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Remberella, a new genus of extinct ericalean flower from the Middle Miocene Latah flora of Washington and Idaho, USA

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ABSTRACT. Small pentamerous floral remains commonly encountered in Middle Miocene lake deposits of the Latah Formation of Washington and Idaho, USA, previously assigned to *Diospyros*, are here shown to represent an extinct genus. Newly recovered specimens preserve characters of the androecium and pollen that were previously unknown. *Remberella microcalyx* (Knowlton) gen. et comb. nov. flowers are actinomorphic, with five basally connate petals having an adnate androecium including ten staminodes and ten stamens. The elongate-triangular anthers contain finely rugulate, triaperturate pollen. The combination of pentamerous sympetalous corolla, ten staminodes in two whorls and ten stamens adnate to the corolla indicates affinity with early divergent superasterids, likely the Ericales, with intriguing similarities to Ebenaceae. Although the Miocene flora includes many genera confidently assigned to extant genera, *Remberella* adds to a growing number of contemporary extinct genera.

KEYWORDS: Ebenaceae, Tertiary, Neogene, western North America, extinct

INTRODUCTION

The Middle Miocene flora of the Latah Formation, representing lacustrine interbeds of the Columbia River Basalt series, is known from sites in eastern Washington and northern Idaho, USA. Best known for fossil leaves (Knowlton, 1926; Berry, 1929; Smiley and Rember, 1979), the sites also yield occasional reproductive structures. The flora represents mixed mesophytic vegetation diverse in temperate taxa, such as *Acer* L. 1753, *Fagus* L. 1753, *Liquidambar* L. 1753, *Liriodendron* L. 1753, *Ostrya* Scop. 1760 and *Platanus* L. 1753. The flora includes many taxa that are exotic to the region today, including some that are centered in eastern Asia today, such as *Cunninghamia* R. Br. 1826, *Metasequoia* Hu et W.C. Cheng 1948, *Cercidiphyllum* Siebold et Zucc. 1846, *Tetracentron* Oliv. 1889, *Trochodendron* Siebold et Zucc. 1839 and *Pterocarya* Kunth 1824 (Smiley and Rember, 1979, 1985; Kvaček and Rember, 2000; Manchester and Chen, 2006; Manchester et al., 2018). Also included are some extinct genera, such as *Pseudofagus* Smiley et Huggins (1981), *Nordenskioeldia* Heer 1870 (Manchester et al., 1991), *Buzekia* Manchester (1999), *Ozakia* Manchester et Uemura (2013) and *Juddicarpon* Smith et Manchester (2019).

Aside from catkins of Betulaceae Gray 1822 and Fagaceae Dumort 1829, one of the more common flower types preserved in the Latah flora is represented by isolated pentamerous perianths that were initially named *Diospyros*? *microcalyx* (Ebenaceae Gürke 1892) by

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Knowlton (1926), then reassigned to *Porana microcalyx* (Convolvulaceae Juss. 1789) by Berry (1929). In their review of Miocene floras of the Columbia Plateau, Chaney and Axelrod (1959), demoted this species to incertae sedis. The identity of these flowers has been difficult to confirm because they are represented only by the corolla, apparently having fallen away from the rest of the flower so that features of gynoecium and androecium have remained unknown.

Newly recovered specimens bearing intact stamens with *in situ* pollen provide more characters for assessment of affinities. Here we describe their morphology in greater detail, and attribute them to a new fossil genus, *Remberella*. We consider its possible affinities relative to extant taxa.

MATERIAL AND METHODS

The fossils considered here are found at sites in eastern Washington, and adjacent northern Idaho, USA, in interbeds of the Columbia River Basalt group (Fig. 1). The flowers initially investigated by Knowlton (1926) and Berry (1929) were collected from a deep railroad cut situated at ~47.6183333°N, 117.4456972°W in eastern Spokane, Washington, USA. The fossil-bearing sediments at that site are associated with the Grande Ronde Basalt (Derkey et al., 2004), indicating an age likely in the range of 16.1–16.5 Ma (Kasbohm and Schoene, 2018; Kasbohm et al., 2023). Many additional specimens were collected by William C. Rember from the sites at Clarkia Race Track (UF loc 15888; 46.991450°N, 116.276600°W) and Emerald Creek (UF 18596, 47.032841°N, 116.338254°W), near Clarkia Idaho, associated with the Priest Rapids Member of the Wanupum Basalt indicating an age in the range of 15.9 to 16.1 Ma (Kasbohm and Schoene, 2018). A few specimens were also recovered from Oviatt Creek, Idaho (~46.7416417°N, 116.2665833°W), believed to be similar in age to the Clarkia Race Track flora, but situated 27 km to the south (Boyd, 1991). The studied specimens are housed in the paleobotanical collections at the University of Idaho, the Florida Museum of Natural History at University of Florida, Gainesville (UF), and the Smithsonian National Natural History Museum, Washington, DC (USNM).

Fossils from the Clarkia Race Track site are organically preserved with intact tissues. Although pristine when collected from the damp shales, the tissues begin to crack and detach from the underlying impression on drying. Therefore, best images were obtained from freshly collected specimens. Standard macrophotographs were taken with a Canon Xsi digital SLR camera equipped with an EFS 60 mm macro lens. High resolution reflected light images were obtained with a Keyence VHX-7000N digital Microscope, using the

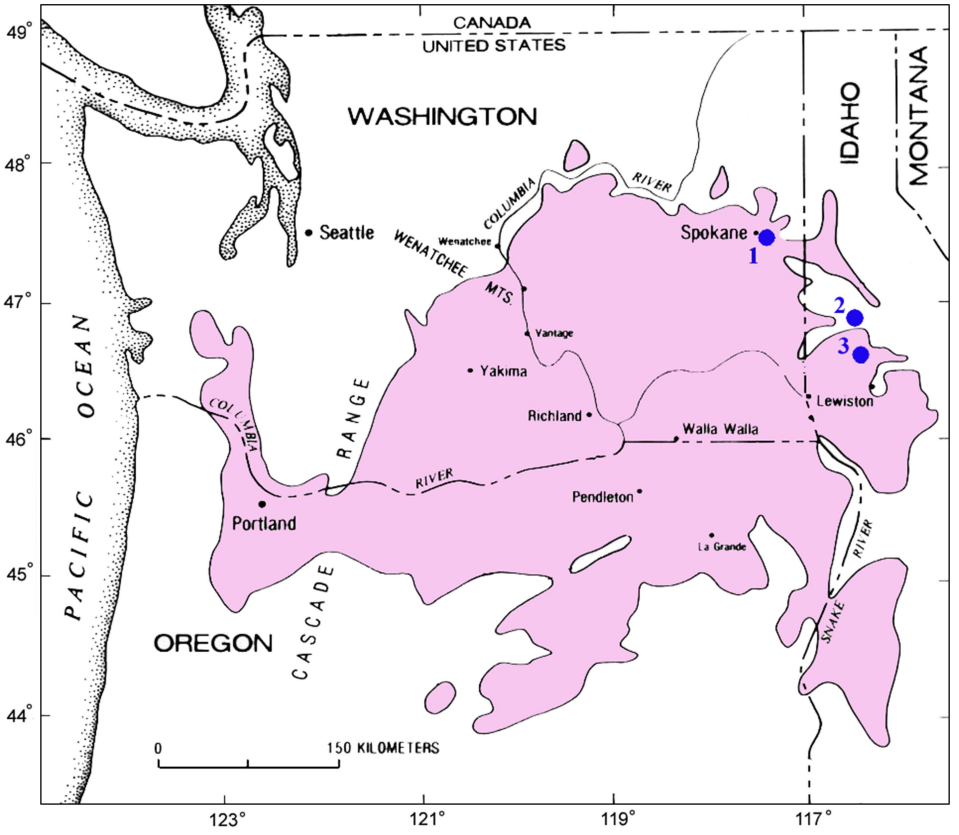

Figure 1. Map showing the sites in Washington and Idaho where *Remberella* flowers have been collected, near the eastern margin of the Middle Miocene Columbia River Basalt Group (shaded in pink). Localities: **1**. Spokane brickyard, **2**. Clarkia race track and Emerald Creek (two sites presented in more detailed map of Smiley and Rember, 1979), **3**. Oviatt Creek. Base map from Swanson and Wright (1981)

shadow effect function to enhance contrast and facilitate observation of cell outlines. Micro-CT scanning was carried out with a GE Phoenix V|Tome|X M dual-tube nano-CT system at the University of Florida Nanoscale Research Facility to reveal attached stamens hidden within the sediment. We used settings of 129 kV and 200 µA, with 2100 images taken at 131 ms, yielding a voxel size resolution of 27.1 µm. CT-generated volumes were visualized with VG studio max and Amira.

SYSTEMATICS

Genus ***Remberella***
Manchester et Judd **gen**. **nov**.

Plant Fossil Names Registry Number. PFN003359 (for new genus).

Generic diagnosis. Flower actinomorphic with corolla of five basally connate petals shed from the gynoecium leaving a central hole in the corolla. Pedicel, calyx and gynoecium unknown. Corolla lobes obovate, 1.4–1.6 times longer than wide, rounded apically, with faint, longitudinal striation from the alignment of epidermal cells. Basal part of the corolla with ten sessile staminodal anthers in two whorls of five, surrounded by ten stamens. Stamens nearly sessile; anthers basifixed, elongate-triangular, basally rounded and apically pointed, about twice as long as wide. Pollen prolate, triaperturate with long colpi, finely rugulate ornamentation.

Species diagnosis. Same as for genus.

Etymology. These little flowers are named in honor of William C. Rember recognizing his contributions to understanding of the geology and paleobotany of fossil floras associated with the Columbia River Basalts in northern Idaho.

Type species. *Remberella microcalyx* (Knowlton) comb. n.

Remberella microcalyx
(Knowlton) **comb**. **nov**.

Figs 2–5

Basionym.

1926 *Diospyros*? *microcalyx* Knowlton 1926, U.S. Geol. Survey Prof. Paper 140-A, p. 46, pl. 22, figs. 5, 6.

1929 *Porana microcalyx* (Knowlton) Berry, 1929, U.S. Geol. Survey Prof. Paper 154, p. 263.

Lectotype. Here designated. USNM36966, from Spokane, Washington (Knowlton, 1926: pl. 22, fig. 5; here refigured, Fig. 2A).

Additional specimens studied. From Emerald Creek, Idaho: UF18596-52581, 18630-59073, 59074. From Oviatt Creek, Idaho: UF18343-25424, 25425. From Clarkia Race Track, Idaho: UF15888-62715, 62716, 62717, 62718, 62719, 62720, 62721, 69863, 69865, 70140, 70142, 70144, 70145, 71376, 71474, 71475, 71476, 71477.

Description. The flowers are preserved as dispersed radially symmetrical, pentamerous corollas 6–8 mm wide, with a central circular hole, ~1.5 mm in diameter, indicating where they detached from the gynoecium and pedicel (e.g. Figs 2F, 3I). Corolla lobes are obovate and rounded apically, slightly reflexed, with faint, longitudinal striations due to alignment of epidermal cells (Figs 2F, 3C) but without obvious venation. Epidermal cells of the thickened inner collar of the corolla relatively large and rectangular, 25 µm wide and 27–67 µm long, while those of the radiating corolla lobes are narrower, 10–13 µm wide. Trichomes apparently absent. The thickened central rim of the corolla is marked by ten sessile staminodia in two whorls, the lowermost opposite the corolla lobes (Figs 2D, 3D, G) and the upper whorl alternating with the corolla lobes (Fig. 3B, H). Stamens are epipetalous, nearly sessile with short filaments (Fig. 3F, J, K), with ten stamens of equal size possibly in a single whorl, or perhaps in two whorls of five (Fig. 3F). Anthers (Figs 2H, I, 3E, F) are basifixed and sagittate, basally rounded, apically pointed, 1–1.2 mm long, 0.4–0.5 mm wide, about twice as long as wide. Pollen (Fig. 4E–I) is prolate, 17–21 µm in polar diameter, 11–13 µm in equatorial diameter. The colpi are long, extending 90% of the length of the grain. We suspect that the grains are tricolporate with indistinct endopores, but were unable to resolve pores with certainty. The grains are psilate by light microscopy but are seen by SEM to possess finely rugulate ornamentation with microspinules on the rugulae (Fig. 4I).

All specimens show the petals to be basally connate. The central hole in the corolla, where it detached from the rest of the flower, is slightly recessed, representing the edge of a short tube to which the staminodes and stamens are attached (Figs 3K, 4A–C). When both shale counterparts of a transversely cleaved specimen are inspected carefully, one side, representing the lower face of the corolla, shows

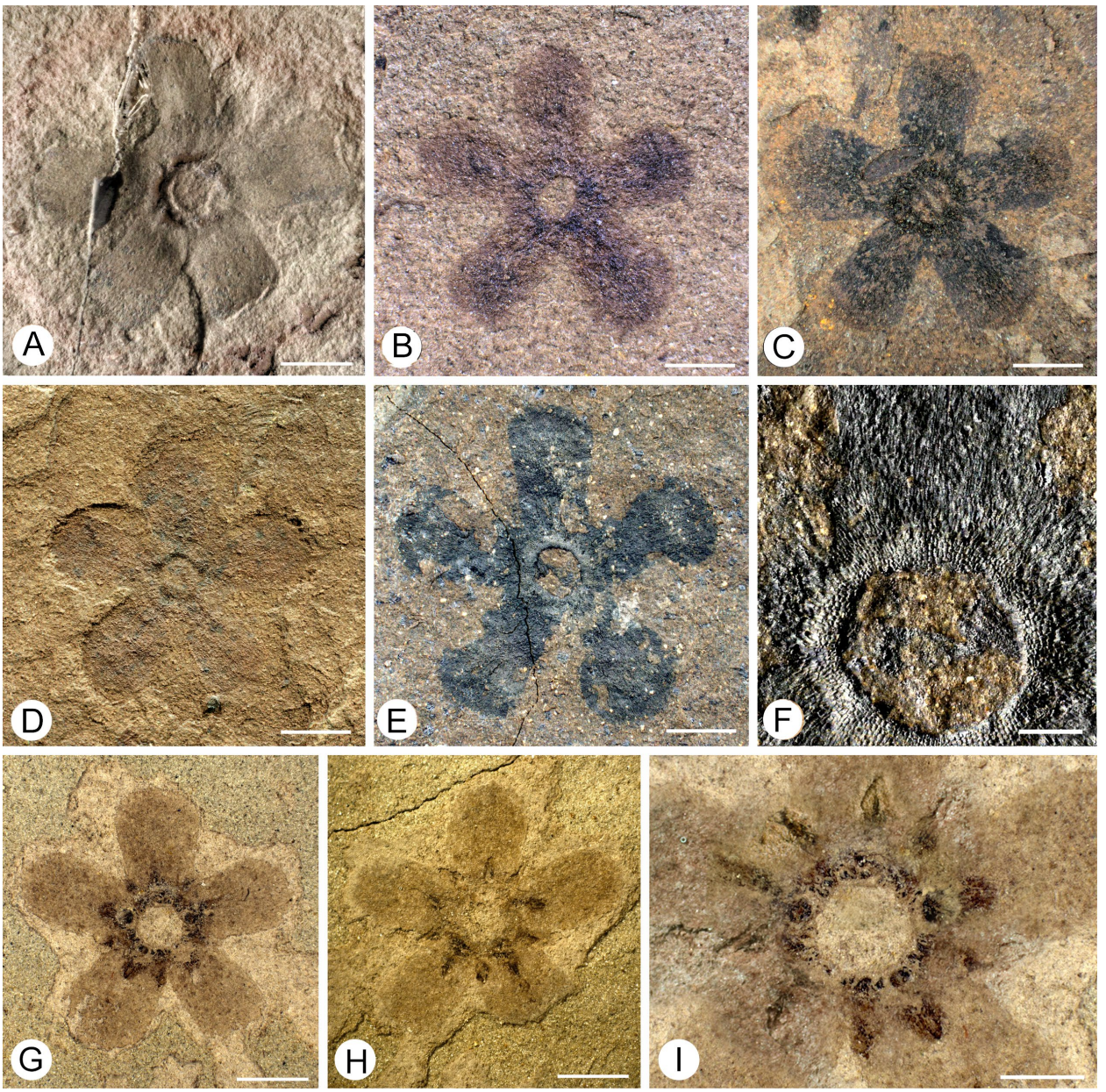

Figure 2. *Remberella microcalyx* (Knowlton) comb. nov. flowers by reflected light. **A**. Lectotype, corolla from Spokane Railroad cut, Washington, USNM36966; **B**. Specimen from Oviatt Cr., Idaho, UF18343-25425; **C**. Corolla showing thickened central rim, from Clarkia race track, Idaho, UF 15888-71475; **D**. Impression specimen showing whorl of five staminodes lining the central rim of the corolla, UF15888-71475; **E**. Freshly collected specimen with intact dark cuticle, UF15888-62717; **F**. Enlargement of the specimen from E, showing cellular striations radiating from the center and running parallel to the long axis of the corolla lobe; **G–I**. Corolla with intact androecium from Emerald Creek, Idaho, UF18596-52581, **G**. Basal counterpart, showing ten staminodes lining the central aperture, surrounded by a circle of partially preserved stamens, **H**. Apical counterpart showing triangular anthers better exposed than in G, **I**. Enlargement of the androecium, blending the images of the two counterparts, G and H, to show the best resolved staminodes and anthers. Scale bars = 2 mm in A–E, G–I, 0.5 mm in F

a cycle of bilobed bulges lining the central hole (Figs 2D, 3A, D, G, 4A, D), one aligned with each lobe of the corolla, which we interpret to be a lower whorl of sessile staminodes. When the other side of the transversely split flower is observed, a second cycle of five bulges (Fig. 3F, I), identical in morphology to those below, is seen to be interspersed, alternating with the corolla lobes (Fig. 3C, E, H). These staminodes are slightly higher in the sediment, indicating they were situated slightly higher on the floral tube. We considered other explanations for these structures, such as filament bases of detached whorls of stamens, but their smooth margins and bilobed appearance with a median cleavage resembles diminutive anthers, supporting the staminode interpretation. Among the numerous specimens studied, no larger, functional stamens were observed in this position, optically or in micro-CT scanning.

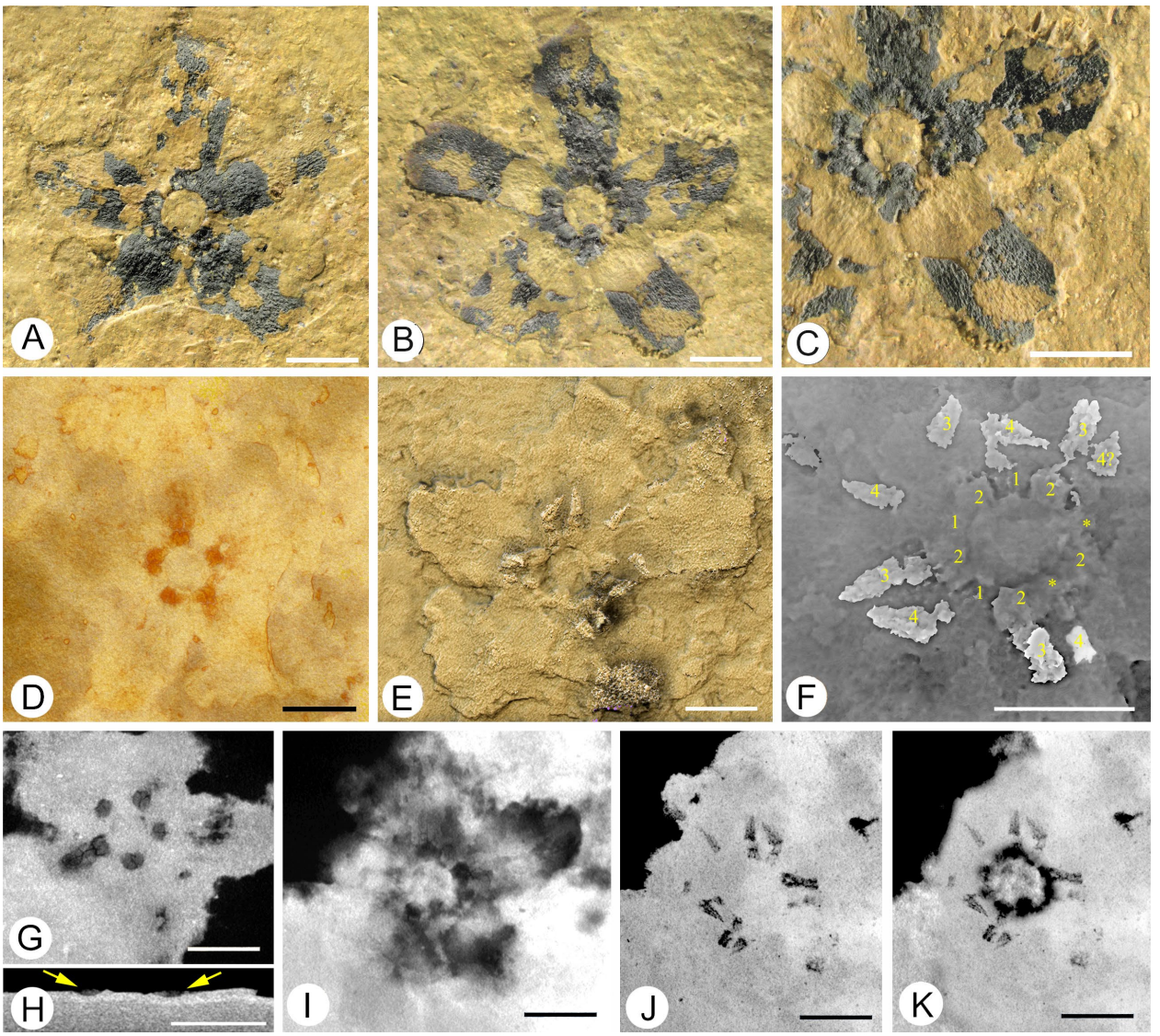

Figure 3. *Remberella microcalyx* (Knowlton) comb. nov., one specimen, part and counterpart (UF15888-62175), from Clarkia Race track, Idaho, by reflected light (A–C), and X-ray (D–J). **A**. Basal counterpart, reflected light, showing five staminodes, each aligned surrounding the central hole in the corolla and positioned opposite each corolla lobe; **B**. Apical counterpart, reflected light, showing ten staminodes including the same whorl seen in A, plus an additional whorl organized alternate with the corolla lobes; **C**. Enlargement from B, showing cellular striation of corolla, and organization of the staminodes at base of the corolla; **D–J**. Micro-CT scan imagery, **D**. Same piece as A, volume rendering with translucency showing sessile, bipartite organization of the staminodal anthers, **E**. Surface rendering of the stamens hidden from optical view of the counterpart in B, C, showing paired stamens encircling the staminodes, **F**. Detail from E, depth map showing successive whorls of the androecium, including lowermost whorl of five staminodes (labeled 1), the next whorl of staminodes (labeled 2), and the stamens inferred to be in two closely adjacent whorls, labeled 3, and 4. Two of the five lower staminodes, indicated by *, are more clearly seen in the counterpart impression shown in A, D and G, **G**. Digital thick section of the specimen in A, skimming the surface, with airspace black, with clear outlines of the five lowest staminodes and outline of two or three stamen anthers, **H**. Digital thick section longitudinal to the flower, transecting two of the staminodia seen in G, **I**. Digital thick section of counterpart specimen from B, C, showing outlines of the ten staminodia, including a second whorl alternate with the corolla lobes that is not visible in H, **J**. Thick section slightly above the level of I, transecting a circle of paired fertile stamens; **K**. Composite image transposing the stamens in J with the staminodia at the level of I. Scale bars = 2 mm

Directly aligned with each of the staminodes, but farther from the central hole, representing a higher level in the flower, are ten triangular anthers that are nearly sessile on very short filaments (Figs 2H, I, 3F, J, K). Most specimens do not show these stamens at the surface, but the anthers are clearly seen on one specimen from Emerald Creek (Fig. 2I), and they are visible by X-ray within the sediment of the upper counterpart of a specimen from Clarkia Race Track (Fig. 3F, G, J, K). It is not obvious in the mature flowers whether the stamens are in a single whorl, or in two closely adjacent whorls of five (Fig. 3F). These observations lead to our illustration of the floral morphology (Fig. 5).

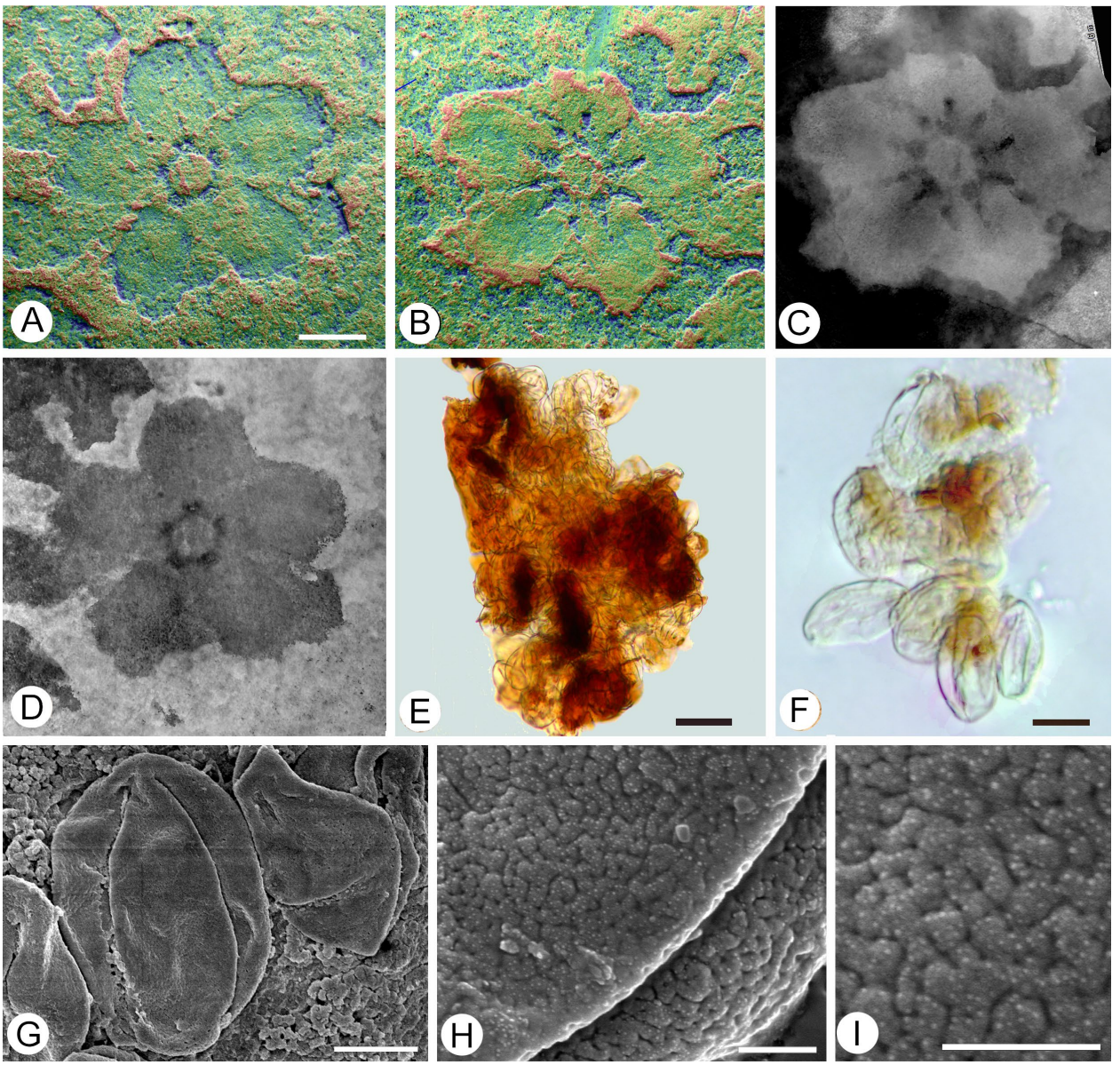

Figure 4. Stamen and pollen from the flower in Fig. 2 G–I, Emerald Creek, Idaho UF18596-52581. **A**, **B**. Optical depth map images of the two counterpart halves with A being the lower half and B being the upper half. Blue color is farther from the viewer, **A**. Part showing one of the whorls of staminodes, each aligned with a corolla lobe, sessile on the inner edge of the corolla, slightly recurved corolla lobe tips, **B**. Counterpart showing the ten staminodes surrounded by ten stamens; **C**. Micro-CT depth map image coinciding with the optical image in B; **D**. Micro-CT depth map image for comparison with the optical image in A; **E–I**. In situ pollen from one of the anthers, **E**, **F**. Transmitted light microscopy showing clumps of prolate tricolpate pollen, **G–I**. Scanning electron microscopy, **G**. Grain showing two of the elongate colpi, **H**. Detail of rugulate ornamentation, **I**. Enlargement showing fine spinules on the rugulae. Scale bars = 2 mm in A (applies also to B–D), 20 µm in E, 10 µm in F, 5 µm in G, 1 µm in H, I

REINTERPRETATION

Only a single whorl of perianth is preserved in the available specimens. In his original description of the flowers, Knowlton (1926: p. 46) stated, “they clearly represent a dry, leathery calyx from which the berry or fruit of some kind has fallen. They are regularly five-lobed, the individual lobes being obovate or oblong and very obtuse and rounded at the apex. The central disk or point of attachment for the berry is over 1 mm in diameter and shows faint outlines of five vascular bundles.” Knowlton’s interpretation that it is a calyx, accepted by Berry (1929), seemed reasonable because the tissues appear to be chartaceous rather than membranous; however, the adnation of androecium to the inner portion of this whorl indicates that it represents the corolla. The calyx likely remained behind, attached to the pedicel and gynoecium on the twig when the corollas were shed. The structures mentioned as outlines of five vascular bundles in the above quotation from Knowlton

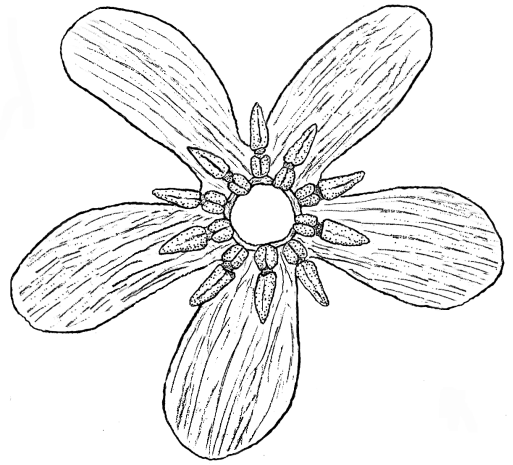

Figure 5. Diagrammatic reconstruction of *Remberella microcalyx* showing the corolla and adnate androecium. Diagram excludes the calyx and gynoecium which remain unknown

are here seen as bipartite staminodal anthers (e.g. Fig. 3G). Although none of the specimens preserves a gynoecium, we conclude that these flowers were probably bisexual because they show a prominent circular aperture at base of the corolla which likely encircled the ovary, and the adnate stamens bear mature pollen.

AFFINITIES

We lack some information that would be helpful to specify the precise affinities of these flowers, such as details of the calyx, gynoecium and fruit type. However, the triaperturate pollen rules out the Magnoliids and indicates a placement in the Eudicots. Furthermore, the pentamerous geometry and synorganized flower (i.e. alternating whorls of floral parts) directs us to the Pentapetalae. Because the corolla is connate, rather than having free petals, it likely represents a member of the Asterid clade (rather than the Rosid clade). Also, the epipetalous stamens support a position among the Asterids (Judd and Olmstead, 2004). Berry (1929) attributed these fossils to *Porana* (Solanales: Convolvulaceae), interpreting the perianth as acrescent in fruit, and considering the central hole to indicate poor preservation of its capsular fruit. However, the organization of stamens (only five) and pollen morphology (Sengupta, 1972) are distinct.

The androecium of this flower is organized in two whorls of five staminodes and ten fertile stamens (Fig. 5). Although we cannot discern that the ten stamens are in two whorls, and we do not have developmental observations for these fossils, the organization of the staminodes is suggestive that development of the entire androecium may have been in four successive whorls of five. Most Asterids have a number of stamens that is equivalent to the number of petals (or fewer), but in this case the number of true stamens is double the number of corolla lobes – a feature characteristic only of some basal members of the Asterids, e.g. Cornales and Ericales (Ronse de Craene, 2010).

The prior assignment to *Diospyros* L. 1753 (Ebenaceae), already questioned by the original author (Knowlton, 1926), deserves reconsideration. The Ebenaceae includes only two extant genera, *Diospyros* and *Euclea* L. 1774, but is quite variable in floral morphology. Some of the general features of *Remberella* coincide with those of Ebenaceae, including sympetalous corolla with reflexed lobes (?) and stamens adnate to the corolla tube with short, flattened filaments (Wallnöfer, 2004). The anthers are apiculate, arrow shaped in dorsiventral view in both, and the pollen ornamentation is, in some cases, similar (Geeraerts et al., 2009). However, the stamens are usually numerous in extant Ebenaceae (2 to ~100 in *Diospyros*, 10 to 30 in *Euclea*; Wallnöfer, 2004), whereas *Remberella* flowers have a fixed number of ten staminodes plus ten stamens. *Diospyros* typically has unisexual flowers, although some species are hermaphroditic, and its perianth ranges from 3- to 8-merous among the species (Wallnöfer, 2004). In Ebenaceae petals are usually reflexed but that condition is not obvious in the fossils. All specimens are preserved in transverse orientation within the sedimentary bedding planes, indicating that the corolla lobes extended outward rather than being apically or basally directed; otherwise, some specimens would be expected to be found lying in lateral orientation. Due to the weight of overlying sediment, we suspect that the corollas became more flattened than in life, but some slight topographic relief (Fig. 4A, B) indicates that they may have been somewhat reflexed.

Diospyros flowers and pollen are confirmed from the Miocene of Denmark (Denk and Bouchal, 2021), showing a similar short corolla tube to that in *Remberella*, but those specimens retain the distinctive accrescent calyx, and do not preserve features of the androecium; the associated isolated pollen grains are distinct in ornamentation from those found within *Remberella* anthers.

Among other ericalean families, Styracaceae DC. et Spreng. 1821 flowers are similar in some respects. They are usually bisexual and actinomorphic with asympetalous corolla that is usually 5 lobed (4–8–lobed), with stamens usually twice the number of corolla lobes, and stamens adnate the corolla tube (Fritsch, 2004; Christenhusz et al., 2017). Although pollen morphology can be similar (Morton and Dickison, 1992), the anthers of Styracaceae are oblong to linear with parallel sides (Dickison, 1993), rather than arrow shaped as in *Remberella* and *Diospyros*.

Although we have not found a precise match with an extant genus, the similarities with *Diospyros* are most intriguing. We conclude that *Remberella* belongs in the Ericales, and may reside in the Ebenaceae as an extinct genus, distinguished from the two extant genera by the unique form of its corolla and androecium. Given the intensity of collecting and abundance of fossil plants in the Clarkia Race Track locality, the absence of any corresponding fruits or accrescent calyces of *Diospyros* dissuades us from hypothesizing that these corollas were produced by that extant genus. The fossil named *Diospyros andersonae* Knowlton from the same site as the type specimens of *R. microcalyx*, verifies the co-occurrence of that genus, however, *D. andersonae* is larger (3 cm) and has a tetramerous rather than pentamerous perianth (Pl. 27, fig. 6 in Knowlton, 1926; USNM 26992; image accessible: http://n2t.net/ark:/65665/m33e80b1a6-25c6-4a4e-989b-77023119e576).

Remberella is the second example of an extinct genus of ericalean affinity to be recognized in the Miocene Latah flora of Idaho. *Juddicarpa* was described based on an inflorescence of campanulate flowers attributed to Ericaceae from the Emerald Creek locality (Smith and Manchester, 2019). Although extant ericalean genera, such as *Lyonia* Nutt. 1818, *Zenobia*, *Eupotrys* D. Don 1834 (Ericaceae Durande 1782) and *Clethra* L. 1753 (Clethraceae Klotzsch 1851) have been recognized from the Miocene of Europe (Friis, 1985), the eastern Columbia Plateau region may have served as a refugium for additional lineages that are now extinct.

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ADDITIONAL INFORMATION

CONFLICT OF INTEREST. The authors have declared that no competing interests exist.

ETHICAL STATEMENT. No ethical statement was reported.

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