Acta Palaeobotanica 59(1): 69–73, 2019 DOI: 10.2478/acpa-2019-0009

Populus erratica Sachse, nom. nov. – not really new, but a stratigraphically informative species from the late Oligocene and early Miocene of Central Europe

MARKUS SACHSE

Rümannstraße 57/V, 80804 Munich, Germany; e-mail: sachse-m@gmx.de

Received 28 January 2019; accepted for publication 13 May 2019

ABSTRACT. A critical review of reports from European localities reveals that the herein newly described *Populus erratica* Sachse, nom. nov. was previously treated under a variety of names. Due to its stratigraphical range from the late Oligocene to early Miocene, it might be a useful tool for age determinations in the terrestrial record. So far it is known only from warm-temperate floodplain forests in Central Europe – possibly even restricted to the alpine area. The taxonomic relationships to some morphologically similar species from other localities cannot be entirely clarified here.

KEYWORDS: Salicaceae, leaves, taxonomy, floodplain forest, palaeoecology, stratigraphy

The genus *Populus* is generally characterized by more or less wide leaves. This may explain why the species described here, with exclusively narrow lanceolate and linear laminae, was previously assigned to various juglandaceous taxa (Ettingshausen 1853, Heer 1856, 1859, Baumberger & Menzel 1914, Hantke et al. 2005). These leaves were found in two Swiss localities.

The plant fossil site in the fluvio-terrestrial facies of the Obere Meeresmolasse from Risi/ Wattwil in St. Gallen Canton was published by Hantke et al. (2005). Leaf macrofossils from this site are kept in the Natural History Museum of St. Gallen (Naturmuseum St. Gallen). The site yielded a considerable number of leaves belonging to a single morphotype, for which the taxonomic assignment is corrected in this brief taxonomic note. Previously described as Carya heerii (Ettingshausen) Heer, they need a new species name, since the systematic position of another taxon – Populus heerii Saporta - cannot be established unambiguously, and its relationship with the fossil species dealt with here remains unclear. A fossil impression from

the type locality (erratic boulders near St. Gallen) is used as a new type specimen, because older specimens are no longer traceable.

Due to the lack of organically preserved cuticles from both localities, the following species definition is based on morphological criteria only (leaf impressions), without support from anatomical characters.

Salicaceae Mirbel 1815 nom. cons.

Populus L. 1753

Populus erratica Sachse, nom. nov.

- 1853 Juglans heerii Ettingsh., p. 811, pl. 2, figs 5–7 [Erratic boulders near St. Gallen, late Oligocene or early Miocene].
- 1856 Juglans heerii Ettingsh. Heer, pl. 99, fig. 23B [Erratic boulders near St. Gallen, late Oligocene or early Miocene].
- 1859 Carya heerii (Ettingsh.) Heer, p. 93, pl. 131, figs 8–17 [Erratic boulders near St. Gallen, late Oligocene or early Miocene].
- ?1862 *Populus heerii* Saporta, p. 87, pl. 7, fig. 3A [Aixen Provence, Chattian or Aquitanian].

- non 1889 *Populus heerii* Saporta Saporta, p. 21, pl. 2, fig. 9 [Chattian or Aquitanian].
- ?1895 Carya heerii (Ettingsh.) Heer Keller, p. 317, pl. 5, fig. 6 [Herisau, Chattian or Aquitanian].
- non 1904 Populus heerii Saporta Brabenec, p. 6, pl. 1, fig. 3 [Holedeč, Chattian].
- non 1909 Populus heerii Saporta Brabenec, p. 87, text-fig. 67 [Holedeč, Chattian].
- 1914 Pterocarya heerii (Ettingsh.) Schimper Baumberger & Menzel, p. 54, pl. 4, fig. 5 [Gnippen am Vierwaldst. See, Chattian].
- ?1937 Populus rottensis Weyland, p. 81, pl. 10, figs 7–9 [Rott, Chattian].
- ?1991 Populus vel Salix Kvaček & Hably, p. 60, pl. 9, fig. 2 [Eger (Wind brickyard), Chattian].
- 2005 Carya heeri (Ettingsh.) Heer partim Hantke et al., p. 9, pl. 2, fig. 5, pl. 3, fig. 8, pl. 5, fig. 6, non pl. 1, fig. 8 [Risi/Wattwil, Ottnang].

Replaced name. *Juglans heerii* Ettingsh. (1853: 811, pl. 2, figs 5–7).

Holotype. Missing.

Neotype (designated here). NMSG F 14383 (Pl. 1, figs 1, 2, illustrated in Heer 1859: pl. 131, fig. 8).

Repository. Natural History Museum of St. Gallen, Switzerland.

Locality. Erratic boulder near St. Gallen.

Stratum. Late Oligocene or early Miocene.

Etymology. Referring to the erratic boulders as well as to the odyssey-like taxonomic history of this species (erraticus, lat. = wandering around).

Additional specimens examined. NMSG F 14191 (Pl. 1, fig. 3), NMSG F 14303 (Pl. 1, fig. 4). Early Miocene (Ottnangian) fluvio-lacustrine marly lens in Risi/Wattwil, Switzerland; Natural History Museum of St. Gallen.

Description. Lamina linear-lanceolate; mostly ca 15 cm long and 1-2 cm wide; base of lamina acute to rounded, apex acute; length of petiole up to 3 cm; midrib strong and straight or slightly curved; margin more or less distinctly coarsely toothed with glandular, widely spaced and spherulate or mucronate teeth; basal side retroflexed to straight, distal side convex or sometimes flexed; secondaries semicraspedodromous or festooned semicraspedodromous, arising at wide or narrow angles, \pm bent upwards. 2–3 intersecondary veins may be present. At base, 1–2 pairs of narrow basal veins emerge at acute angle and run initially parallel to margin

before connecting in a loop with the next-higher secondary veins. Tertiary and higher-order veinlets form irregular or regular reticulum; the former may be locally alternate percurrent in narrow intercostal fields.

Remarks. Such leaves have been assigned a variety of names. Ettingshausen (1853) assigned a single leaf fragment from Erdöbenye (near Tokay, Hungary), and several leaves from erratic boulders of St. Gallen to the genus Juglans. The fragment from the Sarmatian of Erdöbenve, which Ettingshausen (1853) mentioned but unfortunately did not depict, was later compared by Andreansky (1959) unfortunately also without illustration - with Juglans hydrophila Unger. This species in turn was assigned by Kovar-Eder et al. (2004) to Quercus drymeja Unger. Later assignments, also from erratic boulders of St. Gallen, were made to Carya by Heer (1856) and to Pterocarya by Baumberger and Menzel (1914).

Unfortunately, hardly any of the originals can be located. Specimens from Hungary are not included in the type catalogue published by Hably et al. (2001). According to the online versions of the Collections of Vienna and Zurich ("Catalogue of Palaeontological Types in Austrian Collections" and https://ews.e-pics.ethz. ch; also, written comm. from Andreas Müller, ETH from 11/11/2017), the originals of Ettingshausen and Heer are not traceable. On the other hand, the collection of the Natural History Museum of St. Gallen houses one of Heer's figured originals of Carya heerii (Ettingsh.) Heer, hereby designated as neotype. Although indicated on its label, this is not the specimen published in Heer (1856: pl. 99, fig. 2); instead, it is pictured in Heer (1859: pl. 131, fig. 8).

The originals from Ettingshausen and Heer both come from erratic boulders at St. Gallen. Possibly they originated from the same stratigraphic layer but this assumption is not certain. Further finds from such boulders were later reported by Keller (1892).

Weyland (1937) assigned very similar leaves from Rott to the genus *Populus* on account of the reticulate venation pattern, long petiole, and the presence of two or more basal veins. In some *Salix* species at least one pair of basal veins also occurs sporadically, but this is only observed in leaves exposed to drought stress (Buechler 2014), which is not thought to be the case for any of the *P. erratica* sites known



Plate 1. 1. Specimen of the St. Gallen boulders with historical inscriptions from Heer's collection containing *Populus erratica* Sachse, NMSG F 14383; 2. *Populus erratica* Sachse, NMSG F 14383; 3. *Populus erratica* Sachse from Risi/Wattwil, NMSG F 14191; 4. *Populus erratica* Sachse from Risi/Wattwil, NMSG F 14303. Scale bars in figs 2–4: 1 cm

so far. Weyland (1937) nonetheless refrained from making a new combination and instead created his new species P. rottensis Weyland. As compared with *P. erratica*, the pictured specimen does in fact show minor deviations in the size and the straighter or even partly outwards-bending form of the teeth. It cannot be decided here whether they might belong to different species or to ecological or geographical varieties within the same species. Heteromorphism in extant and fossil Populus leaves was documented by Eckenwalder (1980). Also, the single specimen from Eger figured by Kvaček and Hably (1991) cannot be assigned reliably to *P. erratica*, since the leaf margin is not clearly visible.

The assignment of the material from Risi to the genus *Populus* is supported by the fact that *P. erratica* is represented in the parautochthonous association not only by its many leaf remains but also by a number of capsules (Hantke et al. 2005), which, however, were previously interpreted as involucres of *Carya*. According to Kirchheimer (1956), such large 2- to 4-valvate capsules can only come from *Populus*, not from *Salix*.

Saporta (1862) did not refer to the publications of Heer and Ettingshausen when he created the separate species Populus heerii Saporta from upper Oligocene strata at Aix-en-Provence; it was probably not conspecific with P. erratica. It is true that there is a certain similarity in the drawing of the specimen, apart from the uniform dentition, but since the original specimen was not found in the collections in Paris or in Aix-en-Provence (written comm. from Dario De Franceschi, MNHN, 19/09/2018), the exact relationship cannot be clarified here either. Another specimen, figured in Saporta (1889), clearly differs by its broader lamina and more regular dentition. Later, Brabenec (1904) described a leaf with a wide lamina from the Most Basin of the present-day Czech Republic as P. heerii Saporta; it was classified by Teodoridis (2002) as a synonym of Populus zaddachii Heer var. brabenecii Teodoridis. Only narrow leaves with irregularly spaced dentition are known in Populus erratica.

Budantsev (2005) published some Populus leaves characterized by a linear lamina: P. arnaudii (Saporta) Iljinskaya (Aquitanian, Bonnieux in France), P. borissovii Iljinskaja et Akhmetiev (Rupelian, Korablik in Kazakhstan) and P. iljinskajae Akhmetiev (Eocene, Rechnoi in Russia). They all differ in having smaller and more densely spaced teeth.

As the closest extant counterpart to *P. rot*tensis, Weyland (1937) mentioned *P. angustifolia* James from semi-humid to semi-arid riverbank sites in the western United States. This comparison also applies to *P. erratica*. However, the leaves of that extant species show slightly denser dentition and the occasional occurrence of a wider lamina.

P. erratica Sachse nov. nom. was an alluvial forest element which is commonly identified as (almost) the only representative of the willow family at, for example, Risi (even as the dominant element, see Hantke et al. 2005), Lake Lucerne (Baumberger & Menzel 1914), Eger (Kvaček & Hably 1991) and the St. Gallen boulders (Heer 1856, 1859, Keller 1895). Whether and why it was particularly competitive at these locations as a locally developed thicket – possibly it grew mainly in hardwood forests – cannot be clarified at this point. Usually it is accompanied by deciduous and evergreen laurophyllous elements in various communities. At Risi the main components were Cyperaceae, Daphnogene, Ulmus braunii, Acer angustilobum and A. tricuspidatum (Hantke et al. 2005). Heer (1859) mentioned Leguminosae (e.g. Robinia regeli, Acacia parschlugiana), Planera (Zelkova) ungeri, Acer angustilobum, Cinnamomum (Daphnogene) polymorphum and lanceolatum as the most common taxa from the St. Gallen boulders. Further research focusing on the carpoflora of this locality is being done by Jochen Gregor (Olching).

The stratigraphic range known so far includes the Chattian (late Oligocene) and early Miocene. The Ottnangian site at Risi probably represents the youngest reliably dated occurrence. The flora published by Keller (1895) from an excavation of the Herisau water reservoir south-east of St. Gallen is likely of similar age but a precise age cannot be assigned (written comm. from Daniel Kälin, Swisstopo, Jan. 2018), as is the case with the St. Gallen boulders. Heer (1859) attributed them to the "Mainzer Stufe", that is early Miocene, but Kirchheimer (1956) referred them to the late Oligocene or early Miocene. Other Swiss localities (Monod, Rivaz, Lausanne, Uznach near Zürich) listed by Heer (1859) and Schimper (1869) also belong into this interval. From the current perspective the regional spread of this

species seems limited to Central Europe. Possibly it should even be considered as endemic within the Alpine area if the specimens from the Rott and Eger localities are excluded. Further study of leaf variability at those localities is needed to clarify this point.

ACKNOWLEDGEMENTS

I thank Toni Bürgin, Matthias Meier (both Natural History Museum of St. Gallen), Urs Oberli (St. Gallen) and Jochen Gregor (Olching) for their valuable assistance, Thomas Denk (Stockholm) and Heinz Winterscheid (Bonn) for their very helpful reviews, and Graham Shields (London). Work on the collection from Risi/Wattwil was financially supported by the Natural History Museum of St. Gallen).

REFERENCES

- ANDREÁNSZKY G. 1959. Die Flora der sarmatischen Stufe in Ungarn. Akádemiai Kiadó, Budapest.
- BAUMBERGER E. & MENZEL P. 1914. Beitrag zur Kenntnis der Tertiärflora aus dem Gebiete des Vierwaldstätter Sees. Mém. Soc. Paléont. Suisse, 40: 1–84.
- BRABENEC B. 1904. 0 novém nalezisti tfetihomich rostlin ve spodnim pasmu vrstev zateckých (Newly found Tertiary plants in the bottom of the stratum). Rozpr. Čes. Akad. Véd Umeni, II/13: 1–25 (in Czech).
- BRABENEC B. 1909. Souborná květena Českého útvaru třetihorního. Část I. Archiv přírodovědeckého prozkoumání Čech stav dobrý, 14: 1–144.
- BUDANTSEV L.Y. (ed.), 2005. Fossil flowering plants in Russia and adjacent countries. Vol. 4. Nyctaginaceae – Salicaceae. Russian Academy of Sciences Komarov Botanical Institute, St. Petersburg (in Russian).
- BUECHLER W. 2014. Variability of venation patterns in extant genus *Salix* : Implications for fossil taxonomy. Paleobios, 30(3): 89–104.
- ECKENWALDER J.E. 1980. Foliar heteromorphism in *Populus* (Salicaceae), a source of confusion in the taxonomy of Tertiary leaf remains. Systematic Botany, 5(4): 366–383.
- ETTINGSHAUSEN von C. 1853. Beitrag zur Kenntnis der fossilen Flora von Tokay. Sitzungsber. Kaiserl. Akad. Wiss., Wien, Math.-Naturwiss. Cl., 11: 779–816.

- HABLY L., ERDEI B. & KVAČEK Z. 2001. 19th century's palaeobotanical types and originals of the Hungarian Natural History Museum. Budapest.
- HANTKE R., OBERLI U. & GREGOR H.J. 2005. Die mittelmiozäne Megaflora von Risi/Wattwil (Kanton St. Gallen, Schweiz) – Geologie, (Klima-)Stratigraphie und Paläoökologie. Documenta Naturae, 155(3): 1–35.
- HEER O. 1856. Flora Tertiaria Helvetiae. II. J. Wust. Comp., Winterthur.
- HEER O. 1859. Flora Tertiaria Helvetiae. III. J. Wust. Comp., Winterthur.
- KELLER R. 1892. Beiträge zur Tertiärflora des Kantons St. Gallen. Jb. Thätigkeit St. Gallischen naturwissenschaftl. Gesellschaft, 1890/91: 82–117.
- KELLER R. 1895. Beiträge zur Tertiärflora des Kantons St. Gallen. Zweite Mitteilung. Ber. Thätigkeit St. Gallischen naturwissenschaftl. Gesellschaft, 1893/94: 305–330.
- KIRCHHEIMER F. 1956. Die Laubgewächse der Braunkohlenzeit. Knapp, Halle.
- KOVAR-EDER J., KVAČEK Z. & STRÖBITZER-HER-MANN M. 2004. The Miocene Flora of Parschlug (Styria, Austria) – Revision and Synthesis. Ann. Naturhist. Mus. Wien, 105 A: 45–109.
- KVAČEK Z. & HABLY L. 1991. Notes on the Egerian stratotype flora at Eger (Wind brickyard), Hungary, Upper Oligocene. Annales Hist.-Nat. Mus. Nat. Hung., 83: 49–82.
- SAPORTA G. de 1862. Études sur la végétation du Sud-Est de la France à l'époque tertiaire, vol 1. Ann. Sci. Nat., Botanique, ser. 4, 17: 191–311.
- SAPORTA G. de 1889. Derniéres adjonctions à la flore fossile d'Aix-en-Provence. 2ème partie. Ann. Sci. Nat., Botanique, ser. 7, 10: 1–192.
- SCHIMPER W.P. 1869. Traité de paléontologie végétale, ou, La flore du monde primitif dans ses rapports avec les formations géologiques et la flore du monde actuel. J.G. Bailliere, Paris.
- TEODORIDIS V. 2002. Tertiary flora and vegetation of the Hlavačov gravel and sand and the surroundings of Holedeč in the Most Basin (Czech Republic). Acta Mus. Nat. Pragae, ser. B, 57(3-4): 103–140.
- WEYLAND H. 1937. Beiträge zur Kenntnis der rheinischen Tertiärflora. II Erste Ergänzungen und Berichtigungen zur Flora der Blätterkohle und des Polierschiefers von Rott im Siebengebirge. Palaeontographica, B, 83: 67–121.