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

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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 & UPCURCH sp. nov. (Lower–Middle Eocene, northern Washington and southern British Columbia); 2) *Orontium mackii* BOGNER, K. JOHNSON, KVAČEK & UPCURCH sp. nov. (Maastrichtian, New Mexico); and 3) *Symlocarpus hoffmaniae* BOGNER, K. JOHNSON, KVAČEK & UPCURCH 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 & UPCURCH 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. Palaeoökologische Analysen anhand assozierter Blattfossilien 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...
North America, the extant subfamily Orontioideae is represented by *Albertarum pueri* (Bogner et al. 2005) and the extinct subfamily Limnobiyphylloideae, which is represented by *Limbobiophylloides* (Stockey et al.1997; Johnson 2002; Kvaček 2003). In India, the extinct subfamily Monsteroideae is represented by *Rhodospathodendron tomlinsonii* (Bone 2000), while in central Europe, the extant subfamily Orontioideae is represented by *Lysichiton australis* (this paper and J. Kvaček & Herman 2004, 2005, originally described as *Araciphyllites australis*).

The recent 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 Gymnostachyoidae 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 \( n = 13, 14, 15 \) (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 morphospecies 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 (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-Consquences, 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 (Stager 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 Lancian 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 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, KVÁČER & 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 dense 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 areoles 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.


Type locality and age: DMNH 382 (= One Mile Creek, Princeton, loc. B 3389), Eocene.


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, KVÁČEK & UPCHURCH sp. nov., Lower-Middle Eocene of NW North America

4: Leaf fragment with well preserved venation. Republic, One Mile Creek, 56723. 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.

**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 base leaf, 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 lateral veins arising subparallel, only very slightly bent, primary laterals mostly 2–5 mm apart except for the 3–4 primary lateral veins 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 cross veins. 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 (*Dractonium foetidum* L.)
Symplocarpus hoffmaniae BOGNER, K. JOHNSON, KVAČEK & UPCHURCH sp. nov.

**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 Monstroideae 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* OTSUWA & 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.

**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
The correspondence of leaf architecture between the fossils and extant relatives is not as great as in the previous cases of fossil *Orontium. Symlocarpus hoffmaniae* partly differs from extant *Symlocarpus* in its venation, namely in higher-order lateral veins. In contrast to the fossils (Fig. 23) these veins in extant *Symlocarpus* are more often connected with admedially oriented crossovers and tend to form a broader, often quadrangular meshes, as for example in *Symlocarpus 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, *Alberatarum pueri* Bogner et al. (late Campanian, Horseshoe Canyon Formation, Alberta), is indeed related to *Symlocarpus* (Bogner et al. 2005).

**Occurrence:** Dean Street, North Dakota, Upper Cretaceous, uppermost Maastrichtian, Hell Creek Formation, Berwind Canyon, Los Armas 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 *Symlocarpus hoffmaniae* (Mud Buttes) belongs to the HCI1 megaflora sensu Johnson & Hickey (1990) and Johnson (2002). The facies corresponds to fluviatile 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 *Cephalocladus interruptus*) are present. The angiosperms (more than 50 morphotypes) belong mostly to *Platanaceae* (*Platanus marginatus*, *Platanus raynoldsii* and others with lobed leaves) and other primitive eudicots (*Ceratiphyllum* and *Trochodendroides*) types. A few angiosperms are entire-margined, and some of them may correspond to aquatic plants (*Nelumbo montanum*, *Paranymphea hastata*). Coal-forming Metasequoia and other taxa connected with mire faunas 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 HCI1 zone falls into the latest Maastrichtian warming period (Cfa category of Köppen).

The reconstructed paleoenvironment and vegetation of *Symlocarpus 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). *Symlocarpus hoffmaniae* is represented neither in the HCI1 zone of the Hell Creek section, which is predominantly herbaceous, nor in the Paleocene FU1 zone of hydrophytes (Johnson 2002). Hence, this plant obviously belongs to the herbaceous undergrowth in the flatland forests – a typical habitat of *Symlocarpus* 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: *Symlocarpus hoffmaniae* Bogner, K. Johnson, Kvaček & Upchurch sp. nov., Dean Street, North Dakota, loc. 428 (KJ 88102), Upper Cretaceous, uppermost Maastrichtian (22–24) and *Symlocarpus 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 6/11. 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.
Orontium wolfei occur in re-

The distribution of Rosaceae, Salicaceae and va-

tides; and the eudicots

include the conifers Araucarites longifolius (two species), Geinitzia, Alnus, Betula, Palaeocarpinus, Comptonia, Rhinus 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, Lyraceae, Vitaceae, Papaveraceae and others. Of the monocots, abundant araceous seeds and fruits of the Urospa-

thites-type have been described from the chert (Keratosperma allenbyense Cevallos-Perriz & 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, Craugia, Koebreuteria and other Sapindaceae, shrubby Sassafra, Comptonia, Rosaceae, Salicaceae and var-

ious enigmatic dicotyledonous taxa. These are mixed with a few thermophilic and evergreen elements such as Lauraceae, Theaceae, Sabiaceae, Pho tinia, Palaeophytocrene, Ensete, and diverse gymnosperms represented by Ginkgo, Pinaceae including Pinus, Picea, Pseudolarix, Abies, Taxaceae, Cephalota xaceae, 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-
The only extant representative of Orontium, *O. aquaticum*, is a rooted hydrophyte to helophyte that is confined to the warm-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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**Figure 27:** *Symlocarpus boffmaniae* Bogner, K. Johnson, Kváček & Unchurh 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.
5. References


Radtke, M.G., Pigg, K.P. & Wehr, W.C. (2005): Fossil *Corylopsis* and *Fosbergilla* leaves (Hamamelidaceae) from the Lower Eocene


