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A new species of "gigantic" capsular fruits of Vaccinioideae from the Miocene of Idaho

MacKenzie Smith and Steven R. Manchester

ABSTRACT

Large, capsular fruits of Ericaceae have been identified from the Emerald Creek site of the Middle Miocene Clarkia flora of northern Idaho. We recognize the morphological similarity of these fossils to fruits of the subfamily Vaccinioideae, specifically to the extant genus *Oxydendrum* (sourwood), which has a single extant species that lives primarily in the southeastern US and with members of the Lyonieae and Gaultherieae. We present a new species of vaccinioid capsular fruit as *Juddicarpon benewahensis* Smith and Manchester gen. et sp. nov. from an infructescence. The new species has fruits that are twice the size of those in extant *Oxydendrum* and outside the modern size range of vaccinioids with capsular fruit. This fossil is significant as the first record of fossil vacciniod fruit from Western North America.

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INTRODUCTION

The Middle Miocene Clarkia flora of northern Idaho includes a diverse association of mixed mesophytic plants, most of which are exotic to the region today, but with relatives found in eastern North America (Manchester and Chen, 2006). Arborescent elements include several conifers such as *Abies, Amentotaxus, Calocedrus, Cephalotaxus, Chamaecyparis, Cunninghamia, Ketelleeria, Metasequoia, Picea, Pinus, Sequoia, Taxodium, Taxus* and *Thuja* (Kvaček and Rember, 2000, 2007), various deciduous angiosperms such as *Acer, Alnus, Cercidiphyllum, Fagus, Liquidambar, Liriodendron, Lithocarpus, Magnolia, Nyssa, Ostrya, Paliurus, Pseudofagus* and *Pterocarya* (Smiley et al., 1975) and occasional ferns (Pinson

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et al., 2018). Here, we recognize another element of this flora--the heath family, Ericaceae Juss.

The oldest known fossil occurrence of Ericaceae is *Paleoenkianthus sayrevillensis* from the Turonian (ca. 90 Ma) of New Jersey (Nixon and Crepet, 1993). Today the family has a global distribution (Tucker, 2009) and about 124 genera and 4,250 species (Christenhusz and Byng, 2016). Fruit can be a capsule, berry or drupe (Tucker, 2009). The subfamily Vaccinioideae Arn. of the Ericaceae includes 46 genera that are distributed worldwide except for Antarctica and found in almost every biome (Tucker, 2009). Its fruit morphologies are highly diverse and vary in all of the forms mentioned for Ericeaceae (Tucker, 2009). Here, we describe an infructescence conforming morphologically to the Vacciniodeae from the Middle Miocene of Idaho. This represents the first report of a vaccinioid from North America and one of the few occurrences of Ericaceae known from fossil fruits.

MATERIALS AND METHODS

The fossil (UI-P37-2019-1) is preserved in the lacustrine shale of the Clarkia *lagerstätte* upper oxidized zone (Unit 5 of Smiley et al., 1975; Smiley and Rember, 1985) from Emerald Creek, northern Idaho, USA (47.032896° N, 116.338514° W) (Smiley et al., 1975; Smiley and Rember, 1985) (Figures 1 and 2). These sediments belong to the middle Miocene Latah Formation) and are considered to be about roughly 16-15.4 Ma based on their position with respect to flows of the Priest Rapids Member (Wanapum Formation) of the Columbia River Basalt (Ladderud et al., 2015).

The fossil was microCT scanned with a GE Phoenix V|tome|xm240 CT Scanner at the Nanoscale Research Center, University of Florida, Gainesville, Florida. The resulting stack of tiff files was then processed in Avizo 9.0 Lite (FEI Visualization Science Group, Bordeaux, France) to generate an isosurface rendering. Subsequent processing of the isosurface utilized MeshLab (ISTI – CNR, Italy) using the lattice and depth map shaders. The specimen and scans were then compared with modern specimens of *Oxydendrum arboreum* using UF0202 from western Tennessee and UF0203 from the Indiana University arboretum, Bloomington, Indiana, both housed in the modern fruit collection at the Florida Museum of Natural History Paleobotany Collection, Gainesville, Florida and FLAS 32600 L.E. Arnold s.n. from Bristol, Florida, housed in the University of Florida Herbarium (FLAS), Gainesville, Florida.

SYSTEMATIC PALEONTOLOGY

Order ERICALES Bercht. and J.Presl, 1820
Family ERICACEAE Juss., 1789
Subfamily VACCINIOIDEAE Arn., 1832
Genus JUDDICARPON Smith and Manchester
Juddicarpon benewahensis Smith and Manchester gen. et sp. nov.

Figures 3-4

Generic and specific diagnosis. Infructescence is a terminal raceme at least 5.5 cm long with pedicelate fruits drooping to one side of a moderately thick (ca. 1.9 mm thick) axis (secund raceme) with 10, five-valved ovate-elongate capsular fruits (Figure 3.1). Pedicels are curved and about 0.6 cm long and just under 2 mm in diameter (Figures 3.1-3, 4.1-2). Pedicels have one visible bracteole scar (Figure 4.1). Each fruit has five hypogynous persistent, elongate and pointed sepals (Figure 4.3). Fruits are between 0.8-1.1 cm tall and 0.2-0.6 cm wide (with the majority of fruit at the maximum end

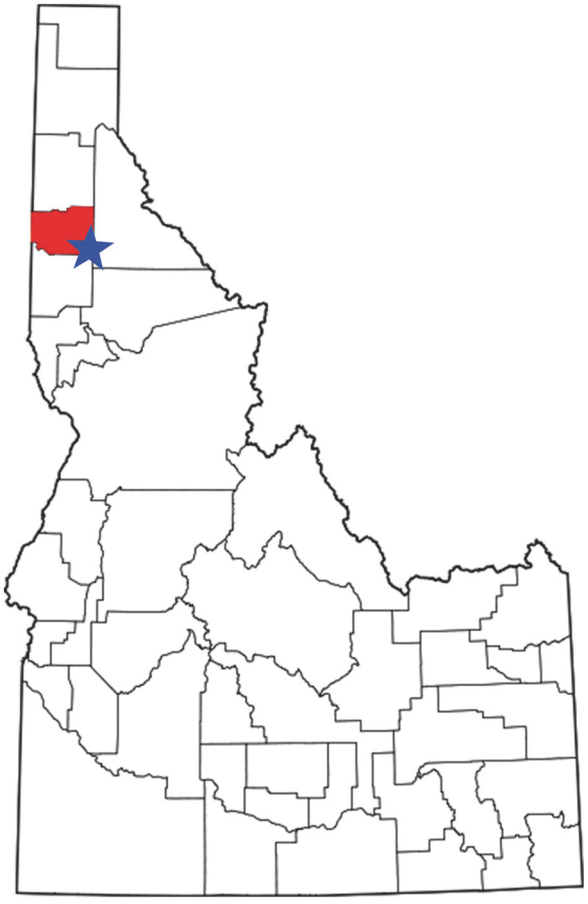

FIGURE 1. Map of Idaho showing position of the Emerald Creek site (star) in Benewah County (red filled).

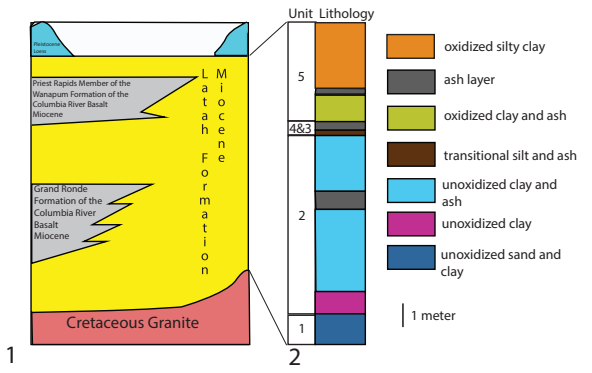

FIGURE 2. Stratigraphic column of the Latah Formation. **1,** Geology at a regional scale from Fairley et al., 2006. **2,** Stratigraphy of the Clarkia Beds from the Latah Formation from Calede et al. 2018 based on Smiley, Gray, and Huggins (1975) and Smiley and Rember (1985). Note not all units are visible at the Emerald Creek site.

of the previous ranges) with long valves lacking thickened sutures (Figures 3.1-3, 4.1-3) and a basal bulge between valves (Figure 4.1). One persistent style with truncated stigma is preserved and extends 6 mm beyond the fruit apex (Figure 3.1-2).

Etymology. The genus *Juddicarpon* honors Walter S. Judd, who shared his expertise on extant Ericaceae with us. The epithet *benewahensis* refers to Benewah County, Idaho, where the fossil was found.

Type locality. Emerald Creek, ID (Clarkia flora)

Age. Burdigalian-Langhian (16-15.4 Ma)

Holotype. Specimen UI-P37-2019-1 housed with the herbarium paleobotanical collections at University of Idaho.

DISCUSSION

The specimen is broken in such a way as to reveal the fruits in longitudinal fracture. In most of the attached fruits only three valves can be counted, but five are inferred from the symmetry (Figures 3.1-3, 4.1-4). Five-valved capsular fruits with persistent hypogynous sepals are present and relatively common within the Ericaceae (e.g., *Enkianthus*, *Pieris* and *Lyonia*), however, the Ericaceae are not the only plant family to have this combination of characters (e.g., other families in the Ericales such as Theaceae and tribe Hibisceae in the family Malvaceae) (Kron et al., 1999; Pfeil et al., 2002; Luna and Ochoterena, 2004). We distinguish this fossil from Theaceae because fruits of that family are generally borne solitary rather than in infructescences. We distinguish it from the Malvaceae based on the combination of features discussed below.

Within the Ericaceae, many members of Vaccinioideae have flowers and fruits borne mainly on one side of the axis, i.e., in secund arrangement (e.g., *Oxydendrum*, *Pieris*, *Lyonia*, *Leucothoë* and *Eubotrys*) (pers. obs.). Because the basal portion of the inflorescence was not collected, it is possible that instead of a raceme it could be one unit of a larger panicle. Among the extant genera of Vaccinioideae with secund infructesences, only the monotypic *Oxydendrum arboreum* (L.) DC has ovate to elongate fruits, non-thickened sutures, a terminal peduncle and occasional bulges at the base between the valves (Figure 4.5-8) (Kron et al., 1999; Kron et al., 2002). Even though septa were not preserved, we interpret the fruit to be loculicidal because the valves open through the basal bulges, a position which seems unlikely for a septum to run through. Loculicidal fruits are a consistent character in the dry-fruited genera of Vaccinioideae. We interpret the infructescence as being determinate because the pedicel of the terminal fruit does not seem to curve laterally. These combined characters also do not exist in the Theaceae or Malvaceae. Thus, we infer that the fossil is closely related to the extant genus *Oxydendrum*.

When comparing the fossil to modern *Oxydendrum arboreum,* a difference that is noticed is the larger size of fossil infructescence and fruits. The pedicels are 2 mm thick in the fossil but less than 1 mm in both studied specimens of *O. arboreum*. In the modern fruit height ranges from 3-5 mm but in the fossil this ranges from 8-11 mm. Additionally, the maximum width for *O. arboreum* fruits is 4 mm, but in the fossil it is 6 mm. Fruit number differs between modern specimens and the fossil with *O. arboreum* having more than 10 fruits and the fossil only having 10 observable fruits. Because of the size difference observed in both the fruits and pedicels and the fruit number, it is relatively easy to distinguish the fossil from *O. arboretum*.

We extended our comparison to include other genera of the Vaccinioideae with capsular fruits such as *Lyonia, Agarista, Pieris* and *Leucothoë*. For phylogenetic context, an ericalean phylogeny by Schwery et al. (2015) shows Vaccinieae and Andromedeae (which includes *Zenobia*) as a clade with Gaultherieae (which includes *Leucothoë*) sister to it, Oxydendreae sister to that and Lyonieae (which includes *Pieris* and *Lyonia*) sister to that. It is possible for *Lyonia* to have secund racemes (e.g., *Lyonia ligustrina* var. *ligustrina* though capsules are globose) and to have elongated capsules (e.g., *Lyonia mariana* although it does not have a

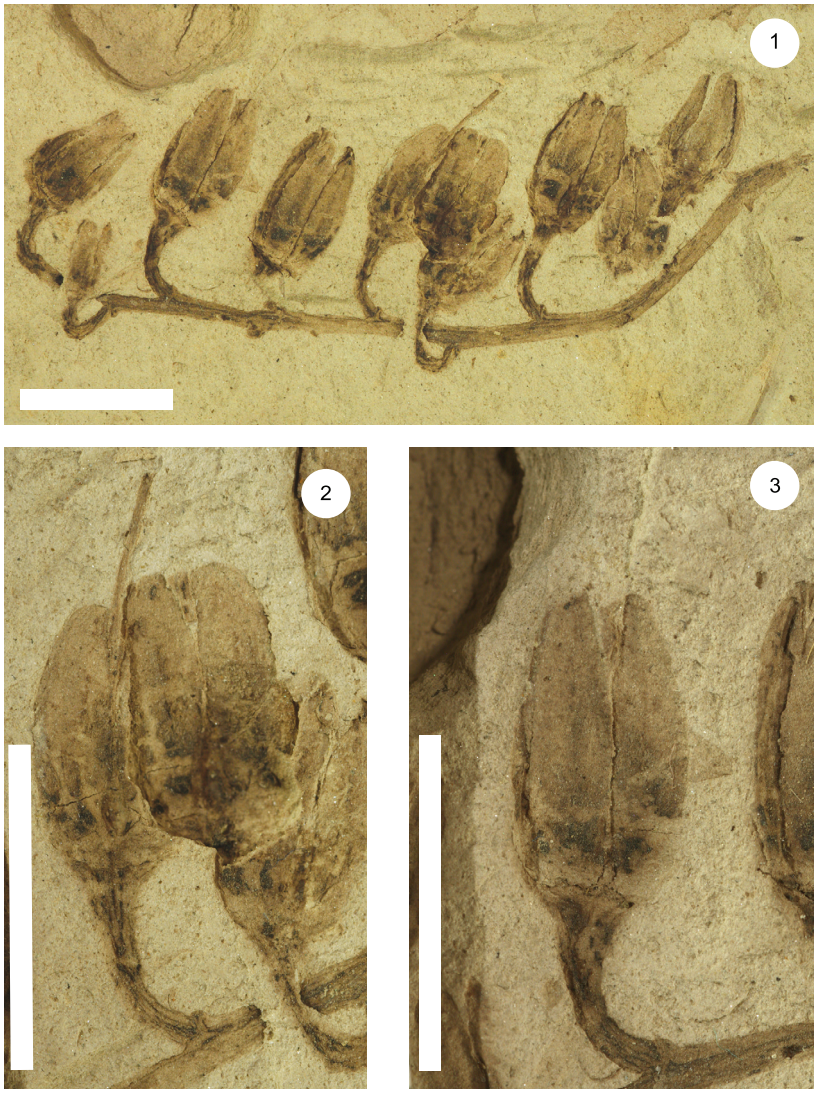

FIGURE 3. Holotype, UI-P37-2019-1 *Juddicarpon benewahensis sp. nov.* Smith and Manchester from the Miocene of Idaho. All scale bars equal 1 cm. **1**, Secund raceme with a terminal fruit and ten capsules total. All fruit are five-valved ovate-elongated capsules. **2,** A fruit with curved pedicel and persistent style. **3,** Fruit lacking persistent style.

secund raceme). However, fruit size does not vary much within species for the dry fruit of Vaccinioideae. Only one specimen, a *Lyonia* (FLAS 53054) unidentified to species level, had varying fruit size on the same branch during our search. Because there is only one living species from which to infer useful characters for identification in the Oxydendreae and in view of the morphological variability within the rest of Vaccinioideae we feel that the combined traits warrant a new genus and species within the Vaccinioideae. It is noteworthy that these fossil fruits are larger than any we have observed among extant Vaccinioideae. Larger capsular fruits occur in other clades of Ericaceae, such as in *Rhododendron*, but the observed morphology fits better with the Vaccinioideae. It seems possible that this extinct genus corresponds to a lineage that combines features of more than one modern clade within Ericaceae. We suppose that the large fruit size may be a plesiomorphic condition within Vaccinioideae, but more fossils and a more comprehensive morphological phylogenetic analysis would be needed to test this.

There are no living vaccinioids in Idaho today with capsular fruit. Instead, the modern genera are located primarily in eastern North America and Asia. A notable exception is *Leucothoë davisiae* from California and Oregon (USDA, n.d.). It is possible that it went extinct due to the region drying

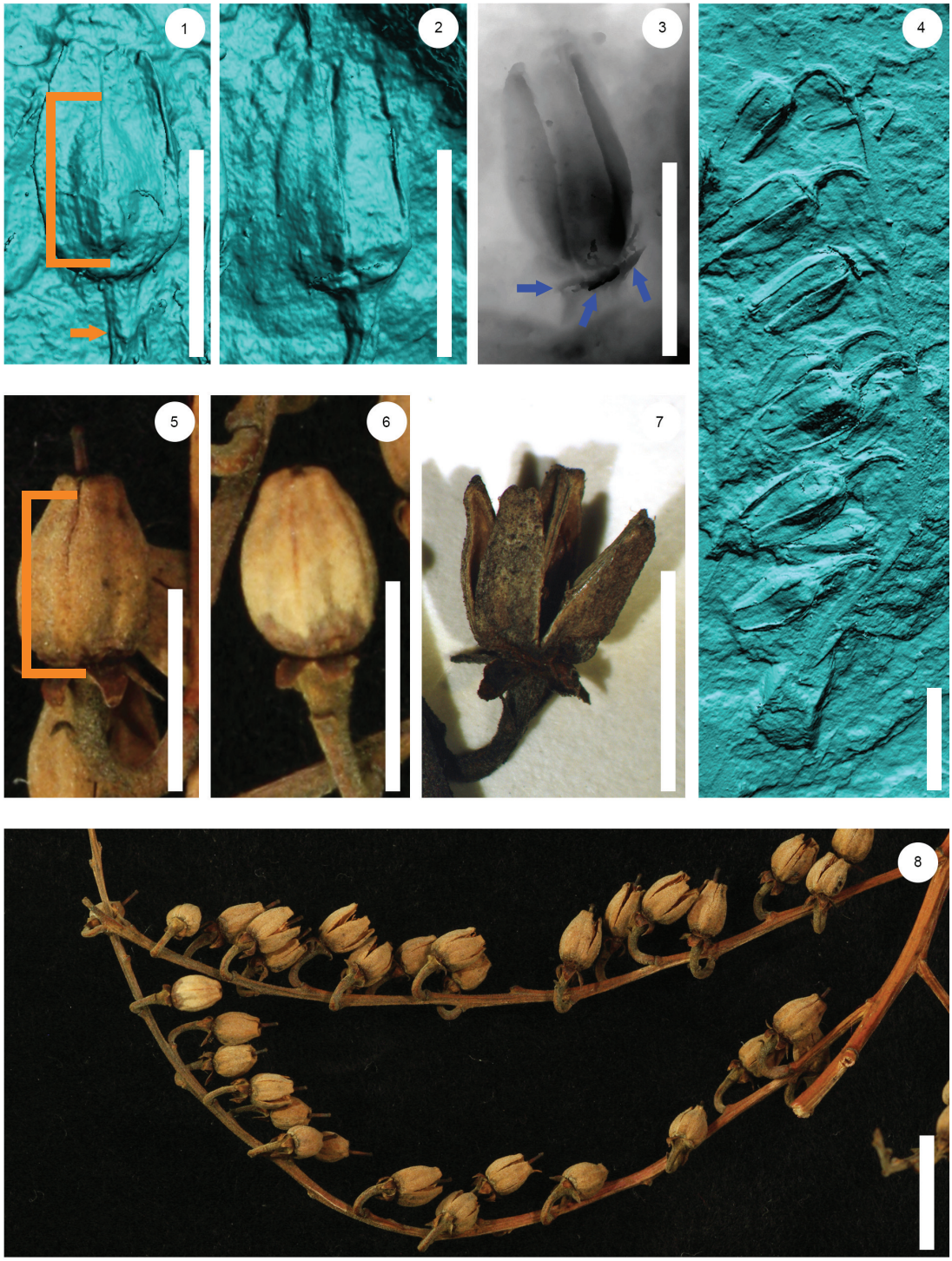

FIGURE 4. 1-2, µCT scan with lattice shading of *Juddicarpon benewahensis* scale bars equal 1 cm. **1,** Fruit with prominent basal bulge in orange bracket between valves and orange arrow pointing at bracteole scar. **2,** Fruit with less prominent basal bulge between valves. **3,** CT scan of *J. benewahensis* with depth map shading showing persistent perianth in blue arrows. Scale bar 1 cm. **4,** CT scan with lattice shading of the entire raceme of *J. benewahensis* with capsules showing two-three valves. Scale bar equals 1 cm. **5-6,** UF0203 *Oxydendrum arboreum* fruit showing basal bulge between valves. Scale bars equal 0.5 cm. **5,** Fruit with persistent style and prominent basal bulge between valves between orange bracket. **6,** Fruit with partial persistent style and less prominent basal bulge. **7,** *O. arboreum* FLAS 32600 open fruit with no style and lacking basal bulge. Scale bar equals 0.5 cm. **8,** UF0203 *O. arboreum* showing secund raceme. Scale bar 1 cm.

and having no refugia to escape because of being surrounded by mountains.

We take this opportunity to comment on the fossils used for calibration of the phylogeny of Ericaceae. Schwery et al. (2015) used the fossil leaf, *Vaccinium creedensis* Axelrod (1987), as a dating calibration point for *Vaccinium*. However, this species was already transferred to *Berberis* by Wolfe and Schorn (1990) based on seven diagnostic characters and is thus inapplicable for calibrating ericalean phylogeny. In general, the assignment of fossil leaves to particular extant genera of Ericaceae should be accepted with caution because of the convergence of leaf architectural patterns both within and outside the family. Fossil fruits and flowers, when available, can provide greater systematic resolution within the Ericaceae.

Few fossil fruit from the Vaccinioideae are known and none were reported previously from North America. European examples include *Lyonia danica* Friis from the Miocene of Denmark and Germany (Friis, 1985; Mai, 2001), *Zenobia fasterholtensis* Friis from the Miocene of Denmark (Friis, 1985), *Eubotrys* sp. from the Miocene of Denmark (Friis, 1985), and *Leucothoë narbonensis* Mai from the Oligocene of Germany (Mai, 1998). *Andromeda brunnea* Dorofeev was recognized from the Oligocene of Siberia (Dorofeev, 1963). *J. benewahensis* is more elongated than these fruit and is at least twice their size. *Juddicarpon* is the first fossil fruit from this subfamily in North America.

CONCLUSION

Juddicarpon benewahensis is the first fossil vaccinioid fruit to be recognized from North America. Its unique combination of characters and large size make it difficult to place precisely within the Vaccinioideae, adding to the subfamily's complex evolutionary history, but it helps explain the timing of how this successful group spread.

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