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New fossil leaves of Araceae from the Late Cretaceous and Paleogene of western North America

By

Josef Bogner¹, Kirk R. Johnson², Zlatko Kvaček^{3*} & Garland R. Upchurch, Jr.⁴

¹Botanical Garden Munich, Menzinger Straße 63, D-80638 Munich, Germany

²Denver Museum of Nature & Science, 2001 Colorado Boulevard, Denver, CO 80205-5798, U.S.A.

³Charles University in Prague, Faculty of Science, Albertov 6, CZ-128 43 Praha 2, Czech Republic

⁴Texas State University, San Marcos, 601 University Drive, San Marcos, Texas 78666-4616, U.S.A.

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Abstract

The fossil record of Araceae is expanded by three new leaf species from the Upper Cretaceous and Paleogene of North America: 1) *Orontium wolfei* BOGNER, K. JOHNSON, KVAČEK & UPCHURCH sp. nov. (Lower–Middle Eocene, northern Washington and southern British Columbia); 2) *Orontium mackii* BOGNER, K. JOHNSON, KVAČEK & UPCHURCH sp. nov. (Maastrichtian, New Mexico); and 3) *Symplocarpus hoffmaniae* BOGNER, K. JOHNSON, KVAČEK & UPCHURCH sp. nov. (uppermost Maastrichtian of North Dakota and lowermost Paleocene of Colorado). A fourth representative of Orontioideae, *Lysichiton austriacus* (J. KVAČEK & A.B. HERMAN) BOGNER, K. JOHNSON, KVAČEK & UPCHURCH comb. nov., is based on a leaf fossil described from the lower Campanian of Grünbach, Austria, central Europe, and its name is re-combined herein from *Araciphyllites*. All species can be assigned to Araceae, subfamily Orontioideae, based on their distinctive patterns of venation, which are directly comparable to those of extant genera. This indicates that the Orontioideae originated sometime during the Cretaceous, and that the lineages related to extant genera were present by the Campanian–Maastrichtian. Climatic analysis of associated leaf assemblages indicates that the thermal tolerances of fossil Orontioideae mostly fall within the range of living representatives.

Key words: Araceae (Orontioideae), Upper Cretaceous, Paleocene, Eocene, foliage, North America, central Europe

Zusammenfassung

Drei neue Araceen Blatt-Taxa werden aus der Oberkreide bzw. dem Paläogen von Nordamerika beschrieben: 1) *Orontium wolfei* BOGNER, K. JOHNSON, KVAČEK & UPCHURCH sp. nov. (Unter–Mittelozeän, nördliches Washington und südliches British Columbia); 2) *Orontium mackii* BOGNER, K. JOHNSON,

KVAČEK & UPCHURCH sp. nov. (Maastricht, New Mexico); und 3) *Symplocarpus hoffmaniae* BOGNER, K. JOHNSON, KVAČEK & UPCHURCH sp. nov. (oberstes Maastricht von North Dakota und unterstes Paläozän von Colorado). Desweiteren wird ein Blattfossil aus dem Unterkampan von Grünbach, Österreich, welches ursprünglich der Morphogattung *Araciphyllites* zugeordnet wurde, neu kombiniert, zur Unterfamilie der Orontioideae gestellt und als *Lysichiton austriacus* (J. KVAČEK & A.B. HERMAN) BOGNER, K. JOHNSON, KVAČEK & UPCHURCH comb. nov. benannt. Alle hier beschriebenen Fossilien können aufgrund einer charakteristischen Aderung, die direkt mit der moderner Arten verglichen werden kann, der Familie der Araceae, Unterfamilie Orontioideae, zugeordnet werden. Dies bedeutet, dass die Orontioideae irgendwann im Laufe der Kreidezeit entstanden sein müssen, und dass Formen, die unmittelbar mit heutigen Gattungen verwandt sind, bereits im Campan–Maastricht existiert haben. Paläoökologische Analysen anhand assoziierter Blattfloren deuten darauf hin, dass die klimatischen Ansprüche der fossilen Orontioideae mehr oder weniger denen heutiger Vertreter dieser Unterfamilie entsprechen.

Schlüsselwörter: Araceae (Orontioideae), Oberkreide, Paläozän, Eozän, Blätter, Nordamerika, Mitteleuropa

1. Introduction

The fossil record of *Araceae* is sparse compared to that of many other families. Most fossil *Araceae* have been reported from the Cenozoic, most often on the basis of detached organs such as inflorescences, infructescences, fruits, seeds, leaves, and pollen, and rarely on the basis of whole plants (KVAČEK 1995; STOCKEY et al. 1997). Few fossil *Araceae* have been reported from the Upper Cretaceous, with unequivocal megafossil records known from only three regions (see MAYO et al. 1997; KEATING 2003; and WILDE et al. 2005 for reviews). In western

*Author for correspondence and reprint requests; E-mail: kvacek@natur.cuni.cz

North America, the extant subfamily Orontioideae is represented by *Albertarum pueri* (BOGNER et al. 2005) and the extinct subfamily Limnobiophylloideae, which is represented by *Limnobiophyllum scutatum* (STOCKEY et al. 1997; JOHNSON 2002; KVAČEK 2003). In India, the extant subfamily Monsteroideae is represented by *Rhodospathodendron tomlinsonii* (BONDE 2000), while in central Europe, the extant subfamily Orontioideae is represented by *Lysichiton austriacus* (this paper and J. KVAČEK & HERMAN 2004, 2005, originally described as *Araciphyllites austriacus*).

The new records described here are based on leaves from the Upper Cretaceous and lower Cenozoic of the western U.S.A. and Canada. Their suite of venational features corroborates their affinity with the subfamily Orontioideae of the Araceae, which together with Gymnostachyoideae forms a grouping of primitive Araceae called "Proto-Araceae" by MAYO et al. (1997). According to recent molecular and morphological studies, "Proto-Araceae" appears to be basal and isolated from the rest of family (L.I. CABRERA, G.A. SALAZAR, M.W. CHASE & S.J. MAYO, personal communication, 2005).

The subfamily Orontioideae is characterized by bisexual flowers with a perigon, anatropous, hemianatropous or orthotropous ovules, sparse or absent endosperm, monosulcate pollen, and chromosome number $\times = 13, 14, 15$ (MAYO et al. 1997). They are herbaceous rhizomatous helophytes (*Orontium* is also a hydrophyte). Diagnostic vegetative features of this clade include undivided leaf blades, a non-geniculate petiole, and continuation of the shoot in the axil of the last leaf preceding the spathe. Leaf venation differs between genera but is distinct from that of all other Araceae.

The Araceae develop variously shaped leaves, which usually do not allow recognizing natural genera, only certain morphological types. Hence, an application of morphogenera for fossils is appropriate in most cases (WILDE et al. 2005). Members of the Orontioideae with the simplified leaf morphology and venation are an exception. The three genera of this subfamily are recognizable according to the following diagnostic traits: Oblong lanceolate leaves of *Orontium* are distinguished by the stout midcosta reaching hardly over the half length of the blade; lateral primary veins arise near the base, arcuately ascending to the leaf apex; primary and lower-order cross veins run obliquely across the blade wide apart at variable angles; the leaf tip is shortly hooded. In the also oblong leaves of *Lysichiton* the midcosta reaches the leaf apex, lateral primaries arise successively along its length, and the higher-order venation is more or less regularly transverse-reticulate forming elongate rectangular meshes. In *Symplocarpus*, the leaf blade is broadly ovate, rounded to cordate at the base, lateral primaries are similarly parallel, but higher-order venation is more complicated at the leaf margin, reticulate to transverse reticulate. Based on the peculiar characteristics of the Orontioideae leaves, the fossils treated below are placed into appropriate extant genera in spite of their considerable age.

2. Material and Methods

The holotype of *Symplocarpus hoffmaniae* was recovered from the Upper Cretaceous (late Maastrichtian) Hell Creek Formation of southwestern Dakota, U.S.A. at site No. 428

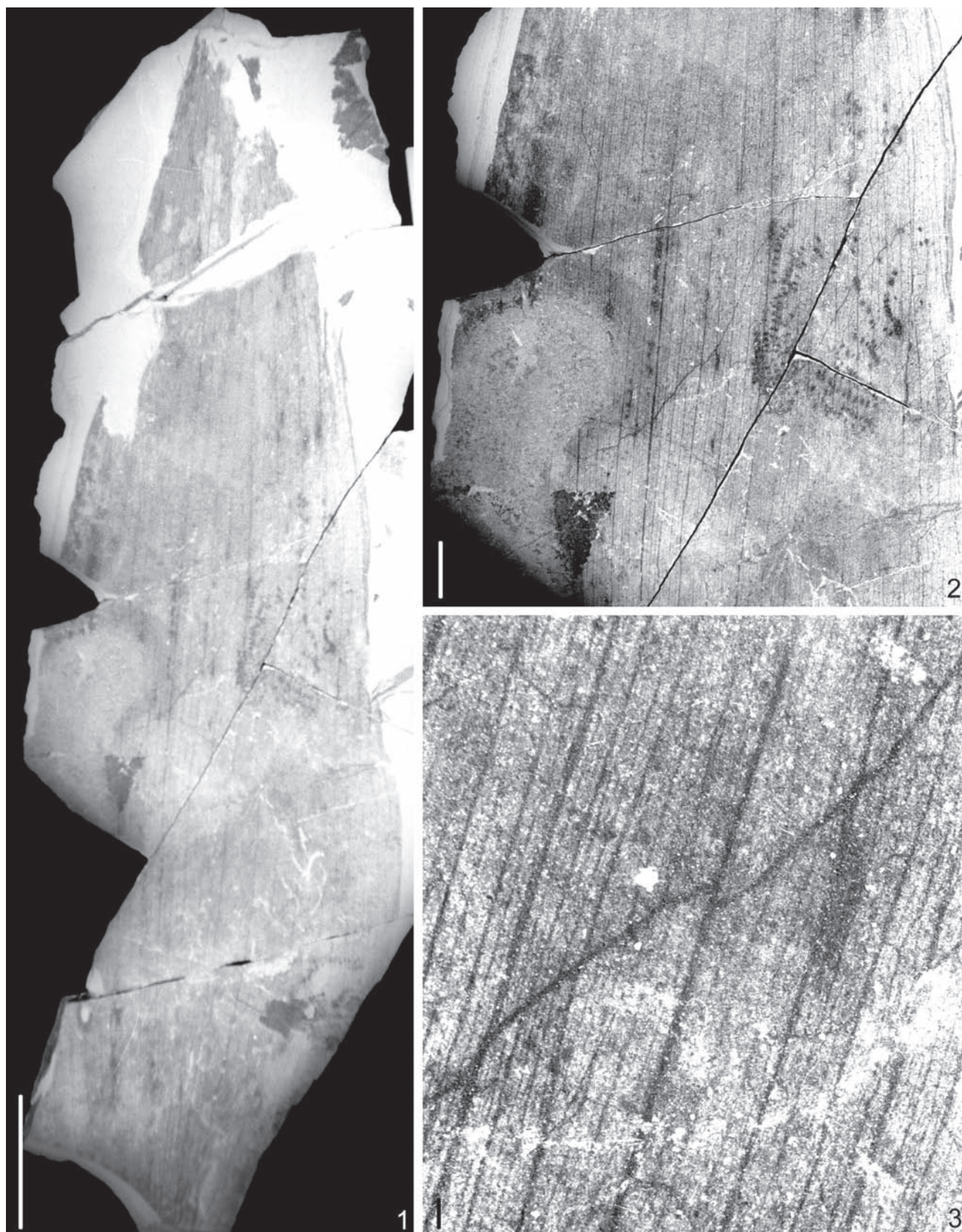
(KJ88102) called the Dean Street (coordinates 46°01' 07" N, 103°45'52" W). This fossil leaf impression was collected in a layer rich in plant remains about 15 m below the Cretaceous/Tertiary (or K/T) boundary in channel deposits of point bar facies. The Hell Creek Formation was dated and subdivided within the late Maastrichtian based on invertebrates, palynology, radiometry, and magnetostratigraphy (for details see JOHNSON 2002; HICKS et al. 2002). The second specimen of *Symplocarpus hoffmaniae* was collected in a similar setting at 30 cm above the K/T boundary impact horizon in the Raton Formation at DMNH loc. 423 (KJ9129), Berwind Canyon, Los Animas Co., Colorado. This is the Berwind Canyon locality reported widely in studies of the non-marine Cretaceous-Tertiary boundary (e.g., WOLFE & UPCHURCH 1987).

Specimens of *Orontium mackii* were collected from three localities near the town of Truth-or-Consequences, New Mexico, in the Jose Creek Member of the McRae Formation. The Jose Creek Member is dated as probable Maastrichtian in age, based on sediment accumulation rates, a conformable contact with the overlying Hall Lake Member, and the occurrence of a suite of conifer megafossils found in other Maastrichtian floras from the southern and central Rocky Mountains (SEAGER et al. 1997; UPCHURCH & MACK 1998). The Jose Creek Member predates the latest Maastrichtian because the lower part of the overlying Hall Lake Member contains dinosaurs indicative of the Lancia land vertebrate age (LOZINSKY et al. 1984). The specimens described in this report occur within fluvial sedimentary sequences and are preserved in re-crystallized volcanic ashes, which are common in the middle to upper part of the Jose Creek Member.

Specimens of *Orontium wolfei* were recovered from the Lower-Middle Eocene of Washington, U.S.A. and Alberta, Canada. The Klondike Mountains Formation in the Republic region, Washington, includes occurrences at Corner Lot, Boot Hill, and Knob Hill. The sites with plant impressions/compressions are concentrated in freshwater mudstone and shale layers in the lower part of the formation. The fossil-bearing deposits formed in lakes that were created by damming from gravity slides. The radiometric ages of lava flows within the formation range from 42 ± 2.0 Ma to 50.3 ± 1.7 Ma, or Early to Middle Eocene. The deposition of the plant-bearing levels took place approximately 48–49 Ma (WOLFE & WEHR 1987).

The Princeton sites from the Allenby Formation in Alberta occur in similar facies to those from Republic. An early K-Ar date of 48 ± 2 Ma placed Princeton in the early Middle Eocene (HILLS & BAADSGAARD 1967), but more recent K-Ar dates of 49 ± 2 and 52 ± 2 Ma from plagioclase and 51 ± 2 Ma from biotite contained within a bentonitic tuff (EWING 1981) indicate a late Early Eocene age (for details see PIGG et al. 2007). The sites include One Mile Creek (loc. B 3389) (= DMNH-26516, the type locality) and Lamont Creek (loc. B 5485) at Princeton.

The fossil material is archived in the paleobotanical collections of the Denver Museum of Nature & Science, Denver CO (numbers preceded by DMNH), Thomas Burke Memorial Washington State Museum, Seattle, Washington (numbers preceded by UWBM), Stonerose Interpretive Centre and Museum, Republic, Washington (SR) and Texas State University, San Marcos TX (numbers preceded by TXSTATE). The extant material for comparison was obtained from the Munich Botanical Garden and the Charles University Herbarium in Prague.



Figures 1–3: *Orontium wolfei* BOGNER, K. JOHNSON, KVAČEK & UPCHURCH sp. nov., Lower–Middle Eocene, DMNH loc. 26516.

1: Fragmentary leaf with well preserved venation. Holotype. Scale bar = 50 mm; 2: Enlarged medial part of the holotype. Scale bar = 10 mm; 3: Venation of the holotype. Scale bar = 5 mm.

The fossils examined in this study all represent leaf impressions. No cuticle appears to be preserved. Venation was studied by reflected light microscopy, with enhancement of detail using digital photography. Extant foliage was studied by transmitted light microscopy following clearing and staining for venation. Leaves were cleared by treatment in 10% KOH followed by short oxidation in commercial bleach. After rinsing, leaves were stained in safranin O and destained in glycerol to differentiate venation.

The terminology used to describe the venation of fossil and living Araceae is that introduced and defined by MAYO et al. (1997).

4. Taxonomy

Family *Araceae* JUSSIEU 1789

Subfamily *Orontioideae* MAYO, BOGNER & P.C.
BOYCE 1997

Genus *Orontium* LINNEUS 1753, *nom. cons.*

Type: *Orontium aquaticum* LINNEUS 1753

Orontium wolfei BOGNER, K. JOHNSON,
KVAČEK & UPCHURCH sp. nov. Figs 1–9

Diagnosis: Leaves oblong elliptic, entire-margined, with shortly hooded leaf tip, venation parallel-pinnate, with inconspicuous midrib, primaries arising near the leaf base, secondary, tertiary and higher order laterals dense, subparallel with primaries, primary cross veins very widely spaced, secondary and lower order crossveins also wide part, oblique, irregular in their broken course, areolation dense, very narrow and elongate.

Description: Leaves falling into the mesophyll to macrophyll size classes, entire-margined, blade oblong-elliptic, 50–150 mm wide, ca. 170 to over 450 mm long (no complete specimens in length), no petiole preserved, leaf tip shortly hooded, venation parallel-pinnate with the midrib area inconspicuous, only at the leaf base demarcated by slightly denser primaries in the medial part of the blade elsewhere without a visible midcosta; primary lateral veins arising near the leaf base, parallel, only very slightly bent, ca. 5–7 mm apart, secondary laterals inconspicuous, subparallel with primaries, tertiary and higher-order laterals very dense, ca. 1 mm or less apart, connected with the ultimate order venation by dense, very narrow and elongate meshes of areolation, primary cross veins very widely spaced, oblique, admedially oriented in the central part and subhorizontally near the margin, often irregular in their broken course, interconnecting primary veins, secondary and lower order crossveins wide part, partly slightly curved, oriented irregularly, partly abmedially, interconnecting lower order laterals.

Holotype here designated: DMNH–26516: Figs 1–3 (coll. Denver Museum of Nature & Science).

Type locality and age: DMNH 382 (= One Mile Creek,

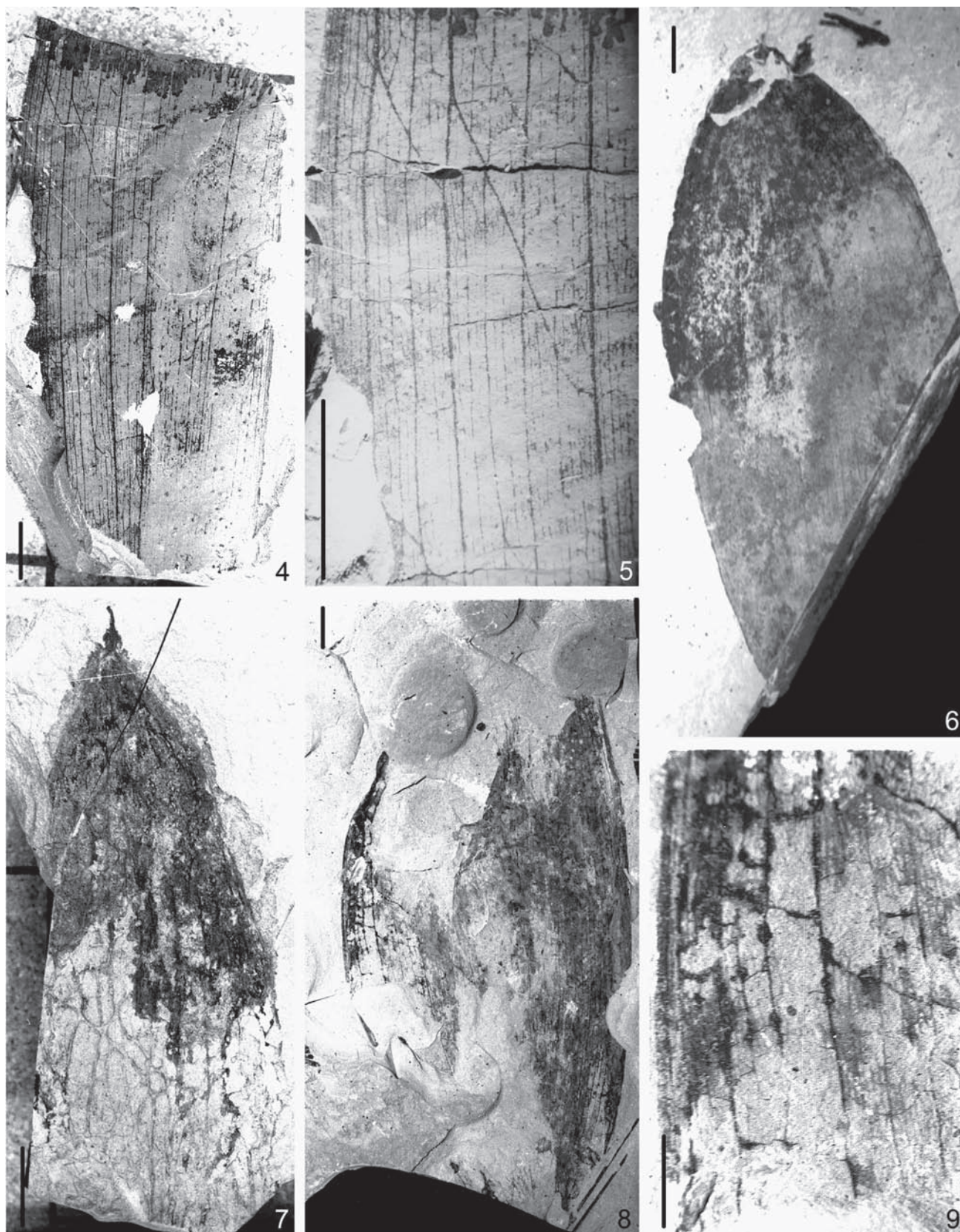
Princeton, loc. B 3389), Eocene.

Other material studied: SR - SR 91-6-13, 92-14-13, 96-11-23, 98-11-12B, 99-6-21A, B (Corner Lot, Republic), UWBM - 54641 (Boot Hill, Republic, loc. B 4131), 56775 (One Mile Creek, Princeton, loc. B 3389), 77650 (One Mile Creek, Princeton, loc. B 3389), 77657 (Knob Hill, Republic loc. B 2737), 77658 A, B (Lamont Creek, Princeton, loc. B 5485): Figs 4–9.

Etymology: The species is named in memory of the late JACK ALBERT WOLFE (1936–2005), who made extensive field studies in the Paleogene of western North America and profoundly contributed to the knowledge of the Cenozoic flora.

Remarks: This kind of monocot leaves was determined in the collections of the Republic flora at UWBM by WOLFE (in sched., not included in the list of WOLFE & WEHR 1987: 3–4) as *Zingiberopsis*, a morphogenus of Zingiberales known from the Upper Cretaceous to Oligocene of western North America (HICKEY & PETERSON 1978; MEYER & MANCHESTER 1997). However, the specimens described here differ markedly from *Zingiberopsis* and all other Zingiberales in lacking a prominent narrow midcosta and in having ultimate venation with oblique, partly irregularly directed crossveins of several orders and very narrow elongate areoles. Foliage with identical venation but of quite variable in size was also recovered by KIRK JOHNSON at One Mile Creek site (DMNH loc. 382). This morphotype matches, in all essential features, the only extant representative of the genus *Orontium*, *O. aquaticum* L., whose venation pattern is unique among aroids (see ERTL 1932; MAYO et al. 1997). Leaves of extant *Orontium* (Figs 16–18) lack a prominent continuous midcosta, which disappears soon after the petiole enters the lamina. Primary veins are all the same thickness including the medial vein, which reaches the leaf tip. Lateral veins diverge in very steep angles from the base of the lamina and are interspaced with laterals of the second and higher orders. The position of the midrib area is only vaguely demarcated by closely spaced laterals. The crossveins of the first-order arise admedially at an angle of 30–40°. Higher-order crossveins are less regularly disposed, wavy and variously oriented. Areoles are very narrow and elongate. *Orontium wolfei* corresponds perfectly in details of the venation (Figs 1–3) and hooded leaf tip to its extant relative, which differs only in having a more prominent midrib area continuing from the petiole and reaching higher above the leaf base (see ERTL 1932: figs 26–27; this paper: Fig. 10). The described leaf fossils of *Orontium wolfei* vary similarly in size from quite large (holotype 150 mm wide, over 450 mm long) to medium (50–60 mm wide and more than 150 mm long).

Leaves of the related genus *Lysichiton* are similar in form (Fig. 24), but differ from *Orontium* in venation (Fig. 25). The midrib is formed by several vascular bundles, which continue into primary laterals towards the leaf apex. These are steeply pinnate and interconnected by transverse reticulate venation of regular, mostly quadrangular meshes of various orders. The fossil *Orontium* that was reported from the Late Eocene Florissant Beds of Colorado (a fragmentary spadix of *Orontium fossile* COCKERELL 1926) is equivocal (MACGINITIE 1953: p. 165; see also MEYER 2005).



Figures 4–9: *Orontium wolfei* BOGNER, K. JOHNSON, KVAČEK & UPCHURCH sp. nov., Lower-Middle Eocene of NW North America

4: Leaf fragment with well preserved venation. Republic, One Mile Creek, 56703. Scale bar = 5 mm; 5: Enlarged detail of Fig. 4. Scale bar = 1 mm; 6: Obovate leaf with a blunt apex. Republic, SR 96-11-23. Scale bar = 10 mm; 7: Leaf fragment with a hooded apex. Princenton, La Mont Creek, 77658A. Scale bar = 10 mm; 8: Fragment of a broadly ovate leaf, Republic, SR 91-6-13. Scale bar = 10 mm; 9: Marginal venation, detail of Fig. 8. Scale bar = 5 mm.

Occurrence: Lower–Middle Eocene - Republic, Princeton (One Mile Creek UWBM 3389, leg. J. WOLFE 1987: DMNH 382, leg. K. JOHNSON; Lamont Creek, UWBM 5485).

Orontium mackii BOGNER, K. JOHNSON,
KVAČEK & UPCHURCH sp. nov.
Figs 10–16

Diagnosis: Leaves oblong elliptic, entire-margined, venation parallel-pinnate, with inconspicuous midrib, primaries arising near the leaf base, secondary laterals indistinctly differentiated in thickness, parallel with primaries, only primary cross veins developed, widely spaced, curved to sinuous, at highly variable angles, areolation dense, very narrow and elongate.

Description: Leaves fragmentary but falling within either the mesophyll or macrophyll size class, mostly medial parts of the lamina preserved, entire-margined, blade oblong-elliptic, 60–90 mm wide in specimens that preserve both margins, well in excess of 275 mm long (longest specimen), petiole over 100 mm long, slightly swollen, apex partially preserved, obtusely rounded near the margin, tip of apex missing, venation parallel-pinnate, with wide midrib area that is more distinct in lower parts of the lamina and consists of dense parallel veins of one order, midrib area 1.5–2.5 cm wide, parallel veins in midrib area ca. 1 mm apart, midrib area primary laterals arising sub-parallel, only very slightly bent, primary laterals mostly 2–5 mm apart except for the 3–4 primary laterals adjacent to the margin, which are more closely spaced, secondary laterals very dense, averaging 0.3 mm apart, indistinctly differentiated in thickness and connected with the ultimate order venation by narrow dense meshes, primary cross veins highly variable in their course and spacing, mostly admedially oblique, typically curved to sinuous, at highly variable angles, partly curved near the margin, interconnecting primary veins and traversing both primary and secondary lateral veins.

Holotype here designated: TXSTATE 1001 – Figs 10, 11.

Paratypes here designated: TXSTATE 1002, 1003, 1005, 1006, 1029 A, B – Figs 12–16.

Holotype locality and age: TXSTATE Paleobotanical Locality 9115, Late Cretaceous (Maastrichtian).

Paratype localities and age: TXSTATE Paleobotanical Localities 9115 and 9116 (same ashfall bed), Late Cretaceous

(Maastrichtian).

Other material studied: TXSTATE Paleobotanical Localities 9115, 9116, 9203; Specimens 1004, 1007–1010, 1012, 1015, 1016, 1018–1022, 1024–1026, 1028.

Etymology: We name this species for Dr. GREGORY H. MACK, discoverer of the localities that yield *Orontium*, and in recognition of his numerous contributions to the geology of New Mexico.

Remarks: The Jose Creek materials have been first mentioned as a new unnamed species of monocot by UPCHURCH & MACK (1998: 216, 217, fig. 5c). While fragmentary, they are clearly relatable to *Orontium*. Diagnostic features include the oblong lamina with an apex that is obtusely rounded below the tip, the broad midrib region with closely spaced parallel veins, and cross veins that are nearly as thick as the primary parallel veins, oblique to the midrib region, irregularly widely spaced, and curved to sinuous in course. Not yet known is whether the lamina bore the hooded tip characteristic of *Orontium aquaticum* and *O. wolfei*. The midrib region of the Jose Creek leaves has a strong tendency to accumulate iron oxides, such that many specimens show a longitudinally oriented brown, orange, or red stripe (e.g., Figs 10, 15). One specimen is broken along the midrib region (Fig. 15, basal half of specimen) and demonstrates that the midrib region is distinctly thickened relative to the lamina.

Orontium mackii differs from *O. wolfei* in having less distinctly differentiated lateral veins of only two orders and one only distinct order of crossveins. The simplicity of venation in *O. mackii* relative to that of *O. wolfei* and *O. aquaticum* implies a trend of venation in *Orontium*, going from a less differentiated pattern in the Maastrichtian to a more differentiated pattern in the Eocene to Recent.

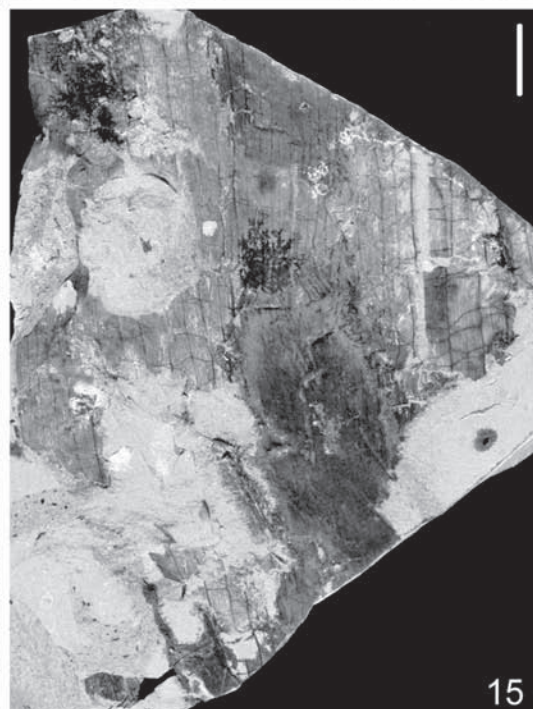
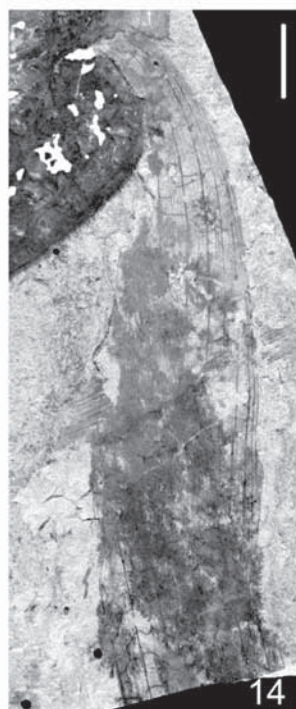
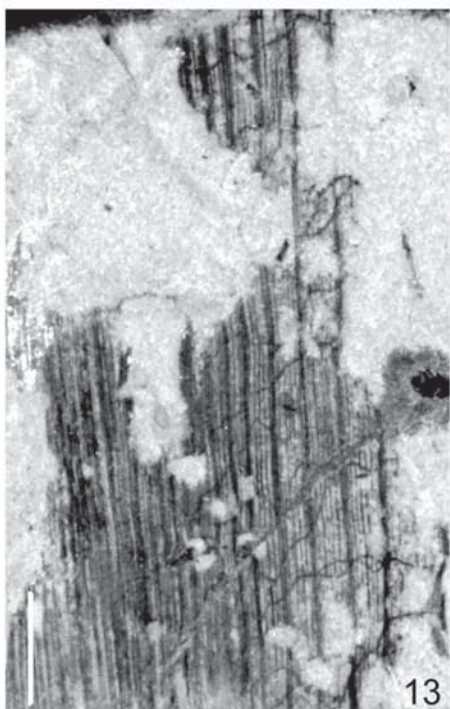
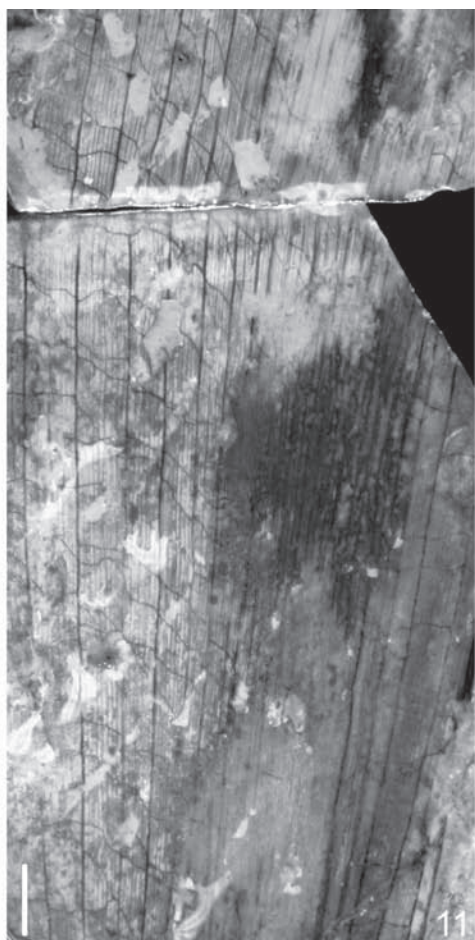
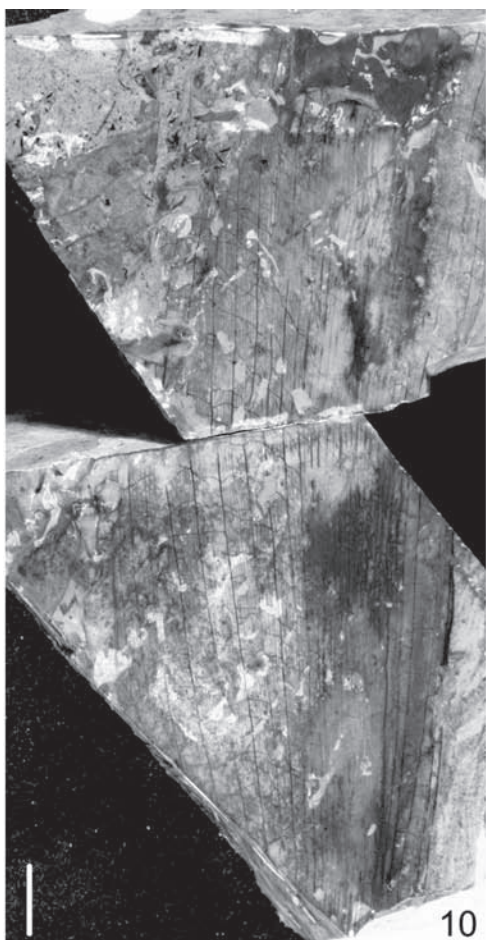
The two localities of the holotype and paratypes form part of the same bed of volcanic ash, and are separated by a distance of no more than 50–100 m. They can be considered to represent the same population of plants at the same instant in geologic time.

Occurrence: Late Cretaceous (probable Maastrichtian), south-central New Mexico, McRae Formation, Jose Creek Member, TXSTATE Paleobotanical localities 9115, 9116, 9203.

Genus *Symplocarpus* SALISB. ex W.P.C. BARTON 1817,
nom. cons.

Type: *Symplocarpus foetidus* (L.) SALISB. ex W.P.C. BARTON 1817 (*Dracontium foetidum* L.)

Figures 10–15: *Orontium mackii* Bogner, K. Johnson, Kvaček & Upchurch sp. n. TXSTATE locs 9115 and 9116 (same bed of volcanic ash), Maastrichtian; **10:** Holotype, TXSTATE 1001. Medial part of an oval leaf showing asymmetrically positioned midrib area with denser primary parallel veins. Scale bar = 10 mm; **11:** Enlarged detail of fig. 10, showing two orders of parallel veins and one order of oblique or curved cross veins. Scale bar = 20 mm; **12:** Paratype, incomplete entire-margined leaf with denser primary laterals near the margin and admedially oblique crossveins. TXSTATE 1002. Scale bar = 10 mm; **13:** Paratype, leaf fragment of medial part with the midrib area (to the left) and adjacent more widely spaced lateral primaries of two orders. TXSTATE 1003. Scale bar = 5 mm; **14:** Paratype, folded fragment of entire-margined leaf showing abrupt rounding of the apex and close spacing of primary laterals by margin. TXSTATE 1005. Scale bar = 10 mm; **15:** Paratype, medial part of a leaf with wide and relatively indistinct midrib area. Crossveins are oblique admedially on both sides and irregularly spaced on the right side. Note how the midrib area is fractured in the lower half of the specimen, showing its thickness. TXSTATE 1006. Scale bar = 10 mm.



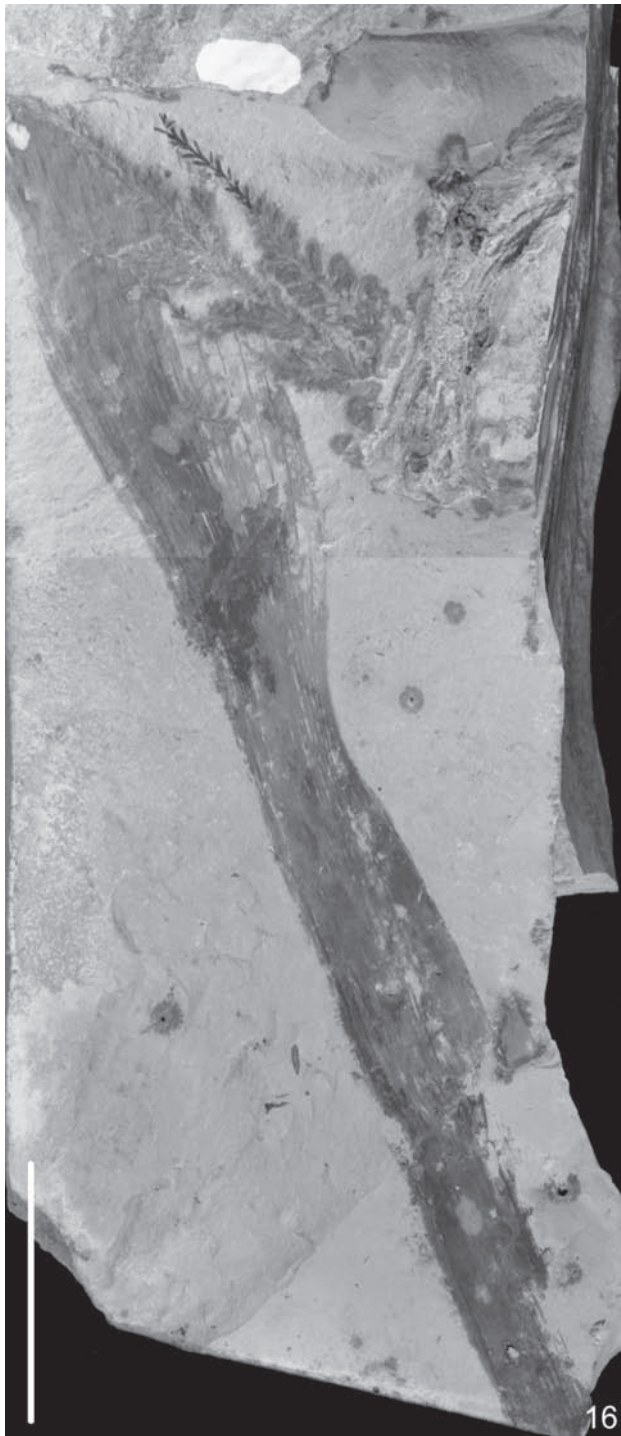


Figure 16: *Orontium mackii* BOGNER, K. JOHNSON, KVAČEK & UPCHURCH sp. nov. TXSTATE locs. 9115 and 9116 (same bed of volcanic ash). Maastrichtian, Paratype, most complete leaf with swollen petiole and basal part slightly folded around midrib. The top part of the specimen is photographed in the normal position. The bottom half is the counterpart, whose image was inverted and overlaid on the top part. A slightly visible seam has been left so that the reader will know it is a composite image. TXSTATE 1029A, B. Scale bar = 50 mm.

Symplocarpus hoffmaniae BOGNER, K. JOHNSON, KVAČEK & UPCHURCH sp. nov.
Figs 22–24

Diagnosis: Leaves cordate to subcordate, entire-margined, petiole non-geniculate, venation pinnate, lowermost primary lateral veins condensed, sending abmedially large loops forming indistinct submarginal (marginal) vein, higher lateral veins weakly differentiated into two orders, higher order veins forming narrow elongate irregular areoles in several orders parallel to primary laterals, crossveins variously oblique.

Description: Leaves incomplete, only the basal half of lamina preserved, entire-margined, blade simple, 120 and 180 mm long (complete length unknown), ca. 65 mm and 130 mm wide, base slightly cordate to subcordate, petiole medium-thick, non-geniculate (ca. 50 mm preserved), venation pinnate, 2–3 lowermost primary lateral veins (max. 0.5 mm thick) condensed on one side of narrow multistranded midrib, lowermost vein successively split shortly above the base, the next higher one sending abmedially series of variously large loops forming indistinct submarginal (marginal) vein, fine details of marginal venation not well preserved, higher lateral veins at an angle of 30–45°, weakly differentiated into two orders, primary veins ca. 10–20 mm apart, straight to slightly bent, secondary veins slightly wavy, not reaching margin and looping admedially with primary veins, higher order veins forming narrow elongate irregular areoles in several orders parallel to primary laterals, steeply fused or joint by variously oblique crossveins.

Holotype here designated: DMNH# 6711 - Fig. 22 (coll. Denver Museum of Nature & Science).

Type locality and age: Mud Buttes (=Dean Street), Bowman County, North Dakota, loc. DMNH 428 (field No. KJ88102), Upper Cretaceous, uppermost Maastrichtian.

Other material studied: DMNH# 26746 - Fig. 27 (coll. Denver Museum of Nature & Science), Berwind Canyon, Raton Fm., Los Animas County, Colorado, DMNH loc. 423 (field No. KJ9129), Puercan, lowermost Paleocene.

Etymology: In honour of GEORGIA HOFFMAN, Calgary, Canada, for her long paleobotanical research activities in northwestern North America.

Remarks: The described new species was first published as aff. *Philodendron* by JOHNSON (2002, p. 347, pl. 4, fig. 4). The fossil leaf fragments differ from the leaves of Aroideae and Monsteroideae with dense parallel-pinnate venation (*Schismatoglottis*, *Homalomena*, *Philodendron*, *Monstera*) in having a slightly cordate base and pinnate venation with widely spaced laterals interconnected in elongate irregular areoles of several orders. They most closely resemble the genus *Symplocarpus* (Figs 25–26). *Symplocarpus* is disjunctly distributed by its five species in temperate western North America and East Asia. Recently two new species have been described: *Symplocarpus egorovii* N.S. PAVLOVA & V. NECHAEV (PAVLOVA & NECHAEV 2005) from East Siberia and *Symplocarpus nabekuraensis* OTSUKA & K. INOUE (OTSUKA, WATANABE & INOUE 2002) from Japan (Honshu), the latter is closely related to *Symplocarpus renifolius* SCHOTT ex MIQ. from East Asia. The other species are *Symplocarpus nipponicus* MAKINO from Japan and Korea and *Symplocarpus foetidus* (L.) W.P.C. BARTON from North America.



Figures 17–19: *Orontium aquaticum* L., cult. Botanical Garden, Munich; 17: Overall form of a leaf. Scale bar = 10 mm; 18: Detail of the medial part. Scale bar = 5 mm; 19: Venation. Scale bar = 2 mm; Figures 20–21: *Lysichiton camtschatcensis* (L.) SCHOTT, cult. Botanical Garden, Munich; 20: Overall form of a leaf. Scale bar = 10 mm; 21: Detail of the venation. Scale bar = 5 mm.

The correspondence of leaf architecture between the fossils and extant relatives is not as great as in the previous cases of fossil *Orontium*. *Symplocarpus hoffmaniae* partly differs from extant *Symplocarpus* in its venation, namely in higher-order lateral veins. In contrast to the fossils (Fig. 23) these veins in extant *Symplocarpus* are more often connected with admedially oriented crossveins and tend to form a broader, often quadrangular meshes, as for example in *Symplocarpus foetidus* (Fig. 26). Unfortunately, details of marginal venation are not sufficiently preserved in the fossils to corroborate generic identification, which must remain somewhat equivocal. More and better preserved specimens are needed. The only Late Cretaceous fossil infructescence from western North America, *Albertarum pueri* BOGNER et al. (late Campanian, Horseshoe Canyon Formation, Alberta), is indeed related to *Symplocarpus* (BOGNER et al. 2005).

Occurrence: Dean Street, North Dakota, Upper Cretaceous, uppermost Maastrichtian, Hell Creek Formation., Berwind Canyon, Los Animas Co. Colorado, Puercan, Paleocene, Raton Formation.

Addendum

Genus *Lysichiton* SCHOTT 1857

Type: *Lysichiton camtschatcensis* (LINNAEUS) SCHOTT 1857 (*Dracontium camtschatcense* L.)

Lysichiton austriacus (J. KVAČEK & A.B. HERMAN) BOGNER, K. JOHNSON, KVAČEK & UPCHURCH comb. nov.

2005 *Araciphyllites austriacus* J. KVAČEK & A.B. HERMAN, p. 4, figs 1, 2, basionym.

Corrected addition to the description: Leaf blade with only primary lateral veins pinnate, higher-order venation ± regularly transverse reticulate between them.

Notes: Due to the delay in publishing the paper by WILDE et al. (2005), where the morphogenus *Araciphyllites* was first established, the species *Araciphyllites austriacus* J. KVAČEK & A.B. HERMAN (2004) from the European Late Cretaceous (Campanian) flora of Grünbach in Austria was at first published invalidly, being connected with the genus *Araciphyllites* before its valid publication. But in the following paper (J. KVAČEK & HERMAN 2005) this species was validated and now can be a valid basionym.

This species is undoubtedly another Late Cretaceous representative of the subfamily Orontioideae. The venation pattern is a good match for that of *Lysichiton* (Figs 19–20) in having simple pinnate primary lateral veins that are connected with regular quadrangular meshes of transverse reticulate higher-order venation (see J. KVAČEK & HERMAN 2004: pl. 1, fig. 4). The original assignment to *Araciphyllites* is, in our opinion, inappropriate. The morphogenus *Araciphyllites* was established for the subfamilies Aroideae and Monsteroideae, and differs in the details of its venation, which is formed by dense parallel-pinnate veins that are weakly differentiated in several orders, as seen in taxa such as *Homalomena pygmaea*

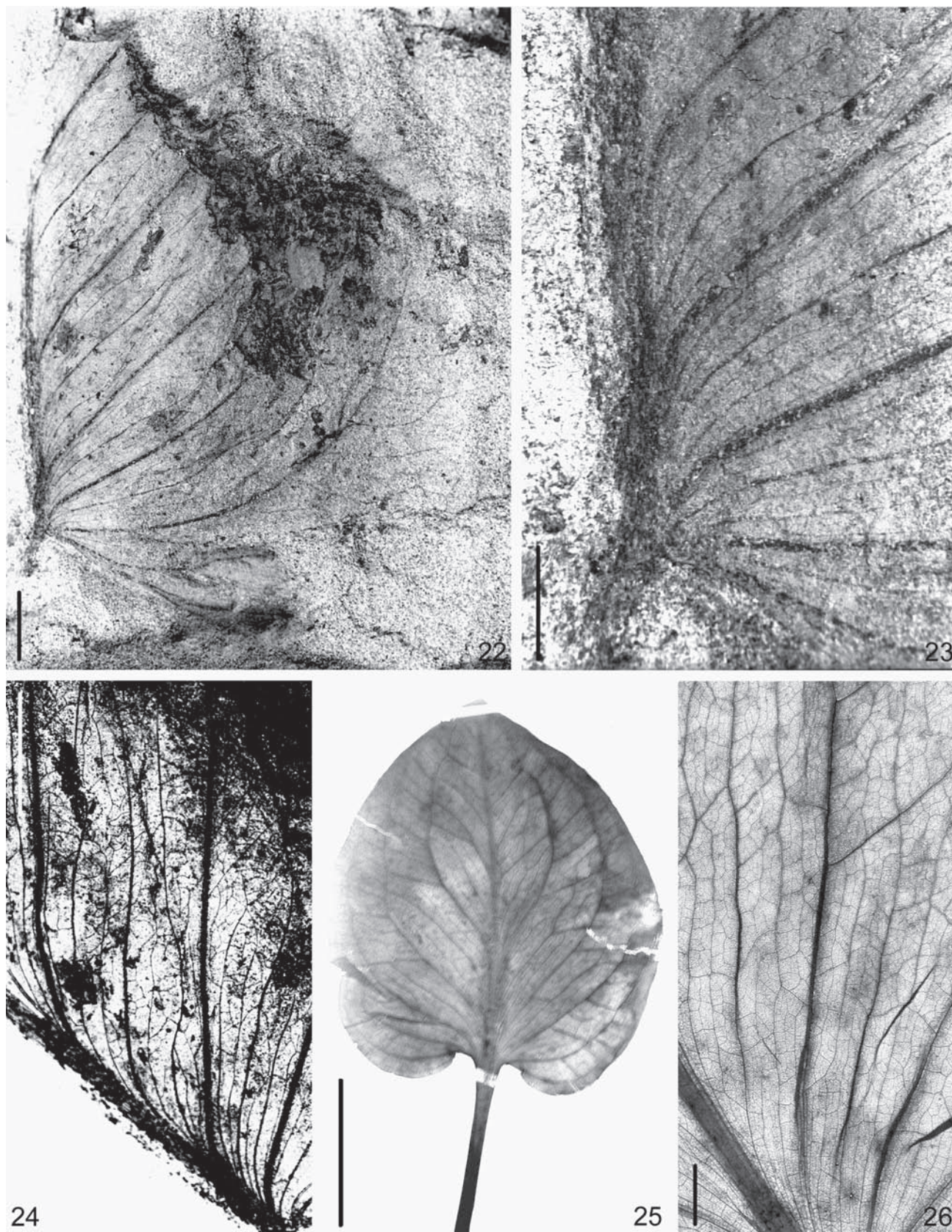
(HASSK.) ENGLER (WILDE et al. 2005: fig. 5E). Because the discussed fossil has the typical gross morphology and venation pattern of *Lysichiton*, we assign it to the extant genus, despite the fact that rare extant genera of angiosperms were present during the Late Cretaceous.

4. Discussion

4.1 Associated Plant Assemblages, Implications on Environment and Climate

The latest Cretaceous plant assemblage of the Hell Creek Formation that contains *Symplocarpus hoffmaniae* (Mud Buttes) belongs to the HCIII megafloora *sensu* JOHNSON & HICKEY (1990) and JOHNSON (2002). The facies corresponds to fluvial channel deposits 15 m below the K/T boundary, which represent the lower part of the Magnetic polarity subchron C29r. This allochthonous assemblage contains a very high diversity of dicot angiosperms. Only three morphotypes of ferns and two morphotypes of conifers (*Elatides longifolius* and *Cupressinocladus interruptus*) are present. The angiosperms (more than 50 morphotypes) belong mostly to *Platanaceae* (*Platanites marginatus*, *Platanus raynoldsii* and others with lobed leaves) and other primitive eudicots (*Cercidiphyllum* and *Trochodendroides* types). A few angiosperms are entire-margined, and some of them may correspond to aquatic plants (*Nelumbago montanum*, *Paranymphea hastata*). Coal-forming *Metasequoia* and other taxa connected with mire facies are absent or scarcely represented at the type locality, Mud Buttes, and rarely occur in other sites and zones of the Hell Creek Formation (JOHNSON 2002). The reconstructed vegetation of the Dean Street consists of angiosperm-dominated woodlands composed of trees frequently with lobed leaves. It can be compared with the Polar Broad-leaved Deciduous Forest *sensu* UPCHURCH & WOLFE (1987), which inhabited flatlands. The presence of palms (*Sabalites*) and leaf margin analysis indicate that the flora of the HCIII zone falls into the latest Maastrichtian warming period (Cfa category of KÖPPEN).

The reconstructed paleoenvironment and vegetation of *Symplocarpus hoffmaniae* largely coincide with the climate and vegetation under which its extant relative *S. foetidus* thrives. Its occurrence in the Hell Creek is consistent with the restriction of *S. foetidus* today to humid mesothermal and microthermal climates from South Carolina to Quebec. Also the ecology of *S. foetidus* corresponds well: “temperate damp woodlands or rarely open wetlands, usually in shaded sites, frequently near water courses” (MAYO et al. 1997). *Symplocarpus hoffmaniae* is represented neither in the HCIIb zone of the Hell Creek section, which is predominantly herbaceous, nor in the Paleocene FU1 zone of hydrophytes (JOHNSON 2002). Hence, this plant obviously belonged to the herbaceous undergrowth in the flatland forests – a typical habitat of *Symplocarpus* today. In its more southerly Paleocene occurrence at Berwind Canyon in the Raton Basin, *S. hoffmaniae* is represented in Phase 3 vegetation – the dicot recolonization phase of WOLFE & UPCHURCH (1987), 30 cm above the iridium-rich Cretaceous-Tertiary boundary clay. The Phase III assemblage at Berwind Canyon is dominated by “*Cissites*” *panduratus* and an unidentified member of Celastrales, with lesser abundance of primitive Lauraceae



Figures 22–26: *Symplocarpus hoffmaniae* BOGNER, K. JOHNSON, KVAČEK & UPCHURCH sp. nov., Dean Street, North Dakota, loc. 428 (KJ 88102), Upper Cretaceous, uppermost Maastrichtian (22–24) and *Symplocarpus foetidus* (L.) SALISB. ex W.P.C. BARTON, Ohio, USA, leg. E. Wilkinson 10757 (Charles University Herbarium) (25–26). 22: *S. hoffmaniae*, holotype, incomplete leaf with one basal lobe. DMNH 6711. Scale bar = 10 mm; 23: Detail of the base of the holotype. Scale bar = 5 mm; 24: Drawing of detailed venation between the lateral primaries. Scale bar = 10 mm; 25: *S. foetidus*, overall form of a leaf. Scale bar = 100 mm; 26: Detailed venation between the lateral primaries. Scale bar = 10 mm.

(*Pandemophyllum*); two species of ferns; and monocots, including palms. Although of low diversity, the reconstructed vegetation indicates wet megathermal conditions (WOLFE & UPCHURCH 1987). The distribution of *S. foetidus* coincides with Northern Hardwood Forest trees such as *Pinus strobus*, *Populus grandidentata*, *Fraxinus nigra*, *Acer spicatum* and *A. saccharum* (cf. MAYO et al. 1997 versus THOMPSON et al. 2000a-c). The temperatures estimated for the Hell Creek are similar to those found in the southerly part of the range of *S. foetidus* in North America, where the ranges of *Symplocarpus* and *Sabal* overlap. The occurrence from the basalmost Paleocene of the Raton Formation (Berwind Canyon) is connected with warmer conditions than those in the Hell Creek.

The Maastrichtian assemblages of the Jose Creek Member of the McRae Formation, New Mexico, where *Orontium mackii* has been recovered, occur in fluvial sandstone, shale, and recrystallized volcanic ash. The Jose Creek assemblages are largely unpublished and contain a mixture of local endemics and taxa found in more northerly floras. Present in the McRae megafloora is a mix of archaic Mesozoic taxa and taxa directly comparable to extant families and genera. Archaic taxa include the conifers *Brachyphyllum* (two species), *Geinitzia reichenbachii*, *Araucarites longifolius*, aff. *Androvettia*, and ?*Widdringtonites complanatus* (UPCHURCH & MACK 1998); the magnoliid dicots aff. *Pabiania* and other palmately veined Laurales; and the eudicots *Trochodendroides* (primitive Trochodendrales or Cercidiphyllales) and *Dryophyllum subfalcatum* (probable Fagaceae). Taxa of more modern aspect include the fern *Woodwardia*, cycads belonging to Zamiaceae, subfamily *Zamioideae* (leaves and cones), isolated conifer leaves comparable to those of extant *Pinus*, pinnately veined Lauraceae, Platanaceae, and monocots assignable to *Sabalites*, *Pandanites* and *Zingiberopsis*, which belong to the families Arecaceae, Pandanaceae, and Zingiberaceae, respectively.

All known specimens of *Orontium mackii* occur in recrystallized volcanic ashes, which occur in the middle to upper part of the Jose Creek Member and the lowermost part of the overlying Hall Lake Member (BUCK & MACK 1995; SEAGER et al. 1997). The aquatic habit of extant *Orontium* implies wet soils and the presence of standing water at the megafossil localities. The localities of the holotype and paratypes (TXSTATE 9115 and 9116) represent the same volcanic ash bed over a distance of 50–100 m and show evidence for standing water, most notably the presence of a fern leaf with well-developed aerenchyma tissue (UPCHURCH, unpublished). However, a third locality that bears two specimens (TXSTATE 9203) has been interpreted as a floodplain with well-drained soils, based on the absence of obvious aquatic plants, the absence of gleying in the underlying paleosol, and ripple structures in the volcanic ash suggestive of wind, rather than water, deposition (BUCK & MACK 1995; GREG MACK, personal communication). This implies that *Orontium mackii* was not an obligate hydrophyte and was capable of living under both terrestrial and aquatic conditions.

The climate of the Jose Creek localities is warm subtropical and conforms to the Cfa type of KÖPPEN, based on foliar physiognomy and the petrology of underlying paleosols (BUCK & MACK 1995; SCHERER et al. 2000). Estimated mean annual temperature ranges from 16–23°C, depending on the model used to quantify modern leaf-climate relationships. Leaf margin

analysis estimates mean annual temperature at either 21–22°C or 16°C, depending on whether the closest modern analogue is vegetation of Asia and North America or Australia (see WILF 1997; GREENWOOD et al. 2004). Cold month means above 5°C are indicated by the common occurrence at *Orontium mackii* localities of zamiod cycads, palms, Pandanaceae, Zingiberaceae, and large-leaved evergreen dicots, all of which are susceptible to hard winter freezes (e.g., WING & GREENWOOD 1995). Estimates of mean annual precipitation based on foliar physiognomy range from 600 to 1200 mm (equations in WIEMANN et al. 1998), with higher estimates supported by associated paleosols (BUCK & MACK 1995). The climate of the Jose Creek Member corresponds to the warm end of the Cfa category of KÖPPEN; that is, subtropical with a cold month mean above 5°C and year-round precipitation. Warm Cfa climate characterizes the southern part of the distributional range of living *Orontium* in southern Florida.

The Early–Middle Eocene flora of Princeton, southern British Columbia is known mainly from the Princeton chert (Allenby Formation) while the leaf impression assemblages containing *Orontium wolfei* remained largely unknown (WOLFE & WEHR 1987: 1) with only recent additions (e.g., PIGG et al. 2003, 2007; MANCHESTER & DILLHOFF 2004). The list of leaf impression taxa indicates many shared elements with the Republic flora, including *Fagus*, *Sassafras*, *Cercidiphyllum*, *Macginitia*, *Alnus*, *Betula*, *Palaeocarpinus*, *Comptonia*, *Rhus* and *Tsukada* (WOLFE & WEHR 1987; GRAHAM 1999). Studies of the Princeton chert have been carried out mainly at the University of Alberta since mid-1970s and continue to the present. The Princeton flora consists of various conifers (*Metasequoia*, *Pinus*) and angiosperms, based mostly on permineralized fruits, seeds and flowers related to the Cabombaceae, Malvaceae, Rosaceae, Lythraceae, Vitaceae, Papaveraceae and others. Of the monocots, abundant araceous seeds and fruits of the *Urospathites*-type have been described from the chert (*Keratoperma allenbyense* CEVALLOS-FERRIZ & STOCKEY 1988). They belong to the Lasiioideae, obviously not in close association with the above described foliage of *Orontium*, and decidedly differ from the smooth seeds of *Orontium* and other Orontioideae in their external sculpture and other details (see SEUBERT 1993). Other monocots in the Princeton flora are not identifiable to this genus (ERWIN & STOCKEY 1991, 1992).

The adjacent Eocene flora of Republic, northern Washington (Klondike Mountains Formation) is probably coeval to Princeton (WOLFE & WEHR 1987: 6; GRAHAM 1999: 215). The Republic macroflora, which also includes *Orontium wolfei*, is dominated by diverse deciduous broad-leaved arborescent dicotyledons, including Cercidiphyllaceae, Platanaceae, Juglandaceae, Ulmaceae, Betulaceae, *Fothergilla*, *Corylopsis*, *Fagus*, *Fagopsis*, *Tilia*, *Craigia*, *Koelreuteria* and other Sapindaceae, shrubby *Sassafras*, *Comptonia*, Rosaceae, Salicaceae and various enigmatic dicotyledonous taxa. These are mixed with a few thermophilic and evergreen elements such as Lauraceae, Theaceae, Sabiaceae, *Photinia*, *Palaeophytocrene*, *Ensete*, and diverse gymnosperms represented by *Ginkgo*, Pinaceae including *Pinus*, *Picea*, *Pseudolarix*, *Abies*, Taxaceae, Cephalotaxaceae, and Cupressaceae including *Metasequoia*, *Cryptomeria*, *Chamaecyparis*, and *Thuja* (WEHR & HOPKINS 1994; GRAHAM 1999; PIGG et al. 2003; MANCHESTER & DILLHOFF 2004; RADTKE et al. 2005). WOLFE & WEHR (1987) interpreted this plant as-

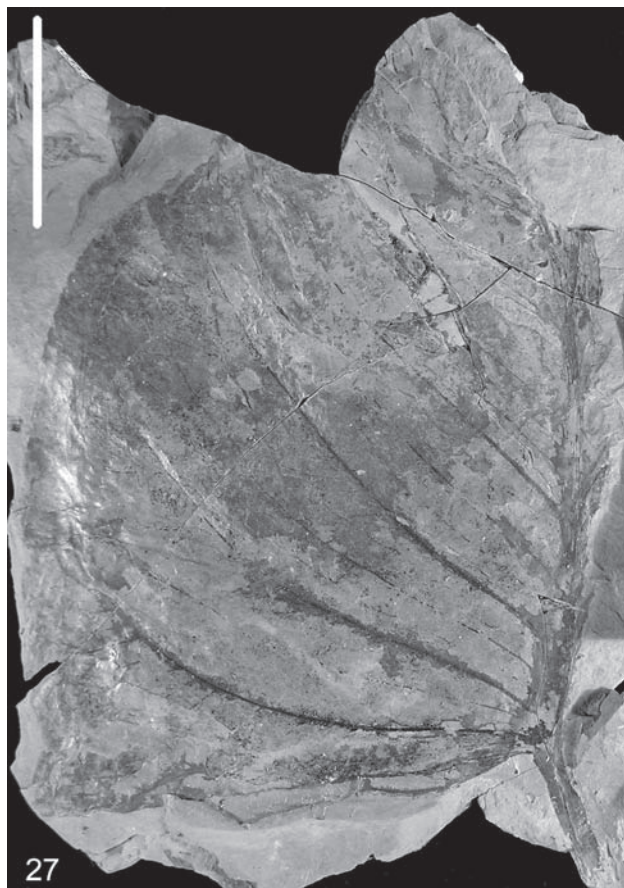


Figure 27: *Symplocarpus hoffmaniae* BOGNER, K. JOHNSON, KVAČEK & UPCHURCH sp. nov., Berwin Canyon, Colorado, loc. 423 (KJ 9129), lowermost Paleocene. Large fragmentary leaf with incompletely preserved basal lobes and petiole. DMNH 26746. Scale bar = 50 mm.

semblage as the Low Montane Mixed Coniferous forest *sensu* WOLFE (1979) with a Mean Annual Temperature of 12–13°C and Mean Annual Range of Temperature about 5°C. This upland Eocene vegetation was characterized physiognomically with a mixture of diverse and dominant coniferous elements, diverse mostly streamside broad-leaved and gymnospermous deciduous higher trees, accessory broad-leaved evergreen and deciduous small trees and shrubs, but no vines (WOLFE & WEHR 1987; GRAHAM 1999). *Orontium* thus represents in this assemblage one of rare aquatic or swamp plants from the lake borders. At Republic, fossil *Orontium* lived under a Cfb or Cfc climate, which is characterized by cooler summer temperatures than Cfa climates (typically less than 20°C).

The only extant representative of *Orontium*, *O. aquaticum*, is a rooted hydrophyte to helophyte that is confined to the warm-temperate to subtropical E and SE USA on borders of shallow fresh waters. Its distribution area from southernmost Florida over Mississippi to Massachusetts coincides with several elements of the Mixed Mesophytic Forest and swamp forests of the Atlantic USA, such as *Taxodium distichum*, *Nyssa sylvatica*, *Diospyros virginiana*, *Liquidambar styraciflua*, *Rhus copallina*, *Myrica cerifera* and *Cephalanthus occidentalis* (cf. MAYO et al. 1997; THOMPSON et al. 2000a-c). The climate over this area is of the Cfa-type with high amount of annual precipitation without any dry period. The mean annual tempe-

perature for the Republic flora is comparable to that experienced by *O. aquaticum* towards the northern part of its range. The precipitation was high enough to call the regime humid although *Orontium* is a hydrophyte or helophyte. Hydrophytes and helophytes are supplied by ground or/and surface waters independent of precipitation regime.

4.2 Phylogenetic Implications

The fossils described here indicate that the Orontioideae is an ancient subfamily of Araceae, with forms comparable to extant genera occurring in the Late Cretaceous. New DNA studies (SALAZAR G., CABRERA L. & CHASE M., personal communication) place them somewhat basal within the family as a whole, a result consistent with morphological characters. In particular, the shoot architecture of Orontioideae is unique within Araceae in having sympodial ramification where the bud in the axil of the last leaf preceding the spathe continues the new shoot. In all other aroids with sympodial ramification the new shoot arises from the bud of the second node before the spathe. The spathe of *Orontium* and *Lysichiton* is inserted at a point of attachment of the inflorescence to the rhizome and envelops the lower part the elongated stipe; in *Orontium* the spathe is inconspicuous (a condition otherwise unknown in aroids). On the other hand, *Symplocarpus* has a true, short peduncle.

The Orontioideae, with the extant genera *Orontium*, *Lysichiton* and *Symplocarpus* and few living species, occur today in North America and East Asia. The fossils described here indicate that both individual genera and the subfamily as a whole had a significantly broader geographic distribution during the Late Cretaceous and Paleogene, a situation well documented for many other East Asian/North American endemics (e.g. *Odocoileus*, *Sequoia*, *Metasequoia*, *Cercidiphyllum*, *Eucommia*, *Sabal* etc.). The discovery of the fossil *Lysichiton austriacus* from Austria in central Europe indicates that members of the Orontioideae were once present throughout the Northern Hemisphere and that the restriction of extant *Lysichiton* to western North America and East Asia is the result of extinction elsewhere. Within North America, *Orontium* and forms similar to *Symplocarpus* were once present in the Western Interior and Pacific Northwest during the Late Cretaceous and Paleogene but are now restricted to the eastern half of the continent. Their present phytogeography is certainly due to exchange of plant populations that was possible by previous proximity or connections between continents in the Northern Hemisphere (see TIFFNEY 1985a, b; SPICER et al. 1994; MANCHESTER 1999).

Today the Orontioideae grow in wet habitats with a temperate to subtropical climate, whereas over 90% of all aroids are restricted to the tropics. Fossil Orontioideae occur in Late Cretaceous and Eocene assemblages that grew under climates ranging from warm subtropical to temperate. This indicates that the relatively cool climatic tolerances of extant Orontioideae evolved no later than the Early Cenozoic.

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