterranea* Unger; Kovar-Eder et al., p. 99, pl. 9, figs 12–16.

Material. Moskenberg: NHMW: 1878/6/3773 (Ett. 1770), a, (*Ulmus plurinervia*); 1878/6/4195 (2192), (*Quercus palaeo-ilex*), Ettingshausen, (1888: p. 289, nomen nudum). Münzenberg: NHMW: 1878/6/7421 (Ett. 5418), (*Betula rectinervis*), Ettingshausen (1888: pl. 2, fig. 12, holotype).

Description. Petiolate leaf and leaf fragments lacking base and apex; petiole 2 mm long, (?) complete; laminar shape broad ovate to elliptic, l × w ~31–60 × 17–32 mm, ratio l/w ~1.8–2.3; base and apex of specimen NHMW 1878/6/7421 (Ett. 5418): base angle

Figure 13. **1**. *Berchemia* (?) sp., IBUG Ett. 6251 (*Dioclea protogaea*); **2**, **3**. *Fagus deucalionis* Unger, **2**. NHMW 1878/6/3576 (Ett. 1573), (*Fagus feroniae*), **3**. LMJ 201.028; **4**, **5**. *Carpinus grandis* Unger, **4**. GBA 2024/0001/0012, B, (*Ulmus prisca*), **5**. GBA 2024/0001/0025, (*Ulmus prisca*); **6–10**. *Quercus gigas* Goepp. emend. Walther et Kvaček 1991, **6**. NHMW 1878/6/9144 (Ett. 7141), (*Castanea atavia*), **7**. NHMW 1878/6/7484 (Ett. 5481), (*C. atavia*), **8**. NHMW 1878/6/9210 (Ett. 7207), (*C. atavia*), **9**. NHMW 1878/6/9141 (Ett. 7138), (*C. atavia*), **10**. NHMW 1878/6/7490 (Ett. 5487), (*C. atavia*); **11–15**. *Quercus drymeja* Unger, **11**. NHMW 1878/6/4102 (Ett. 2099), (*Quercus milleri*), **12**. NHMW 1878/6/4099 (Ett. 2096), A, (*Q. lonchitis*), **13**. NHMW 1878/6/4464 (Ett. 2461), (*Sapindus* sp.), **14**. NHMW 1878/6/8103 (Ett. 6100), (*Rhopalophyllum acuminatum*), **15**. NHMW 1878/6/4098 (Ett. 2095), (*Quercus lonchitis*). For all photographs the scale at bottom right of the figure is 10 mm except for photographs with embedded scale in which the scale is also 10 mm

obtuse, base shape concavo-convex, apex angle acute, apex shape straight-convex on one side, concave on other side; margin simple serrate, one tooth per secondary vein, occasionally 2° teeth; tooth height ~1 mm and >1 and <5 mm, teeth variable, narrow and spine-like or hook-shaped oriented towards apex or outwards, distal and proximal flanks variable, in specimen NHMW 1878/6/7421 (Ett. 5418) mostly straight, more rarely convex or concave; in other specimens distal flank concave, proximal one convex; sinus rounded or angular, apex (blunt) acute; midvein straight or bent near apex; secondaries simple craspedodromous running into tooth apices, course rather straight to slightly curved, angle of origin moderate to wide, tapering towards apex, 2° vein spacing moderate and regular; minor secondaries running into 2° teeth apices; tertiaries hardly visible, percurrent, almost perpendicular to secondaries.

Remarks. Ettingshausen's assignments of two leaves to *Betula* and *Ulmus* are surprising and must be rejected. In the drawing of specimen NHMW 1878/6/7421 (Ett. 5418) (Ettingshausen, 1888: pl. 2, fig. 12) the serration is not correct showing more numerous teeth, i.e. teeth also between those served by secondaries, and the teeth appear less spine-shaped. Denk et al. (2017c) stated that leaf morphotypes of *Q. mediterranea* occur both in Mediterranean as well as Himalayan and East Asian modern species of *Quercus* Group *Ilex*, indicating different climate conditions, i.e. summer-dry climate and fully humid or summer-wet conditions. *Q. mediterranea* leaf morphotypes may comprise more than a single biological species (Denk et al., 2017c) and the assessment of unequivocal nearest living oak species remains unsettled. Moreover, shifts in climatic tolerance of taxa over time should also be considered. These considerations may account for the difficulties in understanding the climate signal of this fossil-taxon.

Quercus rhenana (Kräusel et Weyland) Erw. Knobloch et Kvaček

Figs 14.3–14.8, 24.20

1858 *Quercus undulata* Web.; Ettingshausen, p. 745, pl. 2, fig. 8.

1858 *Ficus joannis* Ettingsh.; Ettingshausen, p. 746, pl. 1 fig. 6, pl. 2 fig. 10.

1858 *Verbenophyllum aculeatum* Ettingsh.; Ettingshausen, p. 749, pl. 2, fig. 11.

1869a *Quercus apocynophyllum* Ettingsh. sp. n.; Ettingshausen, p. 50, pl. 2, fig. 15.

(?) 1869a *Myrsine salicina* Ettingsh. sp. n.; Ettingshausen, p. 72, pl. 4, fig. 9.

1869a *Sapindus moskenbergensis* Ettingsh. sp. n.; Ettingshausen, p. 82, pl. 5, fig. 10.

1869a *Callistemophyllum productum* Ettingsh. sp. n.; Ettingshausen, p. 92, pl. 6, fig. 15.

1888 *Phyllerium palaeo-myricae* Ettingsh. sp. n. on *Myrica lignitum* Unger; Ettingshausen, p. 264, pl. 1, fig. 1.

1888 *Phyllerium palaeo-lauri* Ettingsh. sp. n. on leaf of *Laurus*; Ettingshausen, p. 264, pl. 1, fig. 4.

1888 *Sphaeria palaeo-lauri* Ettingsh. sp. n. p.p. on leaf of *Laurus*; Ettingshausen, p. 265, pl. 1, fig. 6.

1888 *Quercus apocynophyllum* Ettingsh., p.p.; Ettingshausen, p. 287; pl. 2, fig. 17, pl. 3, figs 11, 12.

1888 *Quercus daphnophyllum* Ettingsh.; Ettingshausen, p. 287; pl. 2, figs 18, 19.

1888 *Quercus nereifolia* A. Braun, p.p.; Ettingshausen, p. 287.

1888 *Ficus sagoriana* Ettingsh.; Ettingshausen, p. 296.

1888 *Ficus fridaui* Ettingsh., p.p.; Ettingshausen, p. 297.

1888 *Laurus grandifolia* Ettingsh. sp. n.; Ettingshausen, p. 304; pl. 3, figs 23, 23a.

1888 *Laurus ocoteaefolia* Ettingsh., p.p.; Ettingshausen, p. 304.

1888 *Laurus nectandroides* Ettingsh., p.p.; Ettingshausen, p. 305.

1888 *Apocynophyllum lanceolatum* Unger, p.p.; Ettingshausen, p. 323.

1888 *Apocynophyllum reussii* Ettingsh., p.p.; Ettingshausen, p. 324, pl. 5, figs 23, 24, non figs 21, 22.

1888 *Plumeria stiriaca* Ettingsh. sp. n.; Ettingshausen, p. 325, pl. 6, figs 1–3.

1888 *Eucalyptus oceanica* Unger, p.p.; Ettingshausen, p. 357.

(?) 1888 *Eucalyptus grandifolia* Ettingsh.; Ettingshausen, p. 358.

1888 *Callistemophyllum productum* Ettingsh.; Ettingshausen, p. 358.

1950 *Illicium rhenanum* Kräusel et Weyland; Kräusel and Weyland, p. 50, text-fig. 14, pl. 9, figs 5–7, pl. 10, figs 1, 2, pl. 11, fig. 6.

1976 *Quercus rhenana* (Kräusel et Weyland) Erw. Knobloch et Kvaček; Knobloch and Kvaček; p. 41, pl. 17, figs 6, 8, 14, pl. 21, figs 5, 6, pl. 24, fig. 10.

1996 *Quercus rhenana* (Kräusel et Weyland) Erw. Knobloch et Kvaček; Kovar-Eder, p. 151, pl. 1, figs 19, 21, pl. 2, figs 4–6, pl. 5, figs 1–9.

1999 *Quercus rhenana* (Kräusel et Weyland) Erw. Knobloch et Kvaček; Meller et al., p. 136, pl. 2, fig. 5.

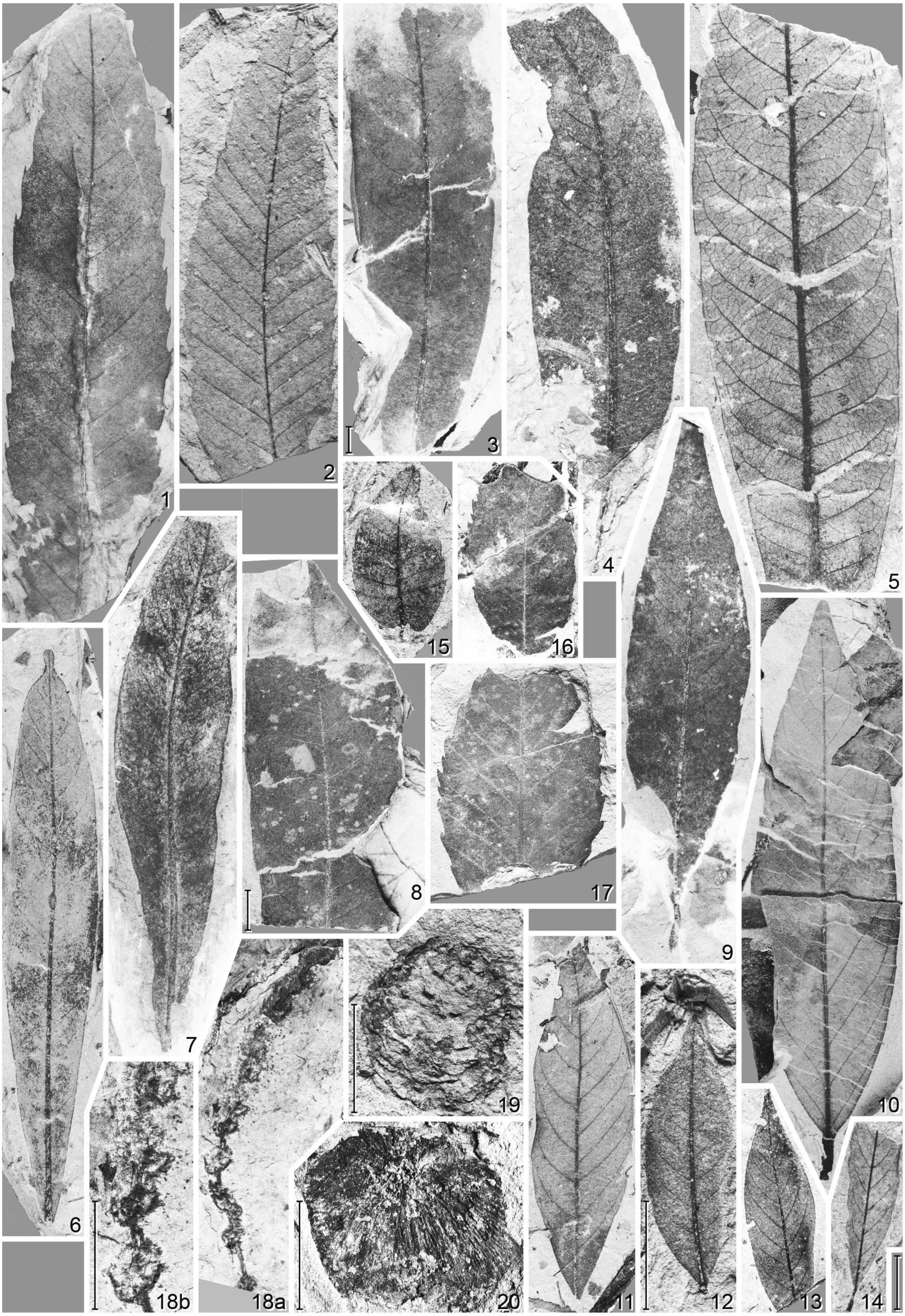
2003 *Quercus rhenana* (Kräusel et Weyland) Erw. Knobloch et Kvaček; Kovar-Eder and Meller, p. 287, pl. 2, fig. 9, pl. 3, fig. 4.

Material. Moskenberg: NHMW: 1878/6/3519 (Ett. 1516), Pb 2275, (*Eucalyptus oceanica*); 1878/6/3561 (1558), (*Apocynophyllum reussii*), Ettingshausen (1888: pl. 5, fig. 23); 1878/6/3600 (1597), B; 1878/6/3709 (1706), (*Laurus nectandroides*); 1878/6/3710 + 3711 (1707 + 1708), (*L. nectandroides*); 1878/6/3724 (1721), b, (*Quercus* sp. in sched.); 1878/6/3788 (1785), a, (*Anona* sp. in sched.); 1878/6/3782 (1779), Pb 1868, (*Sphaeria palaeo-lauri* on leaf of *Laurus*), Ettingshausen (1888: pl. 1, fig. 6); 1878/6/3836 (1833), B, Pb 2038; 1878/6/3861 (1858), (*Quercus daphnophyllum*); 1878/6/3862 (1859), (*Q. daphnophyllum*); 1878/6/3863 (1860), Pb 1986, (*Q. daphnophyllum*), Ettingshausen (1888: pl. 2, figs 18, 18a, syntype); 1878/6/3918 (1915), (*Ficus sagoriana*); 1878/6/3922 (1919), (*Diospyros* sp. in sched.); 1878/6/3923 (1920), A, (*Quercus nereifolia*); 1878/6/3927 (1924), (*Q. nereifolia*); 1878/6/3929 (1926), A, (*Q. nereifolia*); 1878/6/4020 (2017), (*Diospyros* sp. in sched.); 1878/6/4041 (2038), A, listed for *Maesa stiriaca* in Ettingshausen (1888), probably by mistake; 1878/6/4061 (2058), A, (*Apocynophyllum* sp. in sched.); 1878/6/4082 (2079), A, (*Quercus apocynophyllum*); 1878/6/4123 (2120), Pb 1994, (*Apocynophyllum reussii*), Ettingshausen (1888: pl. 5, fig. 24), Ettingshausen (1888: p. 324) listed the number Ett. 2020 instead of Ett. 2120; 1878/6/4168 (2165), Pb 1902, (*Ficus fridaui*); 1878/6/4184 (2181), Pb 1849, (*Sapindus moskenbergensis*), Ettingshausen (1869a: pl. 5, fig. 10, holotype); 1878/6/4194 (2191), Pb 1987, (*Quercus apocynophyllum*), Ettingshausen (1888: pl. 2, figs 17, 17a); 1878/6/4211 (2208), b, (*Apocynophyllum* sp. in sched.); 1878/6/6456 + 6457 (4453 + 4454), Pb 1870, (*Phyllerium palaeolauri* on a leaf of *Laurus*), Ettingshausen (1888: pl. 1, fig. 4); 1878/6/6460 (4457), (*Phyllerium palaeo-myricae* on *Myrica lignitum*), Ettingshausen (1888: pl. 1, fig. 1); 1878/6/7512 (5509) (*Quercus apocynophyllum*); 1878/6/7828 (5825), Pb 1922, (*Laurus ocoteaefolia*); 1878/6/8179 (6176), Pb 1993, (*Apocynophyllum lanceolatum*); 1878/6/8754 (6751), Pb 2078, (*Callistemophyllum productum*), Ettingshausen (1869a: pl. 6, fig. 15, holotype); 1878/6/8755 (6752), Pb 2077, (*C. productum*); 1878/6/8756 (6753), Pb 2075, (*C. productum*); NHMW 1871/38/37. IBUG: Ett. 5714, (*Quercus daphnophyllum* in sched.); Ett. 6018, A, (*Laurus grandifolia* in sched.). Münzenberg: NHMW: 1878/6/4254 (Ett. 2251), Pb 2192, (*Laurus ocoteaefolia*); 1878/6/4255 (2252), Pb 2193, (*L. grandifolia*, syntype); 1878/6/4289 (1879/2286) (Ett. 2286), (*Callistemophyllum productum*); 1878/6/4323 (2320), (*C. productum*); 1878/6/4369 (2366), Pb 2215, (*Plumeria stiriaca*), Ettingshausen (1888: pl. 6, fig. 2, syntype); 1878/6/4370 (2367), (*P. stiriaca*), Ettingshausen (1888: pl. 6, fig. 1, syntype); 1878/6/4371 (2368), Pb 2216, (*P. stiriaca*), Ettingshausen (1888: pl. 6, fig. 3, syntype); 1878/6/4403 (2400), B, Pb 2217; 1878/6/7847 (5844), (*Laurus grandifolia*), Ettingshausen (1888: pl. 3, figs 23, 23a, syntype); 1878/6/7848 (5845), Pb 2194, (*L. grandifolia*, syntype).

Description. Short-petiolate large leaves, petiole at least 4 mm long, thick, rarely preserved; lamina shape oblong, l × w up to at least 130–140 (>200) × 8–20 (50) mm, ratio l/w ~5–9.4, texture firm; base angle narrow acute, base shape straight, i.e. base (narrow) cuneate, apex angle acute, apex shape straight to slightly concave, utmost apex acute to blunt, preserved only exceptionally; margin entire; midvein straight to slightly bent, thick and distinct; secondaries eucamptodromous / brochidodromous, narrow and indistinct, often hardly visible, arising at moderately steep angles, angle of origin somewhat decreasing towards apex; secondaries regularly spaced, curved; intersecondaries occasionally developed, resembling tertiaries; tertiaries (forked-) percurrent, straight, curved to sinuous, angle towards midvein obtuse, decreasing somewhat towards margin, almost perpendicular to secondaries; higher-order veins finely reticulate.

Remarks. The biggest leaf is that described as *Laurus grandifolia* (Ettingshausen, 1888: pl. 3 fig. 23; refigured here Fig. 14.3). Possibly also *Ardisia celastrina* Ettingsh. sp. n. (Ettingshausen, 1869a: pl. 4 fig. 7) represents *Quercus rhenana*, but this specimen has not been detected among the studied material.

Especially the studies of Jähnichen (1966), Knobloch and Kvaček (1976) and Kovar-Eder (1996) rendered this fossil-species in great detail. In those cases, in which rich material is available, the assignment is possible even when cuticles are not preserved, as in the flora from Leoben. *Ficus joannis* Ettingsh., *Quercus undulata* Web., and *Verbenophyllum aculeatum* Ettingsh. from Köflach (Ettingshausen, 1858) very likely also represent *Q. rhenana*. This material is, however, not available (Kovar-Eder, 1996). The description of *Sapindus moskenbergensis* Ettingshausen (1869a)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also predates that of *Illicum rhenanum* Kräusel and Weyland (1950), which is the basionym of *Q. rhenana*, and this specimen is at hand (NHMW 1878/6/4184, Ett. 2181, Pb 1849). As the cuticular features are not preserved in the Leoben material, it is preferable to stick to the combination *Q. rhenana* instead of introducing a new combination.

By general shape foliage of *Quercus rhenana* may be difficult to distiguish from entire-margined *Myrica* leaves. A grossmorphological distinctive feature is the tertiary venation which is distinctly (forked-)percurrent in *Q. rhenana* whereas it is reticulate and more delicate in *Myrica*. (For grossmorphological differentiation from *Trigonobalanopsis rhamnoides* see that chapter.)

Q. rhenana is characteristic of swampy environments and river banks, where it is often present in mass occurrences such as known, among others, from the Oberdorf Basin (Köflach-Voitsberg lignite area at the northwestern margin of the Styrian Basin; Kovar-Eder, 1996) and Bílina (Kvaček, 1998).

***Quercus* sp. 1** – cupule

Fig. 14.19

Material. Münzenberg: NHMW: 1878/6/4234 (Ett. 2331), B; 1878/6/4395 (2392), B.

Description. Cup-shaped cupules, 14 and 15 mm in diameter, scales of the outer surface not well preserved.

Remarks. The cupules are relatively small-sized and the scales were probably short. Following the systematics of Denk et al. (2017a), the surface structure points towards sect. *Quercus*.

***Quercus* sp. 2** – cupule

Fig. 14.20

1888 *Castanea atavia* Unger, p.p.; Ettingshausen, p. 292.

Material. Seegraben Walpurgis-Schacht: NHMW: 1878/6/9186 (Ett. 7183), Pb 2365, (*Castanea atavia*).

Description. Cupule, roundish, almost 20 mm in diameter, surface with dense longitudinal scratch-like ridges running from scar of peduncle to distal margin.

Remark. This cupule differs from the above-described ones by the surface pattern, which, however, may be a result of erosion.

Genus ***Trigonobalanopsis*** Kvaček et H. Walther

Trigonobalanopsis rhamnoides (Rossmässler) Kvaček et H. Walther

Figs 14.9–14.14, 25.1

1840 *Phyllites rhamnoides*; Rossmässler, p. 35, pl. 8, figs 30, 31.
1869a *Ficus tenuinervis* Ettingsh. sp. n.; Ettingshausen, p. 54, pl. 3, fig. 4.
1869a *Cassia leptodictyon* Ettingsh. sp. n.; Ettingshausen, p. 96, pl. 6, fig. 14.
1888 *Myrica studeri* Heer; Ettingshausen, p. 284.
1888 *Quercus daphnophyllum* Ettingsh. sp. n., p.p.; Ettingshausen, p. 287, non pl. 2, figs 18, 19.
1888 *Laurus phoeboides* Ettingsh., p.p.; Ettingshausen, p. 303.
1888 *Cinchonidium bilinicum* Ettingsh., p.p.; Ettingshausen, p. 320, pl. 5, fig. 1, (?) fig. 2.
1888 *Cinchonidium multinerve* Ettingsh.; Ettingshausen, p. 320, pl. 5, figs 3, 4.
1888 *Cinchonidium angustifolium* Ettingsh., p.p.; Ettingshausen, p. 320.

Figure 14. **1**, **2**. *Quercus gigas* Goepp. emend. Walther and Kvaček (1991), **1**. NHMW 1878/6/7482 (Ett. 5479), (*Castanea atavia*), **2**. NHMW 1878/6/9205 (Ett. 7202), (*C. atavia*); **3–8**. *Quercus rhenana* (Kräusel et Weyland) Erw. Knobloch et Kvaček, **3**. NHMW 1878/6/7847 (Ett. 5844), (*Laurus grandifolia*), Ettingshausen (1888: pl. 3, figs 23, 23a, syntype), **4**. NHMW 1878/6/3863 (Ett. 1860), Pb 1986, (*Quercus daphnophyllum*), Ettingshausen (1888: pl. 2, figs 18, 18a, syntype), **5**. IBUG Ett. 5714, (*Q. daphnophyllum*), **6**. NHMW 1878/6/8754 (Ett. 6751), Pb 2078, (*Callistemophyllum productum*), Ettingshausen (1869a: pl. 6, fig. 15, holotype), **7**. NHMW 1878/6/4369 (Ett. 2366), Pb 2215, (*Plumeria stiriaca*), Ettingshausen (1888: pl. 6, fig. 2, syntype), **8**. NHMW 1878/6/4184 (Ett. 2181), Pb 1849, (*Sapindus moskenbergensis*), Ettingshausen (1869a: pl. 5, fig. 10, holotype); **9–14**. *Trigonobalanopsis rhamnoides* (Rossmässler) Kvaček et H. Walther, **9**. NHMW 1878/6/3763 (Ett. 1760), Pb 2010, (*Pomaderris acuminata*), **10**. NHMW 1878/6/3781 (Ett. 1778), Pb 1915, (*Laurus phoeboides*), **11**. NHMW 1878/6/4107 (Ett. 2104), Pb 1937, (*Cinchonidium angustifolium*), **12**. NHMW 1878/6/8611 (Ett. 6608), Pb 2255, (*Rhamnus pusillus*), Ettingshausen (1888: pl. 9, fig. 9, holotype), **13**. NHMW 1878/6/8845 (Ett. 6842), Pb 2140, (*Cassia fischeri*), **14**. NHMW 1878/6/4266 (Ett. 2263), Pb 2302, (*Pterocelastrus elaenus*); **15–17**. *Quercus mediterranea* Unger, **15**. NHMW 1878/6/7421 (Ett. 5418), (*Betula rectinervis*), Ettingshausen (1888: pl. 2, fig. 12, holotype), **16**. NHMW 1878/6/3773 (Ett. 1770), a, (*Ulmus plurinervia*), **17**. NHMW 1878/6/4195 (Ett. 2192), (*Quercus palaeo-ilex*), Ettingshausen (1888: p. 289, nomen nudum); **18a**, **b**. Fagaceae gen. et sp. – male catkin, NHMW 1878/6/9197 (Ett. 7194), A, (*Castanea atavia*), **18b**. detail enlarged; **19**. *Quercus* sp. 1 – cupule, NHMW 1878/6/4234 (Ett. 2331), B; **20**. *Quercus* sp. 2 – cupule, NHMW 1878/6/9186 (Ett. 7183), Pb 2365, (*Castanea atavia*). For all photographs the scale at bottom right of the figure is 10 mm except for photographs with embedded scale in which the scale is also 10 mm

(?) 1888 *Cinchonidium randiaefolium* Ettingsh.; Ettingshausen, p. 321, pl. 5, figs 6, 7.
1888 *Olea stiriaca* Ettingsh., p.p.; Ettingshausen, p. 322.
1888 *Fraxinus primigenia* Unger, p.p.; Ettingshausen, p. 323, (?) pl. 5 fig. 12.
1888 *Apocynophyllum amsonia* Unger, p.p.; Ettingshausen, p. 324.
1888 *Diospyros brachysepala* A. Braun, p.p.; Ettingshausen, p. 329.
1888 *Diospyros lotoides* Unger; Ettingshausen, p. 329.
1888 *Styrax antiquum* Ettingsh. sp. n., p.p.; Ettingshausen, p. 330, pl. 6, figs 15, 15a, (non figs 16–18).
1888 *Pterocelastrus elaenus* Unger, p.p. Ettingshausen, p. 344.
1888 *Rhamnus gaudinii* Heer, p.p.; Ettingshausen, p. 349.
(?) 1888 *Rhamnus aizoon* Unger; Ettingshausen, p. 350, pl. 9, fig. 8.
1888 *Rhamnus pusillus* Ettingsh. sp. n.; Ettingshausen. p. 351, pl. 9, fig. 9.
1888 *Pomaderris acuminata* Ettingsh., p.p.; Ettingshausen, p. 351, pl. 9, figs 11, 11a.
1888 *Cassia phaseolites* Unger, p.p.; Ettingshausen, p. 363.
1888 *Cassia fischeri* Heer, p.p.; Ettingshausen, p. 364.
1888 *Cassia leptodictyon* Ettingsh.; Ettingshausen, p. 364.
1888 *Cassia feroniae* Ettingsh., p.p.; Ettingshausen, p. 364, (?) pl. 9, fig. 24.
1888 *Cassia zephyri* Ettingsh., p.p.; Ettingshausen, p. 365.
1988 *Trigonobalanopsis rhamnoides* (Rossmässler) Kvaček et H.Walther; Kvaček and Walther, p. 405, pl. 49, figs 1–8, pls 50–54, pl. 55, figs 2–7, pl. 56, figs 1–4, pl. 57, text-figs 2–4.
1999 *Trigonobalanopsis rhamnoides* (Rossmässler) Kvaček et H. Walther; Meller et al., p. 137, pl. 3, figs 1–3.
2001a *Trigonobalanopsis rhamnoides* (Rossmässler) Kvaček et H. Walther; Kovar-Eder et al., pl. 3, fig. 3.

Material. Moskenberg: NHMW: 1878/6/3517 (Ett. 1514), Pb 1949, (*Olea stiriaca*); 1878/6/3559 (1556), B; 1878/6/3563 (1560), A, (*Cinchonidium bilinicum*); 1878/6/3592 (1589), B; 1878/6/3736 (1733), Pb 1933, (*C. bilinicum*); 1878/6/3763 (1760), Pb 2010, (*Pomaderris acuminata*); 1878/6/3781 (1778), Pb 1915, (*Laurus phoeboides*); 1878/6/3835 (1832), Pb 1931, (*Fraxinus primigenia*), Ettingshausen (1888: (?) pl. 5, fig. 12); 1878/6/3839 + 3840 (1836 + 1837), Pb 2062, (*Cinchonidium angustifolium*), Ettingshausen (1888: p. 363) listed Ett. 1836 (but not 1837) also for (*Cassia phaseolites*); 1878/6/3995 (1992), (*Rhamnus* sp. in sched.); 1878/6/4051 (2048), (*Rhamnus gaudinii*); 1878/6/4083 (2080), A, Pb 2065, (*Cassia phaseolites*); 1878/6/4107 (2104), Pb 1937, (*Cinchonidium angustifolium*); 1878/6/4143 (2140), (*Cassia feroniae*), possibly Ettingshausen (1888: pl. 9, fig. 24); 1878/6/4160 (2157), a, (*Diospyros brachysepala*); 1878/6/7832 (5829), (*Laurus phoeboides* in sched.); 1878/6/8128 (6125), Pb 1935, (*Cinchonidium bilinicum*); 1878/6/8275 (6272), Pb 2127, (*Diospyros lotoides*); 1878/6/8593 (6590), (*Rhamnus aizoon* in sched.); 1878/6/8610 + 8611 (6607 + 6608), Pb 2255, (*Rhamnus pusillus*), Ettingshausen (1888: pl. 9, fig. 9, holotype); 1878/6/8845 (6842), Pb 2140, (*Cassia fischeri*); 1878/6/8860 (6857), Pb 2289, (*Cassia zephyri*). Münzenberg: NHMW: 1878/6/4235 (Ett. 2232), Pb 2272, (*Pomaderris acuminata*); 1878/6/4237 (2234), (*P. acuminata*); 1878/6/4238 (2235), Pb 2256, (*Rhamnus aizoon*), Ettingshausen (1888: pl. 9, fig. 8); 1878/6/4243 (2240), (*Quercus daphnophyllum*); 1878/6/4246 (2243), Pb 2163, (*Myrica studeri*); 1878/6/4247 (2244), Pb 2164, (*M. studeri*); 1878/6/4266 (2263), Pb 2302, (*Pterocelastrus elaenus*); 1878/6/4330 (2327), Pb 2221, (*Diospyros brachysepala*); 1878/6/4343 (2340), A, Pb 2304, (*Pterocelastrus elaenus*); 1878/6/4377 (2374), Pb 2225, (*Apocynophyllum amsonia*); 1878/6/4396 (2393), Pb 2235, (*Cinchonidium multinerve*), Ettingshausen (1888: pl. 5, fig. 4); 1878/6/4408 (2405), Pb 2254, (*Rhamnus gaudinii*), also listed by Ettingshausen (1888) for (*Rhamnus aizoon*); 1878/6/8132 (6129), A, Pb 2232, (*Cinchonidium multinerve*).

Description. Petiolate leaves, petiole up to 8 mm long, stout, straight to slightly bent, basally slightly widened, laminar shape slender elliptic to almost oblong, l × w ~(25) 43–85 (102) × (8) 10–32 mm, ratio l/w ~(2.7) 3.6–4.3; base angle acute, base shape slightly convex; apex angle (narrow) acute, apex shape almost straight to slightly convex or concave, i.e. acuminate; margin entire; midvein strong, straight, secondaries campto- to brochidodromous, very regularly and medium densely spaced, rather parallel among themselves, angle of origin moderate to narrow, course slightly curved; tertiaries poorly visible, percurrent to more rarely faintly reticulate, position towards midvein wide oblique.

Remarks. Judging from the drawing, the leaf described as *Pomaderris acuminata* (Ettingshausen, 1888: pl. 9, fig. 11) very likely represents *Trigonobalanopsis rhamnoides*, but the assignment of the collection specimen to this figure is doubtful because the l/w ratio of this specimen is smaller (NHMW 1878/6/4236, Ett. 2233).

T. rhamnoides leaves are quite common in the Leoben assemblage. Although devoid of cuticles, there is no doubt about the assignment due to the general laminar shape along with the very regular pattern of secondaries. Probably because of the coriaceous texture of the blades, the tertiaries can only rarely be traced and, if at all, vaguely. The leaves of *T. rhamnoides* are distinct from Lauraceae foliage by their extremely regular pattern of secondaries and percurrent tertiaries. This fossil-species differs from foliage of *Quercus rhenana* by smaller size, smaller l/w ratio and the leaf base which is not elongated cuneate. Nevertheless, in some specimens the unambiguous assignment to either of these fossil-species is not possible (see Supplementary File 2).

Fagaceae gen. et **sp**. – male catkins

Fig. 14.18

Material. Moskenberg: NHMW: 1878/6/7499 (Ett. 5496), (*Castanea atavia*); 1878/6/7500 (5497), (*C. atavia*); 1878/6/9143 (7140), A, (*C. atavia*); 1878/6/9197 (7194), A, (*C. atavia*); 1871/38/39, B, (*C. atavia*). Münzenberg: NHMW: 1878/6/9194 (Ett. 7191), (*C. atavia*).

Description. Catkins up to 70 mm long (incomplete); florets loosely spaced along a single spindle; florets globular, diameter up to 5 mm, stamina numerous, filaments long, anthers inconspicuous.

Remarks. These remains closely resemble male catkins of *Quercus* and *Castanea* Mill. The assignment to *Q*. appears more likely due to the occurrence of several oak species and in particular of *Q. gigas*.

Family MYRICACEAE Kunth

Genus ***Myrica*** L.

Myrica joannis
Ettingsh. emend. Kovar-Eder (1996)

Figs 15.1–15.8, 25.2

1858 *Myrica joannis* Ettingsh.; Ettingshausen, p. 743, pl. 1, fig. 12.

1869a *Myrica subaethiopica* Ettingsh. sp. n.; Ettingshausen, p. 43, pl. 1, figs 29, 30.

1888 *Myrica lignitum* Unger, p.p.; Ettingshausen, p. 283.

1888 *Myrica joannis* Ettingsh.; Ettingshausen, p. 284.

cf. 1888 *Myrica sotzkiana* Ettingsh.; Ettingshausen, p. 284, pl. 2, fig. 10.

1888 *Quercus nereifolia* A.Braun, p.p.; Ettingshausen, p. 287.

1888 *Quercus lonchitis* Unger, p.p.; Ettingshausen, p. 289.

1888 *Castanea atavia* Unger, p.p.; Ettingshausen, p. 292.

1888 *Rhopalophyllum acuminatum* Unger, p.p.; Ettingshausen, p. 314, non pl. 4, figs 16–19.

1888 *Banksia haeringiana* Ettingsh., p.p.; Ettingshausen, p. 317.

1888 *Fraxinus prae-excelsior* Ettingsh. sp. n., p.p.; Ettingshausen, p. 323, non pl. 5, figs 11, 11a.

1888 *Apocynophyllum serratum* Ettingsh. sp. n., p.p.; Ettingshausen, p. 325, pl. 6, figs 6, 7.

1888 *Bombax emarginatum* Ettingsh. sp. n.; Ettingshausen, p. 335, pl. 8, figs 16, 16a.

1888 *Pterocarya denticulata* C.O. Weber, p.p.; Ettingshausen, p. 353, non pl. 9, figs 17, 17a.

1996 *Myrica joannis* Ettingsh. emend. Kovar-Eder; Kovar-Eder, p. 153, pl. 1, figs 1–6, 20, pl. 4, figs 1–8, pl. 5, fig. 10.

2001 *Myrica joannis* Ettingsh. emend. Kovar-Eder 1996; Kovar-Eder and Meller, p. 74.

2003 *Myrica joannis* Ettingsh. emend. Kovar-Eder 1996; Kovar-Eder and Meller, p. 241, pl. 1, fig. 11, pl. 4, figs 1–3.

Material. Moskenberg: NHMW: 1878/6/3725 (Ett. 1722), Pb 2040, (*Pterocarya denticulata*); 1878/6/3733 + 3798 (1730 + 1795), (*Myrica joannis*); 1878/6/3827 (1824), (*Quercus nereifolia*); 1878/6/3871 + 3872 (1868 + 1869, a), Pb 2001, (*Apocynophyllum serratum*), Ettingshausen (1888: pl. 6, fig. 7a, syntype); 1878/6/3880 (1877), Pb 2118, (*Bombax emarginatum*), Ettingshausen (1888: pl. 8, figs 16, 16a, holotype); 1878/6/3906 (1903), (*Myrica joannis*); 1878/6/3999 (1996), Pb 1999, (*Apocynophyllum serratum*), Ettingshausen (1888: pl. 6, fig. 7, syntype); 1878/6/4056 (2053), (*Myrica lignitum*); 1878/6/4104 (2101), (2 leaves), (*M. lignitum*); 1878/6/4124 (2121), (*M. lignitum* var. *angustifolia*); 1878/6/4125 (2122), (*M. lignitum* var. *undulata*); 1878/6/4126 (2123), A, (*M. lignitum* var. *serrata*); 1878/6/4127 (2124), (*M. lignitum* var. *remote dentata* in sched.); 1878/6/4128 + 4129 (2125 + 2126), (*M. lignitum* var. *remote dentata* in sched.); 1878/6/4161, C + 7866, C (2158 + 5863), Pb 1970; 1878/6/4164 (2161), (*Apocynophyllum* sp. in sched.); 1878/6/7999 (5996), B, Pb 1979; 1878/6/8824 (6821), B, Pb 2079; 1878/6/8896 (6893), B; 1878/6/9067 (7064), B;

1878/6/9131 (7128), B, on backside; 1878/6/9143 (7140), B. IBUG: Ett. 5768, (*Castanea atavia*). Münzenberg: NHMW: 1878/6/4245 (Ett. 2242), (*Myrica lignitum* var. *latifolia*); 1878/6/4333 (2330), Pb 2226, (*Apocynophyllum serratum*, syntype); 1878/6/4357 (2354), Pb 2238, (*Banksia haeringiana*); 1878/6/4373 (2370), (*Grevillea* sp. in sched.); 1878/6/4387 (2384), Pb 2236, (*Rhopalophyllum acuminatum*); 1878/6/7340 (5337), Pb 2165, (*Myrica joannis*). IBUG: Ett. 6091, (*Fraxinus prae-excelsior*), Ettingshausen (1888: (?) syntype). Seegraben Walpurgis-Schacht: NHMW: 1878/6/4474 (Ett. 2471), Pb 2337, (*Myrica joannis*). Seegraben Unter-Buchwieser: NHMW: 1878/6/4417 (Ett. 2414), Pb 2360, (*Apocynophyllum serratum*), Ettingshausen, (1888: pl. 6, fig. 6).

Description. Long-petiolate leaves; petiole up to 22 mm long, straight to somewhat bent, base swollen; lamina oblong, more rarely slender elliptic to obovate, l × w ~(42) 70–200 × (6) 10–32 mm, ratio l/w 4.1–7; base angle narrow acute, base shape straight; when midvein bent, one side weakly convex the other weakly concave, decurrent; margin simple serrate, serration usually starting already near base, teeth mostly tiny to very inconspicuous, height <1 mm, more rarely conspicuous, height >1 mm; teeth rather regularly spaced, up to 4 per cm, sometimes teeth only irregularly scattered; often triangular with distal and proximal flanks being straight, sinus acute or narrow rounded, apex acute or blunt; midvein thick, secondaries semicraspedodromous, considerably thinner and more indistinct than midvein, originating at (very) wide angles, running smoothly curved towards margin, forking near margin and looping with adjacent veins, branches of secondaries or exmedial veinlets running into teeth and/or sinus; intersecondaries occasionally present, reaching at least half distance towards margin; tertiaries and higher-order veins reticulate.

Remarks. Ettingshausen (1888) differentiated *Myrica joannis* from *M. lignitum* by a higher number of bent (inter)secondaries intercalated between secondaries reaching the margin and by usually more acute marginal teeth further inclined towards the leaf apex. Ettingshausen stated, however, the difficulties in assigning leaves to either of the fossil-species. Having studied *Myrica* material from the surroundings of Linz (Upper Austria; Kovar, 1982), Parschlug (Kovar-Eder et al., 2004), Oberdorf (Kovar-Eder, 1996; Kovar-Eder and Meller, 2001) and Leoben, the differences regarding secondary venation cannot be confirmed. Grossmorphologically, the differentiation of *M. joannis* is based on the mostly regular and rather densely spaced, often triangular small teeth starting already near the base of the blades. The variability of the marginal serration has been illustrated by Kovar-Eder (1996) and is well reflected in the Leoben material (Fig. 15.1–15.8). In the Leoben assemblage such leaves are more abundant than leaves of *M. lignitum* (see below). In Oberdorf, *M. joannis* is not accompanied by *M. lignitum* (Kovar-Eder and Meller, 2001), whereas in Parschlug *M. lignitum* is among the most abundant fossil-species but evidence of *M. joannis* is not available (Kovar-Eder et al., 2004). These facts underline the probability of two fossil-species rather than a single one with an extremely variable morphology. Furthermore, cuticle studies provided evidence that *M. joannis* differs from *M. lignitum* by a lower density of two-celled trichome bases (Kovar-Eder, 1996). Nevertheless, an unambiguous distinction of the leaves of both fossil-species is not always possible.

The leaves of *Myrica subaethiopica* Ettingsh. sp. n. (Ettingshausen, 1869a: pl. 2, figs 29, 30) from Moskenberg have not been detected among the studied material. They definitely represent *M. joannis*. The specimen on which *Bombax emarginatum* Ettingsh. sp. n. (Ettingshausen 1888: pl. 8, figs 16, 16a) is based also represents, most likely, a leaf of *M. joannis* in which the apex growth was reduced probably due to damage in the juvenile state (refigured here on Fig. 15.5). (For grossmorphological differentiation of almost entire leaves from *Quercus rhenana* see that chapter.)

Myrica lignitum
(Unger) Saporta sensu Ettingshausen et Standfest (1888)

Figs 15.9–15.12, 25.3

1847 *Quercus lignitum* Unger; Unger, p. 113, pl. 31, figs 5–7.

1865 *Myrica lignitum* Unger; Saporta, p. 102, pl. 5, fig. 10.

1888 *Myrica lignitum* Unger, p.p.; Ettingshausen, p. 283, non pl. 2, fig. 9.

1888 *Quercus lonchitis* Unger, p.p.; Ettingshausen, p. 289.

1888 *Apocynophyllum reussii* Ettingsh., p.p.;

Ettingshausen, p. 324, pl. 5, fig. 22, non figs 21, 23, 35.

1888 *Eucalyptus oceanica* Unger, p.p.; Ettingshausen, p. 357.

1888 *Myrica lignitum* Unger; Ettingshausen and Standfest, p. 255, pls 1, 2.

2004 *Myrica lignitum* (Unger) Saporta; Kovar-Eder et al., p. 64, pl. 7, figs 1–6, 8, 9.

2022 *Myrica lignitum* (Unger) Saporta; Kovar-Eder et al., p. 97.

Material. Moskenberg: NHMW: 1878/6/3520 (Ett. 1517), Pb 2276, (*Eucalyptus oceanica*); 1878/6/3521 (1518), (*Myrica lignitum* var. *integrifolia*); 1878/6/3522 (1519), (*M. lignitum* var. *remote dentata*); 1878/6/3532 (1529), B; 1878/6/4083 (2080), B. Münzenberg: NHMW: 1878/6/4241 (Ett. 2238), Pb 2257, (*Quercus lonchitis*); 1878/6/4332 (2329), Pb 2229, (*Apocynophyllum reussii*), Ettingshausen (1888: pl. 5, fig. 22). Leoben: GBA: 2024/0001/0007, (*Fagus castaneaefolia*).

Description. Long-petiolate leaves, petiole up to 8 mm long (incomplete); lamina slender oblong, l × w ~45–140 × 6–22 mm, ratio l/w ~5.6–7.5; base angle narrow acute, base shape straight, decurrent; apex angle narrow acute, apex shape straight, i.e. attenuate, utmost apex not preserved (?) blunt or acute; margin simple serrate, undulate to entire, teeth regularly to irregularely spaced, about one tooth per cm or less, tooth height <1 mm to 1–5 mm, sinus rounded or acute, apex blunt or acute, distal and proximal flanks variable, distal flank straight, convex, concave, sinuate, proximal flank straight, slightly convex or concave; midvein thick, straight, in the basal part occasionally bent; secondaries distinctly weaker than midvein, semicraspedodromous, arising at wide angles from midvein, spacing variable, running curved towards margin, forking mostly near margin, occasionally at a greater distance from it, looping with adjacent veins; branches of secondaries or exmedial veinlets running into teeth; intersecondaries present; tertiaries random reticulate, higher-order veins polygonal reticulate.

Remarks. *Myrica lignitum* has been treated extensively by different authors (Ettingshausen and Standfest, 1888; Knobloch and Kvaček, 1976; Kovar, 1982). Only few leaves unambiguously represent this fossil-species compared to *M. joannis*. In specimen NHMW 1878/6/3522 (Ett. 1519), which Ettingshausen assigned to *M. lignitum* var. *remote dentata*, the venation pattern is best preserved (Fig. 15.9). For the distinction from *M. joannis* see above and of almost entire leaves from *Quercus rhenana* see that chapter.

Myrica (?) **sp.** – fructus

Fig. 15.13

1888 *Myrica lignitum* Unger, p.p.; Ettingshausen, p. 283, pl. 2, figs 9, 9a.

Material. Moskenberg: NHMW: 1878/6/3724 (Ett.1721), a, (*Myrica* sp. in sched.).

Description. Globoid fruit, ~2 mm in diameter.

Remarks. Although Ettingshausen (1888) mentioned *Myrica* fruits from the Leoben assemblage, only a single specimen was detected in the here studied material possibly representing *Myrica*. The warty surface is only partly preserved and indistinct.

Family JUGLANDACEAE Perleb

Genus ***Engelhardia*** Lesch. ex Blume

Engelhardia macroptera (Brongn.) Unger

Fig. 15.23

1828 *Carpinus macroptera* Brongn.; Brongniart, p. 48, pl. 3, fig. 6.

1866 *Engelhardtia macroptera* Brongn.; Unger, p. 52, pl. 16, figs 9–11.

1888 *Engelhardtia macroptera* Saporta, p.p.; Ettingshausen, p. 354, non pl. 8, fig. 15.

1999 *Engelhardia macroptera* (Brongn.) Unger; Ströbitzer, p. 105, pl. 4, fig. 7, pl. 11, fig. 10.

2004 *Engelhardia macroptera* (Brongn.) Unger; Kovar-Eder et al., p. 65, pl. 6, figs 8, 9.

Material. Moskenberg: NHMW: 1878/6/3599 (Ett. 1596) (*Engelhardia brongniartii*).

Description. Fragment of a three-lobed involucrum, fruit indicated by limonitic concretion; central and one lateral lobe of involucrum preserved, shape of lobes oblong, central one slightly widened in apical part; length of central lobe 30 mm, length of lateral one 17 mm (measured from base), width (largest extension of lateral lobes) ~27 mm; each lobe with midvein and an additional one on both sides arising from the lobe base, more or less paralleling midvein; central and lateral veins forking in distal part of involucrum; few secondary veins ascending from the central vein, originating under moderate to steep angles, also forking in distal part


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of lobe; veins partly joining or joined by further veins forming large, irregular meshes.

Remarks. The morphology of this remain corresonds very well with the detailed description provided by Jähnichen et al. (1977). This involucrum is the only unambiguous proof of an *Engelhardia* fructification in the Leoben assemblage. The second specimen listed for *E. brongniartii* by Ettingshausen (1888: p. 354) is a catkin of uncertain systematic position (see paragraph Male catkins and florets gen. et sp.), and the leaf figured by Ettingshausen (1888: pl. 8, fig. 15) has not been detected among the studied material but appears to be of Betulaceae affinity.

Engelhardia orsbergensis
(P. Wessel et C.O. Weber)
Jähnichen, Mai et H. Walther

Fig. 15.14–15.22

1856 *Banksia orsbergensis* P. Wessel et C.O. Weber; Wessel and Weber, p. 146, pl. 25, fig. 9a–d.
1888 *Rhopalophyllum acuminatum* (Unger) Ettingsh., p.p.; Ettingshausen, p. 314, pl. 4, figs 16–19.
1888 *Banksia longifolia* Ettingsh., p.p.; Ettingshausen, p. 316, pl. 4, fig. 9.
1888 *Banksia ungeri* Ettingsh.; Ettingshausen, p. 317.
1888 *Sapindus cassioides* Ettingsh., p.p.; Ettingshausen, p. 343.
1977 *Engelhardia orsbergensis* (P. Wessel et C.O. Weber) Jähnichen, Mai et H. Walther; Jähnichen et al., p. 326, pls 38–49, text-figs 1–3.
2004 *Engelhardia orsbergensis* (P. Wessel et C.O. Weber) Jähnichen, Mai et H. Walther; Kovar-Eder et al., p. 65, pl. 6, figs 10–12.
2022 *Engelhardia orsbergensis* (P. Wessel et C.O. Weber) Jähnichen, Mai et H. Walther; Kovar-Eder et al., p. 94, pl. 6, figs 21–23.

Material. Moskenberg: IBUG: Ett. 6072, (*Banksia longifolia*); Ett. 6073 + 6074, (*Banksia longifolia*). Münzenberg: NHMW: 1878/6/4388 (Ett. 2385), Pb 2237, (*Rhopalophyllum acuminatum*); 1878/6/4401 (2398), (*Cassia* sp. in sched.); 1878/6/4406 (2403), Pb 2258, (*Sapindus cassioides*); 1878/6/8053 (6050), Pb 2199, (*Banksia longifolia*), Ettingshausen (1888: pl. 4, fig. 9.). IBUG: Ett. 6067, (*Rhopalophyllum acuminatum*). Seegraben Walpurgis-Schacht: NHMW: 1878/6/4456 + 4457 (Ett. 2453 + 2454), Pb 2361, (*Banksia ungeri*); Ettingshausen (1888: p. 316) listed Ett. 2154 instead of no. 2454 (likely a printing error); 1878/6/4458 + 4459 (2455 + 2456), (*Dryandroides* sp. in sched.). IBUG: Ett. 6072, (*Banksia longifolia*). Leoben: GBA: 2024/0001/0016, fragmentary pinnate leaf. NATURALIS: RGM.THDB.6761, (*Rhopalophyllum acuminatum*), Ettingshausen (1888: pl. 4, fig. 16); RGM.THDB. 6796, B.

Description. A fragmentary pinnate leaf and isolated, mostly fragmentarily preserved leaflets, (sub)sessile except for terminal one which is long-petiolate, leaflet lamina oblong, l × w ~40–80 × 8–14 mm, ratio l/w ~4–8; base asymmetrical, base angle acute to obtuse, shape convex, in the case of bent midvein convex on one and straight to concave on other side; apex angle narrow acute, shape straight or, in case of bent midvein convex on one and concave on other side; margin simple serrate, teeth widely and irregularly spaced, small, tooth height ~1 mm, triangular, distal flank straight to concave, proximal flank straight, convex or concave; midvein straight or bent, thick; secondairies delicate, faint, brochidodromous,

◄———

Figure 15. **1–8**. *Myrica joannis* Ettingsh. emend. Kovar-Eder (1996), **1**. NHMW 1878/6/7340 (Ett. 5337), Pb 2165, (*Myrica joannis*), **2**. NHMW 1878/6/9131 (Ett. 7128), B, **3**. NHMW 1878/6/4128 (Ett. 2125), (*M. lignitum* var. *remote dentata* in sched.), **4**. IBUG Ett. 6091 (*Fraxinus prae-excelsior*), Ettingshausen (1888: (?) syntype), **5**. NHMW 1878/6/3880 (Ett. 1877), Pb 2118, (*Bombax emarginatum*), Ettingshausen (1888: pl. 8, figs 16, 16a, holotype), **6**. NHMW 1878/6/4124 (Ett. 2121), (*Myrica lignitum* var. *angustifolia*), **7**. NHMW 1878/6/3725 (Ett. 1722), Pb 2040, (*Pterocarya denticulata*), **8**. NHMW 1878/6/9067 (Ett. 7064), B; **9–12**. *Myrica lignitum* (Unger) Saporta sensu Ettingshausen et Standfest (1888), **9**. NHMW 1878/6/3522 (Ett. 1519), (*Myrica lignitum* var. *remote dentata*), **10**. NHMW 1878/6/3521 (Ett. 1518), (*M. lignitum* var. *integrifolia*), **11**. NHMW 1878/6/4241 (Ett. 2238), Pb 2257, (*Quercus lonchitis*), **12**. NHMW 1878/6/3532 (Ett. 1529), B; **13**. *Myrica* (?) sp. – fructus, NHMW 1878/6/3724 (Ett.1721), a; **14–22**. *Engelhardia orsbergensis* (P. Wessel et C.O. Weber) Jähnichen, Mai et H. Walther, **14**. NHMW 1878/6/4401 (Ett. 2398), (*Cassia* sp.), two partly superimposed leaflets of likely one leaf, **15**. IBUG Ett. 6072, (*Banksia longifolia*), **16**. NHMW 1878/6/4458 (Ett. 2455), (*Dryandroides* sp.), **17**. NHMW 1878/6/8053 (Ett. 6050), Pb 2199, (*Banksia longifolia*), Ettingshausen (1888: pl. 4, fig. 9.), **18**. NHMW 1878/6/4406 (Ett. 2403), Pb 2258, (*Sapindus cassioides*), **19**. IBUG Ett. 6067, (*Rhopalophyllum acuminatum*), **20**. NHMW 1878/6/4388 (Ett. 2385), Pb 2237, (*R. acuminatum*), **21a**, **b**. NATURALIS RGM.THDB.6761, (*R. acuminatum*), Ettingshausen (1888: pl. 4, fig. 16); terminal leaflet on rhachis, **21b**. close up of leaflet, **22**. GBA 2024/0001/0016, fragmentary pinnate leaf with several leaflets; **23**. *Engelhardia macroptera* (Brongn.) Unger, NHMW 1878/6/3599 (Ett. 1596) (*Engelhardia brongniartii*); **24**, **25**. *Pterocarya paradisiaca* (Unger) Iljinskaja, **24**. NHMW 1878/6/4214 (Ett. 2211), Pb 2037, (*Pterocarya denticulata*), Ettingshausen (1888: pl. 9, figs 17, 17a), **25**. NHMW 1878/6/3836 (Ett. 1833), A, Pb 2038, (*P. denticulata*). For all photographs the scale at bottom right of the figure is 10 mm except for photographs with embedded scale. If not stated otherwise the embedded scale is also 10 mm

densely spaced, at moderate to wide angles, intersecondaries present.

Remarks. Ettingshausen (1888) already recognised that these remains represent leaflets rather than leaves. The true systematic affinity of such leaflets, however, was recognised only by Jähnichen et al. (1977, 1984). The specimen NATURALIS RGM.THDB.6761 figured by Ettingshausen (1888: pl. 4, fig. 16) as *Rhopalophyllum acuminatum* represents the rhachis with still attached terminal leaflet (refigured here on Fig. 15.21). Except for the fragmentary pinnate leaf, which was detected in the collection of GBA (Fig. 15.22), the two closely spaced leaflets on slab NHMW 1878/6/4401 (Ett. 2398) (Fig. 15.14) indicate that they may derive from a single compound leaf. Specimen NHMW 1878/6/8053 (Ett. 6050) (Fig. 15.17), which is incomplete at the base, has been labelled in the collection by H. Walther as "cf. *Myrica longifolia*". More likely it represents an *Engelhardia* leaflet because *M. longifolia* is restricted to the Paleogene.

Genus ***Juglans*** L.

Juglans reussii Ettingsh.

Fig. 16.1–16.5

1869a *Juglans reussii* Ettingsh. sp. n.; Ettingshausen, p. 46 pl. 52, figs 1, 2.
1888 *Ficus lanceolata* Heer, p.p.; Ettingshausen, p. 296.
1888 *Juglans acuminata* A. Braun, p.p.; Ettingshausen, p. 352.
1888 *Juglans reussii* Ettingsh., p.p.; Ettingshausen, p. 353.

Material. Moskenberg: NHMW: 1878/6/4126 (Ett. 2123), B; 1878/6/8616 (6613), Pb 2052, (*Juglans reussii*). Münzenberg: NHMW: 1878/6/4224 (Ett. 2221), Pb 2048, (*Juglans acuminata*); 1878/6/4314 (2311), Pb 2206, (*Ficus lanceolata*); 1871/38/32. IBUG: Ett. 6210, A + 6211, A; Ettingshausen's determinations of (*Celastrus europaea* in sched.) and (*Sapindus dubius* in sched.) could not be be assigned to the leaves on this slab (see Supplementary File 1). Seegraben Walpurgis-Schacht: IBUG: Ett. 6299, (*Ficus lanceolata*).

Description. Leaflets, mostly fragmentary; lamina shape oblong to broad elliptic to slightly obovate, l × w ~85 to >140 × 44–56 mm, ratio l/w ~1.9–3.1; base angle acute, shape asymmetrical, convex to almost straight; apex angle acute to obtuse (?), shape acute to acuminate (?); margin simple serrate, occasionally basal part entire-margined (IBUG Ett. 6299); teeth often indistinct, tooth height up to ~1 mm, more or less regularly spaced, distal flank very short, straight, proximal flank variable, straight, slightly convex or concave to flexuous; sinus angular, apex acute; midvein straight or bent; secondaries semicraspedodromous, rather regularly, moderately to widely spaced, angle of origin wide to moderate, course curved, rarely forked, inconspicuously looping near margin; exmedial veinlets running into teeth apices and sinus; intersecondaries rare; tertiaries percurrent to forked percurrent, straight to sinuate, angle of tertiaries to midvein oblique, almost perpendicular to secondaries; higher-order venation rarely visible, reticulate.

Remarks. Only one specimen of those listed by Ettingshausen (1888) for *J. reussii* is available. It is rather well preserved, showing the marginal serration and the secondary and tertiary venation (NHMW 1878/6/8616, Ett. 6613; Fig. 16.5). The specimen assigned by Ettingshausen (1888) to *Ficus lanceolata* (NHMW 1878/6/4314, Ett. 2311) shows very tiny and few teeth, as does specimen IBUG Ett. 6299 in the apical part of the leaflet. The margin of leaflet NHMW 1878/6/4224 (Ett. 2221), which Ettingshausen (1888) assigned to *Juglans acuminata*, is also clearly serrate (Fig. 16.3), which is not characteristic of that fossil-species.

Usually entire or nearly entire-margined Juglandaceae leaflets are attributed to *J. acuminata*, reminiscent of modern *J. regia* L. In most modern walnut species, however, the leaf margin is serrate. The teeth of the here summarised leaflets resemble those of *J. cinerea* L. The (forked-)percurrent tertiaries enable the distinction from, e.g. leaflets of *Fraxinus*, in which the tertiaries are reticulate.

Juglans **sp.**

Fig. 16.6

(?) 1888 *Sapindus moskenbergensis* Ettingsh., p.p.; Ettingshausen, p. 342.

Material. Leoben: NATURALIS: RGM. THDB. 6796, A, (*Sapindus moskenbergensis*).

Description. Leaflet lacking apex, petiole short, 4 mm long; lamina elliptic, asymmetrical near base, l × w ~85 × 38 mm, ratio l/w ~2.2, base angle acute, base shape convex; margin entire; midvein straight; secondaries camptodromous to brochidodromous, spacing rather regular and moderately wide, course curved; one to two intersecondaries interspaced between adjacent 2° veins, reaching about one third of distance between midvein and margin; tertiaries (forked-)percurrent, obtuse to midvein, further vein fabric reticulate.

Remarks. This specimen of the collection NATURALIS is labelled as *Sapindus moskenbergensis*. It is uncertain whether the assignment was done by Ettingshausen. Therefore, the synonymy remains equivocal. Likely it represents *Juglans* which is indicated by its shape and the pattern of secondaries and percurrent tertiaries. It differs from *J. reussii* by the entire margin (see paragraph above). Leaflets of *J. acuminata* A. Braun are petiolate and the 2° veins are more densely spaced, hence more numerous, than in the here described specimen. The systematic position of that fossil-species is still a matter of debate (e.g. Kvaček et al., 2011).

Genus ***Pterocarya*** Kunth

Pterocarya paradisiaca (Unger) Iljinskaja

Figs 15.24, 15.25, 25.4

1849 *Prunus paradisiaca* Unger; Unger, p. 7, pl. 14, fig. 22.

1888 *Pterocarya denticulata* C.O. Weber, p.p.; Ettingsh., p. 353, pl. 9, figs 17, 17a.

1962 *Pterocarya paradisiaca* (Unger) Iljinskaja; Iljinskaja, p. 104.

1964 *Pterocarya paradisiaca* (Unger) Iljinskaja; Iljinskaja, p. 130, pl. 2, figs 1–4, pl. 6, fig. 9.

Material. Moskenberg: NHMW: 1878/6/3836 (Ett. 1833), A, Pb 2038, (*Pterocarya denticulata*); 1878/6/4214 + 8644 (2211 + 6641), Pb 2037, (*P. denticulata*), Ettingshausen (1888: pl. 9, figs 17, 17a).

Description. Probably sessile leaflets; lamina shape oblong to slightly elliptic or ovate, asymmetrical in basal part, l × w ~54–65 × 18–21 mm, ratio l/w ~3–3.1; base angle acute, base shape asymmetrical, straight to convex; apex angle acute, apex shape rather straight to somewhat acuminate; margin densely and rather regularly serrate, only near utmost base entire, tooth height up to 1 mm, distal flank mainly straight, proximal flank mostly straight to concave, sinus angular, apex (bluntly) acute; midvein straight to slightly bent near base; secondaries (semi) craspedodromous, moderately and rather regularly spaced, arising almost perpendicular from midvein near base, angle of origin decreasing towards apex, angle near apex moderate; near midvein course of 2° veins straight to curved, near margin distinctly curved, looping with adjacent secondaries; exmedial veinlets further looping near margin; terminal veinlets ending in tooth apices or occasionally in sinus; tertiaries percurrent, partly forked-percurrent, straight to sinuate, near leaf base almost parallel to midvein, in apical part of lamina wide obtuse to midvein; higher-order veins reticulate.

Remarks. *Pterocarya* leaflets are very rare in the Leoben assemblage. Of those listed by Ettingshausen (1888) for *P. denticulata*, one doubtlessly represents *Myrica joannis* (see that section). In *P. leobensis* Ettingsh. (Ettingshausen 1869a: pl. 6, fig. 19; 1888: p. 354, NHMW 1878/6/8645, Ett. 6642) the pattern of secondaries is rather irregular and therefore this generic assignment must be rejected (see *Dicotylophyllum* sp. C).

Juglandaceae gen. et **sp**.

Figs 16.7, 25.5, 25.6

(?) 1888 *Prunus palaeo-cerasus* Ettingsh., p.p.; Ettingshausen, p. 361.

1888 *Phaseolites securidacus* Unger, p.p.; Ettingshausen, p. 362.

Material. Moskenberg: NHMW: (?) 1878/6/3727 (Ett. 1724), a, (*Prunus palaeo-cerasus*). Seegraben Walpurgis-Schacht: NHMW: 1878/6/4468 (Ett. 2465), A, (*Phaseolites securidacus*).

Description. Probably leaflet; NHMW 1878/6/4468 (Ett. 2465, A): laminar shape elliptic to almost oblong, l × w ~42 × 18 mm, ratio l/w ~2.3; base incomplete, angle obtuse, shape convex; apex incomplete, angle acute, shape (?) straight; margin regularly simple serrate, 2–4 teeth between adjacent secondaries, tooth height around 1 mm, distal flank concave or straight, proximal flank slightly convex to straight, sinus angular, apex acute; midvein straight, secondaries semicraspedodromous, regularly spaced, in middle part of lamina at 4–5 mm distance, angle of origin wide, almost perpendicular to midvein in basal part, angle decreasing apically; secondaries curved, sometimes forking once in marginal third of lamina; secondaries


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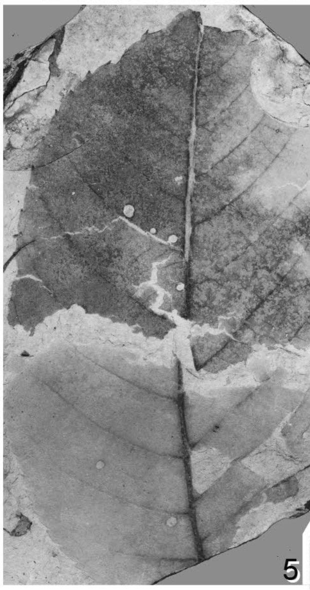
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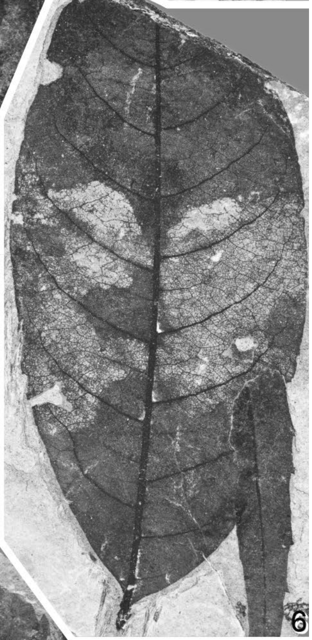
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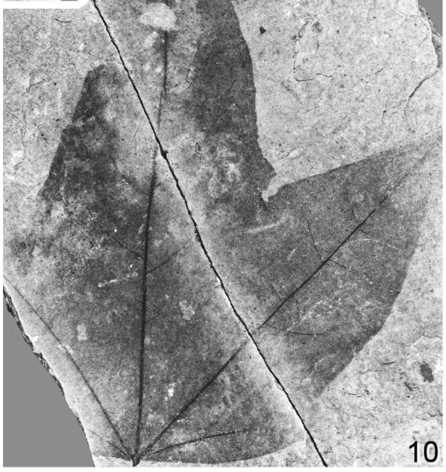
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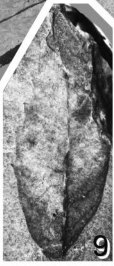
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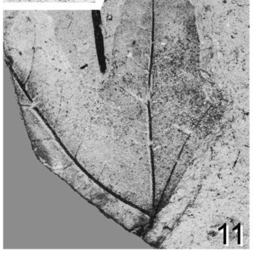
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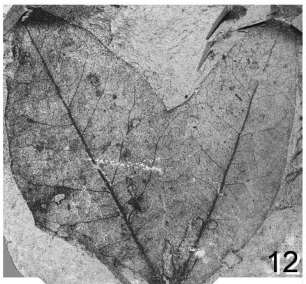
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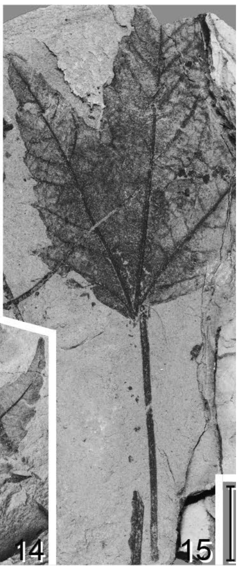
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or their branches more or less distinctly looping; indistinct intersecondaries present, reaching to about one third of distance between midvein and margin; tertiaries percurrent, distinctly weaker than secondaries, almost paralleling midvein and perpendicular to 2° veins, straight to somewhat sinuate; higher-order veins reticulate.

Remarks. It remains unclear why Ettingshausen (1888) listed this specimen as *Phaseolites securidacus*, which is entire-margined. This specimen may rather represent a basal leaflet of a compound Juglandaceae leaf. Tertiaries almost paralleling the midvein do occur in Juglandaceae (own observation). Their angle towards the midvein depends on leaflet shape and position within the leaflet.

Order SAPINDALES Bercht. et J. Presl

Family ANACARDIACEAE R. Brown

Genus ***Toxicodendron*** Auct.

Toxicodendron melaenum (Unger) Doweld

Fig. 16.8, 16.9

1850a *Rhus herthae* Unger; Unger, p. 473.
1850a *Juglans melaena* Unger; Unger, p. 470.
1860 *Rhus herthae* Unger; Unger, p. 42, pl. 20, figs 7–9.
1860 *Juglans melaena* Unger; Unger, p. 38, pl. 19, figs 8–10.
1888 *Acer decipiens* A. Braun, p.p.; Ettingshausen, p. 340, pl. 8, fig. 3, non figs 2, 4, 5.
1888 *Rhus intermedia* Ettingsh. sp. n., p.p.; Ettingshausen, p. 355, (?) pl. 9, fig. 13.
1998 *Toxicodendron herthae* (Unger) Kvaček et H. Walther; Kvaček and Walther, p. 27, pl. 15, figs 3–8; text-fig. 13/16.
2004 *Toxicodendron herthae* (Unger) Kvaček et H. Walther; Kovar-Eder et al., p. 80, pl. 9, figs 17–19.
2007 *Toxicodendron herthae* (Unger) Kvaček et H. Walther; Kvaček and Walther, p. 125, pl. 20, fig. 1, text-fig. 10.
2022 *Toxicodendron melaenum* (Unger) Doweld; Kovar-Eder et al., p. 100, pl. 10, figs 3–9.

Material. Moskenberg: NHMW: 1878/6/4148 (Ett. 2145), Pb 2031, (*Rhus intermedia*), Ettingshausen (1888: (?) pl. 9, fig. 13, syntype). Münzenberg: NHMW: 1878/6/4393 (Ett. 2390), c, Pb 2338, (*Acer decipiens*).

Description. Terminal and lateral leaflet; terminal leaflet NHMW 1878/6/4393 (Ett. 2390, c): probably three-lobed but left lobe incomplete; central lobe distinctly larger than lateral one, 31 mm long; lateral lobe at right much shorter, resembling a big tooth, 18 mm long, maximal width of leaflet 14 mm (incomplete); base angle acute, base shape almost straight; apex angle of central lobe acute, apex shape convex on one and concave on other side, apex angle of lateral lobe almost 90°, apex shape straight, utmost apex of both lobes blunt; sinus between lobes widely rounded; margin entire; venation basal acrodromous; main veins straight, slender, lateral ones running near margin, ending in lobe apices; angle between central and lateral veins 20–30°; secondary veins widely spaced, delicate, straight to slightly curved, brochidodromous.

Lateral leaflet (NHMW 1878/6/4148, Ett. 2145): sessile; lamina elliptic, asymmetrical, l × w ~30 × 13 mm, ratio l/w ~2.3; base distinctly asymmetrical, base angle acute, base shape convex; apex incomplete, angle (?) acute; margin entire in basal part of lamina, simple serrate in upper part, serration starting higher up on more narrow side of lamina than on wider one; teeth rather regularly spaced, 3 teeth per cm, ~1 mm high, distal flank straight to convex, proximal flank concave, sinus angular to rounded, apex bluntly acute; midvein straight; secondaries (?) craspedodromous, arising under wide angle from midvein on wider side of lamina, under moderate angle on more narrow side, spacing wide, course of secondaries moderately curved.

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Figure 16. **1–5**. *Juglans reussii* Ettingsh., **1**. NHMW 1878/6/4314 (Ett. 2311), Pb 2206, (*Ficus lanceolata*), **2**. IBUG Ett. 6299, (*F. lanceolata*), **3**. NHMW 1878/6/4224 (Ett. 2221), Pb 2048, (*Juglans acuminata*), **4**. NHMW 1878/6/4126 (Ett. 2123), B, **5**. NHMW 1878/6/8616 (Ett. 6613), Pb 2052, (*J. reussii*); **6**. *Juglans* sp., NATURALIS: RGM.THDB. 6796, A, (*Sapindus moskenbergensis*); **7**. Juglandaceae gen. et sp., NHMW 1878/6/4468 (Ett. 2465), A, (*Phaseolites securidacus*); **8**, **9**. *Toxicodendron melaenum* (Unger) Doweld, **8**. NHMW 1878/6/4393 (Ett. 2390), c, Pb 2338, (*Acer decipiens*), **9**. NHMW 1878/6/4148 (Ett. 2145), Pb 2031, (*Rhus intermedia*), Ettingshausen (1888: (?) pl. 9, fig. 13, syntype); **10**, **11**. *Acer integerrimum* (Viviani) Massalongo, **10**. IBUG Ett. 6148, (*Sterculia labrusca*), **11**. NHMW 1878/6/4209 (Ett. 2206), C; **12**. *Acer pseudomonspessulanum* Unger emend. Ströbitzer-Hermann (2003), NHMW 1878/6/3569 (Ett. 1566), Pb 2024, (*Acer decipiens*); **13–15**. *Acer tricuspidatum* Bronn, **13**. IBUG Ett. 6333 (*Acer tilobatum*), **14**. NHMW 1878/6/4196 (Ett. 2193), Pb 2030, (*A. trilobatum*), **15**. NHMW 1878/6/3544 (Ett. 1541), (*A. trilobatum*). For all photographs the scale at bottom right of the figure is 10 mm

Remarks. Compared to *Acer pseudomonspessulanum* Unger (formerly *A. decipiens* A. Braun) the lateral lobes of the terminal leaflet of *Toxicodendron melaenum* are distinctly shorter, resembling large teeth. Compared to remains from other sites such as Kundratice (Kvaček and Walther, 1998), Seifhennersdorf (Walther and Kvaček, 2007) and Parschlug (Kovar-Eder et al., 2004, 2022) the lateral leaflet is of smaller size.

Family SAPINDACEAE Jussieu

Subfamily ACEREAE (Durande) Dumortier

Genus ***Acer*** L.

Sect. *Acer*, Ser. *Monspessulana* Pojark.

Acer pseudomonspessulanum Unger emend. Ströbitzer-Hermann (2003)

Figs 16.12, 25.7

1847 *Acer pseudomonspessulanum* Unger; Unger, p. 132, pl. 43, figs (?) 1, 2, non 3 and 4.
1888 *Acer decipiens* A. Braun, p.p.; Ettingshausen, p. 340, non pl. 8, figs 2–4.
1972 *Acer decipiens* A. Braun sensu Walther; Walther, p. 121, pl. 2, figs (?) 5, 6, 7, non 8 and 9, pl. 54, figs 5, 7; non 9.
1975 *Acer pseudomonspessulanum* Unger; Procházka and Bůžek, p. 61, text-figs 1c–f, 21a, b, (?) c, (?) d, e, non f.
2003 *Acer pseudomonspessulanum* Unger emend. Ströbitzer-Hermann; Ströbitzer-Hermann, p. 41, pl. 5, figs 1–6.
2004 *Acer pseudomonspessulanum* Unger emend. Ströbitzer-Hermann (2003); Kovar-Eder et al., p. 77, pl. 10, figs 7–9.
2022 *Acer pseudomonspessulanum* Unger emend. Ströbitzer-Hermann (2003); Kovar-Eder et al., p. 85, pl. 1, fig. 1.

Material. Moskenberg: NHMW: 1878/6/3569 (Ett. 1566), Pb 2024, (*Acer decipiens*).

Description. Trilobate leaf; lacking petiole; base shape rounded, l × w (distance from centre of sinus to sinus) of central lobe 45 × 24 mm, one lateral lobe preserved, l × w (distance from centre of sinus to margin at right angle to main vein) 42 × 17 mm; lobe apices slightly covex, blunt; sinus angular, angle between midveins of lobes 50°; margin entire; venation basal palinactinodromous, 2 of 3 main veins preserved, straight; secondaries brochidodromous, not very regularly spaced, angle of origin moderate to wide, course slightly curved; exmedial veinlets arising from looping secondaries, forming further marginal loops; intersecondaries present, partly very short, partly reaching about halfway of secondaries, networking with tertiaries; tertiaries percurrent to reticulate; 4° veins reticulate, higher-order veins reticulate.

Remarks. The small leaf size and the almost equal length of the blunt lobes with entire margin are characteristic of *A. pseudomonspessulanum*. This is the only leaf representing this maple in the Leoben assemblage, although Ettingshausen (1888) listed several leaves (and winged fruits) for it. The other available collection specimens represent *A. integrilobum*, *A. tricuspidatum* and *Acer* sp. and *Toxicodendron melaenum* (see these sections).

The gross- and micromorphological most similar modern species is *A. monspessulanum* L. (Heer, 1859; Walther, 1972; Hably and Kvaček, 1997; Ströbitzer-Hermann, 2003) which thrives in Central Europe and the Mediterranean primarily in the temperate biome (POWO, accessed September, 2022).

Sect. *Platanoidea* Pax

Acer integerrimum (Viviani) Massalongo

Figs 16.10, 16.11, 25.8

1833 *Acerites integerrimus* Viviani; Viviani, p. 311, pl. 11, fig. 6.
1859 *Acer integerrimum* (Viviani) Massalongo; Massalongo and Scarabelli, pl. 341, pl. 18, fig. 3, pl. 41, fig. 10.
1972 *Acer integerrimum* (Viviani) Massalongo; Walther, p. 107, pls 22, 23, pl. 26, figs 1–4.
1975 *Acer integerrimum* (Viviani) Massalongo sensu Procházka et Bůžek; Procházka et Bůžek, p. 15, text-fig. 1a, b.
2003 *Acer integerrimum* (Viviani) Massalongo; Ströbitzer-Hermann, p. 26, pl. 3, figs 3, 5, 7, pl. 18, figs 3, 4.

Material. Moskenberg: NHMW: 1878/6/4209 (Ett. 2206), C, on backside. Münzenberg: IBUG: Ett. 6148, (*Sterculia labrusca* in sched.).

Description. Palmately five-lobed leaves, petiole not preserved; base shape truncate; central lobe l × w up to ~70–80 × 30 mm (IBUG Ett. 6148); only lateral lobe next to the central one complete, l × w ~60 × 22 mm (IBUG Ett. 6148) and 47 × 12 mm (NHMW 1878/6/4209, Ett. 2206, C); basalmost lobe distinctly smaller, narrow, incomplete; apex angle of lobes (narrow) acute, shape almost straight, slightly convex to long acuminate, straight to slightly bent; angle between midveins of central and lateral lobe ~40 –45°, angle between midveins of lateral and basal lobe ~30°; margin entire to slightly sinuous, specimen (NHMW 1878/6/4209, Ett. 2206, C) with a single, indistinct tooth/lobe on right margin of lateral lobe; venation basal actinodromous with 5 main veins, basalmost slightly curved towards base; secondaries delicate, not very regularly spaced, curved, camptodromous to brochidodromous, arising at moderate to wide angle; short intersecondaries occasionally developed; tertiaries delicate, reticulate, higher-order veins reticulate.

Remarks. These two remains are the only ones recalling *Acer integerrimum* in the Leoben flora. This is unsurprising because in the Miocene Central European floras *A. integerrimum* is known only as an accessory element. Characteristically, leaves of this fossil-species are five-lobed, contrary to *A. integrilobum* which is three-lobed with occasionally a tooth (indistinct lobe) on each side near base. Leaf NHMW 1878/6/4209, C (Ett. 2206) was very likely also five-lobed. The lateral lobe tapers into an elongated, narrow acuminate and bent apex. These features are characteristic of *A. integerrimum*. From Oberdorf, *A.* (?) *integerrimum* (one leaf fragment) was reported from the hanging wall sequence (Kovar-Eder and Meller, 2001).

Among modern maples, *A. cappadocicum* Gled., *A. pictum* subsp. *mono* (Maxim.) H. Ohashi (synonym *A. mono* Maxim.) and *A. truncatum* Bunge (all sect. Platanoidea Pax) are regarded close living relatives (e.g. Walther, 1972; Mai and Walther, 1988, 1991; Ströbitzer-Hermann, 2003). *A. cappadocicum*, which is a tree thrives in Italy and from northern Turkey to China. The latter two species are trees occuring in eastern Asia. All three species occur primarily in the temperate biome (POWO, accessed September, 2022).

Sect. *Rubra* Pax

Acer tricuspidatum Bronn

Figs 16.13–16.15, 17.1–17.5, 25.9

1838 *Acer tricuspidatum* Bronn; Bronn, p. 865, pl. 25, figs 10a, b.

1888 *Platanus aceroides* Goepp.; Ettingshausen, p. 299.

1888 *Liquidambar europaea* A. Braun, p.p.; Ettingshausen, p. 300.

1888 *Acer trilobatum* A. Braun, p.p., Ettingshausen, p. 338.

1888 *Acer decipiens* A. Braun, p.p.; Ettingshausen, p. 340, non figs 2, 4, 5, (?) fig. 3.

(?) 1888 *Cissus fagifolia* Ettingsh., p.p.; Ettingshausen, p. 352, pl. 8, fig. 14.

1972 *Acer tricuspidatum* Bronn; Walther, p. 56, pls 7–18, pl. 24, figs 5–7, pls 39–51.

1975 *Acer tricuspidatum* Bronn sensu Procházka and Bůžek; Procházka and Bůžek, p. 24, text-figs 2, 3, 4d, 5–13, pls 22–24.

1999 *Acer tricuspidatum* Bronn; Ströbitzer, p. 106, pl. 4, figs 9–11, pl. 11, figs 14–16, pl. 12, fig. 1.

2001 *Acer tricuspidatum* Bronn sensu Walther 1972; Kovar-Eder and Meller, p. 87, pl. 1, fig. 13, pl. 3, figs 7–9.

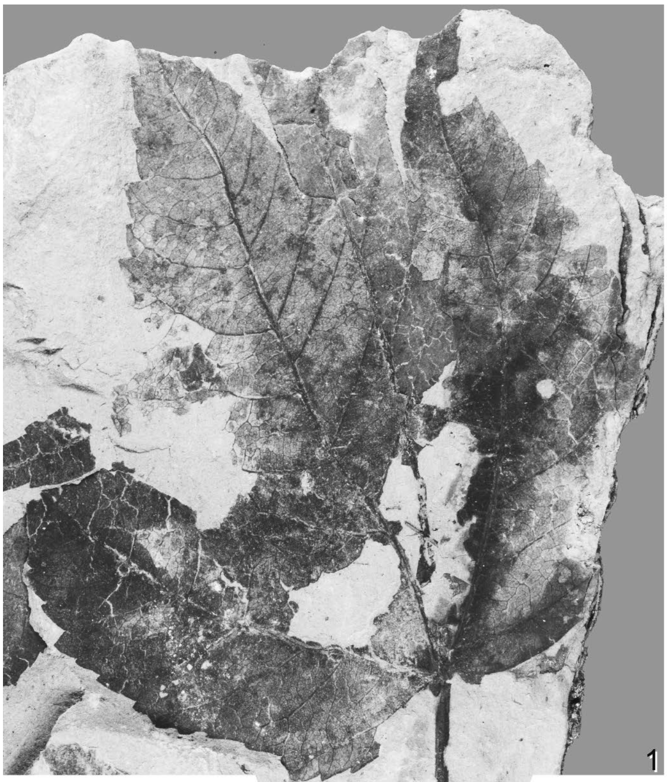
2003 *Acer tricuspidatum* Bronn; Ströbitzer-Hermann, p. 53, pl. 5, figs 16–20, pl. 1, 2, (?) 3, 4, 5, pl. 7, figs 1, 2, pl. 19, figs 5–8.

2004 *Acer tricuspidatum* Bronn; Kovar-Eder et al., p. 77, pl. 10, figs 10–12.

2022 *Acer tricuspidatum* Bronn; Kovar-Eder et al., p. 85, pl. 1, figs (?) 2, 3.

Material. Moskenberg: NHMW: 1878/6/3544 (Ett. 1541) + GBA 2024/0001/0026, (*Acer trilobatum*); 1878/6/3556 (1553), (*A. trilobatum*), two leaves; 1878/6/3557 + 9715 (1554, A + 7712, B), (*A. trilobatum*); 1878/6/3806 (1803), (*A. trilobatum*); 1878/6/3822 + 3823 (1819 + 1820), Pb 2029, (*A. trilobatum*); 1878/6/3993 (1990), (*A. trilobatum*); 1878/6/4114 (2111), (*Liquidambar europaeum*) + 1878/6/7711 (5708), (*Platanus aceroides*); 1878/6/4136 (2133), (*Liquidambar europaeum*); 1878/6/4137 (2134), A, (*L. europaeum*); 1878/6/4160 (2157), b, (*Acer trilobatum*); 1878/6/4196 + 8423 (2193 + 6420), Pb 2030, (*A. trilobatum*); 1878/6/7866 (5863), E, (on backside), Pb 1970; 1878/6/8378 + 8379 (6375 + 6376), (*Vitis teutonica* in sched.). IBUG: Ett. 6223, (*V. plurinervia* in sched.); Ett. 6333 (*Acer tilobatum*). Münzenberg: NHMW: 1878/6/4298 (Ett. 2295), Pb 2307, (*A. decipiens*); 1878/6/4338 (2335), Pb 2345, (*A. trilobatum*); 1878/6/4339 (2336), Pb 2297, (*A. trilobatum*); 1878/6/4411 (2408), Pb 2346, (*A. trilobatum* in sched.). Seegraben Walpurgis-Schacht: NHMW: 1878/6/4476 (Ett. 2473), C, D, (2 leaves on backside).

Description. Palmately tri- (to quinque-) lobate leaves, petiole rarely preserved, up to at least 45 mm long (incomplete); base shape obtuse to slightly cordate; length of central lobe ~30–95 mm, width (distance from centre of sinus to sinus) ~15–30 mm; l × w (distance from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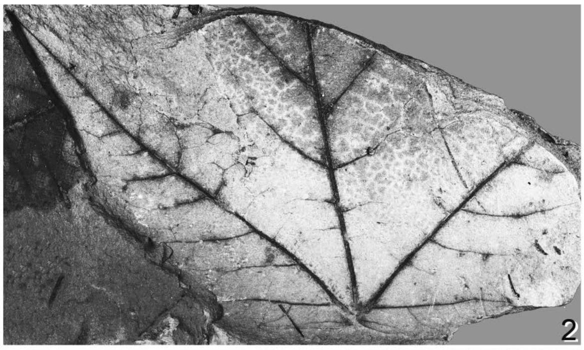
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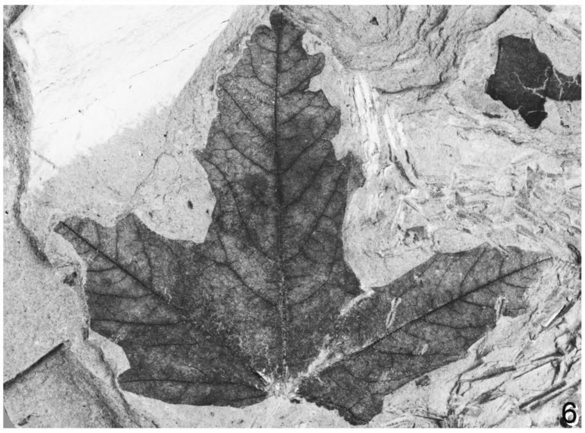
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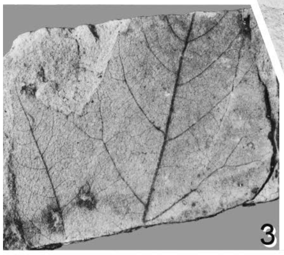
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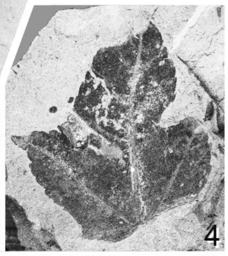
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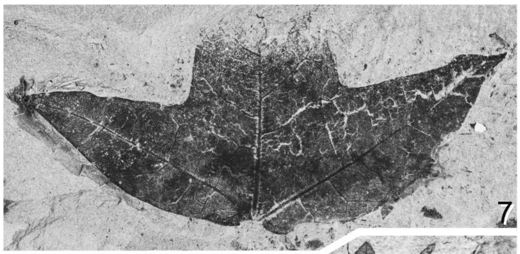
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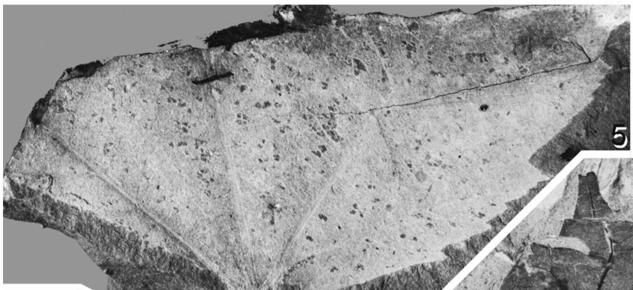
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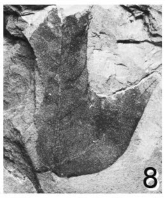
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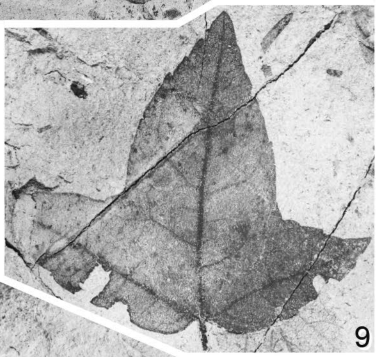
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centre of sinus to margin at right angle to main vein of lateral lobe) ~24–88 × 6–27 mm; central lobe usually wider than lateral ones; angle of lobe apices acute, shape straight to acuminate; angle between central lobe and adjacent lateral lobes ~(30) 45–50°, sinus between lobes angular to narrow rounded; occasionally near base a further small lobe/large tooth developed; margin double-serrate, teeth variable in size and shape, apices and sinus blunt to acute; venation basal actinodromous, three to rarely 5 main veins, central one straight, lateral ones straight occasionally exmedially or admedially bent; secondaries craspedodromous, occasionally forked, running into first-order teeth, to sometimes semicraspedodromous with exmedial veinlets running into tooth apices; secondaries not very regularly spaced, arising at moderate angle, course somewhat curved; intersecondaries present; tertiaries between central and adjacent main veins percurrent, in free lobe parts (forked)percurrent to reticulate, higher-order veins reticulate.

Remarks. Ettingshausen (1888) assigned specimen NHMW 1878/6/4114 (Ett. 2111) to *Liquidambar europaea* A. Braun and NHMW 1878/6/7711 (Ett. 5708) to *Platanus leucophylla* (Unger) Erw. Knobloch (formerly *P. aceroides* Goepp.). Both specimens doubtlessly represent part and counterpart of the same leaf, of which only the base is preserved. The marginal serration excludes the affiliation both to *Liquidambar* and *Platanus* (Fig. 17.5).

The variability of these leaves in size, with short or long lateral lobes and wider or more narrow lobes, is characteristic of *Acer tricuspidatum* which is by far the most common maple in the European Miocene. In the Leoben flora, however, it is rather rare compared to other assemblages reflecting wetland environments and most specimens are incomplete indicating allochthonous deposition.

The most similar modern relatives of *A. tricuspidatum* both by gross- and micro morphology are *A. saccharinum* L., *A. rubrum* L. (Walther, 1972), as well as *A. pycnanthum* K. Koch (Walther, 2000), the latter resembling only grossmorphologically (Ströbitzer-Hermann, 2003). All three species are trees occurring primarily in the temperate biome: *A. saccharinum* L. and *A. rubrum* in eastern Canada and eastern to central U.S.A., *A. pycnanthum* in Honshu (Japan) (POWO, accessed September, 2022).

Sect. *Acer* L.
vel *Rubra* Pax

Acer palaeosaccharinum Stur

Figs 17.6, 25.10

1867 *Acer palaeosaccharinum* Stur; Stur, p. 177, pl. 5, fig. 8.
1888 *Acer trilobatum* Bronn, p.p.; Ettingshausen, p. 338.
1972 *Acer palaeosaccharinum* Stur; Walther, p. 97, pls 19–21, pls 52, 53.
1975 *Acer palaeosaccharinum* Stur; Procházka and Bůžek, p. 48, pls 20, 21, figs 1–5, text-figs 16–20, non 21f.
2003 *Acer palaeosaccharinum* Stur; Ströbitzer-Hermann, p. 38, pl. 4, figs 10–12, (?) 13, 14–16, (?) pl. 38, figs 1–3.

Material. Moskenberg: NHMW: 1878/6/3543 (Ett. 1540), (*Acer trilobatum*) + NHMW 1871/38/38.

Description. Quinquelobate leaf; petiole not preserved; base shape slightly cordate, central lobe l × w (distance from centre of sinus to sinus) ~55 × 23 mm wide; adjacent lateral lobes l × w ~40 × 15 mm and 40 × 17 mm; angle between lobe midveins 50 and 65°; sinus between lobes angular; maximal distance between apices of lateral lobes ~70 mm; basal lobes much smaller, tooth-like (only one preserved); margin of central and adjacent lateral lobes serrate, basalmost lobe entire-margined; teeth large, simple, widely spaced, distal and proximal side of teeth straight to concave, apex acute, sinus angular to rounded; venation basal actinodromous, 5 straight main veins, a further short veinlet running near margin of basal lobe; secondaries mixed craspedodromous (those running into tooth apices) and

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Figure 17. **1–5**. *Acer tricuspidatum* Bronn, **1**. IBUG Ett. 6223 (*Vitis plurinervia*, in sched.), **2**. NHMW 1878/6/3557 (Ett. 1554), A, (*Acer trilobatum*), **3**. NHMW 1878/6/4298 (Ett. 2295), Pb 2307, (*A. decipiens*), **4**. NHMW 1878/6/4137 (Ett. 2134), A, (*Liquidambar europaea*), **5**. NHMW 1878/6/7711 (Ett. 5708), (*Platanus aceroides*); **6**. *Acer palaeosaccharinum* Stur, NHMW 1871/38/38; **7–11**. *Acer integrilobum* C.O. Weber emend. Walther (1972), **7**. NHMW 1878/6/3567 (Ett. 1564), Pb 2108, (*Acer decipiens*), Ettingshausen (1888: pl. 8, fig. 2), **8**. NHMW 1878/6/4095 (Ett. 2092), **9**. IBUG Ett. 6189 (*Acer decipiens*), **10**. NHMW 1999B0003/0001, Pb 5498, (*Acer palaeo-campestre*), Ettingshausen (1869a: pl. 5, fig. 11, syntype), **11**. NHMW 1878/6/3560 (Ett. 1557), (*Sterculia labrusca*). For all photographs the scale at bottom right of the figure is 10 mm

eucamptodromous, irregularly spaced, arising at moderate to acute angles, curved; short intersecondaries interspaced; tertiaries percurrent to reticulate; higher-order venation reticulate.

Remarks. The shape of the leaf margin is rather characteristic for this specimen. It documents the occurrence of this rather rare fossil-species from the Leoben flora. It has been recorded neither from Oberdorf nor from Parschlug.

A. saccharum Marshall and *A. hyrcanum* ssp. *tauricola* (Boiss. et Balansa) Yalt. resemble *A. palaeosaccharinum* grossmorphologically, while the cuticular morphology is closer to *A. saccharum* (Walther, 1972). Additionally, Ströbitzer-Hermann (2003) found the closest cuticular resemblance in *A. saccharinum* L. although that species least resembles the fossil-species in gross morphology. The natural range of *A. saccharum* is southeastern Canada, eastern U.S.A and northeastern Mexico. *A. hyrcanum* ssp. *tauricola* is a shrub or tree native to Turkey, Syria and Lebanon. For *A. saccharinum* see paragraph *A. tricuspidatum*.

Sect. *Palmata* Pax vel *Platanoidea* Pax

Acer integrilobum
C.O. Weber emend. Walther (1972)

Figs 17.7–17.11, 25.11

1852 *Acer integrilobum* C.O. Weber; Weber, p. 196, pl. 22, figs 5a, b.
1869a *Acer palaeo-campestre* Ettingsh. sp. n., p.p.; Ettingshausen, p. 80, pl. 5, fig. 11; non figs 12–14.
1888 *Sterculia labrusca* Unger, p.p.; Ettingshausen, p. 336.
1888 *Acer paulliniaecarpum* Ettingsh., p.p.; Ettingshausen, p. 339.
1888 *Acer decipiens* A. Braun, p.p.; Ettingshausen, p. 340, pl. 8, fig. 2, non figs 3–5.
1972 *Acer integrilobum* C.O. Weber sensu Walther; Walther, p. 111, pls 25, 26, 55.
1999 *Acer integrilobum* C.O. Weber sensu Walther; Ströbitzer, p. 106, (?) pl. 4, fig. 14, pl. 12, fig. 4.
2003 *Acer integrilobum* C.O. Weber sensu Walther (1972); Ströbitzer-Hermann, p. 32, pl. 3, figs 4, 6, 9–16, pl. 4, figs 2, 5, 7–9, (?) figs 3, 4, non figs 1, 6.
2004 *Acer integrilobum* C.O. Weber sensu Walther (1972); Kovar-Eder et. al., p. 78, pl. 10, figs 1–4, non figs 5, 6.
2022 *Acer integrilobum* C.O. Weber sensu Walther (1972); Kovar-Eder et. al., p. 84.

Material. Moskenberg: NHMW: 1878/6/3560 (Ett. 1557), (*Sterculia labrusca*) + GBA 2024/0001/0019, (*Acer decipiens*); 1878/6/3567 (1564), Pb 2108, (*A. decipiens*), Ettingshausen (1888: pl. 8, fig. 2); 1878/6/4095 (2092), (*Phaseolites* sp. in sched.); 1878/6/4180 (2177), Pb 2021, (*Acer decipiens*); 1878/6/8431 (6428), Pb 2103, (*A. paulliniaecarpum*); 1878/6/8973 (6970), (*Sterculia labrusca* in sched.). IBUG: Ett. 6189, (*Acer decipiens*). Leoben: NHMW: 1999B0003/0001, Pb 5498, (*A. palaeo-campestre*), Ettingshausen (1869a: pl. 5, fig. 11, syntype) + GBA 2024/0001/0013. GBA: 2024/0001/0012, A, (*Sterculia labrusca*); 2024/0001/0014.

Description. Palmately trilobate leaves; petiole usually not preserved, in one specimen 4 mm long (incomplete); base shape rounded to minimally cordate; margin entire, usually with a more or less weakly developed shallow, blunt tooth/lobe on each side of central lobe and sometimes also on lateral lobe; IBUG Ett. 6189 with few blunt teeth on central and lateral lobe; l × w (distance from centre of sinus to sinus) of central lobe up to >70 × 10– >30 mm; l × w (distance from centre of sinus to margin at right angle to main vein of lateral lobe) 20–73 × 12–25 mm; angle of lobe apices (narrow) acute, apex shape acuminate, utmost apex blunt or acute; angle between midveins of central and lateral lobes ~45–55 (60)°; sinus between lobes (widely) rounded; venation basal actinodromous, 3 main veins running straight and apically sometimes slightly bent into lobe apices; secondaries eucampto- to brochidodromous in free parts of lobes, delicate, not very regularly spaced, curved, angle of origin moderate in free parts of lobes, moderate to wide on basal sides of lateral lobes; intersecondaries present; tertaries percurrent in area between central and lateral lobes, in free parts percurrent to reticulate; further venation finely reticulate.

Remarks. Specimen NHMW 1878/6/3567 (Ett. 1564) (Fig. 14.7) was assigned to *Acer decipiens* A. Braun (now *A. pseudomonspessulanum*) (Ettingshausen, 1888: pl. 8, fig. 2). The size of this leaf and the fact that the incompletely preserved central lobe was probably longer than the lateral ones indicate rather the affinity to *A. integrilobum*. Ettingshausen (1888) listed specimen NHMW 1878/6/8972 (Ett. 6969) as *Sterculia labrusca* Unger. That specimen, however, was not detected in the course of this study. But specimen NHMW

1878/6/8973 (Ett. 6970) *Sterculia labrusca* Unger (in sched.) closely resembles the leaf assigned to *A.* cf. *integerrimum* from the Cypris Formation (Bůžek et al., 1996: pl. 26, fig. 1). According to those authors this leaf may also belong to *A. integrilobum*.

Walther (1972) mentioned *Acer longipes* Franch. ex Rehder, *A. wilsonii* Rehder and *A. cappadocicum* Gled. as close relatives. Ströbitzer-Hermann (2003) found only gross-morphological similarity of the fossil-species to *A. cappadocicum* but better cuticular similarity in *A. wilsonii*. *A. longipes* and *A. wilsonii* are trees with native range primarily in temperate regions; *A. longipes* thrives in Central China whereas *A. wilsonii* occurs in southern China. For *A. cappadocicum* see paragraph *A. integerrimum*.

Sect. problematic

***Acer* sp.** – leaf

Figs 18.1, 25.12

1888 *Acer decipiens* A. Braun, p.p.; Ettingshausen, p. 340, non pl. 8, figs 2–5.

Material. Moskenberg: NHMW: 1878/6/3570 (Ett. 1567), (*Acer decipiens*).

Description. Trilobate leaf, lacking petiole and lobe apices; base shape rounded; l × w (distance from sinus to sinus) of central lobe ~72 × 31 mm, lateral lobes l × w ~58 × 23 and 63 × 28 mm; sinus between lobes narrowly rounded to almost angular, angle between midveins of central and lateral lobes 40° and 45°; margin entire, giving lobes a general convex shape; venation basal actinodromous, 3 major veins running straight into lobes, exmedially at each side one further less strong main vein developed and an additional short veinlet paralleling margin; secondaries brochidodromous, not very regularly spaced, arising at moderate to wide angle, curved, occasionally forking; intersecondaries interspaced, reaching about half distance between lobe midvein and margin, networking with tertiaries; tertiaries polygonal reticulate to forked percurrent; 4° veins polygonal reticulate, higher-order veins reticulate, areoles well developed.

Remarks. Ettingshausen included this leaf in *Acer pseudomonspessulanum* (former *A. decipiens*), but it differs considerably by the convex shape of the lobes and bigger size. The general shape may resemble *Dombeyopsis lobata* Unger (i.e. *Craigia* W.W. Sm. et W.E. Evans) but the venation differs considerably by generally more delicate veins of different orders, and the delicate polygonal reticulate to forked-percurrent pattern of tertiaries.

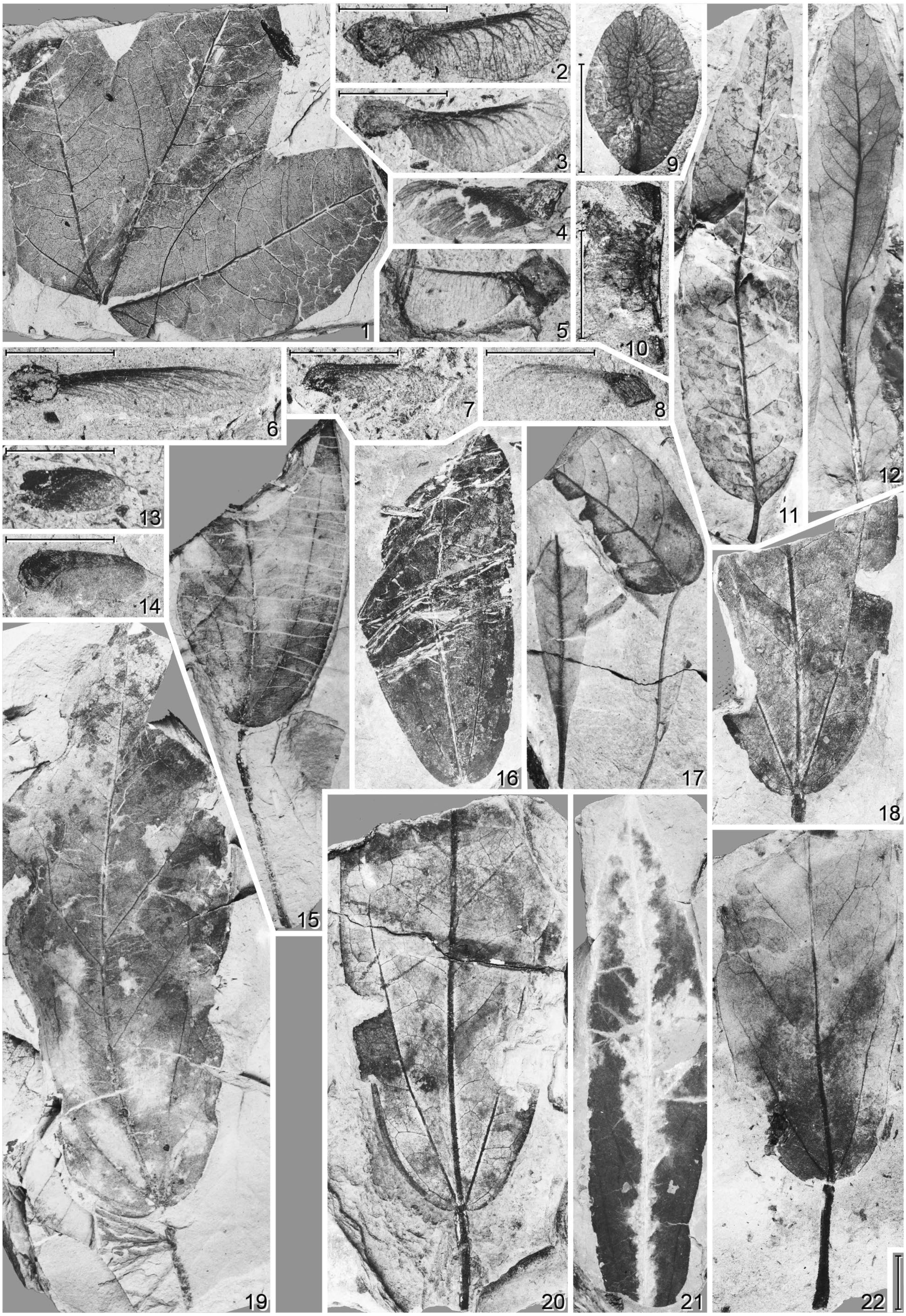
***Acer* sp.** div. – fructus

Fig. 18.2–18.8

The collections of the Leoben flora include several rather variable samaroid fruits of maples. Currently there is no systematic treatment available for maple samaras and, therefore, the intraspecific variability is largely unresolved (see also Kvaček et al., 2011). In *A. pseudoplatanus* L., for example, the variability is considerable (own observations). Mai's (1983) systematic treatment focussed on *Acer* endocarps and cannot be applied to impressions. The occurrence of different fossil-species of leaves supports the presence of different fossil-species of winged fruits in the Leoben flora, but intermediate forms occur as well. A distinction of unequivocal types would, therefore, require more material. The terminology for the samaras follows Wolfe and Tanai (1987).

Material. Moskenberg: NHMW: 1878/6/3542 (Ett. 1539), (*Acer palaeo-campestre*), Ettingshausen (1869a: pl. 5, fig. 14a, syntype); 1878/6/3568 (1565), (*A. decipiens*); 1878/6/4048 + 8433, A (2045 + 6430), Pb 2104, (*A. rhombifolium*), Ettingshausen (1869a: pl. 5, fig. 4, syntype); 1878/6/4132 + 4133 (2129 + 2130), Pb 2027, (*A. trilobatum*); 1878/6/4177 (2174), Pb 2023, (*A. decipiens*); 1878/6/4178 (2175), (*A. decipiens*); 1878/6/4179 (2176), Pb 2022, (*A. decipiens*); 1878/6/8424 (6421), (*A. trilobatum*); 1878/6/8429 (6426), Pb 2102, (*A. paulliniaecarpum*), Ettingshausen (1869a: pl. 5, fig. 6, syntype); 1878/6/8439 (6436), Pb 2020, (*A. decipiens*); 1878/6/9092 (7089), (*A. trilobatum*). IBUG: Ett. 6193, (*A. angustilobum*), Ettingshausen (1888: pl. 8, fig. 7). Münzenberg: NHMW: 1878/6/4297 (Ett. 2294), A, B, Pb 2308, (*A. decipiens*); 1878/6/4395 (2392), A, Pb 2309, (*A. decipiens*). Seegraben Walpurgis-Schacht: NHMW: 1878/6/4436 (Ett. 2433), Pb 2371, (*A. trilobatum*).

Description. Winged fruits variable in size, smallest ones ~13–14 mm long, largest up to >30 mm long; nutlet roundish up to 8–10 mm in diameter to elliptic ~3–6 × 2–4 mm; length of contact line 2–4 to 8–9 mm, attachment angle <30° to almost 90°; wing length 9–24 mm, width 4–12 mm, proximal side straight, somewhat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sinus-shaped, slightly convex, thickened; distal side convex, wing apex rounded, length of wing attachment 2–3 to 5–6 mm; wing venation multiply forking, at very different angle to proximal suture.

Remarks. The samaras differ considerably in size, e.g. NHMW 1878/6/4177 (Ett. 2174), NHMW 1878/6/4395, A (Ett. 2392), are rather small (Fig. 18.7, 18.8). The fruit NHMW 1878/6/4048 + 8433 (Ett. 2045 + 6430, A) is characterised by the distinctly offset nutlet and the narrow wing with strongly oblique venation (Fig. 18.6). A handwritten note by D.H. Mai in sched. indicates sect. Goniocarpa Pojark. for this specimen. The shape of the samaras NHMW 1878/6/9092 (Ett. 7089) and NHMW 1878/6/8439 (Ett. 6436) is distinctly waisted and the proximal suture is concave to straight (Fig. 18.2, 18.3). The issue to determine maple mericarps has been addressed among others by Walther and Kvaček (2007).

Family SIMAROUBACEAE DC. (?)

Genus ***Ailanthus*** Desf. (?)

Ailanthus (?) ***apollinis*** Ettingsh.

Figs 18.11, 25.13

1888 *Ailanthus apollinis* Ettingsh. sp. n., p.p.; Ettingshausen, p. 356, pl. 9, figs 28, 28a, non fig. 29.

Lectotype designated here. IBUG Ett. 6238, Ettingshausen, (1888: pl. 9, figs 28, 28a), refigured on Figs 18.11, 25.13.

Derivatio nominis. Unknown.

Locus typicus. Historical locality Münzenberg near Leoben, Leoben Basin, Styria (Ettingshausen, 1869a).

Stratum typicum. Shales ~2.75 m above the coal seam (Ettingshausen, 1869a), 14.9 ± 0.7 Ma (a tuff layer near the base of the shales overlying the coal seam, Sachsenhofer et al., 2010).

Material. Moskenberg: NHMW: 1878/6/4212 (Ett. 2209), b, Pb 2131, (*Sapindus pythii*). Münzenberg: IBUG: Ett. 6238, (*Ailanthus apollinis*), Ettingshausen (1888: pl. 9, figs 28, 28a, syntype).

Emended diagnosis. Leaflet, petiolule slightly broadened at base; lamina oblong to slightly ovate, base slightly asymmetrical, rounded, apex acute or acuminate, margin entire near base, then remotely undulate except for single, small teeth; secondaries brochidodromous; delicate veinlets or loops running into/touching tooth sinus, a further veinlet running from sinus to tooth apex (?); intersecondaries reaching about half distance between midvein and margin; tertiaries delicate, (forked-)percurrent to reticulate; higherorder veins reticulate.

Description. Petiolulate leaflets, one complete with well-visible venation, the other one incomplete; petiolule up to 7 mm long, almost straight, slightly broadened near base; laminar shape nearly oblong to minimally ovate, l × w ~94 × 22 mm, ratio l/w ~4.2 and (?) ~50 × 14 mm, ratio l/w (?) ~3.5, respectively; base more or less asymmetrical, base angle obtuse to acute, base shape convex to rather straight, apex angle acute, apex shape almost straight, (?) acuminate, utmost apex not preserved; margin entire near base, then slightly undulate except for single, scattered teeth; tooth height ≤ 1 mm, both flanks variable, very short, convex, straight, or concave; sinus

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Figure 18. **1**. *Acer* sp., leaf, NHMW 1878/6/3570 (Ett. 1567), (*Acer decipiens*); **2–8**. *Acer* sp. div. – fructus, **2**. NHMW 1878/6/9092 (Ett. 7089), (*A. trilobatum*), **3**. NHMW 1878/6/8439 (Ett. 6436), Pb 2020, (*A. decipiens*), **4**. NHMW 1878/6/3542 (Ett. 1539), (*A. palaeo-campestre*), Ettingshausen (1869a: pl. 5, fig. 14a, syntype), **5**. NHMW 1878/6/8429 (Ett. 6426), Pb 2102, (*A. paulliniaecarpum*), Ettingshausen (1869a: pl. 5, fig. 6, syntype), **6**. NHMW 1878/6/8433 (Ett. 6430), A, Pb 2104, (*A. rhombifolium*), Ettingshausen (1869a: pl. 5, fig. 4, syntype), **7**. NHMW 1878/6/4177 (Ett. 2174), Pb 2023, (*A. decipiens*), **8**. NHMW 1878/6/4395 (Ett. 2392), A, Pb 2309, (*A. decipiens*); **9**, **10**. *Craigia bronnii* (Unger) Kvaček, Bůžek et Manchester, **9**. NHMW 1878/6/4468 (Ett. 2465), B, **10**. NHMW 1878/6/7577 (Ett. 5574), (*Ulmus bronnii*); **11**. *Ailanthus* (?) *apollinis* Ettingsh., IBUG Ett. 6238, lectotype, (*Ailanthus apollinis*), Ettingshausen (1888: pl. 9, figs 28, 28a, syntype); **12**. *Tilia longebracteata* Andrae, IBUG Ett. 6162, (*Tilia milleri*), Ettingshausen (1888: pl. 8, figs 9, 9a); **13**, **14**. *Saportaspermum* sp., **13**. NHMW 1878/6/7998 (Ett. 5995), A, (*Hakea plurinervia*), **14**. NHMW 1878/6/3888 (Ett. 1885), Pb 1939, (*Embothrium salicinum*), Ettingshausen (1888: pl. 4, fig. 27); **15–22**. *Laria rueminiana* (Heer) G. Worobiec et Kvaček, **15**. NHMW 1878/6/7916 (Ett. 5913), (*Sterculia cinnamomea*), Ettingshausen (1888: pl. 7, fig. 2), **16**. NHMW 1878/6/4181 (Ett. 2178), (*S. cinnamomea*), Ettingshausen (1869a: pl. 4, fig. 19, syntype), **17**. NHMW 1878/6/8824 (Ett. 6821), A, Pb 2079, (*Palaeolobium moskenbergense*), Ettingshausen (1869a: pl. 6, fig. 20, holotype), **18**. NHMW 1878/6/3740 (Ett. 1737), (*Cinnamomum* sp.), counterpart to Ettingshausen (1888: pl. 7, fig. 3), **19**. NHMW 1878/6/3817 (Ett. 1814), (*Cinnamomum* sp.), **20**. NHMW 1878/6/7915 (Ett. 5912), Pb 2119, (*Sterculia cinnamomea*), Ettingshausen (1888: pl. 7, fig. 3), **21**. NHMW 1878/6/7912 (Ett. 5909), (*S. cinnamomea*), **22**. NHMW 1878/6/7913 (Ett. 5910), (*S. cinnamomea*), Ettingshausen (1888: pl. 7, fig. 5). For all photographs the scale at bottom right of the figure is 10 mm except for photographs with embedded scale in which the scale is also 10 mm

angular to rounded, apex acute to blunt; midvein slightly bent, secondaries brochidodromous, spacing moderate to wide, 4–10 mm, originating at moderate to moderately wide angle, angle tapering towards apex; secondaries looping at some distance to margin, delicate veinlets or loops running into/touching tooth sinus, a delicate vein running from sinus to tooth apex (?); commonly (but not always) a single intersecondary interspaced between 2 secondaries, reaching about half distance between midvein and margin; tertiaries delicate, (forked-)percurrent to reticulate; higher-order veins reticulate.

Remarks. Ettingshausen (1888) merged leaflet IBUG Ett. 6238 and a putative fruit under *A. apollinis*. Specimen IBUG Ett. 6237 very likely is that putative fruit figured there (Ettingshausen, 1888: pl. 9, fig. 29), but this remain is incomplete, as faintly indicated in the drawing. It lacks any diagnostically relevant feature and must therefore be regarded as indeterminable. Among the here studied material, no fruit specimen of *Ailanthus* has been detected.

The leaflets from Leoben differ from *A. pythii* (Unger), Kovar-Eder et Kvaček from Parschlug (Kovar-Eder et al., 2004, 2022) and *A. mecsekensis* Hably from the Mecsek area (Hably, 2020) by less densely spaced secondaries arising at a steeper angle. As stated by Kovar-Eder et al. (2004, 2022), *A. mecsekensis* is likely synonymous with *A. pythii*. In *A. pythii* (and *A. mecsekensis*) the tooth shape is very variable, as is the density of teeth so that the teeth of the here described specimen may fall into the variability range. The assessment of possible differences in the tooth innervation is hampered because this feature is rarely unambiguously visible in the material from the different sites. Furthermore, *A.* (?) *apollinis* differs from *A. prescheri* H. Walther (Kleinsaubernitz, Germany, Upper Oligocene; Walther, 1999) by clearly brochidodromous secondaries.

Regarding the material from Parschlug, the taxonomic assignment of specimen IBUG 1641 to "*Quercus*" *daphnes* Unger (Kovar-Eder et al., 2022, pl. 10, fig. 19) must be revised. The incompletely preserved leaf fragments on this slab more likely represent *A. pythii*. Arguments for the reassignment are the position of the fragments implying that they derive from a single pinnate leaf, the vein fabric matching *A. pythii*, and its visibility indicating a chartaceous rather than a coriaceous texture as is characteristic of "*Q.*" *daphnes*. The former assignment was mainly made based on the entire margin.

Although more than 50 modern species of *Ailanthus* have been described, only 6 of them are currently accepted (WFO Plant List accessed June, 2023) which are either entire-margined or variably serrate. Teeth are glandular in *A. altissima* (Mill.) Swingle and *A. excelsa* Roxb. In *A. altissima*, secondaries or their branches or veinlets arising from looping secondaries run directly into the tooth apex (NMNS Cleared Leaf Database accessed June, 2023), and in *A. excelsa* the secondaries terminate in tooth apices (POWO accessed June, 2023), thus differing from the here described specimens and causing uncertainty regarding their generic assignment.

Order MALVALES Bercht. et J. Presl

Family MALVACEAE Jussieu

Subfamily TILIOIDEAE Arn.

Genus ***Craigia***
W.W. Sm. et W.E. Evans

Craigia bronnii
(Unger) Kvaček, Bůžek et Manchester

Fig. 18.9, 18.10

1847 *Ulmus bronnii* Unger; Unger, p. 100, pl. 26, figs 2–4.

1888 *Ulmus bronnii* Unger, p.p.; Ettingshausen, p. 295.

1991 *Craigia bronnii* (Unger) Kvaček, Bůžek et Manchester; Kvaček et al., p. 522.

2004 *Craigia bronnii* (Unger) Kvaček, Bůžek et Manchester; Kovar-Eder et al., p. 66, pl. 6, figs 16, 17.

Material. Moskenberg: NHMW: 1878/6/3547 (Ett. 1544), (*Ulmus bronnii*); 1878/6/4115 + 4116 (Ett. 2112 + 2113), (*U. bronnii*); 1878/6/7577 (5574), (*U. bronnii*). IBUG: Ett. 5960, (*U. bronnii*). Münzenberg: NHMW: 1878/6/4393 (Ett. 2390), b, Pb 2338, (*U. bronnii*). Seegraben Walpurgis-Schacht: NHMW: 1878/6/4468 (Ett. 2465), B, part + counterpart on backside.

Description. Winged capsules (valves), single or two valves still attached to each other, flattened in one plane; stalk not preserved; single valve l × w ~16 × 7 mm; specimens with two valves l × w ~14–15 × 10–12 mm; shape of two attached valves elliptic to slightly obovate, at base somewhat and at apex distinctly retuse; wing venation distinct, reticulate, veins running subparallel and somewhat radiating from central elongated capsule towards wing margin, forming more or less longitudinal meshes with cross veins; specimen NHMW 1878/6/7577 (Ett. 5574) with three abortive seeds in locular region.

Remarks. Ettingshausen (1869a) mentioned fruits of *Ulmus bronnii* without figuring them. Later he listed among the material assigned to *U. bronnii* also the here figured valves (Ettingshausen, 1888). The best-preserved specimen (part and counterpart) is that of NHMW 1878/6/4468, B (Ett. 2465) (Fig. 18.9), which was detected accidently when a small sediment fragment broke off. Specimen NHMW 1878/6/7577 (Ett. 5574) (Fig. 18.10) is preserved fragmentarily but shows abortive seeds in the locular region that are very similar to the specimen of *C. oregonensis* (Arnold) Kvaček, Bůžek et Manchester figured by Kvaček et al. (1991: fig. 4).

For a long time, the systematic assignment of such fruits was problematic and changed from *Ulmus* (Unger, 1847) to *Pteleaecarpum* (Weyland, 1948) and presumable sapindaceous affinity (Bůžek et al., 1989) until the true affinity to *Craigia* was recognised (Kvaček et al., 1991). This assignment was further confirmed by fruits, buds and pollen from the Inden Formation (Lower Rhine Basin, Germany) by Kvaček et al. (2002).

Leaves of *Craigia* have not been detected in the Leoben collection material and, as in many fossil assemblages, *Craigia* fruits occur accessorily in Leoben.

Genus ***Tilia*** L.

Tilia longebracteata Andrae

Fig. 18.12

1888 *Tilia milleri* Ettingsh., p.p.; Ettingshausen, p. 337, pl. 8, figs 9, 9a.
2004 *Tilia longebracteata* Andrae; Kovar-Eder et al., p. 66, pl. 6, figs 13–15.

Material. Moskenberg: NHMW: 1878/6/8433 (Ett. 6430), B. IBUG: Ett. 6162 + 6163, (*Tilia milleri*), Ettingshausen (1888: pl. 8, figs 9, 9a).

Description. Involucrum oblong, slightly obovate in shape, l × w ~97 × 15 mm, ratio l/w ~6.5; base angle acute, shape truncate at very base, then somewhat convex; apex angle acute, shape straight to slightly convex, utmost apex not preserved; margin entire, remotely undulate; midvein thick, tapering along length; secondaries distinct, very irregularly spaced in basal two thirds, more regularly in apical third, angle of origin narrow acute in basal part, angle increasing towards apex; secondaries brochidodromous, festooned brochidodromous in apical part, loops irregular; intersecondaries and epimedial tertiaries numerous; tertiaries percurrent to reticulate; higher-order veins reticulate, (?) ultimate veinlets poorly developed.

Remarks. The shape and venation pattern of the bract IBUG Ett. 6162 + 6163 clearly point towards an involucrum of *Tilia*, although the attachment point of the peduncle is not evident. Ettingshausen (1888) merged these bracts with leaves, which he had described as *T. milleri* from Leoben earlier (Ettingshausen, 1869a). All leaf specimens listed explicitly by Ettingshausen (1888) for *T. milleri*, however, represent leaves of Betulaceae, mostly *Alnus milleri* (see respective paragraph), but no linden leaves have been detected among the Leoben material.

Ettingshausen (1888) indicated that the figured involucrum derived from Münzenberg. The label adhering to specimen IBUG Ett. 6162 + 6163, as well as the Ettingshausen inventory indicate Moskenberg instead.

Tilia brabenecii Bůžek et Kvaček is based on leaves and bracts and the identical cuticular structures of both remains (Bůžek and Kvaček, 1994). An assignment to this fossil-species is not appropriate for the remains from Leoben because neither leaves nor cuticle structures are available. Besides a very similar involucrum described first by Ettingshausen (1869b), fruits of linden are known from Parschlug as *T. longebracteata* Andrae (Kovar-Eder et al., 2004).

Subfamily HELICTEROIDEAE Griseb.

Genus ***Laria*** G. Worobiec et Kvaček

Laria rueminiana
(Heer) G. Worobiec et Kvaček

Figs 18.15–18.22, 25.14

(?) 1855 *Acalypha prevaliensis* Unger; Unger, p. 31, fig. 3.

1859 *Ficus rueminiana* Heer; Heer, p. 183, pl. 152, figs 11, 12.
1859 *Ficus truncata* Heer; Heer, p. 183, pl. 152, fig. 15.
1869a *Sterculia cinnamomea* Ettingsh. sp. n.; Ettingshausen, p. 78, pl. 4, figs 19, 20.
1869a *Palaeolobium moskenbergense* Ettingsh. sp. n.; Ettingshausen, p. 95, pl. 6, fig. 20.
1888 *Sterculia cinnamomea* Ettingsh.; Ettingshausen, p. 336, pl. 7, figs 2–6.
(?) 1877 *Acalypha prevaliensis* Unger; Zwanziger, p. 78, pl. 38.
1971 "*Ficus*" *truncata* Heer sensu novo; Bůžek, p. 92, pls 46, 47, 48, figs 1–4, text-fig. 15.
2010 *Laria rueminiana* (Heer) G. Worobiec et Kvaček; Worobiec et al., p. 903, figs 6, 7.

Material. Moskenberg: NHMW: 1878/6/3649 (Ett. 1646), A; 1878/6/3727 (1724), b, Pb 2092, (*Cinnamomum* sp. in sched.); 1878/6/3740 + 7915 (Ett. 1737 + 5912), Ett. 1737 (*C.* sp. in sched.), Ett. 5912, Pb 2119, (*Sterculia cinnamomea*), Ettingshausen (1888: pl. 7, fig. 3); 1878/6/3778 + 3779 (1775 + 1776), (*S. cinnamomea*); 1878/6/3817 (1814), (*Cinnamomum* sp. in sched.); 1878/6/3855 (1852), (*Sterculia cinnamomea*); 1878/6/3866 (1863), a, (*Cinnamomum scheuchzeri* in sched.); 1878/6/3876 (1873), (*C.* sp. in sched.); 1878/6/3881 (1878), a, (*Xylomites daphnogenes* on C. *polymorphum* in sched.); 1878/6/3882 + 3883 (1879 + 1880), (*Sterculia cinnamomea*); 1878/6/3924 (1921), (*S. cinnamomea*); 1878/6/3981 (1978), (*Cinnamomum* sp. in sched.); 1878/6/4013 (2010), (*C.* sp. in sched.); 1878/6/4119 (2116), (*C.* sp. in sched.); 1878/6/4171 (2168), A, (*C.* sp. in sched.); 1878/6/4181 (2178), (*Sterculia cinnamomea*), Ettingshausen (1869a: pl. 4, fig. 19, syntype); 1878/6/7911 (5908), (*S. cinnamomea*); 1878/6/7912 (5909), (*S. cinnamomea*); 1878/6/7913 (5910), (*S. cinnamomea*), Ettingshausen (1888: pl. 7, fig. 5); 1878/6/7914 (5911), (*S. cinnamomea*); 1878/6/7916 (5913), (*S. cinnamomea*), Ettingshausen (1888: pl. 7, fig. 2); 1878/6/8824 (6821), A, Pb 2079, (*Palaeolobium moskenbergense*), Ettingshausen (1869a: pl. 6, fig. 20, holotype). Münzenberg: NHMW: 1878/6/4328, A + 4336, B (Ett. 2325 + 2333), Ett. 2333 Pb 2196, (*Cinnamomum* sp. n. in sched.). Moskenberg or Münzenberg: NHMW: 1878/6/3982 + 6518 (Ett. 1979 + 4515), Ett. 1979 (*Cinnamomum* sp. in sched.), Ett. 4515 (*Sphaeria muenzenbergensis* in sched.), Ett. 1979 labelled "Leoben I", i.e. Moskenberg, Ett. 4515 labelled "Leoben II", i.e. Münzenberg. Seegraben Unter-Buchwieser: NHMW: 1878/6/4415 (Ett. 2412), b, (*Sterculia cinnamomea*). Leoben: LMJ: 201.001, 201.002. GBA: 2024/0001/0009.

Description. Very long-petiolate leaves; petiole length up to 57 mm, with a pulvinus close to base of lamina; laminar shape slender elliptic to oblong to somewhat obovate, l × w ~(42) 60–100 (140) × 20–54 mm, ratio l/w ~2.1–4.2 (4.6); base obtuse to rounded, usually minimally cordate at very base; apex missing except in one specimen, acute; margin entire; venation basal acrodromous (to actinodromous), i.e. three (to five) veins arising at base; lateral main veins next to midvein strong, mostly straight, more rarely gently curved, reaching into apical half to third of lamina, looping with secondaries arising from central vein; marginal veins (veinlets) arising at base delicate, short, running along margin, occasionally an agrophic vein formed by exmedial veinlets; secondaries arising from midvein irregularly and widely spaced, at moderate to narrow angle depending on leaf width, gently bent, occasionally forked, looping with subsequent secondaries; long and short intersecondaries interspaced with secondaries; exmedial veinlets arising from lateral main veins rather regularly spaced, looping along margin; tertiaries delicate, percurrent to reticulate, sinuate to curved, appearing irregular, angle to midvein very variable; higher-order veins reticulate.

Remarks. The leaf fragment figured by Ettingshausen (1869a: pl. 1, fig. 6) as *Sterculia cinnamomea* with *Dothidea cinnamomea* Ettingsh. very likely also represents *Laria rueminiana*. Ettingshausen clearly was unsure about a systematic assignment of numerous specimens because they were labelled as *Cinnamomum* sp. (in sched.) and were not listed in Ettingshausen's study (1888). Specimen NHMW 1878/6/7912 (Ett. 5909) is an exceptionally slender leaf and the only one with preserved leaf apex (Fig. 18.21). Specimen NHMW 1878/6/3740 + 7915 (Ett. 1737 + 5912) shows an agrophic vein formed by exmedial veinlets (Figs 18.20, 25.14).

The morphological leaf variability of this fossil-taxon appears to differ from site to site. In the Most Basin (northern Bohemia, Early Miocene) it is rather wide. Bůžek (1971) characterised the laminar shape of former "*Ficus*" *truncata* as narrow to (wide) ovate to oblong with 3 to 5 main veins and cuneate to truncate base. From the Bełchatów lignite mine (Lower Silesia, Poland, Middle and Late Miocene), Worobiec et al. (2010) described the leaves to be broader with 5 to 9 (usually 7) main veins, while in the Leoben assemblage narrower, symmetrical leaves with 3 to 5 veins dominate.

This fossil-taxon was long enigmatic and is an impressive example of the realisation of the whole-plant concept, which aims to arrive at a holistic picture of former plants based on detached organs (see, e.g. Sakala, 2004; Kvaček, 2008). Based on the co-ocurrence of fruit valves (*Reevesia hurnikii* Z. Kvaček), seeds (*Saportaspermum*), and leaves (*Laria rueminiana* formerly *"Ficus" truncata*) from the lignite mine Bílina, Kvaček (2006) suspected that these isolated plant parts derive from one biological species of modern *Reevesia* (Malvaceae). Worobiec et al. (2010) introduced the morphogenus *Laria* and, for priority reasons, assigned these leaves to *Laria rueminiana*. Based on the co-occurrence of leaves and pollen in a sample from Bełchatów, Worobiec et al. (2012) further suspected that *Reevesiapollis triangulus* (Mamczar) Krutzsch may represent the corresponding pollen of this fossil-taxon. Most recently, Worobiec and Worobiec (2020) supported this hypothesis by reporting pollen aggregations of *R. triangulus* adhering to *L. rueminiana* from Bełchatów, which disintegrated during the process of cuticle preparation.

For the study of leaf assemblages preserved as impressions lacking cuticles, it is useful to mention that narrow, 3-veined leaves of *L. rueminiana* may resemble those of *"Illicium" limburgense* Kräusel and Weyland (1950) (e.g. Walther, 1999) by prominent and steeply ascending basal secondaries and long petiole. *"I." limburgense* lacks, however, a pulvinus, the texture is coriaceous so that the higher-order venation is poorly known.

Acalyphe prevaliensis described by Unger (1855) and later again by Zwanziger (1877) from Leše near Prevalje in Slovenia (Klagenfurt Basin, Sarmatian/Serravallian; former Liescha near Prävali), may also represent *L. rueminiana*. This assignment, however, remains ambiguous because in the figure the leaf base was completed graphically (Unger, 1855) and the collection specimen was not available to Bouchal et al. (2017) for their revision.

The rich occurrence of *L. rueminiana* in the Leoben assemblage is important because such records are still scanty (see also Worobiec et al., 2010; Worobiec and Worobiec, 2020). Furthermore, the Leoben flora yields, though rarely, *Saportaspermum* seeds (see below) and a capsule not yet dehisced, *Carpolithes* sp. L, which may represent *Reevesia*.

Genus ***Saportaspermum*** Meyer et Manchester

Saportaspermum **sp.**

Fig. 18.13, 18.14

1888 *Embothrium salicinum* Heer; Ettingshausen, p. 315, pl. 4 fig. 27.
1888 *Hakea plurinervia* Ettingsh., p.p.; Ettingshausen, p. 314, non pl. 4, figs 24, 25.
1890 *Embothrium parschlugianum* Ettingsh. sp. n.; Ettingshausen, p. 110, pl. 4, figs 43, 44.
2004 *Saportaspermum* sp.; Kovar-Eder et al., p. 87, pl. 15, figs 6–8.

Material. Moskenberg: NHMW: 1878/6/3888 (Ett. 1885), Pb 1939, (*Embothrium salicinum*), Ettingshausen (1888: pl. 4, fig. 27); 1878/6/7998 (5995), A, (*Hakea plurinervia*).

Description. Winged seeds, l × w ~8–12 × 3.5–4 mm; seed body roundish, l × w ~4 × (?) 2–3.8 mm, dorsally thickened, prolonging into wing margin; seed body rounded basally; angle between long-axes of wing and seed body ~40°; wing attached laterally to seed body, lacking venation, margin smooth, slightly rounded to straight, distal end rounded.

Remarks. Of the winged seeds described by Ettingshausen (1869a, 1888), only few could be identified in the collection material and only two specimens could be assigned to *Saportaspermum*, which represents the seeds of the *Reevesia* plant with leaves of *Laria rueminiana* (see previous paragraph). These seeds differ from the recently described *Mecsekispermum gordonioides* Erdei, Hably (2021) by the more roundish seed body, higher ratio of wing length to seed length, the rounded distal end of wing, the straight to moderately convex margin opposite the thickened seed prolongation (no swelling on ventral side), and the wider angle between the long axes of wing and seed body. For differences from *Carpolithes* sp. B see respective paragraph.

Order CORNALES Dumortier

Family CORNACEAE Bercht. et J. Presl

Genus ***Cornus*** L.

cf. ***Cornus* sp.**

Fig. 19.1, 19.2

1888 *Lonicera prisca* Ettingsh. sp. n., p.p.; Ettingshausen, p. 321, pl. 5, figs 8, 8a.
1888 *Cornus buechii* Heer, p.p.; Ettingshausen, p. 333, pl. 6, figs 22, 23.

Material. Moskenberg: NHMW: 1878/6/3768 + 4026 (Ett. 1765 + 2023), Pb 2120 + Pb 2021, (*Cornus buechii*), Ettingshausen (1888: pl. 6, fig. 22 (Ett. 2023), fig. 23 (Ett. 1765)). IBUG: Ett. 6082, (*Lonicera prisca*), Ettingshausen (1888: pl. 5, figs 8, 8a, syntype).

Description. Petiolate simple leaves; petiole 3–6 mm long; laminar shape elliptic to minimally obovate, l × w ~37–46 × 17–23 mm, ratio l/w ~2–2.2; base angle wide acute, base shape somewhat convex to concave (cuneate) near utmost base, apex angle acute, apex shape smoothly convex to nearly straight, utmost apex incomplete; margin entire; midvein slender, straight to slightly curved; secondaries delicate, brochidodromous to eucamptodromous, spacing variable, 4–11 mm, angle of origin moderate to acute, near origin approaching midvein, further course curved, steeply ascending into upper third of lamina; basal 2° veins subopposite, others alternate; at utmost base, delicate veinlets running along margin; tertiaries delicate, percurrent, not dense, obtuse towards midvein, perpendicular to secondaries.

Remarks. Ettingshausen's (1888) assumption of a chartaceaous texture of these leaves is supported by the slender petiole, slender midvein and delicate 2° veins. The tertiary and higher-order venation is not visible on specimen IBUG 6082, contrary to Ettingshausen's (1888) opinion. In specimen NHMW 1878/6/3768 + 4026 (Ett. 1765 + 2023) the tertiaries are faintly visible only near the base. Their obtuse angle towards the midvein makes the generic assignment to *Cornus* somewhat ambiguous because in that genus the 3° venation is almost perpendicular to the midvein.

Rhamnaceae vel Cornaceae gen. et sp. differs by larger, more slender, occasionally toothed leaves, more numerous and steeper secondaries and the absence of basal secondaries ascending far into the lamina closely approaching to the margin (see respective paragraph).

Family NYSSACEAE Dumortier nom. con.

Genus ***Nyssa*** L.

Nyssa cf. ***haidingeri*** (Ettingsh.) Kvaček et Bůžek

Fig. 19.4, 19.5

1866 *Coccoloba bilinica* Ettingsh.; Ettingshausen, p. 164, pl. 30, fig. 1.
1866 *Laurus haidingeri* Ettingsh.; Ettingshausen, p. 174, pl. 30, figs 5, 8, 9.
1868 *Laurus haidingeri* Ettingsh.; Ettingshausen, p. 196.
1869a *Anacardiophyllum dubium* Ettingsh. sp. n.; Ettingshausen, p. 90.
(?) 1869a *Juglans undulata* Ettingsh. sp. n.; Ettingshausen, p. 88, pl. 6, fig. 8.
1888 *Juglans parschlugiana* Unger, p.p.; Ettingshausen, p. 352.
1888 *Anacardiophyllum dubium* Ettingsh.; Ettingshausen, p. 356.
cf. 1972 *Nyssa haidingeri* (Ettingsh.) Kvaček et Bůžek; Kvaček and Bůžek, p. 373, pl. 1, pl. 2, figs 1, 2, pl. 3, figs 1–3, pl. 4, figs 1–5.

Material. Moskenberg: NHMW: 1878/6/4018 + 4019 (Ett. 2015 + 2016), Pb 2049, (*Juglans parschlugiana*); 1878/6/8724 (Ett. 6721), Pb 2054, (*Anacardiophyllum dubium*), Ettingshausen (1869a: p. 90, very probably holotype).

Description. Basal parts of petiolate leaves, petiole at least up to 13 mm long, (?) complete; lamina wide (?) elliptic, l (incomplete) × w ~(108) × 97 mm and l (incomplete) × w ~(54) × 39 mm; base shape concavo-convex, base angle obtuse; margin entire; midvein straight; secondaries (?) brochidodromous or (?) eucamptodromous, distinctly more delicate than midvein; angle of origin wide, near base almost 90°, at first slightly approaching midvein, then rapidly turning towards margin or immediately running straight across lamina, probably looping closely in front of margin; delicate and short intersecondaries present.

Remarks. Concluding from the description by Ettingshausen (1869a), specimen NHMW 1878/6/8724 (Ett. 6721) is the holotype of

Anacardiophyllum dubium although it was not figured there. That author assumed a leaflet attached to the fragment of the main axis. The fragment/detritus at the base is, however, not connected to the petiole; instead, the fragmentary petiole appears superimposed. Generally, this leaf is poorly preserved, showing scratches of a brush. Tertiaries and higher-order veins mentioned by Ettingshausen (1869a) are not preserved. The assignment to *Nyssa* cf. *haidingeri* is indicated by the combination of laminar shape, size and pattern of secondaries as described by Kvaček and Bůžek (1972).

The leaf NHMW 1878/6/4018 + 4019 (Ett. 2015 + 2016) is very similar, differing mainly by its smaller size. Accordingly, its assignment appears less certain. *Juglans undulata* (Ettingshausen 1869a: pl. 6, fig. 8) may also represent *N.* cf. *haidingeri*. The tertiary venation, which is (forked-) percurrent according to the drawing, accounts for the hesitation in the assignment. The respective specimen has not been detected in the studied collections.

***Nyssa* sp.**

Fig. 19.3

Material. Seegraben Walpurgis-Schacht: NHMW: 1878/6/4441 (Ett. 2438), B.

Description. External imprint of an oblong fruit, l × w ~24.5 × 10 mm, shape of base and apex straight to somewhat concave, utmost base and apex not preserved; surface coarsely ribbed, deepening in the apical part, indicating a germination valve.

Remarks. The shape of the fruit and the deepening (probably resulting from the already missing germination valve) account for the generic assignment (pers. comm. E. Martinetto and V. Teodoridis).

Order CORNALES Dumortier vel ROSALES Perleb

Family CORNACEAE Bercht. et J. Presl vel RHAMNACEAE Juss.

Cornaceae vel **Rhamnaceae gen.** et **sp.**

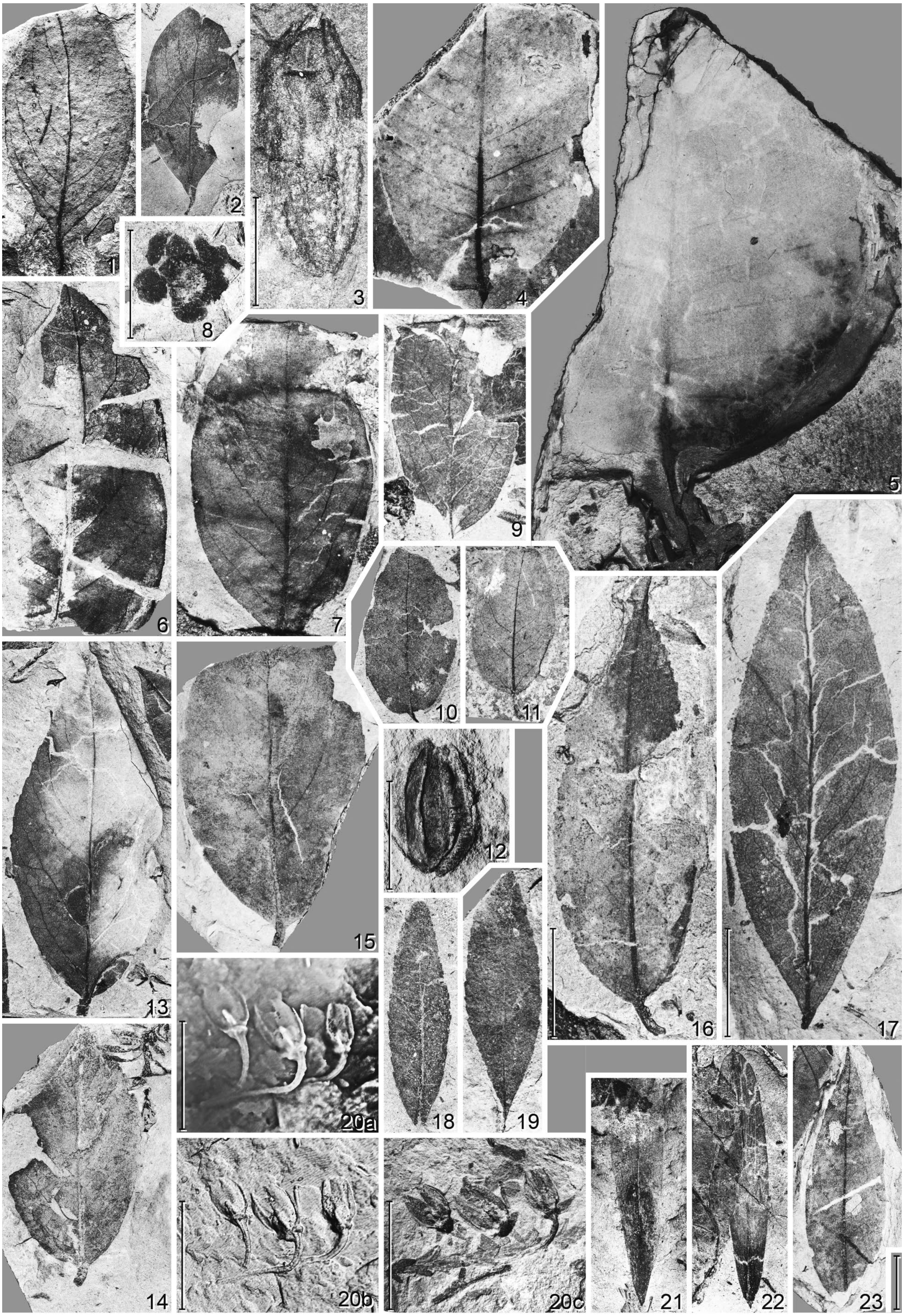
Figs 20.4–20.7, 26.1

1869a *Maytenus integrifolia* Ettingsh. sp. n.; Ettingshausen, p. 84, pl. 5, fig. 18.
1888 *Quercus gmelinii* A. Braun, p.p.; Ettingshausen, p. 290.
1888 *Daphne radobojana* Unger, p.p.; Ettingshausen, p. 311.
1888 *Apocynophyllum lanceolatum* Unger, p.p.; Ettingshausen, p. 323.
1888 *Heteropteris protogaea* Ettingsh., p.p.; Ettingshausen, p. 341.
1888 *Maytenus integrifolia* Ettingsh.; Ettingshausen, p. 345, pl. 9, fig. 6.
1888 *Rhamnus gaudinii* Heer p.p.; Ettingshausen, p. 349.

Material. Moskenberg: NHMW: 1878/6/3514 (Ett. 1511), A, (*Rhamnus gaudinii*); 1878/6/3531 (1528), B; 1878/6/4053 (2050) (*Quercus gmelinii*) + 1878/6/7961 (5958), (*Daphne radobojana*); 1878/6/8178 (6175), Pb 1992, (*Apocynophyllum lanceolatum*); 1878/6/8510 (6507), Pb 2016, (*Maytenus integrifolia*), Ettingshausen (1869a: pl. 5, fig. 18, holotype). IBUG: Ett. 6199, A, (*Heteropteris protogaea*).

Description. Simple leaves, petiole not preserved, lamina shape slender elliptic, l × w ~60–90 (?) 180 × 22–53 mm, ratio l/w ~2.4–3.7; base shape almost straight to slightly convex, base angle acute; apex not preserved, (?) acute or acuminate; margin entire to entire with single very inconspicuous, tiny teeth; midvein straight, distinct; secondaries considerably more delicate, eucamptodromous, angle of origin acute, not very regularly spaced, wide to moderately dense, running steeply and slightly curved towards margin, ascending closely along margin as intramarginal secondary or fimbrial vein; lowermost pair of secondaries paralleling margin; tertiaries delicate, mainly faintly traceable, reticulate to percurrent, angle towards 1° vein obtuse; further venation pattern reticulate.

Remarks. Characteristics of these leaves are the large size and the thick midvein compared to the slender secondaries, which are not very regularly and moderately densely spaced and ascend steeply, paralleling the margin as either intramarginal secondaries or a fimbrial vein. Density and course of the secondaries are reminiscent of *Rhamnus* or *Cornus*. The assignment remains equivocal because of the obtuse angle of the 3° veins towards the midvein. The large size and the steeply ascending secondaries remind of *Dicotylophyllum* sp. 2 from the Mecsek Mts. (Hably, 2020). In that specimen the dotted surface is interpreted as trichome bases and the 3° veins are not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visible. Therefore, it remains open whether the leaf from Mecsek Mts. represents the here described taxon. For differences from cf. *Cornus* sp. see that paragraph.

Order ERICALES Bercht. et J. Presl

Family EBENACEAE Gürke

Genus ***Diospyros*** L.

Diospyros brachysepala
A. Braun sensu Hantke (1954)

Figs 19.6–19.8, 25.15

1845 *Diospyros brachysepala* A. Braun; Braun, p. 170.
1859 *Diospyros brachysepala* A. Braun; Heer, p. 11, 191, pl. 102, figs 1–6, (?) 7 and 8.
1859 *Diospyros anceps* Heer; Heer, p. 12, pl. 102, figs 15–18.
1888 *Diospyros brachysepala* A. Braun, p.p.; Ettingshausen, p. 329, non pl. 6, fig. 9.
1888 *Diospyros anceps* Heer, p.p.; Ettingshausen, p. 329.
1954 *Diospyros brachysepala* A. Braun sensu novo; Hantke, p. 80, pl. 14, figs 4, 5.

Material. Moskenberg: NHMW: 1878/6/8273 (Ett. 6270), Pb 2128, (*Diospyros anceps*); (?) 2023/0072/0004 (coll. Hofmann sine no.). IBUG: Ett. 6121, (*Diospyros brachysepala* in sched.).

Description. Simple leaves lacking utmost base; laminar shape broad elliptic, l × w ~72 × 34–35 mm, ratio l/w ~2.1; apex angle acute, apex shape slightly convex to straight, (?) concave, incomplete; margin entire; midvein straight; secondaries festooned brochidodromous (IBUG Ett. 6121) to (?) eucamptodromous (NHMW 1878/6/8273, Ett. 6270), arising at moderate angle, spacing moderate to wide, not very regular, course curved, looping close to margin (NHMW 1878/6/8273, Ett. 6270) or at some distance from it with somewhat angular loops (IBUG Ett. 6121); fabric of tertiaries percurrent to reticulate, coarsely meshed. NHMW 2023/0072/0004: Four-partite calyx, 9 mm in diameter, sepals broadly rounded, attached with a wide base.

Remarks. While Ettingshausen (1888) listed several specimens as *Diospyros brachysepala* and several more *Diospyros* fossil-species, based on single specimens, only two leaves can be assigned to *Diospyros*. That author distinguished *D. brachysepala* and *D. anceps* although the leaf assigned to the latter fossil-species lacks the base. The differentiation of both fossil taxa by Heer (1859) was, however, based on the shape of the leaf base. Hantke (1954) fused both fossil-species because transitional leaf shapes were present in the flora of Schrotzburg (Germany, Middle Miocene). Bůžek (1971) referred to nomenclatural issues when he dealt the rich material of leaves and calyx remains from Čermníky (Bohemia, Lower Miocene). Furthermore, there is a single remain reminiscent of a four-partite calyx of *Diospyros*. Nonetheless, it is rather small, only ~9 mm in diameter, and diagnostic characters are scarce (Fig. 19.8).

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Figure 19. 1, **2**. cf. *Cornus* sp., **1**. NHMW 1878/6/3768 (Ett. 1765), Pb 2120, (*Cornus buechii*), Ettingshausen (1888: pl. 6, fig. 23), **2**. IBUG Ett. 6082, (*Lonicera prisca*), Ettingshausen (1888: pl. 5, figs 8, 8a, syntype); **3**. *Nyssa* sp., NHMW 1878/6/4441 (Ett. 2438), B; **4**, **5**. *Nyssa* cf. *haidingeri* (Ettingsh.) Kvaček et Bůžek, **4**. NHMW 1878/6/4018 (Ett. 2015), Pb 2049, (*Juglans parschlugiana*), **5**. NHMW 1878/6/8724 (Ett. 6721), Pb 2054, (*Anacardiophyllum dubium*), Ettingshausen (1869a: p. 90, very probably holotype); **6**, **7**. *Diospyros brachysepala* A. Braun sensu Hantke (1954), **6**. NHMW 1878/6/8273 (Ett. 6270), Pb 2128, (*Diospyros anceps*), **7**. IBUG Ett. 6121, (*Diospyros brachysepala*); **8**. (?) *Diospyros brachysepala* A. Braun sensu Hantke (1954), NHMW 2023/0072/0004; **9–11**. Styracaceae (?) gen. et sp., **9**. NHMW 1878/6/4475 (Ett. 2472), b, Pb 2373, (*Elaeodendron striacum*), **10**. NHMW 1878/6/4477 (Ett. 2474), Pb 2354, (*Sophora europaea*), Ettingshausen (1888: pl. 9, fig. 30), **11**. NATURALIS: RGM.THDB.6777; **12**. cf. *Symplocos* sp., NHMW 1878/6/8266 (Ett. 6263), (*Diospyros brachysepala*); **13–15**. *Ternstroemites stiriacus* (Ettingsh.) Kovar-Eder comb. nov., **13**. NHMW 1878/6/4052 (Ett. 2049), a, Pb 1859, paratype, (*Euonymus diversifolius*), Ettingshausen (1888: pl. 8, fig. 19, syntype), **14**. NHMW 1878/6/4111 (Ett. 2108), Pb 1848, (*Ilex dianae*), Ettingshausen (1888: pl. 9, figs 7, 7a, holotype), **15**. NHMW 1878/6/8547 (Ett. 6545), Pb 2005, holotype, (*Elaeodendron stiriacum*), Ettingshausen (1869a: pl. 6, fig. 1, holotype); **16**. *Ternstroemites egeriae* (Ettingsh.) Kovar-Eder comb. nov., NHMW 1878/6/3849 (Ett. 1846), Pb 2095, holotype, (*Sorbus egeriae* Ettingsh.), Ettingshausen (1888: pl. 9, figs 15, 15a, holotype); **17**. *Ternstroemites diversifolius* (Ettingsh.) Kovar-Eder comb. nov., NHMW 1878/6/4140 (Ett. 2137), (*Euonymus diversifolius*), counterpart of NHMW 1878/6/4052, b (Ett. 2049, b), Pb 1859, lectotype, Ettingshausen (1888: pl. 8, figs 18, 18a, syntype); **18**, **19**. Theaceae (?) vel Ericaceae (?) gen. et sp., **18**. NHMW 1878/6/4331 (Ett. 2328), (*Ceratopetalum haeringianum*), **19**. IBUG Ett. 6141 (*C. haeringianum*); **20a–c**. Vaccinioideae gen. et sp., NHMW 1878/6/4047 (Ett. 2044), Pb 1973, (*Cinnamomum polymorphum*), Ettingshausen (1888: pl. 4, fig. 20), **20a**, **b**. different views from CT-scans, **20c.** surface view; **21**, **22**. *Fraxinus macroptera* Ettingsh., **21**. IBUG 6094, (*Fraxinus macroptera*), Ettingshausen (1888: pl. 5, figs 13, 13a), **22**. IBUG 6095, (*Fraxinus macroptera*); **23**. *Fraxinus bilinica* (Unger) Kvaček, NHMW 1878/6/3879 (Ett. 1876), Pb 1958, (*Fraxinus primigenia*). For all photographs the scale at bottom right of the figure is 10 mm except for photographs with embedded scale in which the scale is also 10 mm

Family ERICACEAE Juss.

Subfamily VACCINIOIDEAE Arn.

Vaccinioideae gen. et **sp.**

Fig. 19.20

1888 *Cinnamomum polymorphum* A. Braun, p.p.; Ettingshausen, p. 309, pl. 4, fig. 20.

Material. Moskenberg: NHMW: 1878/6/4047 (Ett. 2044), Pb 1973, (*Cinnamomum polymorphum*), Ettingshausen (1888: pl. 4, fig. 20).

Description. Fragmentary racemose infructescence; 3 pedicillate capsules directed to one side preserved; one capsule still attached to curved pedicel, others closely adjoining main axis; pedicel of attached capsule 6 mm long; calyx persistent, at base of capsule, ovary superior; capsules (?) 4 to (?) 5 valved, elongated, l × w = 8–11 × 6–7 mm with central column, dehiscence probably loculicidal.

Remarks. Ettingshausen (1888) assigned this remarkable specimen to the Lauraceae. The CT-scan performed to reveal details hidden in the sediment hardly provided more information than the surface image. The persistent calyx at the base of each capsule indicates hypogynous flowers. The curved pedicels are consistent with Ericaceae. This curvature is typical for orienting capsules to face upwards in order to avoid shedding their wind-dispersed seeds directly downward (pers. comm. W. Judd). The dehiscence was possibly loculicidal, pointing towards the tribes Oxydendreae, Lyonieae, Gaultherieae, or Andromedeae, although septicidal dehiscence (Ericoideae) cannot be ruled out completely (pers. comm. W. Judd, S. Manchester). No further diagnostic features such as placentation or presence of a terminal style are available. The specimen is reminiscent of *Juddicarpon benewahensis* Smith et Manchester described from the Clarkia flora (Latah Formation, Middle Miocene, 16–15.4 ma, Idaho) with close relations to *Oxydendrum* (Smith and Manchester, 2019), but it is far less well preserved. No other remains as isolated fruits or seeds have been detected in the studied material.

Family STYRACACEAE DC. et Spreng. (?)

Styracaceae (?) **gen.** et **sp.**

Figs 19.9–19.11, 25.16

1888 *Elaeodendron stiriacum* Ettingsh., p.p.; Ettingshausen, p. 346.

1888 *Sophora europaea* Unger; Ettingshausen, p. 363, pl. 9, fig. 30.

Material. Seegraben Walpurgis-Schacht: NHMW: 1878/6/4475 (Ett. 2472), b, Pb 2373, (*Elaeodendron stiriacum*); 1878/6/4477 (2474), Pb 2354, (*Sophora europaea*), Ettingshausen (1888: pl. 9, fig. 30). Leoben: NATURALIS: RGM.THDB.6777.

Description. Simple leaves lacking apex; petiole 2–4 mm long, slightly angular towards midvein; laminar shape ovate, elliptic, l × w ~30–57 × 14–23 mm, ratio l/w ~1.9–2.4; base angle (wide) obtuse, base shape convex to rounded; margin entire/erose to dentate in apical part (NHMW 1878/6/4477, Ett. 2474), tooth height < 1 mm, distal and proximal flanks convex, sinus angular to rounded; apex rounded, blunt, some teeth minutely (?) glandular; midvein slender, straight to minimally sinuate; secondaries (festooned) brochidodromous to (festooned) semicraspedodromous in toothed part, delicate; angle of origin moderate to moderately narrow (NHMW 1878/6/4475, Ett. 2472, b) and moderate to moderately wide (NHMW 1878/6/4477, Ett. 2474); spacing of secondaries not very regular, moderate to wide, general course straight to slightly curved, slightly zigzag; secondaries steeply ascending (NHMW 1878/6/4475, Ett. 2472, b); secondaries forking and looping at some distance from margin; further loops developed towards margin; veinlets arising from marginal loops running into tooth apices; tertiaries forked-percurrent to reticulate; further veins reticulate.

Remarks. The texture of these leaves was probably chartaceous, which is indicated by the preservation of the venation details, although already the secondaries are delicate. Such dentition of the margin is reminiscent of Styracaceae. Nonetheless, reliable fossil records of Styracaceae foliage are extremely rare. *Styrax burdigalensis* Kvaček, Teodoridis et Roiron, described from Arjuzanx (France, Middle Miocene; Kvaček et al., 2011), differs by the cuneate base and probably more slender lamina. The assignment of the leaves from Arjuzanx to *Styrax* is, however, supported by the presence of stellate trichomes.

Family SYMPLOCACEAE Desfontaines

Genus ***Symplocos*** Jacq.

cf. ***Symplocos* sp.**

Fig. 19.12

1888 *Diospyros brachysepala* A. Braun, p.p.; Ettingshausen, p. 329.

Material. Moskenberg: NHMW: 1878/6/8266 (Ett. 6263), (*Diospyros brachysepala*).

Description. External fruit imprint, shape oval, l × w ~12 × 8 mm, with longitudinal ribs.

Remarks. The preservation state does not allow a more precise assignment (pers. comm. E. Martinetto and V. Teodoridis).

Family THEACEAE Ker Gawler

Genus ***Ternstroemites*** Berry

Ternstroemites diversifolius (Ettingsh.) Kovar-Eder comb. nov.

PFNR Unique Identifier: PFN003333

Figs 19.17, 25.17

1888 *Euonymus diversifolius* Ettingsh. sp. n., p.p.; Ettingshausen, p. 347, pl. 8, figs 18, 18a, non 19.

Lectotype designated here. NHMW 1878/6/4052, b + 4140 (Ett. 2049, b + 2137), Pb 1859, (*Euonymus diversifolius*), Ettingshausen (1888: pl. 8, figs 18, 18a, syntype), refigured on Figs 19.17, 25.17.

Basionym. *Euonymus diversifolius* Ettingsh., Ettingshausen (1888: p. 347).

Derivatio nominis. Referring to the morphological variability.

Locus typicus. Historical locality Moskenberg near Leoben, Leoben Basin, Styria (Ettingshausen, 1869a).

Stratum typicum. Shales ~8.2 m above the coal seam (Ettingshausen, 1869a), 14.9 ± 0.7 Ma, dating of a tuff layer near the base of the shales overlying the coal seam, Sachsenhofer et al., 2010).

Material. Moskenberg: NHMW: 1878/6/4052, b + 4140 (Ett. 2049, b + 2137), Pb 1859, (*Euonymus diversifolius*), Ettingshausen (1888: pl. 8, figs 18, 18a, syntype).

Emended diagnosis. Slender elliptic leaf, base and apex acute, margin regularly, very densely and minutely serrate, teeth (?) theoid, secondaries probably festooned brochidodromous, delicate, tertiaries percurrent to reticulate, higher-order veins reticulate.

Description. Shortly petiolate, simple leaf; laminar shape slender elliptic, l × w 46 × 15 mm, ratio l/w 3.1; base angle acute, base straight to minimally convex; apex angle acute, apex shape straight to minimally acuminate; margin regularly, very densely serrate, near base entire to less densely spaced teeth; teeth extremely minute, up to 10–12 teeth per 5 mm (!); apex blunt, (?) theoid (setaceous) already devoid of deciduous projections; midvein straight, secondaries already rather delicate, probably festooned semicraspedodromous, moderately spaced, up to 4–5 mm in middle part of lamina; secondaries arising at moderate angle, slightly curved, ascending steeply, looping at some distance from margin; further loops of higher-order veins developed closer to margin; intersecondaries present, looping with secondaries; tertiaries partly percurrent, partly reticulate; higher-order veins reticulate.

Remarks. Ettingshausen (1888: pl. 8, figs 8, 9) merged two leaves with considerably different morphology under *Euonymus diversifolius*, referring to this fact by the species epithet *diversifolius*. One of them is represented by part and counterpart (NHMW 1878/6/4052, b + 4140 (Ett. 2049, b + 2137), here described as *Ternstroemites diversifolius*. The other leaf is transferred to *T. stiriacus* (Ettingsh.) Kovar-Eder comb. nov., which Ettingshausen (1869a) described as *Elaeodendron stiriacum* Ettingsh. (see respective paragraph). According to the International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code, Turland et al., 2018), the epitethon *diversifolius* must be retained for the here discussed specimen although it is not well-fitting because the variability of this fossil-taxon is still unknown.

Most characteristic of *T. diversifolius* is the minute, dense, (?) setaceous serration (up to 10–12 teeth per 5 mm). The deciduous apical projections appear already shed and it remains equivocal whether the teeth were gland-tipped.

Leaf shape, venation and the extremely minute marginal serration as well as the very short but thick petiole point towards a Theaceae relationship. The assignment to the form-genus *Ternstroemites* Berry is based on the fact that an unequivocal assignment to a modern genus within Theaceae is not possible.

Miocene records of Theaceae foliage have increased steadily during the last decades, e.g. Kvaček and Walther (1984b), Bozukov and Palamarev (1995), Kovar-Eder and Meller (2001), Kovar-Eder et al. (2004), Kvaček et al. (2011), Holý et al. (2012). *Hartia palaeorhodopensis* Bozukov, Palamarev (1995) from the Middle Miocene of Bulgaria is the only fossil-species resembling the here described leaves to some degree. It differs, however, by bigger size, somewhat coarser serration, and less steeply ascending secondaries.

Some former Theaceae genera as *Eurya*, *Visnea* or *Ternstroemia* are now assigned to the Pentaphylacaceae (Stevens, P.F., 2001 onwards) implying the necessity to reconsider the concept of the fossil *Ternstroemites*.

Ternstroemites egeriae

(Ettingsh.) Kovar-Eder comb. nov.

PFNR Unique Identifier: PFN003336

Fig. 19.16

1888 *Sorbus egeriae* Ettingsh. sp. n.; Ettingshausen, p. 360, pl. 9, figs 15, 15a.

Holotype designated here. NHMW 1878/6/3849 + 3859 (Ett. 1846 + 1856), Pb 2095, *Sorbus egeriae* Ettingsh. sp. n., Ettingshausen (1888: p. 360, pl. 9, figs 15, 15a), refigured on Fig. 19.16.

Basionym. *Sorbus egeriae* Ettingsh., Ettingshausen (1888: p. 360).

Derivatio nominis. questionable.

Locus typicus. Historical locality Moskenberg near Leoben, Leoben Basin, Styria (Ettingshausen, 1869a).

Stratum typicum. Shales ~8.2 m above the coal seam (Ettingshausen, 1869a), 14.9 ± 0.7 Ma (a tuff layer near the base of the shales overlying the coal seam, Sachsenhofer et al., 2010).

Material. Moskenberg: NHMW: 1878/6/3849 + 3859 (Ett. 1846 + 1856), Pb 2095, (*Sorbus egeriae*), Ettingshausen (1888: pl. 9, figs 15, 15a, holotype).

Emended diagnosis. Simple leaf, petiole thick, angular towards midvein, bent; lamina ovate to slender elliptic, small, base convex, apex long-acuminate, somewhat offset; margin regularly simple serrate, teeth small, probably theoid, tooth apices blunt, devoid of deciduous projections; secondaries considerably more delicate than midvein.

Description. Petiolate, simple leaf; petiole angular towards midvein, bent, ~4 mm long and 1 mm wide; lamina ovate to elliptic, l × w ~42 × 13 mm, ratio l/w ~3.2; base angle ~90°, base shape convex; apex angle narrow acute, apex shape long-acuminate, somewhat offset; margin regularly simple serrate, teeth small, probably theoid (setaceous), distal flank straight to convex, proximal flank mainly straight to slightly concave, sinus rounded, apex blunt, probably devoid of deciduous projection; midvein almost straight, thick; secondaries probably semicraspedodromous, considerably more delicate, arising at moderate angle, moderately spaced (3–6 mm in central part), straight to slightly bent; tertiaries faint, partly percurrent.

Remarks. Ettingshausen (1888) did not explain which features of this leaf point towards *Sorbus* L. The thick petiole indicates an evergreen fossil-species rather than a deciduous one, as suspected by Ettingshausen, and the faint appearance of the lamina is probably a preservational artefact rather than indicating chartaceous texture. While the venation is only poorly preserved, the marginal serration looks like the teeth had shed their apices (theoid or setaceous type), which is a feature characteristic of Theaceae. The thick petiole in angular position to the midvein also occurs in Theaceae. A somewhat offset, long-acuminate leaf apex occurs in several Theaceae genera, e.g. *Camellia tsaii* H.H. Hu (e.g. Kvaček and Walther, 1984a: pl. 25, fig. 6. Specimen DR 047619 in JACQ – Virtual Herbarium JACQ, accessed April, 2023). *T. egeriae* differs from *T. diversifolius* by bigger and less dense teeth.

Ternstroemites stiriacus

(Ettingsh.) Kovar-Eder comb. nov.

PFNR Unique Identifier: PFN003338

Figs 19.13–19.15, 25.18

1869a *Elaeodendron stiriacum* Ettingsh. sp. n.; Ettingshausen, p. 85, pl. 6, fig. 1.

1888 *Elaeodendron stiriacum* Ettingsh., p.p.; Ettingshausen, p. 346.

1888 *Euonymus diversifolius* Ettingsh. sp. n., p.p.; Ettingshausen, p. 347, pl. 8, fig. 19, non figs 18, 18a.

1888 *Ilex dianae* Ettingsh. sp. n.; Ettingshausen, p. 348, pl. 9, figs 7, 7a.

Holotype designated here. NHMW 1878/6/8547 + 8548 (6544 + 6545), Pb 2005, (*Elaeodendron stiriacum*), Ettingshausen (1869a: pl. 6, fig. 1, holotype), refigured on Fig. 19.15.

Basionym. *Elaeodendron stiriacum* Ettingsh., Ettingshausen (1869a: p. 85).

Paratype. NHMW 1878/6/4052 (Ett. 2049), a, Pb 1859, (*Euonymus diversifolius*), Ettingshausen (1888: pl. 8, fig. 19, syntype), refigured on Fig. 19.13.

Derivatio nominis. Referring to the occurrence in Styria.

Locus typicus. Historical locality Moskenberg near Leoben, Leoben Basin, Styria (Ettingshausen, 1869a).

Stratum typicum. Shales ~8.2 m above the coal seam (Ettingshausen, 1869a), 14.9 ± 0.7 Ma, dating of a tuff layer near the base of the shales overlying the coal seam, Sachsenhofer et al., 2010).

Material. Moskenberg: NHMW: 1878/6/4052 (Ett. 2049), a, Pb 1859, (*Euonymus diversifolius*), Ettingshausen (1888: pl. 8, fig. 19, syntype); 1878/6/4111 (2108), Pb 1848, (*Ilex dianae*), Ettingshausen (1888: pl. 9, figs 7, 7a, holotype); 1878/6/8547 + 8548 (6544 + 6545), Pb 2005, (*Elaeodendron stiriacum*), Ettingshausen (1869a: pl. 6, fig. 1, holotype).

Emended diagnosis. Short-petiolate leaves, petiole very thick, curved or angular towards midvein; lamina elliptic to slightly obovate, base convex, apex acuminate; margin entire near base, then crenate-serrate, teeth loosely, not very regularly spaced, sinus angular, tooth apices blunt to minimally mucronate, (?) glandular; midvein thick, slightly undulate; secondaries slender, (festooned) semicraspedodromous, widely, not very regularly spaced, partly undulate; tertiaries reticulate to percurrent, somewhat undulate; higher-order veins finely reticulate.

Description. Short-petiolate, simple leaves; petiole thick, 3 mm long, up to 2 mm wide, curved or angular towards midvein; lamina elliptic to slightly obovate, l × w ~45–69 × 20–34 mm, ratio l/w ~2.3–3.8; base angle obtuse, base shape convex to rounded; apex angle (narrow) acute, apex shape acuminate; margin entire near base, then (indistinctly) crenate-serrate; teeth small, height <1 mm, loosely and not very regularly spaced, slightly varying in size, distal and proximal flanks convex, sinus angular, tooth apices blunt to minimally mucronate, (?) glandular; midvein thick in basal part, tapering considerably towards apex, straight to slightly undulate; secondaries slender, (festooned) semicraspedodromous, widely and not very regularly spaced, arising at moderate angles, course moderately bent, slightly undulate especially in the exmedial part; secondaries sometimes forking in exmedial third of lamina; secondaries and further veins looping near margin, most marginal loops giving rise to veinlets that run into teeth; intersecondaries occasionally developed; tertiaries reticulate to percurrent, somewhat undulate; higher-order veins finely reticulate.

Remarks. Ettingshausen (1869a, 1888) described 3 new fossil-species based on these leaves (see synonymy and paragraph *Ternstroemites diversifolius*) of which the first species-epitethon is *stiriacum*. The respective specimen described as *Elaeodendron stiriacum* (Ettingshausen, 1869a) is not very well preserved (refigured here on Fig. 19.15). Therefore, the best-preserved specimen (NHMW 1878/6/4052, Ett. 2049, a) has been selected here as paratype in addition to the holotype. Ettingshausen (1888) synonymises *Elaeodendron oligoneure* (Ettingshausen, 1869a; NHMW 1878/6/8549, Ett. 6546) with *E. stiriacum*. This reassignment must be rejected because this leaf or leaflet is long-petiolate, has much bigger teeth and a different venation pattern (see paragraph *Clematis oligoneure*).

Laminar shape, marginal serration with sometimes slightly mucronate, (?) glandular teeth and festooned secondaries point towards a Theaceae relationship.

The very thick petiole of *Ternstroemites stiriacus* again indicates an evergreen fossil-species rather than a deciduous one. *T. stiriacus* differs from *T. diversifolius and T. egeriae* by the somewhat undulate venation course and less regular serration with some minimally mucronate teeth. It differs further from *T. diversifolius* by laminar shape, and bigger, less densely spaced teeth, and from *T. egeriae* by the bigger lamina.

Theaceae (?) vel **Ericaceae** (?) **gen**. et **sp**.

Fig. 19.18, 19.19

1888 *Ceratopetalum haeringianum* Ettingsh., p.p.; Ettingshausen, p. 334.

Material. Moskenberg: IBUG: Ett. 6141 + 6142, (*Ceratopetalum haeringianum*). Münzenberg: NHMW: 1878/6/4331 (Ett. 2328), (*Ceratopetalum haeringianum*).

Description. Petiolate simple, probably coriaceous leaves; petiole 3 mm long, incomplete in length and width; laminar shape slender elliptic to oblong, l × w ~43–49 × 12–14 mm, ratio l/w ~3.5–3.6; base angle acute, base shape straight to slightly convex; apex angle acute, apex shape straight, utmost apex (?) convex; margin simple serrate, entire at base, teeth < 1 mm, more or less equal in size, rather regularly spaced, moderately dense (4–5 per cm in middle part), distal flank very short, convex, proximal flank straight to slightly convex, sinus angular, apex rounded, blunt; midvein straight; secondaries very faint, delicate, arising at (?) moderate angle.

Remarks. These leaves are almost complete, the texture was likely coriaceous and the teeth were not setaceous. Essential venation details are not preserved, hampering a comparison with those Theaceae that are similar in size and laminar shape and serration, such as *Gordonia hradekensis* (Kvaček et Bůžek) Bozukov et Palamarev (e.g. Holý et al., 2012), or with *Ternstroemites pereger* (Unger) Kovar-Eder et Kvaček (Kovar-Eder et al., 2004). An Ericaceae affinity is also possible because of the probably non-setaceous teeth.

Order LAMIALES Bromhead

Family OLEACEAE Hoffmanns. et Link

Genus ***Fraxinus*** L.

Fraxinus bilinica (Unger) Kvaček

Figs 19.23, 25.19

1849 *Juglans bilinica* Unger, p.p.; Unger, p. 126 (non pl. 14, fig. 20).

1850a *Juglans bilinica* Unger, p.p.; Unger, p. 469.

1888 *Fraxinus primigenia* Unger, p.p.; Ettingshausen, p. 323, non pl. 5, fig. 11.

2000 *Fraxinus bilinica* (Unger) Kvaček et Hurnik; Kvaček and Hurnik, p. 19, pl. 8, fig. 7, text-figs 4.2, 4.7.

Material. Moskenberg: NHMW: 1878/6/3879 (Ett. 1876), Pb 1958, (*Fraxinus primigenia*).

Description. (?) Leaflet lacking base, laminar shape elliptic, l × w ~46 × 14 mm, ratio l/w ~3.3; base angle (?) acute, base shape (?) moderately convex; apex angle acute to acuminate; margin entire in basal part then simple serrate; teeth spacing neither dense nor regular, tooth height < 1 mm, distal and proximal flanks straight, convex, proximal flank straight to convex, sinus angular to rounded, apex blunt; midvein straight, distinctly thicker than secondaries, tapering along length; secondaries delicate, brochidodromous near base then semicraspedodromous, looping in marginal third of lamina; secondaries moderately spaced, angle of origin moderate, course initially straight, then curved; exmedial veinlets forming further loops, veinlets serving teeth but not running into tooth apex; tertiaries and higher-order veins reticulate; areoles well developed, freely ending veinlets multiply branched.

Remarks. The assumption is that this remain represents a leaflet rather than a leaf because its well-preserved further morphological features match well with those of *Fraxinus*. Ettingshausen (1888) assigned 5 leaf remains explicitely to *Fraxinus*, three of them to *F. primigenia* and two to *F. praeexcelsior* Ettingsh. *Fraxinus* leaflets are characterised by brochidodromous to eucamptodromous secondaries not running into the tooth apices and by a reticulate 3° vein fabric. The secondaries may touch the tooth sinus or the veinlets may run into the sinus. Veinlets serving the tooth apex are rare. The here described specimen represents the only ash leaflet, while the others represent different taxa (see paragraphs *Alnus julianiformis*, *Trigonobalanopsis rhamnoides*, Supplemantary File 2).

Kvaček and Hurnik (2000) referred to the nomenclatural issues, introducing the combination *F. bilinica*, which is followed here.

Fraxinus macroptera Ettingsh.

Fig. 19.21, 19.22

1868 *Fraxinus macroptera* Ettingsh. sp. n.; Ettingshausen, p. 213, pl. 36, figs 9, 10.

1888 *Fraxinus macroptera* Ettingsh.; Ettingshausen, p. 323, pl. 5, figs 13, 13a.

Material. Moskenberg: IBUG: Ett. 6094, (*Fraxinus macroptera*), Ettingshausen (1888: pl. 5, figs 13, 13a); Münzenberg: IBUG: Ett. 6095, (*Fraxinus macroptera*).

Description. Bilaterally symmetrical samaroid fruits, IBUG Ett. 6095 complete, IBUG Ett. 6094 incomplete distally; l × w ~(44 incomplete) –47 × 7–10 mm; slender oblong; base acute, distal end short acuminate (Ett. 6095), margin entire, with strong longitudinal keel and numerous fine, parallel, somewhat diverging veins; pedicel incomplete; oval seed at base.

Remarks. In the heading for this taxon, "sp. n." (Ettingshausen, 1888) is clearly a printing mistake because *F. macroptera* was described first from the flora of Bilina (Ettingshausen, 1868). The figured specimen (Ettingshausen, 1888: pl. 5, figs 13, 13a) is incomplete distally. The better-preserved specimen is IBUG Ett. 6095 (Fig. 19.22). *F. primigenia* from Parschlug (Kovar-Eder et al., 2004) appears smaller and narrower.

Order DIPSACALES Bercht. et J. Presl

Family VIBURNACEAE Raf.

Genus ***Sambucus*** L.

Sambucus ettingshausenii Kovar-Eder sp. n.

PFNR Unique Identifier: PFN003340

Figs 20.1, 25.20

Holotype designated here. IBUG 6085 A, B.

Derivation nominis. In honour of Constantin von Ettingshausen, who presented the first monograph of the Leoben flora (Ettingshausen, 1869a, 1888).

Locus typicus. Historical locality Moskenberg near Leoben, Leoben Basin, Styria (Ettingshausen, 1869a).

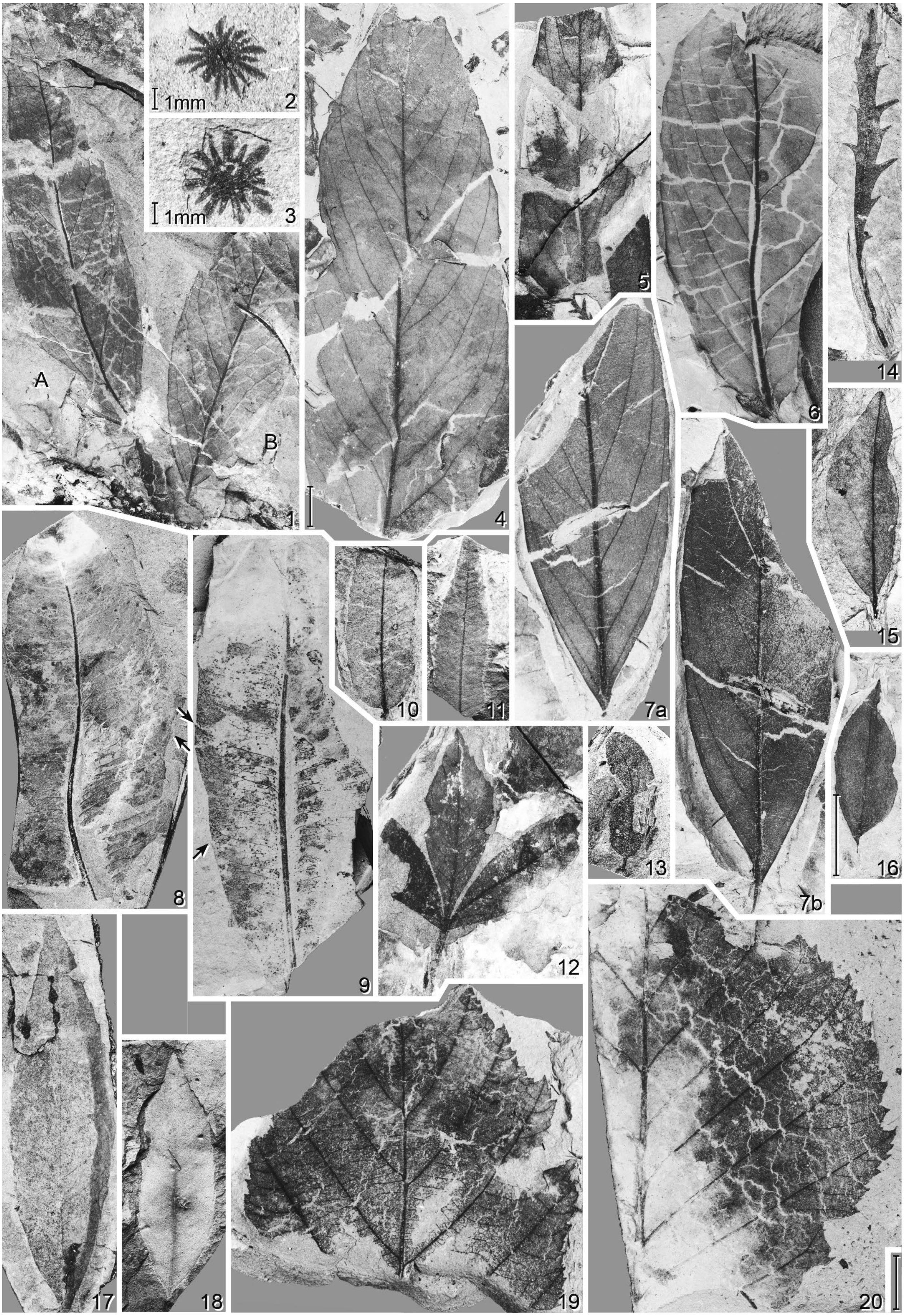
Stratum typicum. Shales ~8.2 m above the coal seam (Ettingshausen, 1869a), 14.9 ± 0.7 Ma (a tuff layer near the base of the shales overlying the coal seam, Sachsenhofer et al., 2010).

Material. Moskenberg: IBUG: Ett. 6085 A, B, (*Sambucus miocenica* sp. n. in sched.).

Diagnosis. (?) subsessile leaflets, lamina slender elliptic, base almost cuneate, apex acute, slightly (?) acuminate; margin simple serrate, teeth distantly spaced, tiny, (?) glandular; midvein slender, secondaries festooned semicraspedodromous, lowermost pair arising at base, running parallel to margin; tertiaries widely spaced, percurrent to irregular reticulate, large-meshed; quaternaries reticulate and also large-meshed; veinlets arising from marginal loops running into tooth sinus.

Description. Two leaflets of probably one compound leaf; petiolule 2–3 mm long, (?) complete; laminar shape slender elliptic symmetrical to somewhat asymmetrical, l × w of the more complete leaflet A ~83 × 24 mm, ratio l/w ~3.5, that of leaflet B ~(?) 67–72 × 24 mm; base angle acute, base shape almost cuneate to slightly convex; apex angle narrow acute, apex shape straight, (?) slightly acuminate; margin simple serrate with irregularly, widely spaced teeth; teeth up to 1 mm high, proximal flank very short, distal flank straight, near tooth apex convex, sinus angular, apex bluntly acute, (?) glandular; midvein almost straight, near base somewhat bent, slender; secondaries slender, festooned semicraspedodromous, spacing moderately dense, more or less regular, angle of origin narrow to moderate, course straight to minimally sinuate, near margin curved, finally looping; lowermost pair of secondaries arising at base, running parallel to margin; tertiaries widely spaced, mainly percurrent transient to irregular reticulate, curved to sinuate, angle towards midvein from perpendicular to wide obtuse, forming large meshes; quaternaries reticulate and also large-meshed; veinlets arising from marginal loops running into tooth sinus.

Remarks. As recognised by Ettingshausen (note in the handwritten inventory of IBUG), the position of these leaflets in the sediment implies that they probably belong to a single compound leaf. Unfortunately, the organical contact is not preserved. The fabric of the secondaries and tertiaries resembles that in *Sambucus*, the serration is usually more dense and regularly spaced. Glandular teeth do occur and such teeth are bigger, with veinlets running into the tooth apex (NMNS Cleared Leaf Database, POWO, accessed July, 2023). Therefore, the generic assignment remains somewhat equivocal. While seeds of *Sambucus*


1
A
B
2
1mm
3
1mm
4
5
6
7a
7b
8
9
10
11
12
13
14
15
16
17
18
19
20

are well known from the European Miocene, reliable foliage records are not known to the author, which may be related to rapid decay as observed in modern *S. nigra* L. (own observation).

Leaves incertae sedis

"*Apocynophyllum*" *hunteriaeforme* Ettingsh.

Figs 20.8, 20.9, 26.2

1869a *Apocynophyllum hunteriaeforme* Ettingsh. sp. n.; Ettingshausen, p. 70, pl. 4, figs 5, 6.

1878b *Achras lycobroma* Unger with *Sphaeria achreia* Ettingsh. sp. n.; Ettingshausen, p. 84, pl. 5, fig. 4.

1888 *Apocynophyllum hunteriaeforme* Ettingsh.; Ettingshausen, p. 325.

Material. Moskenberg: NHMW: 1878/6/3562 + 8193 (Ett. 1559 + 6190), Pb 1998, (*Apocynophyllum hunteriaeforme*), Ettingshausen (1869a: pl. 4, figs 5, 6, holotype); 1878/6/6497 (4494), as (*Achras lycobroma*) with fungus (*Sphaeria achreia*), Ettingshausen (1878b: pl. 5, fig. 4).

Description. Leaves or leaflets, lacking base and apex, lamina shape oblong, l × w ~70 and 85 mm × ~30 and 32 mm (both specimens incomplete); margin almost entire and distantly undulate, except for very distant, single, tiny, acute teeth; midvein thick and prominent, straight to sinuate; secondaries brochidodromous/eucamptodromous to semicraspedodromous if teeth are present; secondaries very delicate compared to midvein, very densely spaced, interspacing with intersecondaries; differentiation between secondaries and intersecondaries not always unequivocal; secondaries and intersecondaries arising from midvein under narrow angles, initially approaching midvein, soon turning and running rather straight towards margin, looping close to margin, forming narrow, elongated meshes; exmedial veinlets looping further; tertiaries percurrent to reticulate, not very regular, percurrent ones almost straight to irregularly sinuous, angle towards midvein wide obtuse; higher-order veins admedially ramifying, areoles not clearly delimited; ultimate veinlets branched to ramifying.

Remarks. Ettingshausen (1878b and 1888) described the fungus S*phaeria achreia* on the leaf of *Achras lycobroma* Unger but, astonishingly, did not further treat this latter fossil-taxon for the Leoben flora. Without any doubt, both leaves represent a single fossil-species. Ettingshausen (1888) listed specimen NHMW 1878/6/3562 (Ett. 1559) both as *Apocynophyllum hunteriaeformae* and *Cinchonidium bilinicum* Ettingsh. The latter assignment was probably a mistake and, instead, should be Ett. 1560, as is evident from the NHMW inventory.

Although the margin and venation pattern are very characteristic, the systematic affinity is obscure.

"*Cassia*" *lignitum* Unger

Fig. 20.13

1888 *Cassia lignitum* Unger, p.p.; Ettingshausen, p. 365.

Material. Moskenberg: NHMW: 1878/6/8868 (Ett. 6865), Pb 2137 (*Cassia lignitum*).

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Figure 20. **1**. *Sambucus ettingshausenii* Kovar-Eder sp. n., IBUG 6085 A, B, holotype, (*Sambucus miocenica* sp. n. in sched.), two leaflets of probably one compound leaf; **2**, **3**. *Antholithes stiriacus* (Ettingsh.) Kovar-Eder et Kvaček, **2**. IBUG Ett. 5596, (*Asterocalyx styriacus*), **3**. NHMW 2023/0072/0007, Ettingshausen (1888: pl. 3, fig. 2); **4–7**. Cornaceae vel Rhamnaceae gen. et sp., **4**. IBUG Ett. 6199, A, (*Heteropteris protogaea*), **5**. NHMW 1878/6/8178 (Ett. 6175), Pb 1992, (*Apocynophyllum lanceolatum*), **6**. NHMW 1878/6/3514 (Ett. 1511), A, (*Rhamnus gaudinii*), **7a**, **b. 7a**. NHMW 1878/6/7961 (Ett. 5958), (*Daphne radobojana*), **7b**. NHMW 1878/6/4053 (Ett. 2050) (*Quercus gmelinii*), part and counterpart; **8**, **9**. "*Apocynophyllum*" *hunteriaeforme* Ettingsh., arrows indicating tiny teeth, **8**. NHMW 1878/6/8193 (Ett. 6190), Pb 1998, (*Apocynophyllum hunteriaeforme*), counterpart of Ettingshausen (1869a: pl. 4, figs 5, 6, holotype), **9**. NHMW 1878/6/6497 (Ett. 4494), as (*Achras lycobroma*) with fungus (*Sphaeria achreia*), Ettingshausen (1878b: pl. 5, fig. 4); arrows indicating tiny teeth; **10**, **11**. *Dicotylophyllum* sp. B, **10**. NHMW 1878/6/8685 (Ett. 6682), Pb 2033, (*Rhus tenuifolia*), Ettingshausen (1869a: pl. 6, fig. 6, holotype), **11**. NHMW 1878/6/4350 (Ett. 2347), Pb 2248, (*Rhus prisca*); **12**. "*Cytisus*" *palaeolaburnum* Ettingsh., NATURALIS: RGM.THDB.6799, (*Cytisus palaeo-laburnum*), Ettingshausen (1888: pl. 9, fig. 27, holotype); **13**. "*Cassia*" *lignitum* Unger, NHMW 1878/6/8868 (Ett. 6865), Pb 2137; **14**. "*Dryandroides*" *grevilleaefolia* Ettingsh., NATURALIS: RGM.THDB.6757, (*Dryandroides grevilleaefolia*), Ettingshausen (1888: pl. 4, figs 15, 15a, holotype); **15**, **16**. "*Celastrus*" *myrtillifolius* Ettingsh., **15**. NHMW 1878/6/4227 (Ett. 2224), (*Cassia berenices*), **16**. NHMW 1878/6/4134 (Ett. 2131), (*Celastrus myrtillifolia*), Pb 2014, Ettingshausen (1888: pl. 9, figs 2, 2a, holotype); **17**, **18**. *Dicotylophyllum* sp. A, **17**. NHMW 1878/6/9828 (Ett. 7825), Pb 1956, (*Fraxinus prae-excelsior*), Ettingshausen (1888: pl. 5, fig. 11, syntype), **18**. NHMW 1878/6/8392 (Ett. 6389), Pb 2129, (*Ceratopetalum haeringianum*); **19**, **20**. "*Corylus*" *palaeoavellana* Ettingsh., **19**. NHMW 1878/6/7455 (Ett. 5452), A, (*Corylus palaeo-avellana*), **20**. NHMW 1878/6/3536 (Ett. 1533), A, (*C. palaeo-avellana*), Ettingshausen (1888: pl. 2, fig. 20). For all photographs the scale at bottom right of the figure is 10 mm except for photographs with embedded scale. If not stated otherwise the embedded scale is also 10 mm

Description. Petiolate leaf (or leaflet); petiole (petiolule) sturdy, straight, ~2.5 mm long; lamina shape oblong, curved in apical part, l × w ~23 × 7 mm, ratio l/w ~3.3; base angle obtuse, base shape convex to rounded, apex angle obtuse, apex shape convex, utmost apex rounded or (?) slightly emarginate; margin (?) entire; midvein bent in apical part; secondaries brochidodromous, arising at wide angles, moderately curved, lowermost pair running approaching margin; secondaries rather regularly interspacing with intersecondaries, which reach almost half the distance between midvein and margin.

Remarks. The petiole (or petiolule) appears rather robust and long relative to the small size of the lamina. This may indicate a leaf rather than leaflet. The assignment to *Cassia*, which is a genus with distribution mainly in the Southern Hemisphere, is unlikely.

“***Celastrus***” ***myrtillifolius*** Ettingsh.

Fig. 20.15, 20.16

1888 *Celastrus myrtillifolius* Ettingsh. sp. n.; Ettingshausen, p. 343, pl. 9, figs 2, 2a.

1888 *Cassia berenices* Unger, p.p.; Ettingshausen, p. 363.

Material. Moskenberg: NHMW: 1878/6/4134 (Ett. 2131), (*Celastrus myrtillifolia*), Pb 2014, Ettingshausen (1888: pl. 9, figs 2, 2a, holotype). Münzenberg: NHMW: 1878/6/4227 + 8132 (Ett. 2224 + 6129, B), Pb 2057, (*Cassia berenices*).

Description. Simple, petiolate leaves; petiole straight, 2 mm long (incomplete); laminar shape elliptic to slightly obovate, l × w ~21 × 9 mm and 38 × 19 mm, ratio l/w ~2.4 and 2; base angle acute, base shape straight to slightly convex; apex angle acute, apex shape straight to slightly acuminate; margin minutely crenate-serrate, partly entire especially near base, tooth height <1 mm, distal flank very short, proximal flank straight to slightly convex, sinus acute to rounded, apex blunt; midvein straight, distinct; secondaries brochidodromous, delicate, faint, widely spaced, originating at acute angle, steeply ascending, looping in front of margin.

Remarks. These leaves were probably rather coriaceous, which may account for the poor visibility of the venation fabric. In both specimens the margin is preserved only partly. In specimen NHMW 1878/6/4134 (Ett. 2131) the serration is distinct (Fig. 20.16), while in the other specimen a crenation is discernible in the apical part, but the basal part appears entire-margined (Fig. 20.15). *Ternstroemites diversifolius* differs by probably setaceous and even smaller, more densely spaced teeth along the whole margin except for the utmost base and more numerous (more densely spaced) secondaries. Leaves of *T. diversifolius* were probably less coriaceous than those of “*Celastrus*” *myrtillifolius*.

“***Corylus***” ***palaeoavellana*** Ettingsh.

Fig. 20.19, 20.20

1869a *Corylus palaeo-avellana* Ettingsh. sp. n.; Ettingshausen, p. 47.

1888 *Corylus palaeo-avellana* Ettingsh.; Ettingshausen, p. 293, pl. 2, fig. 20.

Material. Moskenberg: NHMW: 1878/6/3536 (Ett. 1533), A, (*Corylus palaeo-avellana*), Ettingshausen (1888: pl. 2, fig. 20) + GBA 2024/0001/0027, (*Corylus palaeo-avellana*); 1878/6/7455 (5452), A, (*Corylus palaeo-avellana*).

Description. Fragments of large, simple leaves lacking base and distalmost apex; lamina (?) broad elliptic to broad obovate, l × w ~70–100 × 56–92 mm, ratio l/w ~1.1–1.3; apex angle wide acute, apex shape (?); margin double serrate, teeth conspicuous, triangular, bigger above secondaries; up to 5 teeth in between those served by secondaries; on some teeth, tiny further teeth present; distal flank concave, acuminate to almost straight, proximal flank acuminate, convex to almost straight or concave; sinus angular, apex acute, acuminate; midvein straight; secondaries craspedodromous, terminating in tooth apices, arising suboppositely to alternate at moderate angles, straight to slightly curved near margin, forking several (up to 5) times, sending minor secondaries into tooth apices; tertiaries (forked-)percurrent, sinuate, ~3 per cm between secondaries, more densely spaced between midvein and secondaries, angle of tertiaries obtuse towards midvein; 4° and higher-order veins reticulate, areoles well developed.

Remarks. The specimens assigned by Ettingshausen (1869a, 1888) to *Corylus* both lack base and apex. The specimen from collection IBUG is even more fragmentary, representing the upper lamina part only. The assignment to *Corylus* is not very probable because the bigger-sized teeth (1° and 2°) are served by secondaries and their exmedial branches (minor secondaries), whereas in modern *Corylus* small-sized teeth are commonly served by higher-order veinlets and 1° teeth frequently show small teeth both on the proximal and distal flanks, which is not the case in the fossil remains. Moreover, unambiguous Miocene records of hasel are not available from Central Europe. Compared to *Alnus menzelii*, leaves of "*Corylus*" *palaeoavellana* are broader with more prominent and more abundant minor secondaries serving the marginal teeth. No other Betulaceae appears to be a possibility. "*Corylus*" *palaeoavellana* differs from Ulmaceae vel Betulaceae gen. et sp. by broader blades, distinct minor secondaries serving teeth between those above secondaries, and more distinct size differentiation of 1° and 2° teeth. Although incomplete, these leaves were probably not asymmetrical, as is characteristic of *Ulmus*.

"***Cytisus***" ***palaeolaburnum*** Ettingsh.

Fig. 20.12

1888 *Cytisus palaeo-laburnum* Ettingsh. sp. n.; Ettingshausen, p. 361, pl. 9, fig. 27.

Material. Münzenberg: NATURALIS: RGM. THDB.6799, (*Cytisus palaeo-laburnum*), Ettingshausen (1888: pl. 9, fig. 27, holotype).

Description. Trifoliate leaf; petiole ~12 mm long, leaflets sessile, central one symmetrical, lateral ones asymmetrical near base; leaflet shape slender elliptic to slightly obovate, l × w ~33–36 × 10–12 mm, ratio l/w ~2.9–3.5; base angle narrow acute, base shape rather straight, i.e. cuneate; apex preserved only in central leaflet, angle acute, apex shape straight to slightly concave, i.e. acute to somewhat acuminate; margin entire in basal part of leaflets, apical part of central and one lateral leaflet simple serrate, other lateral leaflet incomplete; teeth less distinct and smaller on lateral than on central leaflet, tooth height variable, up to 1 mm, spacing wide, not very regular, distal flank straight to slightly convex, proximal flank almost straight to slightly concave or convex; sinus rounded to angular, tooth apex blunt; midvein straight, thick; secondaries delicate, brochidodromous, angle of origin acute near base, then moderate, spacing wide, up to 5–6 mm in central part of leaflets; basalmost pair running along margin; loops of 2° veins angular near margin; exmedial veinlets arising from 2° veins looping further; veinlets running into tooth apices; one to several intersecondaries interspaced between two adjacent 2° veins, reaching about half distance between midvein and margin; tertiaries (?) reticulate.

Remarks. Ettingshausen (1888) described this specimen as entire-margined and the respective drawing shows an entire-margined leaf. Nevertheless, the specimen at hand definitely is the original specimen of "*C.*" *palaeolaburnum*. No isolated leaflets are available which could be assigned to this fossil-taxon. The assignment to the Fabaceae is improbable because of the marginal serration. The trifoliate maples *A. griseum* (Franch.) Pax, *A. mandshuricum* Maxim., *A. maximowiczianum* Miq. and *A. triflorum* Kom. differ by usually larger leaflets, at least short-petiolate central leaflet and percurrent tertiaries. Furthermore, in the former three species the teeth are larger and blunt and the base of the lateral leaflets is not cuneate to decurrent.

Dicotylophyllum **sp. A**

Fig. 20.17, 20.18

1888 *Fraxinus prae-excelsior* Ettingsh. sp. n., p.p.; Ettingshausen, p. 323, pl. 5, fig. 11.

1888 *Ceratopetalum haeringianum* Ettingsh., p.p.; Ettingshausen, p. 334.

Material. Moskenberg: NHMW: 1878/6/8392 (Ett. 6389), Pb 2129, (*Ceratopetalum haeringianum*); 1878/6/9828 (7825), Pb 1956, (*Fraxinus prae-excelsior*), Ettingshausen (1888: pl. 5, fig. 11, syntype).

Description. Two (almost) complete, probably petiolate symmetrical leaves, petiole <1 mm long (incomplete); lamina oblong, l × w = 43 × 14 mm, ratio l/w = 3.1 and ~75 × 19 mm, ratio l/w ~3.9; base angle acute, base shape slightly convex; apex angle acute, shape acute to slightly acuminate; margin regularly simple serrate, only near base entire, one tooth per secondary vein; teeth small, spine-like, slender, distal flank convex to straight, proximal flank concave to straight, sinus angular, apex acute; midvein straight, delicate; secondaries simple craspedodromous, delicate, moderately dense but not very regularly spaced, angle of origin moderate, course rather straight to curved, terminating in tooth apices; visible only in specimen NHMW 1878/6/8392, (Ett. 6389) (Fig. 20.18): basalmost pair of secondaries originating suboppositely, running close to and parallel along margin; one, two or even more short intersecondaries interspaced between secondaries; tertiaries very faint, probably percurrent, dense, angle to midvein obtuse.

Remarks. Although specimen NHMW 1878/6/8392 (Ett. 6389) is a rather colourless adpression, its morphology is clearly perceivable. In the other specimen the venation details are less well preserved. Nevertheless, leaf shape, serration, and the features of midvein and secondaries warrant the assignment to the same fossil-taxon.

Beyond the extremely unlikely affiliation to the Australo-Asian Cunoniaceae R. Br. (*Ceratopetalum* Sm.), the slightly spine-like teeth contradict an affiliation to *Fraxinus*. A Fagaceae relationship must also be excluded because of the secondaries, which are not very regularly spaced and curved, and the lowermost pair of secondaries running closely spaced parallel to the margin.

***Dicotylophyllum* sp. B**

Figs 20.10, 20.11, 21.1, 26.3

1869a *Rhus tenuifolia* Ettingsh. sp. n.; Ettigshausen, p. 90, pl. 6., fig. 6.

1888 *Carya bilinica* Unger, p.p.; Ettingshausen, p. 353.

1888 *Rhus prisca* Ettingsh., p.p.; Ettingshausen, p. 354, non pl. 9, fig. 41.

1888 *Rhus tenuifolia* Ettingsh., p.p.; Ettingshausen, p. 355.

Material. Moskenberg: NHMW: 1878/6/8637 + 8638 (Ett. 6634 + 6635), Pb 2042, (*Carya bilinica*); 1878/6/8685 (6682), Pb 2033, (*Rhus tenuifolia*), Ettingshausen (1869a: pl. 6, fig. 6, holotype). Münzenberg: NHMW: 1878/6/4350 (Ett. 2347), Pb 2248, (*Rhus prisca*).

Description. (?) Leaflets; short-petiolulate; laminar shape oblong to slender elliptic, l × w ~34–95 × 9–29 mm, ratio l/w ~2.8–>5.1; base angle obtuse, base shape convex, rounded, slightly asymmetrical; apex angle (narrow) acute, apex shape (?) straight (incomplete); margin entire at base, then finely, more or less regularly simple serrate, tooth height <1 mm, distal flank very short, proximal flank straight to convex, sinus angular to rounded, apex (bluntly) acute; midvein straight, thick; secondaries semicraspedodromous, delicate, (moderately) dense, originating at wide angles, initially shortly converging towards midvein, then running almost straight to slightly convex or concave towards margin, looping close to margin, veinlets arising from loops serving teeth; mostly one intersecondary vein between adjacent secondaries, reaching into exmedial area between midvein and margin.

Remarks. Although these specimens differ considerably in size, they resemble each other by laminar shape, venation and tiny, densely spaced teeth. In the specimen described by Ettingshausen (1869a) as *Rhus tenuifolia* (NHMW 1878/6/8685, Ett. 6682, Fig. 20.10), some teeth on the upper left are narrower and more pointed than in the other specimens. Specimen (NHMW 1878/6/4350, Ett. 2347, Fig. 20.11) is more slender than the other specimens. All specimens lack any indications of percurrent tertiaries, as is characteristic of *Carya* and other Juglandaceae.

***Dicotylophyllum* sp. C**

Figs 21.2–21.4, 26.4

1869a *Pterocarya leobensis* Ettingsh. sp. n., p.p.; Ettingshausen, p. 89, pl. 6, fig. 19, (non 18).

1888 *Celastrophyllum venosum* Ettingsh. sp. n.; Ettingshausen, p. 345, pl. 8, fig. 10.

1888 *Juglans melaena* Unger; Ettingshausen, p. 353.

1888 *Pterocarya leobensis* Ettingsh., p.p.; Ettingshausen, p. 354.

Material. Moskenberg: NHMW: 2023/0072/0008 (1878/6/XXXX (Ett. 16XX)); 1878/6/4135 (Ett. 2132), Pb 2015, (*Celastrophyllum venosum*), Ettingshausen (1888: pl. 8, fig. 10, holotype); 1878/6/4163 (2160), (*Ficus* sp. in sched.); 1878/6/8645 (6642), Pb 2036, (*Pterocarya leobensis*), Ettingshausen (1869a: pl. 6, fig. 19, syntype).

Description. Fragments of (?) leaflets, base and apex incomplete; utmost base not preserved; laminar shape oblong to elliptic, more or less asymmetrical, l × w up to 80 × 16–26 mm, ratio l/w up to ~4; base angle acute, base shape slightly convex; apex angle acute, apex shape (?) straight; margin entire to widely undulate; midvein thick, S-shaped to straight; secondaries brochidodromous, originating at variable distances and wide to moderate angle, looping irregularly, forming angular loops at a distance from margin; 2° to

4° veins forming distinct irregular, relatively large meshes.

Remarks. The assignment to *Pterocarya* of leaflet NHMW 1878/6/8645 (Ett. 6642) (Ettingshausen, 1869a) must be rejected because of the irregular reticulate venation pattern. Leaflets of *Pterocarya* and other Juglandaceae are characterised by a rather regular network of secondaries and percurrent tertiaries. Contrary to Ettingshausen's description of a serrate margin in the upper part of the lamina of *Pterocarya leobensis* (Ettingshausen, 1869a: pl. 6, fig. 19), the margin near the apex is complete only on the right side and it is entire.

***Dicotylophyllum* sp. D**

Fig. 21.5

Material. Moskenberg: NHMW: 1878/6/3671 (Ett. 1668), B, backside.

Description. Part of an ± oblate, medially asymmetrical leaf, l × w ~50 × 55 mm, ratio l/w ~0.9; base incomplete, shape convex on one side; apex not preserved; margin serrate, tooth height ~1 mm, distal and proximal flanks slightly convex, sinus angular to rounded, apex rounded; venation basal actinodromous, 4–5 curved major veins on one side of lamina; widely spaced agrophic veins developed along outer major veins; central vein with widely spaced secondaries; secondaries corresponding to lateral major veins in thickness, originating at acute to moderate angle, course of proximal ones slightly curved, distal ones almost straight; tertiaries indistinct, somewhat undulate, percurrent, widely spaced.

Remarks. This very faint impression of one half of the lamina still provides some essential features. The assignment to *Byttneriophyllum tiliifolium* (A. Braun) Knobloch et Kvaček must be excluded due to the serrate margin, and *Cercidiphyllum crenatum* (Unger) R.W. Br. must be rejected due to the asymmetrical shape of the lamina. The systematic affinity therefore remains open.

***Dicotylophyllum* sp. E**

Fig. 21.10

Material. Moskenberg: NHMW: (?) 1878/6/9197 (Ett. 7194), C. IBUG: Ett. 6247 + 6294, a, (*Prunus palaeo-cerasus* in sched.).

Description. IBUG Ett. 6247 + 6294, a: Leaf (or leaflet) lacking petiole; laminar shape elliptic, l × w ~97 × 43 mm, ratio l/w ~2.3; base angle obtuse, base shape rounded; apex angle acute, apex shape slightly acuminate; margin simple to double serrate to almost crenate along whole margin; 1° and 2° teeth often of similar size, height ~1 mm, distal flank very short, proximal flank mostly slightly convex, sinus angular, apex bluntly acute; midvein straight; secondaries craspedodromous to semicraspedodromous, sometimes running into tooth apex sometimes into sinus, arising under moderate angle, moderately dense, regularly spaced, course curved and parallel; near margin up to at least 3 exmedial veinlets arise from secondaries serving 2° teeth; some teeth are served by minor veinlets arising from looping veins; tertiaries (forked-)percurrent, dense, 5–8 per cm.

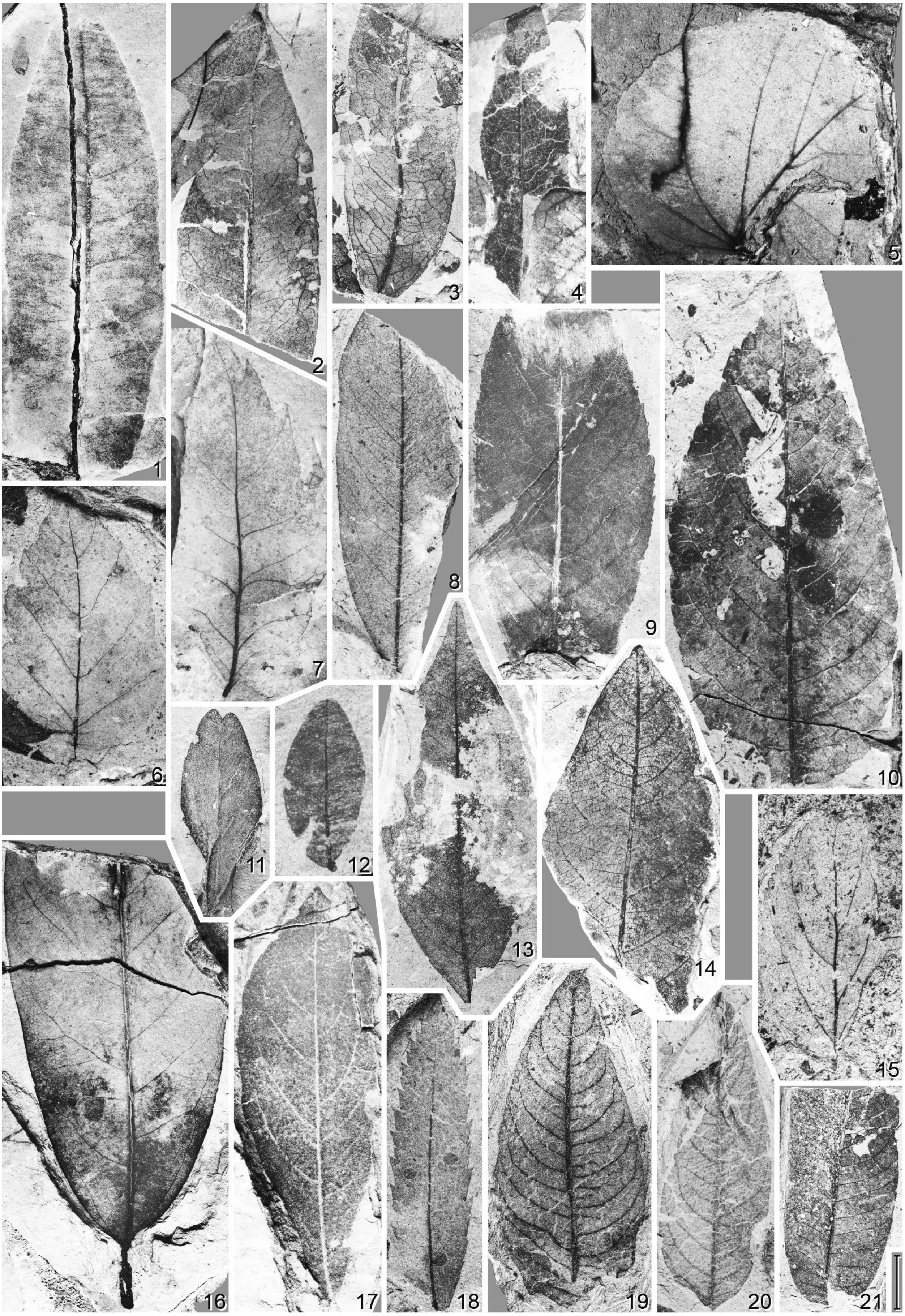
Remarks. The description is restricted to the more complete specimen. Both specimens resemble each other by tooth shape and tooth size as well as the laminar shape. Ettingshausen assigned specimen IBUG Ett. 6247 + 6294, a to *Prunus palaeo-cerasus* (in sched.), which he had described earlier (Ettingshausen, 1869a: pl. 6, figs 12, 13). None of those figured specimens conform to the here described leaves (see paragraphs *Alnus gaudinii* and Supplementary File 2).

***Dicotylophyllum* sp. F**

Figs 21.9, 26.5

Material. Seegraben Walpurgis-Schacht: IBUG: Ett. 6297, (*Photinia eratonis* in sched.).

Description. Simple leaf lacking base and apex; laminar shape slender elliptic, l × w ~95 × 33 mm, ratio l/w ~2.9; margin double serrate, teeth variably shaped, height ≤ 1 mm, 2–3 teeth between those above secondary veins; distal flank short, straight to slightly concave to convex, proximal flank straight to slightly convex, sinus angular to rounded, apex acute to blunt; midvein straight; secondaries craspedodromous, running to tooth sinus, spacing moderately dense at distances of 6–10 mm, alternate, angle of origin moderate, tapering towards apex, course slightly curved, (?) looping close to margin, delicate veinlets serving teeth; 3° veins delicate, indistinct, percurrent, at obtuse angle towards midvein.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Remarks. This specimen is definitely not conspecific with *Photinia eratonis* Ettingsh. (Ettingshausen, 1888), which is based on a single specimen reassigned in this study to *Sloanea serratifolia* (see respective paragraph). *Dicotylophyllum* sp. F differs from *S. serratifolia* by the elliptic laminar shape and the double serrate margin with bigger and differently shaped teeth and craspedodromous secondaries.

***Dicotylophyllum* sp. G**

Fig. 21.12

Material. Münzenberg: IBUG: Ett. 5984, (*Planera ungeri* in sched.).

Description. Short-petiolate or petiolulate, small leaf or leaflet; petiole < 1 mm long, thick, angular towards midvein; laminar shape elliptic, slightly asymmetrical, l × w ~16 × 7 mm, ratio l/w ~2; base angle almost 90°, base shape slightly convex, asymmetrical; apex angle acute, apex shape almost straight, at utmost apex incomplete; margin entire; midvein straight, thick near base, tapering considerably along length; secondaries brochidodromous, very delicate, faintly discernible, spacing ~2 mm, angle of origin near base moderate, higher up wide.

Remarks. The identification in the IBUG inventory was very likely a mistake because Ettingshausen would definitely not have assigned this leaf to former *Planera ungeri* Ettingsh. (now *Zelkova* or *Cedrelospermum*). This remain is classified here as *Dicotylophyllum* because of the very thick and somewhat angular petiole, otherwise it could represent a leaflet assignable to *Leguminophyllum*. The thick petiole and the only faintly visible secondaries point towards a non-deciduous fossil-species.

***Dicotylophyllum* sp. H**

Figs 21.8, 26.6

1888 *Cassia phaseolites* Unger, p.p.; Ettingshausen, p. 363.

Material. Seegraben Walpurgis-Schacht: NHMW: 1878/6/4476 (Ett. 2473), a, Pb 2357, (*Cassia phaseolites*).

Description. Probably leaf, incomplete at base and apex; laminar shape slender elliptic, l × w ~75 × 22 mm, ratio l/w ~3.4; base angle acute, base shape slightly convex; apex angle acute, apex shape (?); margin entire, smoothly undulate; midvein straight, secondaries delicate, (festooned) brochidodromous, arising at moderate angle, spacing not very regular, 5–12 mm in middle part of lamina, course slightly curved, looping at variable distance from margin, loops angular; intersecondaries developed, usually one between adjacent secondaries, reaching about half the distance between midvein and margin; tertiaries and higher-order veins reticulate.

Remarks. The texture of this leaf appears to be chartaceous, as is characteristic of deciduous taxa. Although superficially resembling *Leguminophyllum* sp. 4, this leaf type differs by the probably chartaceous texture, steeper ascending secondaries, reticulate pattern of tertiaries and well-visible reticulate higher-order veins.

***Dicotylophyllum* sp. I**

Fig. 21.6

1888 *Betula dryadum* Brongn., p.p.; Ettingshausen, p. 285.

Material. Moskenberg: NHMW: 1878/6/4108 (Ett. 2105), (*Betula dryadum*).

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Figure 21. **1**. *Dicotylophyllum* sp. B, NHMW 1878/6/8637 (Ett. 6634), Pb 2042, (*Carya bilinica*); **2–4**. *Dicotylophyllum* sp. C, **2**. NHMW 1878/6/4163 (Ett. 2160), (*Ficus* sp.), **3**. NHMW 1878/6/4135 (Ett. 2132), Pb 2015, (*Celastrophyllum venosum*), Ettingshausen (1888: pl. 8, fig. 10, holotype), **4**. NHMW 1878/6/8645 (Ett. 6642), Pb 2036, (*Pterocarya leobensis*), Ettingshausen (1869a: pl. 6, fig. 19, syntype); **5**. *Dicotylophyllum* sp. D, NHMW 1878/6/3671 (Ett. 1668), B; **6**. *Dicotylophyllum* sp. I, NHMW 1878/6/4108 (Ett. 2105), (*Betula dryadum*); **7**. *Dicotylophyllum* sp. J, IBUG Ett. 6231, (*Carya bilinica*); **8**. *Dicotylophyllum* sp. H, NHMW 1878/6/4476 (Ett. 2473), a, Pb 2357, (*Cassia phaseolites*); **9**. *Dicotylophyllum* sp. F, IBUG Ett. 6297, (*Photinia eratonis* in sched.); **10**. *Dicotylophyllum* sp. E, IBUG Ett. 6247, (*Prunus palaeo-cerasus* in sched.); **11**. *Dicotylophyllum* sp. M, NHMW 1878/6/4467, (Ett. 2464), b, Pb 2359, (*Terminalia* sp.); **12**. *Dicotylophyllum* sp. G, IBUG Ett. 5984, (*Planera ungeri*); **13**. *Dicotylophyllum* sp. O, NHMW 1878/6/3841 (Ett. 1838), Pb 1909, (*Ficus tenuinervis*); **14**. *Dicotylophyllum* sp. N, IBUG Ett. 6001, (*Ficus lobkowitzii*); **15**. *Dicotylophyllum* sp. R, NHMW 1878/6/4206 (Ett. 2203), (*Celtis stiriaca*); **16**. *Dicotylophyllum* sp. L, IBUG Ett. 6019, (*Laurus prae-nobilis* in sched.); **17**. *Dicotylophyllum* sp. K, NHMW 1878/6/4249 (Ett. 2246), Pb 2166, (*Quercus tephrodes*); **18**. *Dicotylophyllum* sp. P, NHMW 1878/6/4120 (Ett. 2117), Pb 1858, (*Rhus intermedia*) with (*Xylomites moskenbergensis*), Ettingshausen (1888: pl. 1, fig. 12, syntype of *R. intermedia*, holotype of fungus); **19**, **20**. *Salix* sp., **19**. NHMW 1878/6/7670 (Ett. 5667), Pb 1905, (*Ficus fridaui*), Ettingshausen (1869a: pl. 2, fig. 5a, holotype), **20**. NHMW 1878/6/7672 (Ett. 5669), Pb 1904, (*F. fridaui*); **21**. "*Juglans*" *parschlugiana* Unger, NHMW 1878/6/4118 (Ett. 2115), Pb 2050, (*Juglans parschlugiana*). For all photographs the scale at bottom right of the figure is 10 mm

Description. Simple leaf; petiole >2 mm, incomplete; laminar shape ovate, l × w ~48 × 31 mm, ratio l/w ~1.6; base angle wide obtuse, base shape rounded; apex angle acute, apex shape (?) acute; margin double serrate with few rather big 1° teeth; 2° ones small, confined to proximal flank of 1° ones, one to three per 1° tooth, irregularly spaced; tooth height of 1° teeth >1 and <5 mm, height of 2° teeth <1 mm; distal flank convex, slightly sinuate to straight, proximal flank of 1° teeth convex, concave to straight, sinus angular, apex acuminate to bluntly acute, (?) glandular; 2° teeth similarly shaped, probably non-glandular; midvein straight, slender, tapering considerably and slightly bent towards apex; secondaries delicate, craspedodromous, originating at moderate angle, widely spaced, course slightly sinuate, terminating in apices of 1° teeth; exmedial branches of secondaries running into 2° teeth; near leaf base a pair of short, minor veins arising from midvein, running along margin.

Remarks. The assignment to Betulaceae appears unlikely.

***Dicotylophyllum* sp. J**

Fig. 21.7

Material. Münzenberg: IBUG: Ett. 6231, (*Carya bilinica* in sched.).

Description. Leaf or leaflet; petiole ~2 mm long, (?) complete, angular towards midvein; laminar shape elliptic or ovate, l × w ~64 × (?) 33 mm, ratio l/w ~1.9; base angle almost 90°, base shape near lowermost base almost straight, cuneate, then concave on one side and concavo-convex on the other; apex angle acute, apex shape straight to (?) acuminate; margin entire near base then simple serrate with few, rather big teeth, tooth height >1 and <5 mm, distal flank almost straight, proximal flank straight to concave, sinus rounded, apex acute; midvein nearly straight, slightly bent near apex; secondaries (semi-)craspedodromous, delicate, widely, irregularly spaced, angle of origin narrow to moderate near base, wide in central part of lamina, tapering towards apex; 2° veins in basal part initially approaching midvein then turning and running curved or straight towards margin, forking in marginal area of lamina, branches looping or running into tooth apices; basalmost pair of veins originating from midvein weaker and shorter than secondaries, running along margin; single intersecondaries occasionally developed, length variable; tertiaries (forked-)percurrent, only faintly visible.

Remarks. Although no assignment is proposed here, that to Juglandaceae must be rejected.

***Dicotylophyllum* sp. K**

Fig. 21.17

1888 *Quercus tephrodes* Unger; Ettingshausen, p. 289.

Material. Münzenberg: NHMW: 1878/6/4242 (Ett. 2239), Pb 2167 + 4249 (Ett. 2246), Pb 2166, (*Quercus tephrodes*).

Description. Simple leaf, laminar shape obovate, l × w ~77 × 28 mm, ratio l/w ~2.7; base angle acute, base shape straight, cuneate, apex angle nearly 90°, apex shape straight, acute; margin entire from base to upper third, then serrate-crenate; tooth height ~1 mm, teeth widely spaced, both flanks straight to convex, sinus angular, apex blunt, rounded; midvein straight; secondaries (?) semicraspedodromous, widely, not very regularly spaced, angle of origin moderate, curved.

Remarks. The assignment to *Quercus* is rejected because of the serrate to crenate margin, which is not oak-like. From Parschlug *Dicotylophyllum* sp. V (Kovar-Eder et al., 2022: pl. 5, figs 15–17) resembles in size and general shape but differs by smaller and acute teeth and more densely spaced, hence more numerous secondaries arising at wider angle from the midvein.

This leaf differs from (?) *Platanus neptuni* by the narrower base, more steeply ascending secondaries and more irregularly, wider spaced teeth. Based on leaf shape and widely spaced and curved secondaries, it is reminiscent of *Sloanea serratifolia* but differs considerably by the serrate to crenate margin with larger and blunt teeth.

***Dicotylophyllum* sp. L**

Figs 21.16, 26.7

Material. Münzenberg: IBUG: Ett. 6019, (*Laurus prae-nobilis* in sched.).

Description. Basal half of a petiolate, simple leaf; petiole 10 mm long, thick; laminar shape (?) elliptic to (?) oblong, l × w at least 120 × 36 mm, ratio l/w >3; base angle acute, base shape convex, almost rounded; margin entire; midvein thick, straight; secondaries delicate, (festooned) brochidodromous; first pair originating directly at base, running almost parallel to margin, steeper than all other secondaries, looping with next pair; further secondaries alternate, angle of origin moderate, widely spaced, up to 16 mm, course slightly curved; some secondaries forking at different distances from margin, looping with branches of neighbouring 2° vein; tertiaries widely spaced, (forked-)percurrent to reticulate, forming large meshes.

Remarks. The texture of this leaf was probably coriaceous. The difference in thickness between midvein and secondaries as well as the basalmost pair of secondaries do not point towards a Lauraceae affinity.

***Dicotylophyllum* sp. M**

Fig. 21.11

Material. Seegraben, Walpurgis-Schacht: NHMW: 1878/6/4467, (Ett. 2464), b, Pb 2359, (*Terminalia* sp. in sched.).

Description. Apical part of an entire-margined leaf; laminar shape (?) slender elliptic to (?) spatulate, l × w ~35 × 15 mm, ratio l/w ~2.3; apex angle acute, apex shape straight, utmost apex emarginate; midvein straight, secondaries faint, eucampto- to brochidodromus, angle of origin acute, spacing regular, moderately wide, course rather straight, steeply ascending, looping close to margin.

Remarks. This is the only specimen with an emarginate apex.

***Dicotylophyllum* sp. N**

Figs 21.14, 26.8

1888 *Ficus lobkowitzii* Ettingsh., p.p.; Ettingshausen, p. 297.

Material. Münzenberg: IBUG: Ett. 6001, (*Ficus lobkowitzii*).

Description. Apical part of an entire-margined leaf; laminar shape (?) elliptic, l × w (?) ~80 × 31 mm, ratio l/w (?) ~2.6; apex angle acute, apex shape straight to slightly convex, bluntly acute; margin entire; midvein straight, thick; secondaries brochidodromous, slender, alternate, angle of origin moderate, spacing rather regular, course smoothly curved, looping close to margin; intersecondaries/tertiaries arising almost perpendicular to midvein, running horizontally across lamina before forking and forming an angle to connect with next lower 2° vein; tertiaries between secondaries percurrent, occasionally forked, dense, somewhat undulate, angle towards midvein obtuse; 4° and 5° vein fabric reticulate.

Remarks. Most characteristic of this leaf are the intersecondaries/tertiaries originating perpendicular to midvein and running horizontally into the lamina, forking and forming an angle to connect with the next lower 2° vein. Futhermore, the densely spaced percurrent to forked-percurrent tertiaries are remarkable.

***Dicotylophyllum* sp. O**

Figs 21.13, 26.9

1888 *Ficus tenuinervis* Ettingsh., p.p.; Ettingshausen, p. 297.

Material. Moskenberg: NHMW: 1878/6/3841 (Ett. 1838), Pb 1909, (*Ficus tenuinervis*).

Description. Simple, entire-margined leaf lacking petiole; laminar shape elliptic, l × w 75 × 27 mm, ratio l/w 2.7; base angle acute, base shape moderately convex, apex angle acute, apex shape acuminate; midvein straight, thick near base, distinctly tapering towards apex; secondaries brochidodromous, delicate, moderately to densely spaced, angle of origin moderate, slightly increasing towards apex, course moderately curved; one to several intersecondaries between adjacent secondaries; tertiaries and higher-order veins similarly thick, well visible, small-meshed reticulate.

Remarks. The texture of this leaf was probably firm, implying non-deciduous phenology. The small-meshed regular venation pattern characterises this leaf. Comparisons with Moraceae Gaudich (*Ficus* Tourn. ex L.), Oleaceae (*Fontanesia* Labill., *Ligustrum* L.) and Rutaceae Juss. (*Citrus* L.) (NMNS Cleared Leaf Database, accessed July, 2023) did not reveal a similarity of the venation pattern.

***Dicotylophyllum* sp. P**

Fig. 21.18

1888 *Rhus intermedia* Ettingsh. sp. n., p.p.; Ettingshausen, p. 355, pl. 1, fig. 12, non pl. 9, figs 12, 13.

Material. Moskenberg: NHMW: 1878/6/4062 + 4120 (Ett. 2059 + 2117), Pb 1858, (*Rhus intermedia*) with (*Xylomites moskenbergensis*), Ettingshausen (1888: pl. 1, fig. 12, syntype of *R. intermedia*, holotype of fungus).

Description. Simple leaf lacking petiole; laminar shape oblong, l × w ~60 × 16 mm, ratio l/w ~3.8; base angle acute, base shape straight, incomplete, apex angle acute, apex shape straight; margin simple serrate, teeth regularly spaced, tooth height ~2 mm, distal flank rather straight, proximal flank straight to slightly concave, sinus angular, apex acute; secondaries extremely delicate and faint, craspedodromous, ending in tooth apices.

Remarks. This leaf may be reminiscent of *Myrica lignitum* but in serrate species of *M. lignitum* the teeth are blunt and the secondaries are usually semicraspedodromous, whereas in the specimen at hand the secondaries run into the tooth apices. Furthermore, in *Myrica* the number of secondaries does not necessarily correspond with the number of teeth, but is higher in the toothed part of the lamina, and the angle of origin of the secondaries is wider than in *Dicotylophyllum* sp. P. *D*. sp. P differs from *Sorbus* (?) sp. by bigger size, symmetrical shape, straight shape of the base and teeth that are less strongly directed towards leaf apex. From Parschlug, *Dicotylophyllum* sp. 6 resembles to some degree the here described specimen (Kovar-Eder et al., 2004, 2022), but in that fossil-taxon the laminar shape is more elongate and slender (the base is unknown), the secondaries are stronger and the proximal flank of the teeth is convex, i.e. the tooth shape is different.

Dicotylophyllum sp. Q

Figs 22.2, 22.3, 26.10

1869a *Cissus celtidifolia* Ettingsh. sp. n.; Ettingshausen, p. 76, pl. 4, fig. 14.

1888 *Ulmus plurinervia* Unger, p.p.; Ettingshausen, p. 295.

Material. Moskenberg: NHMW: 1878/6/4186, A + 8376 (Ett. 2183 + 6373), Pb 2098, (*Cissus celtidifolia*), Ettingshausen (1869a: pl. 4, fig. 14, holotype); 1878/6/9846 + 9847 (7843 + 7844), (*Ulmus plurinervia*).

Description. (?) Leaves or (?) leaflets; petiole/petiolule ~5 mm long (NHMW 1878/6/9846 + 9847, Ett. 7843 + 7844); laminar shape ovate to elliptic, asymmetrical, l × w ~ 52–58 × 22–23 mm, ratio l/w ~2.4–2.5; base angle acute, base shape asymmetrical, straight on one side, convex on other one, apex angle acute, apex shape straight to slightly acuminate; margin serrate, entire-margined near base on straight side, tooth size slightly variable, tooth height ~1 mm, teeth densely spaced; in specimen NHMW 1878/6/9846 + 9847, (Ett. 7843 + 7844) distal and proximal flanks rather straight, sinus angular, apex acute; in specimen NHMW 1878/6/4186, A + 8376 (Ett. 2183 + 6373) tooth size more variable, in apical part of lamina distal and proximal flanks flexuous (not well preserved); midvein curved or straight; further venation visible only in specimen NHMW 1878/6/4186, A + 8376 (Ett. 2183 + 6373): secondaries festooned semicraspedodromous, angle of origin moderate, spacing moderate, course curved, looping in marginal quarter of lamina, giving rise to further loops, ultimate loops occasionally touching sinus, ultimate veinlets arising from marginal loops running into tooth apex; tertiaries forked percurrent, slightly sinuate, not dense, 3 within 0.5 mm, almost perpendicular to secondaries and wide obtuse towards midvein; further venation small-meshed reticulate.

Remarks. Specimen NHMW 1878/6/9846 + 9847 (Ett. 7843 + 7844) is much better preserved than the other specimen, showing well the margin and venation detail. This remain clearly shows a petiole/petiolule, while in specimen NHMW 1878/6/4186, A + 8376 (Ett. 2183 + 6373) the margin is less well preserved, the venation details are hardly visible and the base lacks a petiole/petiolule. Due to the very similar general laminar shape and the asymmetry of the base, they may represent the same fossil-taxon. An assignment to Vitaceae is unlikely because of the rather dense serration. *Ulmus* must be excluded because in *Ulmus* the secondaries are simple craspedodromous. *Celtis* L. is not an option because in this genus the proximalmost pair of secondaries should arise almost directly at the laminar base. The systematic position of these leaves therefore remains open.

Dicotylophyllum sp. R

Figs 21.15, 26.11

1888 *Celtis stiriaca* Ettingsh., p.p.; Ettingshausen, p. 296.

Material. Moskenberg: NHMW: 1878/6/4206 (Ett. 2203), (*Celtis stiriaca*).

Description. Simple petiolate leaf; petiole straight, 2 mm long, (?) complete; laminar shape elliptic, l × w ~45 × 25 mm, ratio l/w ~1.8; base angle probably nearly 90°, base shape convex, apex angle acute, apex shape slightly convex, incomplete; margin regularly, densely simple crenate-serrate along whole length, tooth height ~1 mm, sinus acute, apex rounded, glandular; midvein slender, slightly sinuate, secondaries delicate, festooned semicraspedodromous, widely spaced, 4 to 5 pairs, basal pair almost opposite, further pairs alternate, angle of origin acute to moderate, course curved; secondaries looping with exmedial branches of superimposed 2° veins; ultimate veinlets arising from marginal loops entering teeth; tertiaries very faint, reticulate.

Remarks. While most other leaves assigned by Ettingshausen (1888) to *Celtis stiriaca* represent Betulaceae, mainly *Alnus* (see Supplementary File 2), this specimen definitely represents another family. The margin is somewhat similar to *Cercidiphyllum crenatum* (Unger) R.W. Brown, but in *Cercidiphyllum* the laminar shape is roundish with cordate base and the major venation tends to be actinodromous with more than 3 main veins. Glandular teeth may occur in modern *C. magnificum* (Nakai) Nakai (NMNS Cleared Leaf Database, accessed December, 2022). The systematic position therefore remains open.

"***Dryandroides***" ***grevilleaefolia*** Ettingsh.

Fig. 20.14

1888 *Dryandroides grevilleaefolia* Ettingsh. sp. n.; Ettingshausen, p. 318, pl. 4, figs 15, 15a.

Material. Münzenberg: NATURALIS: RGM. THDB.6757, (*Dryandroides grevilleaefolia*), Ettingshausen (1888: pl. 4, figs 15, 15a, holotype).

Description. Long-petiolate leaf; petiole ~18 mm long; excluding teeth, laminar shape linear, including teeth, shape oblong, l × w (including teeth) ~47 × 10 mm; base angle very narrow acute, base shape nearly straight, i.e. narrow cuneate to decurrent; apex incomplete, apex angle narrow acute, apex shape straight; margin coarsely and asymmetrically serrate, one side entire near base then with 5 spine-like teeth, other side with 7 teeth, starting near base; teeth differently sized, tooth height up to nearly 5 mm, distal flank convex to straight, proximal flank concave to nearly straight, teeth curved outwards, sinus acute to narrow rounded, apex acute; midvein strong, minimally sinuate, approaching one or the other margin of lamina, i.e. not always running in middle of lamina; secondaries already very faint, craspedodromous, secondaries terminating in tooth apices and (?) camptodromous in between, arising at moderate angle; secondaries running into teeth straight to curved towards apex; further fabric not discernible.

Remarks. The assignment to the Proteaceae as assumed by Ettingshausen (1888) is unlikely because that family thrives in the southern hemisphere. An assignment to *Engelhardia orsbergensis* (terminal leaflet) is excluded because of the craspedodromous secondaries, the large size of the teeth and the sinuous course of the midvein approaching the left or right margin and thus dividing the lamina into uneven parts.

"***Juglans***" ***parschlugiana*** Unger

Figs 21.21, 26.12

1860 *Juglans parschlugiana* Unger; Unger, p. 37, pl. 19, figs 1–6, non 7.

1888 *Juglans parschlugiana* Unger, p.p.; Ettingshausen, p. 352.

2004 "*Juglans*" *parschlugiana* Unger; Kovar-Eder et al., p. 75, pl. 9, figs 15, 16.

2022 "*Juglans*" *parschlugiana* Unger; Kovar-Eder et al., p. 95, pl. 6, figs 16–20, pl. 10, figs 17, 18.

Material. Moskenberg: NHMW: 1878/6/4118 (Ett. 2115), Pb 2050, (*Juglans parschlugiana*).

Description. Basal half of a (?) sessile leaflet; laminar shape oblong, somewhat asymmetrical, l × w (?) ~50 × 20 mm, ratio l/w (?) ~2.5; base angle obtuse, base shape rounded, asymmetrical; margin entire; midvein thick, straight; secondaries slender, brochidodromous, arising at wide angle from midvein; on smaller side of lamina, secondaries initially approaching midvein then turning towards margin; spacing regular, dense; course of secondaries rather straight, curved close to margin, looping directly in front of it; intersecondaries occasionally interspaced; tertiaries (alternate) pecurrent, almost perpendicular to secondaries, very wide obtuse to midvein.

Remarks. Ettingshausen (1888) stated this specimen to be the best preserved one. During the here presented study, this was the only one detected in the studied collections. Compared to the richer record from Parschlug this leaflet is more slender. This feature, however, may be well within the morphological variability. According to Kovar-Eder et al. (2004) a relationship with legumes is more likely than with Juglandaceae.

The here described leaflet differs from *Salix* sp. by the laminar shape, very regularly, densely spaced secondaries, fewer and less distinct intersecondaries between adjacent secondaries as well as by the tertiaries positioned almost perpendicular to the secondaries.

"***Rhus***" ***appendiculata*** Ettingsh.

Fig. 22.5

1869a *Rhus appendiculata* Ettingsh. sp. n.; Ettingshausen, p. 90, pl. 6, fig. 7.
1888 *Rhus appendiculata* Ettingsh.; Ettingshausen, p. 355.

Material. Moskenberg: NHMW: 1878/6/8686 + 8687 (Ett. 6683 + 6684), Pb 2032, (*Rhus appendiculata*), Ettingshausen (1869a: pl. 6, fig. 7, holotype).

Description. Sessile leaflet; lamina slender elliptic, asymmetrical, l × w ~26 × 9 mm, ratio l/w ~2.9; base distinctly asymmetrical, base angle acute, base shape slightly convex; apex angle acute, apex shape (?) acuminate; margin entire in basal part of lamina, simple serrate in upper part; teeth rather regularly spaced, 3–4 teeth per cm, tooth height <1 mm, distal flank very short, straight to convex, proximal flank concave, sinus angular, apex bluntly acute; midvein straight, thick; secondaries brochidodromous, delicate, angle of origin wide, steeper on one side than on other, spacing ~1–2 mm, course of secondaries moderately curved.

Remarks. This specimen definitely represents a sessile leaflet. It differs in the size of lamina and of teeth from the lateral leaflet of *Toxicodendron melaenum* (NHMW 1878/6/4148, Ett. 2145) (compare Fig. 16.9 and respective chapter).

Other remains incertae sedis

Genus ***Antholithes*** Brongn.

Antholithes stiriacus Kovar-Eder et Kvaček

Fig. 20.2, 20.3

1888 *Asterocalyx stiriacus* Ettingsh. sp. n., p.p.; Ettingshausen, p. 281, pl. 3, fig. 2; non figs 1, 3, 4.
1890 *Asterocalyx stiriacus* Ettingsh.; Ettingshausen, p. 83, pl. 2, figs 34–40.
2004 *Antholithes stiriacus* Kovar-Eder et Kvaček; Kovar-Eder et al., p. 86, pl. 15, figs 13–15.
2020 *Antholithes stiriacus* Kovar-Eder et Kvaček; Hably, p. 104, pl. 27, figs 5–11.

Material. Münzenberg: IBUG: Ett. 5596, (*Asterocalyx styriacus* in sched.). Leoben: NHMW: 2023/0072/0007 (coll. Hofmann sine no.), (*Asterocalyx stiriacus*), Ettingshausen (1888: pl. 3, fig. 2, syntype).

Description. Actinomorphic, octomeric flower, (half-) epigynous (?); calyx shortly synsepalous, diameter of calyx 3.6–3.8 mm, free parts 0.8–1 mm long, 0.3 mm wide at base, narrow, apex bluntly acute; corolla shortly (?) sympetalous, diameter ~4.4 mm; free parts of petals somewhat spatulate, ~1.4 mm long, maximum width 0.5–0.6 mm, with a central vein, apex rounded.

Remarks. Specimen NHMW 2023/0072/0007 is marked as being from the collection Hofmann and lacks an Ettingshausen collection file number. Most likely it represents the original figured by Ettingshausen (1888: pl. 3, fig. 2) because Ettingshausen (1888: p. 281) mentioned material from that collection but did not list any specimen from the NHMW collection. In the collection IBUG a second specimen was detected during the here presented study; it was likely not yet available for Ettingshausen's (1888) monograph because Ettingshausen did not mention a specimen from "N. Coll. Ett." (i.e. collection IBUG). The other flower specimens figured as *Asterocalyx stiriacus* (Ettingshausen, 1888: pl. 3, figs 1, 3) must be excluded because neither are they octomerous nor do they show a differentiation of sepals and petals and the leaf (Ettingshausen, 1888: pl. 3, fig. 4) represents *Smilax* as already stated by Kovar-Eder et al. (2004). These authors explicated further that the generic name *Asterocalyx* proposed by Ettingshausen (1888) should be rejected because it endangers the name of *Asterocalyx* Merril (Melastomataceae) in current use.

Besides the occurrences in Parschlug and Leoben, *A. stiriacus* has been reported from the flora of Schönegg (Styria, Early Miocene; Ettingshausen, 1890) and recently from the Mecsek Mts, especially from Magyaregregy (Hungary, Early Miocene, late Burdigalian, Karpatian) with numerous specimens (Hably, 2020).

Male catkins and **florets gen**. et **sp**.

Fig. 22.32–22.36

Material. Moskenberg: NHMW: 1878/6/9865 (Ett. 7862), A, (*Engelhardia brongniartii* in sched.).

Description. Male catkin, l × w > 32 × 9 mm, central axis rather thick, stamina very numerous and dense, pollensacs ~1 mm long, proximally thicker than distally, opening into two valves along suture (Fig. 22.34).

Material. Moskenberg: NHMW: 1878/6/3947 (Ett. 1944), (*Populus latior*).

Description. Fragment of male catkin, 16 mm long (incomplete), 6 mm wide, florets distinct, loosely (?) opposite or (?) helically arranged; florets petiolate, each floret cluster- to disc-like; stamina numerous, filaments short (Fig. 22.35).

Material. Moskenberg: NHMW: 1878/6/4106 (Ett. 2103), (*Betula blanchetii* in sched.); IBUG: Ett. 5697, (*Quercus apocynophyllum*), Ettingshausen (1888: pl. 2, fig. 16).

Description. Male catins, main axis 27 and 28 mm long (incomplete) with several, loosely arranged sessile or shortly petiolate florets; bracts and elements of corolla indistinct, organisation unclear; up to (?) 7 stamina, filaments slender, 1–2 mm long, anthers slender elliptic to bean-shaped, up to 2 mm long, connective distinct, straight to slightly bent (Fig. 22.32, 22.33).

Material. Seegraben Walpurgis-Schacht: IBUG: Ett. 5749, (*Castanea atavia*).

Description. Isolated male floret, corolla elements ~2 mm long, curved, number and organisation unclear; at least 6 stamina, filaments thin, up to ~3 mm long, anthers slender spindle-shaped, ~1.5–2.5 mm long, (Fig. 22.36).

Remarks. Except for male catkins of *Pinus*, Betulaceae, and Fagaceae (see respective paragraphs), these catkins certainly represent different taxa. Attempts to extract pollen from selected specimens failed (see also paragraph Material) so that the systematic assignment must remain open. Included here are only specimens that show some details.

Flower gen. et **sp**.

Fig. 22.37

Material. Leoben: NHMW: 2023/0072/0010.

Description. Stalked, funnel-shaped flower; stalk 4 mm long, corolla 9 mm high, max. width 7 mm; calyx tiny, <1 mm high; 3 or (?) 4 petals visible, base forming funnel of 6 mm height and max. 5 mm width, free part of petals skin-like, broadly rounded, margin entire.

Remarks. Based on the position of the visible petals, it may be hypothesized that the complete number of petals was five and that, due to the funnel-shaped corolla, the ovary was likely inferior. Neither the shape of sepals nor details of the gynoecium or stamina are evident.

Carpolithes Brongn.

The proposal to maintain the generic name *Carpolithus* as nomen conservandum was rejected (TAXON 64(6) 2015, p. 1307).

***Carpolithes* sp. A**

Fig. 22.13, 22.14

Material. Moskenberg: NHMW: 1878/6/4059 (Ett. 2056), B; 1878/6/4061, (2058), C + 4082, (2079), B; 1878/6/9884 (7881) (*Betula prisca* in sched.).

Description. Narrow-winged nutlets, l × w (including wings) ~4.2–4.5 × 2.3–2.9 mm; nutlets slender elongate, l × w ~2–3 × 1.5 mm; wings very narrow, slightly protruding nutlet at base, distally protruding distinctly.

Remarks. These fruits differ from *Alnus* sp. by nutlet shape, by the proximal as well as distal extension of the wings and by the lack of style remnants.

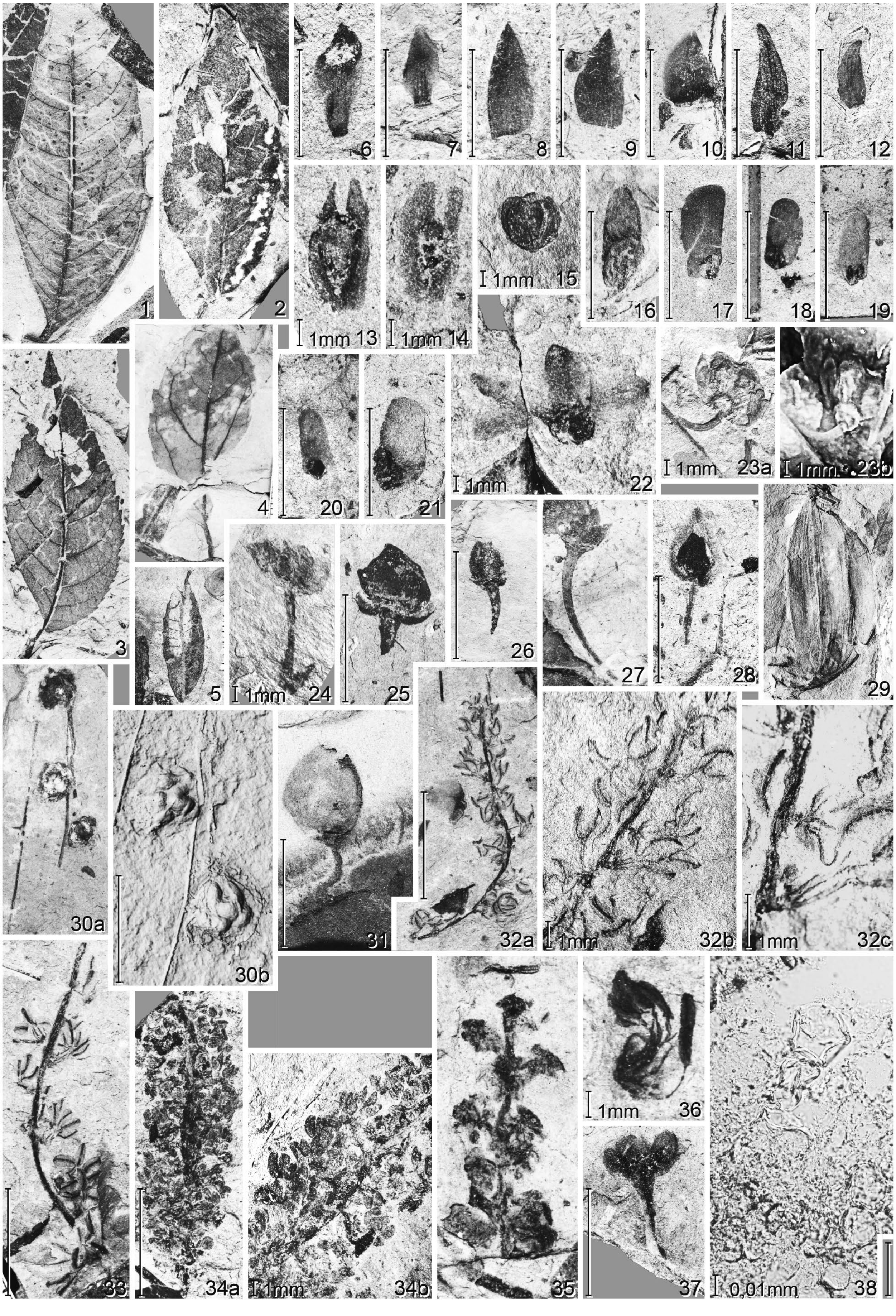
***Carpolithes* sp. B**

Fig. 22.16

Material. Moskenberg: NHMW: 1878/6/3929 (Ett. 1926), B.

Description. Winged seed; l × w ~11 × 4 mm, wing length (?) complete, distally probably rounded, margin smooth, no venation visible; seed body oval, l × w ~6 × 3.5 mm, proximally acute, dorsally thickened, thickening prolonging into wing margin.

Remarks. This seed differs from *Saportaspermum* by the lower ratio between wing length and length of seed body, the acute base of the seed body and further by the long axes of the seed body and wing, which are almost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parallel to each other. It differs further from *Gordonia* sp. (Hably, 2020), i.e. *Mecsekispermum gordonioides* (Erdei and Hably, 2021), by the symmetrical and broader seed body and the absence of the swelling on the ventral side of the wing.

Carpolithes sp. C

Fig. 22.17

1869a *Banksia longifolia* Ettingsh.; Ettingshausen, p. 66, pl. 3, fig. 18.

Material. Moskenberg: NHMW: 1878/6/9905 (Ett. 7902), Pb 1978, (*Banksia longifolia*), Ettingshausen (1869a: pl. 3, fig. 18).

Description. Winged seed, l × w ~9 × 4 mm; seed body oval l × w ~2.4 × 2 mm, (?) asymmetrical; wing straight on one side, convex on other, proximal end straight, distal end broadly rounded, margins unthickened; wing surface with delicate, dense striae, i.e. (?) venation running nearly parallel to long axis of wing.

Remarks. The wing of this specimen is complete and the striae may indicate dense venation, which distinguishes this specimen from *Carpolithes* sp. E.

Carpolithes sp. D

Fig. 22.18–22.20

1888 *Banksia haeringiana* Ettingsh., p.p.; Ettingshausen, p. 317, non pl. 4, fig. 10.

Material. Moskenberg: NHMW: 1878/6/3585 (Ett. 1582), (*Banksia* sp. in sched.); 1878/6/3586 (1583), (*Banksia haeringiana*) + 9718 (7715), b, (*B. haeringiana* in sched.); 1878/6/8936 (6933), (*B. haeringiana* in sched.).

Description. Isolated scales or wings with 2 (?) immature or (?) abortive seeds; 6–7 mm long, 2.5–3 mm wide.

Remarks. In specimen NHMW 1878/6/3585 (Ett. 1582) the seeds appear to be partly superimposed. In NHMW 1878/6/3586 (Ett. 1583) the scale or wing is incomplete.

Carpolithes sp. E

Fig. 22.21

(?) 1869a *Embothrium affine* Ettingsh.; Ettingshausen, p. 66, pl. 3, fig. 17.

1888 *Embothrium affine* Ettingsh.; Ettingshausen, p. 315, pl. 4, figs 28, 29.

Material. Moskenberg: IBUG: 6070, (*Embothrium affine* in sched.).

Figure 22. **1**. *Salix* sp., NHMW 1878/6/7675 (Ett. 5672), Pb 1899, A, (*Ficus fridaui*); **2**, **3**. *Dicotylophyllum* sp. Q, **2**. NHMW 1878/6/4186, A (Ett. 2183), Pb 2098, (*Cissus celtidifolia*), Ettingshausen (1869a: pl. 4, fig. 14, holotype), **3**. NHMW 1878/6/9847 (7844), (*Ulmus plurinervia*); **4**. *Clematis oligoneure* (Ettingsh.) Kovar-Eder comb. nov., NHMW 1878/6/8549 (Ett. 6546), holotype, (*Elaeodendron oligoneure*), Ettingshausen (1869a: pl. 6, fig. 2, holotype); (*Elaeodendron stiriacum*), Ettingshausen (1888); **5**. "*Rhus*" *appendiculata* Ettingsh., NHMW 1878/6/8686 (Ett. 6683), Pb 2032 (*Rhus appendiculata*), Ettingshausen (1869a: pl. 6, fig. 7, holotype); **6**, **7**. Scales or corolla elements, **6**. NHMW 1878/6/7494 (Ett. 5491), B, **7**. NHMW 1878/6/7492 (Ett. 5489), (*Castanea atavia*); **8–10**. Bud scales, **8**. NHMW 1878/6/4093 (Ett. 2090), (*Ramentites latior*), **9**. NHMW 1878/6/4069 (Ett. 2066), (*R. latior*), **10**. NHMW 1878/6/9190 (Ett. 7187), (*Castanea atavia*); **11**, **12**. Scales, bracts or corolla elements, **11**. NHMW 1878/6/4470 (Ett. 2467), (*Ramentites* sp.), **12**. NHMW 1878/6/8199 (Ett. 6196), B, Pb 2106; **13**, **14**. *Carpolithes* sp. A, narrow-winged nutlets, **13**. NHMW 1878/6/4059 (Ett. 2056), B, **14**. NHMW 1878/6/4061 (Ett. 2058), C; **15**. *Carpolithes* sp. N, NHMW 1878/6/4027 (Ett. 2024), Pb 2003, (*Diospyros brachysepala*), Ettingshausen (1888: pl. 6, fig. 9); **16**. *Carpolithes* sp. B, NHMW1878/6/3929 (Ett. 1926), B; **17**. *Carpolithes* sp. C, NHMW 1878/6/9905 (Ett. 7902), Pb 1978, (*Banksia longifolia*), Ettingshausen (1869a: pl. 3, fig. 18); **18–20**. *Carpolithes* sp. D, **18**. NHMW 1878/6/3586 (Ett. 1583), (*Banksia haeringiana*), **19**. NHMW 1878/6/8936 (Ett. 6933), (*B. haeringiana*), **20**. NHMW 1878/6/3585 (Ett. 1582), (*Banksia* sp.); **21**. *Carpolithes* sp. E, IBUG 6070, (*Embothrium affine*); **22**. *Carpolithes* sp. I, IBUG 6200 (*Tetrapteris minuta*), counterpart of Ettingshausen (1888: pl. 7, fig. 11, holotype); **23a**, **b**. *Carpolithes* sp. H, NHMW 1878/6/4192 (Ett. 2189), Pb 2007, (*Euonymus moskenbergensis*), Ettingshausen (1869a: pl. 6, fig. 4, syntype), **23a**. surface view, **23b**. CT-scan; **24**. *Carpolithes* sp. G, NHMW 2023/0072/0009; **25**, **26**. *Carpolithes* sp. J, **25**. IBUG 6120, (*Diospyros brachysepala*), **26**. NHMW 2023/0072/0011; **27**. *Carpolithes* sp. K, IBUG 6130, (*Macreightia longipes*), probably Ettingshausen (1869a: pl. 4, fig. 10, syntype); **28**. *Carpolithes* sp. M, NHMW 1878/6/7811 (Ett. 5808), (*Polygonites deperditus*), Pb 1990, Ettingshausen (1869a: pl. 3, fig. 15, holotype); **29**. *Carpolithes* sp. L, IBUG 5597, (Palmae in sched.); **30a**, **b**. *Carpolithes* sp. F, NHMW 1878/6/7715 (Ett. 5712), (*Platanus gracilis*), Ettingshausen (1869a: pl. 3, fig. 3, holotype), **30a**. surface view, **30b**. CT-scan; **31**. Shoot fragment with bud, NHMW 1878/6/3989, (Ett. 1986), B; **32–36**. Male catkins and florets gen. et sp., **32a–c**. NHMW 1878/6/4106 (Ett. 2103), (*Betula blanchetii*), **32a**. view of complete specimen with loosely arranged florets, **32b**, **c**. details, bracts and corolla elements indistinct, filaments long, anthers slender elliptic to bean-shaped along distinct connective, **33**. IBUG Ett. 5697, (*Quercus apocynophyllum*), Ettingshausen (1888: pl. 2, fig. 16), with indistinct bracts and corolla elements, filaments long, anthers slender elliptic to bean-shaped along distinct connective, **34a**, **b**. NHMW 1878/6/9865 (Ett. 7862), A, (*Engelhardia brongniartii*), **34b**. detail of 34a., pollensacs opening into two valves, **35**. NHMW 1878/6/3947 (Ett. 1944), (*Populus latior*), **36**. IBUG Ett. 5749, (*Castanea atavia*), male floret with at least 6 stamina, corolla elements and stamina larger than in the catkins figured afore; **37**. Flower gen. et sp., NHMW 2023/0072/00010; **38**. Betulaceae gen. et sp., pollen of catkin NHMW 1878/6/3615 (Ett. 1612) (*Populus latior*). For all photographs the scale at bottom right of the figure is 10 mm except for photographs with embedded scale. If not stated otherwise the embedded scale is also 10 mm


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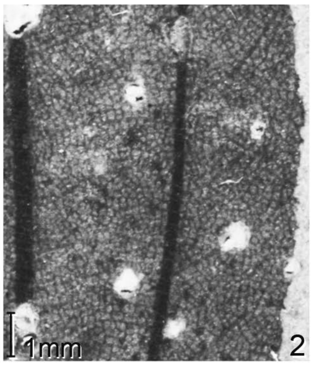
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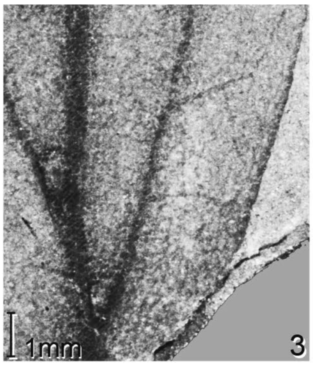
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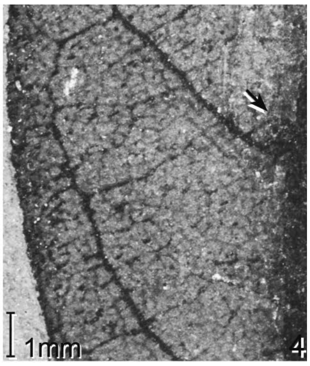
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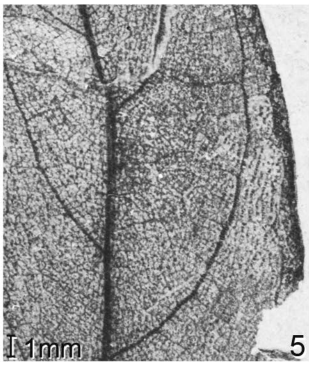
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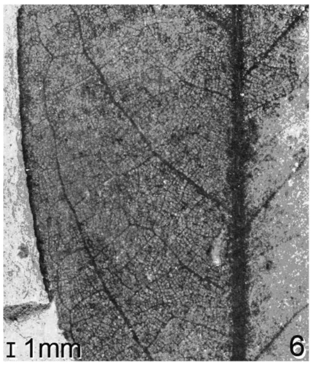
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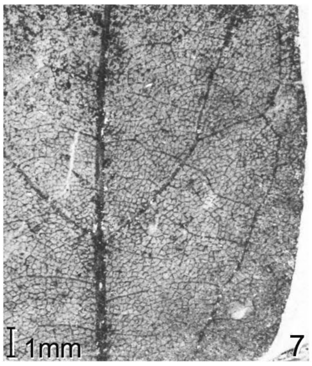
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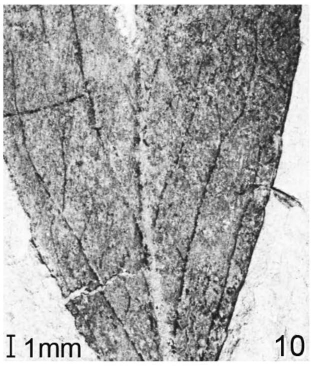
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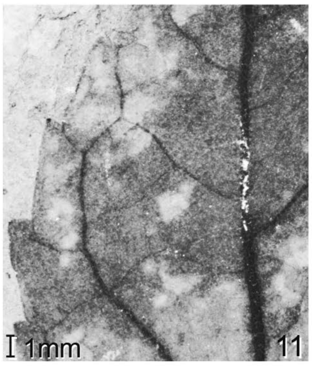
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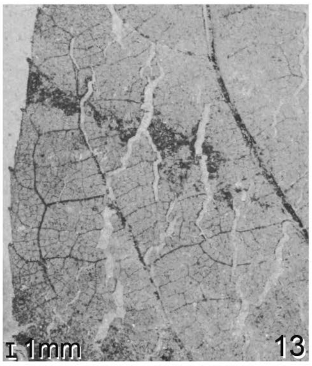
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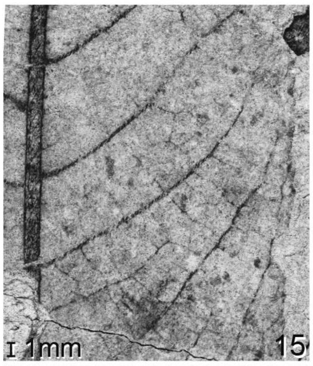
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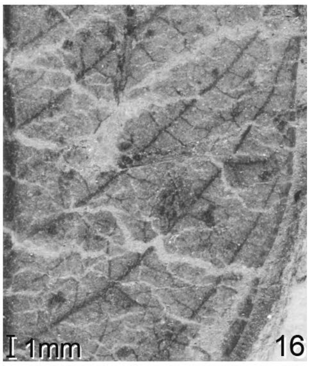
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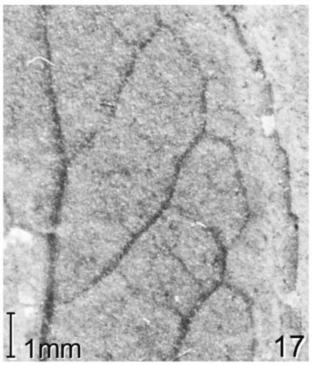
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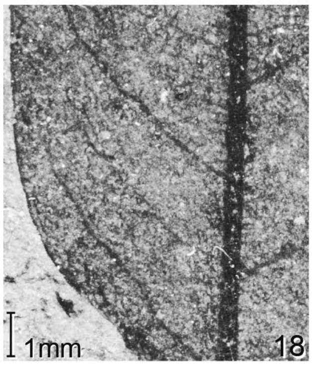
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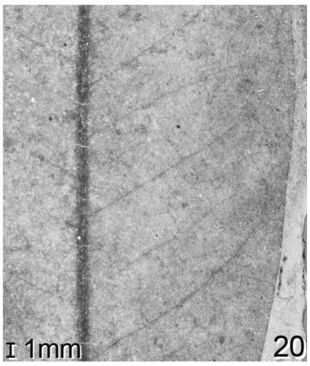
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Description. Winged seed, l × w ~8.5 × 4.5 mm, seed body l × w ~4 × 2 mm, spindle-shaped, proximally bluntly acute, distally rounded; wing incomplete, clasping half of the seed body from base to apex; angle between long axis of wing and seed body probably very narrow, no venation visible.

Remarks. Wing length and width of this specimen appear incomplete. The figures in Ettingshausen (1869a and 1888, see synonymy) resemble the specimen described here regarding the position of the seed body related to the wing, but none of the specimens listed by Ettingshausen (1888) for *E. affine* matches those figures.

Carpolithes sp. F

Fig. 22.30

1869a *Platanus gracilis* Ettingsh. sp. n.; Ettingshausen, p. 56, pl. 3, fig. 3.

Material. Moskenberg: NHMW: 1878/6/7715 (Ett. 5712), (*Platanus gracilis*), Ettingshausen (1869a: pl. 3, fig. 3, holotype).

Description. Four globoid heads on slender main axes; three loose fragments of axes, longest fragment 42 mm long; diameter of heads 7–8 mm, consisting of several oval or bean-shaped fruits, ~3 mm long, surrounded by a (?) fleshy exocarp; attachment of fruiting heads to axes unclear.

Remarks. The attachment of the fruiting heads to the axes fragments is not evident or, in other words, it remains open how many fruiting heads were attached to the axes. Ettingshausen (1869a) misinterpreted the surrounding shadow (“verschwommene Umrandung”) of one of these heads as remnants of trichomes. The CT-scan, however, indicates the existence of a probably (?) fleshy exocarp.

Carpolithes sp. G

Fig. 22.24

Material. Leoben: NHMW: 2023/0072/0009.

Description. Stalked infructescence; stalk ~6 mm long with a triangular bract at base, fruiting head terminal, bowl-shaped, ~3 mm high and 5 mm in diameter with at least 3 oval seeds.

Remarks. The number of seeds was possibly higher than the number visible here.

Carpolithes sp. H

Fig. 22.23

1869a *Euonymus moskenbergensis* Ettingsh. sp. n., p.p.; Ettingshausen, p. 83, pl. 6, fig. 4, non fig. 3.

1888 *Euonymus moskenbergensis* Ettingsh.; Ettingshausen, p. 346.

Material. Moskenberg: NHMW: 1878/6/4192 (Ett. 2189), Pb 2007, (*Euonymus moskenbergensis*), Ettingshausen (1869a: pl. 6, fig. 4, syntype).

Description. Stalked, globoid fruiting head; stalk curved, ~3 mm long; fruiting head ~3.3 mm high, max. width 5.5 mm; receptacle disc-shaped, swollen; gynoecium superior, 3 (?) capsules visible, gynoecium surrounded by coriaceous rounded (?) sepals with smooth margin.

Remarks. Ettingshausen (1869a, 1888) probably correctly estimated a pentamerous

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Figure 23. Venation details. If not stated differently major vein is midvein; **1**. *Magnolia* cf. *liblarensis* (Kräusel et Weyland) Kvaček, NHMW 1878/6/6917 (Ett. 4914), C; **2**. *Daphnogene polymorpha* (A. Braun) Ettingsh., NHMW 1878/6/3807, (Ett. 1804), Pb 1971, (*Cinnamomum polymorphum*); **3**. *Ocotea* sp., NHMW 1878/6/7867 (Ett. 5864), B, Pb 1982, domatia at the origin of secondaries near base; **4**. *Laurophyllum* sp. 1, NHMW 1878/6/4150 (Ett. 2147), B, Pb 2044; shade of domatium at the origin of a secondary vein (arrow); **5**. *Laurophyllum* sp. 2, NHMW 1878/6/9085 (Ett. 7082), Pb 1923, (*Laurus primigenia*), Ettingshausen (1869a: pl. 3, figs 11, 11 a); **6**. *Laurophyllum* sp. 3, NHMW 1878/6/3706 (Ett. 1703), Pb 1917, (*Laurus princeps*); **7**. *Laurophyllum* sp. 4, NHMW 1878/6/3802 (Ett. 1799), Pb 1969, (*Oreodaphne stiriaca*); **8**. Araceae (?) gen. et sp., IBUG Ett. 5531, B; **9**. *Berberis mahonioides* Kovar-Eder sp. n., IBUG Ett. 6147, holotype, (*Nymphaeophyllum denticulatum* sp. n. in sched.); **10**. *Berberis* cf. *teutonica* (Unger) Kovar-Eder et Kvaček, NHMW 1878/6/8509 (Ett. 6506), Pb 2018, (*Maytenus submarginata*), Ettingshausen (1869a: pl. 5, fig. 17, holotype); **11**. *Clematis oligoneure* (Ettingsh.) Kovar-Eder comb. nov., NHMW 1878/6/8549 (Ett. 6546), holotype, (*Elaeodendron oligoneure*), Ettingshausen (1869a: pl. 6, fig. 2, holotype), (*Elaeodendron stiriacum*), Ettingshausen (1888); **12**. *Parthenocissus rhombifolia* (Ettingsh.) Kovar-Eder comb. nov., NHMW 1878/6/4049 (Ett. 2046), Pb 2105, lectotype, (*Acer rhombifolium*), Ettingshausen (1869a: p. 80, pl. 5, fig. 5, syntype); **13**, **14**. *Sloanea serratifolia* (Ettingsh.) Kovar-Eder comb. nov., major veins are secondaries, **13**. NHMW 1878/6/7710 (Ett. 5707), Pb 1977, lectotype, (*Artocarpidium serratifolium*), Ettingshausen (1869a: pl. 3, fig. 2, syntype), **14**. NHMW 1878/6/3750 (Ett. 1747), paratype, (*Persea heeri*); **15**. *Salix varians* Goepp., NHMW 1878/6/7801 (Ett. 5798), (*Salix varians*); **16**. *Salix* sp., NHMW 1878/6/7675 (Ett. 5672), Pb 1899, A, (*Ficus fridaui*); **17**. *Leguminophyllum* sp. 1, NHMW 1878/6/8815 (Ett. 6812), Pb 2085, (*Dalbergia haeringiana*); **18**. *Leguminophyllum* sp. 2, NHMW 1878/6/8816 (Ett. 6813), Pb 2086, (*D. haeringiana*); **19**. *Leguminophyllum* sp. 3, NHMW 1878/6/8817 (Ett. 6814), Pb 2087, (*Dalbergia pterocarpoides*), Ettingshausen (1869a: pl. 6, fig. 9, holotype); **20**. *Leguminophyllum* sp. 4, NHMW 1878/6/8836 (Ett. 6833), Pb 2066, (*Cassia phaseolites*)


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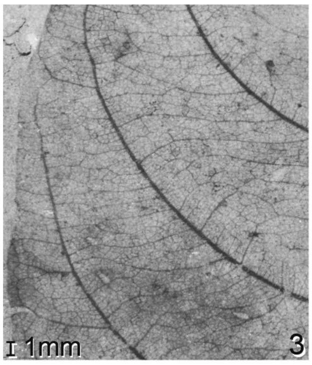
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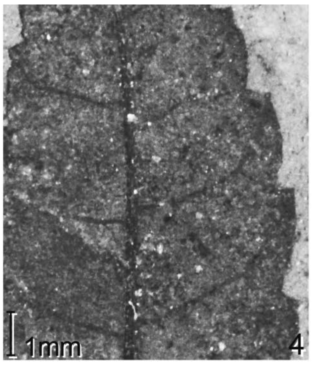
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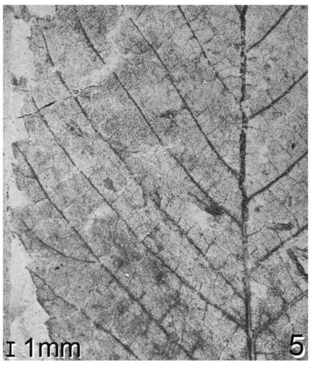
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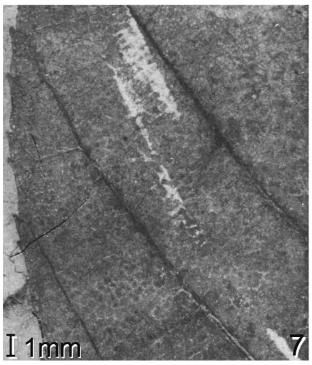
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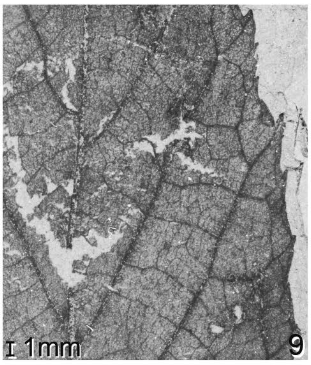
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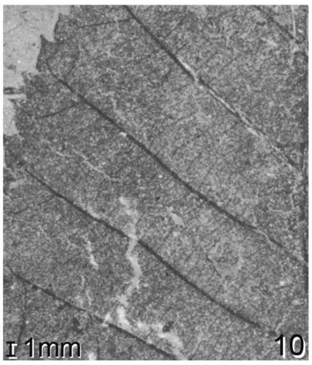
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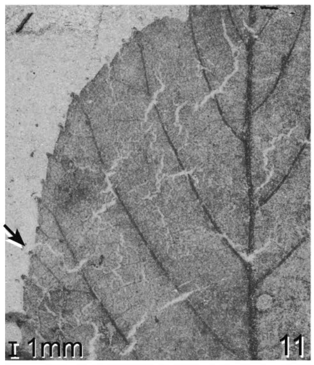
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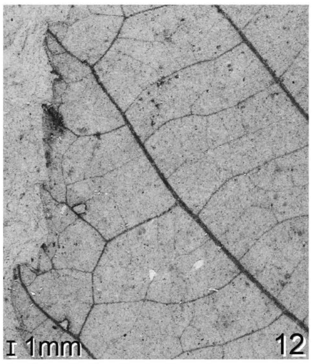
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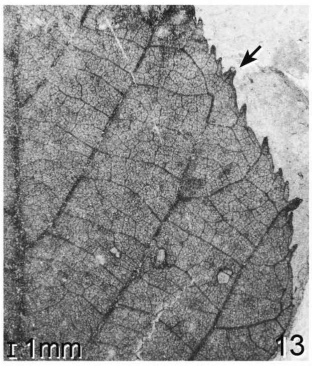
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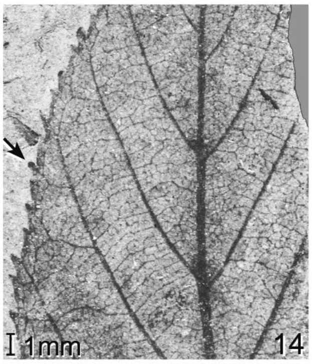
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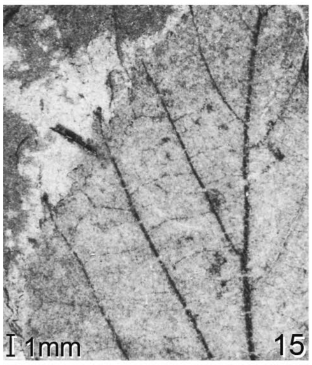
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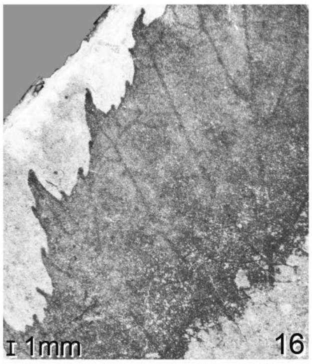
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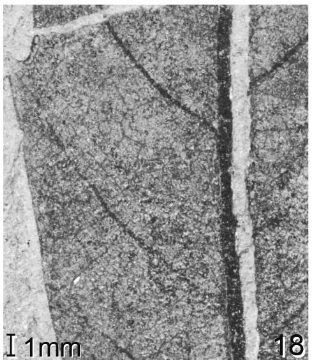
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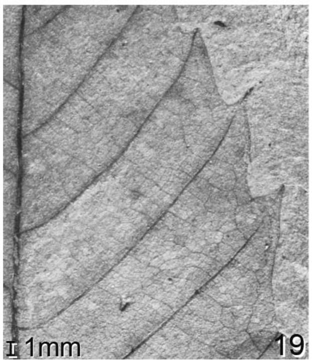
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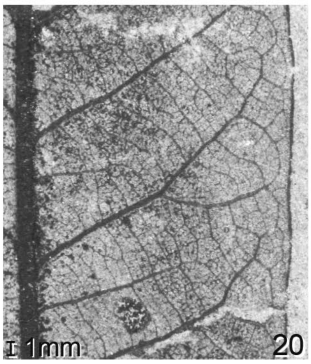
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structure of this specimen. The gynoecium was possibly choricarp.

Carpolithes sp. I

Fig. 22.22

1870 *Tetrapteris minuta* Ettingsh. sp. n.; Ettingshausen, p. 888, pl. 2, figs 8a, b.

1888 *Tetrapteris minuta* Ettingsh., p.p.; Ettingshausen, p. 341, pl. 7, figs 10, 11.

Material. Münzenberg: NHMW 1878/6/4394 (Ett. 2391), a, Pb 2132, (*Tetrapteris minuta*) + IBUG 6200 (*Tetrapteris minuta*), Ettingshausen (1888: pl. 7, fig. 11), part + counterpart.

Description. Four-winged fruit, max. width ~10.5 mm; fruit body roundish, diameter ~2.5–2.8 mm; wings elongated, l × w up to 5 × 2 mm, parallel-sided, with up to 4 veins parallel to wing longitude; wings attached with broad base to fruit, distal end rounded.

Remarks. This specimen was already figured by Ettingshausen (1870). The leaf that Ettingshausen (1888) also assigned to this taxon is an indeterminable fragment (Supplementary File 2). Ettingshausen (1870, 1888) saw affinities to the modern genus *Tetrapterys* Cav. (Malphigiaceae), a genus native to Mexico and tropical America (POWO, accessed December, 2023), but the preserved details are too scarce for such an assignment. As Hably and Manchester (2000) stated, there are no affinities of the here described specimens to *Tetrapteris harpyarum* Unger emend. Hably et Manchester due to the minute size and more equal size of wings of *Carpolithes* sp. I. Moreover, the wings show fewer veins than *T. harpyarum*.

Carpolithes sp. J

Fig. 22.25, 22.26

1888 *Macreightia longipes* Ettingsh. p.p.; Ettingshausen, p. 330, pl. 6, fig. 14, non figs 12, 13.

Material. Münzenberg: IBUG: 6120, (*Diospyros brachysepala* in sched.). Leoben: NHMW: 2023/0072/0011 (coll. Hofmann sine no.).

Description. Infructescences attached to thick stalk, length of stalk at least 5 mm, incomplete; calyx elements attached to receptacle, number uncertain, (?) coriaceous or (?) woody, 1–3.5 mm long, apex acute, clasping only basal region of fruit body; fruit body ~5.8 × 6.7 mm and 3.8 × 3.4 mm.

Remarks. Both specimens differ in size, which may reflect different states of maturity. The shape of the fruit body is smoothly curved in specimen NHMW 2023/0072/0011 but bluntly hexagonal in specimen IBUG Ett. 6120. The latter appearance may be an artefact due to compactation during fossilisation. Otherwise both specimens resemble each other closely.

Today, *Macreightia* A. DC. is regarded as being synonymous to *Diospyros* L. (POWO, accessed December, 2023). Ettingshausen's assignment of these fossils to this genus was probably based on the persistent coriaceous or woody calyx. Nonetheless, the number of calyx elements is uncertain in the specimens from Leoben.

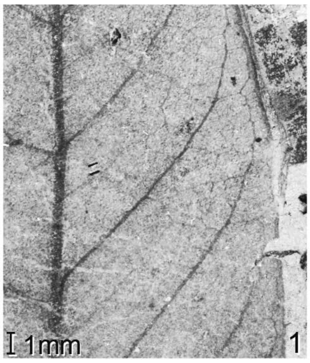
Carpolithes sp. K

Fig. 22.27

1869a *Macreightia longipes* Ettingsh. sp. n., p.p.; Ettingshausen, p. 74, pl. 4, fig. 10, non 11.

◄

Figure 24. Venation details. If not stated differently major vein is midvein. **1**. *Leguminophyllum* sp. 6, IBUG Ett. 5811, B; **2**. *Leguminophyllum* sp. 7, NHMW 1878/6/7692 (Ett. 5689), Pb 2168, (*Ficus rachoyana*), Ettingshausen (1888: pl. 2, fig. 26, holotype); **3**. *Berchemia* (?) sp., IBUG Ett. 6251 (*Dioclea protogaea*), major veins are secondaries; **4**. *Cedrelospermum ulmifolium* (Unger) Kovar-Eder et Kvaček, NHMW 1878/6/3580 (Ett. 1577), (*Planera ungeri*); **5**. *Ulmus pyramidalis* Goepp., NHMW 1878/6/3546 (Ett. 1543), (*Ulmus bronnii*); **6**. *Ulmus* (?) *prisca* Unger, NHMW 1878/6/6455 (Ett. 4452), Pb 1800, (*Phyllerium palaeo-carpini* on *Carpinus heeri*), Ettingshausen (1888: pl. 1, figs 3, 3a, holotype of fungus); **7**. *Alnus gaudinii* (Heer) Erw. Knobloch et Kvaček, NHMW 1878/6/3523 (Ett. 1520), B, (*Prunus palaeo-cerasus*), major veins are secondaries; **8**, **9**. *Alnus julianiformis* (Sternberg) Kvaček et Holý, **8**. NHMW 1878/6/3553 (Ett. 1550) (*Alnus kefersteinii*), **9**. NHMW 1878/6/8373 (Ett. 6370), Pb 2096, (*Cissus fagifolia*), Ettingshausen (1869a, pl. 5, fig. 1, syntype); **10**. *Alnus menzelii* Raniecka-Bobrowska, NHMW 1878/6/7450 (Ett. 5447), (*Carpinus heeri*); **11**. *Alnus milleri* (Ettingsh.) Kovar-Eder comb. nov., NHMW 1878/6/3572 (Ett. 1569), Pb 2110, lectotype, (*Tilia milleri*), Ettingshausen (1869a: pl. 5, fig. 2, syntype); teeth probably glandular; **12**. *Alnus* aff. *cecropiifolia* (Ettingsh.) Berger, NHMW 1878/6/7426 (Ett. 5423), (*Alnus kefersteinii*), major veins are secondaries; **13**. *Alnus* cf. *oberdorfensis* Kovar-Eder, NHMW 1878/6/3658 (Ett. 1655), (*A. kefersteinii*), see glandular teeth (arrow); **14**. *Betula similis* (?) (Goepp.) Zastawniak et Walther, NHMW 1878/6/4015 (Ett. 2012), (*Betula prisca*), see domatia at origin of secondaries, glandular tooth apices (arrow); **15**. *Betula* sp. 1 – leaf, IBUG 6296, a, (*Betula brongniartii*), some tooth apices (?) glandular; **16**. *Betula* sp. 2 – leaf, NHMW 1878/6/4445 (Ett. 2442), Pb 2334, (*Betula brongniartii*), glandular tooth apices; **17**. *Carpinus grandis* Unger, NHMW 1878/6/3741 (Ett. 1738), (*Carpinus heeri*), major veins are secondaries; **18**. *Quercus drymeja* Unger, NHMW 1878/6/4102 (Ett. 2099), (*Quercus milleri* in sched.); **19**. *Quercus gigas* Goepp. emend. Walther and Kvaček (1991), NHMW 1878/6/9141 (Ett. 7138), (*Castanea atavia*); **20**. *Quercus rhenana* (Kräusel et Weyland) Erw. Knobloch et Kvaček, IBUG Ett. 5714, (*Quercus daphnophyllum*)



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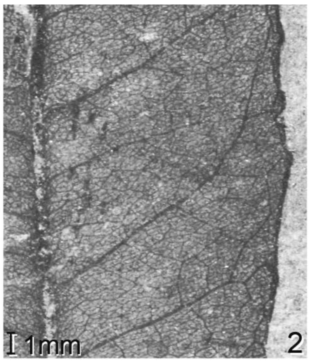

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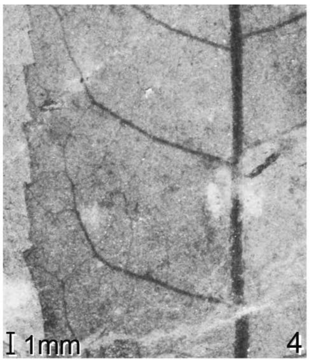

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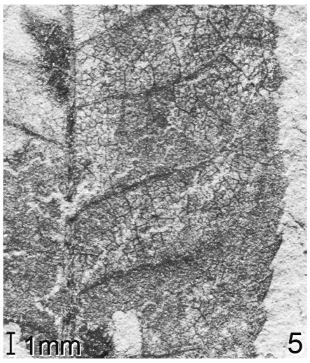

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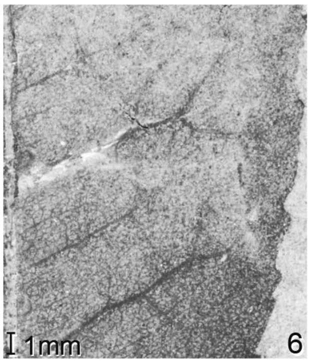

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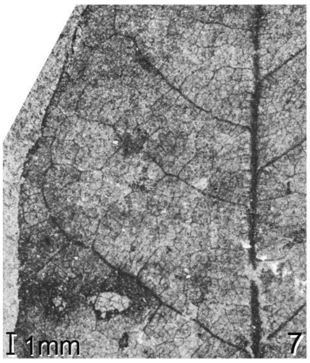

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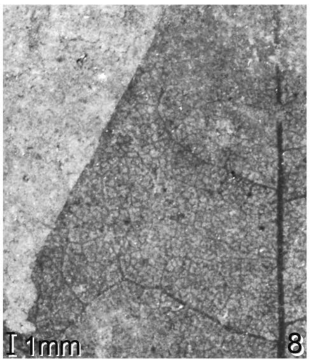

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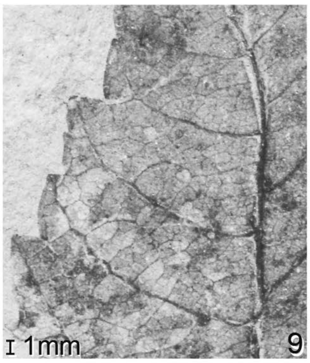

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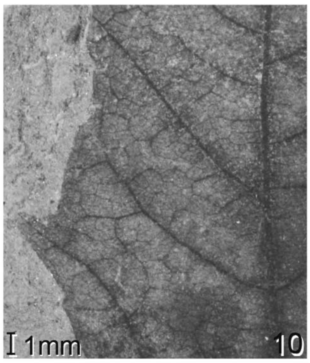

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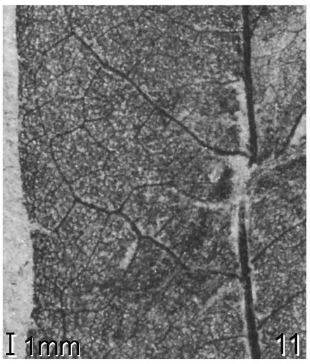

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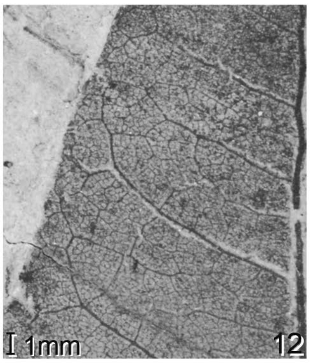

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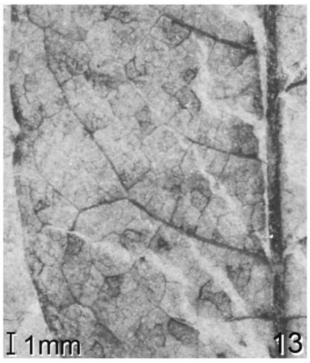

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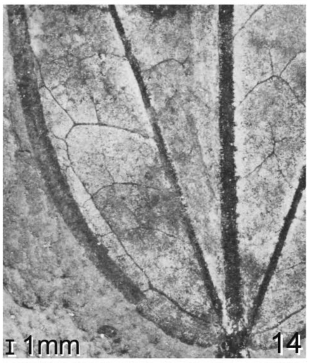

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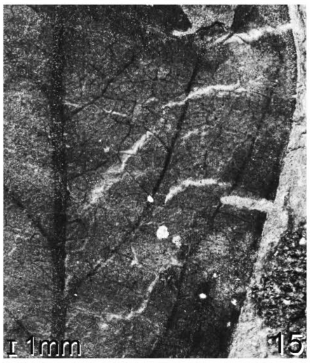

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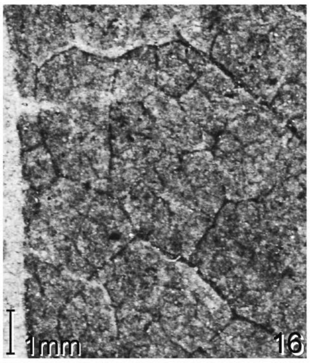

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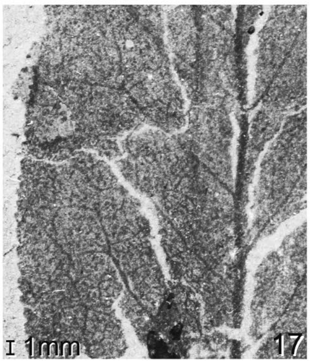

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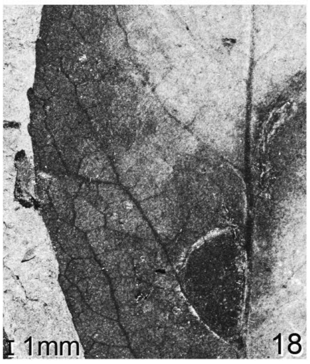

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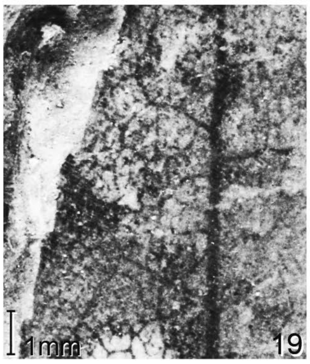

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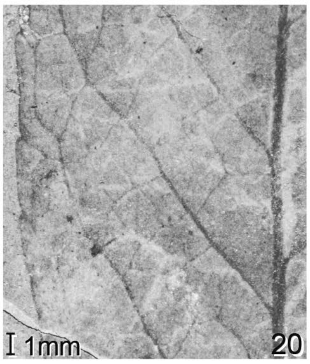

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Material. Moskenberg: IBUG: 6130, (*Macreightia longipes*), probably Ettingshausen (1869a: pl. 4, fig. 10, syntype).

Description. Long-stalked infructescence; stalk curved, ~22 mm long, (?) complete, widened in transition to receptacle; two coriaceous calyx elements complete, ~5.5–7.5 mm long, third one damaged apically; calyx elements attached with broad base to receptacle, apex blunt acute.

Remarks. The specimen at hand resembles closely that figured by Ettingshausen (1869a: pl. 4, fig. 10) although it is now damaged. It differs from *Carpolithes* sp. J by larger size of the calyx elements, which would have clasped a potential fruit to a greater extent.

***Carpolithes* sp. L**

Fig. 22.29

Material. Moskenberg: IBUG: 5597, (Palmae in sched.).

Description. Broad spindle-shaped, not yet dehiscent capsule, l × w ~35 × 17 mm, proximal and distal ends (?) acute, surface finely ribbed, ribs paralleling fruit length, 3 (?) valves indicated by 2 longitudinal (?) dehiscence lines.

Remarks. Although Ettingshausen (1888) identified two fossils as fragmentary palm fronds of *Sabal major* Unger, no fragments of palm fronds were discovered during the restudy of the Leoben material. Slab NHMW 1878/6/7316 (Ett. 5313) listed by Ettingshausen (1888) was located and it represents a poorly preserved fragment of monocotylean affinity (see Supplementary File 2). If palms were present at all in the lake surroundings, fragmented palm fronds would be expected to occur more likely than large-sized fructifications in the fine-grained sediments deposited under low water energy regime. The size of this specimen is similar to capsules of *Reevesia hurnikii* Kvaček (Kvaček, 2006; Worobiec and Worobiec, 2020), whose leaves (*Laria rueminiana*) are abundant in the Leoben assemblage. Nevertheless, the lack of diagnostically relevant features hampers a definite systematic assignment.

***Carpolithes* sp. M**

Fig. 22.28

1869a *Polygonites deperditus* Ettingsh. sp. n.; Ettingshausen, p. 58, pl. 3, fig. 15.
1888 *Persoonia daphnes* Ettingsh., p.p.; Ettingshausen, p. 313, non pl. 4, figs 22, 23.

Material. Moskenberg: NHMW: 1878/6/7811 (Ett. 5808), Pb 1990, (*Polygonites deperditus*), Ettingshausen (1869a: pl. 3, fig. 15, holotype); 1878/6/7975 (Ett. 5972), Pb 1959, (*Persoonia daphnes*).

Description. Long-stalked fruits; stalk up to 6.3 mm long, straight; fruit body heart-shaped, l × w ~4.4 × 3.3 and 3.7 × 3.7 mm; in NHMW 1878/6/7811 (Ett. 5808) seed body surrounded by shadowly preserved, also heart-shaped (?) wing or (?) flesh, l × w of complete specimen ~7 mm × 5 mm.

Remarks. Both specimens definitely represent the same taxon of uncertain affinity.

◄———

Figure 25. Venation details. If not stated differently major vein is midvein; **1**. *Trigonobalanopsis rhamnoides* (Rossmässler) Kvaček et H. Walther, NHMW 1878/6/4107 (Ett. 2104), Pb 1937, (*Cinchonidium angustifolium*); **2**. *Myrica joannis* Ettingsh. emend. Kovar-Eder (1996), IBUG Ett. 6091, (*Fraxinus prae-excelsior*), Ettingshausen (1888: (?) syntype); **3**. *Myrica lignitum* (Unger) Saporta sensu Ettingshausen and Standfest (1888), NHMW 1878/6/3522 (Ett. 1519), (*M. lignitum* var. *remote dentata*); **4**. *Pterocarya paradisiaca* (Unger) Iljinskaja, NHMW 1878/6/3836 (Ett. 1833), A, Pb 2038, (*Pterocarya denticulata*); **5**. Juglandaceae gen. et sp., NHMW 1878/6/4468 (Ett. 2465), A, (*Phaseolites securidacus*); **6**. (?) Juglandaceae gen. et sp., NHMW 1878/6/3727 (Ett. 1724), a, (*Prunus palaeo-cerasus*); **7**. *Acer pseudomonspessulanum* Unger emend. Ströbitzer-Hermann (2003), NHMW 1878/6/3569 (Ett. 1566), Pb 2024, (*Acer decipiens*), detail of central lobe; **8**. *Acer integerrimum* (Viviani) Massalongo, IBUG Ett. 6148, (*Sterculia labrusca*), detail of right lateral lobe; **9**. *Acer tricuspidatum* Bronn, IBUG Ett. 6223, (*Vitis plurinervia*), detail of central lobe; **10**. *Acer palaeosaccharinum* Stur, NHMW 1871/38/38, detail of central lobe; **11**. *Acer integrilobum* C.O. Weber emend. Walther (1972), NHMW 1999B0003/0001, Pb 5498, (*A. palaeo-campestre*), Ettingshausen (1869a: pl. 5, fig. 11, syntype), detail of right lateral lobe; **12**. *Acer* sp., leaf, NHMW 1878/6/3570 (Ett. 1567), (*Acer decipiens*), detail of right lateral lobe; **13**. *Ailanthus* (?) *apollinis* Ettingsh., IBUG Ett. 6238, lectotype, (*Ailanthus apollinis*), Ettingshausen (1888: pl. 9, figs 28, 28a, syntype); **14**. *Laria rueminiana* (Heer) G. Worobiec et Kvaček, NHMW 1878/6/7915 (Ett. 5912), Pb 2119, (*Sterculia cinnamomea*), Ettingshausen (1888: pl. 7, fig. 3); **15**. *Diospyros brachysepala* A. Braun sensu Hantke (1954), IBUG Ett. 6121, (*Diospyros brachysepala*); **16**. Styracaceae (?) gen. et sp., NHMW 1878/6/4477 (Ett. 2474), Pb 2354, (*Sophora europaea*), Ettingshausen (1888: pl. 9, fig. 30); **17**. *Ternstroemites diversifolius* (Ettingsh.) Kovar-Eder comb. nov., NHMW 1878/6/4140 (Ett. 2137), Pb 1859, lectotype, (*Euonymus diversifolius*), counterpart of NHMW 1878/6/4052 (Ett. 2049), b, Ettingshausen (1888: pl. 8, figs 18, 18a, syntype); **18**. *Ternstroemites stiriacus* (Ettingsh.) Kovar-Eder comb. nov., NHMW 1878/6/4052 (Ett. 2049), a, Pb 1859, paratype, (*Euonymus diversifolius*), Ettingshausen (1888: pl. 8, fig. 19, syntype); **19**. *Fraxinus bilinica* (Unger) Kvaček, NHMW 1878/6/3879 (Ett. 1876), Pb 1958, (*Fraxinus primigenia*); **20**. *Sambucus ettingshausenii* Kovar-Eder sp. n., IBUG 6085 A, B, holotype, (*Sambucus miocenica* sp. n. in sched.), detail of leaflet B

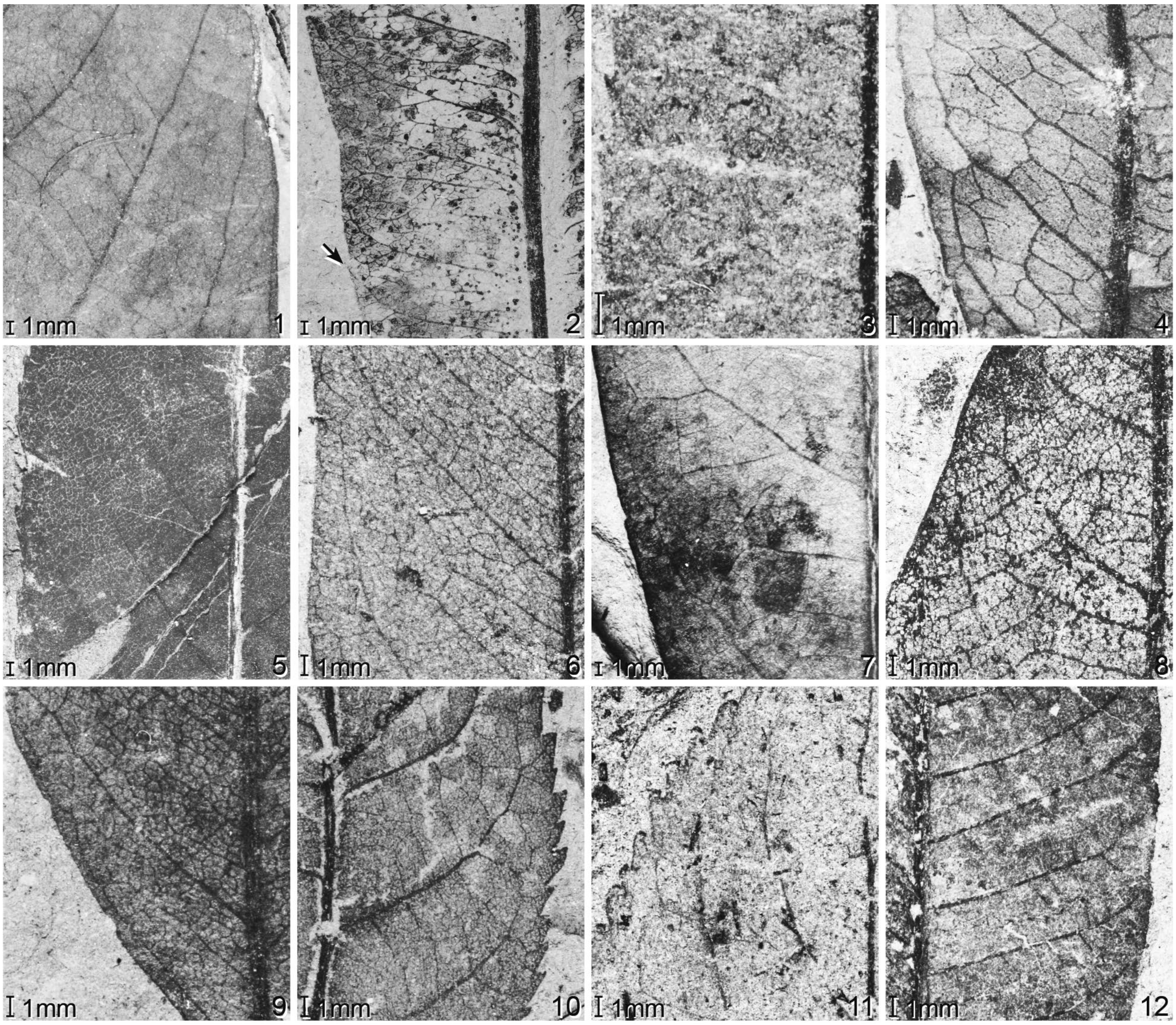

Figure 26. Venation details. If not stated differently major vein is midvein; **1**. Cornaceae vel Rhamnaceae gen. et sp., IBUG Ett. 6199, A, (*Heteropteris protogaea*); **2**. "*Apocynophyllum*" *hunteriaeforme* Ettingsh., NHMW 1878/6/6497 (Ett. 4494), as (*Achras lycobroma*) with fungus (*Sphaeria achreia*), Ettingshausen (1878b: pl. 5, fig. 4), arrow indicating inconspicuous tooth; **3**. *Dicotylophyllum* sp. B, NHMW 1878/6/8685 (Ett. 6682), Pb 2033, (*Rhus tenuifolia*), Ettingshausen (1869a: pl. 6, fig. 6, holotype); **4**. *Dicotylophyllum* sp. C, NHMW 1878/6/4135 (Ett. 2132), Pb 2015, (*Celastrophyllum venosum*), Ettingshausen (1888: pl. 8, fig. 10, holotype); **5**. *Dicotylophyllum* sp. F, IBUG Ett. 6297, (*Photinia eratonis*); **6**. *Dicotylophyllum* sp. H, NHMW 1878/6/4476 (Ett. 2473), a, Pb 2357, (*Cassia phaseolites*); **7**. *Dicotylophyllum* sp. L, IBUG Ett. 6019, (*Laurus prae-nobilis*); **8**. *Dicotylophyllum* sp. N, IBUG Ett. 6001, (*Ficus lobkowitzii*); **9**. *Dicotylophyllum* sp. O, NHMW 1878/6/3841 (Ett. 1838), Pb 1909, (*Ficus tenuinervis*); **10**. *Dicotylophyllum* sp. Q, NHMW 1878/6/9847 (Ett. 7844), (*Ulmus plurinervia*); **11**. *Dicotylophyllum* sp. R, NHMW 1878/6/4206 (Ett. 2203), (*Celtis stiriaca*), see glandular teeth; **12**. "*Juglans*" *parschlugiana* Unger, NHMW 1878/6/4118 (Ett. 2115), Pb 2050, (*Juglans parschlugiana*)

Carpolithes sp. N

Fig. 22.15

1888 *Diospyros brachysepala* A. Braun, p.p.; Ettingshausen, p. 329, pl. 6, fig. 9.

Material. Moskenberg: NHMW: 1878/6/4027 (Ett. 2024), Pb 2003, (*Diospyros brachysepala*), Ettingshausen (1888: pl. 6, fig. 9).

Description. Roundish, syncarp fruit, 3.6 mm in diameter; base rounded, apex region indicating at least 3 parts, each of them rounded, centre of apex depressed; seed bodies crescent to inverted drop-shaped, l × w ~2.4–2.6 × 1.1 mm.

Remarks. Ettingshausen's (1888) figure does not show any details, but judging from the discussion for *Diospyros brachysepala* this specimen is the original of the fruit figured there.

Shoot fragment with bud

Fig. 22.31

Material. Moskenberg: NHMW: 1878/6/3989 (Ett. 1986), B.

Description. Shoot fragment with (?) two stalks, one with bud attached; stalks bent, ~4 mm long; bud ~8.3 × 7.3 mm upon disc-shaped receptacle, bud scales broad bowl-shaped, imbricative.

Remarks. The impression of the bud is quite faint and at first look somewhat resembles a drupe. The conture of the outermost scale upon the inner one is, however, visible though indistinct. The attachment of the other stalk (lacking a bud) to the twig is uncertain.

Bud scales

Fig. 22.8–22.10

1869a *Ostrya stenocarpa* Ettingsh. sp. n.; Ettingshausen, p. 47, pl. 2, figs 8–10.
1888 *Castanea atavia* Unger, p.p.; Ettingshausen, p. 292.
1888 *Ostrya stenocarpa* Ettingsh.; Ettingshausen, p. 295.

Material. Moskenberg: NHMW: 1878/6/4069 + 4086, A (Ett. 2066 + 2083), (*Ramentites latior* in sched.); 1878/6/4092 (2089), (*R. latior* in sched.); 1878/6/4093 (2090), (*R. latior* in sched.); 1878/6/7493 + 7494 (5490 + 5491), A, (*Castanea atavia*); 1878/6/7495 (5492), (*C. atavia*); 1878/6/9190 (7187), (*C. atavia*). Münzenberg: IBUG: Ett. 6278, (*Ramentites ovatus* in sched.).

Description. Scales (broad) triangular, more or less symmetrical, lateral flanks convex, in some specimens base somewhat constricted, thickened; l × w ~4–10 × 3–7 mm, ratio l/w = 1.2–2.6; apex (bluntly) acute, acuminate, sometimes bipartite, parallel veins very faint.

Remarks. The bud scales labelled *Ramentites latior* (NHMW 1878/6/4069 + 4086, A (Ett. 2066 + 2083), Fig. 22.9, NHMW 1878/6/4092 (Ett. 2089), NHMW 1878/6/4093 (Ett. 2090), Fig. 22.8) closely resemble those figured as *Ostrya stenocarpa* (Ettingshausen (1869a: pl. 2, figs 8–10), although it is not possible to assign individual specimens unambiguously to one of the figures, and Ettingshausen (1888: p. 295) did not provide collection numbers for this fossil-taxon.

The specimens regarded as nuts of *Castanea atavia* (Ettingshausen, 1888) (NHMW 1878/6/7493 + 7494 (Ett. 5490 + 5491), A, NHMW 1878/6/7495 (Ett. 5492), NHMW 1878/6/9190 (Ett. 7187), Fig. 22.10) and IBUG Ett. 6278 differ by a lower length/width ratio and somewhat constricted and thickened base and sometimes bipartite apex from the other specimens. Scales with bipartite apex do occur, e.g. in *Quercus* (own observaton). Bud scales of oaks are quite resistant to decay and known to become commonly fossilised. The innervation consists of numerous parallel but hardly visible veins (Tomlinson, 1985).

Scales, **bracts** or **corolla elements**

Fig. 22.11, 22.12

1869a *Ostrya atlantidis* Unger, p.p.; Ettingshausen, p. 46, pl. 2, figs 11, 12, non 13.

Material. Moskenberg: NHMW: 1878/6/8199 (Ett. 6196), B, Pb 2106. Seegraben Walpurgis-Schacht: NHMW: 1878/6/4469 + 4470 (Ett. 2466 + 2467), (*Ramentites* sp. in sched.).

Description. Scales, bracts or corolla fragments, l × w ~6–10 × 2–3 mm, ratio l/w ~2.6–3.3; base slightly thickened, shape oblong, asymmetrical, apically bent, one side convex; the other straight to convex in lower part, apically concave; apex blunt acute, with 5 to 6 parallel veins, central one running into apex, slightly thicker than lateral ones; NHMW 1878/6/4470 (Ett. 2467) with a (?) nutlet at base.

Remarks. In the specimen preserved as part and counterpart (NHMW 1878/6/4469 + 4470, Ett. 2466 + 2467), one half possibly shows a small nutlet (Fig. 22.11) near base, which would indicate a bract rather than a bud scale. Although this specimen closely resembles the figures of Ettingshausen (1869a: pl. 2, figs 11, 12), it remains open whether it represents the original because the figures would be mirror-inverted.

Scales or **corolla elements**

Fig. 22.6, 22.7

1888 *Acer decipiens* A. Braun, p.p.; Ettingshausen, p. 340, non pl. 8, figs 2–5.

Material. Moskenberg: NHMW: 1878/6/3745 (Ett. 1742), (*Acer decipiens*); 1878/6/7492 (5489), (*Castanea atavia*); 1878/6/7493 + 7494 (5490 + 5491), B; IBUG Ett. 6281 (*Ramentites ovatus* in sched.).

Description. Scales or fragments of corolla; narrowed and thickened at base, base like a compressed ring; upper part somewhat broadened, l × w ~7.5–10.5 × 3.5–5 mm, ratio l/w ~2.2–2.5; apex blunt acute, with numerous parallel veins, veins dichotomising in specimen NHMW 1878/6/7494 (Ett. 5491), B.

Remarks. These remains differ from the afore-described ones by their shape and symmetry and in being narrowed near their base.

(SEMI)QUANTITATIVE ASSESSMENT OF VEGETATION, MODERN VEGETATION PROXIES AND PALAEOCLIMATE – RESULTS

INTEGRATED PLANT RECORD (IPR) VEGETATION ANALYSIS

For the Leoben assemblage three score variants (variants A–C) were applied to test the robustness of the results (Table 3, Supplementary File 3[3]). In variants A and C more taxa (or share of taxa) are scored as azonal than in variant B. In variant C, additionally all taxa "incertae sedis" are scored as problematic taxa. The results of variants A–C vary, however, only minimally: The BLD component ranges from 50.3% (variant A) to 54% (variant C), the BLE component varies between 29.3% (variant C) and 31.6% (variant A), and the SCL+LEG component counts from 16.8% (variant C) to 18.1% (variant A) of zonal woody angiosperms. Based on these percentages the predicted major vegetation type is the ecotone between mixed mesophytic forest and broad-leaved evergreen forest (sensu Teodoridis et al., 2011a, 2011–2021).

SIMILARITY APPROACH (APPLICATION OF DRUDGE 1)

Drudge 1 of the Similarity Approach was applied to the scoring variants A–C of the IPR vegetation analysis. Drudge 2 was not employed because herbaceous plants assignable to zonal vegetation are hardly documented in the Leoben assemblage.

Unit China 60 (Mixed Mesophytic Forest – Southern Anhui) (Teodoridis et al., 2020: appendix 7) received the highest number of scores, i.e. two similarity hits (of 3 possible ones) in each of variants A–C, followed by Japan 01 (Shirakami Sanchi – Broad-leaved Deciduous Forest – Lindera membranacea-Fagus crenata comm.), which received two hits in variants A and C and one hit in variant B (Table 4, Fig. 27A, Supplementary File 4[4]).

On the higher level of vegetation types (East Asia) and vegetation formations (Europe), each type/formation can potentially achieve a maximum of 15 scores (5 in each of the IPR Similarity, Taxonomic Similarity and Results Mix). The vegetation type BLDF Upper Yangtze, Honshu (sensu Kovar-Eder et al., 2021: table 3) is delivered as the most likely modern vegetation proxy (4 similarity hits in each variant), followed by MCF China, Japan (4 hits in variant C and 3 hits in each of variants A and B), and MMF China (3 hits in each of variants B and C, and 2 hits in variant A) (Fig. 27B, Supplementary File 5[5]). The European Vegetation Formations C, D, F, the BLDF N and NE Provinces, China and the BLEF China, Japan received fewer similarity hits. In the MCF China, Japan the similarity hits are distributed rather equally over four units out of 18 possible ones, namely Japan 06, Japan 16, Japan 18, China 81. None of them received more than a single hit within each of the variants A–C. In the BLDF Upper Yangtze, Honshu, which comprises 10 units, the scores are also distributed over 4 units (Japan 01, Japan 05, China 66, China 67), of which Japan 01 received more hits than the other units and, as stated above, the second most of all delivered proxies. In the MMF China, comprising 7 units, 3 of them received scores (China 58, China 60, China 61). Of these, China 60 received by far the most scores in the MMF China and at the same time, as stated above, the most scores of all units delivered as proxies at all (2 in each of variants A–C).

CLIMATE LEAF ANALYSIS MULTIVARIATE PROGRAM (CLAMP)

Based on the methodology proposed on the CLAMP website (Spicer, 2011–2021), the CLAMP calibration data set PhysgAsia2 (HresGridMetAsia2) was determined to be the most suitable to derive the palaeoclimate parameters for the Leoben flora

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[3] Supplementary File 3. Scoring sheet of the Leoben flora for the IPR vegetation analysis and results. Different organs of probably one plant species are scored only once. Three variants were performed in which the scorings of some taxa were modified as follows: in variant A more taxa are assumed to be at least partly azonal, i.e. preferring wetland habitats than in variant B based on presumed autecology and abundance. In variants A and B, differently scored taxa are marked by an asterisk. In variant C, taxa incertae sedis are not scored according to foliar physiognomy but are instead assigned to "Problematic taxa"

[4] Supplementary File 4. Modern vegetation proxies as delivered by the Similarity Approach (application of the Drudge 1 tool) for Leoben (variants A–C) at the level of units. Only those units that received similarity hits are shown

[5] Supplementary File 5. Modern vegetation proxies as delivered by the Similarity Approach (application of the Drudge 1 tool) for Leoben (variants A–C) at the level of vegetation types (Asia) and vegetation formations (Europe)

Table 3. Results of the IPR vegetation analysis for Leoben and comparison with the results for Oberdorf, Parschlug (Kovar-Eder et al., 2022), Mecsek Mts. (Kovar-Eder et al., 2021) and the Cypris Formation (Teodoridis and Kvaček, 2015). The results for Leoben and the Cypris Formation indicate an ecotone between mixed mesophytic and broad-leaved evergreen forest, whereas the most likely major vegetation type predicted for Oberdorf is broad-leaved evergreen forest and for Parschlug and Mecsek Mts. subhumid sclerophyllous forest

Localities	IPR-vegetation analysis results													Predicted major vegetation type
	Zonal components						Number of taxa of azonal components							
	Percentage of zonal woody angiosperms				Percentage of zonal taxa									
	BLD component	BLE component	SCL + LEG component	ZONPALM	DRY HERB component	MESO HERB component	Azonal woody component	Azonal non-woody component	Aquatic component	Number of zonal taxa	Number of zonal woody angiosperms	Number of problematic taxa	Total number of taxa	
Leoben – variant A (this paper)	50.3	31.6	18.1	0.0	0.0	1.7	30.0	10.5	3.0	89.4	78.1	18.0	151	ecotone mixed mesophytic forest/ broad-leaved evergreen forest
Leoben – variant B (this paper)	52.8	30.1	17.1	0.0	0.0	1.5	19.0	10.5	3.0	100.4	88.6	18.0	151	
Leoben – variant C (this paper)	54.0	29.3	16.8	0.0	0.0	2.4	30.0	10.5	3.0	63.4	52.1	44.0	151	
Oberdorf	49.3	46.5	4.1	0.0	2.2	7.8	25.6	25.9	7.0	108.6	92.2	5.0	172	broad-leaved evergreen forest
Parschlug – variant 1 (Kovar-Eder et al., 2022)	43.0	20.9	36.1	0.0	0.0	1.0	6.7	3.0	1.0	100.0	94.0	4.0	114	subhumid sclerophyllous forest
Parschlug – variant 2 (Kovar-Eder et al., 2022)	44.1	21.4	34.5	0.0	0.0	1.0	6.7	3.0	1.0	100.0	94.0	4.0	114	
Parschlug – variant 3 (Kovar-Eder et al., 2022)	45.0	23.0	32.0	0.0	0.0	1.0	6.7	3.0	1.0	100.0	94.0	4.0	114	
Mecsek Mts. (Kovar-Eder et al., 2021)	41.5	29.2	27.7	1.6	0.0	0.0	8.2	6.5	1.0	68.3	60.8	12.0	96	subhumid sclerophyllous forest
Cypris Formation (Teodoridis and Kvaček, 2015)	58.6	33.8	7.6	0.0	0.0	3.0								ecotone mixed mesophytic forest/ broad-leaved evergreen forest

(Supplementary File 6[6]), resulting in the following proxies: MAT 16.9 (±2.3)°C, WMMT 27.5 (±2.8)°C, CMMT 4.9 (±3.6)°C, GROWSEAS 9.8 (±1.1) months, GSP 196.7 (±60.6) cm, MMGSP 20.5 (±6.1) cm, 3_WET 86.7 (±35.8) cm, 3_DRY 29.3 (±9.5) cm, RH 71.3 (±8.4) %, SH 9.4 (±1.9) g/kg, ENTHAL 32.7 (±0.9) kJ/kg. The MAP indirectly derived from CLAMP parameters is 238.9–240.5 cm (Table 5).

Using the tool developed by Teodoridis et al. (2011b, 2012, update in Kovar-Eder et al., 2022), PhysgAsia1 (HiResGRIDMetAsia1) is the most suitable to predict the palaeoclimate for the Leoben flora. The respective results are: MAT 13.3 (±2.5)°C, WMMT 24.2 (±3.0)°C, CMMT 3.6 (±4.1)°C, GROWSEAS 7.75 (±1.3) months, GSP 140.6 (±49.7) cm, MMGSP 15.35 (±5.5) cm, 3_WET 78.5 (±23.9) cm, 3_DRY 20.5 (±10.4) cm, RH 66.9 (±7.4) %, SH 6.5 (±1.8) g/kg, ENTHALP 31.2 (±0.9) kJ/kg and MAP 169.3–191.1 cm (derived from CLAMP predictions) (Table 5).

TAPHONOMY

Some fossil taxa are represented by different organs, e.g. *Glyptostrobus* (twigs, cones, seeds), *Alnus* (leaves, female strobili, male catkins, seeds), *Quercus* (leaves, male catkins, cupules). Roots are extremely rare and only a single rhizome fragment (not in situ) and some disintegrated diaphragmas of Nymphaeaceae or Nelumbonaceae were observed. Occasionally leaves or leaflets of one fossil-taxon are found closely spaced because they fell apart only during deposition (e.g. Figs 11.5, 15.14, 15.22, 20.1). These facts point to parautochthonous deposition primarily of all of the abundant fossil-species represented by vegetative and fertile organs, but also of numerous well-preserved, rare fossil-species, e.g. Araceae (?) gen. et sp. (Fig. 6.21). Frequent

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[6] Supplementary File 6. Leaf physiognomy character scoring according to the CLAMP analysis

Table 4. Results of the Similarity Approach. Shown are the five best suited results as delivered by Drudge 1 for the Leoben assemblage (scoring variants A–C) for the IPR Similarity, Taxonomic Results (TS) and Results Mix. Hence, 15 proxies are shown for each of the scoring variants A–C. For the IPR Similarity the mathematical difference is provided, the TS is shown in percentage and the Results Mix shows the total difference. For modern vegetation unit designations see Teodoridis et al. (2020: appendix 7). The modern vegetation proxies predicted in the IPR Similarity, the Taxonomic Similarity (TS) and Results Mix are fairly similar in all three variants. They differ mainly by their ranking of the delivered vegetation units. Furthermore, the IPR Similarity indicates a closer leaf physiognomic relationship of the Leoben assemblage to European than to East Asian vegetation, while the TS and the Results Mix infer strong relations to the vegetation in China and Japan

	Modern vegetation	Mathematical difference/Taxonomic Similarity/ Total difference	Modern vegetation	Mathematical difference/Taxonomic Similarity/ Total difference	Modern vegetation	Mathematical difference/Taxonomic Similarity/ Total difference
	Variant A		Variant B		Variant C	
IPR Similarity	D030	1.7	Japan 18	1.5	F148	1.9
	F136	3.6	F148	3.4	Japan 18	1.9
	D011	3.6	F136	3.4	Japan 16	3.6
	Japan 18	3.8	D030	4.3	C041	3.6
	F026	4.6	D011	4.7	F136	4.0
Taxonomic Similarity	China 68	28.7%	China 68	31.5%	China 68	38.7%
	Japan 06	27.7%	Japan 05	29.6%	Japan 06	37.3%
	China 60	27.7%	Japan 06	29.6%	China 60	37.3%
	China 81	26.7%	China 60	28.7%	China 81	36.0%
	Japan 01	26.7%	China 81	28.7%	Japan 01	36.0%
Results Mix	China 67	81.0	Japan 01	78.5	Japan 01	71.2
	Japan 01	81.5	China 67	79.8	China 67	72.0
	China 66	81.9	China 60	81.2	China 60	73.0
	China 36	82.7	China 66	81.6	China 66	73.2
	China 60	83.5	China 61	82.8	China 58	75.5

traces of plant-insect interactions indicate that most of the leaf material was deposited in the advanced vegetation period (e.g. Figs 6.7, 7.12, 7.21, 11.8). These traces are both frequent and diverse, deserving a separate study.

Most leaf material is incompletely preserved, with potentially four-fold reasons: (1) the sediment did not split properly along the surface of plant organs; (2) the slabs broke apart during sampling; (3) diagenetic pressure fractured the specimens (e.g. Fig. 9.27; see paragraph Preservation); (4) the material was already damaged when it was deposited. The last reason would indicate some transport of the material of those taxa that are rare and poorly preserved, but it is also possible that this material was less resistant to decay than that of other taxa. Quiet sedimentation conditions are indicated by disarticulated fish skeletons. Sedimentary evidence of an elevated energy transport is limited to bedding planes with accumulations of plant debris, which are documented on very few collection specimens. Possibly such bedding planes are underrepresented in the collection material because they appeared less attractive to historical collectors. The only specimens of *Betula* seeds were discovered on such a bedding plane (Fig. 12.16, 12.17). The diversity and partly also abundance of winged seeds, samaras (*Acer*, *Alnus*, *Betula*, *Cedrelospermum*, *Craigia*, *Pinus*, *Saportaspermum*, *Tilia*, *Ulmus* and *Carpolithes* sp. A–E) and of flowers/florets and inflorescences (*Antholithes stiriacus*, male catkins of Betulaceae, Fagaceae, Pinaceae and Male catkins and florets gen. et sp. and others) indicate that aeolian transport contributed to the accumulation of the plant material.

The leaf imprints of *Alnus* and *Betula* as well as of some Lauraceae show dark spots in the axils, mainly between primary and (basal) secondary veins. Heer (1856: p. 88, pl. 94, figs 21, 23, 24) observed this phenomenon within Lauraceae (Heer´s *Cinnamomum polymorphum* representing probably *Ocotea* sp.) and Ettingshausen (1894) recognised it for leaves of former *Alnus kefersteinii* and *Fagus feroniae* (all Betulaceae, partly *Alnus julianiformis*) from Leoben. Heer (1856) concluded that these patches indicate domatia, while Ettingshausen (1894) concluded that such spots represent artefacts. In the Leoben material, own observations indicate that such dark patches are restricted to taxa in which domatia in axils of veins are known today. In modern Betulaceae, tufts of hairs in vein axils are common. Among Lauraceae, different kinds of domatia are known, as has been showcased for Lauraceae from the

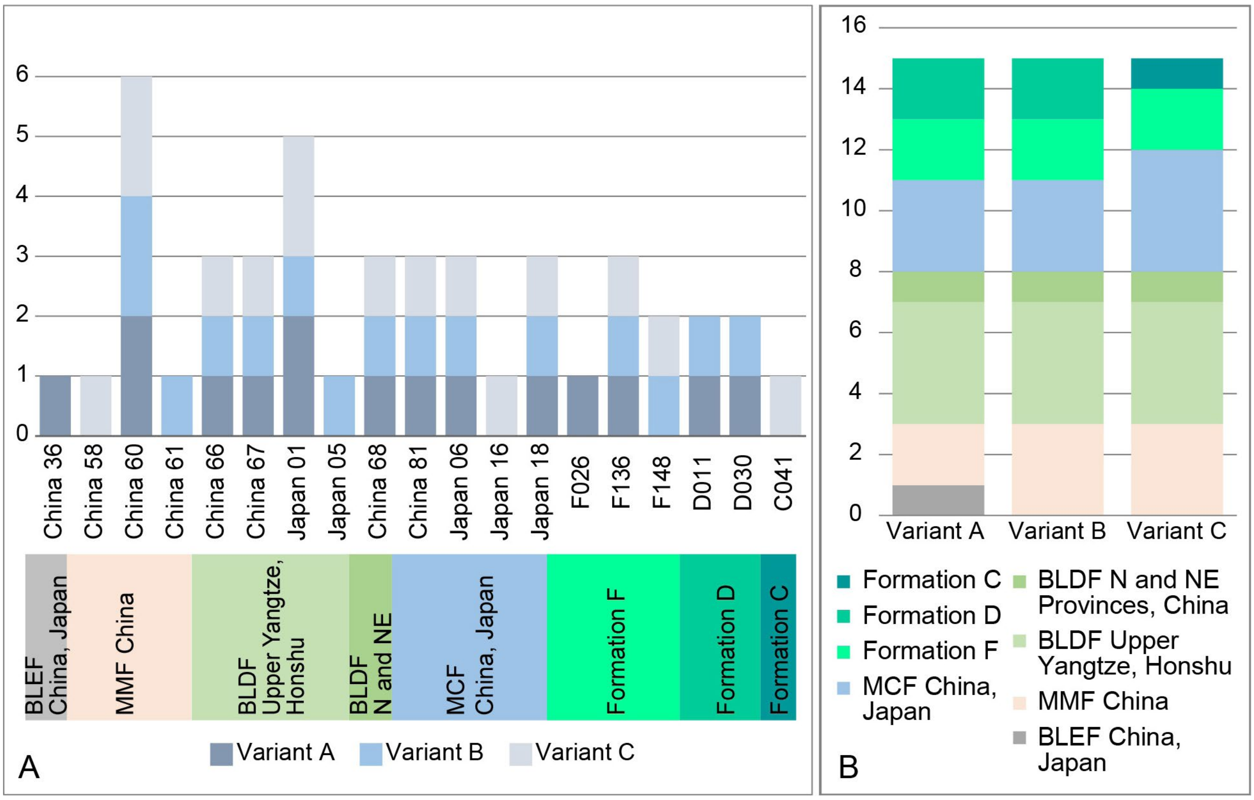

Figure 27. **A**. Modern vegetation proxies at the level of vegetation units delivered by the Similarity Approach (Drudge 1) for the Leoben flora in the tested variants A–C. Units China 60 and Japan 01 received the highest numbers of similarity hits. For more details see Table 4 and Supplementray File 4. Only those units are shown that were delivered as proxies. For the full set of vegetation units see Teodoridis et al. (2020: appendix 7); **B**. Modern vegetation proxies summarised to the higher level of vegetation formations (Europe) and vegetation types (Asia) delivered by the Similarity Approach (Drudge 1) for the Leoben flora in the tested variants A–C. The major vegetation type BLDF Upper Yangtze, Honshu received the highest number of similarity hits followed by MCF China, Japan and MMF China. For more details see Table 4 and Supplementary File 5. Only those East Asian vegetation types and European vegetation formations are shown that were delivered as proxies. For the full set of vegetation types/formations see Kovar-Eder et al. (2021, table 3)

Canary Islands (Nickol, 1998). In *Laurus azorica* (Seub.) Franco and *Ocotea foetens* (Aiton) Baill., domatia are pockets covered by hairs. In the Leoben material some leaves are preserved as part and counterpart in which only one of them (supposedly reflecting the abaxial leaf surface) shows distinct dark spots at the origin mainly (but not necessarily only) of basal secondaries (e.g. Figs 6.5, 6.6, 6.12b, 6.13, 10.10a). This fact and the occurrence restricted to fossil taxa in which domatia are known from modern representatives but lacking in other fossil taxa, lead to the conclusion that these dark patches indicate domatia in the Leoben material (see also paragraphs *Ocotea* sp., *Laurophyllum* sp. 1, *Alnus julianiformis* and further Betulaceae). One hypothesis is that the surface relief caused an increased capture of oxidised mineral substance. This result is of taxonomic and ecological value because domatia may serve as a diagnostically relevant trait and they indicate plant-animal interactions to which more attention should be paid in the fossil record.

FLORISTIC EVALUATION, PHYTOSOCIOLOGY, MODERN VEGETATION PROXIES AND PALAEOCLIMATE

FLORISTIC COMPOSITION (TABLE 6)

Based on the here presented revision (study of more than 4000 plant remains), the number of fossil-species described by Ettingshausen (1869a, 1888) has been reduced from 382 (fungi excluded) to ~175 and ~150 fusing different organs of probably one biological fossil-species. The Leoben flora is characterised by high diversity although the floristic resolution is limited by the lack of organic material, which prevents cuticular analysis. Especially prevailingly laurophyllous families such as Ericaceae, Lauraceae or Theaceae are very difficult to assess based solely on gross morphology.

In the Leoben assemblage, spore-producing, herbaceous plants are very rare and not diverse. With the exception of single remains

Table 5. Palaeoclimate estimates for Leoben, Oberdorf (Bruch and Kovar-Eder, 2004), Parschlug (Kovar-Eder et al., 2022), Mecsek Mts. (Hably, 2020) and the Cypris Formation (Teodoridis and Kvaček, 2015). Estimates for Leoben and Parschlug derived by CLAMP, estimates for Oberdorf and Mecsek Mts based on the Coexistence Approach (CA), for the Cypris Formation estimates derived by CLAMP and CA are available. The updated tool for selecting the best-suited modern CLAMP calibration dataset (Kovar-Eder et al., 2022) yielded the PhysgAsia1 dataset as best suited for Leoben, whereas following the CLAMP website (Spicer 2011–2021) the PhysgAsia2 calibration dataset is the best suited. Abbreviations: STDEV – standard deviation, MAT – Mean Annual Temperature, WMMT – Warmest Month Mean Temperature, CMMT – Coldest Month Mean Temperature, GROWSEAS – Length of the Growing Season, GSP – Growing Season Precipitation, MMGSP – Mean Monthly Growing Season Precipitation, 3_WET – Precipitation Mean during 3 Consecutive Wettest Months, 3_DRY – Precipitation Mean during 3 Consecutive Driest Months, RH – Relative Humidity; SH – Specific Humidity, ENTHAL – Enthalpy. *MAP – For CLAMP palaeoestimates, MAP has been derived by simple calculations based on 3-WET, 3-DRY, GSP and MMGSP (see paragraph Methods, Climate Leaf Analysis Multivariate Program (CLAMP))

	CLAMP calibration data set	MAT (STDEV)	WMMT (STDEV)	CMMT (STDEV)	GROW-SEAS (STDEV)	GSP (STDEV)	MMGSP (STDEV)	3_WET (STDEV)	3_DRY (STDEV)	RH (STDEV)	SH (STDEV)	ENTHAL (STDEV)	*MAP	Method applied
		°C	°C	°C	months	cm	cm	cm	cm	%	g/kg	kJ/kg	cm	
Leoben	Physg3brcAZ_GRIDMet-3brAZ (144)	12.8 (2.1)	24.1 (2.5)	2.5 (3.4)	7.35 (1.1)	175.4 (31.7)	22.9 (3.8)	99.1 (22.9)	18.2 (5.9)	64.7 (8.6)	6.15 (1.7)	31.0 (0.8)	203.7–254.6	CLAMP
Leoben	Physg3arcAZ_GRIDMe-t3arAZ (173)	12.4 (2.8)	24.6 (3.0)	0.25 (3.8)	7.2 (1.3)	180.3 (30.0)	23.6 (+3.6)	79.8 (22.1)	18.8 (5.9)	58.1 (10.5)	6.0 (1.7)	30.9 (0.8)	212.4–240.0	CLAMP
Leoben	PhysgAsia1_HiResGRID-MetAsia1 (189)	13.3 (2.5)	24.2 (3.0)	3.6 (4.1)	7.75 (1.3)	140.6 (49.7)	15.35 (5.5)	78.5 (23.9)	20.5 (10.4)	66.9 (7.4)	6.5 (1.8)	31.2 (0.9)	169.3–191.1	CLAMP
Leoben	PhysgAsia2_HiResGRID-MetAsia2 (177)	16.9 (2.3)	27.5 (2.8)	4.9 (3.6)	9.8 (1.1)	196.7 (60.6)	20.5 (6.1)	86.7 (35.8)	29.3 (9.5)	71.3 (8.4)	9.4 (1.9)	32.7 (0.9)	238.9–240.5	CLAMP
Leoben	PhysgGlobal_HiResGRID-MetGlobal (378)	12.7 (4.0)	23.0 (3.9)	2.0 (6.7)	8.3 (1.9)	114.1 (54.9)	11.3 (6.0)	60.3 (32.2)	10.1 (13.0)	71.3 (9.3)	7.0 (2.0)	31.35 (1.1)	131.4–138.3	CLAMP
Oberdorf		15.7–17.6	26.6–27.5	9.6–11.7									118.7–1322	CA
Parschlug	PhysgAsia1_HiResGRID-MetAsia1 (189)	17.1 (2.5)	27.1 (3.0)	6.4 (4.1)	9.7 (1.3)	177.7 (49.7)	17.6 (5.5)	76.6 (23.9)	27.3 (10.4)	69.6 (7.4)	9.2 (1.8)	32.7 (0.9)	209.3–218.3	CLAMP
Parschlug	PhysgAsia2_HiResGRID-MetAsia2 (177)	14.1 (2.3)	24.1 (2.8)	5.6 (3.6)	8 (1.1)	133.2 (60.6)	14.3 (6.1)	75.4 (35.8)	20.8 (9.5)	65.5 (8.4)	6.65 (1.9)	31.3 (0.9)	161.7–182.2	CLAMP
Parschlug	PhysgGlobal_HiResGRID-MetGlobal (378)	12.3 (4.0)	22.8 (3.9)	1.7 (6.7)	8.3 (1.9)	98.8 (54.9)	9.6 (6.0)	53.5 (32.2)	9.5 (13.0)	68.9 (9.3)	6.5 (2.0)	31.1 (1.1)	114.2–120.7	CLAMP
Mecsek Mts		15.6–16.6	24.7–27.9	5–6.2									82.3–135.6	CA
Cypris Fmt.	PhysgAsia1_HiResGRID-MetAsia1 (189)	13.1 (1.3)	25.1 (1.7)	2.9 (2.6)				57.4 (16.6)	13.2 (5.0)					CLAMP
Cypris Fmt.		15.7–17.0	24.9–27.5	5.6–13.3									114.6–121.3	CA

of *Osmunda parschlugiana* and *Pronephrium stiriacum*, ferns are represented by tiny fragments of sterile fronds (Pteridophyta gen. et sp.) only. A single rhizome fragment documents the presence of horsetails (*Equisetum parlatorii*). Monocotyledons are generally rare, confined to Poales, *Potamogeton* sp. (aquatic) and Araceae (?) gen. et sp. ((?) aquatic) and woody lianas *Smilax sphenophylla* and *Smilax* sp. Among Poales, "*Typha*" *latissima* and Poales gen. et sp. 1–6 are differentiated, all represented by single or very few remains of leaf or stem fragments. The specimen of Araceae (?) gen. et sp. may represent a yet unknown aquatic plant. Nymphaeaceae vel Nelumbonaceae are represented by floating leaves ("*Nelumbium*" *buchii*), a rhizome fragment and rare isolated diaphragmas. The isolated cluster of rather large stamina and single stamina possibly derive from Nymphaeaceae vel Nelumbonaceae, which is assumed based on their large size (Nymphaeaceae (?) vel Nelumbonaceae (?) gen. et sp. – stamina). Unfortunately, it was not possible to extract pollen from these findings (pers. comm. R. Zetter), so that their taxonomic assignment remains tentative.

In the Leoben assemblage the great majority of plant remains derives from woody taxa. The cycad *Ceratozamia hofmannii* (Ettingsh.) (Ettingshausen, 1887) was confirmed by Kvaček (2004), but no other remain resembling cycads was detected among the rich studied material. Conifers are rather diverse, represented by at least 8 genera among which *Glyptostrobus europaeus* and *Pinus* div. sp. are most common, represented by vegetative and fertile remains. Among Cupressoideae, *Calocedrus suleticensis* and *Tetraclinis salicornioides* are documented by a few shoot fragments, and *T. salicornioides* additionally by seeds. Shoots and cones and possibly a seed of *Sequoia abietina* do occur but are not abundant, *Taiwania* cf. *paracryptomerioides* is rare and *Amentotaxus* sp., *Cephalotaxus* vel *Torreya* sp. and *Taxus* vel *Cephalotaxus* sp. are represented by single needles or twig fragments only.

The Leoben assemblage is definitely dominated by deciduous and evergreen, woody angiosperms. Most abundant and diverse are Betulaceae (3–4 genera, ~12 fossil-species, fertile remains not counted separately) followed by Fagaceae (3 genera, 6 fossil-species, fertile remains not counted separately) and Lauraceae (8 fossil-species). Among Betulaceae, foliage of *Alnus julianiformis* is most abundant and even the most common angiosperm taxon in the Leoben assemblage as such, while *A. gaudinii*, *A. menzelii*, *A. milleri*, *A.* aff. *cecropiifolia* and A. cf. *oberdorfensis* are far less common and *Betula* sp. div., *Carpinus grandis* and *C.* vel *Ostrya* sp. are represented by single or few specimens only. Among fertile remains, two types of female cones of alder can be distinguished: *A. gracilis* and *A. kefersteinii*. The former is usually regarded to represent the fruiting cones of *A. julianiformis* leaves and the latter that of *A. gaudinii* foliage (e.g. Kvaček et al., 2004a), but an unambiguous assignment to leaf taxa is not possible for Leoben because of the occurrence of more than two alder fossil-species of leaves. Male catkins of Betulaceae do occur, but pollen preparation was successful in only one of them, showing tetra- to pentaporate pollen grains (Fig. 22.38). Besides rare leaves of *Betula*, some bracts of female cones and two-winged seeds were encountered. In contrast, the leaf records of *Carpinus* and *Ostrya* are not supported by samaras; the samara of *Carpinus* figured by Ettingshausen (1888: pl. 3, fig. 9) was not detected among the collection material. Among Fagaceae, most abundant are *Quercus rhenana* and the deciduous oak *Q. gigas*. *Trigonobalanopsis rhamnoides* (evergreen) also occurs quite frequently, whereas *Quercus drymeja* and *Q. mediterranea* are documented by very few specimens only and beech is represented by only two (but unequivocal) leaves (*Fagus deucalionis*). As for Betulaceae, no unequivocal assignment of male catkins and cupules to one or the other leaf taxa of oaks is possible. Foliage of Lauraceae are rather abundant but, except for *Daphnogene polymorpha*, *Laurophyllum* cf. *pseudoprinceps*, *Ocotea* sp. and cf. *Sassafras* sp., their diversity is difficult to assess because no cuticles are preserved. Four further fossil-species (*Laurophyllum* sp. 1–4) distinguished grossmorphologically are at least likely. Numerous lauroid leaves were classified to the family level only (see Supplementary File 2).

Leaves of *Myrica joannis* are very abundant, those of *M. lignitum* less common. Surprisingly, only a single impression of a putative fruit (*Myrica* (?) sp. – fructus) was located in the studied collection material. While *M. lignitum* is very common in many Miocene European lignite deposits, e.g. Most Formation, Cypris Formation (northern Bohemia, Early Miocene; Bůžek et al., 1992, 1996), Wackersdorf (Bavaria, Early/Middle Miocene; Knobloch and Kvaček, 1976), *M. joannis* mass occurrences are known so far only from Oberdorf (Styria, Early Miocene; Kovar-Eder, 1996) and Leoben. Further quite common leaf taxa in the Leoben assemblage are *Sloanea serratifolia* (Elaeocarpaceae) and *Laria rueminiana*. Grossmorphologically, *S. serratifolia* resembles *S. artocarpites* but that latter fossil-species is restricted to the Paleogene (Kvaček et al., 2001, 2018; Hably, 2007; Hably et al., 2007). Rich occurrences of *Laria rueminiana*, as found in Leoben, are rather rare, e.g. Most Basin (Bůžek, 1971). Leaves of *L. rueminiana*, *Saportaspermum* (seeds), and possibly *Carpolithes* sp. L represent different organs of modern *Reevesia* (Malvaceae) (Kvaček, 2006; Worobiec et al., 2010; Worobiec and Worobiec, 2020). *Saportaspermum* sp. is documented by few specimens in the Leoben assemblage, and *Carpolithes* sp. L possibly represents an undehisced capsule of *Reevesia hurnikii*.

Five fossil-species of maple leaves are distinguished, among which *Acer tricuspidatum* is the most common (but not abundant) followed by *A. integrilobum*, whereas *Acer integerrimum*, *A. palaeosaccharinum* and *A. pseudomonspessulanum* are documented by single specimens only. Maple samaras are associated, but the number of specimens is insufficient to properly differentiate the morphological variability of types.

Engelhardia orsbergensis (leaves)/*E. macroptera* (samara), *Juglans reussii*, *Juglans* sp., *Pterocarya paradisiaca*, and Juglandaceae gen. et sp. represent the Juglandaceae. Although not abundant, remains of *E. orsbergensis* are more numerous than remains of the other members of the walnut family. Very few leaves are assignable to Theaceae: *Ternstroemites diversifolius*, *T. egeriae*, and *T. stiriacus*. Magnoliaceae are represented by leaves of *Magnolia* cf. *liblarensis*. Ulmaceae proofs are restricted to few elm leaves (*Ulmus pyramidalis*) and two samaras (*Ulmus* sp.), a single foliated twig of *Cedrelospermum ulmifolium* and one winged seed (*Cedrelospermum* sp.), one twig and a single leaf of *Zelkova zelkovifolia*, and *Ulmus* (?) *prisca*. The latter taxon is represented by several leaf remains with quite characteristic marginal serration, but the generic assignment is nevertheless uncertain. Salicaceae are documented by very few leaves of *Salix varians*, *Salix* sp. and very few and fragmentary leaves of *Populus latior*, but no fertile remains of these genera were encountered.

Other taxa represented both by leaf and infructescences are *Fraxinus* (*Fraxinus bilinica*, leaf, *Fraxinus macroptera*, samara) and possibly *Diospyros brachysepala*. Taxa represented by infructescences only are *Craigia bronnii* (several specimens), and single remains of *Leguminocarpon* sp., *Nyssa* sp., cf. *Symplocos* sp., *Tilia* sp. (involucrum), and Vaccinioideae gen. et sp. The latter finding is a fragmentary racemose infructescence with three capsules.

Clematis oligoneure, *Parthenocissus rhombifolia* and *Vitis stricta* probably represent dicotyledonous lianas in addition to *Smilax* (see above). Further taxa, many of them represented by single or few specimens only, are *Ailanthus* (?) *apollinis*, *Berchemia* (?) sp., cf. *Cornus* sp., *Leguminophyllum* sp. 1–7, *Sambucus ettingshausenii*, *Sorbus* (?) sp., Styracaceae (?) gen. et sp., *Toxicodendron melaenum*, Rhamnaceae vel Cornaceae gen. et sp., and taxa of uncertain systematic position such as *Antholithes stiriacus*, *“Apocynophyllum” hunteriaeforme*, *“Cassia” lignitum*, *“Celastrus” myrtillifolius*, *“Corylus” palaeoavellana*, *“Cistus” palaeolaburnum*, *Dicotylophyllum* sp. A–R, *“Dryandroides” grevilleaefolia*, *“Juglans” parschlugiana*, *“Rhus” appendiculata*. Unfortunately, additional remains of flowers, inflorescences, bud scales and *Carpolithes* sp. A–N cannot be assigned further. Finally, the scarcity of legumes in the Leoben assemblage is remarkable.

Although most of the original material of Ettingshausen’s studies (1869a, 1888) has been located, it is important to mention that some quite remarkable specimens were not found. This concerns, among others, *Quercus cruciata* (Ettingshausen, 1888: pl. 3, fig. 14, (fig. 15 stems from Radoboj)), *Asterocalyx stiriacus* (ibidem, pl. 3, fig. 4) representing *Smilax*, *Embothrium stiriacum* (ibidem, pl. 4, fig. 32), and *Porana oeningensis* (ibidem, pl. 9, fig. 19) probably representing *Chaneya*.

The Leoben flora represents a key assemblage of the “Florenkomplex Langenau-Leoben” (Mai, 1995). That author listed *Calamus daemonorops* (Unger) Chandler and *Sabal major* (Unger) Heer as so-called Mediterranean (“eumesogäische”) xerophytic elements for Leoben. However, neither xerophytic elements nor

Table 6. The Leoben assemblage compared to the floras of Oberdorf (Kovar-Eder et al., 2001b), Parschlug (Kovar-Eder et al., 2004, 2022), Mecsek region (Hably, 2020) and the Cypris Formation (Bůžek et al., 1996). Abundances: A – 1 specimen, B – 2–4 specimens, C – 5–9 specimens, D – 10–19 specimens, E ≥ 20 specimens. Note that the position of "(?)" is applied here as for the taxa described from the Leoben flora, i.e. behind the genus name – referring to the genus name, behind the species name – referring to the species name, in front of the genus name – referring to the taxon as such (see also paragraph Methods)

Order	Taxa Leoben	Leoben abundance	Oberdorf	Parschlug	Mecsek region	Cypris Formation
Charales			*Lychnothamnus* sp.			*"Chara" neogenica*
	Muscites sp.	A	Bryophyta gen. et sp.			
Selaginellales			*Selaginella* sp. div.			
Equisetales	*Equisetum parlatorii*	A			X	
Polypodiidae	*Osmunda parschlugiana*	B	X	X		*Osmunda* sp.
	Pronephrium stiriacum	A		X		X
	Pteridophyta gen. et sp.	B	Polypodiaceae gen. et sp.	*Adiantum renatum*, *Salvinia* cf. *mildeana*	*Woodwardia muensteriana*, Polypodiaceae, *Salvinia* (?) sp.	*Lygodium gaudinii*, *Salvinia* sp., Polypodiaceae
Cycadales	*Ceratozamia hofmannii*	A				
Pinales	*Pinus* sp. – two-needled fascicles	D		X	X	*P. hepios*
	Pinus sp. – 4 (?) 5-needled fascicles	C		*Pinus* sp. div.	*Pinus* sp. 3-needled fascicle, *Pinus* sp. seed, *Abies* sp.	*P. rigios*, *P.* cf. *saturni*, *Pinus* sp. (catkins, cones, seeds)
	Pinus sp. – cluster of needles	B				
	Pinus sp. – male catkins	D				
	Pinus sp. – winged seeds, isolated wings	D				
	Pinus cortesii	A				
	Pinus sp., cones	C				
			Pinaceae gen. et sp.	*Cathaya* (?) sp.		cf. *Cathaya roseltii*
Cupressales	*Glyptostrobus europaeus*	E	X	X	X	X
	Tetraclinis salicornioides	C	X		X	X
	Calocedrus suleticensis	A(B)		*Cupressus* (?) sp.	Cupressaceae gen. et sp.	*Chamaecyparis* (?) sp.
	Sequoia abietina	C	X			
	Taiwania cf. *paracryptomerioides*	B				
	Amentotaxus sp.	A				
	Cephalotaxus vel *Torreya* sp.	A	*Cephalotaxus miocenica*, *C. europaea* (?)			
	Taxus vel *Cephalotaxus* sp.	A	*Taxus* sp.			
Nymphaeales	*"Nelumbium" buchii*	D	*Irtyshenia* cf. *lusatica*			*Nymphaea szaferi*, Nymphaeaceae gen. et sp.
	Nymphaeaceae vel Nelumbonaceae gen. et sp.	B				
	Nymphaeaceae (?) vel Nelumbonaceae (?) gen. et sp., stamina	B				
Austrobaileyales						*Schisandra* sp.
Magnoliales	*Magnolia* cf. *liblarensis*	C	*M. liblarensis*, *M. burseracea*, *M.* (former *Manglietia*) *germanica*, *M.* sp.		cf. *Magnolia* sp.	*M. kristinae*, *M. burseracea*
Laurales	*Daphnogene polymorpha*	E	X	X	*D. cinnamomifolia*, *D.* sp.	X
	Ocotea sp.	C				*O. hradekense*
	cf. *Sassafras* sp.	A				X
	Laurophyllum cf. *pseudoprinceps*	C	*L. pseudoprinceps*			*L. pseudoprinceps*
	Laurophyllum sp. 1	C	*Laurus abchasica*, *Laurophyllum markvarticense*, *L. pseudovillense*, *L. rugatum*, *"Litsea" sonntagii*	*L.* sp.	*L. markvarticense*, *L.* sp., *Laurocarpum* sp.	*Laurus abchasica*, *Laurophyllum markvarticense*, *L. medimontanum*, *L. nechranicense*, *L. rugatum*, *L.* sp.
	Laurophyllum sp. 2	C				
	Laurophyllum sp. 3	C				
	Laurophyllum sp. 4	B				
Piperales			*Saururus bilobatus*			
Alismatales	Araceae (?) gen. et sp.	A	Araceae gen. et sp.			
	Potamogeton sp.	A	*Potamogeton* spp.			X
			Stratiotes kaltennordheimensis, *S.* sp.			*Stratiotes* sp., *Limnocarpus longipetiolatus*, *L. medardii*

Table 6. Continued

Order	Taxa Leoben	Leoben abundance	Oberdorf	Parschlug	Mecsek region	Cypris Formation
Liliales	*Smilax sphenophylla*	A		*Smilax sphenophylla* (formerly *Mahonia (?) sphenophylla)*, *S. sagittifera*	*Smilax* cf. *weberi*, *Cladyocarya* sp.	*Smilax sagittifera*
	Smilax sp.	C				
Arecales					*Palmacites* sp.	
Poales	*“Typha“ latissima*	C	cf. Typha sp., *Scirpus* sp., *Dulichium* vel *Scirpus* sp., cf. *Dulichium* sp., *Carex* div. sp., Cyperaceae gen. et sp., *Sparganium haentzschelii*, *S.* sp., *Urospathites dalgasii*, *U.* cf. *dalgasii*, *U.* cf. *visimense*, *U.* sp.	Monocotyledoneae gen. et sp.	Monocotyledonae gen. et sp.	*Cladium* sp., *Cladiocarya chomutovensis*, *C. trebovensis*, *C.* cf. *lusatica*, *Glumophyllum* sp. div., Monocotyledoneae gen. et sp. div.
	Poales gen. et sp. 1	A				
	Poales gen. et sp. 2	A				
	Poales gen. et sp. 3	A				
	Poales gen. et sp. 4	A				
	Poales gen. et sp. 5	A				
	Poales gen. et sp. 6	A				
Ceratophyllales			*Ceratophyllum* spp.			
Ranunculales	*Clematis oligoneure*	A			*Clematis csabae*	
	Berberis mahonioides	A		*Berberis teutonica*, *B.* (?) *ambigua*	*Berberis andreanszkyi*, *Mahonia* sp.	
	Berberis cf. *teutonica*	C				
			Ranunculus sp., *Sinomenium militzeri*			
Proteales	(?) *Platanus neptuni*	B		*Platanus leucophylla*		*Platanus neptuni*
			Meliosma wetteraviensis, *M. pliocenica*, *M. miessleri*, *M.* sp., *Sabia europaea*			*Meliosma pliocenica*
Buxales				*Buxus* cf. *egeriana*	*Buxus* sp.	*Buxus egeriana*
Saxifragales			*Cercidiphyllum crenatum*, *Distylium fergusonii*, *D. uralense*, *Liquidambar* sp., *Parrotia pristina*, Hamamelidaceae gen. et sp.	*Liquidambar europaea*	*Liquidambar europaea*	*Cercidiphyllum crenatum*, *Distylium fergusonii*, *Liquidambar europaea*, cf. *L.* sp.
			Proserpinaca sp.			
Vitales	*Parthenocissus rhombifolia*	A	*Parthenocissus britannica*, *P.* sp., *Vitis globosa*, *V.* cf. *teutonica*, *V.* sp., *Ampelopsis malviformis*, *A. rotundata*, *A.* sp., *Tetrastigma* cf. *lobata*, *T.* cf. *chandleri*, *T.* sp.			*Parthenocissus* sp., *Tetrastigma* sp., cf. *Cayratia* sp., *Ampelopsis* cf. *rotundatoides*
	Vitis stricta	A				
Celastrales					Celastraceae gen. et sp.	
Oxidales	*Sloanea serratifolia*	E				
Malphigiales	*Populus latior*	C		X, *Populus* sp., fructus	*Populus populina*, *P. zaddachii*, *P. baslamoides*, *Populus* sp. catkin	X
	Salix varians	B	X			
	Salix sp.	C	X			
			Poliothyrsis eurorimosa			
			Viola sp.			
Fabales	cf. *Leguminosites palaeogaeus*	A		X	X	*Podocarpium podocarpum*, Fabaceae gen. et sp. div.
	Leguminophyllum sp. 1	A		*“Acacia” parschlugiana*, *Podocarpium podocarpum*, *Phaseolites securidacus*, *Leguminosites* div. sp., *Leguminophyll.* sp. A–J	Leguminosae gen. et sp., *Acacia parschlugiana*, *Podocarpium podocarpum*, *Leguminocarpum Mecsekense*, cf. *Gleditsia* sp.	
	Leguminophyllum sp. 2	A				
	Leguminophyllum sp. 3	B				
	Leguminophyllum sp. 4	A				
	Leguminophyllum sp. 5	B				
	Leguminophyllum sp. 6	A				
	Leguminophyllum sp. 7	B				

Table 6. Continued

Order	Taxa Leoben	Leoben abundance	Oberdorf	Parschlug	Mecsek region	Cypris Formation
Rosales	*Berchemia* (?) sp.	A		*B. multinervis*, *Paliurus tiliifolius*, *P. favonii*	*B. multinervis*, *Paliurus favonii*, *Ziziphus paradisiaca*	*Ziziphus paradisiaca*
	Sorbus (?) sp.	A	*Prunus* sp., *Rubus* sp.	cf. *Rosa* sp., *Prinsepia serra*	*Rosa* sp., cf. *Prinsepia serra*, Rosaceae gen. et sp.	cf. *Prunus* sp.
	Cedrelospermum ulmifolium	A		X	*C. flichei*	
	Cedrelospermum aquense	A		X	X	*C. leptospermum*
	Zelkova zelkovifolia	B	X, *Zelkova* sp.	X	X	X
	Ulmus pyramidalis	C	*Ulmus* (?) sp.	*U. plurinervia*, *U. parschlugiana*	*Ulmus braunii*, *U.* div. sp., Ulmaceae gen. et sp.	*Ulmus* sp., *Celtis* cf. *lacunosa*
	Ulmus sp.	B				
	Ulmus (?) *prisca*	D				
			Celtis lacunosa, *Gironniera verrucata*, *G. neglecta*, Moraceae			
Fagales	*Alnus gaudinii*	C		X		X
	Alnus julianiformis	E		X		*A.* cf. *julianiformis*
	Alnus gracilis	C				*Alnus* sp.
	Alnus kefersteinii	B				
	Alnus menzelii	C				
	Alnus milleri	D				
	Alnus aff. *cecropiifolia*	D				
	Alnus cf. *oberdorfensis*	C	*A. oberdorfensis*			
	Alnus sp. – leaves	C	X			
	Alnus sp. – winged seeds	B				
	Betula similis	C				*Betula* sp.
	Betula sp. 1 – leaf	A				
	Betula sp. 2 – leaf	A				
	Betula sp. – bracts	B				
	Betula sp. – winged seeds	B		*B.* cf. *dryadum*		X
	Carpinus grandis	B	*Carpinus* sp.			
	Carpinus vel *Ostrya* sp.	A	X		*Ostrya* sp.	
	Betulaceae gen. et sp., catkins	D				
	Fagus deucalionis	B	*Fagus* sp., *F.* cf. *deucalionis*	*Fagus* sp.	*Fagus* sp.	
	Quercus drymeja	C		X	X	*Q.* cf. d*rymeja*
	Quercus gigas	E				
	Quercus mediterranea	B		*X*		
	Quercus rhenana	E	X			*X*
	Quercus sp. 1 – cupule	B				
	Quercus sp. 2 – cupule	A				
	Trigonobalanopsis rhamnoides	E	*T. rhamnoides/exacantha*			*T. rhamnoides/ exacantha*
	Fagaceae gen. et sp., male catkins	C	*"Castanopsis" bavarica*, *C. salinarum*	*Quercus zoroastri*	*Quercus kubinyii*	*Quercus kubinyii*
	Myrica lignitum	C		X	X	X
	Myrica joannis	E	X	*M. oehningensis*		*Myrica vindobonensis*, *M.* cf. *minima*, *Comptonia acutiloba*, *C. srodoniowae*
	Myrica (?) sp., fructus	A	*Myrica* sp., *M. boveyana* et/vel *M. ceriferiformoides*, *M.* spp.	X		
	Engelhardia macroptera	A		X	X	X
	Engelhardia orsbergensis	D		X	X	X
	Juglans reussii	C			*Carya serrifolia*, Juglandaceae gen. et sp. div.	
	Juglans sp.	A				
	Pterocarya paradisiaca	B	*Pterocarya* spp.			cf. *Pterocarya* sp.
	Juglandaceae gen. et sp.	A	*Carya ventricosa*, *Cyclocarya* (?) sp.			*Carya* sp., *Cyclocarya nucifera*
Myrtales			*Decodon gibbosus*, *Decodon* spp.			*Decodon globosus*
Crossosomatales			*Turpinia ettingshausenii*, *Staphylea bessarabica*, *Staphylea* sp.			

Table 6. Continued

Order	Taxa Leoben	Leoben abundance	Oberdorf	Parschlug	Mecsek region	Cypris Formation
Sapindales	*Toxicodendron melaenum*	B		*T. melaenum*		
				Cotinus (?) *aizoon*	*Cotinus* sp., *Rhus* sp.	
	Acer pseudomonspessulanum	A		X	*Acer* sp.	*A.* cf. *pseudomonspessulanum*
	Acer tricuspidatum	D	X	X		X
	Acer integrilobum	C	X	X		*A.* cf. *integrilobum*
	Acer integerrimum	B	*A. integerrimum* (?)			*A.* cf. *integerrimum*
	Acer palaeosaccharinum	A				*A. angustilobum*, *Acer* sp., cf. *Sapindus falcifolius*
	Acer sp. – leaf	A				
	Acer sp. div. – fructus	D	*Acer* spp.	X		
	Ailanthus (?) *apollinis*	B		*Ailanthus pythii*, *A. confucii*	*A. confucii*, *A. Mecsekensis*	*Ailanthus confucii*
			Toddalia latisiliquata, *T. latisiliquata* vel *naviculiformis*, *Zanthoxylum giganteum*, *Sapindoidea margaritifera*, *Fagaropsis* (?) *koeflachensis*			*Toddalia maii*, *Zanthoxylum* cf. *ailanthiforme*
Malvales	*Craigia bronnii*	C		X	X	X
	Tilia longebracteata	B		X	*Tilia* sp.	*Tilia* sp.
	Laria rueminiana	E				
	Saportaspermum sp.	B		X		
					Sterculia sp., *Daphne oeningensis*	
Santalales			*Viscum morlotii*, *V.* et/vel *Loranthus* sp.			
Caryophyllales			*Moehringia* spp., Caryophyllaceae gen. et sp.		Polygonaceae gen. et sp.	
Cornales	cf. *Cornus* sp.	B	*Cornus* vel *Swida* sp., *Swida* cf. *bugloviana*, *S.* cf. *gorbunovii*, *S.* cf. *discimontana*, *S.* spp.			*Swida bugloviana*
	Nyssa cf. *haidingeri*	B	*Nyssa ornithobroma*, *N.* sp.		*Nyssa gyoergyi*, *N. gergoei*, *Nyssa* sp. div.	*Nyssa ornithobroma*
	Nyssa sp.	A				
			Eomastixia holzapfelii vel *E. saxonica*, *Mastixia amygdaliformis*, *M.* cf. *lusatica*			*Mastixia amygdaliformis*
Cornales vel Rosales	Cornaceae vel Rhamnaceae gen. et sp.	C				
Ericales	*Diospyros brachysepala*	B			*Diospyros* ? *microcalyx*	
	Vaccinioideae gen. et sp.	A	Ericaceae, Arbutoideae gen. et sp.		*Arbutus* sp.	
	Styracaceae (?) gen. et sp.	B				*Sinojackia* sp.
	cf. *Symplocos* sp.	A	*Symplocos lignitarum*, *S. poppeana*, *S. salzhausensis*, *S.* cf. *pseudogregaria*, *S.* cf. *pseudoschereri*, *S.* cf. *schereri*, *S.* spp.			*Symplocos lignitarum*, *S. minutula*, *S. ludwigii*, *Sphenotheca* cf. *incurva*
	Ternstroemites diversifolius	A	*Cleyera* (?) *schilcheriana*, *C.* (?) *boveyana*, *Eurya stigmosa*, *Gordonia* (?) *oberdorfensis*, *Ternstroemites reniformis*, *T. waltheri*	cf. *Gordonia oberdorfensis*, *Ternstroemites pereger*	*Ternstroemites pereger*, *Gordonia* sp.	*Gordonia hradekensis*, *Ternstroemites sequoioides*
	Ternstroemites egeriae	A				
	Ternstroemites stiriacus	B				
	Theaceae (?) vel Ericaceae (?) gen. et sp.	B				
			Actinidia sp., cf. *Naumburgia* sp.			

Table 6. Continued

Order	Taxa Leoben	Leoben abundance	Oberdorf	Parschlug	Mecsek region	Cypris Formation
Gentianales			*Cephalanthus* cf. *pusillus*	*Nerium* sp.		
Solanales			cf. *Hyoscyamus* spp., Solanaceae gen. et sp.			
Lamiales	*Fraxinus bilinica*	A	*F. ungeri*			*Fraxinus* sp.
	Fraxinus macroptera	B	*F.* sp.	*Fraxinus primigenia*	cf. *Fraxinus* sp.	
Aquifoliales			*Ilex saxonica*, *I. ahrensii*, *Ilex* sp.			
Apiales			*Pentapanax tertiarius*, *Aralia pusilla*, *A.* aff. *crassa*, *A.* cf. *lucida*, Araliaceae gen. et sp., *Umbelliferopsis molassicus*, Apiaceae gen. et sp.			
Dipsacales	*Sambucus ettingshausenii*	A	*Sambucus* sp.			
			Torricellia bonesii			
					cf. *Hedera* sp.	*Hedera* sp.
Incertae sedis	*“Apocynophyllum” hunteriaeforme*	B	*Dicotylophyllum dieteri*	*“Celastrus” europaea*, *“Cornus” ferox*, *“Quercus” daphnes*, *Cypselites* sp., ? *Chaneya* sp., *Dicotylophyllum* sp. 1, 3–6, D. sp. A–JJ	*Dicotylophyllum* sp. 1–10, *“Ilex” falsani*, Ceratophyllaceae?	cf. *Viburnum atlanticum*, *Dicotylophyllum* sp. 1–3
	“Cassia” lignitum	A				
	“Celastrus” myrtillifolius	B				
	“Corylus” palaeoavellana	B				
	“Cytisus” palaeolaburnum	A				
	Dicotylophyllum sp. A	B				
	Dicotylophyllum sp. B	B				
	Dicotylophyllum sp. C	B				
	Dicotylophyllum sp. D	A				
	Dicotylophyllum sp. E	B				
	Dicotylophyllum sp. F	A				
	Dicotylophyllum sp. G	A				
	Dicotylophyllum sp. H	A				
	Dicotylophyllum sp. I	A				
	Dicotylophyllum sp. J	A				
	Dicotylophyllum sp. K	A				
	Dicotylophyllum sp. L	A				
	Dicotylophyllum sp. M	A				
	Dicotylophyllum sp. N	A				
	Dicotylophyllum sp. O	A				
	Dicotylophyllum sp. P	A				
	Dicotylophyllum sp. Q	B				
	Dicotylophyllum sp. R	A				
	“Dryandroides” grevilleaefolia	A				
	“Juglans” parschlugiana	A		X		
	“Rhus” appendiculata	A				
	Antholithes stiriacus	B		X	X	
	Male catkins and florets gen. et sp.	C				
	Flower gen. et sp.	A			*Carpolithes* 1–6	*Hartziella* cf. *rosenkjaeri*, *Carpolithes* sp. 1–2
	Carpolithes sp. A	B				
	Carpolithes sp. B	A				
	Carpolithes sp. C	A				
	Carpolithes sp. D	B				
	Carpolithes sp. E	A				
	Carpolithes sp. F	A				
	Carpolithes sp. G	A				
	Carpolithes sp. H	A				
	Carpolithes sp. I	A				
	Carpolithes sp. J	B				
	Carpolithes sp. K	A				
	Carpolithes sp. L	A				
	Carpolithes sp. M	B				
	Carpolithes sp. N	A				

palm remains were encountered in the present revision of the Leoben assemblage (see paragraph *Carpolithes* sp. L).

VEGETATION RECONSTRUCTION

In the Leoben Basin the sapropelic, up to 18-m-thick shales superimposing the coal seam represent lacustric sediments, indicating the drowning of the lignite-forming, raised mire due to rapid basin subsidence (Gruber and Sachsenhofer, 2001). The plant-bearing layers from which all collection material derives occur near the base of these shales, i.e. from the beginning of the drowning stage (see paragraph Geology and Stratigraphy). Plant material from different stages of basin development and different sediment facies is not available. Consequently, the assignment of taxa to the habitats from the basin to the upland is restricted to the autecology of modern relatives, to the observation of the fossil-species in the Leoben assemblage regarding preservation, abundance, cooccurrence of vegetative and fertile organs, as well as to occurrences at other sites. A detailed reconstruction of the ecosystem development as provided for the Oberdorf Basin (Styria; Kovar-Eder et al., 2001b; see below) or the Most Basin (northern Bohemia; Kvaček et al., 2004b) is, therefore, not possible.

Representatives of a floating-leaf plant zone are *Potamogeton* and Nymphaeaceae vel Nelumbonaceae (leaves of "*Nelumbium*" *buchii*, rhizome and isolated diaphragmas, possibly a cluster of stamina and isolated stamina) and Araceae (?) gen. et sp. Ferns (*Osmunda parschlugiana*, *Pronephrium stiriacum*, Pteridophyta gen. et sp.) and Poales foliage ("*Typha*" *latissima*, Poales gen. et sp. 1–6), which are both scarce and fragmentarily preserved, indicate undergrowth of swamp vegetation and reed and sedges at the lake margin.

Woody taxa characteristic of swampy habitats are, above all, *Glyptostrobus europaeus*, *Alnus julianiformis*, *Myrica joannis* and *Quercus rhenana*, all of them abundant in the Leoben assemblage. The abundance and good preservational state of the large leaves of *Quercus gigas* imply that this oak also favoured the swampy environment at the initial state of the drowning mire. The numerous remains of *Pinus* sp. – two-needled fascicles, male catkins, seeds and female cones – indicate that a pine also favoured this environment. The ecological tolerance of *Daphnogene polymorpha* and *Laurophyllum* cf. *pseudoprinceps* was probably wide because both taxa are known from very different sedimentological settings, among them also coal-bearing sequences. Their leaves are common in the Leoben assemblage and therefore they probably occurred in the swampy environment of the drowning mire and outside as well. The leaves of *Laria rueminiana* (Malvaceae) and *Sloanea serratifolia* (Elaeocarpaceae) are numerous and well preserved, providing evidence of growing close to the depositional site. These taxa are therefore inferred to have favoured a swamp environment. Further taxa characteristic of swamp habitats are *Alnus menzelii*, *Magnolia* cf. *liblarensis*, *Myrica lignitum* and *Nyssa*, which are represented by fewer remains than the aforementioned taxa. The fragmentarily preserved infructescence Vaccinioideae gen. et sp. (Ericaceae) may represent a shrub in this environment. The differentiation of Ericaceae foliage is equivocal in the Leoben assemblage (Theaceae (?) vel Ericaceae (?) gen. et sp.) because cuticles are not preserved. Parts of compound leaves partly still organically connected of *Engelhardia orsbergensis*, *Sambucus ettingshausenii* and "*Cytisus*" *palaeolaburnum* also point to very little transport of these remains prior to sedimentation (Figs 15.14, 15.22, 20.1, 20.12).

The vegetation near the lake margin and along streams outside the swampy habitats is assumed to be diverse, including the conifer *Sequoia abietina* and woody, mainly deciduous and to a minor extent evergreen angiosperms: Betulaceae (*Alnus gaudinii*, *A. milleri*, *Betula similis*, *Betula* sp., *Carpinus grandis*), Fagaceae (*Trigonobalanopsis rhamnoides*), Juglandaceae (*Engelhardia orsbergensis*/*E. macroptera*, *Juglans reussii*, *Juglans* sp., *Pterocarya paradisiaca*), Lauraceae (*Daphnogene polymorpha*, *Ocotea* sp.), Salicaceae (*Populus latior*, *Salix varians*, *S.* sp.), Sapindaceae (*Acer integrilobum*, *A. tricuspidatum*), Ulmaceae (*Ulmus pyramidalis*, *Ulmus* (?) *prisca*, *Zelkova zelkovifolia*, *Cedrelospermum ulmifolium*/*C. aquense*), Cornaceae vel Rhamnaceae gen. et sp.. Of these fossil-species, only *Trigonobalanopsis rhamnoides*, *Daphnogene polymorpha* and *Ocotea* sp. were non-deciduous.

The forests around the lake at Leoben and along streams gradually segued into mesophytic hinterland forests composed of conifers, the rare cycad *Ceratozamia hofmannii* in the undergrowth, as well as both deciduous and evergreen, woody angiosperms. In addition to fossil-species listed in the context of the forests near the lake margin and along streams, the following taxa likely occurred there: *Amentotaxus* sp., *Calocedrus suleticensis*, *Cephalotaxus* vel *Torreya* sp., *Pinus* sp. – 4 (?) 5-needled fascicles, *Taiwania* cf. *paracryptomerioides* and *Tetraclinis salicornioides* – all conifers – and the angiosperms Berberidaceae (*Berberis mahonioides*), Betulaceae (*Carpinus* vel *Ostrya* sp.), Cornaceae (cf. *Cornus* sp.), Ebenaceae (*Diospyros brachysepala*), Fagaceae (*Fagus deucalionis*, *Quercus drymeja*, *Q. mediterranea*), Lauraceae (cf. *Sassafras* sp.), legumes (*Leguminocarpon* sp., *Leguminophyllum* sp. div.), Malvaceae (*Tilia* sp., *Craigia bronnii*), Oleaceae (*Fraxinus bilinica*, *F. macroptera*), Rhamnaceae (*Berchemia* (?) sp.), Sapindaceae (*Acer integerrimum*, *A. palaeosaccharinum*, *A. pseudomonspessulanum*), Simaroubaceae (*Ailanthus* (?) *apollinis*), Theaceae (*Ternstroemites diversifolius*, *T. egeriae*, *T. stiriacus*). The lianas *Clematis oligoneure*, *Parthenocissus rhombifolia*, *Smilax sphenophylla*, *Smilax* sp., *Vitis stricta*, and *Toxicodendron melaenum*, represented by single specimens only, may have flourished in the forests of the lake surroundings and the hinterland. Further taxa are of unknown systematic affinity, preserved by single or very few and often poorly preserved specimens, indicating that they likely did not grow very close to the depositional site.

The results of the IPR vegetation analysis indicate the ecotone between mixed mesophytic and broad-leaved evergreen forest as the most likely zonal vegetation type for the Leoben flora (Table 3).

MODERN VEGETATION PROXIES

The modern vegetation proxies predicted in the IPR Similarity, the Taxonomic Similarity (TS) and Results Mix are fairly similar in all three variants (Table 4). They differ mainly by their ranking of the delivered vegetation units. The IPR Similarity indicates a closer leaf physiognomic relationship of the Leoben assemblage to European than to East Asian vegetation, while the TS and the Results Mix infer strong relations to the vegetation in China and Japan. This pattern is not surprising because it was already detected in the study of the Paleogene and Neogene European plant record (Kovar-Eder et al., 2021). The close relationship to East Asia in the TS and the Results Mix compared to the much lower one to Europe has two explanations: the floristic depletion of the modern European vegetation due to the repeated changes between warm and cold periods of the Quaternary Ice Age, and the west/east oriented orogenes in Europe hampering the north-south migration of plants, whereas the effects on the East Asian flora was minor.

The BLDF Upper Yangtze, Honshu (sensu Kovar-Eder et al., 2021), which received highest number of scores of all major vegetation types (East Asia) and vegetation formations (Europe) (Fig. 27A, B), include vegetation units in Sichuan (evergreen oak and *Schima* forests, evergreen oak and deciduous hardwood forests, mixed deciduous forests in mountain regions), broad-leaved deciduous forests of western Hubei (at 1000–1100 m) and eastern Guizhou (at 1700–1850 m) (Wang, 1961) and in northwestern most Yunnan on the Meili Snow Mountains broad-leaved deciduous forests (at altitudes >2000 m). In Japan, this includes broad-leaved forests in Shirakami Sanchi (Shirakami Mountains) on Honshu on the northern part of the Sea of Japan side at low elevations and on Mt. Fuji on the Pacific side of Honshu at 600–1800 m (Teodoridis et al., 2011a).

The Broad-leaved Deciduous Forest – *Lindera membranacea-Fagus crenata* comm. of Shirakami Sanchi (unit Japan 01) is the second-placed proxy unit following unit China 60 (Fig. 27A, Supplementary File 4). The Shirakami Sanchi region belongs to the cool-temperate deciduous broad-leaved forest region in Japan. The climate is characterised by precipitation maxima in winter and heavy snowfall in the mountains. The snow cover enables evergreen woody taxa to survive in the shrub layer. The *Lindera membranacea-Fagus crenata* comm. is a major community in the *Fagus crenata* area (Hukushima et al., 1995). It includes more than 80 woody taxa of which *Cephalotaxus harringtonia* (Knight ex J. Forbes) K. Koch and *Pinus parviflora* var. *pentaphylla* (Mayr) A. Henry are the only conifers. Deciduous angiosperms are most diverse and evergreen taxa occur in the shrub layer (*Aucuba japonica* var. *borealis* Miyabe et Kudô, *Daphne miyabeana* Makino, *Daphniphyllum macropodum* var. *humile* (Maxim.

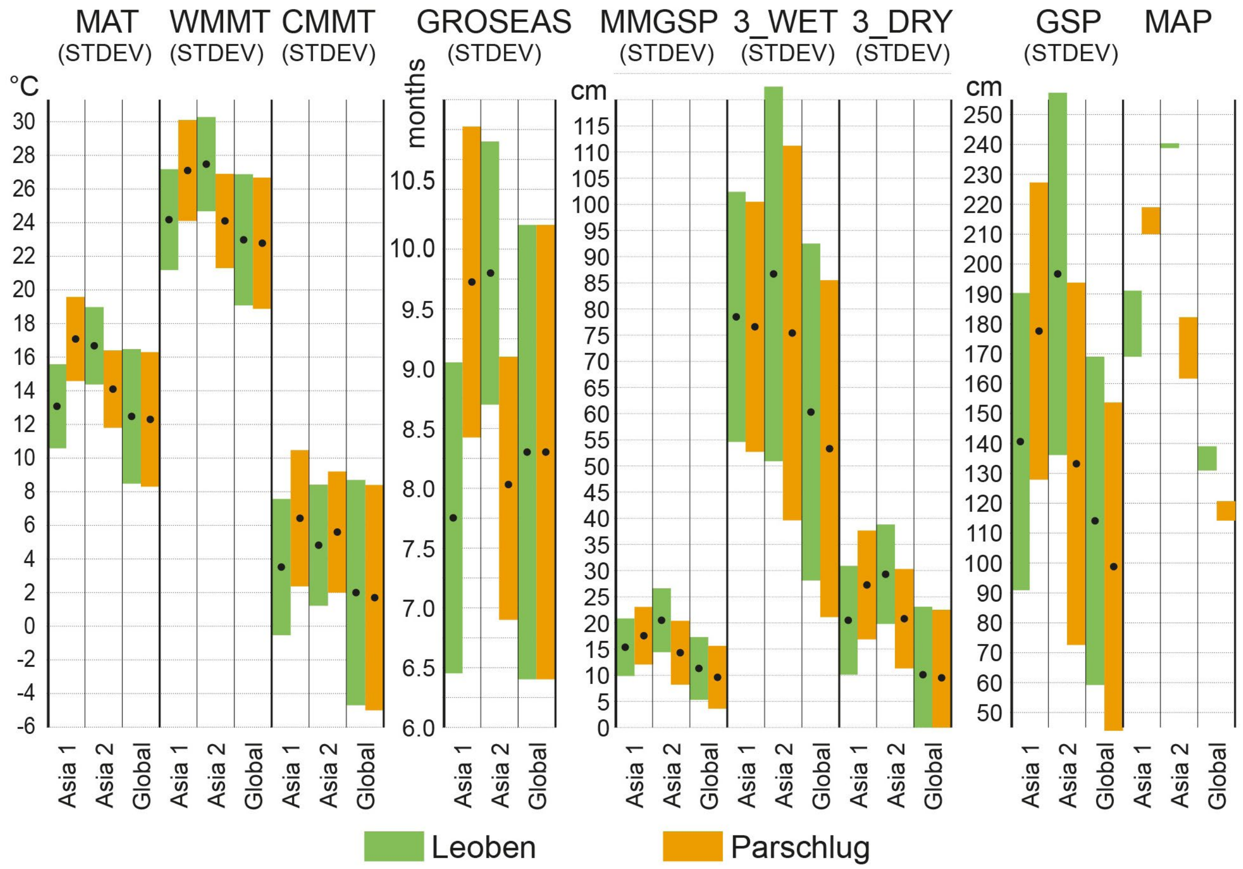

Figure 28. Palaeoclimate estimates including Standard Deviations (STDEV) for the floras of Leoben and Parschlug derived by CLAMP. For Leoben, the choice of the best suited calibration dataset is equivocal. Therefore, the selected palaeoclimate estimates are shown based on the datasets PhysgAsia1 (Asia 1), PhysgAsia2 (Asia 2) and Global378 (Global). *MAP – For CLAMP palaeoestimates, MAP has been derived by simple calculations based on 3-WET, 3-DRY, GSP and MMGSP (see paragraph Methods, Climate Leaf Analysis Multivariate Program (CLAMP)). CLAMP abbreviations as in Table 5

ex Franch. et Sav.) K. Rosenthal, *Epigaea asiatica* Maxim., *Euonymus fortunei* var. *radicans* (Miq.) Rehder, *Ilex leucoclada* (Maxim.) Makino, *Rhododendron brachycarpum*, *Skimmia japonica* Thunb.). The deciduous woody angiosperms include *Acer*, *Betula*, *Euonymus*, *Fraxinus*, *Hydrangea*, *Ilex*, *Magnolia*, *Menziesia*, *Prunus*, *Rhododendron*, *Toxicodendron*, *Vaccinium and Viburnum* – all represented by more than one species – and one species each of *Fagus*, *Hamamelis*, *Pterocarya*, *Quercus*, *Smilax*, *Tilia*, *Ulmus*, *Vitis* and *Zelkova*. The IPR vegetation analysis classification of this unit is the ecotone between broad-leaved deciduous forests and mixed mesophytic forests. The comparability of this unit with the Leoben flora may, however, be limited because the survival of evergreen woody taxa is confined to the shrub layer favoured by the snow cover in winter (see above). (For taxa list and results of the IPR vegetation analysis of unit Japan 01 see Teodoridis et al., 2020: appendix 4.)

The MMF China (sensu Kovar-Eder et al., 2021) occurs in hilly regions of southern Jiangsu (Kiangsu), southern Anhui (Anhwei), northern Zhejiang (Chekiang) and northern Jiangxi (Kiangsi) (Wang, 1961). The woody flora of the Mixed Mesophytic Forest – Southern Anhui (unit China 60) is estimated to comprise ~500 species and varieties, of which ~30 are regarded to be characteristic of the broad-leaved evergreen region. Such forests occur on the Hwang Shan at ~900–1500 m on the northern side and 800–1200 m on the southern side, and on Chiuhua Shan at ~900 m. A characteristic feature is that no species are dominant although the following may be abundant locally: *Carpinus cordata* Blume, *Emmenopterys henryi* Oliv., *Fagus engleriana* Seemen ex Diels, *Fortunearia sinensis* Rehder et E.H. Wilson, *Lindera obtusiloba* Blume, *Magnolia sieboldii* subsp. *japonica* K. Ueda. The IPR vegetation analysis places unit China 60 in broad-leaved deciduous forest. (Wang, 1961; for taxa list and results of the IPR vegetation analysis see Teodoridis et al., 2020: appendix 4.)

The MCF China, Japan (Kovar-Eder et al., 2021) is not treated here in more detail because none of the respective vegetation units received more than a single score in each of the variants A–C (see also the results of the Similarity Approach, Fig. 27).

The results of the two approaches (IPR, Similarity) are not fully congruent. The IPR vegetation analysis indicates the ecotone between mixed mesophytic and broad-leaved evergreen forest as the most likely major vegetation type for Leoben. The modern proxies delivered by the Similarity Approach, in turn, are BLDF Upper Yangtze, Honshu, MMF China (and to a minor extent MCF China, Japan). This is because the results of the former analysis imply higher proportions of broad-leaved evergreen taxa than the results of the latter approach. This discrepancy probably also reflects the low taxonomic resolution of laurophyllous versus deciduous taxa in the Leoben assemblage due to the preservation as mere impressions. While the IPR vegetation analysis takes advantage of fossil-species and morphotypes of unknown systematic affinity, morphotypes and taxa resolved to the family level only cannot be evaluated for the Taxonomic Similarity and the Results Mix of the Similarity Approach. The Similarity Approach may therefore indicate more temperate vegetation proxies than expected from the IPR vegetation analysis.

PALAEOCLIMATE

The most appropriate calibration data set as determined by the recommendations on the CLAMP website (Spicer, 2011–2021) is PhysgAsia2 (HresGridMetAsia2), whereas the tool (Teodoridis et al., 2011b, 2012; Kovar-Eder et al., 2022) predicts PhysgAsia1 (HiResGRIDMetAsia1) as best-fitted. The differences in the palaeoclimate proxies derived by these calibration data sets are considerable regarding both the temperature and humidity parameters. PhysgAsia1 indicates lower temperature parameters (MAT, WMMT, CMMT), a shorter growing season and lower precipitation values (GSP, MMGSP, 3_WET, 3_Dry) than does PhysgAsia2 (Table 5, Fig. 28). MAP calculated from CLAMP parameters (see section Methods) is also lower when PhysgAsia1 is applied. Including the standard deviations, the values of the temperature parameters delivered by these calibration data sets overlap.

The differences in the palaeoclimate proxies predicted by the Asian data sets are likely related to the fact that PhysgAsia1 includes 45 sites from different regions in China while PhysgAsia2 includes sites from tropical Asia (southern China, Thailand, India) but excludes other sites from China.

Based on PhysgAsia2, the results for Leoben would be closer to the climate estimates for the Younger Mastixioid flora (sensu Mai, 1964) of Wackersdorf (Early/Middle Miocene, Bavaria) and otherwise only for Late Eocene and Early Oligocene floras of northern Bohemia and eastern regions of Germany based on CLAMP (PhysgAsia1) (Teodoridis and Kvaček, 2015). This discussion must keep the progress of the CLAMP technique in mind. Specifically, the PhysgAsia2 data set, which was determined to be the best-suited for the Leoben flora, was not yet included when Teodoridis and Kvaček (2015) performed their analyses for the floras of northern Bohemia and eastern parts of Germany. Considering the results of the IPR vegetation analysis (ecotone between broad-leaved evergreen and mixed mesophytic forest) and the Similarity Approach (TS and Mixed Results pointing towards BLDF Upper Yangtze, Honshu and MMF China) for Leoben, the results retrieved by the calibration data set PhysgAsia1 appear to be more reasonable.

LEOBEN COMPARED TO THE EARLY TO MIDDLE MIOCENE FLORAS OF THE PARATETHYS REGION AND SURROUNDINGS

LEOBEN AND OBERDORF (TABLE 6)

The Köflach-Voitsberg lignite deposits developed at the northwesternmost margin of the Styrian Basin, which itself constitutes the westernmost extension of the Pannonian Basin system. The Oberdorf Basin is part of the Köflach-Voitsberg lignite area. The plant assemblages, leaves, fruits and pollen studied from the lignite-bearing sequence of Oberdorf derived from very different positions within the sequence, i.e. from the base of the main seam, from seam partings and the hanging wall (Kovar-Eder, 1996; Kovar-Eder and Meller, 2001, 2003; Kovar-Eder et al., 1998, 2001a; Meller, 1998; Meller et al., 1999). In contrast, all the material from Leoben derives from the basal layers of the lacustric sediments overlying the coal seam. Micro-mammals from the hanging wall sequence were dated to MN4 (middle Burdigalian/Ottnangian) (Daxner-Höck et al., 1998), and magnetostratigraphic results enabled correlating this part of the Oberdorf sequence to chron 5Dn of the Geomagnetic Polarity Time Scale (Mauritsch and Scholger, 1998). Consequently, the Leoben flora, which derives only from the sapropelic shales overlying the main seam in the Leoben Basin, is ~3 million years younger than the Oberdorf flora. The leaf material from Oberdorf is preserved as compressions, enabling cuticular analysis, whereas the impressions from Leoben do not. The taxonomic resolution, especially of laurophyllous leaf taxa, is therefore higher in Oberdorf. Nevertheless, the number of leaf taxa recorded from Oberdorf is much lower. For the Oberdorf flora, swamp and riparian (azonal) habitats, as well as mesophytic (zonal) habitats were differentiated (Kovar-Eder et al., 2001b). Leoben and Oberdorf share mainly taxa that presumably preferred azonal habitats. Such shared taxa are *Glyptostrobus europaeus*, *Acer tricuspidatum*, *Myrica joannis*, *Osmunda parschlugiana*, *Potamogeton*, *Quercus rhenana* and possibly also *Alnus oberdorfensis* and *Magnolia liblarensis*. The abundance of some taxa differs considerably at Oberdorf and Leoben, and the autecological tolerance of some taxa may have been wider than that of others (compare Supplementary File 3, in which the autecology of some Leoben taxa was scored differently for the IPR vegetation analysis). Such taxa include *Sequoia abietina*, *Fraxinus*, *Nyssa*, *Pterocarya* and *Salix varians*, which were common in some layers in Oberdorf but rare in Leoben. Joint taxa that probably preferred mesophytic habitats are *Tetraclinis salicornioides*, *Acer integrilobum*, *Daphnogene polymorpha*, *Fagus*, *Trigonobalanopsis rhamnoides*, *Zelkova zelkovifolia* and possibly *Taxus*, *Acer integerrimum*, *Cornus* and *Laurophyllum pseudoprinceps*. *Cornus*, *Parthenocissus*, *Sambucus* and *Vitis*, documented by seeds or fruits from Oberdorf, are represented in the leaf assemblage of Leoben, although the generic assignment of the former three is equivocal there. Beyond a few taxa such as *Daphnogene polymorpha*, *Quercus rhenana* or *Trigonobalanopsis rhamnoides*, the concordance of laurophyllous taxa is difficult to assess because of the different preservation state of the leaf material at the two locations. One evident result, however, is that the diversity of presumably deciduous taxa is higher in Leoben. Numerous such taxa are represented by single or few specimens only, and they probably derived from mesophytic rather than wetland habitats. Among them are *Acer pseudomonspessulanum*, *A. palaeosaccharinum*, *Ailanthus* (?) *apollinis*, *Clematis oligoneure*, *Craigia bronnii*, *Tilia*, *Sambucus ettingshausenii*, *Ulmus* (?) *prisca*, Styracaceae (?) gen. et sp., "*Corylus*" *palaeoavellana* and *Dicotylophyllum* D–F, I, J, P–R. To the author´s knowledge, some of them are not known from elsewhere. This discrepancy between Leoben and Oberdorf is reflected in the IPR vegetation analysis (Table 3), which indicates the ecotone between mixed mesophytic and broad-leaved evergreen forest as the zonal vegetation type for Leoben. In contrast, broad-leaved evergreen forest is predicted for Oberdorf. This conforms to the palaeoclimate estimates, which predict lower mean values for MAT, WMMT and CMMT for Leoben than for Oberdorf based on PhysgAsia1 (Table 5) albeit it must be kept in mind that the palaeoclimate estimates for Leoben and Oberdorf are based on different methodologies, i.e. the assessment for Oberdorf is based on the Coexistence Approach (Mosbrugger and Utescher, 1997). The modern vegetation proxies for Leoben derived by the Similarity Approach are primarily BLDF Upper Yangtze, Honshu and MMF China, whereas for Oberdorf the closest relationship is predicted to BLEF China, Japan (Kovar-Eder et al., 2021). Briefly summarising, the Leoben flora signals a more temperate flora and a cooler palaeoclimate than the Oberdorf flora.

LEOBEN AND PARSCHLUG
(TABLE 6)

The Parschlug Basin is situated ~20 km NE of the Leoben Basin (Fig. 1). It is also one of the basins along the Mur/Mürz fault system that developed during the Early/Middle Miocene (see paragraph Geology and Stratigraphy). Similarly to Leoben, the plant-bearing sediments (marlstone-ironstone, clays and marls) represent lacustric deposits of a lake overlying the coal seam, indicating the drowning of the mire. The Parschlug flora is considered to be of late Early/early Middle Miocene (Upper Burdigalian/Lower Langhian, Karpatian/Lower Badenian) age based on the radiometric dates from the adjacent basins (Kovar-Eder et al., 2004). Contrary to Leoben, the plant remains are not densely packed and the sediment does not easily split along bedding plains. Although the here presented revision has reduced the floristic diversity in Leoben by ~60% compared to Ettingshausen`s monograph (1888), it is nonetheless more diverse (~150 fossil-species and morphotypes) than that of Parschlug (123 fossil-species and morphotypes).

In Parschlug, aquatic plants are confined to *Salvinia*. The two sites therefore do not share any aquatic fossil-species. Both have herbaceous plants of the lake margin and undergrowth in common: *Osmunda parschlugiana*, *Pronephrium stiriacum* and monocots. In Parschlug, oligotypic gallery forests were deduced from the fossil-species *Glyptostrobus europaeus*, *Liquidambar europaea* and *Myrica lignitum*, which are dominant there. *Zelkova zelkovifolia*, which is abundant in Parschlug, was probably also a member of this association. Leoben and Parschlug share only the dominance of *G. europaeus*, but in Leoben *M. lignitum* is far less common, *Z. zelkovifolia* is very rare and *L. europaea* has not been recorded. In Leoben, dominant species besides *G. europaeus*, are *Alnus julianiformis*, *Myrica joannis*, *Quercus gigas* and *Q. rhenana*, followed by *Daphnogene polymorpha*, *Laria rueminiana*, *Sloanea serratifolia* and *Trigonobalanopsis rhamnoides*, indicating swampy environments (forests, woodland or scrub). In Parschlug, *D. polymorpha* and *A. julianiformis* are rare, whereas the other fossil-species are absent.

The shared taxa in the lake surroundings at the two sites and their hinterland are: *Pinus* sp. div., *Acer pseudomonspessulanum*, *A. integrilobum*, *Acer* sp. (fruits), *Alnus gaudinii*, *Betula* sp. (winged seeds), *Cedrelospermum ulmifolium/aquense*, *Craigia bronnii*, *Daphnogene polymorpha*, *Engelhardia orsbergensis/macroptera*, *Fagus*, *Fraxinus* (fruits), “*Juglans*” *parschlugiana*, *Laurophyllum* sp., *Populus latior*, *Quercus drymeja*, *Q. mediterranea*, *Saportaspermum*, *Smilax sphenophylla* (former *Mahonia* (?) *sphenophylla*), *Smilax*, *Tilia longebracteata*, *Toxicodendron melaenum*, *Antholithes stiriacus* and possibly *Berberis teutonica* and *Leguminosites palaeogaeus*. But *Quercus drymeja*, *Q. mediterranea* and *Smilax sphenophylla* are far more abundant in Parschlug.

Remarkable differences between both sites are the distinctly higher diversity of conifers in Leoben comprising *Calocedrus suleticensis*, *Tetraclinis salicornioides*, *Sequoia abietina*, *Taiwania* cf. *paracryptomerioides*, *Amentotaxus* sp., *Cephalotaxus* vel *Torreya* sp. and *Taxus* vel *Cephalotaxus* sp. – all restricted to Leoben – whereas records of *Cathaya* (?) sp. and *Cupressus* (?) sp. are restricted to Parschlug. In Leoben the diversity of Betulaceae, Fagaceae and Juglandaceae both on the generic and species level is higher than in Parschlug. In Parschlug, five different types of legume pods are documented, whereas Leoben yielded only a single pod of cf. *Leguminosites palaeogaeus*. Legume leaves are usually difficult to assess and to differentiate properly, except for *Podocarpium podocarpum* (A. Braun) Herendeen and “*Acacia*” *parschlugiana* Unger. Both fossil-species occur in Parschlug but are absent in Leoben. *Ulmus* is represented at both sites but by different fossil-species: *U. plurinervia* and *U. parschlugiana* (samara) in Parschlug; *U. pyramidalis*, *U.* sp. (samara), *U.* (?) *prisca* in Leoben. Morphologically characteristic taxa of Parschlug such as *Prinsepia serra* (Unger) Kovar-Eder et Kvaček, *Paliurus*, *Cotinus* (?) *aizoon* or *Nerium* have not been detected in Leoben. None of the Theaceae documented are shared by both sites. Both sites feature numerous leaf taxa of unknown systematic affinity, but only a few of them are shared.

The IPR vegetation analysis indicates differences in the overall leaf physiognomy of the zonal forests, whereby Parschlug is characterised by a very high proportion of the legume-like and sclerophyllous components (LEG + SCL) to the detriment of the broad-leaved deciduous (BLD) and broad-leaved evergreen (BLE) components. Accordingly, subhumid sclerophyllous forest is the most likely major vegetation type here (Kovar-Eder et al., 2022), whereas the result for Leoben is ecotone between mixed mesophytic and broad-leaved evergreen forest (Table 3). The Similarity Approach indicates the European vegetation formation G (sensu Teodoridis et al., 2020), i.e. Thermophilous mixed deciduous broadleaved forests of southern and southeastern Europe (sensu Bohn et al., 2004), as the most similar modern vegetation proxies for Parschlug, but BLDF Upper Yangtze, Honshu and MMF China for Leoben.

CLAMP palaeoclimate estimates for Parschlug were derived based on the calibration data set PhysgGlobal378 (Kovar-Eder et al., 2022) (Table 5). Comparing these proxies to Leoben based on PhysgAsia1, the temperature estimates for Parschlug are somewhat lower (MAT, WMMT and CMMT), and the humidity parameters (GSP, MMGSP, 3_WET, 3_DRY and MAP) are considerably lower than for Leoben. The precipitation of 3_WET exceeds that of 3_DRY more than 5 times, expressing a much stronger precipitation seasonality for Parschlug (Table 5, Fig. 28).

Comparing the CLAMP proxies based on the calibration sets derived as proposed on the CLAMP website (Spicer, 2011–2021), i.e. using PhysgAsia2 for Leoben and PhysgAsia1 for Parschlug, indicate generally higher temperatures than derived by the afore-discussed pair of results. Furthermore, they predict slightly higher MAT and CMMT for Parschlug, whereas WMMT and GROWSEAS are very similar for both sites. GSP, MMGSP, 3_WET, 3_DRY and MAP are somewhat lower for Parschlug but are generally very high, MAP exceeding 200 cm. The difference between 3_WET and 3_DRY indicating precipitation seasonality is similar for both sites. Considering the big differences in both the floristic composition and leaf physiognomy between both sites reflected by the results of the IPR vegetation analysis and the Similarity Approach these results appear to be less plausible.

One can argue that the Leoben and Parschlug Basins are situated very close to each other, the age difference is probably minor, and therefore the same calibration data set should be used for palaeoclimate predictions. Accordingly, the results for both sites were compared based on the calibration data sets PhysgAsia1, PhysgAsia2 and PhysgGlobal378, respectively (Fig. 28). The predictions based on PhysgAsia1 indicate higher temperature values for Parschlug. 3_WET is predicted fairly similar for both sites whereas 3_DRY would be somewhat higher for Parschlug. MAP would be higher for Parschlug indicating low plausibility. The PhysgAsia2 results show somewhat lower MAT and WMMT, higher CMMT and shorter GROWSEAS for Parschlug, along with lower precipitation values (GSP, MMGSP, 3_WET, 3_DRY) for that site. The predictions based on PhysgGlobal378, which is supposed to be least exact because it includes sites from both the northern and southern hemisphere (Spicer 2011–2021), show the lowest and similar values of MAT, WMMT and CMMT for both Parschlug and Leoben, as well as fairly similar precipitation values.

Summarising the comparison of the two assemblages, floristic differences are definitely partly caused by the different habitats recorded in the two basins. Swamp environments are well represented only by the Leoben assemblage, while oligotypic gallery forests are documented only from the Parschlug Basin. The regional geology does not provide arguments for considerable differences in elevation of both lakes nor for mountain ranges separating the two adjacent basins (see also paragraph Geology and Stratigraphy). The differences in the floristic composition of the mesophytic vegetation in the surroundings of the lakes at Parschlug and Leoben are reflected by the results of the IPR vegetation analysis, the Similarity Approach and of the palaeoclimate assessment, although the palaeoclimate signals remain equivocal.

LEOBEN AND MECSEK AREA
(TABLE 6)

The Mecsek region (Hungary) is situated in the SW of the Pannonian Basin. The flora derives mainly from the Komló Claymarl Member (Feked Formation), which is regarded to be of lacustrine origin (Hably, 2020). K/Ar dating of tuff interbeds indicates an age of 16.82 ± 0.65 Ma for these sediments, i.e. Early Miocene, late Burdigalian/ Karpatian (Sebe et al., 2019) and therefore ~2 Ma older than the Leoben flora.

Although the record of the Mecsek flora is based on almost 10 000 specimens and comprises more than 100 taxa (Hably, 2020), the number of taxa shared with Leoben is very limited. Moreover, conifer diversity is higher in Leoben, but *Abies* sp. and Cupressaceae gen. et sp. are restricted to the Mecsek assemblage. In that flora the record of Betulaceae is restricted to *Ostrya*, while it is diverse both on the generic and fossil-species level in Leoben. Fagaceae are represented by several fossil-species in both assemblages: they share *Fagus* and *Quercus drymeja*, but *Q. kubinyii* (Kováts ex Ettingsh.) Berger is restricted to the Mecsek assemblage whereas *Q. gigas*, *Q. mediterranea*, *Q. rhenana* and *Trigonobalanopsis rhamnoides* occur only in Leoben. Although both sites yield Theaceae, they do not share any of them. Similarly, the genus *Populus* occurs in both floras but with differences at the fossil-species level. *P. populina* (Brongn.) Erw. Knobloch (younger synonym of *P. latior*) from Mecsek Mts. differs from true *P. latior* by a more minute marginal crenation. Maples are rather diverse in Leoben although not abundant except for *Acer tricuspidatum*, whereas their record is restricted to a few leaves of *Acer* sp. and numerous samaras in the Mecsek flora. Finally, *Palmacites* sp. is documented only from Mecsek area. The palms were probably already rare there because the record is based on a single fan-shaped leaf among the extremely rich material. Overall, the floristic similarities of the two assemblages are mainly restricted to taxa of azonal habitats. Otherwise, the Mecsek flora is more similar to Parschlug than to Leoben. This result is consistent with those deduced from the IPR vegetation analysis, which proposes subhumid sclerophyllous forest as the most likely zonal vegetation for both Mecsek area and Parschlug. The climate estimates for Mecsek area based on the Coexistence Approach (Mosbrugger and Utescher, 1997) were derived by Erdei et al. (2007), indicating higher MAT and CMMT than for Leoben (based on PhysgAsia1), similar WMMT for both sites and considerably lower MAP for the Mecsek flora than for Leoben (Table 5).

LEOBEN AND THE CYPRIS FORMATION (TABLE 6)

The Cypris Formation developed in the Cheb and Sokolov Basins (northwestern Bohemia, Czech Republic). The sediments consist of mostly well-bedded, bituminous claystones which developed immediately above the coal seams there (Bůžek et al., 1996). The flora here is dated to the Mammal Neogene Zone MN 4b and 5 (currently Upper Burdigalian to Lower Langhian/ Karpatian to Lower Badenian). The depositional setting is comparable to that of Leoben and both assemblages are close in age. Contrary to Leoben, the leaves and fruits from the Cypris Fmt. are preserved as compressions. Hence, the taxonomic resolution of laurophyllous leaf taxa and fruits is higher there than in Leoben. Both assemblages include only few aquatic taxa, of which they share Nymphaeales and *Potamogeton*. Among woody taxa from swampy habitats, both floras share *Glyptostrobus europaeus*, *Pinus*, *Myrica lignitum*, *Nyssa*, *Quercus rhenana* and probably *Alnus julianiformis*, Poales are quite diverse in both floras.

The diversity of Lauraceae is high both in Leoben (8 fossil-species) and the Cypris Fmt. (at least 9); they share *Daphnogene polymorpha*, *Ocotea* and probably *Laurophyllum pseudoprinceps* and *Sassafras*. Beyond these Lauraceae the comparison at the species level in the Lauraceae is hampered because of the lack of cuticles in Leoben. Both floras share further the diversity of maples and on the species level *Acer tricuspidatum* and probably *A. integrilobum*, *A. integerrimum* and *A. pseudomonspessulanum*.

Further shared taxa are *Tetraclinis salicornioides*, *Alnus gaudinii*, *Betula*, *Cedrelospermum*, *Craigia*, *Engelhardia*, *Fraxinus*, *Magnolia*, *Populus latior*, *Smilax*, *Tilia*, *Trigonobalanopsis rhamnoides*, *Ulmus*, *Zelkova zelkovifolia* and possibly *Ailanthus*, *Quercus drymeja*, *Parthenocissus*, *Pterocarya* and *Symplocos*. *Platanus neptuni* is common in the Cypris Fmt., whereas only few remains probably of this plane tree were recovered in Leoben. This difference may reflect the probably somewhat younger age of the Leoben flora. Fabaceae do not play an important role in either assemblage except for *Podocarpium podocarpum* in the Cypris Fmt., whereas this fossil-species is completely absent in Leoben.

Otherwise the Leoben assemblage differs by a higher diversity of conifers, Betulaceae and Theaceae, a lower diversity of Myricaceae including the absence of *Comptonia* and, among others, the absence of Saxifragales and *Mastixia*. The absence of *Mastixia*, as well as of other taxa whose remains are confined to sievable sediments may be related to the different preservational settings of the two sites.

The ecotone vegetation between the Notophyllous Evergreen Broad-leaved Forest and the Mixed Mesophytic Forest sensu Wolfe (1979) was proposed as a modern living analogue for the mesophytic forests of the Cypris Formation (Bůžek et al., 1996). The IPR vegetation analysis predicts the ecotone between mixed mesophytic forest and broad-leaved evergreen forest as the major vegetation type for the Cypris Fmt. (Teodoridis and Kvaček, 2015), which is coherent with the predictions for Leoben (Table 3). For the Cypris Fmt., the palaeoclimate proxies (MAT, WMMT, CMMT) based on CLAMP (PhysgAsia1) (Teodoridis and Kvaček, 2015) are fairly close to those for

Leoben (PhysgAsia1) but 3_WET and 3_DRY are considerably lower. Based on the Coexistence Approach the temperature parameters for the Cypris Fmt. are fairly close to those predicted by CLAMP (PhysgAsia2) for Leoben, but MAP for the former is considerably lower than for the latter (Table 5).

THE FLORA OF LEOBEN IN THE CONTEXT OF THE MIOCENE CLIMATE OPTIMUM AND THE MIDDLE MIOCENE CLIMATE TRANSITION

The floristic composition of the Leoben flora is more similar to assemblages of the Younger Mastixioid type (sensu Mai, 1964) than to floras of the Middle Miocene Transition. The rare specimens of (?) *Platanus neptuni* and *Calocedrus suleticensis* represent "old" taxa, while taxa characteristic of Middle and Late Miocene assemblages are restricted to *Quercus gigas*. The high diversity of Lauraceae, the presence of Theaceae and evergreen Fagaceae along with *Ceratozamia* (Zamiaceae) and *Sloanea* (Elaeocarpaceae), as well as the diversity of subtropical conifers are characteristic for the Leoben assemblage. The taxonomic results are supported by the major vegetation type predicted by the IPR vegetation analysis (ecotone between mixed mesophytic and broad-leaved evergreen forest), by the modern vegetation proxies assessed by the Similarity Approach, and by the palaeoclimate predictions based on CLAMP. These approaches all imply that the Leoben flora accumulated during the Miocene Climate Optimum rather than during the Middle Miocene Climate Transition.

CONCLUSIONS

The flora of Leoben is very diverse, comprising ~175 fossil-species and morphotypes and, when different organs of probably one biological fossil-species are fused, ~150. This result reduces the number of taxa (382 excluding fungi) described by Ettingshausen (1869a, 1888) by 54 and 60%. Several taxa are represented by different organs (leaves, inflorescences, fructifications): *Pinus*, *Glyptostrobus*, *Sequoia*, *Acer*, *Alnus*, *Betula*, *Cedrelospermum*, *Englhardia*, *Fraxinus*, Nymphaeaceae vel Nelumbonaceae, *Nyssa*, *Quercus*, *Reevesia* (*Laria*, *Saportaspermum*, possibly *Carpolithes* sp. L) and *Ulmus*.

Horsetails are documented by a single specimen of rhizome bulbs, and fern fronds are very fragmentary and few (*Osmunda parschlugiana*, *Pronephrium stiriacum*). Conifer diversity is rather high. While *Glyptostrobus europaeus* and *Pinus* sp. div. are abundant, *Tetraclinis* and *Sequoia* are less common, and *Calocedrus*, *Taiwania*, *Amentotaxus* and others are rare. Among angiosperms, Betulaceae (3–4 genera), Fagaceae (3 genera), Lauraceae (8 fossil-species), Sapindaceae (5 fossil-species) are most diverse, followed by Ulmaceae and Juglandaceae (each 3–4 fossil-species), Theaceae (3 fossil-species) and Smilacaceae, Berberidaceae, Vitaceae, Salicaceae, Myricaceae, Malvaceae and Oleaceae (each 2 fossil-species). All other families are represented by one fossil-species. Remains of Poales and presumable Fabaceae foliage are rare but comprise several morphotypes each. Taxonomically unassignable morphotypes of leaves and fructifications are also numerous.

Berberis mahonioides Kovar-Eder sp. n. and *Sambucus ettingshausenii* Kovar-Eder sp. n. are described for the first time. New combinations introduced here are *Alnus milleri* (Ettingsh.) Kovar-Eder comb. nov., *Clematis oligoneure* (Ettingsh.) Kovar-Eder comb. nov., *Parthenocissus rhombifolia* (Ettingsh.) Kovar-Eder comb. nov., *Sloanea serratifolia* (Ettingsh.) Kovar-Eder comb. nov., *Smilax sphenophylla* (Unger) Kovar-Eder comb. nov., *Ternstroemites diversifolius* (Ettingsh.) Kovar-Eder comb. nov., *Ternstroemites egeriae* (Ettingsh.) Kovar-Eder comb. nov. and *Ternstroemites stiriacus* (Ettingsh.) Kovar-Eder comb. nov. Furthermore, remarkable is the isolated finding of an Ericaceae infructescence (Vaccinioideae gen. et sp.) consisting of 3 pedicillate capsules.

Phytosociologically the flora represents plants of a floating-leaf plant zone, the lake margin and the undergrowth of swampy environments. Swampy forests are indicated by mass occurrences of several taxa. Forest communities outside swampy environments but near the lake margin and along streams are assumed to be diverse, including conifers and mostly deciduous angiosperms. These forests gradually segued into mesophytic hinterland forests, which were probably even more diverse, including a cycad, conifers, as well as deciduous and laurophyllous woody angiosperms, which are rare or even represented by single specimens only. Woody lianas are rather diverse and may have flourished in the forests of the lake surroundings and the hinterland.

The Integrated Plant Record (IPR) vegetation analysis indicates the ecotone between mixed mesophytic and broad-leaved evergreen forest (sensu Teodoridis et al., 2011a, 2011–2021). In the Similarity Approach, the IPR Similarity indicates closer leaf physiognomic relationship of the Leoben flora to European than to East Asian vegetation today. The Taxonomic Similarity (TS) and the Results Mix, in turn, point to strong relations to the vegetation in China and Japan. This divergence has already been described for other Miocene European floras. The close relationship to East Asia in the TS and Results Mix compared to the much lower one to Europe is explained by the floristic depletion of the modern European flora due to the repeated climatic oscillations during the Quaternary Ice Age. The most likely modern vegetation proxies assessed by applying this technique are BLDF Upper Yangtze, Honshu and MMF China (sensu Kovar-Eder et al., 2021).

Palaeoclimate predictions based on CLAMP are equivocal, depending on the calibration data set applied. The proxies derived by applying PhysgAsia1 are MAT 13.3 (±2.5)°C, WMMT 24.2 (±3.0)°C, CMMT 3.6 (±4.1)°C, GROWSEAS 7.75 (±1.3) months, GSP 140.6 (±49.7) cm, MMGSP 15.35 (±5.5) cm, 3_WET 78.5 (±23.9) cm, 3_DRY 20.5 (±10.4) cm, MAP (calculated indirectly from CLAMP parameters) 169.3–191.1 cm. Based on the data set PhysgAsia2, the proxies are MAT 16.9 (±2.3)°C, WMMT 27.5 (±2.8)°C, CMMT 4.9 (±3.6)°C, GROWSEAS 9.8 (±1.1) months, GSP 196.7 (±60.6) cm, MMGSP 20.5 (±6.1) cm, 3_WET 86.7 (±35.8) cm, 3_DRY 29.3 (±9.5) cm, MAP (calculated indirectly from CLAMP parameters) 238.9–240.5 cm.

Floristically, Leoben is more similar to the Younger Mastixioid type (sensu Mai, 1964) such as in the Cypris Formation and Oberdorf than to Parschlug and the Mecsek Mts. It corresponds closer to floras of the Miocene Climate Optimum than to those of the Middle Miocene Transition. This result is congruent with the rare occurrence of the ancient taxa *Ceratozamia hofmannii*, *Calocedrus suleticensis*, (?) *Platanus neptuni* and *Sloanea*, while taxa characteristic of Middle to Late Miocene are confined to *Quercus gigas*.

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ADDITIONAL INFORMATION

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