A fossilized aroid infructescence, *Albertarum pueri* gen.nov. et sp.nov., of Late Cretaceous (Late Campanian) age from the Horseshoe Canyon Formation of southern Alberta, Canada

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Abstract: A fossilized aroid infructescence has been recovered from the Horseshoe Canyon Formation in southern Alberta, Canada. Its stratigraphic position places it near the end of the Campanian Stage of the Late Cretaceous Epoch, at an absolute age of approximately 72 million years before present. It is one of the few Cretaceous aroid fossils known at present, and it represents a new genus of Araceae, here named *Albertarum*. The infructescence is fertile to the apex, and the flowers must have been bisexual. Flowers bear remains of a long, attenuated style, surrounded by a perigone of six tepals. A fracture reveals ellipsoid seeds with a thick, ribbed testa and traces of a raphe, arranged in groups of three. The gynoecium was probably trilocular with one ovule per locule, and ovules were anatropous, probably with apical–parietal or axile placentation. Bisexual, perigoniate flowers occur in subfamilies Gymnostachydoideae, Orontioideae, Pothoideae, Monsteroideae, and Lasioideae, no genera of which have ribbed seeds, but the infructescence and stylar region of *Albertarum* resemble those of extant *Symplocarpus* (Orontioideae). The Horseshoe Canyon Formation was deposited in a delta plain setting, and like *Symplocarpus*, *Albertarum* probably grew in a wetland environment.

Key words: fossil, Araceae, *Symplocarpus*, *Albertarum*, *Limnobiophyllum*, *Mayoa*.

Résumé : Les auteurs ont découvert une infructescence aroïde fossilisée, dans la formation de Horse Shoe Canyon du sud de l'Alberta, au Canada. Sa position stratigraphique la situe vers la fin du stade Campanien de la fin de l'époque Crétacée, avec un âge absolu de 72 millions d'années avant le présent. Il s'agit d'un des rares fossiles aroïdes connus à ce jour, et il représente un nouveau genre d'Araceae, ci-nommé l'*Albertarum*. L'infructescence est fertile jusqu'à l'apex, et les fleurs étaient sans doute bisexuelles. Les fleurs portent les restants d'un long style atténué, entouré d'un périgone à six pétales. Une fracture révèle des graines ellipsoïdes, avec un tégument épais et rainuré ainsi que les traces d'un raphé, arrangées en groupes de trois. Le gynécée était probablement triloculaire avec une ovule par loge, et ces ovules étaient anatropes, probablement avec une placentation apico-pariétale ou axile. On retrouve des fleurs périgoniées bisexuelles dans les sous-familles Gymnostachydoideae, Orontioideae, Pothoideae, Monsteroideae, et Lasioideae, dont aucun genre ne possède des graines rainurées, mais les infructescences et la région du style de l'*Albertarum* ressemblent à celles des *Symplocarpus* (Orontideae) actuels. La formation de Horse Shoe Canyon s'est déposée dans une plaine d'alluvions en delta, et comme les *Symplocarpus*, l'*Albertarum* poussait probablement dans un environnement humide.

Mots clés: fossile, Araceae, *Symplocapus, Albertarum, Limnobiphyllum, Mayoa*.

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Introduction

When the fossil record of the Araceae was reviewed by Gregor and Bogner (1984, 1989), there were almost no fossils older than Eocene that could be ascribed to the family with confidence. A clearer picture is now emerging. Recently described fossil pollen from Early Cretaceous sediments indicates that Araceae is one of the oldest families of monocots (Friis et al. 2004). Convincingly araceous fossils from the Cretaceous Epoch remain rare, however, and no araceous macrofossils older than the Campanian Stage of the Late Cretaceous are known at present.

This paper describes a new macrofossil from Late Campanian Stage sediments in south-central Alberta, Canada. It is an isolated infructescence that is permineralized with silica. The remains of its flowers, gynoecium, and seeds are remarkably well preserved, and its affinity to Araceae is clearly apparent. Compared to the other known fossils and extant Araceae, this specimen exhibits a unique combination of characters, many of which are considered plesiomorphic in the family. It is clearly a

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new taxon, here described as *Albertarum pueri* gen.nov. et sp.nov., and it sheds new light on the phylogeny, diversity, and biogeography of early Araceae.

Materials and methods

Location

Only one specimen (TMP 2001.51.01) has been found to date. It is housed in the collections of the Royal Tyrrell Museum of Palaeontology in Drumheller, Alberta, Canada. It was collected in the Red Deer River valley near Drumheller, at the Royal Tyrrell Museum's 2001 Day Digs Site, located at 51°28′33.7″N, 112°45′43.4″W (12U0377631, UTM 5704236 accuracy ± 8 m; Dominion Land Survey SW1/4-2-16-29-20-W4M).

Preservation

The specimen was permineralized with silica before any significant decay or compression had occurred, and many details of both the external and internal morphology are clearly apparent. This type of preservation is not common in plant fossils, and it is especially rare in those of Cretaceous age.

Preparation

The specimen is about 2.0 cm in height, with a diameter that measures about 2.0 cm × 2.5 cm. It was cleaned with a sharpened tungsten carbide rod to remove adhering mudstone, and it was studied and photographed under a binocular microscope.

Geological setting

The Royal Tyrrell Museum's 2001 Day Digs Site encompasses strata between Coal Zones 7 and 8 in the lower Horseshoe Canyon Formation (Fig. 1). The Horseshoe Canyon Formation is interpreted as a succession of delta plain and estuarine sediments (Eberth 2004; Hamblin 2004). It was deposited along the western margin of an interior seaway that is represented by the marine sediments of the Bearpaw Formation (Fig. 1).

Age

The Campanian–Maastrichtian boundary occurs just below Coal Zone 10 in the Horseshoe Canyon Formation (Lerbekmo and Braman 2002; Hamblin 2004). The specimen was found as float between Coal Zones 7 and 8 (Fig. 1), and it apparently had weathered from a bed within that stratigraphic interval. This establishes the age of the fossil as Late Campanian, which correlates with an absolute age of about 72 Ma (Eberth 2002).

Results

Characters

The fossil represents about three-quarters of a fertile infructescence that has been permineralized with silica (Fig. 2). A natural fracture provides a cross-sectional view of the interior, revealing ribbed seeds in groups of three (Fig. 3). A scar where the stipe was attached is present at the base of the specimen (Fig. 4).

The specimen is fertile to the apex, indicating that the flowers were bisexual. In aroids with unisexual flowers, the upper portion of the spadix is occupied by male, never female, flowers (Mayo et al. 1997). Each flower bears a long attenuated and faceted style (Fig. 5) that is similar in form to those of extant *Symplocarpus* (L.) Salisbury ex Nuttall. The style is surrounded by a perigone that consists of six tepals, arranged in two whorls of three. Remains of a tepal that is arched or falcate toward the style are present on one flower.

The natural fracture reveals that the gynoecium includes seeds in groups of three, or in one example, two (Fig. 3). The seeds are slightly arched ellipsoids, with a thick, prominently ribbed testa (Figs. 6, 7). Traces of a raphe can be seen on the fractured seeds (Fig. 7), recessed between the ribs on the ventral surface and extending from the apex to near the base of the seed. The ribs that flank the raphe are strongly developed.

The tissues needed to confirm ovule attachment are not visible, but it is possible to deduce some aspects of ovular placement by examining the seed groups. The gynoecium appears to have a trilocular ovary, with one ovule per locule, rather than a unilocular ovary with three ovules. In the example with two seeds, the remains of a third aborted seed can be discerned. The presence of a raphe indicates that the ovules were anatropous. The longitudinal position of the fruits, their slightly arched shape, and uniform extension of the raphe suggest an apical–parietal or at least mid- to upper-axial attachment of the ovule to the placenta with a short funicle.

Systematic description

Class	Liliopsida
Order	Arales Lindl.
Family	Araceae Jussieu
Subfamily	Orontioideae Mayo, Bogner & Boyce

GENUS AND SPECIES: *Albertarum pueri* Bogner, G.L. Hoffman & Aulenback, gen.nov. et sp.nov.

DIAGNOSIS: *Albertarum pueri* a genere extanti *Symplocarpo*, flore 6 tepalis instructo, gynoecii ovario 3-loculare, loculis uniovulatis, ovulo anatropo, semine ellipsoideo, testa crassa et costata, raphe distincta differt.

HOLOTYPUS: TMP 2001.51.01, Royal Tyrrell Museum of Palaeontology.

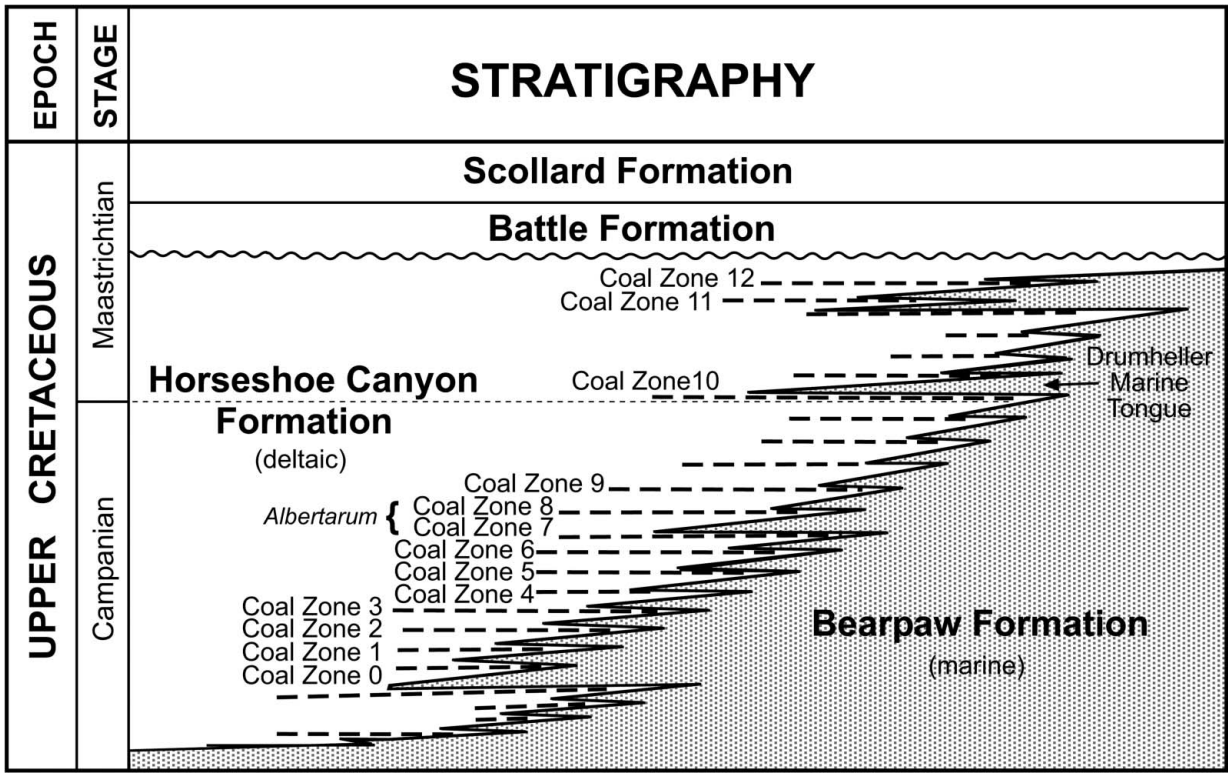
GENERIC DESCRIPTION: Infructescence stipitate, subglobose. Flowers bisexual, perigoniate; tepals six, fornicate, imbricate. Gynoecium with a trilocular ovary, one ovule per locule, placenta apical-parietal or possibly mid-axial; ovules anatropous; stylar region long attenuate. Seed ellipsoid; testa thick, prominently ribbed; raphe present.

TYPUS OF THE GENUS: *Albertarum pueri* Bogner, G.L. Hoffman & Aulenback, sp.nov.

SPECIES: *Albertarum pueri* Bogner, G.L. Hoffman & Aulenback, sp.nov.

SPECIFIC DESCRIPTION: Infructescence stipitate, subglobose, about 2.0 cm in length and 2.5 cm in width. Flowers bisexual, perigoniate, about 6.0–7.0 mm in diameter; tepals 6, fornicate, imbricate. Gynoecium with a trilocular ovary, one

Fig. 1. Stratigraphic setting of the Horseshoe Canyon Formation (modified from Hamblin 2004). *Albertarum pueri* came from the interval between Coal Zones 7 and 8.



ovule per locule, placentation apical parietal or possibly mid-axial. Stylar region attenuate, about 4.0 mm in length. Seed ellipsoid, about 3.0 mm in length and 1.8–2.0 mm in diameter, slightly arched. Testa about 0.25–0.30 mm thick, prominently ribbed. Raphe present, inset between ribs on ventral face, extending the length of the seed.

HOLOTYPUS: TMP 2001.51.01, Royal Tyrrell Museum of Palaeontology.

ETYMOLOGY: The generic name refers to the Province of Alberta and the genus *Arum* L., from which the family Araceae takes its name. The specific epithet honours the finder, an unknown boy who visited the collecting site.

TYPE LOCALITY: The Royal Tyrrell Museum of Palaeontology 2001 Day Digs site (12U0377631, UTM 5704236).

STRATIGRAPHIC POSITION: Lower Horseshoe Canyon Formation between Coal Zones 7 and 8 (Fig. 1).

AGE: Late Cretaceous, Latest Campanian; approximately 72 Ma.

Discussion

Affinity

The fossil flowers are bisexual and perigoniate. Bisexual flowers occur in subfamilies Gymnostachydoideae, Orontioideae, Pothoideae, Monsteroideae, Lasioideae, and Calloideae. In Gymnostachydoideae, Orontioideae, and Pothoideae, all genera are perigoniate. In Monsteroideae, only three genera (*Spathiphyllum* Schott, *Holochlamys* Engler, and *Anadendrum* Schott) have a perigone (Engler and Krause 1908). In Lasioideae, all genera except one (*Pycnospatha* Thorel ex Gagnepain) have a perigone. The single genus of Calloideae, *Calla* L., lacks a perigone (Krause 1908).

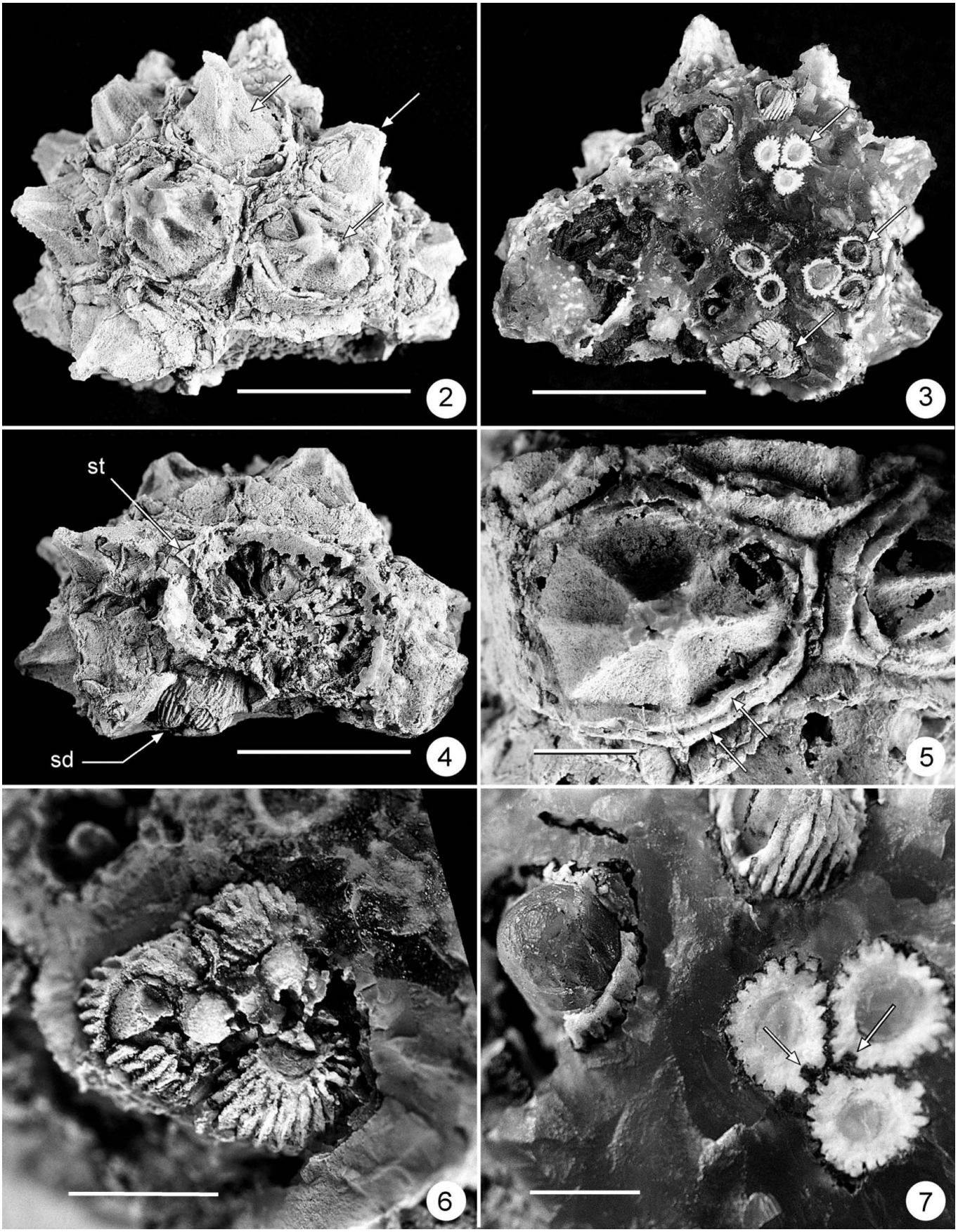
The fossil is referred to subfamily Orontioideae. It is excluded from subfamily *Calloideae* by its perigone and from subfamilies Gymnostachydoideae, Pothoideae, Monsteroideae, and Lasioideae by the morphology of the stylar region. In those subfamilies, only some species of *Spathiphyllum* have a similar stylar region, but they have a cylindric rather than globose infructescence, and their seeds are not ribbed like those of the fossil (Seubert 1993).

There are three extant genera in subfamily Orontioideae: *Symplocarpus*, *Lysichiton* Schott, and *Orontium* L. (Mayo et al. 1997). The fossil shares a few characters with each of them, but there are significant differences (Table 1); therefore, the new genus *Albertarum* is erected for the fossil.

Albertarum is most similar to *Symplocarpus* (Table 1). The morphology of the stylar region is quite similar, and both have a globose to subglobose infructescence (Figs. 8, 9). *Albertarum* is distinguished by its trilocular ovary, however, and its ellipsoid, ribbed seeds. It also differs in the number of tepals, and the anatropous ovules.

Paleoenvironment

The extant genera of subfamily Orontioideae typically grow in wetlands and swamps, and along the margins of ponds and streams (Mayo et al. 1997). The geological setting suggests a similar habitat for *Albertarum*. The lower Horseshoe Canyon Formation, from which the specimen was



Figs. 2–7. *Albertarum pueri* gen.nov. et sp.nov. Fig. 2. Exterior of the infructescence, with remains of flowers (arrows). Scale bar = 1 cm. Fig. 3. Cross-sectional view of the infructescence, exposed by a natural fracture. Note ribbed seeds in groups of three (arrows). Scale bar = 1 cm. Fig. 4. Base of the specimen, showing scar where the stipe attached (st). Note seeds (sd) exposed where flower remains have broken away. Scale bar = 1 cm. Fig. 5. Flower with remains of style, surrounded by remains of two whorls of tepals (arrows). Scale bar = 2 mm. Fig. 6. Group of three seeds, showing the ribbed testa. Scale bar = 2 mm. Fig. 7. Group of three seeds broken near their base, showing position of the raphe (arrows). Two partially exposed, broken seeds are nearby. Scale bar = 2 mm.

Table 1. Comparison of *Albertarum* with extant genera of subfamily Orontioideae.

	Genus			
	Albertarum	*Symplocarpus*	*Lysichiton*	*Orontium*
Flowers				
Bisexual	Yes	Yes	Yes	Yes
Perigoniate	Yes	Yes	Yes	Yes
Tepals	6	4	4	6 or 4
Gynoecium				
Locules	3	1	2	1
Ovules per locule	1	1	1 or 2	1
Ovules	Anatropous	Orthotropous	Orthotropous	Anatropous
Placentation	Apical–parietal or mid-axial	Apical parietal	Axile	Basal
Stylar region	Long attenuate	Long attenuate	Attenuate	± Absent
Infructescence				
Shape	Globose to subglobose	Globose to subglobose	Subcylindric	Conical
Base of spadix	Stipitate	Stipitate	Very long stipitate	Very long stipitate
Seed				
Shape	Ellipsoid, curved	Globose	Ellipsoid	Globose to subglobose
Raphe	Inconspicuous	None	None	Conspicuous
Testa	Thick	Thin	Thick	Thin
Texture	Ribbed	Smooth	Smooth	Smooth

collected, is interpreted as a vertically aggrading sedimentary succession that was deposited along the western margin of the Western Interior Seaway (Gibson 1977; Rahmani and Hills 1982; Dawson et al. 1994; Straight and Eberth 2002; Eberth 2004; Hamblin 2004). The sedimentary succession records a variety of estuarine, shoreline, and poorly drained wetland environments adjacent to fluvial and distributary channels (Straight and Eberth 2002; Eberth 2004; Hamblin 2004).

Although the *Albertarum* specimen was found as float, it is apparent from the location and geography of the site that it weathered out from one of several thin, laterally discontinuous lenses of mudstone that occur between Coal Zones 7 and 8. The mudstones are massive, poorly sorted, and locally rich in coaly organic fragments. They are interpreted as poorly drained flood-basin deposits associated with swampy settings, small meandering channels, and minor splays. Sedimentation was probably influenced largely by seasonal rainfall and storm activity (D.A. Eberth, personal communication, 2004).

Other fossils from the same collecting site also indicate a wetland setting. The assemblage includes *Equisetum* L., a *Dennstaedtia*-like fern, the heterosporous ferns *Marsilea* L. and *Azolla* Lam., and foliage and cones of taxoidaceous conifers. There are also leaves and rhizomes of a *Trapa*-like floating aquatic dicot (Stockey and Rothwell 1997). Faunal remains include caddisfly larval casings and small freshwater gastropods. The site also hosts a bonebed consisting of the disarticulated remains of the dinosaur *Edmontosaurus*, a hadrosaur.

Paleoclimate

Calla palustris L. (Calloideae) is the only aroid that grows in Alberta today (Moss 1983). However, the distribution of extant genera of subfamily Orontioideae flanks Alberta to both the east and the west (Fig. 10), and it is probable that Orontioideae grew in the area during times of milder climate.

Paleoclimate information for the Horseshoe Canyon Formation has been summarized by Hamblin (2004). The climate during the deposition of the Lower Horseshoe Canyon Formation (up to Coal Zone 10; Fig. 1) was interpreted by Srivastava (1970) to have been generally subtropical and humid, on the basis of detailed palynological analysis. Remains of taxodiaceous conifers, cycads, and ginkgoes, which are consistent with a humid and largely frost-free climate, are common in the megaflora (e.g., Bell 1949; McIver and Aulenback 1994). The abundance of coal and a lack of evidence of desiccation are also consistent with a humid climate (Nurkowski and Rahmani 1984).

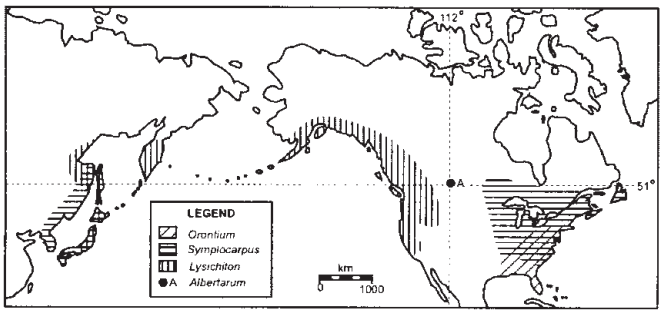
Cretaceous Araceae

Although the fossil record of early Araceae remains quite sparse, a number of distinctive new fossils have been described since the reviews by Gregor and Bogner (1984, 1989). They indicate that the family was present during

Fig. 8. Inflorescence of *Symplocarpus foetidus* (L.) Salisbury ex Nuttall, showing spadix surrounded by spathe. In *S. foetidus*, the spathe is typically 6.0–10.0 cm long from base to apex. Photograph by J. Bogner.

Fig. 9. Infructescences of *Symplocarpus foetidus*. In *S. foetidus*, the infructescence is typically 2.5–3.0 cm in diameter. Photograph by J. Bogner.

Fig. 10. The distribution of extant genera of subfamily Orontioideae (after Mayo et al. 1997) and the location of *Albertarum pueri*.



Early Cretaceous time, and by the end of the Cretaceous Epoch, it was both diverse and widespread.

At present, the strongest evidence of Araceae during the Early Cretaceous comes from *Mayoa portugallica* Friis, Pedersen & Crane, a palynomorph from Late Barremian to Early Aptian Stage sediments at the Torres Vedras locality in western Portugal (Friis et al. 2004). The specimen consists of large masses of pollen attached to a small cutinized fragment. The pollen grains are inaperaturate with a very distinctive striate exine, a morphology very similar to that of pollen of *Holochlamys* Engler (subfamily Monsteroideae, tribe Spathiphylleae), an extant genus from the New Guinea area. There is also a zona-aperturate palynomorph from the same beds and several other localities that could be araceous (cf. *Gonatopus* Hooker f. ex Engler, subfamily Aroideae).

Although these palynomorphs strongly resemble pollen of extant Araceae, no supporting araceous macrofossils from the Early Cretaceous are known at present, and even in the Late Cretaceous the fossil record is still very limited. There are currently four published examples, two from the Campanian Stage (J. Kvaček and Herman 2004; this paper), and two from the Maastrichtian (Z. Kvaček 1995; Bonde 2000).

From the Early Campanian, J. Kvaček and Herman (2004) have described an araceous leaf fragment from Austria as *Araciphyllites austriacus* nom. invalid. The specimen is a large, elongate–lanceolate leaf blade with a massive midrib. The base and apex are lacking, but the venation pattern is like that of extant *Lysichiton* (subfamily Orontioideae). It will be validly described as *Lysichiton austriacus* J. Kvaček & A.B. Herman ex Bogner, K. Johnson & J. Kvaček (J. Bogner, personal communication, 2005).

Albertarum, of Late Campanian age, is the oldest aroid infructescence known at present, and it provides new evidence of ancestral characters for the family. The evolution of unisexual flowers in monoecious inflorescences from bisexual, perigoniate flowers like those of *Albertarum* is considered to be the basic trend in Araceae (Mayo et al. 1997); therefore, *Albertarum* is relatively plesiomorphic. Both *Albertarum* from the western interior of Canada and *Lysichiton austriacus* from central Europe are referred to subfamily Orontioideae; thus, the subfamily appears to have had a much different and probably wider distribution during Late Campanian time that it does at present (Fig. 10).

Limnobiophyllum Krassilov sensu Z. Kvaček (1995) demonstrates that by Late Maastrichtian time, more derived forms were present and were spread throughout the northern hemisphere. *Limnobiophyllum* is considered to represent a link between the families Araceae and Lemnaceae (e.g., Z. Kvaček 1995; Stockey et al. 1997), and botanists now recognize Lemnaceae only as a subfamily of Araceae, the

Lemnoideae. In that view, *Limnobiophyllum* represents a highly derived example of Araceae. The genus persisted from the Late Maastrichtian until at least the mid-Tertiary and was geographically widespread, with occurrences reported from western North America, central Europe, and eastern Asia (Z. Kvaček 1995; Govaerts and Frodin 2001; Z. Kvaček 2003). Fertile specimens with attached remains of flowers and pollen are known from the Late Paleocene of Alberta (Stockey et al. 1997).

Rhodospathodendron Bonde provides an example from the Late Maastrichtian of India (Bonde 2000). It is based on a single specimen that, like *Albertarum*, is permineralized with silica so that details of its cellular structure are preserved. It consists of a thin aerial stem with root scars and remains of leaf sheaths. The axis has a distinct cortex, a thin periderm, and a vascular region with amphivasal vascular bundles (Bonde 2000). The remainder of the plant is not known, but the stem anatomy is consistent with subfamily Monsteroideae, and Bonde (2000) feels that it most closely resembles that of extant *Rhodospatha* Poeppig, a neotropical genus of Monsteroideae.

Additional studies of early Araceae are currently in progress. The pollen record of the family is being reviewed by M. Hesse (J. Bogner, personal communication, 2005). The morphology and affinity of plant fossils from a variety of Late Cretaceous localities that have been erroneously attributed to the genus *Pistia* L. (subfamily Aroideae) as *Pistia corrugata* Lesquereux (1878) are under study (Johnson et al. 1999; R.A. Stockey, personal communication, 2005). A leaf from the Late Cretaceous of North America is being described by J. Bogner, K. Johnson, and J. Kvaček (J. Bogner, personal communication, 2005). Friis et al. (2004) mention unpublished seeds similar to those of *Spathiphyllum* Schott and *Epipremnum* Schott from the Late Cretaceous Mira locality in western Portugal. Clearly, we can look forward to more information about early Araceae in the near future.

Acknowledgements

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