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AROID SEEDS FROM THE MIDDLE EOCENE PRINCETON CHERT (*KERATOSPERMA ALLENBYENSE*, ARACEAE): COMPARISONS WITH EXTANT LASIOIDEAE

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A reinvestigation of more than 200 new specimens of *Keratosperma allenbyense* Cevallos-Ferriz et Stockey from the Middle Eocene Princeton chert allows a more detailed comparison with living Araceae and provides evidence for the evolution of the lasioid clade. The anacampylotropous seeds possess a warty seed coat, single dorsal ridge, and two lateral ridges. Idioblasts that may have contained raphides are scattered in the outer integument. The seed has a thin micropylar cover and an epistase, with evidence of mucilage in the space between these two structures. The raphe is embedded in the seed coat and parallels the concave surface of the seed. At the chalazal end of the seed, there is a prominent hypostase and podium. Endosperm tissue with dark contents and monocotyledonary embryo are present, but in most specimens these tissues are replaced by fungal hyphae. Anatomical comparisons with the extant lasioid taxa *Cyrtosperma merkusii* (Hassk.) Schott and *Urospatha sagittifolia* (Rudge) Schott were made. A reconstruction of *K. allenbyense* constructed from serial sections allowed the fossil to be compared with the extant genera of Araceae, subfamily Lasioideae, on the basis of external seed morphology of 22 taxa. *Keratosperma* appears to be a distinct genus among aroids having many shared characters with extant Lasioideae and represents the oldest known member of the lasioid clade.

Keywords: Araceae, aroid, *Cyrtosperma*, Eocene, *Keratosperma*, Lasioideae, seed, *Urospatha*.

Introduction

The diverse fossil flora from the Middle Eocene Princeton chert of southern British Columbia has been extensively studied in the past 20 yr. This exceptional site contains a wide variety of well-preserved silicified plants, including pteridophytes, conifers, angiosperms, and their associated fungi (Cevallos-Ferriz et al. 1991; LePage et al. 1994; Pigg and Stockey 1996; Stockey et al. 1999).

Monocots are often not well preserved in the fossil record, partially because of their primarily herbaceous habit (Herendeen and Crane 1995). The Princeton chert, however, is unique, having numerous vegetative and fertile monocot remains preserved for families that have an otherwise poor fossil record (Pigg and Stockey 1996). Monocot vegetative remains in the Princeton chert include *Uhlia allenbyense* (Arecaceae) (Erwin and Stockey 1991*a*, 1994), *Heleophyton helobiaeoides* (Alismataceae) (Erwin and Stockey 1989), *Soleredera rhizomorpha* (Liliales) (Erwin and Stockey 1991*b*), and *Ethela sargantiana* (Juncaceae/Cyperaceae) (Erwin and Stockey 1992). In addition to these vegetative remains, flowers, fruits, and seeds of alismatid affinity (Stockey 1994) and seeds of Araceae, subfamily Lasioideae, have also been identified in the chert. These seeds, described as *Keratosperma allenbyense* Cevallos-Ferriz et Stockey (1988), represent the earliest known seeds for this subfamily.

Since the original description, several hundred new specimens of *K. allenbyense* seeds have been found. In this study, we examine the new material anatomically and morphologically along with the type specimens to reevaluate seed anatomy in light of recent detailed studies of aroid structure (Hay 1992; Seubert 1993, 1997; Mayo et al. 1997). Further anatomical details of the micropylar and chalazal region have allowed a comparison of these seeds to additional extant taxa of Araceae, subfamily Lasioideae, on the basis of anatomy and external morphology.

Material and Methods

The fossil specimens were collected from the Princeton chert outcrop, located on the east bank of the Similkameen River, approximately 8.4 km south of Princeton, British Columbia, near the abandoned mining town of Allenby. This outcrop consists of interbedded layers of chert and coal with an occasional ash bed replacing a chert layer (Stockey 1983). There are at least 49 layers of exposed chert that have been recorded and systematically sampled. The outcrop is part of the Princeton Group, Allenby Formation (Boneham 1968), and has been dated as Middle Eocene using data from freshwater fish (Wilson 1977, 1982), mammals (Russell 1935; Gazin 1953), and K-Ar dates (Hills and Baadsgaard 1967). H. Baadsgaard (personal correspondence, 1999) currently places the ash in layer 22 as 48.7 million years.

Chert blocks from several layers were cut into slabs and studied using the cellulose acetate peel technique modified for concentrated (48%) hydrofluoric acid (Joy et al. 1956; Bas-

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Table 1

Extant Lasioid Seeds Examined for Morphology

Species	Material examined	Source	Location
Anaphyllopsis americana (Engl.) A. Hay	MO 05096784 Cremers & Crozier 15019	French Guiana	ALTA 109368
Cyrtosperma carrii A. Hay	J. Bogner 2451, in cult., BGM	Papua New Guinea	J. Boos, personal collection
Cyrtosperma merkusii (Hassk.) Schott	J. Bogner 1510, in cult., BGM	Malay Peninsula (Johore)	ALTA 106077
Dracontioides desciscens (Schott) Engl.	J. Boos, in cult., FL	Brazil	ALTA 109369
Dracontium asperum K. Koch	Proctor 48047	Puerto Rico	ALTA 109370
Dracontium grayumianum G. Zhu	Zhu & Croat 1506	Panama	ALTA 109371
D. grayumianum G. Zhu	Stern et al. 93	Panama	ALTA 109372
Dracontium plowmanii G. Zhu	Gentry & Nunez 69383	Peru	ALTA 109374
Dracontium polyphyllum L.	Martineli 6815	Brazil	ALTA 109375
Dracontium purdieanum (Schott) Hook. f.	Liesner & Gonzalez 13060	Venezuela	ALTA 109376
Dracontium soconuscum Matuda	Bartlett & Lasser 16831	Panama	ALTA 109377
Dracontium spruceanum (Schott) G. Zhu	Vasquez et al. 3005	Peru	ALTA 109378
Lasia spinosa (L.) Thwaites	J. Boos, in cult., FL	Tropical Asia	ALTA 109379
Lasimorpha senegalensis Schott	MO 3435216 Thompson 1486	Cameroon	ALTA 109380
L. senegalensis Schott	Jongkind & Abbin 2089	Ghana	ALTA 109381
L. senegalensis Schott	J. Bogner 691, in cult., BGM	Gabon, West Africa	ALTA 109382
Urospatha grandis Schott	MO 2072643 T. Croat & D. Porter 16500	Panama	ALTA 109383
U. grandis Schott	J. Boos, in cult., FL	Costa Rica	ALTA 109384
Urospatha sagittifolia (Rudge) Schott	J. Bogner s.n., in cult., BGM	Tropical South America	ALTA 106122
Urospatha sp. 1	MO 2395070 T. Croat 35764	Costa Rica	ALTA 109385
Urospatha sp. 2	J. Boos, in cult., FL	Venezuela	ALTA 109386
Urospatha sp. 3	E. Goncalves	Brazil	ALTA 109387
Urospatha sp. 4	MO 3475831 Vasquez & Jaramulbo 7210	Peru	ALTA 109388
Urospatha sp. 5	MO 2403609 Daryer & McBride 9813	Ecuador	ALTA 109389
Urospatha sp. 6	MO 2272377 T. Croat	Peru	ALTA 109390
Urospatha sp. 7	E. Goncalves 176	Brazil	ALTA 109391

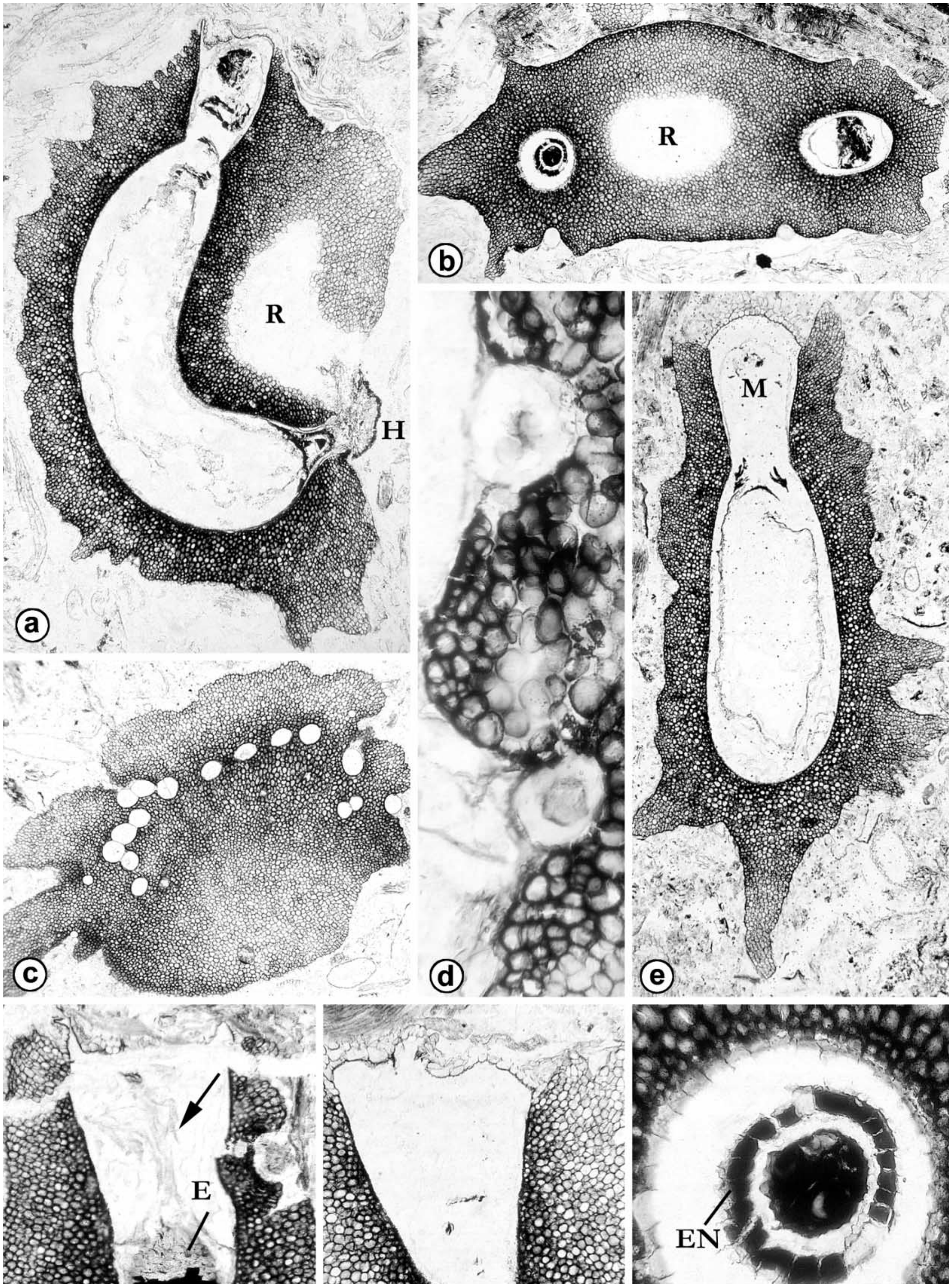
Note. Abbreviations: MO = Missouri Botanical Garden; ALTA = University of Alberta herbarium; BGM = Botanischer Garten München; FL = Florida.

inger and Rothwell 1977; Basinger 1981). Slides of the peels were made using Eukitt (O. Kindler, Freiberg, Germany) xylene-soluble mounting medium.

Since previous work on *Keratosperma* indicated possible similarities to *Cyrtosperma* (Cevallos-Ferriz and Stockey 1988), fossil seeds were compared anatomically with the extant lasioid taxa *Cyrtosperma merkusii* (Hassk.) Schott and *Urospatha sagittifolia* (Rudge) Schott. These seeds were prepared using paraffin histology (Johansen 1940), using a Histomatic 166 tissue embedding processor center and a sliding microtome. Standard safranin/fast green staining procedure was used (Johansen 1940), and paraffin sections were mounted using DPX mounting medium. Cevallos-Ferriz and Stockey (1988) originally compared *Keratosperma* with *Urospatha friedrichsthalii* Schott, but since there is some question as to the taxonomic placement of *U. friedrichsthalii* (Hay 1992), closer comparisons of the fossil with another species of *Urospatha* was necessary. *Urospatha sagittifolia* was chosen because of the reliable source material from the Botanischen Garten München and its external similarity to our fossil seeds.

Fossil specimens were compared with seeds of several extant genera (table 1). The fossil seeds were reconstructed by camera lucida drawings of serial sections through the entire seed. These were then magnified, cut out of 1-mm-thick beeswax, and assembled to form a scale model ×40 larger than the actual specimen; a reconstruction drawing was made from the model.

Fig. 1 *Keratosperma allenbyense* Cevallos-Ferriz & Stockey. *a*, Longitudinal section of seed showing micropyle (top), raphe, and hypostase. P5836 E_1 bot 2b, ×37. *b*, Transverse section of seed showing two seed cavities and raphe. P2613 E bot 34, ×36. *c*, Section of seed integument showing numerous surficial idioblasts. P5937 G bot 10, ×42. *d*, Idioblasts with contents that appear organic. P5956 D top 11, ×217. *e*, Longitudinal section of seed showing integumentary ridges appearing as spines and funnel-shaped micropyle covered by micropylar cap. P5836 D_4 bot 3, ×39. *f*, Longitudinal section of micropyle showing mucilage (arrow) and epistase at apex of nucellus. P2613 D_2 bot 35, ×77. *g*, Longitudinal section of micropyle showing micropylar cover two cells thick. P5836 B_1 top 36, ×85. *h*, Transverse section of seed cavity showing dark, cuboidal endosperm cells surrounding an embryo. P2613 E bot 34, ×204. *R* = raphe, *H* = hypostase, *M* = micropyle, *E* = epistase, *EN* = endosperm.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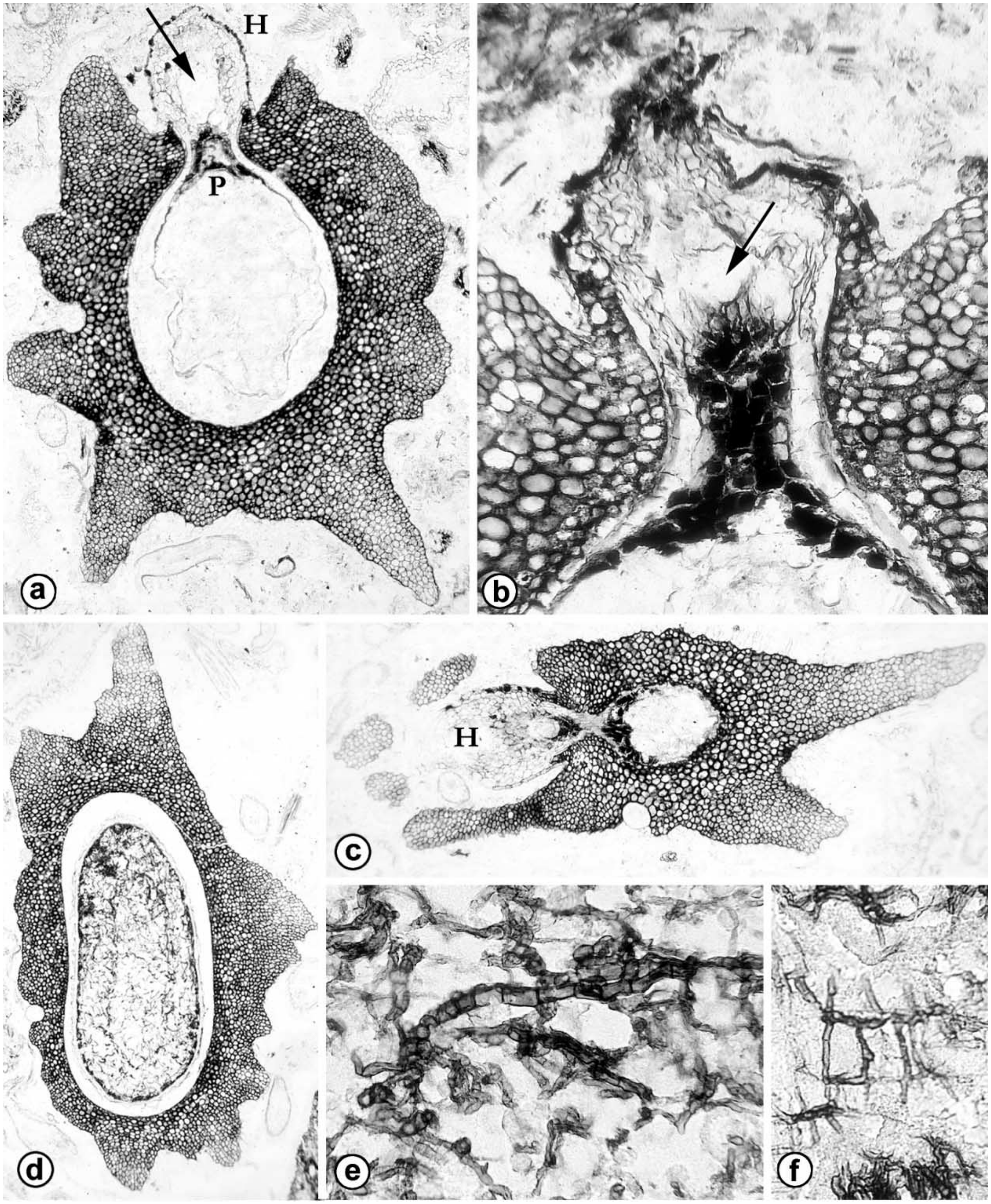

Fig. 2 *Keratosperma allenbyense* Cevallos-Ferriz & Stockey. *a*, Longitudinal section of seed at chalazal end showing protruding hypostase, podium, and integumentary ridges. Arrow indicates the probable zone of mucilage as in extant seeds. P5836 E_1 bot 14a, ×57. *b*, Longitudinal section through hypostase, with thicker, dark outer layer, center without cells, and podium of dark cuboidal cells. Arrow indicates the probable zone of mucilage as in extant seeds. P2613 Ebot 23, ×245. *c*, Section of seed showing hypostase surrounded by integumentary ridges. P5153 Cbot 3, ×49. *d*, Section of seed showing fungal contents that outline the endosperm and embryo. P6025 G 27, ×38. *e*, Septate fungal hyphae in seed cavity. P6025 G 27, ×250. *f*, Fungi in seed cavity replacing cell walls of endosperm. P6025 G 18, ×200. *H* = hypostase, *P* = podium.

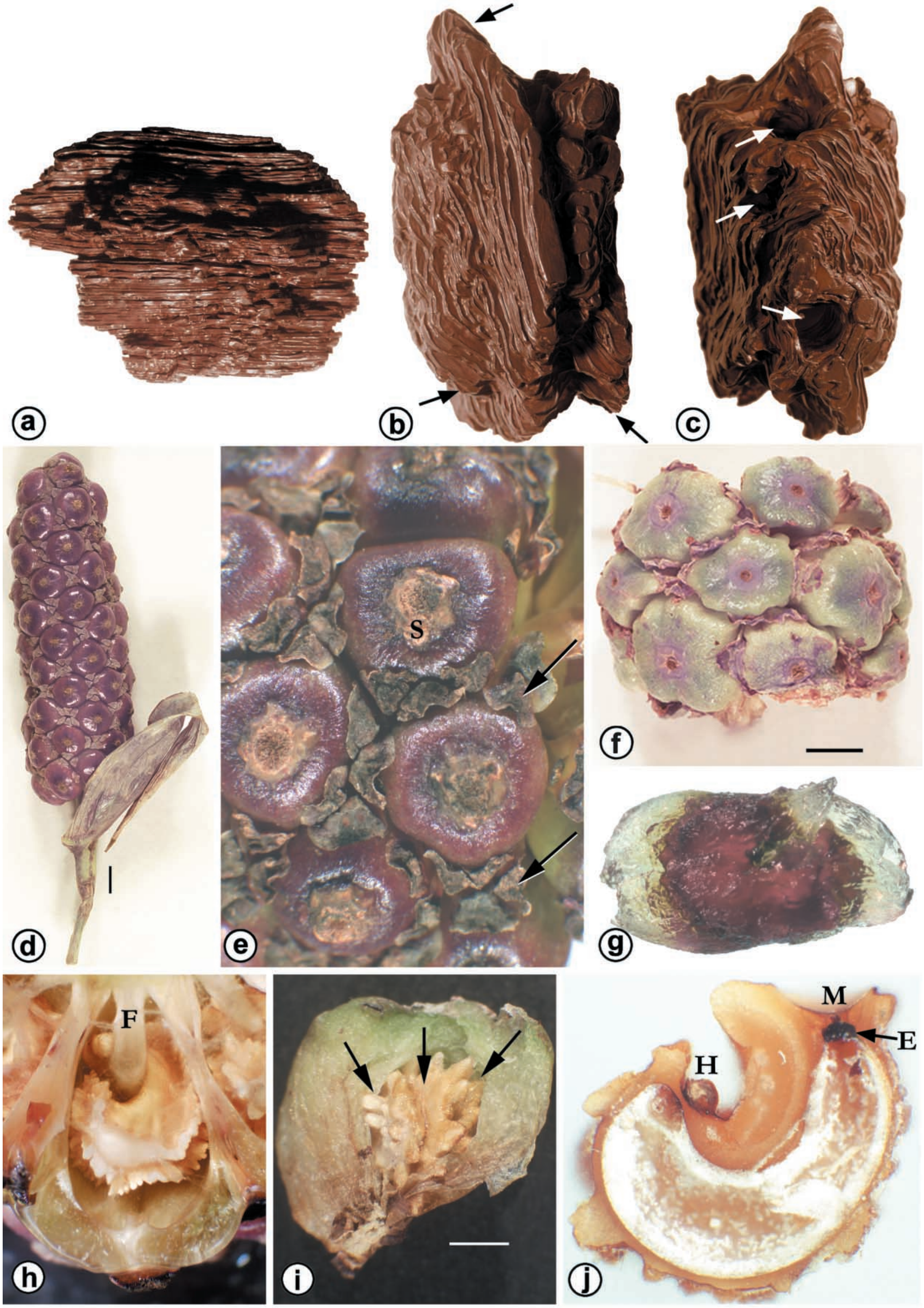

Fig. 3

Results

Systematics

Class—Liliopsida Cronquist, Takhtajan, & Zimmermann

Order—Alismatales Lindley

Family—Araceae de Jussieu

Subfamily—Lasioideae Engler

Genus—Keratosperma *Cevallos-Ferriz et Stockey emend. Smith et Stockey*

Species—Keratosperma allenbyense *Cevallos-Ferriz et Stockey emend. Smith et Stockey*

Generic diagnosis. Seeds 2.5–3.2 mm long × 1.8–2.3 mm high × 1.1–1.6 mm in diameter; flattened ventrally and expanded dorsally with single, large dorsal ridge and smaller, more irregular ridge on either side, remaining seed coat warty; micropyle dorsal to hilum, reflexed ca. 140°. Integumentary dorsal ridge up to 0.8 mm high. Integument of pitted, isodiametric, radially aligned sclereids, 15–27 μm in diameter, with thinner walls around raphe area and near seed periphery; outer integumentary layer containing scattered circular to oval, enlarged, thick-walled idioblasts. Micropylar region of seed expanded and conical; integument thinning greatly near micropylar end to form micropylar cover; epistase present. Hypostase and podium present at chalazal end of seed. Nucellus fused to integument and continuous with epistase and podium. Endosperm of nearly cuboidal cells with dark contents. Embryo curved, monocotyledonous.

Specific diagnosis. Seeds are as described in generic diagnosis.

Holotype. P4268 D bot and E.

Paratypes. P2613 B bot, D bot, E bot, G, P2541 D, and P2592 B bot.

Topotypes. P2613 D_2 bot, P5153 C bot, P5836 B_1 top, D_4 bot, E_1 bot, P5937 G bot, P5956 D top, P6025 G.

All specimens are housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA).

Description

The additional specimens of *Keratosperma allenbyense* have provided new data to Cevallos-Ferriz and Stockey's original description (1988) on the structure of the seed. Only the new information will be presented in detail here. The seeds are small, spiny, and anacampylotropous, i.e., they have a curved seed axis, and the antiraphal (dorsal) side is more developed than the raphal (ventral) side (fig. 1*a*). On the ventral side of the seed, the raphe extends from micropylar to chalazal ends. Vascular tissue is often not preserved, giving the appearance of a cavity in the outer integument (fig. 1*a*, 1*b*). The raphe is found parallel to the concave (ventral) side of the seed and is nearly enclosed by the outer integument, with only a small opening left for the funiculus to pass through. The seed coat is composed of isodiametric, pitted sclereids and idioblasts that may represent raphide sacs (fig. 1*b*–1*d*). These cells protrude from the outer integument (fig. 1*b*–1*d*) or are found a few cells from the outside edge of the outer integument. Idioblasts are scattered and are commonly found in the low areas between ridges or raised areas, on the sides of protrusions but not at the tips. The contents of these cells sometimes appear to be organic rather than crystalline.

The micropyle is funnel shaped and has a thin, micropylar cover formed by the integument. This cover can be up to three or four cells thick (fig. 1*e*–1*g*). These seeds also show an epistase, or nucellar cap, which appears as a small, darkly pigmented conical structure of compacted, rectangular cells that are attached to and seemingly part of the nucellus (fig. 1*f*). Between the epistase and micropylar cover, a noncellular, transparent substance is preserved that we interpret to be mucilage (fig. 1*f*, arrow). The nucellus is fused to the integument and is continuous with the epistase and hypostase. In many specimens, the nucellus appears to be detached from the integument.

At the chalazal end of the seed, the integument forms a small tube through which a large protuberance emerges (fig. 1*a*; fig. 2*a*–2*c*). We interpret this structure as a hypostase, an outgrowth from the chalazal end of the seed through which the funiculus passes (Seubert 1997). The hypostase is composed of thin-walled cells that often appear somewhat collapsed (fig. 2*a*, 2*b*). In some sections, a hollow interior is seen that probably corresponds to a mucilage-filled area (fig. 2*a*–2*c*, arrow), as has been reported in the hypostase of extant lasioid seeds (Seubert 1997).

A single curved monocotyledonous embryo has been found (Cevallos-Ferriz and Stockey 1988). Endosperm cells are cuboidal with dark contents (fig. 1*h*). The endosperm cells extend into the hypostase (fig. 1*a*; fig. 2*a*, 2*b*), forming a structure that has been referred to as a "podium" (Seubert 1997) or "hypostasenkork" (Netolitzky 1926) in living aroid seeds. This

Fig. 3 Lasioid fruits and seeds. *a*, Lateral view of a scale model (× 40) reconstruction of *Keratosperma allenbyense* showing prominent dorsal ridge and smaller lateral ridge; micropylar end is at bottom, × 0.6. *b*, Dorsal view of model in fig. 4*a* showing prominent dorsal ridge and two lateral ridges (arrows), × 0.7. *c*, Ventral view of model in fig. 4*a* showing (at arrows) micropyle (bottom), raphe (middle), and hypostase region (top); note seed ridges, × 0.7. *d*, Spathe and spadix of *Cyrtosperma merkusii* in fruit stage. Scale bar = 5 mm. *e*, Red berries and hooded tepals (arrows) of *Cyrtosperma merkusii*, × 4. *f*, Part of spadix of *Urospatha sagittifolia*. Scale bar = 5 mm. *g*, Seed of *Cyrtosperma merkusii* covered by mucilage, × 5. *h*, Transverse section through spadix of *Cyrtosperma merkusii* showing longitudinal section of fruit containing anacampylotropous seed in mucilage, and funiculus, × 4. *i*, Green berry of *Urospatha sagittifolia* showing three spiny seeds. Scale bar = 2 mm. *j*, Longitudinal section of seed of *Cyrtosperma merkusii* embedded in paraffin showing hypostase, epistase, micropylar cover, and some mucilage between the epistase and micropylar cover, × 11. *S* = stylar region, *F* = funiculus, *H* = hypostase, *M* = micropylar cover, *E* = epistase.

protrusion of the endosperm and the nucellus is usually present when a hypostase is produced by the seed (Seubert 1997).

Fungi are frequently found in *Keratosperma* seeds (fig. 2*d*–2*f*). They often fill the seed cavity (fig. 2*d*) and are also seen in the integument and idioblasts. Fungi in the cavity tend to take the form of a loose network of septate hyphae but can be very dense. Often they have invaded and replaced the cell walls of endosperm cells (fig. 2*e*, 2*f*).

The tissue previously described as fruit was reexamined during this study. This tissue has been found wrapped around clusters of eight or more *Keratosperma* seeds (Cevallos-Ferriz and Stockey 1988; their fig. 22). Alternating large and small circular vascular bundles are present in a poorly preserved ground tissue. The large bundles show radially aligned tracheary elements with scalariform and helical thickenings. Surrounding the bundles is a parenchymatous sheath two to three cells thick. Inside this "fruit" tissue, we have observed small thin bands of crushed tissue nearer the seeds.

The reconstruction based on serial sections shows that the seeds have a prominent ridge along the antiraphal side that extends from the micropyle to the hypostase area (fig. 3*a*–3*c*). On either side of this are smaller, more irregular ridges. The remaining seed coat is warty. In section, the integument is formed of isodiametric cells that are more thickened to the inside of the seed and slowly grade into thinner-walled cells (fig. 5*h*).

Extant taxa. Aroid inflorescences are spadices, and among lasioids they take on different morphologies. We examined spadices of *Cyrtosperma merkusii* and *Urospatha sagittifolia* that were in fruit; these show four to six hooded tepals (fig. 3*d*–3*f*). Between the tepals and the fruit, stamens with broad, flat filaments and dehisced anthers are found. Fruits are sessile on the spadix. Berries have different colors in different genera (Mayo et al. 1997); *C. merkusii* has red berries (fig. 3*d*, 3*e*), while in *U. sagittifolia* they are green (fig. 3*f*, 3*i*). Seeds are embedded in mucilage within the fruit (fig. 3*g*, 3*h*). Lasioid fruits may contain more than one seed, as in *Urospatha* (fig. 3*i*), and seeds are anacampylotropous with a hypostase and an epistase (fig. 3*j*).

Seed specimens of seven of the 10 extant lasioid genera including 22 taxa were compared with the fossils on the basis of external morphology (table 1; fig. 4), while seeds of the other three genera were compared from the literature. All seeds examined are anacampylotropous. Seeds of *Anaphyllopsis* are somewhat reniform, with two thick dorsal (antiraphal) ridges that merge into one at the micropylar end of the seed and with a lateral ridge on either side (fig. 4*a*). Seeds of *Cyrtosperma carrii* A. Hay are nearly spherical and very smooth (fig. 4*b*), while those of *C. merkusii* are C-shaped and have a flattened dorsal side with verrucose lateral margins (fig. 4*c*). *Dracontioides desciscens* (Schott) Engl. seeds are C-shaped with numerous rows of small spines (fig. 4*d*). In *Dracontium asperum* K. Koch, seeds are rounded and C-shaped, with smooth lateral surfaces and a rugose dorsal side (fig. 4*e*). Seeds of *Dracontium grayumianum* G. Zhu are semicircular in outline, with four thin but prominent main ridges that are sometimes connected by perpendicular ridges (fig. 4*f*). The nearly spherical seeds of *Dracontium plowmanii* G. Zhu and *Dracontium polyphyllum* L. are smooth with a slightly rugose, thin area on the dorsal side (fig. 4*g*, 4*h*). The curved seeds of *Dracontium purdieanum* (Schott) Hook f. have thick anastomosing ridges similar to but not as prominent as in *Anaphyllopsis* (fig. 4*i*). Seeds of *Dracontium soconuscum* Matuda are nearly semicircular with a rugose dorsal surface (fig. 4*j*), while those of *Dracontium spruceanum* (Schott) G. Zhu are narrow with a mostly smooth surface and some discontinuous ridges (fig. 4*k*). *Lasia spinosa* (L.) Thwaites seeds are large with a greatly expanded dorsal side, appearing conical; the dorsal tip, micropylar end, and chalazal end develop small ridges (fig. 4*l*). *Lasimorpha senegalensis* Schott seeds have numerous, irregularly shaped and irregularly occurring spines (fig. 4*m*). Seeds of *Urospatha* show varying morphologies, but all are C-shaped with ridges and spines of various lengths. Those of *Urospatha grandis* Schott have several ridges that are sometimes large and not continuous (fig. 4*n*, 4*o*). *Urospatha sagittifolia* seeds have prominent spines arranged in four rows (fig. 4*p*). Other *Urospatha* species show thin, flat, and expanded ridges (fig. 4*q*), rows of blunt, short projections (fig. 4*r*, 4*s*), or intermediate states with very irregularly shaped protuberances (fig. 4*t*).

Internal anatomy. Seeds of *C. merkusii* are curved with an irregular integumentary outline (fig. 5*a*, 5*b*). Copious endosperm is present, and cells are full of contents (fig. 5*c*) that are probably lipids and proteins (Seubert 1997). Idioblasts containing druses are scattered throughout the outer integument (fig. 5*d*). The raphe has xylem with helical thickenings (fig. 5*e*). The inner integument is very thin and "collapsed" (Seubert 1997) (fig. 5*i*). The outer integument is formed of strongly thickened, elongated cells toward the inside of the seed that quickly grade into thin-walled isodiametric cells externally (fig. 5*i*).

Urospatha sagittifolia seeds are curved and have prominent spines (fig. 5*f*, 5*g*) usually in four rows. Very strongly thickened isodiametric cells are found to the inside of the outer integument, while the cells to the outside are thin walled (fig. 5*j*). The two zones are separated by an area of cells with dark-staining contents, probably tannins (Seubert 1993). Raphides are rare in the integument, and the inner integument is collapsed, as in *Cyrtosperma*.

Discussion

The fossil seeds of *Keratosperma* are anacampylotropous, with a generally warty integument, a main dorsal ridge, and two lateral ridges. Internal tissues are rarely preserved, since fungi have invaded the seed cavities, but endosperm is sometimes present in small amounts. The fossil seeds have an epistase and thin micropylar cover, with probable mucilage found between the two structures. The raphe is surrounded by the integument and parallels the concave ventral surface of the seed. At the chalazal end of the seed, a hypostase and podium are described for the first time for these seeds.

Within Araceae, the subfamilies Monsteroideae and Lasioideae contain taxa with seeds that have irregular surfaces (Madison and Tiffney 1976; Cevallos-Ferriz and Stockey 1988). More detailed knowledge of anatomy of *Keratosperma* and other lasioid seeds (Seubert 1993, 1997) reinforces the placement of *Keratosperma* in Araceae, subfamily Lasioideae. Seeds of taxa from this subfamily are characterized as anacampy-

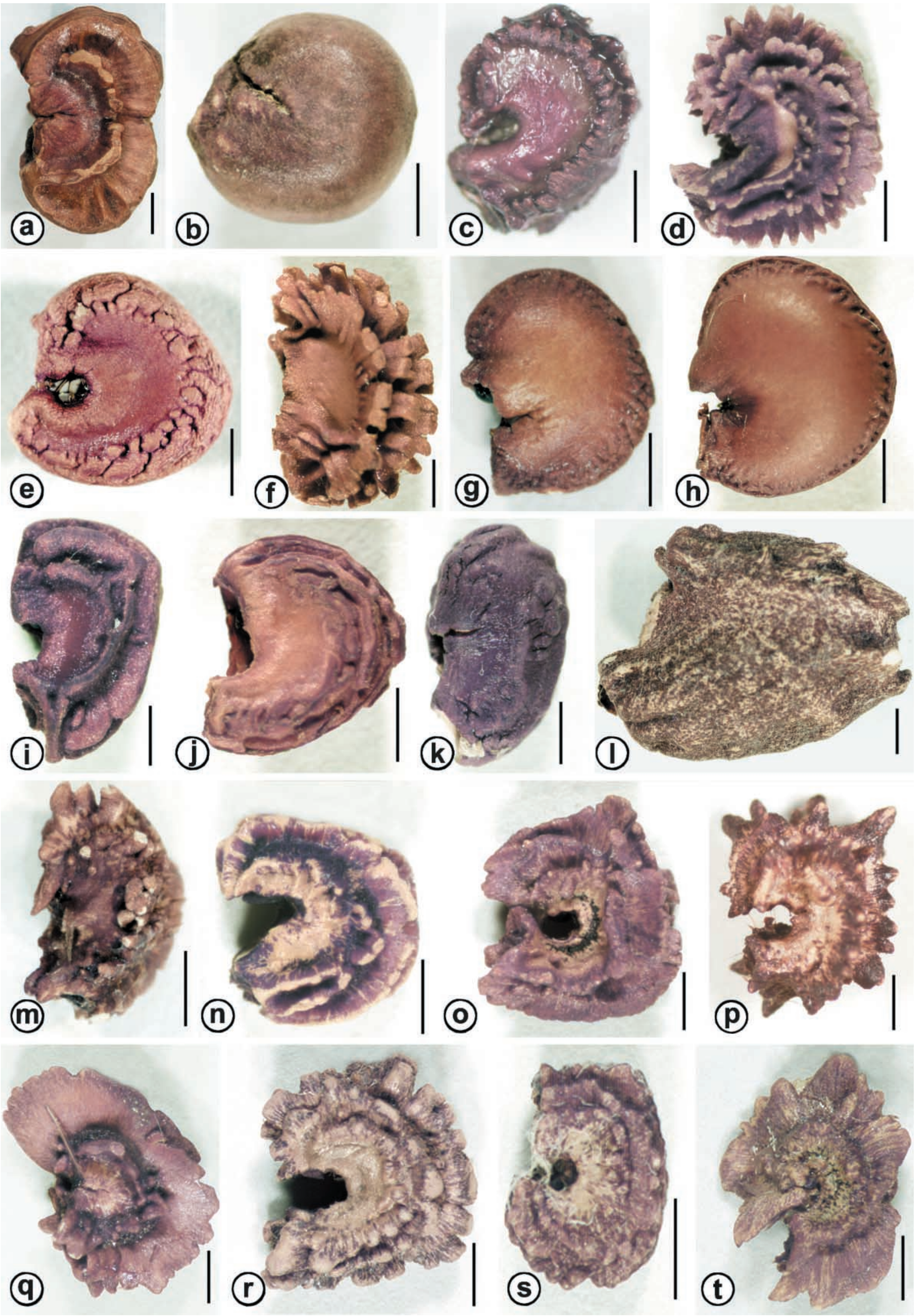

Fig. 4 External views of extant lasioid seeds. Scale bar = 2 mm. *a*, *Anaphyllopsis americana*. *b*, *Cyrtosperma carrii*. *c*, *C. merkusii*. *d*, *Dracontioides desciscens*. *e*, *Dracontium asperum*. *f*, *D. grayumianum*. *g*, *D. plowmanii*. *h*, *D. polyphyllum*. *i*, *D. purdieanum*. *j*, *D. soconuscum*. *k*, *D. spruceanum*. *l*, *Lasia spinosa*. *m*, *Lasiomorpha senegalensis*. *n*, *Urospatha grandis*. *o*, *U. grandis*. *p*, *U. sagittifolia*. *q*, *Urospatha* sp. 1. *r*, *Urospatha* sp. 2. *s*, *Urospatha* sp. 3. *t*, *Urospatha* sp. 4.

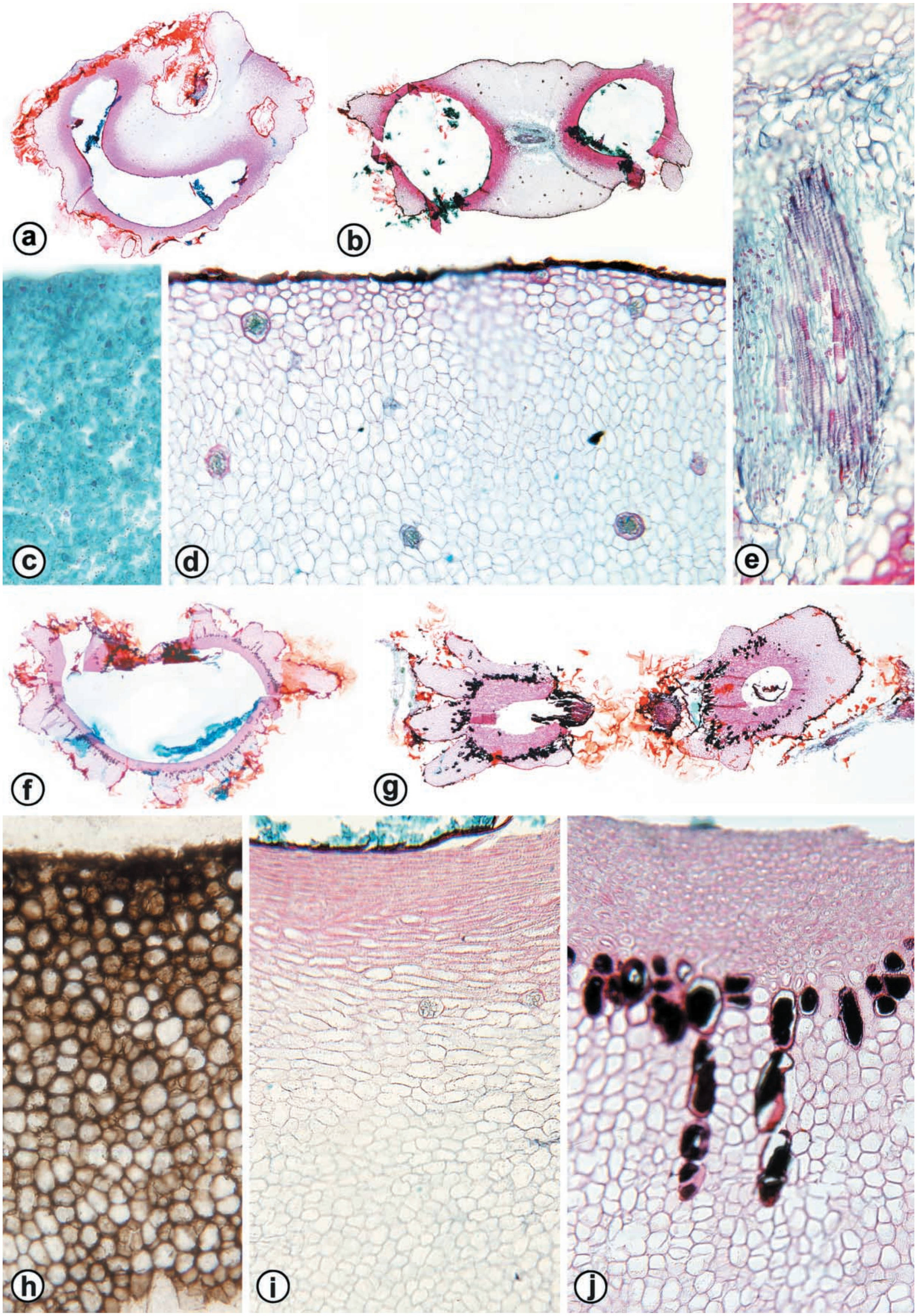

Fig. 5

lotropous, having a hard seed coat with crests and warts, starch-free endosperm, and curved embryos (Seubert 1997). In addition, specialized micropylar and chalazal regions are not common among Araceae but are found in most Lasioideae (Seubert 1997). Therefore, it seems that our fossil seeds can be placed with some confidence in this subfamily.

Keratosperma allenbyense seeds have an external morphology unlike seeds of any of the 22 extant taxa examined during this study. While original interpretations of the seeds suggested they were covered with prominent spines, our reconstruction suggests instead that these seeds possessed a prominent dorsal ridge, with two lateral ridges, and an otherwise irregular warty surface.

Seeds with prominent spines in extant Lasioideae include *Dracontioides desciscens*, *Dracontium grayumianum*, *Lasimorpha senegalensis*, *Urospatha sagittifolia*, and other *Urospatha* species. Seeds with smooth integuments are found in *Cyrtosperma carrii*, *Dracontium plowmanii*, and *Dracontium polyphyllum*. *Lasia spinosa* seeds, with their greatly expanded dorsal side and lack of ridges, do not resemble *K. allenbyense*. *Anaphyllopsis* seeds have two dorsal ridges merging into one, unlike the single dorsal ridge of *K. allenbyense*. Many of the extant seeds have an even number of ridges (often four), unlike the three ridges seen in the fossil seeds. *Keratosperma* also differs from *Anaphyllum* Schott and *Podolasia* N. E. Brown, whose seeds are ovoid, smooth, and more or less spherical (Mayo et al. 1997). Seeds of *Pycnospatha* Thorel ex Gagnepain are reniform and verrucose (Mayo et al. 1997), unlike *Keratosperma* with its ridged integument. Therefore, on the basis of external morphology, *Keratosperma* appears to have seeds distinct from all 10 known genera of living lasioids.

Sections of *Cyrtosperma merkusii* do not show the spiny ridges found in *Keratosperma*. However, they do have cells with druses scattered throughout the outer integument. While *Keratosperma* does have idioblasts in the seed coat, these are confined to the outer cell layer of the outer integument, unlike the scattered idioblasts in *Cyrtosperma*. The two-zoned outer integument of *Cyrtosperma* contrasts with the gradual thickening of the outer integumentary cells toward the center of the seed of *Keratosperma*. The strongly thickened and elongated cells of the inner part of the outer integument of *Cyrtosperma* differ from the thick-walled, isodiametric cells of the inner region of the outer integument of *Keratosperma*.

Most aroid workers agree that the genus *Urospatha* is in need of a monographic revision (Hay 1992; Seubert 1997; J. Bogner, personal communication, 2000; P. Boyce, personal communication, 2000). Therefore, many of the *Urospatha* seeds examined in this study were not assignable to species. Sections of *Urospatha* seeds show very prominent spines, more prominent than the spines observed in sections of *Keratosperma*. The outer integument of *Urospatha* possesses an outer zone of thin-walled cells and an inner zone of thick-walled cells (fig. 5*j*), distinctly different from the fossil where there is little difference in wall thickness from the inside to outside. In addition, the outer integument of *Urospatha* has a band of cells with darkly staining contents that separates the two layers, a character not observed in the integument of *Keratosperma*.

Seubert (1993) examined the integuments of several lasioid seeds, illustrating strongly differentiated inner and outer zones to the outer integument in species of all lasioid genera except *Anaphyllum*, which has a fairly uniform cell wall thickness throughout the outer integument. This is unlike the gradually thinning outer integument seen in *Keratosperma*. Seed coat ornamentation in *K. allenbyense*, with three unequal ridges and an otherwise warty surface, while similar to most lasioids, differs from the seeds of any of the 22 lasioid taxa examined here or the additional six taxa described by Seubert (1993). Integumentary anatomy is also different; the fossil seed coat shows a gradual thickening of cell walls toward the inside. On the basis of these anatomical and morphological comparisons, it appears that *Keratosperma* does indeed represent a unique genus within Araceae, subfamily Lasioideae.

One of the reasons that *K. allenbyense* was originally most closely compared with *Cyrtosperma* is that the fossil seeds were found in what was interpreted as fruit tissue with eight or more seeds per locule. *Cyrtosperma* can have up to seven seeds per ovary (Mayo et al. 1997). However, on reinvestigation of the fossil fruit material, it appears that these seeds are enclosed in leaf tissue, similar to that of the aquatic dicot *Eorhiza arnoldii* Robison et Person, which possesses alternating major and minor vascular bundles (Stockey and Pigg 1994). The radially aligned tracheary elements are like those reported in *Eorhiza* leaves (Robison and Person 1973). While *Eorhiza* has monocot-like ensiform ensheathing leaves similar to Iridaceae, the major bundles show secondary xylem, distinguishing them from monocot foliage in the chert (Stockey and Pigg 1994). *Keratosperma* seeds probably collected in clumps by being washed between the leaves in the rotting vegetation. Their abundance and tendency to form clumps indicate that they were probably produced not far from the site of deposition. Small pieces of tissue inside these *Eorhiza* leaves may actually be the remains of fruit walls; however, preservation of this

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Fig. 5 Lasioid seed anatomy. *a*, Longitudinal section of seed of *Cyrtosperma merkusii* showing mucilage outside seed (red) and outer integument with two zones. Slide 12367, ×8. *b*, Transverse section of seed of *C. merkusii* showing two seed cavities, raphe, and zoned outer integument. Slide 12368, ×11. *c*, Endosperm of *C. merkusii*. Slide 12369, ×136. *d*, Outer integument of seed of *C. merkusii* showing numerous cells with druses. Slide 12368, ×132. *e*, Raphe area of seed of *C. merkusii* with helical xylary thickenings. Slide 12368, ×77. *f*, Longitudinal section of seed of *Urospatha sagittifolia* showing prominent integumentary spines, micropyle, and red staining mucilage on outside of seed. Slide 12370, ×8. *g*, Transverse section of seed of *U. sagittifolia* showing zoned outer integument, prominent integumentary spines, and hypostase. Slide 12371, ×12. *h*, Outer integument of *Keratosperma allenbyense* showing inner, thick-walled cells (top) and outer, thin-walled cells (bottom). P5836 B_1 top 36, ×204. *i*, Outer integument of *C. merkusii* showing strongly thickened, elongate cells to inside of seed (top) and outer thin-walled cells. Slide 12372, ×154. *j*, Outer integument of *U. sagittifolia* showing strongly thickened isodiametric cells to inside of seed (top) and outer thin-walled cells, separated by a layer of cells with darkly staining contents. Slide 12370, ×128.

tissue is poor. At this time, therefore, we cannot compare fruits of *Keratosperma* with those of known taxa.

Although four monocots have been described from the Princeton chert on the basis of vegetative remains (Erwin and Stockey 1989, 1991*a*, 1991*b*, 1992, 1994), there are many monocots as yet undescribed. It is possible that one of these types might represent the vegetative body of *Keratosperma*. In the future, we hope that this plant may be reconstructed and its affinities determined on the basis of a whole plant concept encompassing anatomical and morphological characters of vegetative and reproductive parts.

The fossil record of Araceae consists of leaves, pollen, spadices and infructescences, and fruits and seeds. Fossils that can be placed with confidence in the Araceae s. s. first occur in the Eocene, although putative aroid pollen is known from the Paleocene (Mayo et al. 1997). The best-known fossils are seeds of Araceae of the subfamilies Monstereae and Lasioideae, placed in the genera *Epipremnites* Gregor et Bogner, *Scindapsites* Gregor et Bogner, and *Urospathites* Gregor et Bogner, found in European deposits of Oligocene, Miocene, and Pliocene age (Gregor and Bogner 1989; Mayo et al. 1997). Externally, seeds of *Urospathites avimontanus* (Gregor) Gregor et Bogner from the Miocene of Salzhausen near Nidda, Vogelsberg, Germany, and of *Urospathites visimensis* (Dorofeev) Gregor et Bogner from the Oligocene of Nowy Log, Siberia, Russia, show circular small pits or "grübchen" (Gregor and Bogner 1989), which may represent idioblasts similar to those of *Keratosperma*.

The Princeton seeds, *K. allenbyense*, are unique in their external morphology and integumentary anatomy but share features such as an epistase, hypostase, podium, and presence of mucilage with the extant taxa of Lasioideae. Therefore, we confidently place them within this subfamily of Araceae. The anacampylotropous seeds have a main dorsal ridge with smaller, more irregular lateral ridges and an otherwise warty outer integument that is not seen in extant taxa. This is the first time hypostase, epistase, podium, and mucilage have been described for these seeds. To date, *K. allenbyense* represents the earliest known occurrence of Lasioideae in the fossil record.

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