



# FIRST WATER LILY, A LEAF OF *NYMPHAEA* SP., FROM THE MIOCENE CLARKIA FLORA, NORTHERN IDAHO, USA: OCCURRENCE, TAPHONOMIC OBSERVATIONS, FLORISTIC IMPLICATIONS

CAROLE T. GEE<sup>1,2,\*</sup>, DAVID WINSHIP TAYLOR<sup>3</sup>, WILLIAM C. REMBER<sup>4</sup>

<sup>1</sup> Institute of Geosciences, Division of Paleontology, University of Bonn, Nussallee 8, 53115 Bonn, Germany; e-mail: cgee@uni-bonn.de.

<sup>2</sup> Huntington Botanical Gardens, 1151 Oxford Road, San Marino, California 91108, USA.

<sup>3</sup> Department of Biology, Indiana University Southeast, 4201 Grant Line Road, New Albany, Indiana 47150, USA.

<sup>4</sup> Department of Geological Sciences, University of Idaho, Moscow, Idaho 83844, USA.

\*corresponding author

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**Abstract:** Although the Miocene Clarkia locality in Idaho, USA, is a well-known fossil lagerstätte, this 16-million-year-old flora is especially renowned for its abundant leaves with excellent preservation. The exquisite condition of its dicot leaves has resulted in detailed research on systematics, morphology, venation, epidermal structure, cell ultrastructure, biochemistry, and even molecular biology. However, new discoveries continue to emerge, even after five decades of research. Here we describe the first water lily leaf from the Clarkia flora as *Nymphaea* sp. based on its form, petiole attachment, and venation. The eccentric peltate leaf is ovate with a cordate base, a deep basal sinus, entire margins, and actinodromous primary venation. Its small, unblemished condition and leathery texture suggests that it is a young floating leaf. While rare in the Clarkia Lake deposits, the occurrence of a single water lily leaf among tens of thousands of dicot and conifer leaves follows the taphonomic pattern of nearby Middle Miocene floras, two of which have yielded *Nymphaea* pollen. The recognition of *Nymphaea* at Clarkia supplements the taxonomic composition of the flora, confirms the presence of water lilies in region during the Middle Miocene, and completes our understanding of plant life in the Pacific Northwest 16 million years ago.

**Key words:** Clarkia local flora, Columbia River Basalt Group, fossil aquatic macroflora, fossil aquatic macrophyte, leaf fossil, Miocene Climatic Optimum, Nymphaeaceae, Nymphaeales, plant taphonomy, Wanapum Formation

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## Introduction

Although there are a number of Cenozoic lagerstätte with abundant foliage, the Miocene Clarkia flora is especially well-known for the excellent preservation of its dicot leaves. In addition to a plethora of specimens, the fossil leaves commonly show higher orders of leaf venation (e.g., Smiley and Rember 1985b), the epidermal structure of the cuticle (Huggins 1985), and the cellular anatomy of epiphyllous fungi (Williams 1985, Phipps and Rember 2004). Even the ultrastructure of dicot leaf cells is preserved; membrane-bound organelles such as chloroplasts, mitochondria, and nuclei have been documented by the transmission electron microscopy (Niklas and Brown 1981, Niklas et al. 1985). Lipids have also been found in the fossil leaves as well as in the sedimentary rock (Yang and Huang 2003).

The most unusual feature of the Clarkia flora, however, is that some leaves have been reported as exhibiting original

pigment colors when freshly excavated (e.g., Smiley and Rember 1985a, Rember 2007, Taylor et al. 2009, Kim 2019, Steinthorsdottir and Coxall 2019). Chlorophyll derivatives such as pheophorbides, pristane, and phytane have been extracted in quantifiable amounts from dicot leaves from one Clarkia site (P-33; Giannasi and Niklas 1977, Niklas and Brown 1981). Similarly, traces of carotenoids, flavonoids, and proanthocyanidins, as well as other organic compounds and biomarkers have been documented in fossil dicot leaves from the Clarkia flora at two sites (P-33 and P-37; Giannasi and Niklas 1977, 1985, Niklas and Brown 1981, Niklas and Giannasi 1985, Otto et al. 2003, 2005). Thus, the excellent preservation of the Clarkia leaves offers much potential for further biochemical and molecular work, particular in regard to the confirmation, characterization, and quantification of leaf pigments (Gee and McCoy 2021).

Another example of the excellent preservation at Clarkia is the amplification and sequencing of fossil genetic

material from two dicot leaves from *Clarkia* (Kim et al. 2004). However, there is some controversy about the source of this DNA, as it has been claimed that it may have come from contamination by bacterial sources (Sidow et al. 1991, Lindahl 1993).

The *Clarkia* locality is both a conservation and concentration lagerstätte dominated by leaves deposited in a freshwater lake during Miocene times (Smiley 1985 and chapters therein; Wang et al. 2017). Most of the fossil leaves come from broadleaved trees of a mixed mesophytic forest that include the following genera which are listed here in alphabetical order: *Acer* L., *Betula* L., *Castanea* MILL., *Gleditsia* J. CLAYTON, *Halesia* J. ELLIS ex L., *Liquidambar* L., *Lithocarpus* BLUME, *Magnolia* L., *Nyssa* GRONOV. ex L., *Ostrya* SCOP., *Quercus* L., *Platanus* L., *Pseudofagus* C. J. SMILEY et HUGGINS, *Symplocos* JACQ., *Zenia* CHUN, *Zizyphoides* sensu Seward and Conway (1935), as well as members of the Lauraceae JUSS. (Manchester et al. 1991, Rember 1991). Fossil conifer leaves found at *Clarkia* include *Abies* MILL., *Amentotaxus* PILG., *Cathaya* CHUN et KUANG, *Chamaecyparis* SPACH, *Calocedrus* KURZ, *Cunninghamia* R. BR., *Glyptostrobus* ENDL., *Metasequoia* HU et W. C. CHENG, *Pinus* L., *Sequoia* ENDL., *Taxodium* RICH., and *Taxus* L. (Rember 1991, Kvaček and Rember 2000), which represent trees growing along the shoreline, in the littoral zones in the lake, or alongside the broadleaved trees in the mixed mesophytic forest. The diversity of conifers in the *Clarkia* flora is greater than any other of the many Miocene floras associated with the Columbia River Basalt Group in the western United States.

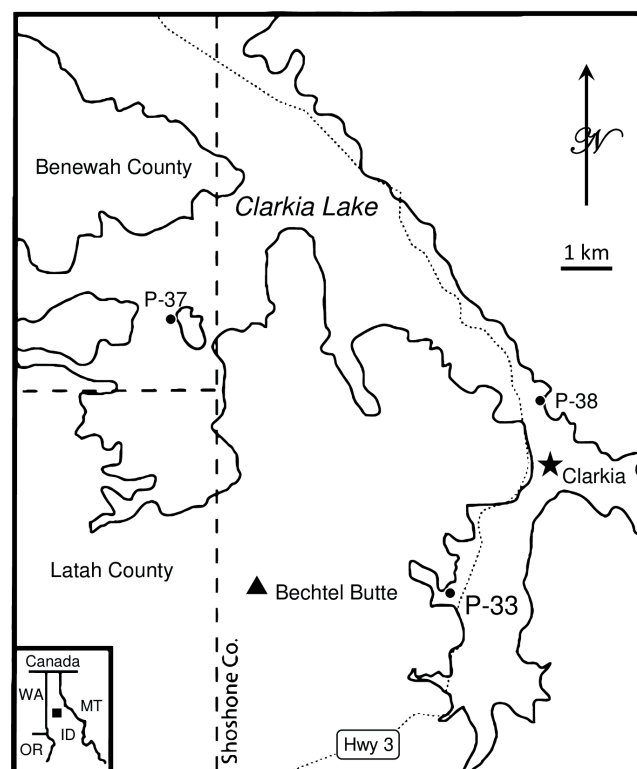
Yet, among the over 100 taxa of leaves, fruits, and seeds from the vast collections with many thousands of leaves from *Clarkia* site, only four fossil leaves have been found that pertain to aquatic macrophytes. Three leaves have been identified as *Caldesia* PARL. (Smiley and Rember 1985a, Haggard and Tiffney 1997, Rember, own data), while the fourth leaf was provisionally assigned to *Nuphar* SM. (Rember 1991). This fourth leaf had been noted in floral lists, but had not received systematic attention until now.

Here we formally describe the second taxon of an aquatic macrophyte from the Miocene *Clarkia* flora. Using morphological study and phylogenetic analysis, the leaf can be assigned to the water lily genus *Nymphaea* L. based on its leaf form, petiole insertion, and primary and secondary venation.

## Geological setting

The *Clarkia* flora comes from *Clarkia* Valley in northern Idaho, about 2.5 km south of the small town of *Clarkia* located 80 km northeast of Moscow, Idaho, USA. Here, the St. Maries River is part of the local drainage system and was responsible for depositing the Neogene valley fill (Smiley and Rember 1985a). The bedrock in the St. Maries River area consists of Precambrian schist and quartzite.

The first fossil leaves from the *Clarkia* area were discovered in the early 1970's (Smiley and Rember 1979). In the last five decades, several fossiliferous localities in the *Clarkia* basin have been discovered, which represent sites in and along the shoreline of the Miocene *Clarkia* Lake.



**Text-fig. 1.** Locality map with the approximate extent of *Clarkia* Lake during Miocene times in what is today northern Idaho, USA. Black dots mark three of the localities yielding the Miocene *Clarkia* flora; the fossil leaf of *Nymphaea* sp. described here comes from locality P-33. Other symbols: Dashed lines for county boundaries; a thin dotted line for Idaho State Hwy 3; a triangle for the local peak of Bechtel Butte; and a star for the town of *Clarkia*. Inset: Location of the map in northern Idaho. Abbreviations: WA – Washington state, OR – Oregon, ID – Idaho, MT – Montana. Map redrawn from Ladderud et al. (2015).

The fossil specimen described here was collected by one of us (WCR) in the winter of 1976 from the best-known site yielding the *Clarkia* flora, P-33, which is also known as the Fossil Bowl Race Track site. Locality P-33 is located on privately owned land west of Idaho State Highway 3 (Text-fig. 1).

The fossil-bearing sediments at P-33 pertain to the Wanapum Formation of the Columbia River Basalt Group. The section at the outcrop consists of 9 m of soft, laminated, unoxidized, lacustrine clay horizons intercalated with barren volcanic ash layers (Smiley et al. 1975, Smiley and Rember 1985a). The fossil specimen described here was recovered from the main section, section A, from a horizon 115.5 cm down from the top of the section measured by Rember (1991: fig. 5).

In the Miocene, the clay layers were deposited in the narrow, deep ancient lake of *Clarkia* Lake (Text-fig. 1) formed by the damming of lava flows in the valley. Cold, anoxic conditions in the original bottom of the lake and rapid sedimentation are thought to be responsible for the excellent preservation of the fossil leaves (Rember 2007). A geologically instantaneous drop in water level prompted a change in depositional conditions from those forming a conservation deposit to those promoting a concentration

deposit (Wang et al. 2017). At P-33, the fossiliferous sediments are poorly lithified and have not been significantly affected by tectonic movements or burial. Radiometric dating of the ash layers gave the age of the *Clarkia* flora as between 15.4 to 16.0 Ma (Ladderud et al. 2015), but more recent dating using U-Pb zircons from the interbedded ash layers at P-33 pinpoints the age as  $15.78 \pm 0.039$  Ma (Höfig et al. 2021). The fossil leaves of the *Clarkia* flora thus represent the local vegetation during the Miocene Climatic Optimum (Höfig et al. 2021), the last climatic highpoint in the Cenozoic before the present day.

## Materials and methods

The fossil material under study here is represented by a single leaf adpression (sensu Shute and Cleal 1987), which is a slightly darker shade of brown than the light brown clay matrix. The specimen is deposited in the *Clarkia* fossil collections in Morrill Hall at the University of Idaho in Moscow, Idaho, USA, and has no inventory number. Because of the uniqueness of this taxon in the *Clarkia* flora, it was not possible to borrow the specimen, so it was studied, measured, and photographed onsite in natural sunlight.

The fossil leaf was later coded using the 55 diagnostic characters given by Taylor and Gee (2014) and the updated data set constructed with the 34 living taxa of Nymphaeales and outgroups of Gee and Taylor (2019). The leaf had 18 traits preserved within the first 23 characters and was coded 110221112(1-2)221111?01 (in which a question mark denotes “unknown”); the remaining characters were not preserved and coded as unknown. Maximum parsimony analyses were conducted using PAUP\* version 4.0a169 (Swofford 2003). In all cases, *Amborella* BAILL. was defined as the outgroup. All characters were unordered, and heuristic

searches were made using 10 random addition replicates with tree-bisection-reconstruction branch swapping with MULTREES on. Multistate characters were considered polymorphic, and bootstrap values were based on 100 replicates with simple addition.

The terminology and characters used here are defined in the Manual of Leaf Architecture (Leaf Architecture Working Group 1999, Ellis et al. 2009), as well as in publications by Taylor (2008) and Taylor and Gee (2014).

## Systematic palaeobotany

Clade Angiospermae LINDL., 1830

Order Nymphaeales SALISB. ex BERCHT. et J. PRESL., 1820

Family Nymphaeaceae SALISB., 1805 nom. cons.

Genus *Nymphaea* L., 1753

*Nymphaea* sp.

Text-fig. 2a, b

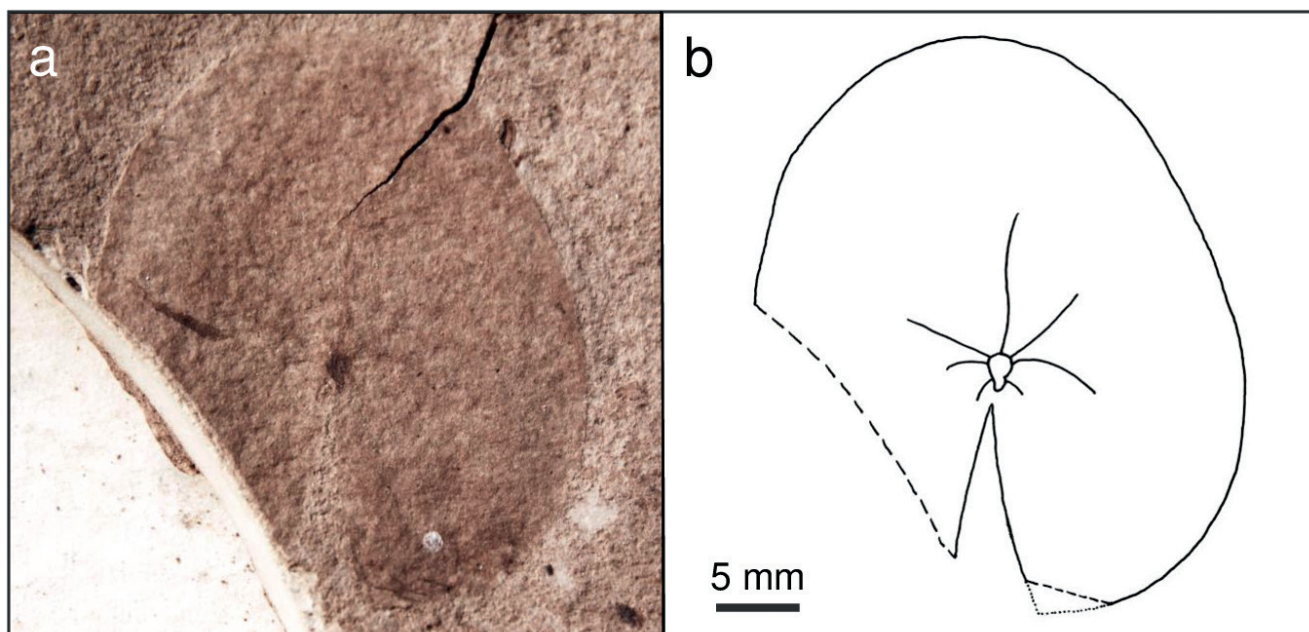
1991 *Nuphar* sp.; Rember, table 1 on p. 52, appendix B on pp. 117, 122 (leaf not figured).

**Provenance.** Locality P-33 at the Fossil Bowl Racetrack site, 115.5 cm down from the top of the section A as measured by Rember (1991: 32, fig. 5); Idaho, USA.

**Stratigraphy.** Wanapum Formation of the Columbia River Basalt Group.

**Age.**  $15.78 \pm 0.039$  Ma, Middle Miocene (cf. Höfig et al. 2021).

**Repository.** *Clarkia* fossil collections, Morrill Hall, University of Idaho in Moscow, USA (no inventory number).



Text-fig. 2. *Nymphaea* sp. from the Miocene Clarkia Lake flora, Locality P-33. a: Photograph of the fossil leaf. b: Sketch of leaf showing the salient features of shape, basal lobes and margin, eccentric insertion point of the abaxial petiole, and primary actinodromous venation. Dashed lines represent torn edge of lamina; dotted line is outline of right basal lobe. Line drawing by P. Martin Sander. Scale bar applies to both photo and drawing.

**Description.** The fossil leaf is represented by a single specimen, which is oriented with its adaxial surface facing upward on the sediment surface (Text-fig. 2a, b). It has the eccentric peltate petiole attachment typical of many aquatic leaves. A dark spot on the adaxial side of the lamina represents the point of petiole insertion on the abaxial side of the leaf. The petiole insertion point is dark, robust, and located about 1 mm distal to the basalmost leaf margin. The petiole itself is not visible, because it is presumably attached at an angle to the abaxial side of the leaf lamina.

Using the morphological characters and character states given by the Leaf Architecture Working Group (1999) and Ellis et al. (2009), the fossil specimen can be described as follows. The leaf is simple and has an entire margin without any undulations. The leaf measures 3.8 cm in maximal length, from leaf apex to the end of basal lobe, and 3.2 cm in maximal width at its widest point which is about 2.3 cm from the leaf apex. Hence, the leaf laminar area defines a microphyll, with a laminar length/width ratio of 1.2, and leaf shape is widely ovate in general outline. Leaf apex angle is obtuse, while the leaf apex shape is rounded. Leaf base angle is acute, and leaf base shape is cordate, whereby the leaf base is embayed in a narrow sinus with extremely straight margins until it curves at the end of the lobes. The leaf sinus between the basal lobes is deep, measuring 1.2 cm or 30 % of leaf length.

The venation on the lamina is visible only near the base of the leaf. The primary vein category is basal actinodromous, with at least three lateral primaries radiating from the petiolar insertion point on either side of the slightly thicker medial primary vein. The medial primary vein, or midvein, runs toward the leaf apex and would measure 2.2 cm when it reaches the margin, but is only clearly visible in the proximal 1 cm of its length. The lateral primaries are visible for a few millimeters to roughly 6 mm of their length. Lateral secondary veins and higher venation cannot be observed.

**Remarks.** The characteristics preserved in the Clarkia leaf are well within the range of variation in living water lilies of the Nymphaeaceae (cf. Taylor 2008, Taylor and Gee 2014, Gee and Taylor 2019), not only morphologically as described above, but also after a more critical analysis of single characters using phylogenetic analysis. To examine its relationship to the family Nymphaeaceae and living genera, we first entered the data of the Clarkia leaf into a previously constructed data matrix comprised of the living-taxa data of Gee and Taylor (2019), then conducted the analysis. The phylogenetic analysis shows that the fossil leaf is well-embedded within the order Nymphaeales and family Nymphaeaceae. Even with the lack of fine venation, the phylogenetic analysis yields bootstrap support for the fossil leaf within Nymphaeales (68 %), but not within the *Nuphar* clade. Furthermore, mapping the Clarkia *Nymphaea* leaf on fig. 5 of Gee and Taylor (2019) also shows that it shares many synapomorphies with the Nymphaeales: 5, floating leaves usually peltate; 10, leaf base angle wide obtuse; 11, leaf apex angle obtuse; 19, primary veins actinodromous. Characters 5 and 10 are universally found in the order. Synapomorphies for Nymphaeaceae are also shared: 9, sinus length ratio 0.21 to 0.40; 12, leaf base cordate; 14, base margin curved; 15, cordate lobe shape with rounded point;

16, peltate base very eccentric. In this case, character 12 is universal for the Nymphaeaceae.

The Clarkia leaf differs in several ways from *Nuphar* leaves by exhibiting characters not found in *Nuphar*: 8, length/width ratio 1 to 1.29; 13, apex rounded; 18, medial slightly thicker than lateral primaries; 19, actinodromous. These differences restrict the relationship of the fossil leaf to the clade that encompasses *Nymphaea*, *Barclaya* WALL., and *Euryale* SALISB./*Victoria* LINDL.

Within the *Nymphaea-Barclaya-Euryale/Victoria* clade, the Clarkia leaf lacks the short cordate base of *Barclaya*, as well as the nearly central peltate attachment of the petiole and palinactinodromous primary venation of the *Euryale/Victoria* clade. Its placement is confirmed when the Clarkia leaf is put into a key of leaves of living Nymphaeaceae genera (cf. Taylor 2008). Based on the characters preserved in the Clarkia leaf, it fits best in the genus *Nymphaea*. Thus, the phylogenetic analysis is consistent with our assignment of the fossil leaf based on gross morphology to *Nymphaea*. The lack of details in the higher venation merely precludes identification at the species level, but not at the generic level.

**Frequency in the leaf assemblage.** The single specimen of *Nymphaea* in the Clarkia leaf flora is a rare occurrence. It is the only such leaf in the entire collection made by Rember in 1976. If the leaf count made in only the 90 to 120 cm interval of section A is considered, the water lily leaf makes up 0.1 % of the 774 leaves found in this 30 cm stratigraphic interval. If the entire Clarkia collection described by Rember in 1991 is taken into account, the frequency of water lily leaves in the assemblage becomes even smaller, amounting to 0.01 % of the 10,641 specimens collected in the systematic sampling of section A.

## Discussion

As discussed above, there is overwhelming morphological and phylogenetic evidence supporting the identification of the Clarkia leaf to *Nymphaea*. Both the morphological and phylogenetic analyses are consistent with one another. Despite the lack of details in the higher venation, the Clarkia leaf can be confidently identified to the genus level. Hence our assignment of the fossil leaf to *Nymphaea* sp.

### Leaf size

The *Nymphaea* sp. leaf from Clarkia is small in size. However, there are some living species of *Nymphaea* that have small leaves. *Nymphaea tetragona* GEORGI growing in northern Russia, for example, has small leaves averaging from 5 to 9 cm in length (Volkova and Shipunov 2007). The lower size range of *N. tetragona* reaches 4 cm, which is comparable to the Clarkia leaf length of 3.8 cm.

The well-known species *Nymphaea odorata* AITON, has floating leaves that grow from 12.7 to 30.5 cm in length in Missouri, USA (e.g., Whitley et al. 1999). However, the submerged leaves of a *Nymphaea* species with relatively large floating leaves can be quite small. When the leaves of *N. odorata* were studied in Florida, it was observed that juvenile leaves that were submerged in 30, 60, or 90 cm in depth measured only 2.5, 3.5, or 3.4 cm long on average,

respectively (Richards and Cao 2012). The sizes of these young, submerged leaves are considerably smaller than that of the *Clarkia Nymphaea* leaf.

It should also be noted that there is a major difference in morphology and lamina thickness between floating and submerged leaves of *Nymphaea*. The floating leaves have a deep sinus, are ovate to orbicular in shape, and have a leathery lamina, while the submerged leaves of *Nymphaea* spp. are usually sagittate, filmy, and delicate (Cook 1996).

Given the small size of the *Clarkia Nymphaea* leaf, plus its orbicular shape and thick leathery lamina, it is highly likely that the *Clarkia* fossil represents an immature floating leaf. Another line of evidence supporting the leaf as young and newly emerged is the unblemished state of the lamina which shows no evidence of insect herbivory. Most leaves in the *Clarkia* fossil flora are riddled with numerous instances of insect herbivory, such as hole feeding, margin feeding, and galls (Gee, own observations), which is not unexpected given what must have been a sizeable insect fauna in the warm climate of the Miocene Climate Optimum at *Clarkia* Lake (Harris 2016).

In addition to the morphological and phylogenetic results discussed in the previous section, additional botanical, evolutionary, palaeontological, floristic, and taphonomic aspects of the *Nymphaea* sp. leaf in the *Clarkia* flora can be considered.

#### Affinities based on venation

The *Nymphaea* sp. leaf from *Clarkia* is clearly peltate. Among angiosperms, peltate leaves are relatively rare (Cook 1996), and most aquatic plants with peltate leaves share a lack of agrophic support veins in their basal lobes (Taylor and Gee 2014). In the leaves of terrestrial plants, the agrophic veins appear to provide support for the basal lobes, while in the peltate leaves of floating aquatic plants, these veins are unnecessary as the water supports the entire leaf. Since agrophic veins are similar in vein size to the lateral vein from which they originate, if the *Clarkia* leaf were to pertain to a terrestrial plant, we would expect to see them even in this moderately preserved fossil. However, agrophic veins do not occur in the *Clarkia* leaf. Thus, the combination of the peltate shape of the leaf and a lack of agrophic veins is an additional line of evidence supporting the assignment of the *Clarkia* leaf to a floating aquatic angiosperm, and not to a terrestrial plant.

Among aquatic angiosperms, only two families have similar, peltate leaves: the Nymphaeaceae and Menyanthaceae DUMORT. Many members of Menyanthaceae are aquatic (Cook 1996), however, there is only one genus – *Nymphoides* SEG. – that has floating, cordate or peltate leaves that are palmately veined with a medial primary with three pairs of lateral primaries, an ovate shape, a blunt apex, and a strongly curved-sided, open sinus. While technically not a true water lily, which is limited to the order Nymphaeales or family Nymphaeaceae, the leaves of *Nymphoides* are superficially similar in appearance to *Nymphaea*, hence its Latin name. The fossil leaf from *Clarkia* does show many of these characteristics, except it does not share the distinctive curved-sided, open sinus of the cordate base of extant *Nymphoides* leaves. Instead, the fossil leaf's cordate

base has a straight-sided to slightly curved sinus margin and is narrowly closed. Thus, based on the morphology of the leaf base, in addition to the well-embedded placement of the fossil leaf in the genus *Nymphaea* as shown by phylogenetic analysis, an assignment to *Nymphoides* is quite unlikely.

#### Comparison of deep-time records

It should also be noted that the very different palaeontological records of *Nymphaea* and *Nymphoides* argue strongly against the occurrence of *Nymphoides* at *Clarkia*. In *Nymphoides*, seed characteristics are highly diagnostic (Tippery and Sokolik 2020). If *Nymphoides* had evolved by the Miocene, we would expect to find a fossil record of its seeds. Instead, beyond a few reports of *Nymphoides* seeds or pollen from the Plio-Pleistocene (e.g., Watts 1971, Bhandari et al. 2009, 2010), *Nymphoides* fossils from deeper-time Cenozoic, and in particular, leaves, are unknown. More importantly, molecular clock analyses suggest a base age of 6.7 million years for the living crown species of *Nymphoides* (Tippery et al. 2018). Thus, from palaeontological and molecular perspectives, it is most likely that the *Clarkia* leaf pertains to *Nymphaea*, a genus with a deep and extensive fossil record that starts in the Late Cretaceous, continues through the Paleogene and Neogene, and survives to the present day.

#### Geological record of *Nymphaea*

Water lilies are some of the very first angiosperms to appear on earth and show up in the fossil record in the Early Cretaceous (Friis et al. 2001). The order Nymphaeales has been identified through fossil leaves, fruits, seeds, and rhizomes since the onset of palaeobotanical publishing some 166 years ago (e.g., de Saporta 1861, Engelhardt 1922, Cevallos-Ferriz and Stockey 1989, Wehr and Manchester 1996, Dobruskina 1997, Friis et al. 2001, 2009, Gee and Mörs 2001, Chen et al. 2004, Gandolfo et al. 2004, Taylor et al. 2006, 2008, Mohr et al. 2008, Taylor 2008, Coiffard et al. 2013, Taylor and Gee 2014, DeVore et al. 2015, Gee and Taylor 2016, 2019).

The oldest leaves that can be assigned to the genus *Nymphaea* come from the Late Cretaceous (Dobruskina 1997, Taylor and Gee 2014), whereas the geological records of *Nuphar* first begin in the late Paleocene (DeVore et al. 2015 and references therein). Up to now, fossil *Nuphar* has been identified by reproductive parts such as flowers, fruits, and seeds, or occasionally as rhizomes with roots and leaf scars (DeVore et al. 2015 and references therein). It should be noted that fossil leaves have not been assigned to *Nuphar* leaves with confidence (DeVore et al. 2015), although a leaf form transitional between *Nuphar* and *Nymphaea*, the extinct genus *Nuphaea* GEE et DAVID W. TAYLOR has been described from the Eocene (Gee and Taylor 2019).

#### Palaeoclimate

Among living Nymphaeaceae with leaves showing eccentric peltate petiole attachment, *Nymphaea* and *Nuphar* grow in temperate climates, while *Victoria* and *Euryale* thrive under more tropical conditions. In the mid-Miocene, the plants growing in what is now northern Idaho would have enjoyed a warm temperate climate without

freezing temperatures; it has been estimated that mean annual temperatures were above 11 °C and coldest month mean temperatures were above 5 °C (Harris 2016). For the Middle Miocene flora Red Lake macroflora in nearby southern British Columbia, Canada, the climate was reconstructed as similarly temperate and mesic, with mild winters. Here, climatic parameters were further refined to reflect mean annual temperatures between 11 to 13 °C, with a coldest month mean temperature of ca. 3 °C, and moderate seasonality which also shows up in differences in precipitation (Greenwood et al. 2020). In general, aquatic plants are less affected by water stress so that drier conditions due to reduced precipitation would have played a lesser role in their biogeography.

### Fossil *Nymphaea* pollen

Fossil *Nymphaea* pollen has not been reported from the Clarkia Lake deposits, but it is difficult to rule out the occurrence of *Nymphaea* in the Clarkia flora on this basis, because extensive palynological studies have not been carried out (cf. Smiley et al. 1975, Gray 1985). However, it should be noted that *Nymphaea* pollen has been described from other, coeval lake deposits from the Middle Miocene of the Pacific Northwest, namely at Succor Creek in Oregon and Palouse Falls in Washington state (Dillhoff et al. 2014). *Nymphaea* water lilies were thus members of the aquatic macroflora of the freshwater lakes in the Pacific Northwest during the Miocene Climatic Optimum.

### Taphonomic observations

When water lilies colonize freshwater habitats today, their leaves occur in huge abundance. If Cenozoic Nymphaeaceae had a similar growth habit, this profusion of leaves increases the likelihood of at least one leaf entering the fossil record, compensating for the rapid decay of water lily leaf tissue and their susceptibility to insect damage (cf. Klok and van der Velde 2019), both of which diminish the changes of fossilization. Thus, it would be expected that fossil water lily leaves in an ancient pond or lake would make up a sizeable proportion of any fossil plant assemblage in these depositional environments. Yet, the remains of aquatic macrophytes are strangely uncommon in freshwater deposits of the Cenozoic (e.g., Gee and Mörs 2001, Gee and Taylor 2016), even if the occurrence of one nymphaealean leaf or seed indicates that water lilies had colonized that body of water. As mentioned earlier, in the Clarkia flora, the rate of occurrence of aquatic macrophyte fossils is low, at 0.01 % among 10,000 fossils. In other ancient freshwater deposits well known as conservation lagerstätten, such as the Eocene lake at Messel or the Oligocene lake at Rott, both Germany, water lily fossils make up a very small proportion of the entire fossil flora (e.g., Collinson et al. 2012, Gee and Taylor 2016, 2019), although *Nymphaea* or *Nuphar* may have actually been a common water plant in those Cenozoic lakes. Instead, the leaves of dicot trees dominate the fossil assemblages. Most of these broadleaved trees would have grown in the drier, wooded areas surrounding the lake. The conifer foliage also found in the pond and lake facies would have mostly pertained to conifers that preferred the moist soils along the lake shoreline.

### Floristic implications

Besides the Clarkia fossil lagerstätte, there are nearly 20 other Miocene sites in the American Pacific Northwest and southwestern Canada – from Washington state in the west to Idaho in the east, from British Columbia in the north to Oregon in the south – with extensive Miocene leaf floras (most recently summarized by Greenwood et al. 2020). Like the Clarkia flora, these plant assemblages are dominated by dicot and conifer foliage of the mixed mesophytic forest (e.g., Berry 1929, 1934, Hollick 1927, Brown 1935, Smith 1941, Graham 1963, Baghai and Jorstad 1995, Buechler et al. 2007, Dillhoff et al. 2014, Greenwood et al. 2020). When compared to the Neogene of Europe, the conifer floras in Clarkia and Europe share nearly all genera (Kvaček and Rember 2000).

Although most of the floras in the Pacific Northwest were deposited in freshwater facies, as was the Clarkia flora, megafossil evidence of aquatic macrophytes is uncommon and, until now, have been limited to eight specimens pertaining to five taxa among the tens of thousands of dicot leaf specimens. One leaf of *Caldesia* was reported from the Clarkia flora (Smiley and Rember 1985b, Haggard and Tiffney 1997), while two others are still undescribed (Rember, own data). One leaf each of *Potamogeton* L. and *Palaeopotamogeton* KNOWLT. occur in the Spokane flora in Washington state (Berry 1929). In Idaho, a single fruit of *Trapa* L. was described from Potlatch Creek (Brown 1935), while two specimens of *Ceratophyllum* L. shoots were found at Pickett Creek (Buechler et al. 2007). The single leaf of *Nymphaea* sp. from Clarkia newly described here constitutes the ninth specimen of six taxa of aquatic macrophytes, as well as the first megafossil leaf evidence that water lilies were also been part of the Miocene aquatic macroflora in the Pacific Northwest.

Occurrence of these aquatic macrophytes, however rare, suggest that the Miocene freshwater plant assemblages in North America may have been similar to and as species-diverse as those in the Miocene of Europe (cf. Mai 1985, 1995, Martín-Closas 2003). *Ceratophyllum*, *Nymphaea*, *Potamogeton*, and *Trapa*, including *T. kvacekii* WÓJCICKI et D. VELITZELOS (Wójcicki and Velitzelos 2007), are common Miocene water plants in the open water habitat in Central Europe (Mai 1995: 526) and are also found in the La Cerdanya flora of Spain (Martín-Closas 2003). The unusually low numbers of water plants in the Miocene lacustrine record of the Pacific Northwest and southwestern Canada, as discussed here, can thus be attributed to taphonomic factors. While a deeper biostratigraphic analysis of the scarcity of fossil water plants in lacustrine facies is beyond the scope of this paper, it should be noted the single occurrence of an aquatic macrophyte among the vast numbers of dicot and conifer leaves collected for the last half century from the ancient freshwater Clarkia Lake follows the taphonomic pattern observed in other nearby Miocene plant assemblages.

### Conclusions

A single fossil leaf from the Miocene Clarkia flora is identified here as a young, floating leaf of *Nymphaea* sp., Nymphaeaceae, on the basis of its form, petiole attachment, venation, and lamina thickness. The eccentric peltate leaf is

ovate in shape with a cordate base, a deep basal sinus, entire margins, and actinodromous primary venation. Despite the lack of details in higher venation, phylogenetic analysis of existing characters is consistent with this assignment. In addition to its morphology and venation, the extensive palaeontological history of the genus *Nymphaea* from the Late Cretaceous onwards and the growth habit of the living genus are also taken into consideration. The small, unblemished nature of the leaf points to a newly emerged leaf of *Nymphaea* sp. The occurrence of a single water lily leaf among tens of thousands of dicot and conifer leaves in a lacustrine environment follows the taphonomic pattern of other nearby Miocene floras. Describing and identifying this leaf supplements the taxonomic composition of the well-known Clarkia flora, supports the likely presence of *Nymphaea* water lilies in region during the Middle Miocene, and helps to complete our understanding of Miocene plant life in the Pacific Northwest 16 million years ago.

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