Zingiberalean fossils from the Late Paleocene of North Dakota, USA and their significance to the origin and diversification of Zingiberales

by

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ABSTRACT

The Zingiberales, including the gingers (*Zingiber*), bananas (*Musa*) and ornamental flowers (*Strelitzia*, *Canna*, and *Heliconia*) are a diverse group of monocots that occupy the tropics and subtropics worldwide. The monophyly of the order is well supported, although relationships between families are not well resolved. A rapid divergence of the Zingiberales has been proposed to explain the poor resolution of paraphyletic families in the order, and direct fossil evidence shows members of both of these lineages of Zingiberaceae and Musaceae were present by the Late Cretaceous. Comparisons of the fossils with extant relatives and their systematic placement have been limited because variation within modern taxa is not completely known. The current study focuses on describing zingiberalean fossil material from North Dakota that includes seeds, leaves, buds, adventitious roots and rhizomes. A survey of extant zingiberalean seeds was conducted, including descriptions of those for which data were previously unknown, in order to resolve the taxonomic placement of the fossil material. Upon careful examination, anatomical characters of the seed coat in fossil and extant seeds provide the basis for a more accurate taxonomic placement of the fossils and a better understanding of character evolution within the order.

DEDICATION

To Mitsuko and Shiro, Always there when I need support, or to just to help motivate me to get off my lazy butt and go for a walk.

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INTRODUCTION

Introduction to the Zingiberales

The Zingiberales Griseb. is an order of commelinid monocotyledons that includes many ornamentals (Bird-of-paradise, *Strelitzia* Ait; Canna-lilies, *Canna* L., prayer plants, *Maranta* L.) and edible fruits and spices (Bananas, *Musa* L.; Cardamom, *Elettaria* Maton; Tumeric, *Curcuma* Roxb; and Ginger, *Zingiber* Boehm.; Hutchinson 1973; Prince and Kress 2002; Kress and Specht 2005, 2006). They are common components of the understory of tropical and subtropical forests as small (less than one meter) to medium-sized rhizomatous herbs, but can also be large arborescent herbs such as *Musa* or some *Heliconia* species that are over seven meters tall. Less commonly the order includes lianas (some Marantaceae), and, rarely, fully aquatic plants (e.g., *Alpinia aquatic* Roscoe.; Dahlgren et al. 1985; Anderson 1998c; Kress et al. 2001; Prince and Kress 2002; Kress and Specht 2005, 2006). Members of the order are easily distinguished from other monocots by having leaves with a prominent midrib (costa) and relatively large lamina, and often showy and colorful zygomorphic flowers or bracts that attract a wide array of pollinators (Kress 1990; Kress and Specht 2005). Many taxa have large rhizomes, with *Zingiber* and other Zingiberaceae being of nutritional and medicinal commercial value (Larsen et al. 1998). Fruits are typically triloculate, and either loculicidal capsules, or less commonly, drupes, berries or pyrenes (Dahlgren et al. 1985).

The order has a rich fossil record of both vegetative and reproductive remains extending from the Late Cretaceous to the Pliocene from throughout the New World and Eurasia (Jain 1965; Koch and Friedrich 1970; Daghlian 1981; Boyd 1992; Manchester and Kress 1993; Rodriguez-de la Rosa and Cevallos-Ferriz 1994; Fischer et al. 2009). The fossils attributed to the order have been difficult to classify to family because the variation of characters that distinguish families in the order, in particular of fruits and seeds, are not known comprehensively (Rodriguez-de la Rosa and Cevallos-Ferriz 1994).

Recently discovered seeds, leaves, buds adventitious roots and rhizomes have been recovered from the Late Paleocene Almont and Beicegel Creek floras from the Williston Basin of North Dakota, USA (Benedict et al. 2007; Benedict 2011b). These fossil remains are anatomically preserved, allowing for a critical analysis and comparison with extant members of the order to determine the correct taxonomic placement of the fossils, which was the basis for this dissertation research. To accurately describe the fossils in a systematic context, it was necessary to gain a better understanding of the variation of extant fruits and seeds within the order, and a broad survey was conducted. Once characteristic features of extant members were described it was possible to address the systematic placement of the Late Paleocene fossils, as well as that of several other fossils attributed to this order of ecologically and economically important plants.

The order includes eight families with over 2500 species and can be divided into two informal groups, the “Bananas” and the “Gingers” (Bartlett and

Specht 2010, 2011). The paraphyletic banana group is sister to the ginger group and includes the four families: Musaceae Jussieu, Heliconiaceae Vines, Strelitziaceae Hutchinson, and Lowiaceae Ridley (Kress et al. 2001). The terminal ginger group includes the remaining four families: Cannaceae Jussieu, Marantaceae R. Brown, Costaceae Nakai, and Zingiberaceae Martinov. The idea of the ginger group as a monophyletic lineage is well-supported, based on molecular and morphological data, and within the lineage, the Zingiberaceae plus Costaceae and Cannaceae plus Marantaceae are considered well-supported sister taxa (Kress et al. 2001). A brief synopsis of each family is presented below.

Musaceae. Musaceae contains three genera, *Ensete* Horan, *Musa* L. and *Musella* (Franch.) H.W. Li with approximately 41 species that are distributed in Africa and from Southeast Asia to northern Australia (Fig. 1A; Stevens 2001 onwards). Plants of this family are large herbs that attain arborescence ("pseudostems" of Anderson 1998c). The clasping bases of elongate petioles that provide support for the stem and allow some species to achieve heights up to 13 meters (Dahlgren et al. 1985). Zingiberalean plants are usually distichous, but those of the Musaceae are arranged helically.

Flowers are bisexual, but functionally unisexual with fertile pistillate flowers being produced first at the base of the lateral cyme (cincinni) and staminate flowers developing later, more distally and acropetally (Dahlgren et al. 1985). Ovaries are trilocular with two or more rows of ovules per locule. Fruits are mostly indehiscent berries with a hard, leathery pericarp and softer tissue that surrounds the numerous seeds. The fleshy tissue or ‘pulp’ that encapsulates the seeds and has been overexpressed in the commercial, edible banana are enlarged trichomes derived from the epidermis of the axile placenta (Anderson 1998c). Seeds are operculate with a thick seed coat derived from the outer integument and have a short bulbous to mushroom-shaped embryo with little perisperm, but abundant starchy endosperm (Anderson 1998c). There have been reports of an arillate structure on the seed, but this tissue is not derived from the funiculus, instead it is interpreted as the remnants of trichomes on the surfaces of the flower's placenta (Friedrich and Strauch 1975; Grootjen and Bouman 1981; Manchester and Kress 1993; Anderson 1998c).

Heliconiaceae. Heliconiaceae is monogeneric with *Heliconia* L. containing 100-200 species as defined by different authors (Anderson 1998a). *Heliconia* has its broadest range in the Neotropics but also can be found in the Philippines (Fig. 1*B*; Stevens 2001 onwards). Plants are small or large herbs achieving arborescence in the same manner as Musaceae, but can be distinguished by their distichous phyllotaxy (Dahlgren et al. 1985; Kress 1990). Flowers are perfect, bisexual and actinomorphic, but are somewhat masked by the very flashy red to orange bracts that subtend them and attract hummingbird (New World) or bat (Old World) pollinators (Kress 1990; Kirchoff 2009). Fruits are mostly blue, 3-seeded and drupaceous, breaking apart upon maturity to release single seeded disseminules called pyrenes (Roth 1977; Simão et al. 2006). Seeds are operculate, exarillate, triangular-pyramidal and have an elongate embryo with copious perisperm in the embryo sac. Unlike any other family in the order, the mechanical layer of the diaspore is derived from the endocarp and not the testa (Simão and Scatena 2001; Simão et al., 2006).

Strelitziaceae. Strelitziaceae contains three genera and seven species that are distributed disjunctly in the tropics of South American along the Amazonian waterways (*Phenakospermum guianense* [Rich.] Endl. Ex Miq., a single species); in southern Africa (*Strelitzia*, five species); and Madagascar (*Ravenala madagascariensis* Sonnerat, a single species)(Fig. *1C;* Dahlgren et al. 1985; Stevens 2001 onwards). Plants are large to medium-sized arborescent herbs and closely resemble Heliconiaceae because of the strong distichous nature of their phyllotaxy. They can be distinguished by their showy perianth parts and green bracts (Dahlgren et al. 1985; Anderson 1998d).

Flowers are perfect, complete and zygomorphic with a very showy perianth, typified by the ornamentally important *Strelitzia reginae* Aiton (Bird-of-paradise). Fruits are loculicidal capsules that recurve upon maturity, displaying the very colorful arils of the seeds. Seeds are large, cylindrical and operculate with a large showy aril that is either hair-like or lobed and can cover the micropylar portion of the seed (Dahlgren et al. 1985). The embryo is large and the embryo sac contains large amounts of starchy endosperm.

Lowiaceae. Lowiaceae contains a single genus *Orchidantha* N. E. Brown with 15 species. The family name is based on the formerly recognized genus *Lowia* that has now been merged with *Orchidantha.* The family named was conserved at the International Botanical Code of Nomenclature Session held 26-30 July 1999 in conjunction with the XVI International Botanical Congress in St. Louis, Missouri. This family has the most limited distribution within the banana group, extending from southern China to Borneo (Fig. 1*D*; Stevens 2001 onwards). Plants are small rhizomatous herbs with a distichous phyllotaxy and leaves with a short petiole and broad lamina.

Flowers are zygomorphic and very showy, much like that of an Orchid (hence the generic name). Fruits are loculicidal capsules that dehisce upon maturity, releasing the seeds within. Seeds are globose to pyriform, smooth or hairy, exoperculate and have an aril comprised of 3-4 hollow tubes (Dahlgren et al. 1985; Wen et al. 1997; Larsen 1998b).

Cannaceae. Cannaceae is a monogeneric family of 10 species of *Canna* L. that are confined to a distribution in the tropical and subtropical Americas, but are planted ornamentally around the world (Fig. 1*E* Dahlgren et al. 1985; Stevens 2001 onwards). Plants are small to medium-sized herbs with helically arranged leaves and a starchy rhizome (Kubitzki 1998).

Flowers are large with inconspicuous sepals and showy petals. The androecia are modified into large fleshy and showy staminoids and surround a large fleshy style (Dahlgren et al. 1985; Kubitzki 1998). Fruits are triloculate, apically dehiscing capsules with a hard warty surface and persistent sepals (Grootjen and Bouman 1988). Seeds are axially arranged in one or two rows of each locule and are spherical and smooth. The seeds have been interpreted by some authors to be exoperculate, and instead have a seed coat that is modified at the apex to create an imbibition lid (Grootjen and Bouman 1988; Kubitzki 1998). Like those of Musaceae, seeds of this family have arillate structures not derived of funicular tissue and should be regarded as ‘arilloid’ and not ‘true arils’ (Grootjen and Bouman 1981, 1988; Manchester and Kress 1993).

Marantaceae. Marantaceae is the second largest family in the order with 31 genera and 550 species and has a pantropical distribution with a large presence in the Americas (Fig. 1*F*; Stevens 2001 onwards). Plants are small to medium-sized rhizomatous herbs, sometimes lianas, with a distichous phyllotaxy (Anderson 1998b). Leaves have a long petiole, and wide lamina with a distinctly pointed apex.

Flowers are zygomorphic or asymmetric with paired flowers being mirrored images, bisexual with distinct sepals and petals (Anderson 1998b). Fruits are triloculate capsules, but many genera appear uniloculate at maturity because only one of the three locules ever develops. Seeds are basally attached and there is a single seed per locule. Seed shape is dependent on the number of locules in the mature fruit. Triloculate fruits contain triangular pyramidal seeds while those in uniloculate fruits are subglobose. They can be arillate or not, but all are operculate with a micropylar collar and some genera have been shown to have a perisperm canal, a feature unique for the group (Anderson and Chase 2001; Dahlgren et al. 1985; Delser 1994).

Costaceae. Costaceae is also pantropical with many of its 6 genera and 110 species found in the Americas (Fig. 1*G*; Stevens 2001 onwards). The small to medium sized rhizomatous plants have spirally arranged leaves with closed sheaths and a ligule at the apex of each sheath (Dahlgren et al. 1985; Specht et al. 2001; Specht and Stevenson 2006).

Flowers have showy petals and two sets of three sepals with the outer whorl often basally fused. Fruits are trilocular capsules or bilocular with the abortion of a locule (*Dimerocostus* Kuntze), and have axile placentation. Seeds are arillate, operculate, and have a micropylar collar and small chalazal chamber or hypostase (Desler 1994; Larsen et al. 1998). Embryos are cylindrical and elongate and contain chalazosperm and perisperm but lack endosperm. Costaceae has been treated as a subfamily of Zingiberaceae by many authors, but lack the ethereal oils characteristic of members of the Zingiberaceae (Dahlgren et al. 1985; Kress 1990; Larsen et al. 1998).

Zingiberaceae. Zingiberaceae is the largest family in the order with 46-52 genera and somewhere between 1075 and 1300 species and has a pantropical range with a center of diversity in southeast Asia (Fig. 1*H*; Stevens 2001 onwards). Plants are either large or small perennial, aromatic herbs and have rhizomes that contain a considerable amount of starch (Dahlgren et al. 1985; Larsen et al. 1998). Leaves are distichous with a long or short petiole and a relatively broad lamina.

Flowers are strongly zygomorphic, bisexual, and show considerable variation in morphology. Fruits are mostly triloculate with axile placentation or less commonly uniloculate with basal placentation. Fruits are either berries or loculicidally dehiscent capsules. Seeds are often cylindrical or variously shaped, arillate, operculate, with micropylar collars and a chalazal chamber. Embryos are variously shaped but most often cylindrical and elongate and nutrient tissue is often stored in the form of perisperm with scant endosperm directly surrounding the embryo (Dahlgren et al. 1985; Kress 1990; Kress et al. 2001).

Relationships within Zingiberales

Traditional circumscription of the group has changed markedly from recognizing the group as a family or an order and as to how many unique subgroupings should be included (Table 1; Kress 1990). Bentham and Hooker (1883) recognized the family Scitamineae with four subfamilies: Museae, Zingibereae, Maranteae and Canneae. Shortly afterwards, Engler and Prantl in a series of publications in *Die Natürlichen Pflanzenfamilien* from 1889 to 1930 separated *Heliconia* into its own tribe within Musaceae, changed the rank of the group to ordinal status, and separated the plants into many of the families and subfamilies that we recognize today (e.g. Cannaceae, Marantaceae, Musaceae and Zingiberaceae; Kress 1990). Hutchinson's first and second edition of *The Families of Flowering Plants* subsequently spilt Musaceae into Musaceae, which included *Musa*, and Strelitziaceae, which included *Heliconia* (Hutchinson 1934; Hutchinson 1959; Kress 1990). Nakai (1941) created the family Heliconiaceae and was the first author to differentiate the eight families recognized today. Since then, many authors have adapted this revision (e.g. Tomlinson 1962, Takhtajan 1980, Cronquist 1981, Dahlgren et al. 1985). In 1990, Kress established a suite of suborders and superfamilies for the banana and ginger groups based first on morphology alone (Kress 1990) and later with the addition of molecular data (Kress et al. 2001).

The Zingiberales have long been recognized as a natural group and recent phylogenetic studies have supported the monophyly of these plants with a combination of molecular and morphological data (Kress 1990; Smith et al. 1993; Kress et al. 2001; Specht et al. 2001). Current phylogenetic hypotheses place the Zingiberales as sister to the Commelinales within the informal clade ‘commelinid monocots’ based predominately on molecular data (Chase 2004; Chase et al. 2006; Davis et al. 2004; APG 2009). Members of the Zingiberales are easily distinguished from other commelinid monocots by a variety of apomorphies, the most prominent of which, an inferior ovary, may have played a pivotal role in the evolution of this group (Simpson 2010; Endress et al. 2011). Other apomorphies of the order include penni-parallel venation, petiolate air chambers and supervolute ptxyis (Kress et al. 2001; Simpson et al. 2010).

Although the monophyly of the order is well recognized, interfamilial phylogenetic relationships are less robustly supported (Kress et al. 2001; Kress and Specht 2005, 2006). The most comprehensive work on the order to date is based on 36 morphological characters and chloroplast sequence data from *rbcL* and *atpB* genes and nuclear 18S rDNA gene (Kress et al. 2001). The combined dataset from molecules and morphology shows the order to be made up of two major clades: the well supported and terminal ginger clade and the weakly supported and paraphyletic banana families (Kress et al. 2001). The data place Musaceae as sister to the rest of the order (bootstrap value: 55%) and Heliconiaceae as sister to the ginger families (bootstrap value: <50%) but these are the two most weakly supported nodes on the tree (Fig. 2, Kress et al. 2001). Recent reviews of the monocots as a whole continue to emphasize this lack of resolution of paraphyletic families and it continues to be an unresolved issue within Zingiberales (Davis et al. 2004; Chase et al. 2004; Chase et al. 2006).

Since the ordinal phylogenetic study of Zingiberales by Kress et al. in 2001, many publications have focused on a particular family to better understand interfamilial relationships. These include the following: Musaceae: Wong et al. 2002; Bartoš et al. 2005; Liu et al. 2010; Christelova et al. 2011; Heliconiaceae: Marouelli et al. 2010; Strelitziaceae: Cron et al. 2012; Lowiaceae: Johansen 2005; Cannaceae: Prince 2010; Marantaceae: Anderson and Chase 2001; Price and Kress 2006; Suksathan et al. 2009; Costaceae: Specht 2001, 2006; Specht and Stevenson 2006; Zingiberaceae: Kress et al. 2002, 2005, 2007; Pedersen 2004; Williams et al. 2004; Xia et al. 2004; Leong-Škorničková et al. 2011. From these studies a much clearer picture of the generic relationships within the families have been shown. One exception is the Alpiniodieae, which is in need of a generic revision as the genus *Alpinia* has been shown to be paraphyletic and polyphyletic, with nine genera within the *Alpinia* clade in a recent analysis (Kress et al. 2007).

The Fossil Record of Zingiberales

Zingiberales have a good fossil record that extends from the Late Cretaceous to the Pliocene of Europe and the late Cretaceous to Eocene in North America (Daghlian 1981; Boyd 1992; Manchester and Kress 1993; Rodriguez-de la Rosa and Cevallos-Ferriz 1994; Fischer et al. 2009). The fossil record includes leaves, rhizomes, fruits and seeds, but, because these plants are monocots, lacks wood. Pollen in this order typically has an exine with little to no sporopollenin (Kress and Stone 1983). A single putative pollen grain assignable to the order has been described from the Middle Miocene Ponzholt flora of Germany, but this occurrence needs to be investigated further (Fischer et al. 2009).

Vegetative Fossil Remains of Zingiberales

Taxonomic characters from leaves. To date, the only taxonomically informative characters to delimit ordinal and family status in Zingiberales are leaves with a supervolute ptxyis and large midrib. A ligule is present at the junction of the base of the lamina and apex of the petiole in Costaceae and Zingiberaceae (Tomlinson 1969; Kress et al. 2001; Simpson 2010; W. John Kress, National Museum of Natural History, Washington DC, personal communication, January 2012).

Several fossil monocot leaf types have been assigned to the order Zingiberales or to families within the order on the basis of venation, interstitial fiber patterns within the lamina, and leaf shape (Tables 2-7). To evaluate the different leaf patterns found within extant and extinct Zingiberales, some authors have developed a tool resembling barcode labeling of commercial products to identify species based on the different widths and thicknesses of secondary veins and the relative spacing they have to each other (Hickey 1977; Hickey and Peterson 1978; Boyd 1992). Just as barcodes differ in the width, number and distance of vertical lines for each product to create a unique symbol, the width of veins in the leaves were shown to be unique to particular taxa in the Zingiberales (Hickey and Petersen 1978). The relative width of the veins or fibers in relation to each other is represented with capital letters denoting large veins (e.g. A) and lowercase thin veins (e.g. "d").

Boyd (1992) used this "barcode" identification approach to show differences in Musaceae, Strelitziaceae, and Heliconiaceae. Studies are currently underway at the ordinal level to determine if additional details of leaf venation and phytolith data are diagnostic at the family level (Selena Y. Smith, University of Michigan, Ann Arbor, personal communication, December 2011).

In North America, *Zingiberopsis* Hickey (Zingiberaceae) is the best-known fossil leaf genus in the order and has four species currently recognized, three of which are from North America and one from Germany (Hickey 1977, Hickey and Peterson 1978; Knobloch 1979; Wilf et al. 2000; Peppe et al. 2007). Taxa in the genus are characterized by having large blades with acuminate tips and a long exligulate petiole and a thick costa or midvein with secondaries diverging parallel to each other (Hickey and Peterson 1978). The oldest occurring species, *Zingiberopsis magnifolia* (Knowlton) Hickey, is known from the Late

Cretaceous Vermejo Formation of Walsenburg, Colorado, Medicine Bow Formation of Wyoming, Lance Formation of Wyoming and South Dakota and the Fox Hills Formation of North Dakota (Peppe et al. 2007). It is distinguished from the other species of *Zingiberopsis* by having a unique set of secondary veins with the formula “AdCdBdCdBdCdBdCdA” (Hickey 1977; Hickey and Peterson 1978; Peppe et al. 2007). In the Paleocene, three species have been described: *Z. attenuata* Hickey and Peterson from the Paskapoo Formation of Alberta, Canada; *Z. isonervosa* Hickey and Peterson from Wyoming and North Dakota and *Musophyllum complicatum* Lesquereux from the Fort Union Formation of Colorado. These three species can be readily recognizable by their venation patterns as *Z. attenuata* has a formula of “BdCdBdCdBdCdBdCd”, *Z. isonervosa* has simple venation of uniform secondaries, or formula “d” and *M. complicatum* has an entirely different type of secondary venation and angle of divergence of the veins most likely does not belong in the Zingiberales though superficially it looks similar to *Musa* (Hickey 1977; Boyd 1992).

Zingiberopsis occurs at numerous localities in the western North American Late Cretaceous through Paleogene, particularly in the Western Interior Williston Basin, as well as the Joffre Bridge locality of Canada (Peppe et al. 2007; Kathleen B. Pigg, Arizona State University, personal observation). This taxon has been shown to contain stereotypical feeding patterns on its epidermis that has preserved quite well in the fossil record (Wilf et al. 2000) that consists of individual or multiple strips of tissue being removed parallel to the secondary veins and fibers of the leaves (Wilf et al. 2000). This damage pattern was correlated with a group of rolled leaf beetles (family Chrysomelidae, subfamily Hispinae, tribes Cephaloleniini and Arescini) that today feed on a wide variety of zingiberalean leaves. Although insect fossils were not found in association with these leaves, an ichnotaxon *Cephaloleichnites strongi* Wilf et al.was established for this damage pattern, extending the record of hispine beetles back 20 million years earlier than previously known (Wilf et al. 2000).

Recently, the validity of *Cephaloleichnites* as a member of the hispine beetles has been brought into question (Garcia-Robledo and Kuprewicz 2007; Garcia-Robledo and Staines 2008). Garcia-Robledo and Staines performed trials documenting what insects may produce the characteristic feeding pattern reported on the *Zingiberopsis* leaves and found that both hispine and non-hipsine beetles (members of Lepidoptera and Curculionidae respectively, Coleptera) could have been responsible for the damage patterns reported. They propose that members of the curculionid beetles may be a better fit for explaining the damage patters as there are fossil Curculionidae known from the late Cretaceous of South America, though they hesitate with a formal revision as their data suggest that it is more likely a result of the physiology (silica bodies and large fiber bundles) of the leaf rather than a feeding method unique to a specific group of beetles (Donato et al. 2003; Garcia-Robledo and Staines 2008).

The European floras have many reports of leaves assigned to Zingiberales extending from the Cretaceous to the Pliocene and, to date, at least seven have been described. The most significant and accepted reports are discussed below (Koch and Friedrich 1970, 1971; Boyd 1992; Fischer 2009). *Zingiberopsis rigguaensis* Knobloch is reported from the Late Cretaceous (Cenomanian-Turonian) strata of Bavaria, Germany and differs from the North American species with respect to its secondary venation pattern. This occurrence extends the geographic range of the genus to Europe, which makes this the most widely distributed fossil leaf type in the order (Knobloch 1979)

The most dominant zingiberid fossil leaf type found throughout Europe is *Zingiberoideophyllum liblarense* Kräusel and Weyland. This type is known from the Oligocene into the Neogene and has been postulated by a number of authors to be the leaf type borne by the parent plant of the fruit and seed genus *Spirematospermum* (Kräusel and Weyland 1954; Kvaček and Wilde 2006; Fischer et al. 2009). *Zingiberoideophyllum liblarense* was revisited recently by Kvaček and Wilde (2006) who revised many of the initial identifications of Kräusel and Weyland and confirmed its identity as Zingiberaceae.

Also from Europe are *Cannophyllites virlettii* Brongniart (Cannaceae), *Cannophyllites* sp. in the Paleocene Firkanten Formation of Spitzberg, *Heliconia europea* Schweigert (Heliconiaceae) from the Lower Miocene of Engelwies, Germany, and multiple *Musophyllum* species (Musaceae) from the Miocene to Pliocene (Saporta 1862, 1888; Kownas 1955; Livisc 1965; Boyd 1992; Schweigert 1992; Hably 2006).

The genus *Cannophyllites* was originally established by Brongniart for *Cannophyllites virlettii.* However, this name is is invalid as the genus was previously used for the seed fern *Megalopteris* (Dawson) Andrews and fossils described to this genus name need to be renamed (Table 2; Andrews 1875; Hickey 1977; Hickey and Peterson 1978).

Boyd (1992) described, *Musopsis groenlandicum* Boyd, a unique zingiberalean leaf type from the Late Paleocene to Early Eocene of Greenland. Although he could not place it in a family, he compared *Musopsis* comprehensively with extant and extinct members of the order and provided a detailed look into the record of fossil leaves described to the Zingiberales.

Fossil zingiberid leaves from India have been placed in *Cannaites intertrappea* Trivedi and Verma (Cannaceae), and *Musophyllum indicum* Prakash et al. (Musaceae), and are known in association with the pseudostem *Musocaulon indicum* Jain (Musaceae), and the inflorescence axis *Musostrobocaulon skutchii* Bonde (Musaceae) (Jain 1963b, 1965; Trivedi and Verma 1971; Prakash et al. 1977; Bonde 2008). These fossils all come from the Deccan Interappen Beds in India, which range in age from Maastrictian to Eocene in age (Bonde 2008).

Zingiberalean fossils are unknown from Asia with the exception of *Musophyllum nipponicum* Tanai, a single Oligocene leaf from Hokkaido, Japan. Its assignment to Musaceae has been questioned by Boyd on the basis of departure angles of the secondary veins and he recommends it not be considered a part of Musaceae, Strelitziaceae or Heliconiaceae (Tanai 1970; Boyd 1992).

In South America many leaves attributed to Zingiberales have been reported in the fossil record, most of which come from Edward Berry's extensive work in the region in the early to mid 20th century (Table 3, Berry 1921a, Berry 1921b, 1922, 1925a, 1925b, 1935, 1939; Boyd 1992). Two species of *Heliconiophyllum, H. elegans* and *H. falanense* are known from Colombia (Pons 1965); *Heliconia tertiaria* from the late Pliocene of Boliviam and two other species of *Heliconia*, one fromfrom the Oligocene of Costa Rica and the other from the Late Miocene of Cuba (Berry 1921a, 1922, 1939). Berry also described *Heliconia elegans* Berry from the Late Miocene of Venezuela, although this report has been questioned by Boyd (Berry 1921b; Boyd 1992). Recently, paleoenvironmental studies from the Paleocene Cerrejon Formation of Colombia have reported many leaves that are not identified to a particular taxon, but possibly belong to Zingiberales (CJ65 and CJ49 in Wing et al. 2009). To date, there is no fossil record reported for Lowiaceae, Marantaceae, Strelitziaceae, or Costaceae.

Reproductive Fossil Remains of Zingiberales

Reproductive remains of Zingiberales are well documented in the fossil record and extend from the Late Cretaceous to Pliocene in North and South America, Europe, and India. The oldest known reproductive structures are found from the Late Cretaceous (Santonian) of North Carolina in the Black Creek Formation and consist of isolated seeds of *Spirematospermum chandlerae* Friis (Friis 1988). Two fossil genera of Zingiberales have been described from the Late

Cretaceous (Campanian) of Coahuila, Mexico based on permineralized fruits and seeds (Rodriguez-de la Rosa and Cevallos-Ferriz 1994). *Striatornata sanantoniensis* Rodriguez-de la Rosa and Cevallos-Ferriz is a distinctive triloculate fruit with numerous seeds that is placed in Musaceae based on the presence of a chalazal chamber, a character reported by Manchester and Kress (1993) as a synapomorphy for Musaceae. The seeds differ from other members of Musaceae in construction of the seed coat (Rodriguez-de la Rosa and Cevallos-Ferriz 1994).

A second taxon from the same strata, *Tricostatocarpon silvapinedae* Rodriguez-de la Rosa and Cevallos-Ferriz, is also included in Zingiberales based on the characters of triloculate fruits with axile placentation and operculate seeds with a seed coat construction similar to other fossil members classified in the order. However, they could not be placed in a family, in part, because of a lack of diagnostic information about seeds of extant taxa (Rodriguez-de la Rosa and Cevallos-Ferriz 1994).

Also from North America are isolated seeds and a single fruit of *Ensete oregonense* Manchester and Kress from the Middle Eocene Clarno Nut Beds of Oregon (Manchester and Kress 1993; Manchester 1994, 1995). The seeds are small, cylindrical, operculate with a conspicuous chamber in the chalazal region and are quite similar to extant *Ensete* of the Musaceae (Manchester and Kress 1993). Possibly conspecific with *Ensete oregonense* are seed casts from Golden, Colorado that were originally described as *Viburnum goldianum* by Leo

Lesquereux (Steven R. Manchester, Florida Museum of Natural History, personal communication, June 2011).

A fossil fruit illustrated from the latest Early Eocene Republic flora of northeastern Washington was initially identified as *Ensete* sp. (Wehr and Manchester 1996; http://www.burkemuseum.org/paleontology/stonerose). These fossils are currently under study and reevaluation suggests taxonomic assignment to Nelumboaceae (Pigg et al. 2009).

In South America, seeds attributed to Musaceae were described by Berry from the Tertiary of Colombia (Berry 1925; Manchester and Kress 1993; Rodriguez-de la Rosa and Cevallos-Ferriz 1994). These fossils, named *Musa enseteformis* Berry, were thought to come from an unknown horizon of probable Oligocene age around Bogota, Colombia (Berry 1925). In 1960, Jain renamed these fossils *Ensete berryi* Jain based on the reevaluation of the Musaceae by Cheeseman (Cheesman 1948; Jain 1960). These seeds were reevaluated by Manchester and Kress (1993) and were found to be mummified extant seeds rather than fossils. Based on carbon isotope data, they are 300-year-old specimens of *E. ventricosum*, a species that is still grown in the region today.

In Europe, the fossil record of zingiberalean reproductive structures extends from the Late Cretaceous to Pliocene. The fruit and seed genus *Spirematospermum* (Heer) Chandler was a common component of many floras ranging from the Late Cretaceous to Pliocene. *Spirematospermum friedrichii* Knobloch and Mai is the oldest report of Zingiberales in Europe and is found in the Late Cretaceous (Maastrictian) gray clays of Eisleben, Germany (Knobloch and Mai 1986). These isolated seeds are very similar to *S. wetzleri* from the Miocene of Denmark and the Late Cretaceous *S. chanderae* of North Carolina, but are considerably smaller (*S. wetzleri* 5-10 mm compared to *S. friedrichii* 2-3.5 mm long; Koch and Friedrich 1971; Knobloch and Mai 1986; Friis 1988).

The best-known species with the longest record, extending almost 50 million years, is *S. wetzleri* (Fischer et al. 2009). Fruits of this species are triloculate with axile placentation and 2 rows of seeds per locule. Seeds are cylindrical with a slight taper towards the chalazal region, operculate, arillate, and have a distinct spirally striate seed coat (Koch and Friedrich 1970, 1971; Friedrich and Koch 1970, 1927; Friedrich 1991). This combination of characters was shown to be very similar to *Alpinia oxymitrum* K. Schum [Formerly *Cenolphon oxymitrum* (K. Schum) Holttum] in the Zingiberaceae. The taxonomic placement of *Spirematospermum* will be addressed in the discussion chapter of this work.

In the Eocene Lagerstätten flora and fauna of Messel, a single fossil has been found that closely resembles *Ensete* and is currently being described by other authors (Selena Y. Smith, University of Michigan, personal communication, December 2011; Steven R. Manchester, Florida Museum of Natural History, personal communication, July 2011). *Alpinia arnensis* (Chandler) Mai has been described from the Miocene flora of Phoenix-Nord of England based on isolated seeds and was shown to be very similar to *A. japonica* (L.) of the Zingiberaceae (Chandler 1962; Chandler 1964; Mai and Walther 1985)

In India, zingiberalean silcified fossil plants occur in the well-known Deccan Intertrappan beds (Prakash 1960). The fossil *Musa cardiosperma* Jain was based on well-preserved permineralized fruits and seeds and placed within the Musaceae due to its similarity with *Musa* (Jain 1963a; Jain 1965). Fruits found in compression preservational states from the Decans that are considered to be conspecific with *M. cardiosperma* were named *Callistemonites indicus* Bande et al. (Bande et al. 1986, 1993; Mehrotra 2003; Bonde 2008). Upon reexamination of fruits of *M. cardiosperma*, Manchester and Kress (1993) proposed that the fossil seeds lack essential characters of Musaceae, in particular, the chalazal chamber, which was proposed as a synapomorphy for the family. Because of this it was suggested that *M. cardiosperma* be retained as a member of Zingiberales but not placed in a particular family (Manchester and Kress 1993; Rodriguez-de la Rosa and Cevallos-Ferriz 1994; Benedict et al. 2007; Benedict 2011b).

In surveying the fossils of Zingiberales it is clear that the record is strong with several distinctive taxa being present by the Late Cretaceous and throughout the Tertiary. The limitation is the relationship of these fossil taxa to their living relatives. If the relationships of these problem taxa can be understood, then the larger picture of the radiation and evolution of this important group of monocots can be better evaluated.

The Goal of This Dissertation. The goal of this dissertation is three-fold, 1) to describe new fossil material of zingiberalean relationship from the Late Paleocene of North Dakota, 2) to evaluate these new fossils in the rich context of fossil plants within the Zingiberales, and 3) to compare fossils with a survey of extant fruits and seeds within the order to understand the variation within the groups and to infer character evolution for the order. As noted by many authors, the seeds and fruits in this order are quite distinctive but, to date, the sample sizes of seeds surveyed have been quite narrow and little attention has been given to the anatomical details as well as the overall morphology. It is with this mindset that I have begun this dissertation.

The layout of this dissertation is as follows: Chapter 1 Introduction to Zingiberales; Chapter 2 Materials and Methods; Chapter 3 Nomenclature of Seed Characters; Chapter 4 Results Part 1 Extant Studies of Seeds; Chapter 5 Results Part 2: Fossil Studies; Chapter 6: Discussion.

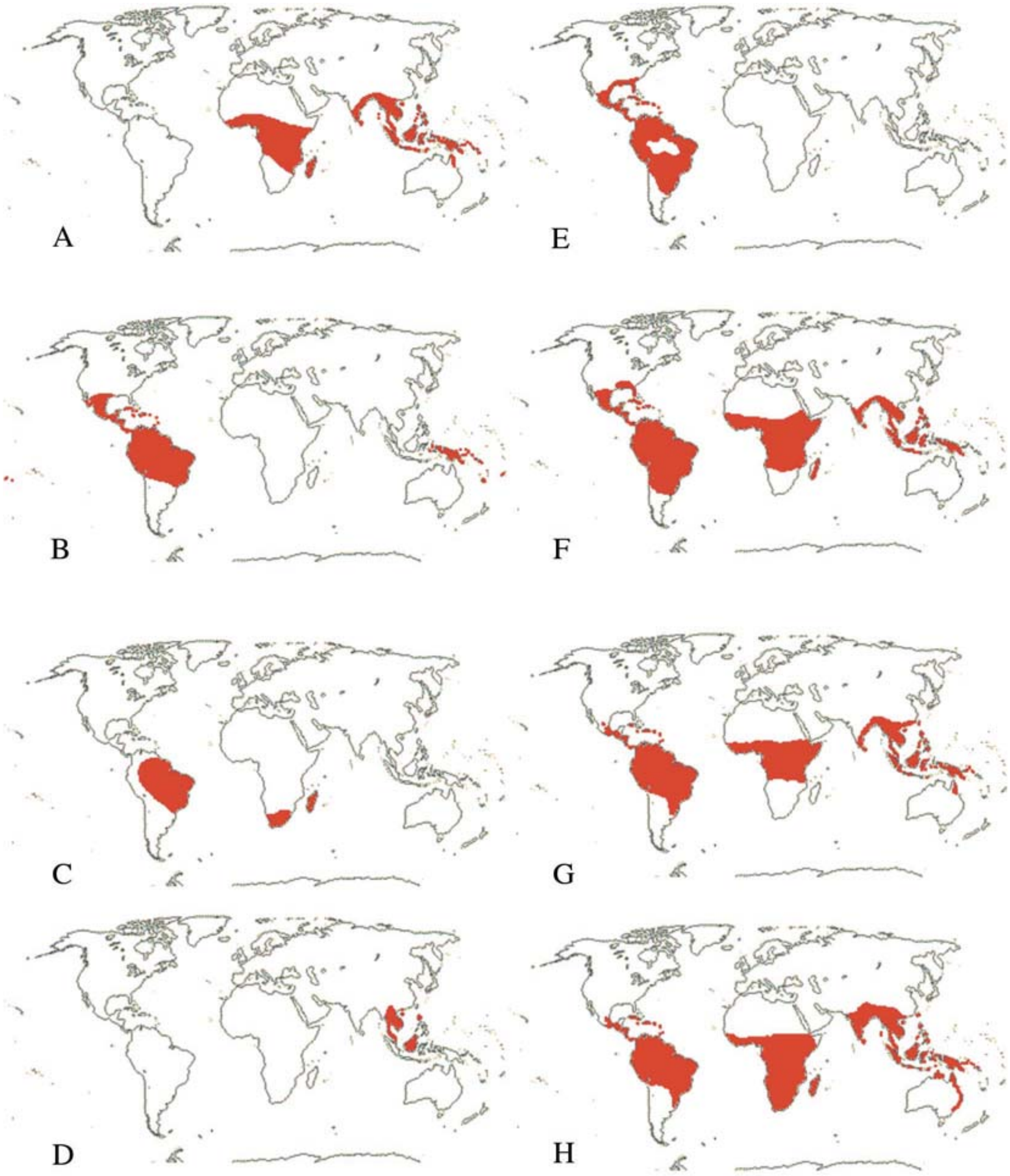


Fig. 1 The current distribution of the families of the order Zingiberales. A, Musaceae. B, Heliconiaceae. C, Strelitziaceae. D, Lowiaceae. E, Cannaceae. F, Marantaceae. G, Costaceae. H, Zingiberaceae. Images modified from Stevens (2001 onwards).

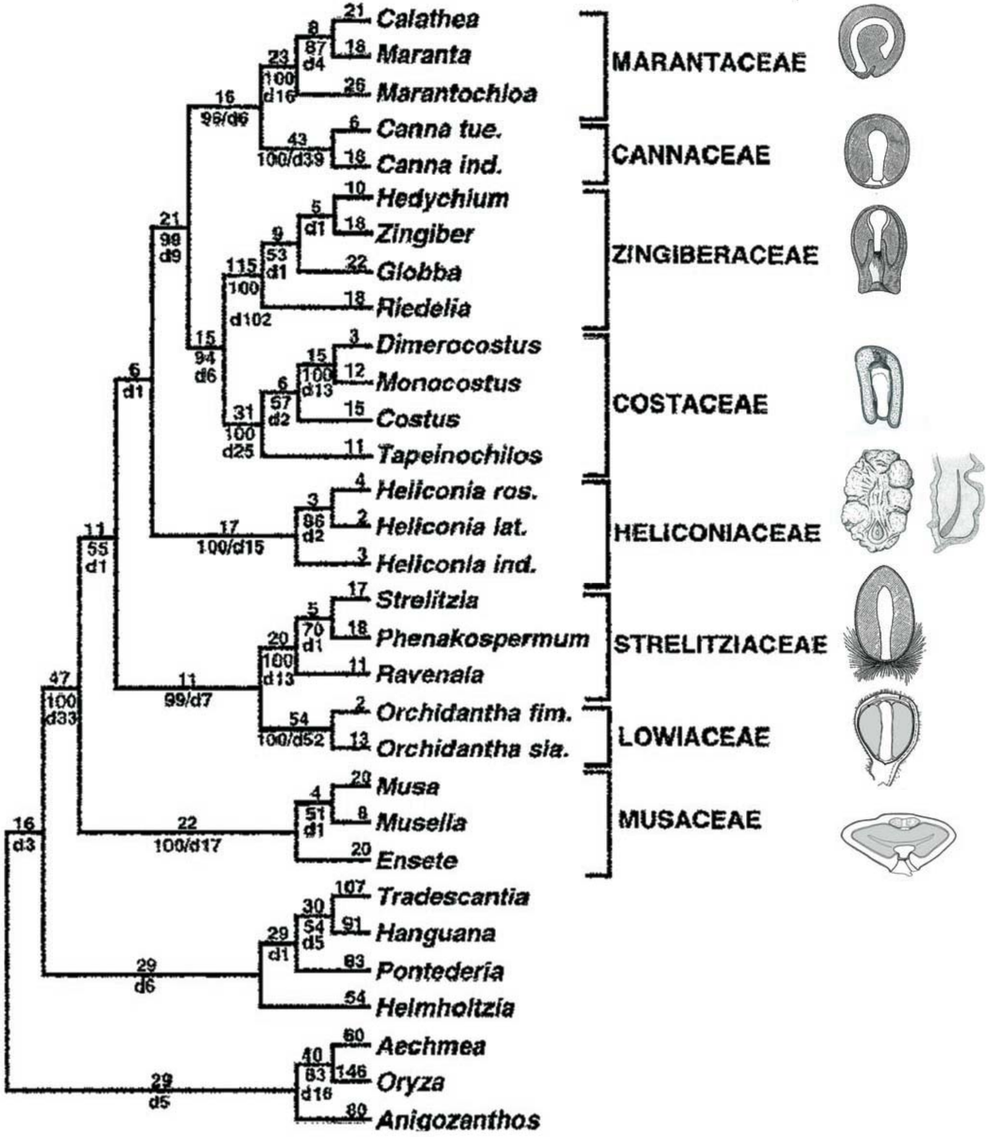
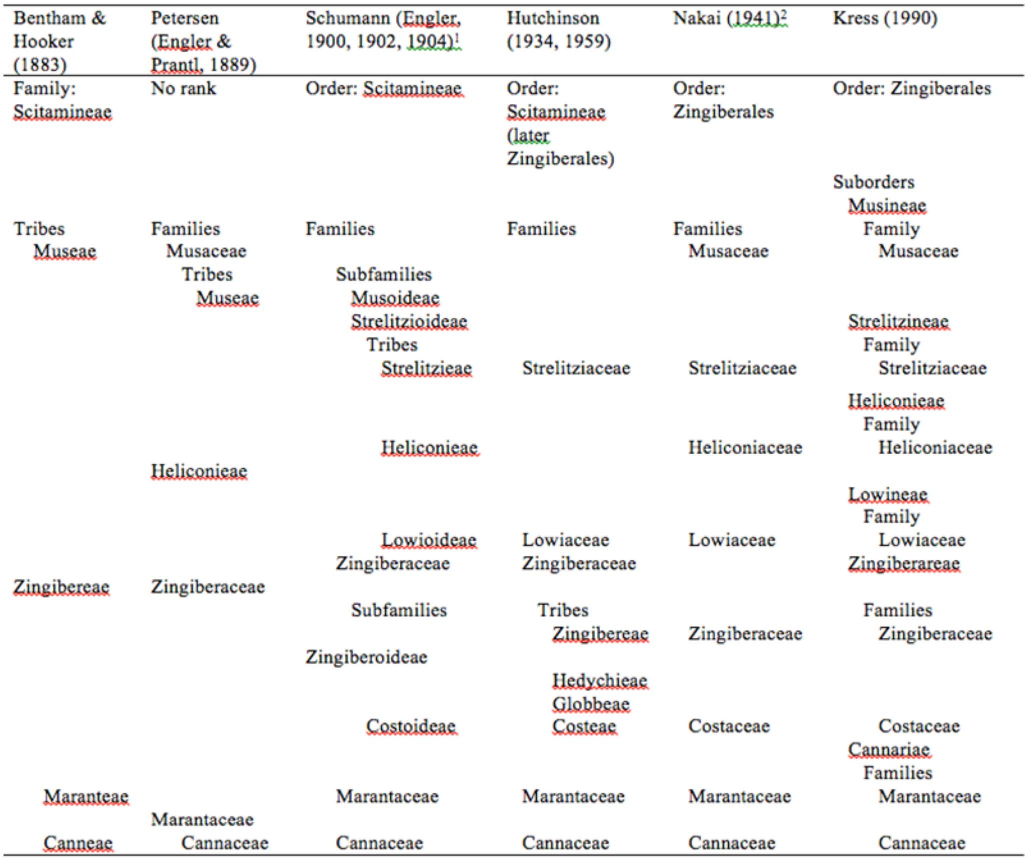


Fig. 2 The Relationships of the families in Zingiberales based on the single most parsimonious tree obtained from 36 morphological characters and molecular data from chloroplast *rbcL* and *atpB* genes and nuclear 18S sequence data. Modified from Figure 8 of Kress et al. 2001. Numbers above the branches indicate branch

lengths. Bootstrap and decay indices (d) are indicated below the line. Figures at right depict seed shape in longitudinal section, with white area indicating embryo shape, and are redrawn from: Marantaceae (*Thalia* sp., Watson and Dallwitz 1992 onwards); Cannaceae (*Canna* sp., Watson and Dallwitz 1992 onwards); Zingiberaceae (*Renealmia* sp., Watson and Dallwitz 1992 onwards) Strelitziaceae (*Strelitzia* sp., Watson and Dallwitz 1992 onwards); Costaceae (*Costus speciosus*, Loesener 1930); Heliconiaceae (*Heliconia* sp., Simão et al. 2006); Lowiaceae (*Orchidantha chinensis*, Wen et al. 1996); and Musaceae (*Musa* sp., Graven et al. 1996).

Table 1. History of the taxonomic relationships of the Zingiberales



Bentham & Hooker (1883)	Petersen (Engler & Prantl, 1889)	Schumann (Engler, 1900, 1902, 1904)[1]	Hutchinson (1934, 1959)	Nakai (1941)[2]	Kress (1990)
Family: Scitamineae	No rank	Order: Scitamineae	Order: Scitamineae (later Zingiberales)	Order: Zingiberales	Order: Zingiberales
					Suborders
					Musineae
Tribes	Families	Families	Families	Families	Family
Museae	Musaceae			Musaceae	Musaceae
	Tribes	Subfamilies			
	Museae	Musoideae			
		Strelitzioideae			Strelitzineae
		Tribes			Family
		Strelitzieae	Strelitziaceae	Strelitziaceae	Strelitziaceae
					Heliconieae
					Family
		Heliconieae		Heliconiaceae	Heliconiaceae
	Heliconieae				
					Lowineae
					Family
		Lowioideae	Lowiaceae	Lowiaceae	Lowiaceae
		Zingiberaceae	Zingiberaceae		Zingiberareae
Zingibereae	Zingiberaceae				
		Subfamilies	Tribes		Families
			Zingibereae	Zingiberaceae	Zingiberaceae
		Zingiberoideae			
			Hedychieae		
			Globbeae		
		Costoideae	Costeae	Costaceae	Costaceae
					Cannariae
					Families
Maranteae		Marantaceae	Marantaceae	Marantaceae	Marantaceae
	Marantaceae				
Canneae	Cannaceae	Cannaceae	Cannaceae	Cannaceae	Cannaceae

[1] Other publications including the same relationships Schumann (Engler, 1900, 1902, 1904): Winkler; Loesener (Engler & Prantl, 1930) [2] Other publications including the same relationships as Nakai 1941: Tomlinson (1962); Takhtajan (1980); Cronquist (1981); Dahlgren et al. (1985). Modified from Kress et al. 2001.

Table 2. Reports of Cannaceae in the fossil record

Taxon	Author	Locality	Age	Organ
Canna eocenica	Berry 1916	Grenada Flora, Oxford, Mississippi, USA	Eocene	Leaf
Canna flaccideafolia	Berry 1924	Claiborne, Louisiana, USA	Eocene	Leaf
Canna jacksoniana	Ball (cf. Boyd 1992)	Texas	Eocene	Leaf
?Canna magnifolia	Lozinsky et al. 1984	Jose Creek Member of McRae Formation, New Mexico, USA	Late Cretaceous	Leaf
Cannaites intertrappea	Trivedi and Verma 1971	Deccan Intertrappean beds	Late Cretaceous – Paleocene (Eocene?)	Rhizome and Roots
Cannophyllites sp.	(Kramer 1974) Bande and Prakash 1986	Sumatra	Neogene	Leaf
Cannophyllites sp.	(Tobler 1923) Bande and Prakash 1986	Indonesia	Neogene	Leaf
Cannophyllites varieseanus	(Göppert 1854) Bande and Prakash 1986	Java	Eocene	Leaf
Cannophyllites sp.	Livsic 1965	Firkanten Formation, Spitzberg, Germany	Paleocene	Leaf

Table 3. Reports of Heliconiaceae in the fossil record

Taxon	Author	Locality	Age	Organ
Heliconia bahiana	Berry 1935	Bahia, Brazil	Pliocene	Leaf
Heliconia europea	Schweigert 1992	Baden-Wuerttemberg, Germany	Lower Miocene	Leaf
Heliconia sp.	Berry 1921a	Costa Rica	Miocene	Leaf
Heliconia sp.	Berry 1939	Matanzas, Cuba	Miocene	Leaf
Heliconia tertiaria	Berry 1922	Pisllypampa, Bolivia	Pliocene	Leaf
Heliconiophyllum elegans	Pons 1965	Colombia	Tertiary	Leaf
Heliconiophyllum falanense	Pons 1965	Colombia	Tertiary	Leaf

Table 4. Reports of Musaceae in the fossil record

Taxon	Author	Locality	Age	Organ
Ensete oregonense	Manchester and Kress 1993	Clarno Nut Beds, Oregon, USA	Eocene	Seed
Musocaulon indicum	Jain 1963b	Deccan Intertrappean Beds, India	Late Cretaceous-Eocene	Rhizome
Musophyllum indicum	Jain 1963b	Deccan Intertrappean Beds, India	Late Cretaceous-Eocene	Rhizome
Musophyllum nipponicum	Tanai 1970 (cf Boyd 1992)	Hokkaido, Japan	Oligocene	Leaf
Musophyllum polonicum	Kownas 1955	Dobrzyn, Poland	Miocene	Leaf
Musophyllum speciosum	Saporta 1862, 1888 (cf Boyd 1992)	France, Romania	Oligocene-Pliocene	Leaf
Musophyllum tárkányense	Hably 2006	Felsőtárkány, Hungary	Miocene	Leaf
Musophyllum trinitense	Hollick 1924	West Indies	Late Miocene?	Leaf
Musophyllum sp.	Geyler 1887 (Bande and Prakash 1986)	Borneo	Paleogene	Leaf
Musostrobocaulon skutchii	Bonde 2008	Deccan Intertrappean Beds, India	Late Cretaceous-Eocene	Inflorescence Axis
Striatornata sanantoniensis	Rodriguez-de La Rosa and Cevallos-Ferriz 1994	Coahuila, Mexico	Late Cretaceous	Fruit

Table 5. Reports of Zingiberaceae in the fossil record

Taxon	Author	Locality	Age	Organ
Alpinia arnense	(Chandler 1962) Mai and Walther 1985	Arne in Pool, England	Lower Eocene	Seed
Alpinia bivascularis	Mai 1999	Saxony and Brandenburg, Germany	Lower Miocene	Seed
Spirematospermum chandlerae	Friis 1988	Potomac, North Carolina, USA	Santonian or Campanian	Seed
Spirematospermum friedrichii	Knobloch and Mai 1986	Kreide	Late Cretaceous	Seed
Spirematospermum wetzleri	Koch and Friedrich 1971	Fasterholt, Denmark	Miocene (Eocence to Pliocene)	Fruit
Zingiberites dubius	(Lesquereux 1878) Brown 1962	Denver Formation, Colorado, USA	Paleocene	Leaf
Zingiberites petiolaris	Saporta 1988	France	Oligocene	Leaf
Zingiberoideophyllum liblarense	(Krausel and Weyland 1954) Kvacek and Wilde 2006	Rhenish Browncoal, Germany	Miocene	Leaf with cuticle
Zingiberopsis attenuata	Hickey and Peterson 1978	Joffre Bridge, Paskopoo, Canada and North Dakota, USA	Paleocene, and Late Cretaceous	Leaf
Zingiberopsis isonervosa	Hickey 1977	Golden Valley Flora, North Dakota, USA, and others	Early Eocene	Leaf
Zingiberopsis rigguaensis	Knobloch 1979 (cf Boyd 1992)	Bavaria, Germany	Cretaceous	Leaf
Zingiberopsis magnifolia (=Canna magnifolia Brown 1962)	Hickey and Petersen 1978	Lance Formation, Wyoming, USA, and others	Late Cretaceous	Leaf

Table 6. Reports of fossils attributed to Zingiberales without family placement

Taxon	Author	Locality	Age	Organ
"Musa cardiosperma"	Jain 1963a	Deccan Intertrappean Beds, India	Late Cretaceous-Eocene	Fruit
Musophyllum complicatum	(Lesquereux 1878) Hickey 1977	Ft. Union Fm, CO, many localities	Paleocene-Eocene	Leaf
Musopsis groenlandicum	Boyd 1992	Thyra Island Fm, Greenland	Late Paleocene or Early Eocene	Leaf
Tricostatocarpon silvapinedae	Rodriguez-de La Rosa and Cevallos-Ferriz 1994	Coahuila, Mexico	Late Cretaceous	Fruit

Table 7. Previous reports of fossil Zingiberales that are no longer accepted

Taxon	Author	Locality	Age	Organ	Notes
"Ensete sp."	Wehr and Manchester 1996	Republic, WA, USA	Eocene	Fruit	Possibly the receptacle of Nelumbo (Nelumbonaceae)
"Musa enseteformis"	Berry 1925 (Jain 1960, 1965)	Colombia	Recent	Seeds	Modern mummified seeds determined by Manchester and Kress 1993
"Heliconia elegans"	Berry 1921b	Venezuela	Miocene	Leaf	Not *Heliconia* determined by Boyd 1992

Chapter 2

MATERIALS AND METHODS

Stratigraphy and Geological Setting

The Almont and Beicegel Creek floras are located in central and western North Dakota, respectively, and occur within the Williston Basin, the largest and easternmost Cretaceous/Paleocene/Eocene depositional basin in the Western Interior in North America (Fig. 3*A*-*D*; Gibson 1995; Bluemle 2000; Harrington et al. 2005; Peppe 2010; Pigg and DeVore 2010). The Williston Basin is one of 13 basins that were formed during the Laramide Orogeny of the second series of uplifts that created the Rocky Mountains (Fig. 3*B*). The strata within the basin extend from the Late Cretaceous to Eocene and contain many floras that have been studied in detail. The oldest megafloral localities are from the Late Cretaceous Hell Creek Formation, which has been well studied (see Johnson 2002 for a review). The flora can be divided into three megafloral zones (HCI-III) that document an increase in leaf size and a warming trend from the earliest to the latest Maastrictian and into the early Paleocene (Shoemaker 1966; Johnson 1989, 2002). The floristic region has been interpreted as a woodland of small to mid-sized trees with many aquatic plants that was dominated by angiosperms (Johnson 2002).

The Paleocene Fort Union Formation rests conformably above the Hell Creek Formation and contains four members; the early Paleocene Ludlow Member, the marine Cannonball Member which “interfingers” with the Ludlow, the Tongue River Member and the Sentinel Butte Member (Hickey 1977; Peppe et al. 2009; Peppe 2010; Pigg and DeVore 2010; Fig. 4). Commercially outcrops of the Fort Union Formation have become quite important and they are the primary source of lignites ("clean coal") for North Datoka (Flores and Keighin 1999; Bluemle 2000).

Of these four Paleocene members, Ludlow (65.47 – 62.99 Ma, Pollen zone 3, Williston Basin I-II, Figs. 4 and 5) has been extensively surveyed and is interpreted as representing fluvial depositional systems with a combination of channels, ponds and crevasse splays (Peppe 2009, 2010). The most common components of the flora include *Paranymphaea crassifolia*, "*Cornus" nebrascensis*, "*Populus" nebrascensis*, *Quereuxia angulate*, *Nyssidium eckmanii* and the leaf morphotype LM29. Although a comprehensive description of the flora and its interpretation in a paleoecological context is pending, Peppe suggests a general cooling event and decrease in species richness during the time of active deposition of the Ludlow Member (Peppe 2010).

The Cannonball Member is a marine time-transgressive deposit representing the Cannonball Sea of North and South Dakota (Blumele 2000; Johnson 2002). Although it lacks notable plant material besides *Teredo*-bored petrified wood, (the state fossil of North Dakota, Blumele 2000), it represents the remnants of the Cretaceous Seaway that was adjacent to the Tongue River and Sentinel Butte Formations during their time of active deposition in the late Paleocene (Royse 1970; Bluemle 2000; Peppe 2010). The Cannonball Sea interfingers in the Ludlow Member and was thought previously to have been present in the early Paleocene but is now extended into the late Cretaceous (Flores and Keighin 1999; Johnson 2002; Peppe 2010). It was fed by rivers in what is now Montana and Wyoming and subsequently retreated northward by the middle Paleocene, dissapearing by the late Paleocene (Flores and Keighin 1999; Fig. 6).

The Tongue River and Sentinel Butte Formations constitute the most extensive Paleocene outcrops in the Williston Basin (Royse 1970). The Tongue River has been considered a fresh waterdeposit but marine(?) ostracodes, bivalves, and diatoms and various ichnogenera have been recoded suggesting fluctuations between salt and freshwater deposits (Belt 2005). The Sentinel Butte is rich in megafloral remains and contains the Almont and Beicegel Creek floras of which the fossils for this study were deposited and its flora will be explained below (Pigg and DeVore 2010).

Above the Fort Union Formation lies the younger Golden Valley Formation that contains the latest Paleocene to early Eocene Bear Den Member and the Early Eocene Camels Butte Member, both of which have well documented megafloral plant communities (Hickey 1977; Clechenko et al. 2007; Pigg and DeVore 2010). The plant communities found within these three formations and are summarized in Appendix A.

The Almont and Beicegel Creek floras of the Sentinel Butte Formation of the Fort Union Group and are Late Paleocene in age (~56 MYA), Tiffanian 3, based on the occurrence of mammal and mollusk faunas from underlying sediments (Crane et al 1990; Pigg and DeVore 2010; Zetter et al. 2011). Based on the palynomorph assemblage, Almont flora can be placed in Pollen Zone 5 *sensu* Nichols and Ott (2006), which further supports a Late Paleocene age for the floras (Figure 7*A*).

A recent overview of the palynomoph flora of the Almont site documents the pollen and spore assemblage through light microscopy (LM) and scanning electron microscopy (SEM) using the same-grain analysis technique (Zetter et al. 2011). The palynoflora is dominated by bisaccate conifer pollen Juglandaceae, and Betulaceae. Well-known pollen morphotypes include *Pistillipollenites macgregori* Rouse, *Incertae sedis*, a distinctive grain found throughout the Cretaceous to Eocene in North America, Europe and Japan, and two species of *Erdtmanipollis* Krutzsch. and is generally regarded as similar to extant *Pachysandra* and assignable to Buxaceae. However, no megaflora record of this family is known at Almont.

Although not formally described, preliminary pollen and spore data from Beicegel Creek are quite similar to the profile at Almont (Michael D. Nowak, Duke University, unpublished data; Kathleen B. Pigg, personal communication; Benedict personal observation). The two floras are separated by 120 km and differ in preservation type and presumably in depositional environment, yet contain many of the same plant mega- and microfossils and are regarded as of similar age (Manchester et al. 2004; Pigg and DeVore 2010).

Fossil Localities and Preservation

The Almont fossils are preserved in a light to dark brown siliceous mudstone matrix that is found in thin layers (50 cm max) directly under the topsoil of an agricultural field in Morton County, North Dakota about 22 km North of the town of Almont (Crane et al. 1990; Manchester et al. 2004; Pigg and DeVore 2010; Taylor 2010; Fig. 5). The fossils can be seen on weathered surfaces of the rocks and are often white due to oxidation and leaching of the organic material within the plant during the process of preservation. The layers of fossil material extend no more than a few meters below ground, but have a lateral range of “several hundred meters” (Crane et al. 1990) and can be seen throughout the agricultural field, and up to at least several kilometers to the north (Newbrey and Bozek 2003; Taylor et al. 2006). Excavations from the sides of the road show areas where weathering has exposed large plates of the hard siliceous rocks (Crane et al. 1990; Benedict personal observation 2005). The Almont matrix often contains fine discrete laminations, relatively complete and unfragmented plant remains including whole leaves, rarely fish and fish scales (Newbrey and Bozek 2003) and is deposited in thin, lens-type beds. Originally described as a large lake (Crane et al. 1990) the depositional environment has been interpreted more recently as possibly a series of overlapping oxbow lakes that were subsequently permeated with siliceous and iron-rich solutions (Pigg and DeVore 2010).

The more recently discovered fossil flora of Beicegel Creek flora lies 120 km to the west of Almont in McKenzie County, North Dakota. This flora occurs in silicified shale found as several discrete outcrops atop adjacent buttes. Fossil plant remains occur throughout the sections as compressions, petrified stumps, paper shales and in clinker (DeVore personal communication 2007). This permineralized flora is preserved in a hard, siliceous shale and ranges from a light orange to dark purple based on the relative abundance of carbon, weathering, oxidation and leaching of minerals during the fossilization process. Fossil material can be seen on the surface of the rocks as white weathered compressions and impressions, often times as dense accumulations of fragmented plant material. In contrast to the Almont flora, which is thought to have been developed in a relatively low energy environment, such as a small pond or perhaps an oxbow lake, as part of a larger fluvial system (Pigg and DeVore 2010), fossil plant remains from Beicegel Creek are highly fragmented and often densely distributed throughout the block of chert. Because of this very fragmentary nature of the matrix it can be interpreted as being part of a higher-energy fluvial system such a flood plain, abandoned channel or crevasse splay (Pigg and DeVore 2010).

The Almont and Beicegel Creek Floras

The Almont flora has been extensively collected for the past 30 years and has led to the publication of over 20 papers, two masters theses and one Ph.D. dissertation documenting its diverse flora (Manchester et al. 1982; Crane et al. 1990; Crane et. al 1991; Pigg et al. 1993; Manchester et al. 1999; Manchester 2001, 2002a, 2002b; Xiang et al. 2003; Manchester et al. 2004; Chen et al. 2005; Pigg and DeVore 2005; Pigg et al. 2006; Taylor et al. 2006; Matthews 2007;

Benedict et al. 2008; Pigg et al. 2008a, 2008b; Manchester et al. 2009; Manchester and O'Leary 2010; Manchester et al. 2010; Taylor 2010; Zetter et al. 2011; Zhou et al. 2012). The Almont and Beicegel Creek floras when considered together are a complex arrangement of deciduous woody tress, shrubs, rare aquatics, ferns and herbaceous understory plants. The most common components of the flora include fruits, seeds and leaves of many deciduous woody plants including the gymnosperms cf. *Parataxodium sp.* (Cupressaceae; Crane et al. 1990), *Ginkgo cranei* Zhou, Quan & Liu (Gingkoaceae, formerly *G. adiantoides*; Zhou et al. 2012) and the woody angiosperms *Palaeocarpinus dakotensis* Manchester, Pigg & Crane (Betulaceae; Manchester et al. 2004), *Corylites* sp. leaves (Betulaceae; Manchester et al. 2004), *Amersinia obtrullata* Manchester, Crane & Golovneva (Cornales, Manchester et al. 1999), *Beringiaphyllum cupanoides* (Newberry) Manchester, Crane & Golovneva (Cornales; Manchester et al. 1999), *Cornus piggae* Manchester, Xiang, & Xiang (Cornaceae, Manchester, Xiang, & Xiang 2010) *Cyclocarya brownii* Manchester (Juglandaceae, Manchester and Dilcher 1982; Taylor 2010), *Melisoma rostellata* (Lesquereux) Crane, Manchester & Dilcher (Meliosmaceae; Crane et al. 1990), *Acer* sp. (Sapindaceae; Crane et al. 1990), *Nordinskioldia borealis* (Heer) Crane, Manchester, & Dilcher (Trochodendraceae; Crane et al. 1991), and *Zizyphoides flabella* (Newberry) Crane, Manchester, & Dilcher (Trochodendraceae, Crane et al. 1991). Many of these taxa are common members of Paleocene floras of the Northern Hemisphere and typify the low diversity floras of this time period

(Crane et al 1990, Pigg and DeVore 2010, Taylor 2010).

Less abundant, but notable components of the combined Almont and Beicegel Creek flora include the pteridiophytes *Woodwardia sp., Isoetes* cf. *horridus* and filicalian ferns that have yet to be formally named, found only at Beicegel Creek (Pigg et al. 2006; Matthews et al. 2006, 2007; Pigg and DeVore 2010). Two genera of the aquatic family Nymphaeaceae, *Susiea newsalemae* Taylor, DeVore and Pigg and *Nuphar* cf. *wutuensis* Chen, Manchester and Chen are known primarily from the Almont site, based on seeds (Chen et al. 2004; Taylor et al. 2006). Understory trees or shrubs that were also an important part of the flora include *Hamawilsonia boglei* Benedict, DeVore and Pigg (Hamamelidaceae), a mosaic taxon whose nearest living relatives are shrubs to medium sized trees that are often confined to riparian habitats, most commonly the banks of streams (Benedict et al. 2008); *Meliosma rostellata* (Meliosmaceae) a genus of trees and shrubs distributed in the Neo- and Paleotropics (Watson and Dallwitz 1992 onwards); *Paleomyrtinea sp.* (Myrtaceae) an extinct genus related to guavas (*Psidium* L.) and most likely a small tree or shrub as are many of the members of the family (Pigg et al. 1993); *Ochna sp.* (Ochnaceae) is a rare but also represented at both Almont and Beicegel Creek and living members of this genus are Old World tropical trees and shrubs.

Another interesting component of the flora are the number of taxa that have affinities with vine producing plants (lianas). *Ampelocissus sp.* (Vitaceae), *Paleosecuridaca curtisii* (Polygalaceae; Pigg et al. 2008a), *Icacinacarya* *collinsonia* and *Icacinacarya dictyota* (Icacinaceae; Pigg et al. 2008b), cf. *Saurauia* (Actinidiacae; Pigg and DeVore 2003) and *Porosia verrucosa* (*Incertae sedis* though compared with *Sabia sp.* [Sabiaceae] in Manchester 2002b) are all genera within families with a large proportion vine producing plants that are mostly restricted to tropical and subtropical environments.

Two possibly herbaceous to smaller understory plants in the flora are *Paleoactaea nageli* Pigg and DeVore (Ranunculaceae) and the zingiberalean fossil described in this study (Pigg and DeVore 2003; Benedict et al. 2006, 2007; Benedict 2011b). These less common components of the Almont and Beicegel Creek Floras add a level of detail to the paleoflora not observed by only observing the most abundant species preserved. The flora could be considered a deciduous hardwood to conifer forest that would imply a more temperate environment than was probably the case. If the less common understory shrubs, tress, ferns, herbs and aquatic plants are incorporated into the reconstruction, we can infer that the environment was much warmer and did not have a coldest month below a few degrees Celsius as the aquatics, vines and especially the zingiberalean plant would not have been able to survive a hard freeze.

Fossil Monocotyledonous Remains from Almont and Beicegel Creek

Fossil monocot seeds, leaves and leaf buds occur rarely in the original Almont locality in Morton County and are much more common in the Beicegel Creek locality of North Dakota (Crane et al. 1990, Pigg and DeVore 2010). Over 100 seeds, 20 leaf buds and numerous leaf fragments of zingiberalean affinity have been recovered from the Beicegel Creek locality, and a few (currently four identified) seeds as well as leaf fragments have been found within the original Almont flora where the fragmented seeds were described as “clavate structures” and the leaf fragments as “monocotyledonous remains” (Crane et al. 1990 Figs. 26D-F and 29A-B). Similar types of leafy buds have been described from other Paleocene floras of western North America, from the Alberta Basin of Canada, the Fort Union localities in the Rockies, and the Golden Valley sites (Brown 1962; Hickey 1977; Hoffman 2002).

Preparation Techniques of Fossil Plant Material: Fossil material was photographed from surface fractures using a Nikon D70s or D90 camera body (Nikon Inc. Melville, NY, USA) with a 60 mm flat field macro lens with a TIFFIN 62 mm Standard hot mirror lens (AF MICRO NIKKOR 60 mm 1:2.8). For details of surface fractures, specimens were photographed using reflected light from a Fiber-light High intensity illuminator, series 180 (Dolan-Jenner Industries Boxborough, MA, USA) on a Nikon SMZ1500 stereomicroscope with a phototube and C-F mount extension to allow the Nikon D90 body to fit on the microscope. For anatomical details specimens were imaged using transmitted light on a Nikon Eclipse E800 compound microscope outfitted for the Nikon D90 camera as well. Images were obtained using Nikon’s Camera Control Pro 2 version 2.8.0 software on an Acer Aspire 5810TZ-4784 laptop computer (Acer America Corporation, San Jose, CA, USA) or an 20 inch iMac mid 2007 model desktop computer (Apple Corporation Cupertino, CA, USA). Images were edited using Adobe Photoshop software version CS or CS2 (Adobe Systems Incorporated San Jose, CA, USA).

Two different techniques were used to study the internal anatomy of the fossils depending on their particular type of preservation and matrix composition. For fossil plant material that was preserved in a matrix high in organic matter, the cellulose acetate peel technique was used, but modified with hydrofluoric acid (HF) for use with siliceous rocks (Joy et al. 1956; Basinger and Rothwell 1977). Large blocks of chert that were suitable for the cellulose acetate peel technique were mapped and then cut into three to four centimeter thick slabs perpendicular to the depositional laminations to expose the maximum amount of plant material contained in the chert. The cut sections were indicated on the map and individual slabs were labeled Newly exposed sections of the block were then polished using a series of silicon carbide (SiC) or carborundum powder from 100 to 1000 grit to smooth the face in preparation for etching with HF.

Blocks were then subject to high concentration (55%) hydrofluoric acid to dissolve the siliceous matrix and ‘free’ the preserved plant material. After 45 seconds to one minute of exposure to HF, blocks were quickly placed in a large bath of sodium bicarbonate to neutralize the acid and stop the etching process. Once neutralized, blocks were rinsed with deionized water and placed on a bed of rocks to dry. Once dried each polished and etched face was lightly rinsed with acetone and then covered with a thin layer of cellulose acetate that was slightly larger than the face of the block. Care was taken to insure that no air bubbles were trapped between the face of the block and the acetate peel because bubbles inhibit the fusion of the freed carbonized matrix with the acetate peel. Once all acetone had evaporated from the peel the cellulose acetate peel was carefully removed from the block and if a portion of the peel remained fused to the block a razorblade was used to carefully remove it from the block ensuring the acetate sheet remained complete. Each face of each block was peeled individually and upon peeling the block the same face was polished and etched multiple times to acquire a series of peels for a given specimen.

Fossils that were preserved in a matrix low in organic matter were wafered observed with reflected light, a technique that was duplicated for extant material. Fossil material were embedded in Ward's Bio-plastic Synthetic Resin (Ward's Natural Science, Rochester, NY). To properly catalyze the resin, a mixture of 2% catalyst (Methyl ethyl ketone peroxide) was added to the Bio-plastic polymer. In the cases where specimens were denser than the Bio-plastic and sank, a thin layer (~3 mm) of resin was added to the molding container prior to placing the specimen. This allowed for a supporting layer to encase the specimen so it would be completely enveloped in the polymer. On the other hand, if specimens were less dense than the Bio-plastic, they were either added to the base supporting layer or a thin layer of Bio-plastic was added on top of the specimen after it had been added to the catalyzed Bio-plastic. After 24 hours of placing the specimens in Bio-plastic, they were put in a 60°C oven to allow for the final curing of the polymer. The material was then removed from the mold and sectioned using a

Buhler Isomet low-speed lapidary saw or Buhler Isomet 1000 precision lapidary saw with a diamond blade (BUEHLER, a division of Illinois Tool Works Inc., Lake Bluff, Illinois, USA). Individual sections were made ranging from 0.4 mm to 1.0 mm thick depending on the individual specimen being sectioned. Once sectioned specimens were either removed from the Bio-plastic or retained and were mounted on glass slides using U-154 adhesive (The Company, Lakewood, Colorado, USA). Specimens were then ground down via a carborundum powder series from rough to fine grit to obtain a single layer of cells for anatomical details if necessary (Benedict et al. 2008; Taylor et al. 2009).

Preparation Techniques of Extant Plant Material: Various methods of standard histology were investigated for sectioning extant Zingiberales seeds. Because silica cells (phytoliths) are present in the seed coats standard microtome techniques involving serial alcohol series, embedding in waxes or synthetic resins, and sectioning obtaining sections using traditional histological techniques is very difficult. Two of the most common methods used previously for this type of plant tissue were freezing microtomy (Desler 1994) or microtomy with the use of hydrofluoric acid treatment of the seeds to remove the phytoliths from seed coats (Liao and Wu 1996; 2000). Due to the fact that these methods were either difficult to employ (Freezing microtomy) or introduced artifacts to the plants material (HF destroys data) extant seeds were treated in the same manner as fossil material and embedded and wafered using the same protocol as described above (Benedict et al. 2008; Taylor et al. 2009).

Synchrotron Radiation-Based X-ray Tomographic Microscopy: Fossil and extant fruits and seeds were also studied using Synchrotron Radiation-Based X-ray Tomographic Microscopy (SRXTM) done in collaboration with Dr. Selena Smith (University of Michigan) at the Advanced Photon Source (APS) at Argonne National Laboratory, Lemont IL. X-ray tomography was completed using the 2-BM beamline operated by Dr. Xianghui Xiao and configured with a White Beam (2-BM-A), Pink, or Monochromatic (multilayer) Beam (2-BM-B) (Beamline information: http://www.aps.anl.gov/Xray_Science_Division/Xray_Microscopy_and_Imaging/Beamlines/2_BM/). Fossil specimens were analyzed using the high energy White Beam at 40 keV with a 5 x objective and exposures were taken every 300 milliseconds, which yielded 1501 exposures per scan. Extant material was examined using the low energy pink beam at 16 keV with an objective of either 2.5 x or 4 x. Exposures were taken every 300 milliseconds and yielded 1024 files for the 2.5 x objective and 1536 files for the 4 x objective.

To view specimens in real time to verify that the specimen was in line with beam and would be completely captured during the scan, the program CCD Image Grabber v.4.2.1 was used. The alignment of the specimen was achieved by adjusting the vertical placement of the specimen using the “Tomo-Y” and 360° rotations were checked at 0°, 180°, and 90° using the two picomotors to verify the specimen would stay in the beamline throughout the entire scan. Specimens taller than the beamline were captured in a series of scans from the base to the apex of the specimen and each scan covered approximately 2.7 mm of vertical distance.

To acquire the beamline data Tomo script v.2.3.0 was used which created new sample folders for each scan, which contained the data sets. Preliminary data sets stored in the sample folders were incorporated into a cluster file, which allowed us to find the frame shift of the scan. To obtain trial reconstructions the first section of the cluster file was edited to remove "#" from the script to allow for the preliminary file to be processed. Once preliminary data in sample folders were captured and the cluster file was edited to allow the script to run the file was submitted to the Orthos server with produced frame shift numbers.

To calculate frame shift numbers of each scan 150 Hierarchical data format (HDF) files were viewed in ImageJ with an "HDF_Reader" plugin. Each file was imported and compared to each other to find the image with least distortion, which indicated the frame shift number of that scan. Once the frame shift number was found it was entered into the original cluster file and the file was submitted to the Orthos server to acquire a full reconstruction of the sample. The full reconstruction folders produced HDF files, which were then converted into files that were usable with three dimensional reconstruction programs. HDF files were converted a single RAW file using the program "HDF_to_binary" in IDL. These single raw files were then imported into the program Aviso® (http://www.vsg3d.com/avizo) and analyzed and converted into TIFF files to be viewed with other three dimensional reconstruction programs such as the open source program UCSF Chimera (http://www.cgl.ucsf.edu/chimera/). In these programs seeds and fruit data were edited to show external and internal morphological details. Individual slices or sections of the data were also acquired to show anatomical details of the seed coat and opercula.

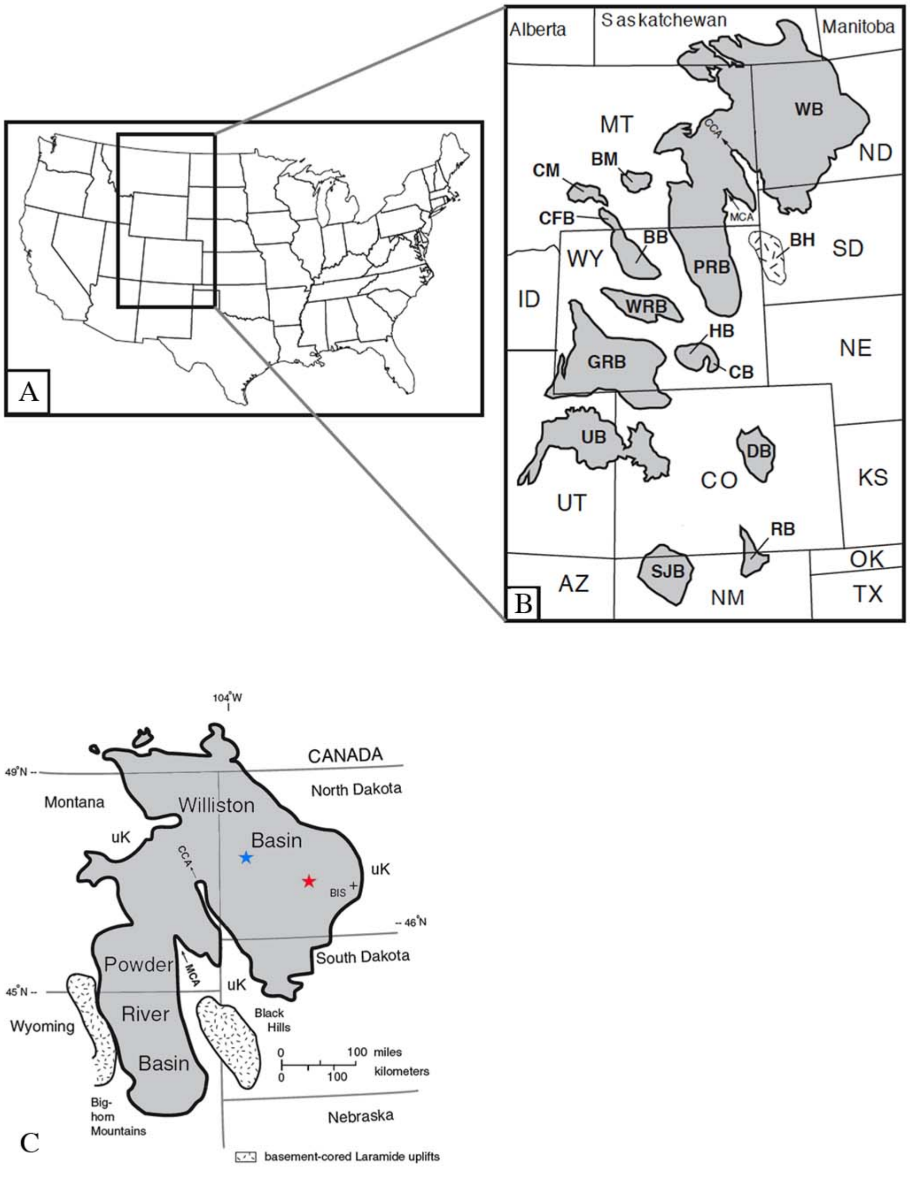


Fig. 3 The Williston Basin of Western Interior, North America. A, Map of the continental United States of America with the region of the Williston Basin outlined in the rectangle. B, Inset of A with the Williston Basin outcrops shaded in grey. C, Williston Basin with stars indicating the Almont flora (Red) and

Beicegel Creek flora (Blue) locations in North Dakota, USA. WB=Williston Basin, BM=Bull Mountain, CM=Crazy Mountains, CFB=Clark's Fork Basin, BB=Bighorn Basin, PRB=Powder River Basin, WRB=Wind River Basin, HB=Hanna Basin, CB=Carbon Basin, GRB=Green River Basin, UB=Uinta Basin, DB=Denver Basin, RB=Raton Basin, SJB=San Juan Basin, BH=Black Hills, CCA=Cedar Creek Anticline, MCA=Miles City Arch. C. Locality map of floral localities in the Little Missouri River Valley in southwestern North Dakota. Figures A and B after Peppe 2010. Figure C after Belt et al. 2004.

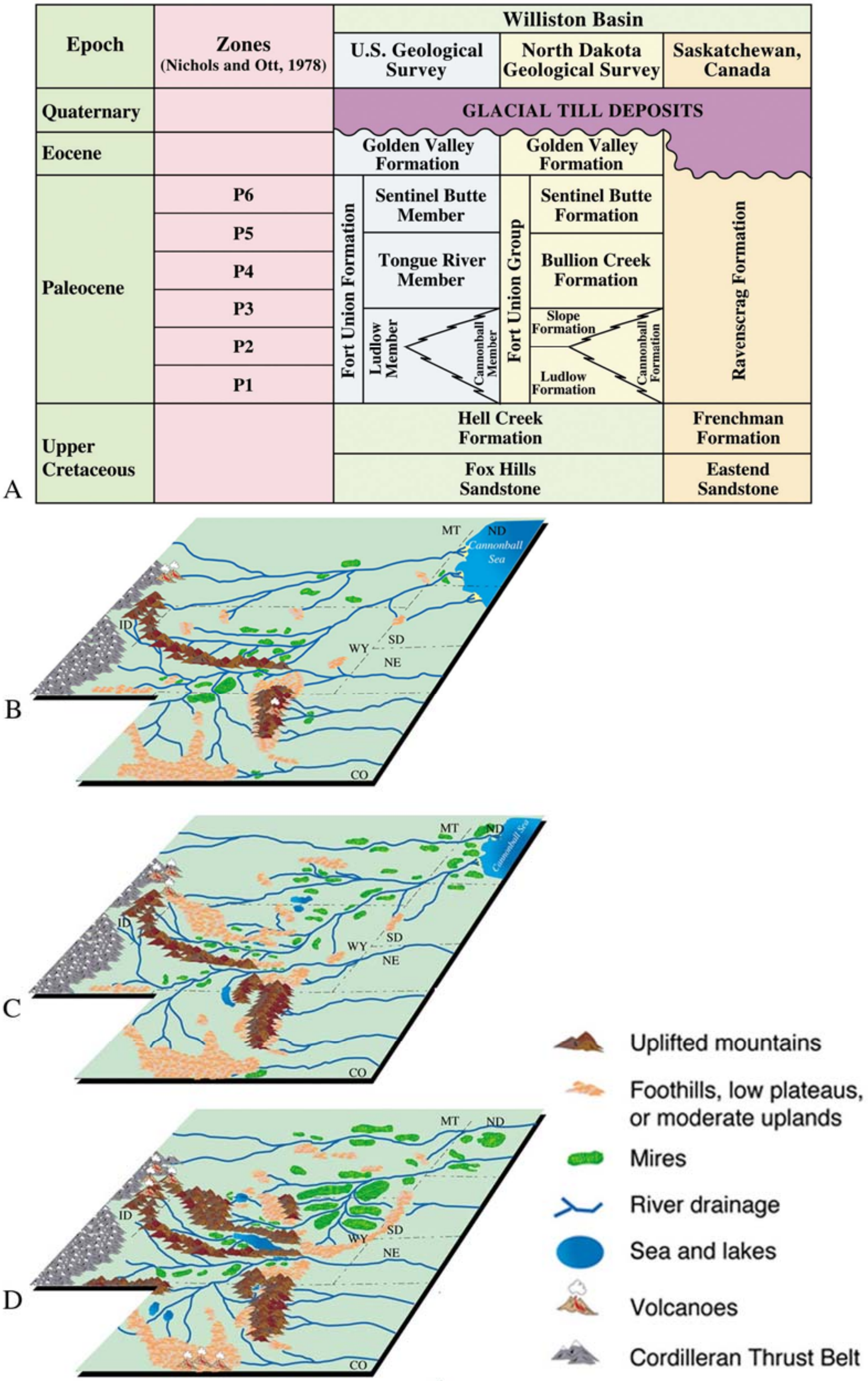

A
Epoch
Zones (Nichols and Ott, 1978)
Williston Basin
U.S. Geological Survey
North Dakota Geological Survey
Saskatchewan, Canada
Quaternary
GLACIAL TILL DEPOSITS
Eocene
Golden Valley Formation
Golden Valley Formation
Paleocene
P6
P5
P4
P3
P2
P1
Fort Union Formation
Sentinel Butte Member
Tongue River Member
Ludlow Member
Cannonball Member
Fort Union Group
Sentinel Butte Formation
Bullion Creek Formation
Slope Formation
Ludlow Formation
Cannonball Formation
Ravenscrag Formation
Upper Cretaceous
Hell Creek Formation
Frenchman Formation
Fox Hills Sandstone
Eastend Sandstone
B
MT
ND
Cannonball Sea
ID
WY
SD
NE
CO
C
MT
ND
Cannonball Sea
ID
WY
SD
NE
CO
D
MT
ND
ID
WY
SD
NE
CO
Uplifted mountains
Foothills, low plateaus, or moderate uplands
Mires
River drainage
Sea and lakes
Volcanoes
Cordilleran Thrust Belt

Fig 4. The Williston Basin stratigraphic column and physiographic map. A, A stratigraphic column diagram of the Williston Basin displaying the Sentinel Butte Formation in within the Late Paleocene, between pollen zones P5 and P5 sensu Nichols and Ott (1976) After figure WS-3 in Flores and Keighin (1999). B-D, Physiographic diagrams of the Williston Basin in Early Paleocene (B), the Middle Paleocene (C), and the Late Paleocene (D). Figures B-D after figures IN-12, IN-13 and IN-14 in Flores and Nichols 1999.

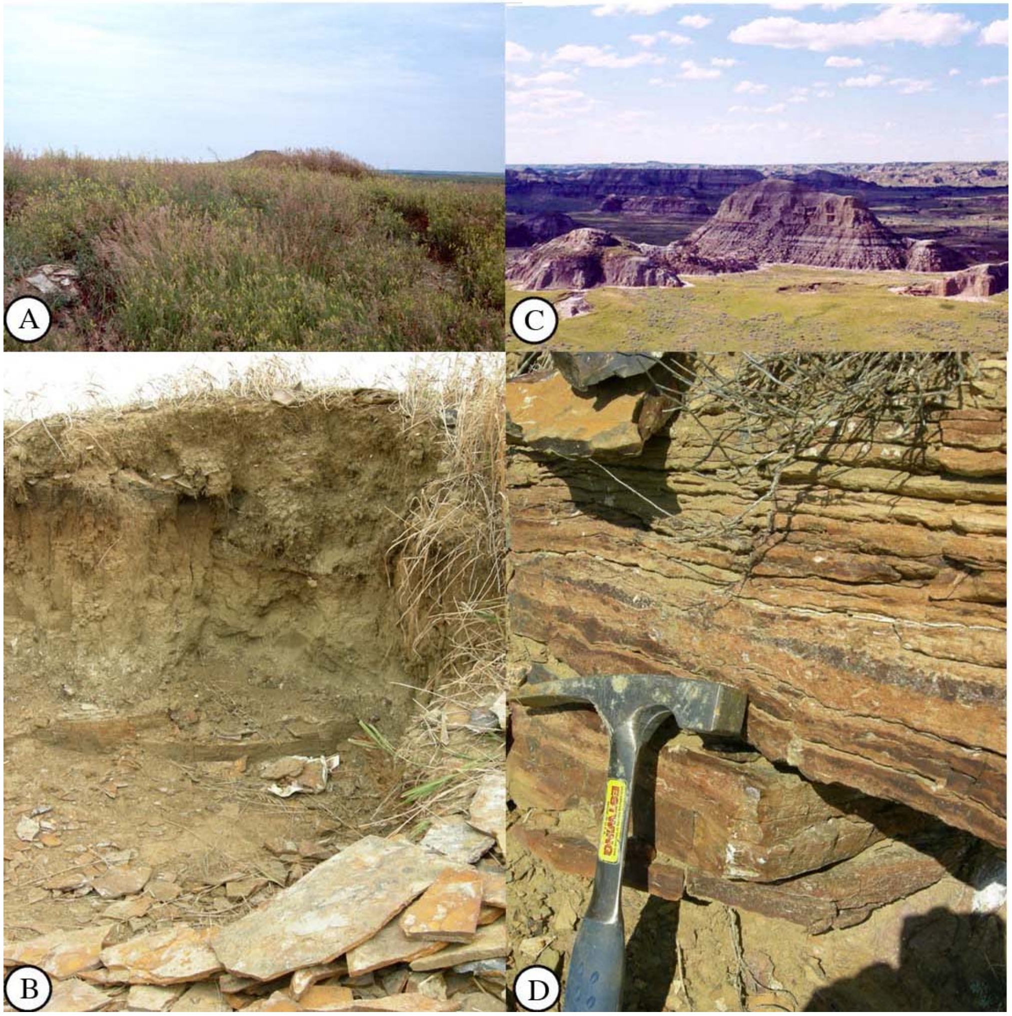


Fig. 5 Photographs of the Almont and Beicegel Creek Localities. A, The Almont locality outcrop in the middle of a corn field. B, The Almont fossil outcrop directly under the topsoil. C, An overview of the Beicegel Creek outcrop located in situ near the summit of the butte in the picture. D, The Beicegel Creek outcrop in situ and comprises discrete laminations. Images A and C courtesy of Dr. Kathleen B. Pigg, and B and D courtesy of Dr. Melanie L. DeVore.

Chapter 3

NOMENCLATURE OF ZINGIBERALES FRUITS AND SEEDS

Fruits of Zingiberales have a wide range of morphological and anatomical variation and range from single seeded pyrenes to triloculate capsules to fleshy berries (Dahlgren et al. 1985; Simão et al. 2006). Seeds of the order also have a great deal of morphological variation including having arils, opercula, micropylar collars, chalazal chambers, stomata or trichomes on the exotesta, the type of nutrient tissue stored in the seed (endosperm, chalazosperm, perisperm), the size and shape of the embryo and the anatomical variation of the seed coat (Rudall et al 1999; Kress et al. 2001; Benedict 2011a, 2011b). Below I provide a history of the studies of Zingiberales seeds as well as a list of characters used to identify Zingiberalean seeds that have often been misused or has changed since original publication.

Historical Studies of the Seeds of Zingiberales

The first detailed review of the seed development and anatomy in a systematic approach for the Zingiberales (Scitamineae) was made by Humphry 1896 where he studied seven genera in detail (*Alpinia mutica* Roxb., *Amomum elongatum* (Teijsm. et Binn.), *Canna indica L., Costus sp., Heliconia psittacorum, Strelitzia reginae* and *Thalia dealbata* Fraser.). Humphry noted many of characters of gross morphology of the seeds including the presence or absence of a micropylar canal, aril, operculum and type of nutrient tissue present in the seeds of the various families in order to compare them in a systematic context.

Some of the most significant finds he made at the time include: 1) supporting the separation of Cannaceae and Marantaceae, an idea that was proposed by other authors at the time. He found Cannaceae to be a unique family in Zingiberales based on the presence of stomata in the seed coat, absence of an operculum and instead a ‘germinal slit’ and that the majority of the seeds developed from the chalazal region of the seed; (2) *Heliconia* fruits are unique among Zingiberales because they are pericarps unlike the capsules and berries of all other genera; (3) *Costus* and some Zingiberaceae contain a ‘discoid patch’ at the chalazal region of the seed that can be seen with the naked eye and upon sectioning of these seeds it produces a chalazal mass that can be either small (*Costus*) to quite large and occupying up to half of the seed (*Alpinia mutica*). He postulated this to be a homologous structure within these genera and evidence of their close relationship to each other.

Most interesting is the final paragraph of his 1896 paper that reads, “In respect to seed-development, the Musaceae are a heterogeneous group. Perhaps the nearest affinity with the Zingiberaceae is shown by *Musa*. *Strelitzia* lacks the most characteristic Scitamineous feature, the micropylar collar and lid, but is, in a measure, saved by its aril. In *Heliconia*, the supplanting to the testa by the endocarp precludes the supposition of a close affinity with other genera.” This short statement summarizes much of what we know to be true about the order today, including the separation of *Strelitzia* and *Heliconia* from Musaceae. Also, the close relationship of *Musa* to Zingiberaceae based on seed characters is one that was returned to in light of fossil evidence throughout the 20th century and with the uncertainty of Musaceae in relation to the other families in Zingiberales these data seem quite relevant still today.

In 1981 and 1983, the first attempts were made to understand the morphological and anatomical variation of the seeds in a systematic context focusing on the aril, operculum and micropylar collar characters (Grootjen and Bouman 1981; Grootjen and Bouman 1983). Taktajan's 1985 comparative anatomy of Monocotyledons expanded our knowledge of seed variation in the Zingiberales quite dramatically by compiling a broad synopsis of publications to date of the seed and fruit variation within the order to date in 1985 in combination with his own observations.

In the early 1990's to early 2000's a series of papers were written by authors working at the South China Botanical Garden and focused of the integumentary structure of seeds in mostly the Zingiberaceae and to a lesser extent others in the order (See Liao and Wu 2000 and Tang et al. 2005 for a review). In 1994, Bridgette Desler published her dissertation regarding the seed anatomy in Zingiberales with an emphasis on the seeds of Marantaceae. She sampled 42 species from seven of the eight currently recognized families and produced a large set of characters she observed in her study, although they were never extrapolated into a systematic context.

In 1993 and 1994 two pivotal papers were written describing fossil fruits and seeds in the Zingiberales, which were described in the context of known data from the seeds and fruits of extant members. Manchester and Kress (1993) described *Ensete oregonense* (Musaceae) concurrently with an ordinal analysis of the seeds from seven of the eight families in the order, with insights on their gross morphology, but no anatomical details. From this analysis it was concluded that the chalazal chamber found in Musaceae was a synapomorphic character for the group and because Musaceae was considered basal and sister to the rest of order at the time, it may also represent the plesiomorphic character state of seeds in the order.

In the following year, Rodriquez-de la Rosa, and Cevallos Ferris (1994) published on two Cretaceous fossil fruits from Mexico that also fit well within the order. In their comparison they analyzed 13 seeds from six of the eight families of the order as well, but expanded their study to incorporate data of the composition of the seed coats. Although this study was limited in its sample size it provided a framework to analyze the fossil fruits and seeds in a systematic context. From the analyses of seed coats they observed coupled with previously published resources they were able to assign *Striatornata sanantoniensis* to Musaceae, but the other Cretaceous fossil *Tricostatocarpon silvapinedae* was resolved only to order and placed as *incertae sedis* with respect to its family status. After a broader analysis of the fossil and living seeds in the order Rodriguez-de la Rosa and Cevallos-Ferriz (1994) noted that, "The seed structures of *Striatornata sanantoniensis, Tricostatocarpon silvapinedae, Spriematospermum friedrichii, S. chandlerae, S. wetzleri,* and *Musa cardiosperma* share more characters among themselves than with any extant group of plants in the Zingiberales (pg. 800).”

Simão et al. (2006) described the integumentary anatomy and more importantly mechanical layer of the endocarp in the Heliconiaceae. This study helped to address erroneous or sporadic reports of which layers of the integument or ovary act as the mechanical or protective layer of the embryo within members of the order. Interestingly, this study showed the development of the endocarp as the mechanical layer of the embryo in Heliconiaceae, which is unique among the order.

Assessing Seed and Fruit Character States in Zingiberales

In this current study over 80 seeds of extant and extinct members of Zingiberales were studied in detail to add to the current understanding of morphology and anatomy of the order. The terminology used to describe seed and fruit characters of Zingiberales have been interpreted in various ways by many authors, and their meanings have changed through time. In order to use these characters to address ideas of phylogenetic relationships and character evolution within the group it is necessary to define what is meant by the various character states. Below is a definition of various fruit and seed characters I have surveyed as well as their different character states observed in Zingiberales.

Fruit Characters

1. Perianth insertion- ovaries can be epigynous (inferior), hypogynous (superior) or perigynous.

2. Fruit type- fruits range from berries, to drupes, to pyrenes, to dehiscent (loculicidal) or indehiscent capsules.

3. Placentation- Placentation ranges from laminar, basal, marginal, apical, axile, parital, free central.

4. Number of locules per fruit- Locules in Zingiberales are commonly 1 or 3, though 2 are known from *Dimerocostusm Monocostus,* and *Tapeinochilos* (Costaceae) (Specht 2006).

5. Ovules (seeds) per locule- Ovules range from 1 to many per locule.

6. Rows of seeds per locule- Rows of seeds range from 1 to many.

Seed Characters

1. Arillate seeds: Seeds of Zingiberales may or may not contain an arillate structure (exarilloid). Arils can be divided into two groups, those of funicular origin, or true arils, and those derived of from tissue other than the funiculus and are not exostomal in origin and are called "arilloid" (Corner 1976, 2009; Grootjen and Bouman 1983; Manchester and Kress 1993).

2. Operculum: The operculum is a lid that covers an opening in the seed coat, which is also derived of seed coat tissue and dislodges to allow for the internal embryo to escape the seed during the early stages of germination. Ontogenetically, the operculum is derived from the outer integument and raphe (Grootjen and Bouman 1983).

3. Micropylar collar: The micropylar collar is a ring of tissue also derived from dermal and raphe tissue and acts as a point of contact for the operculum to attach

to the remainder of the seed coat. It is derived form the proliferation of meso and endotesta cells that divide and protrude into the nucellus (Grouten and Bouman 1981, J. Benedict personal observation). The size of this ring can be quite variable throughout the order from lacking to small or indistinct, to large and extending quite deeply in the seed.

4. Chalazal Chamber: The chalazal chamber is produced by a septum that separates the internal cavity of the seed into two sections, the embryo cavity and chalazal cavity or chamber. It comprises three distinct layers, a portion of the outer integument, the vascular tissue or raphe, and a portion of the inner integument and its cuticle (McGahan 1961; Bouharmont 1963; Manchester and Kress 1993; Graven et al. 1996). Within this chamber that is created inside the separated outer integument is the "chalazal mass." This group of cells is hydroscopic and gelatinous when exposed to water (McGahan 1961). The presence of both a well-differentiated septum comprised of the three layers stated above as well as the chalazal mass in combination will be considered necessary for this character state and is currently only known for members of Musaceae.

5. Perisperm Canal- The perisperm canal is an empty tunnel-like void in seeds of Marantaceae. It is derived from an internal penetration of the chalazal region of the nucellus into the perisperm that subsequently degenerates upon maturation of the seed. Three states of this character have been reported from strait, "a straight unbranched one, a straight, distally ramifying one whose branches partly embrace the curvature of the embryo; and a basally branched one whose ramifications lie

parallel to the curved embryo" (Grootjen 1981; Anderson and Chase 2001).

6. Hypostase- The hypostase, also called the chalazal pigment cell group, or diaphragm, is used by many authors to describe various modifications found at the chalazal region of the seed in Zingiberales (Desler 1994, Humphry 1896, Liao and Wu 1996, 2000). Its definition is unfortunately vague with two contrasting ideas. One, inherently broad interpretation is that it refers to any structure found at the chalazal region of the seed (Tilton 1980b discussed in Rudall 1997). Another more precise definition states it is a modified region of the nucellus adjacent to the embryo sac at the chalazal region (Schnarf 1929; Maheshwari 1950 see Rudall 1997). Because this second definition requires a developmental study be required to identify the presence or absence of a hypostase, it is less useful for the current study on fossil and mature seeds and the general term of any tissue or growth at the chalazal region of the seed derived from the seed coat. It is contrasted with the chalazal chamber as it does not necessitate a thickened septum and is most often comprised of a single layer of cells.

7. Mechanical Layer of Seed Coat- The mechanical layer of the seed coat is defined by which part of the seed coat is functioning as a hard protective layer of the embryo. In Zingiberales the mechanical layer can be derived from the exotesta, exotesta and endotesta, or endocarp tissue.

8. Seed coat layer composition- Most often the mechanical layer of Zingiberales is the outer integument, and thus is the hardest and thickest to provide protection to the embryo inside. This layer is quite variable and can range in width,

orientation, type and number of cells, especially within Zingiberaceae.

9. Hilar rim- In some members of Musaceae (e.g. *Ensete*), a ring of tissue is formed from the integument to form a ring around the hilar region of the seed (Manchester and Kress 1993).

10. Micropylar region thickenings- In some members of the Zingiberales the micropylar region can be differentially thickened. This is particularly evident in many of the fossil members, but can also be seen in some members of the Zingiberaceae. Previously this character has been referred to as a "Caruncle-like structure" (Liao and Wu 2000) for outgrowths observed in seeds of *Globba* and *Zingiber*, but this term seemed too specific for these genera and could not be applied to all members with micropylar thickenings. This character is contrasted with a hilar rim, which is a thickening that protrudes out of the seed coat into a ring at the periphery of the micropylar region of the seed, whereas micropylar region thickenings do not create an obvious ring or extend out of the seed coat.

11. Trichomes on seed coat- Simple unicellular, uniseriate hairs on the epidermis (usually exotestal) of seeds may or may not be present.

12. Embryo shape- Embryo shape can range from elongate and strait to curved to mushroom shaped.

13. Pigments in Embryo- All embryos in Zingiberales are well developed at the mature seed stage, but some families have embryos with pigments and others do not.

14. Chalazosperm- Perisperm tissue that is very hard and starchy has been referred to as chalazosperm and has been used to distinguish families of Zingiberales (Definition from Cannaceae in Kubitzki 1998 pg 103; Kress 1990; Rudall et al. 1999; Kress et al. 2001).

Table 8. Fruit characters in Zingiberales

Family	Fruit Characters					
	1	2	3	4	5	6
Musaceae	inferior	berry/ dehiscent capsule	axile	3	many	2 - many
Heliconiaceae	inferior	pyrene	basal	3	1	1
Strelitziaceae	inferior	dehiscent capsule	axile	3	many	2 - 4
Lowiaceae	inferior	dehiscent capsule	axile	3	many	2
Cannaceae	inferior	dehiscent capsule	axile	3	many	2
Marantaceae	inferior	dehiscent capsule	basal	3	1	1
Costaceae	inferior	dehiscent capsule	axile or parietal	3 or 2	many	2 - 4
Zingiberaceae	inferior	dehiscent capsule	axile or parietal	3 or 1	many	1 - 4

Modified from: Humphrey (1896), Mauritzon (1936), Davis (1966), Grootjen and Bouman (1981), Grootjen (1983), Bouman (1984), Kronestedt and Walles (1986), Grootjen and Bouman (1988), Dahlgren et al. (1985), Johri et al. (1992), Kirchoff (1992), Danilova et al. (1995), Andersson (1998b), Larsen (1998), Kress et al. (2001), Simão et al. (2006), Fischer et al. (2009).

Table 9. Seed characters in Zingiberales

Character	Family							
	MU	HE	ST	LO	CA	MA	CO	ZI
Aril	-[1]	-	+	+	-1	+	+	+
Operculum	+	+	-[2]	+	-	+	+	+
Micropylar Collar	+	-	-	-	-	+	+	+/-[3]
Chalazal Chamber	+	-	-	-	-	-	-	-
Perisperm Canal	-	-	-	-	-	+	-	-
Hypostase	-	-	-	+[4]	-	-	+	+
Mechanical Layer of Integument	exotesta	fruit wall	exo and endotesta	testa	chalazal and exotesta	exo and endo testa	endo testa	endo or exo testa
Hilar Rim	+	-	-	-	-	-	-	-
Micropylar Thickening	-	-	-	-	-	-	-	-/+
Epidermal Trichomes	-/+	-	-	+/(-?)	+	-	-	-/+
Embryo shape	bulb	elongate	elongate	elongate	elongate	elongate	elongate	varies
Embryo Pigments	-	-	-	-	-	-	-	+

[1]= arilloid strctures. [2]= present, but not functional. [3]= Micropylar reported absent in *Caulokaempferia* and *Cautleya* in Liao and Wu 2000. [4]= Hypostase for Orchidantha reported in Wen et al. 1997. Modified from: Humphrey (1896), Mauritzon (1936), Davis (1966), Grootjen and Bouman (1981), Grootjen (1983), Bouman (1984), Kronestedt and Walles (1986), Grootjen and Bouman (1988), Dahlgren et al. (1985), Johri et al. (1992), Kirchoff (1992), Danilova et al. (1995), Andersson (1998b), Larsen (1998), Kress et al. (2001), Simão et al. (2006), Fischer et al. (2009).

Chapter 4

RESULTS PART I: DESCRIPTIONS OF EXTANT SEEDS

In the efforts to better understand the relationships of the various fossil fruits and seeds attributed to Zingiberales in the past, I have conducted a survey of extant fruits and seeds in the order. To date, this study includes representatives from all eight families in the order, though only seven families were available for histological studies. Specimens were studied using a variety of techniques including transmitted and reflected light microscopy, wafer sections, and Synchrotron Radiation-Based X-ray Tomographic Microscopy. Seed descriptions follow the style of Corner (1976), and Martin and Barkley (1961)

Musaceae

Ensete glucum (Roxb.) Cheesman

Seeds large, smooth, brown, cylindrical and slightly tapering towards the chalazal region of the seed. Aril absent, but funicular tissue residual at the apex of the seed. Operculum present and nested within a conspicuous micropylar collar. Hilar rim present. Embryo mushroom shaped and nested under the operculum and surrounded by abundant starchy perisperm. Chalazal chamber present and infiltrated by a depression of the seed coat into the chamber. Seed coat composed of inner and outer integuments, with the outer providing most of the mechanical support. The outer integument highly sclerified and contains a dark substance (tannins?) in the outer most regions (Fig. 6A-E).

Musa sikkimensis Kurz

Seeds medium sized, verrucose, generally triangular pyramidal, though often contorted. Seed strongly compressed vertically causing the chalazal region to be much wider than the micropylar region. No aril present, though reminants of trichomes (of funicular origin?) can be seen surrounding the operculum. Operculum present and nested within the micropylar collar. Embryo bulbous, situated directly under the operculum and surround by abundant starchy, white perisperm. Chalazal chamber present, large, and filled with parenchymatous, gelatinous red cells. The chamber is formed by both integuments. Seed coat is highly sclerified and also formed of both integuments. Outer integument highly sclerified and the majority of the seed coat. Inner integument two cells thick and also sclerified (Fig 7A-G).

Heliconiaceae

Heliconia bihai (L.) L – Macawflower

Disseminules (seeds with endocarp) large, surrounded by endocarp and triangular pyramidal because they are often borne three to a fruit (Pyrenes). Fruit exocarp brown and leathery upon fruit desiccation and endocarp thickened and forming the mechanical layer of the disseminule. Seeds without aril, operculum absent, but a operculum-like structure created from the endocarp present and situated slightly off center on the disseminule. Embryo elongate and nested within abundant starchy perisperm. Seed coat highly reduced, with the endocarp forming the mechanical layer (Fig 8A-F).

Strelitziaceae

Strelitzia reginae Aiton – Bird of Paradise

Seeds large (13.5 mm long x 7 mm wide) ellipsoid, dark brown, and smooth. Aril large, orange and composed of many hollow tubular hairs. True operculum absent, but apically tapering tissue resembling an operculum present in micropylar region of the seed. This tissue containing a centralized vascular bundle. Embryo cylindrical straight extending from the micropylar region to the chalazal region. Micropylar collar absent. Majority of the embryonic cavity is occupied by white endosperm. Seed coat comprised of the inner and outer integument, though inner integument reduced to a single layer of cells. Exotesta forming slight striations of the seed coat and almost clear in color. Mesotesta following the orientation of the exotesta, and approximately eight cells thick. Endotesta approximately eight cells thick and isodiametric in longitudinal sections of the seed (Fig 9A-F).

Lowiaceae

Orchidantha vietnamica

Seeds medium sized light in color tapering towards the apex with a conspicuous aril. Seed coat smooth with small trichomes. Seed coat composed of two layers, the outer layer thin and the inner layer of palisade cells that do not cover the entire base of the seed (Fig. 10A-F).

Cannaceae

Canna paniculata Ruiz & Pav. – Andean canna

Seeds large (6.5 mm long x 6 mm wide) spherical to ellipsoid with brown to black ‘camouflage’ pigmentation. Seed coat smooth with stomata giving it a foveate appearance. Aril lacking, though white tuffs of hairs present on at the micropylar region of the seed. Operculum absent, instead an inhibition lid comprised of the seed coat present off center of the micropylar region of the seed. Micropylar collar present and comprised of red endotestal cells. Embryo contained within micropylar collar and extending ¾ way to the chalazal region. Endosperm present and occupies the majority of the embryo chamber. Outer layer of the seed coat two cell types, one type thickened into elongate palisade cells that are a light tan pigment and other type are stomata. Inner layer of cells approximately 15 cells thick, transverse in longitudinal section and dark brown in color (Fig. 11A-H).

Marantaceae

Ctenanthe lanceolata Petersen

Seeds large (6 mm long x 4.25 mm wide) elliptical, smooth and light brown in color. Aril large, tan, shinny composed of two flattened blade-like structures covering the micropylar region of the seed. Operculum present, not significantly tapering towards the apex. Micropylar collar absent. Micropylar canal present, simple and extending at least hallway through the seed. Embryo directly below operculum, cylindrical and curving around the micropylar collar. Hypostase absent (Fig. 12A-G)

Costaceae

Dimerocostus argenteus (Ruis & Pav) Maas

Seeds small (4 mm long x 2.5 mm wide), smooth, black, elongate, cylindrical and somewhat compressed due to tight packing in the fruit. The aril covers the micropylar portion of the seed and is easily removed. Operculum large, apically tapering with outer perimeter slightly uplifted and nested within the large micropylar collar. At the base of the seed is a distinct chalazal dimple (hypostase), or impression in the seed coat. The hypostase is small, square and formed from the exotesta. In longitudinal section the embryo is well developed, elongate and extends from the operculum to the chalazal chamber. The remaining embryonic cavity is filled with white perisperm. The cells inside of the chamber are distinct, though can be somewhat lacking as seen in the SRXTM section (Fig. 13A-G).

Zingiberaceae

Alpinia boia Seem.

Seeds medium sized and of various shapes, though often elongated and tapering at both ends. Aril presumably present, though not observed in specimens studied. Operculum present and nested within a micropylar collar. Hypostase present and slightly off center. Embryo elongate and touches hypostase (Fig. 14A-G).

Etlingera linguiformis (Roxb.) R.M. Smith

Seeds small and slightly tapering towards the apex. Seeds when dry have a fusion of arils to fall out as a mass. Embryo elongate, slightly flared at base, and nested within endosperm and both covered in perisperm. Seed coat composed mainly on large sclerenchymatous palisade cells (Fig. 15A-G)

Hedychium borneense R.M. Smith

Seeds medium sized, tubular, and with a conspicuous hair-like orange aril. Operculum absent, though a micropylar collar is present. Embryo nested within micropylar collar and elongated throughout the entire embryo cavity. The chalazal region has a small gap in the mestotesta and pigmented cells within the mesotesta cell layer. The endotesta is composed of simple parenchymatous orange cells (Fig. 16A-F).

Hemiorchis sp. Kurz

Seed small and cylindrical with a conspicuous apical thickening of the seed coat. Epidermal hairs present and covering the seed. Operculum absent, though micropylar collar present. Hypostase absent in the chalazal region, but often the region in contorted upon maturity. Embryo a large mass filling most of the seed. Seed coat very thin, though composed of the three layers of the testa. Endotesta of small orange parenchymatous cells. (Fig. 17A-F).

Pleuranthodium sp. (K. Schum.) R.M. Smith

Seeds small and triangular pyramidal with a shiny dark black seed coat and light colored aril. Operculum present and slightly nested within the micropylar collar of the seed. Embryo straight and slightly bulbous towards chalazal region. Hypostase present and composed of a small proliferation of mesotesta cells. Seed coat composed of three layers, the palisade exotesta, a multiple layered mesotesta and a single layered endotesta of square sclerenchymatous cells (Fig. 18).

Aframomum melegueta K. Schum.

Seeds small and cylindrical with a shinny, dark seed and light aril. Operculum present and nested within the micropylar collar. The micropylar region mesotesta cells distinctly proliferated to create a large mass of cells that surrounds the operculum. Embryo straight, elongated and surrounded by endosperm towards the chalazal region. Hypostase present and composed of a proliferation of mesotesta cells. Seed coat three layers, a single exotestal layer, a mesotesta of multiple layers of thickness depending on the region of the seed and a single endotestal layer of square sclerenchymatous cells (Fig. 19A-H).

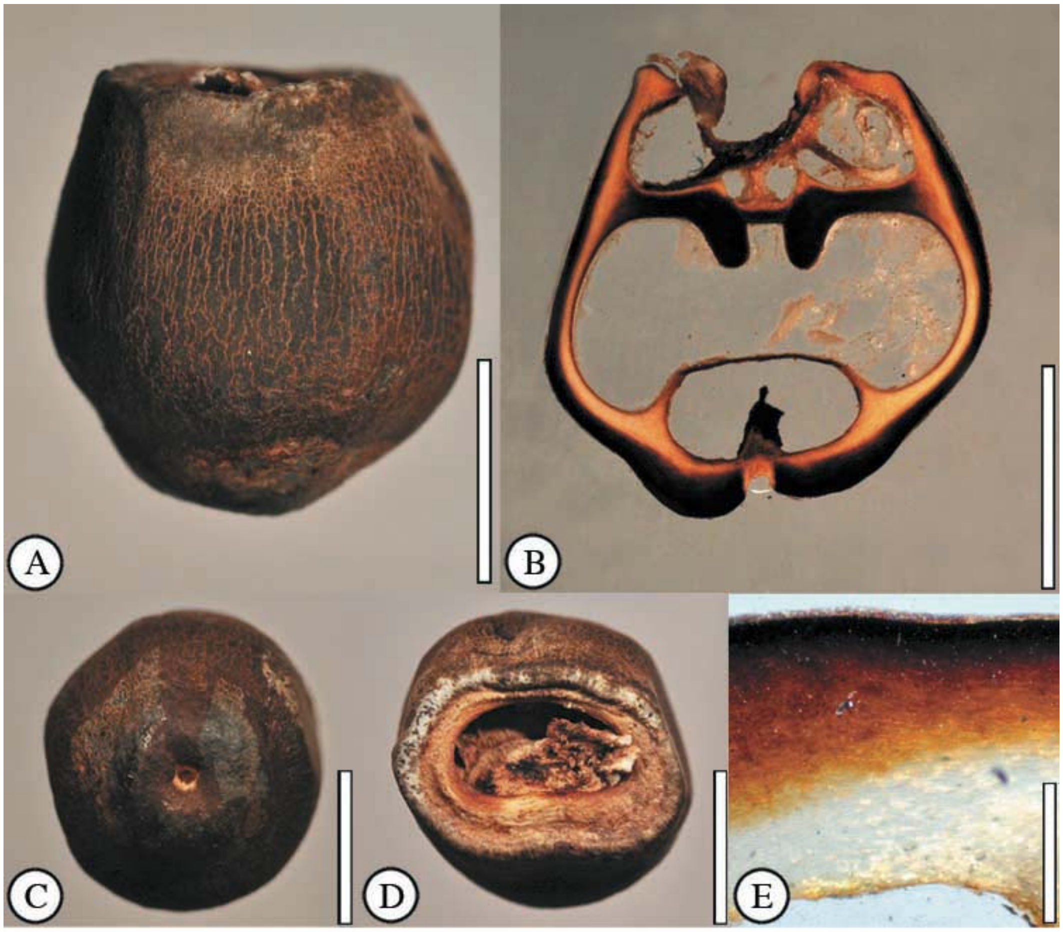


Fig. 6 Seed morphology and anatomy of *Ensete glucum* (Roxb.) Cheesman (Musaceae). A, Side view of the seed. B, Longitudinal section of the seed. Note the hilar rim extending upwards on the seed creating a "pseudochamber" above the operculum. C, A view of the base of the seed with a conspicuous dimple in the seed coat. D, A view of the top of the seed. E, A longitudinal section of the sclerified seed coat from top , dark outer integument to the lighter region. A-D scale bar = 5 mm. E scale bar = 0.5 mm

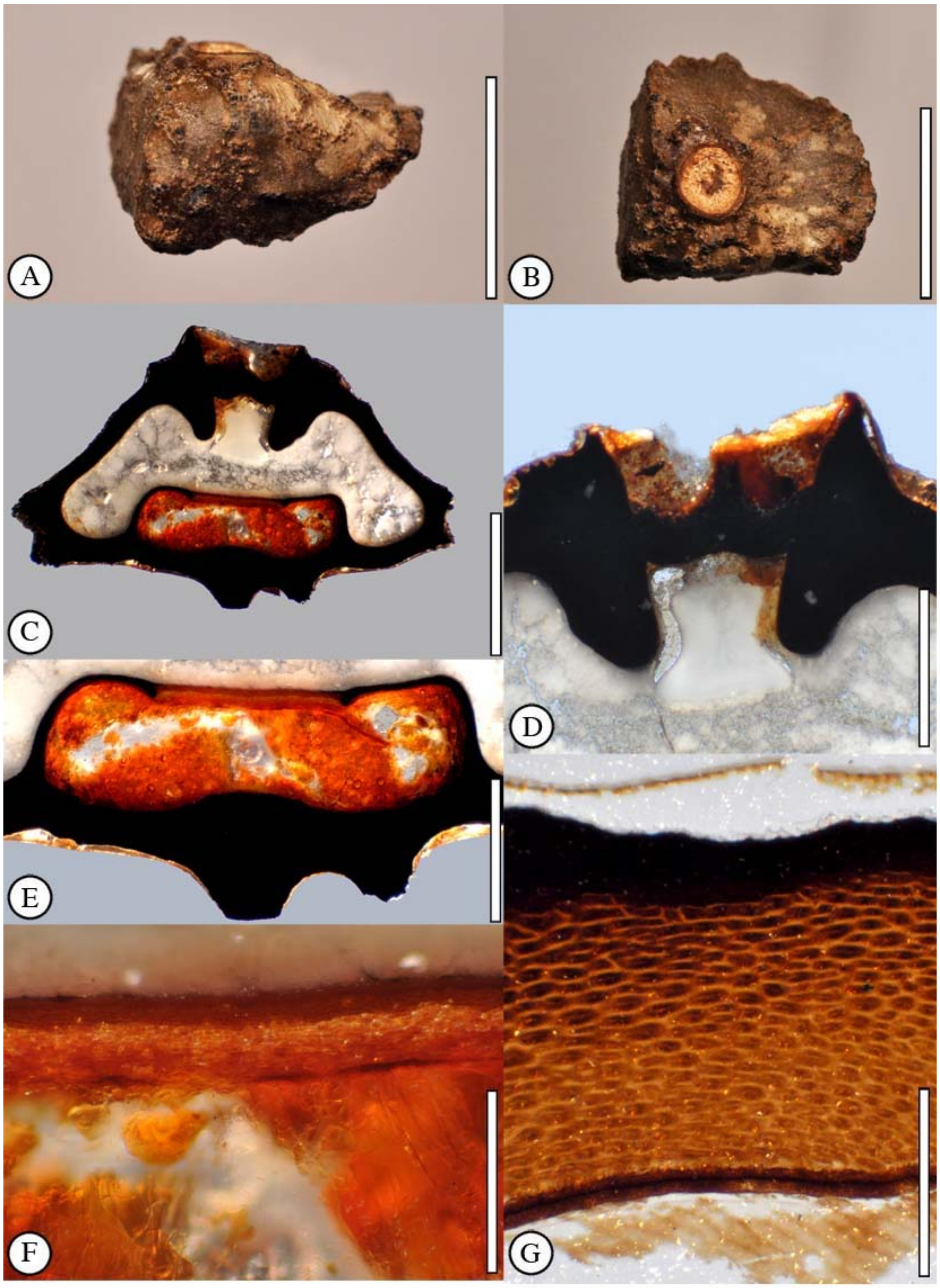


Fig. 7 Seed morphology and anatomy of *Musa sikkimensis* Kurz (Musaceae). A, Side view of the seed with B, Top view of the seed showing the operculum with light yellow trichomes nested within. C, Longitudinal section of the seed showing its internal morphology D, Detailed view of the operculum nested within the

micropylar collar. Note the small white bulbous embryo situated directly below the operculum. E, Detailed view of the chalazal chamber with orange gelatinous cells within. F, Detail of the inner and outer integuments within the chalazal chamber. G, Longitudinal section of the seed coat integumentary layers. The outer integument ranges from near black cells to the thick layer of lighter brown sclereids, round in section. Inner-most layer, two cells thick is the inner integument. A-B scale bar = 5 mm, C scale bar = 2 mm, E and D scale bar = 0.5 mm, F and G scale bar = 0.25 mm

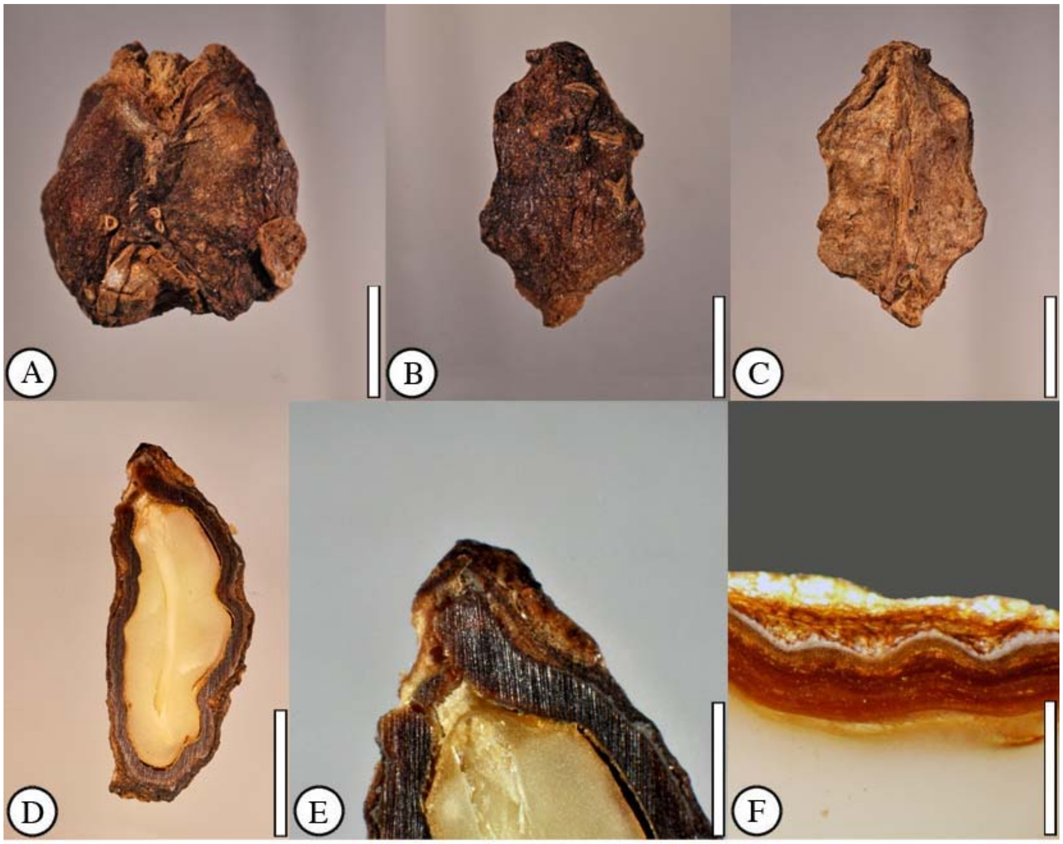


Fig. 8 Seed morphology and anatomy of *Heliconia bihai* (L.) L. (Heliconiaceae). A, Three seeded pyrene of *Heliconia*, though this specimen contains only two seeds. B, A distal view of a single pyrene relative to the axis. C, A proximal view of the pyrene relative to the axis. D, Longitudinal section of a pyrene showing the internal morphology and the elongate embryo. E, The micropylar region of the disseminule showing the endocarp originated operculum. Note striations on the surface are an artifact of preparation and not part of the seed coat. F, Detail of the fruit and seed anatomy. The outermost region is the exocarp with the mechanical layer of the disseminule derived from the endocarp. A-D scale bar = 5 mm, E scale bar = 2 mm, E scale bar = 1 mm.

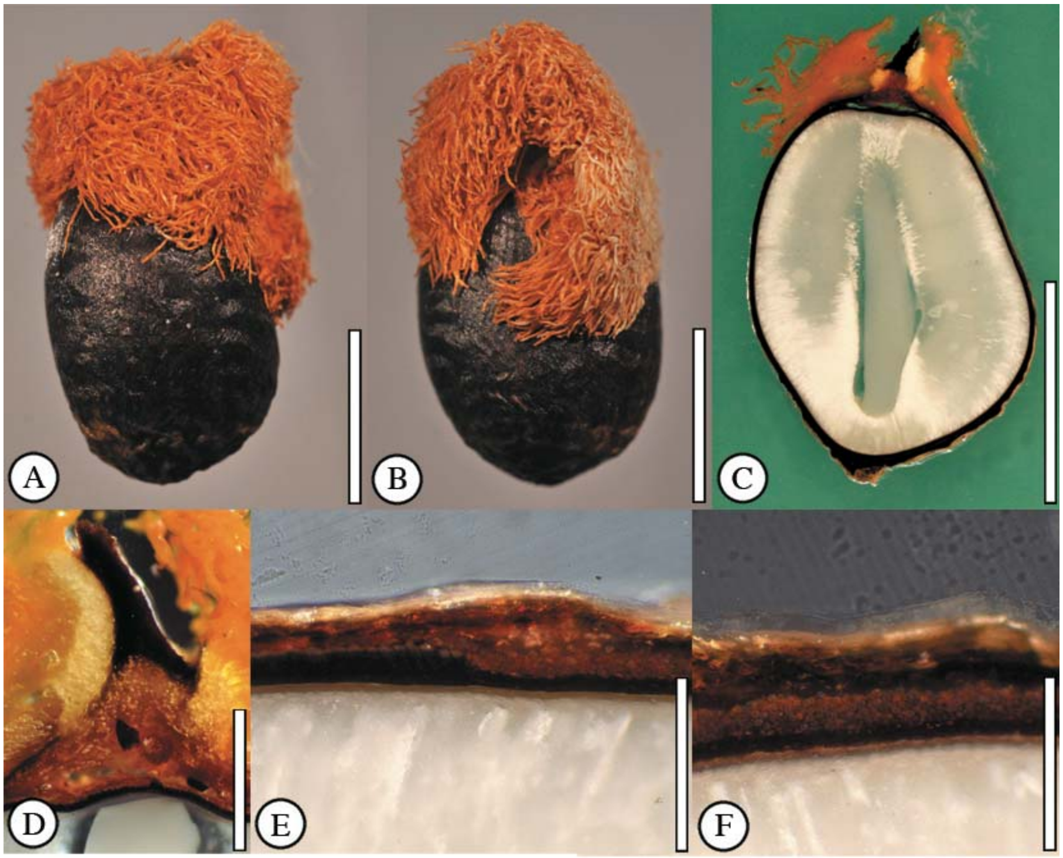


Fig. 9 Seed morphology and anatomy of *Strelitzia reginae* Aiton (Strelitziaceae). A, Overview of the seed with a prominent hair-like aril. B, A different view of the same seed. C, Longitudinal section of the seed showing the elongate embryo and rudimentary operculum. D, Detail of the operculum. E, Longitudinal section of the seed coat in the middle of the seed. F, Longitudinal section of the seed at the chalazal region. A-C scale bar = 5 mm, D scale bar = 1 mm, E and F scale bar = 0.25 mm.

Fig. 10 Seed and fruit morphology and anatomy of *Orchidantha vietnamica* (Lowiaceae). A, Overview of the triloculate capsule with one locule removed to show axile placentation of the seeds. B, Side view of a seed showing its pyriform shape, the aril (large white protrusion) and epidermal trichomes. C, SRXTM vortex image of the seed. D, SRXTM image of the seed showing the internal morphology of the seed. Note the palisade like layer of the seed lacking at its base. E, Top view of the seed showing the origin of the aril and the point of attachment of the seed to the fruit. F, SRXTM image of the seed coat showing two distinct layers. A-E scale bar = 5 mm, F scale bar = 1 mm. Images 10A, 10B, and 10E courtesy of Dr. Jana Leon-Skornickova of the Singapore Botanical Garden. Images 10D and 10F courtesy of Dr. Selena Y. Smith of the University of

Michigan, Margaret Collinson of the Royal Holloway University of London and the beamline staff Drs. Federica Marone and Julie Fife of the TOMCAT beamline, Swiss Light Source, Paul Scherrer Institute, Villigen, Switzerland.

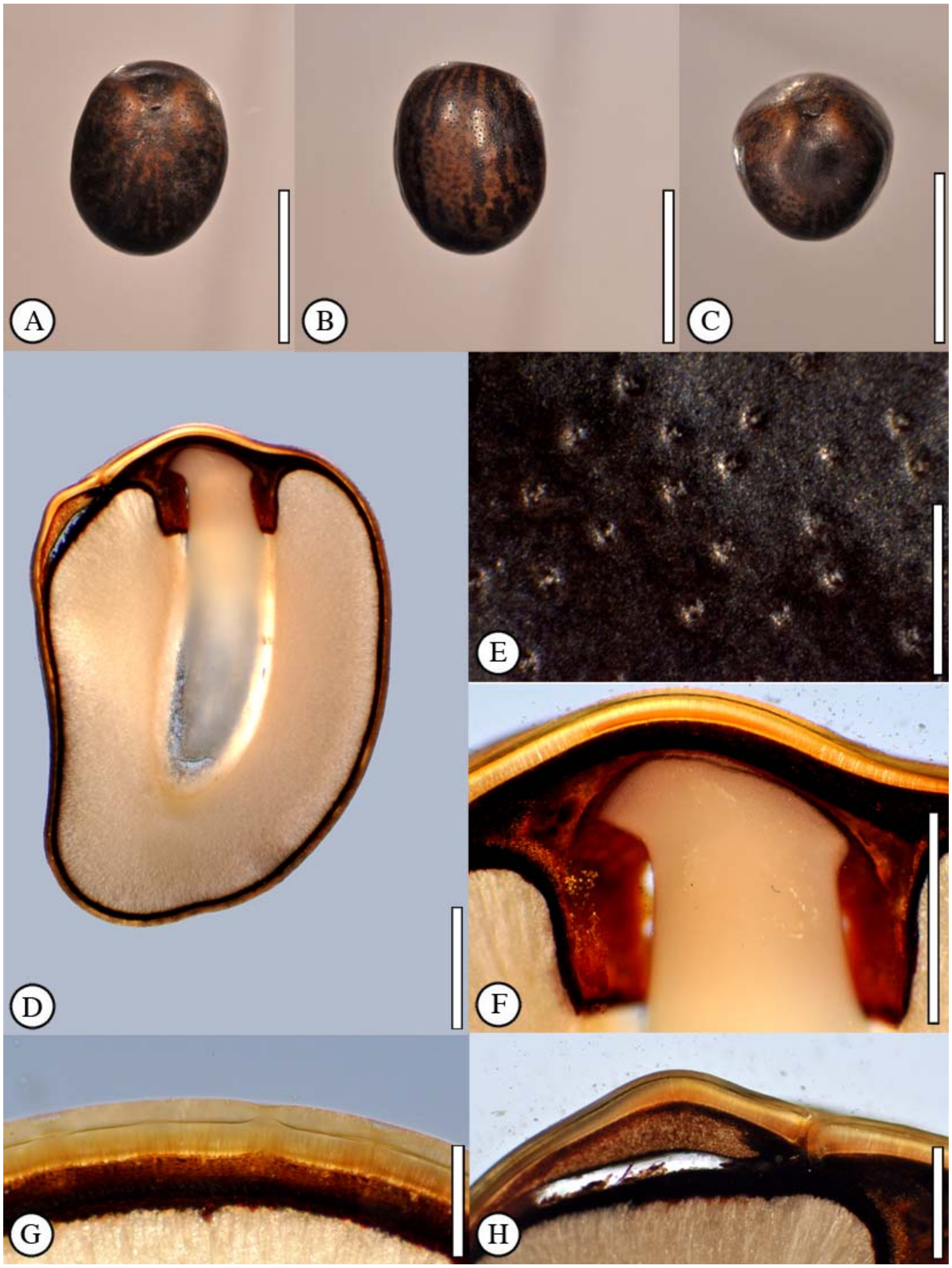


Fig. 11 Seed morphology and anatomy of *Canna paniculata* Ruiz & Pav. (Cannaceae). A, Overview of the seed showing the hilar scar. B, The other side of the seed showing the dark brown to brown camouflage. C, Apical view showing

the inhibition lid. D, Longitudinal section of the seed showing the internal morphology. E, F, G, H, I, A-C scale bar = 5 mm, D scale bar = 2 mm, E scale bar = 0.5 mm, F scale bar = 1 mm

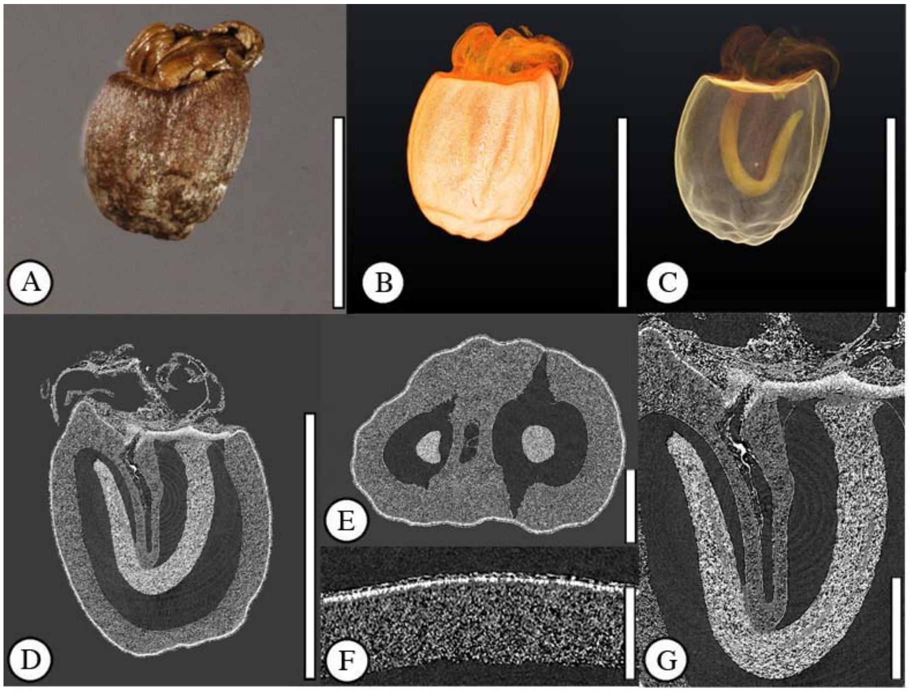


Fig. 12 Seed morphology and anatomy of *Ctenanthe lanceolata* Petersen (Marantaceae). A, Overview of the seed B, XRSTM image showing the external morphology of the seed and its aril. C, XRSTM image showing the internal morphology, in particular, the elongated embryo. D, Longitudinal section of the seed showing the elongated embryo curving around the perisperm canal. E, Transverse section of the seed showing the relative thickness of the seed coat, perisperm, and embryo. F, Transverse section of the seed coat (upper) and perisperm (lower). Note the seed coat is very thin and the perisperm is the bulk of material figured in this image. G, Detailed view of the embryo and the perisperm canal, of which the embryo is curved around. A-D scale bar = 5 mm, E and G scale bar = 1 mm, F scale bar = 0.5 mm.

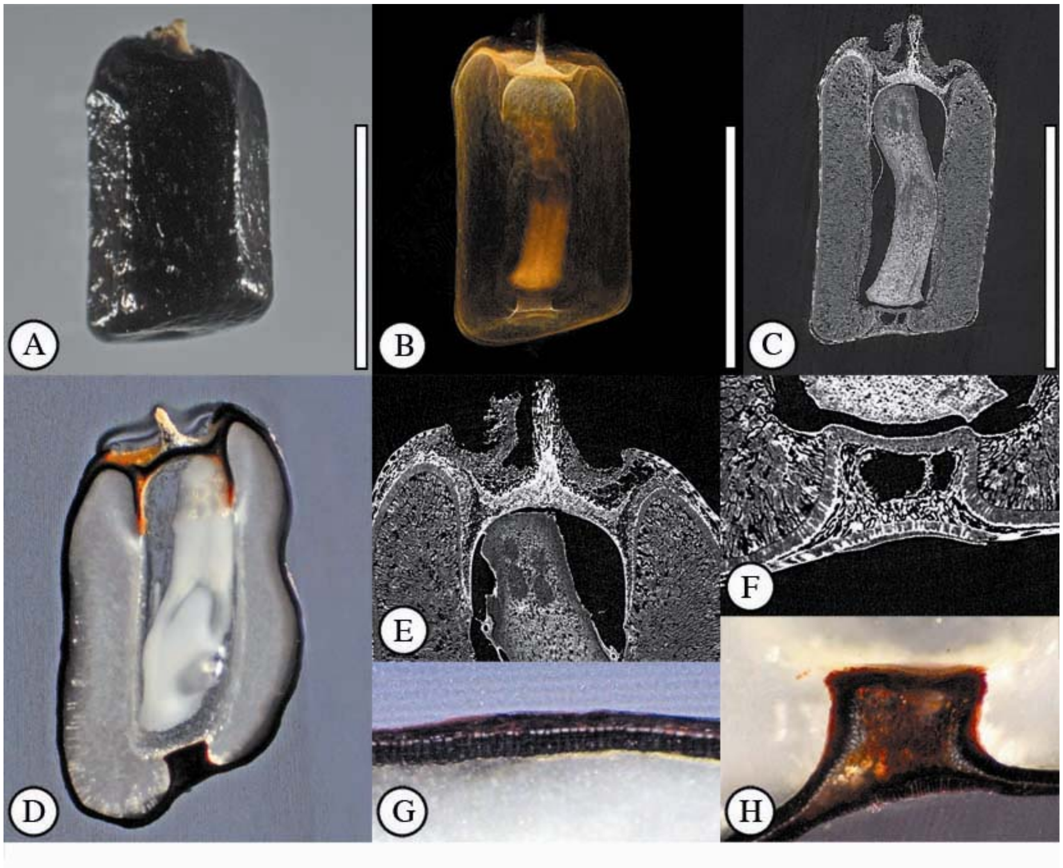


Fig. 13 Seed morphology and anatomy of *Dimerocostus argenteus* (Ruis & Pav) Maas (Costaceae). A, Overview of the seed depicting its jet black coloring and yellow operculum at the apex of the seed. B, SRTXM image showing the general morphology of the seed. Note the shape of the operculum and the cylindrical shape of the micropylar collar. C, SRTXM longitudinal reconstruction showing internal morphology of the seed and embryo. D, Longitudinal section the seed showing the internal morphology of the seed. E, Detailed view of the operculum and its shallow resting position within the seed. F, Detailed view of the hypostase of the seed. Note how the inner layer of the inner integument (Endotesta) is thickened and delimits the encroachment of the hypostase into the seed. G,

Detailed view of the composition of the seed coat. The endotestal cells are palisade like and form the mechanical layer of the seed coat. H, Detailed view of the hypostase. Note the proliferation of the mesotestal cells determine the size of the hypostase. A-D scale bar = 2 mm, E scale bar = 1 mm, F and H scale bar = 0.5 mm, G scale bar = 0.25 mm.

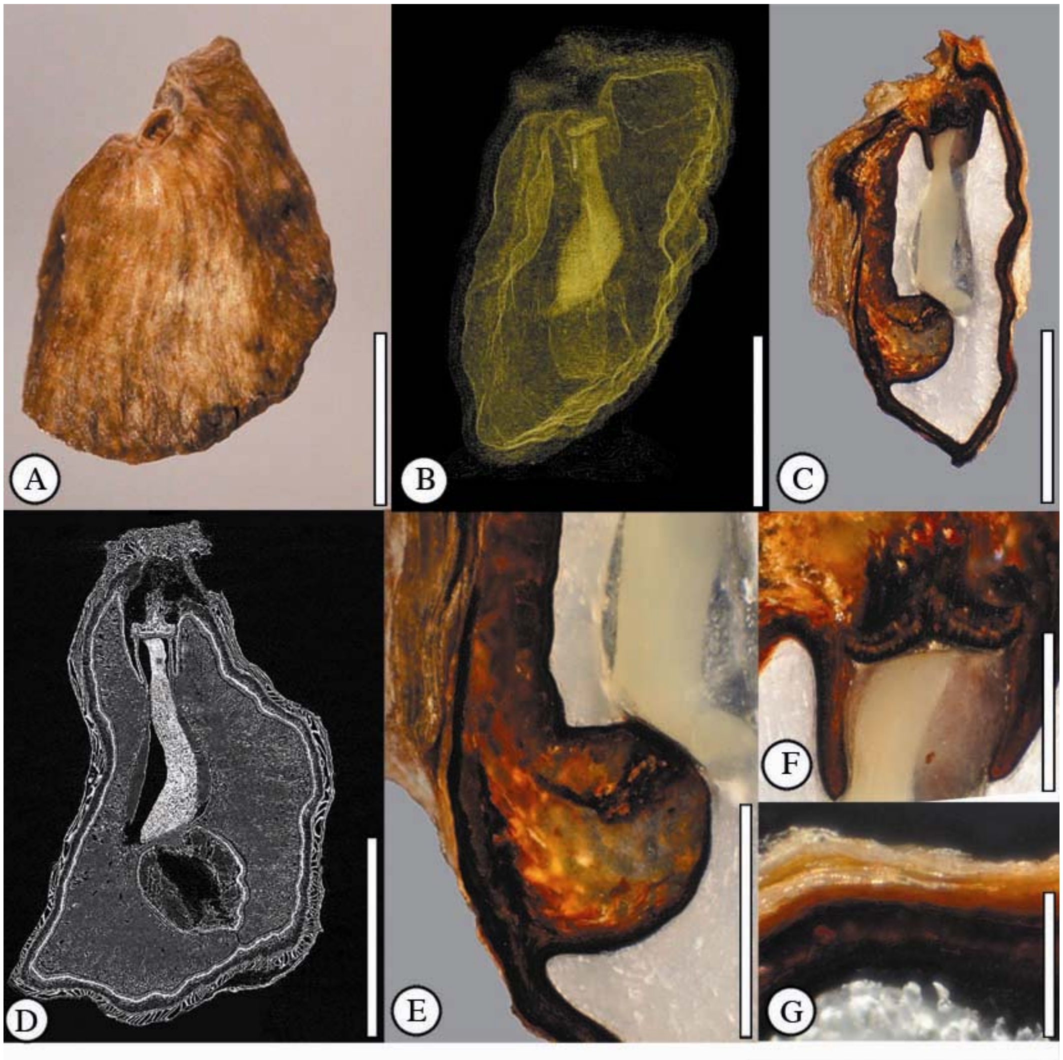


Fig. 14 Seed morphology and anatomy of *Alpinia boia* Seem. (Zingiberaceae). A, Overview of the seed showing its external morphology. B, SRXTM vortex image of the seed showing its internal and external morphology. C, Longitudinal section of the seed showing its internal morphology. D, SRXTM longitudinal reconstruction showing internal morphology. E, Detail of the hypostase derived from a proliferation of the mesotestal cells. Note how the embryo touches the seed

coat. F, Detail of the operculum nested at the top of the micropylar collar. G, Detail of the seed coat anatomy, with the outermost (Exotesta) palisade, multi layered mesotesta and a single layer of the endotesta. A-D scale bar = 2 mm, E and F scale bar = 1 mm. G scale bar = 0.25 mm.

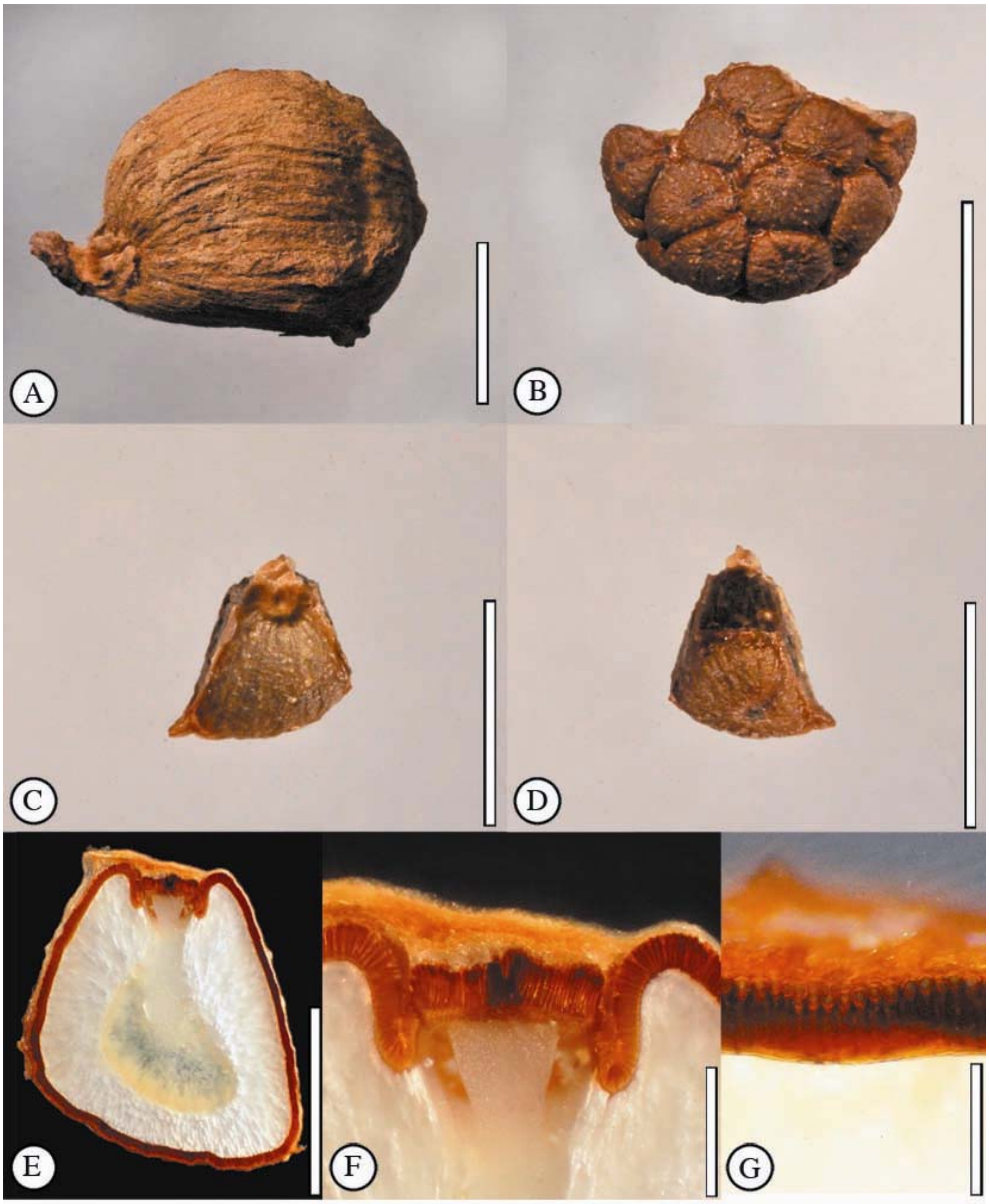


Fig. 15 Seed morphology and anatomy of *Etlingera linguiformis* (Roxb.) R.M. Smith (Zingiberaceae). A, Overview of the fruit with the base towards the right.

B, A segment of seeds removed from the fruit. Note how the seeds disperse as a single unit due to the fusion of the arils. C, Overview of the seed with the operculum pointed upwards. D, Another view of the seed. E, Longitudinal section of the seed showing internal morphology. Note embryo directly below the operculum and nested with light yellow translucent endosperm with the remaining seed in-filled with grainy perisperm. F, Detail of the operculum nested within the micropylar collar. G, Detail of the seed coat with. The palisade cells are the sclerified endotesta that make up the mechanical layer of the seed. A and B scale bar = 10 mm, C and D scale bar = 5 mm, E scale bar = 2 mm, F scale bar = 0.5 mm, G scale bar = 0.125 mm

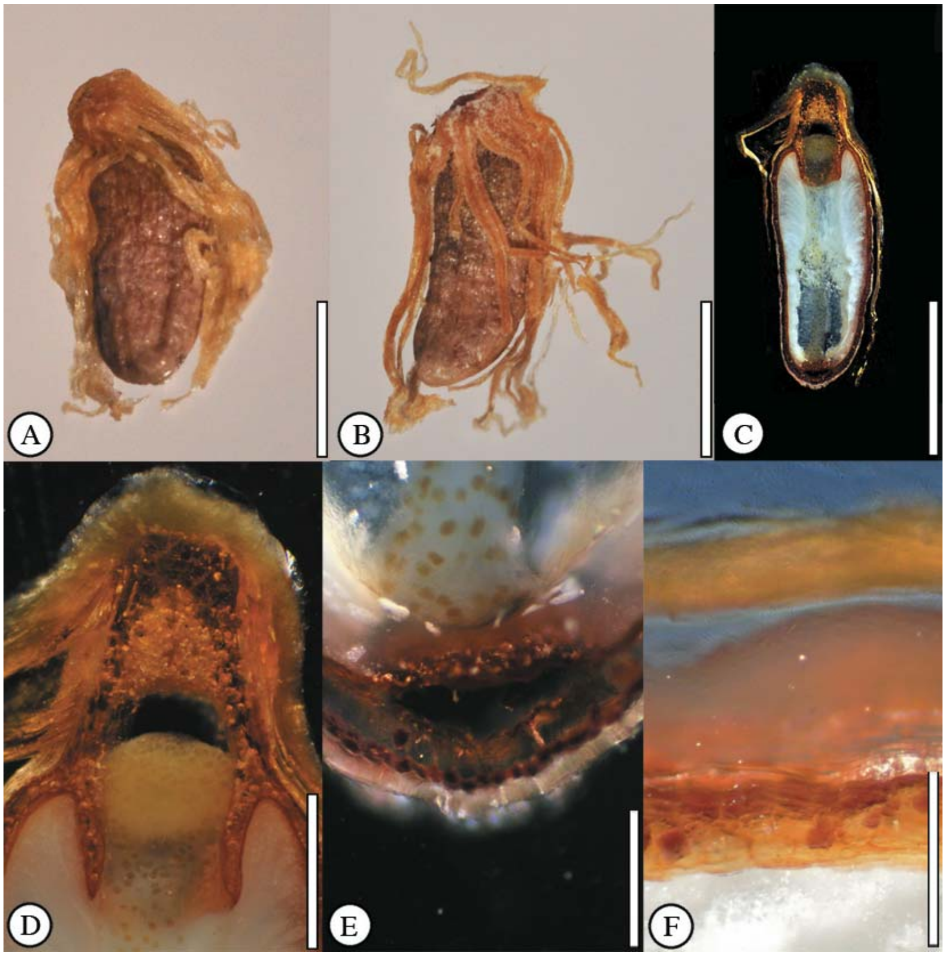


Fig. 16 Seed morphology and anatomy of *Hedychium borneense* R.M. Smith (Zingiberaceae). A, Overview of the seed with a conspicuous aril, hair-like aril. B, A different view od the same seed. C, Longitudinal section of the seed to show internal morphology. D, Detailed view of the micropylar region of the seed to show the presence of a micropylar collar and the absence of an operculum. E, Chalazal region of the seed showing pigmented cells and a gap in the mesotesta. F, Detailed view of the seed coat composition with the exotesta towards the top. A-C scale bar = 2 mm, D scale bar = 1 mm, E scale bar = 0.25, F scale bar = 0.125.

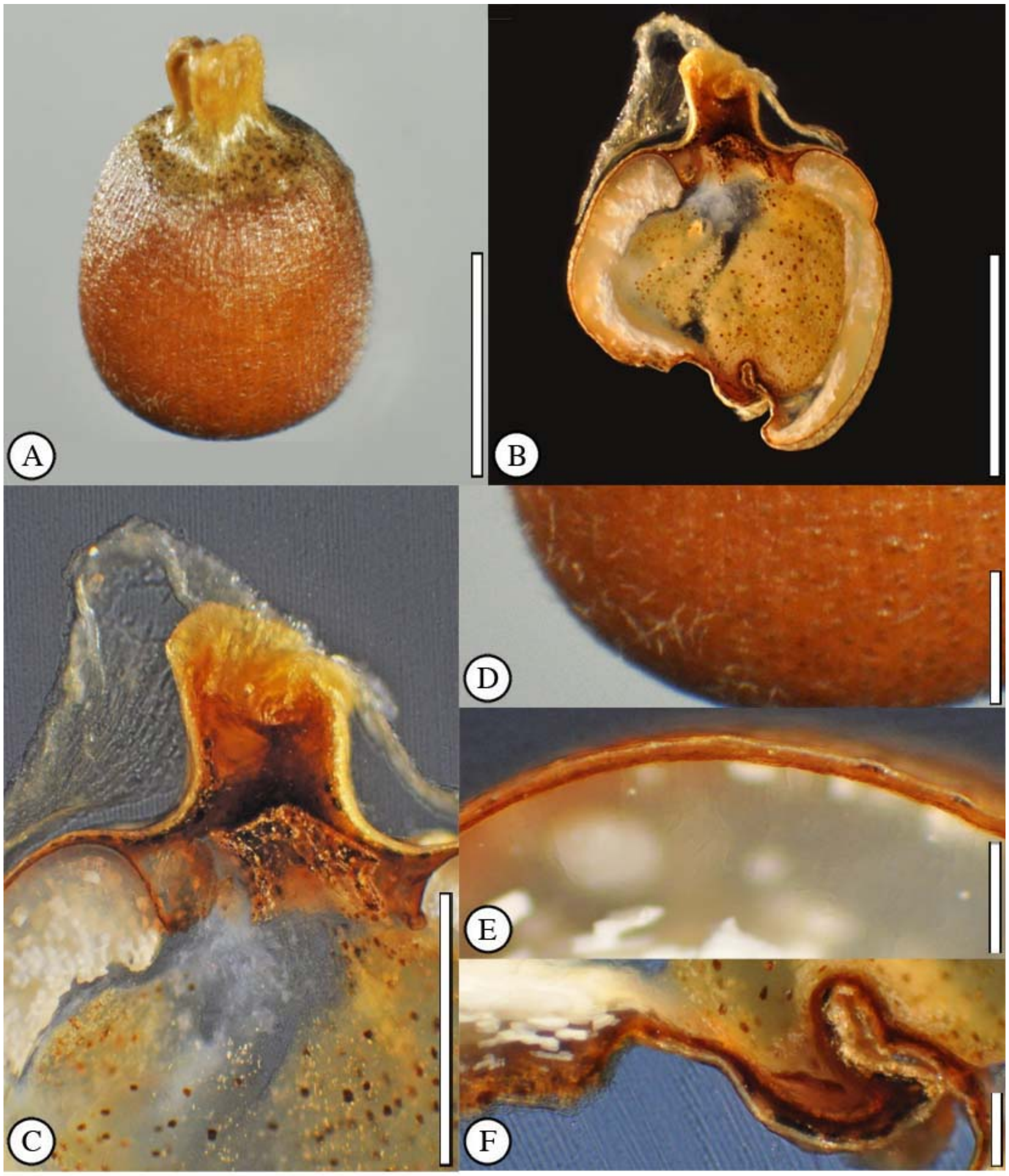


Fig. 17 Seed morphology and anatomy of *Hemiorchis* sp. Kurz (Zingiberaceae). A, Overview of the seed showing apical, carnucle-like projection and epidermal trichomes. B, Longitudinal section of the seed showing internal morphology of the seed and amorphous embryo. C, Detail of apical region of the seed showing micropylar collar and the lack on an operculum. D, Detail of the epidermal

trichomes. E, Longitudinal section of the seed coat showing its simple construction. F, Detail of the chalazal region of the seed. A and B scale bar = 2 mm, C scale bar = 1 mm, D scale bar = 0.5 mm, E scale bar = 0.125, F scale bar = 0.25.

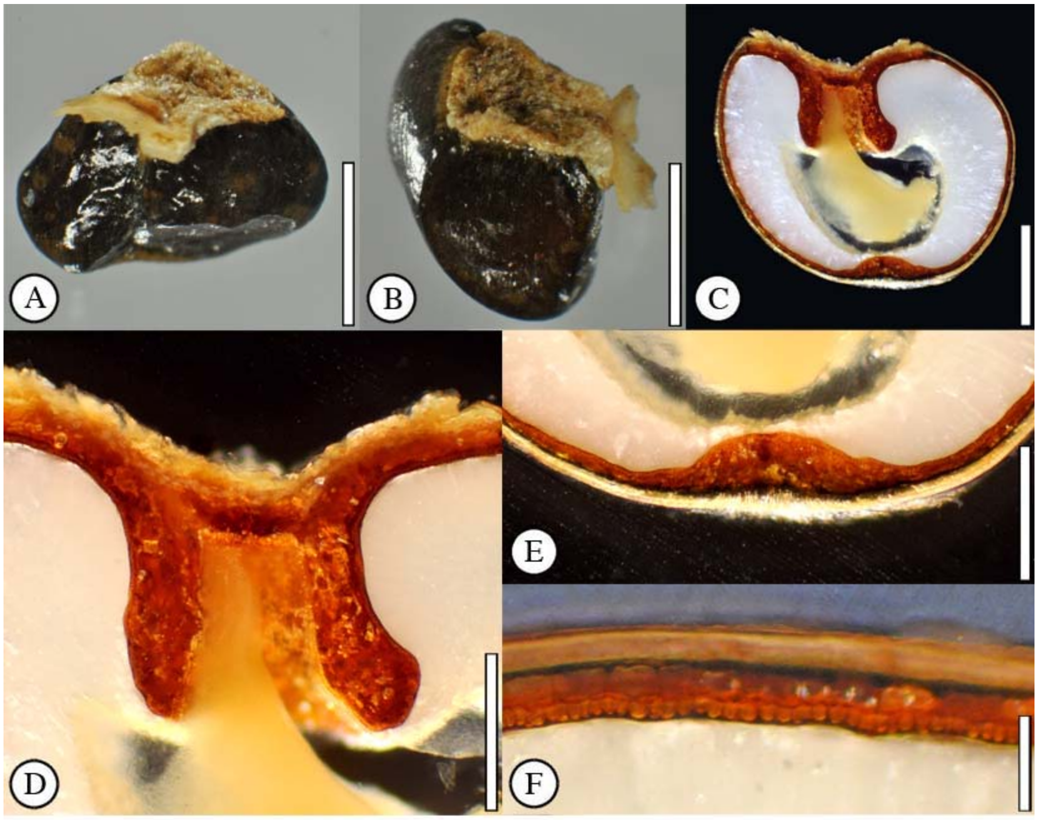


Fig. 18 Seed morphology and anatomy of *Pleuranthodium* sp. (K. Schum.) R.M. Smith (Zingiberaceae). A Overview of the seed with a partially removed aril. B, An apical view of the seed showing aril. C, Longitudinal section of the seed showing internal morphology and slightly bulbous shape of the embryo. D, Detail of the micropylar region of the seed showing the operculum and distinctly thickened micropylar collar surrounding the embryo. E, Detail of the chalazal region of the seed showing a hypostase derived from the proliferation of mesotesta cells. F, Detail of the seed coat anatomy. Note the exotesta (upper most layer), large mesotesta cells and sclerified square endotestal cells. A and B Scale bar = 2 mm, C scale bar = 1 mm, D and E scale bar = 0.5 mm, F scale bar = 0.25 mm.

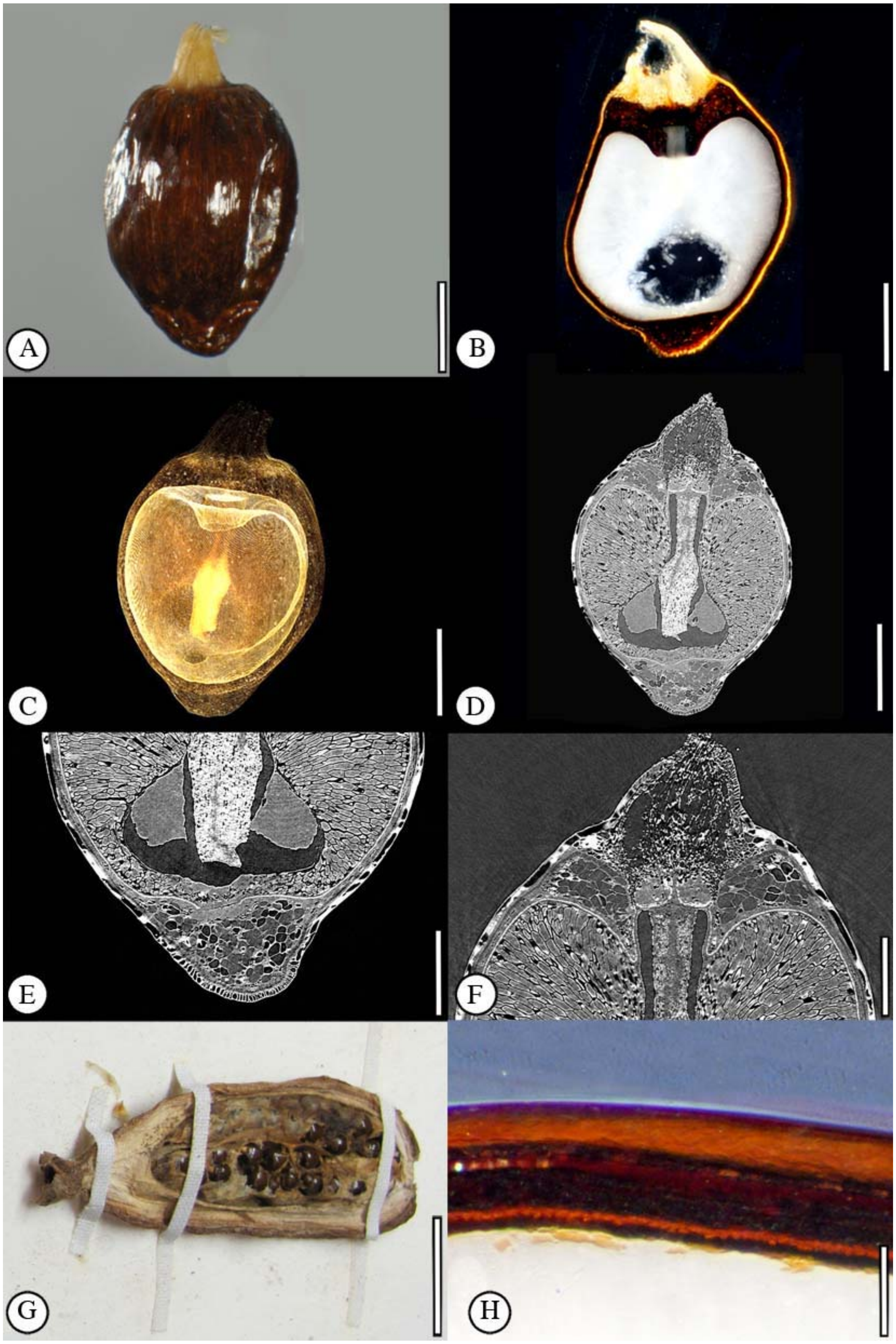

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Fig. 19 *Aframomum melegueta* seed and fruit detail. A, Overview of the seed. B, Longitudinal section of the seed. C, SRXTM image showing 3D shaped of the seed. D, SRXTM image showing internal anatomy of the seed. E, Close up of the hypostase. F, Close up of the apical thickening of the seed. G, Longitudinal section of the fruit. H, Longitudinal section of the seed coat showing the single exotesta layer, multiple mesotesta layers, and the single layer of sclerified endotesta cells. A-D scale bar = 1 mm, E and F scale bar = 0.5 mm, G scale bar = 10 mm, H scale bar = 0.675 mm.

Chapter 5

RESULTS PART I: SYSTEMATICS AND DESCRIPTION

Systematics and Description

Class—Liliopsida Cronquist, Takhtajan and Zimmerman, 1966

Order-- Zingiberales Grisebach, 1854

Family—Zingiberaceae Lindley 1835

Genus—Kressia *gen. nov. Benedict*

Type species—Kressia dakotensis *sp. nov. Benedict*

(Figs. 20A-20I, 21A-21G, 22A-22F)

Generic Diagnosis. Seeds anatropous, elongate and cylindrical with an enlarged chalazal region, operculate with a micropylar collar and exarillate. Outer surface of seed coat finely striate. Internal cavity separated into two distinct areas, the embryo cavity and chalazal chamber. Embryo cavity obovate with ellipsoid elongate embryo occupying more than half the cavity. Chalazal chamber large, separated from the embryo cavity by a septum formed from the seed coat.

Species Diagnosis. Seeds (6.5) 5 (4) mm long x (3) 2 (1) mm wide; Seed coat 0.23 mm thick in transverse section comprising three distinct layers. Outer layer one cell thick of elongate palisade cells with thickened walls, giving a spirally striate appearance to seed. In transverse section cells 0.11 mm in length and 0.02 mm wide. Middle layer up to 15 cells wide, cells isodiametric with thickened walls composed of two layers. Inner layer 0.12 mm thick, individual cells 0.01 mm in diameter. Inner seed coat diverges from outer seed coat approximately two-thirds from the micropylar region to separate the seed cavity into an embryo cavity and chalazal cavity or chalazal chamber. Septum dividing the two chambers, 4 cells thick, is derived from inner seed coat layer. The chalazal cavity comprises isodiametric thin walled cells 0.03 mm in diameter.

Prior Citation. "Clavate structure" Crane PR, SR Manchester and DL Dilcher 1990. Fieldiana Geology New Series, No. 20 Publication 1418. p. 41-43; Fig. 26D-F.

Type locality. Near Beicegel Creek, McKenzie County, North Dakota (Pigg and DeVore 2010).

Stratigraphy. Williston Basin, Sentinel Butte Formation

Age. Late Paleocene (~57 Ma), Tiffanian 3 (NALMA), Pollen zone 5 (Nicholas and Ott 1979; Kihm and Hartman 1991; Manchester et al. 2004)

Holotype. (figs. 21-22).

Etymology. The generic name *Kressia* is in honor of W. John Kress in recognition of his considerable efforts in understanding the relationships within and evolution of the Zingiberales. The specific epithet, *dakotensis*, refers to the occurrence in North Dakota, USA.

Description of Kressia dakotensis**.** The description of *Kressia dakotensis* is based on around 200 specimens, 60 of which are known from complete surface fractures (fig. 20A-F, 20I) and 12 from anatomically from cellulose acetate peels preparations showing internal cellular structure (fig. 20G, 20H, fig. 21, fig. 22). The most complete specimen shows a partially preserved operculum, and a demarcation within the embryo cavity that corresponds to the general shape of the embryo (fig. 23A).

External Morphology. Seeds are elliptical-elongate and distinctly spirally striate with an expanded chalazal region and tapering toward the micropylar end. Seeds are mostly radially symmetric on their long axis, though oftentimes the seed coat is compressed in the chalazal region (fig. 21C, 21E). At the micropylar end the operculum is triangular and nested within the seed coat when it is still attached to the seed. When preserved the operculum is tightly compressed against the inner seed coat, although both tissues are readily distinguishable. The septum separating the embryo cavity from the chalazal region can be seen in both surface fractures (fig. 20A-F) and serial sections (fig. 20G-H) and differentiates the large mass of cells in the chalazal region from the embryo cavity, which is often infilled with silica. Centrally located within the locule apical to the septum is a collection of cells that produce a circular impression or dimple on the embryonic cavity (fig 20I).

Internal Anatomy. The most recognizable feature of the seed is the spirally striate texture derived from the single layer of the outer seed coat (fig. 22D-3F). This single layer of palisade cells is 0.11 mm thick and 0.02 wide in transverse section and comprises half of the total width of the seed coat (fig. 22D-22F). The inner seed coat is 15 cells thick at it widest part and 0.12 mm in width (fig. 22D-22F).

The cells of the inner seed coat are isodiametric to spherical in shape and are 0.01 mm in diameter (fig. 22D-22F).

The seed coat is unevenly thickened as a result of differing numbers of cells in the inner seed coat layer. The inner seed coat is thinnest at the micropylar region where it is in direct contact with the operculum (fig. 20H, 21B, 21E-21G). As the operculum narrows, the inner seed coat increases in thickness to a maximum of approximately 14 cells (fig 21B, 21E). Approximately half way through the embryo cavity the inner seed coat thins again as the embryonic cavity enlarges to a light-bulb shaped structure (fig. 21E). As the embryo cavity tapers the innermost layer of the inner seed coat separates into the septum that delimits the embryo cavity from the mass of chalazal cells (fig 22G). The chalazal region comprises large isodiametric cells that are approximately 0.03 mm in diameter (fig 22E-22F, 22H). These cells are nested in between the inner most layer of the inner seed coat and the outer inner layer of the seed coat. At the chalazal region of the seed, the outer layer of the inner seed coat is approximately 0.08 mm thick and comprises roughly 10 cells. These cells range in size with the largest towards the outer seed coat and become quite small just before the transition into the chalazal region cells. They are highly sclerified with reticulate secondary wall thickenings (fig. 22H).

Systematics and Description

Class—Liliopsida Cronquist, Takhtajan and Zimmerman, 1966

Order-- Zingiberales Grisebach, 1854

Family—Zingiberaceae Lindley, 1835

Genus—Zingiberopsis Hickey, 1977

Type species—Zingiberopsis hickeyi *Benedict sp. nov.* (Figs. 23A, 23C-23F)

Species diagnosis. Leaves with strongly pinnate venation with veins of close spacing and equal vein width. Transverse vein spacing farther than parallel veins and only connecting two adjacent parallel veins. Both sets of veins produce distinctly rectangular "box" patterning to fossils. Epidermal cells minute and rectangular and in the same orientation of the "box" pattern produced by the veins. Epidermal cells 0.03 mm wide and 0.10 mm long. Stomata tetracytic, infrequent and sporadically distributed throughout the epidermis. Stomatal pore 0.018 mm wide and 0.030 mm long. Guard cells two and equal. Each stoma subtended by a pair of lateral subsidiary cells.

Prior Citation. "Monocotyledonous Leaf Fragments" Crane PR, SR Manchester and DL Dilcher 1990. Fieldiana Geology New Series, No. 20 Publication 1418. p. 44-47; Fig. 29A-B.

Type locality. Near Beicegel Creek, McKenzie County, North Dakota (Pigg and DeVore 2010).

Stratigraphy. Williston Basin, Sentinel Butte Formation

Age. Late Paleocene (~57 Ma), Tiffanian 3 (NALMA), Pollen zone 5

(Nicholas and Ott 1979)

Holotype. (fig. 23A, 23C-23F).

Etymology. The specific epithet, *hickeyi*, is in honor of Leo J. Hickey for his work on Zingiberales leaves and documenting characters that can be used to identify fossil leaves to the order.

Description of Zingiberopsis hickeyi. The description of *Zingiberopsis hickeyi* is based on observations from 12 specimens, of which one specimen was discovered to have epidermal cells including stomata preserved. The venation pattern of *Z. hickeyi* is uniformly pinnate with spaces between parallel veins measuring 0.5 mm. Veins transverse to the parallel veins are approximately 2.0 mm apart producing the characteristic box pattern seen in the fossil leaves from surface fractures (Fig 23D). Epidermal cells are small and rectangular, 0.03 mm wide and 0.100 mm long, and are oriented in the same manner as the boxes produced by the veins. Stomata are surrounded by two subsidiary cells, roughly the same crescent shape as the guard cells do not fully surround the stomata leaving the terminal ends exposed.

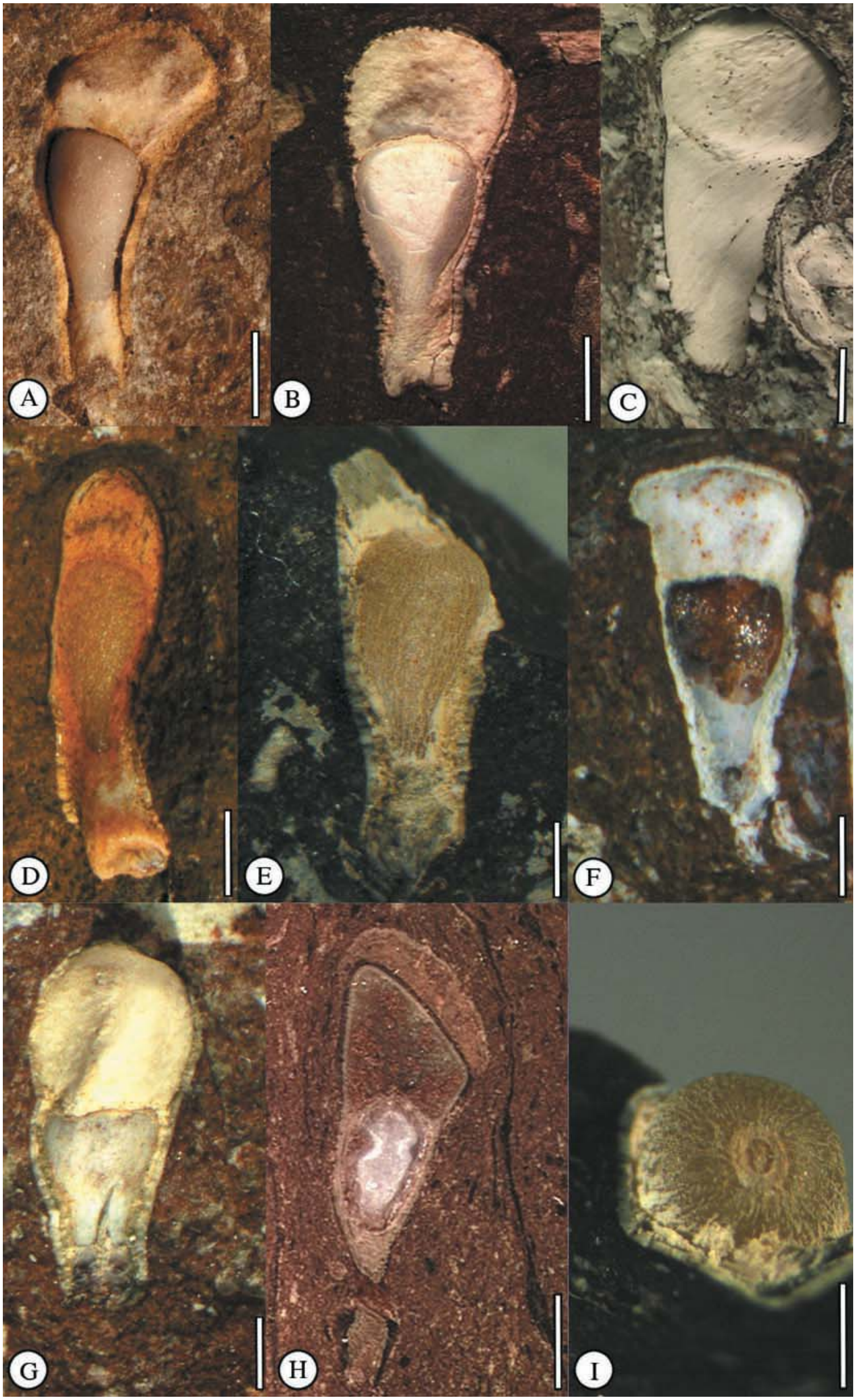
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Fig. 20 *Kressia dakotensis* general seed overview. A, Surface fracture of the Almont specimen figured in Crane et al. 1990. B, Surface fracture of specimen from Beicegel Creek. C, Surface fracture showing outermost spirally striate layer of the seed coat. D, Surface fracture showing an intact operculum at the base. E, Surface fracture showing "light bulb" shape of the embryo cavity. F, Surface fracture with white chalazal region and mud filled embryo cavity. G, Longitudinal section of a specimen showing general internal morphology. H, Longitudinal section of a specimen detailing internal morphology of the seed. I, Close up view of the chalazal region of 20E showing a chalazal scar on the embryo cavity. Scale bar = 1 mm

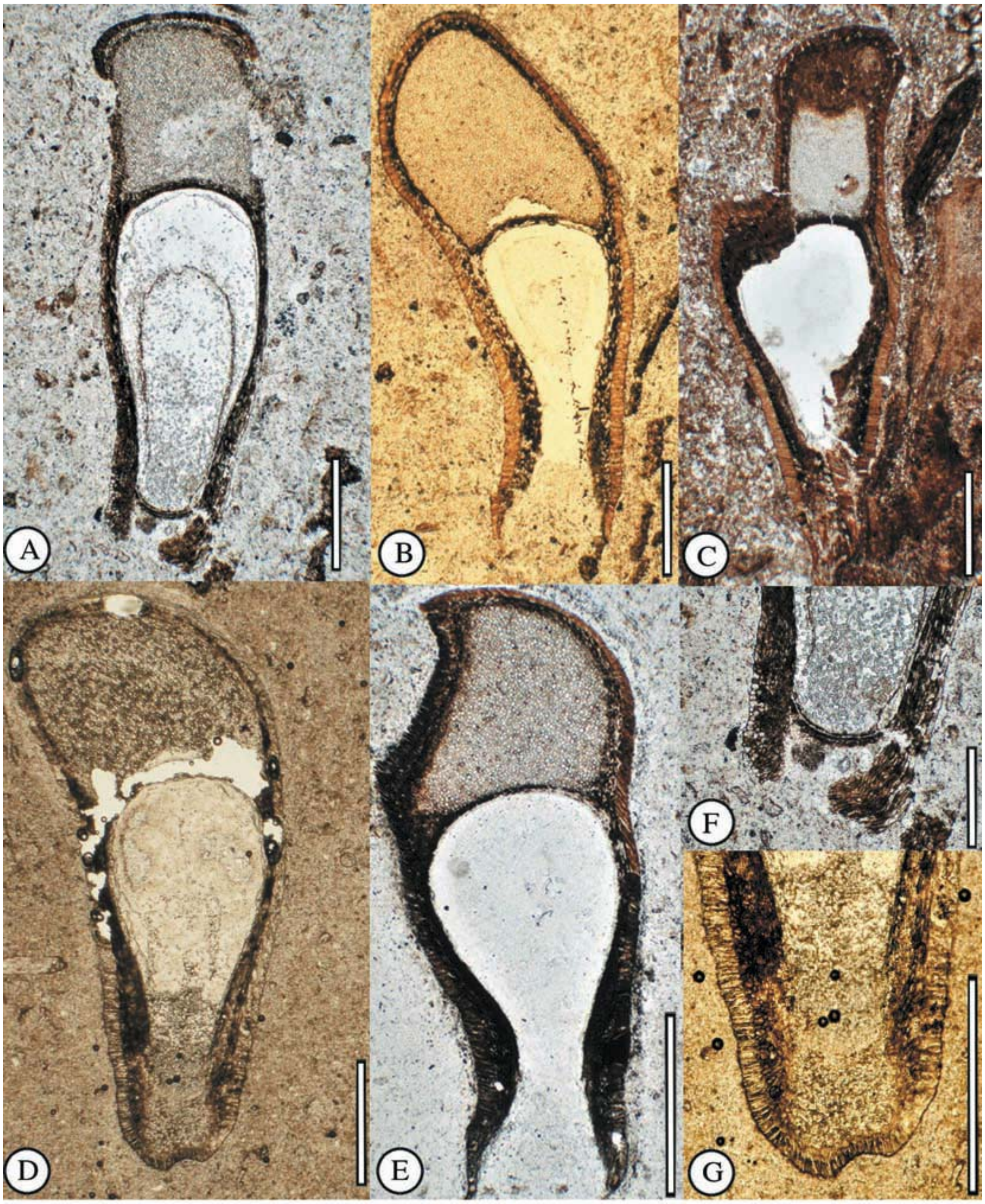

Fig. 21 Internal Anatomy of *Kressia dakotensis*. A, Longitudinal section of the seed showing internal morphology and an outline of the embryo. B, Longitudinal section of the seed showing internal morphology. Note a slight degradation of the

cells within the chalazal region. C, Longitudinal section of a specimen that is slightly contorted. D, Longitudinal section of a seed with an intact operculum. E, Longitudinal section of a seed showing a slightly contorted chalazal region. F, Close up view of the micropylar region of the seed in 21A showing remnants of the operculum. G, Close up of the micropylar region of the seed in 21D showing an intact operculum. A-E scale bar = 1 mm, F-and G scale bar = 0.5 mm.

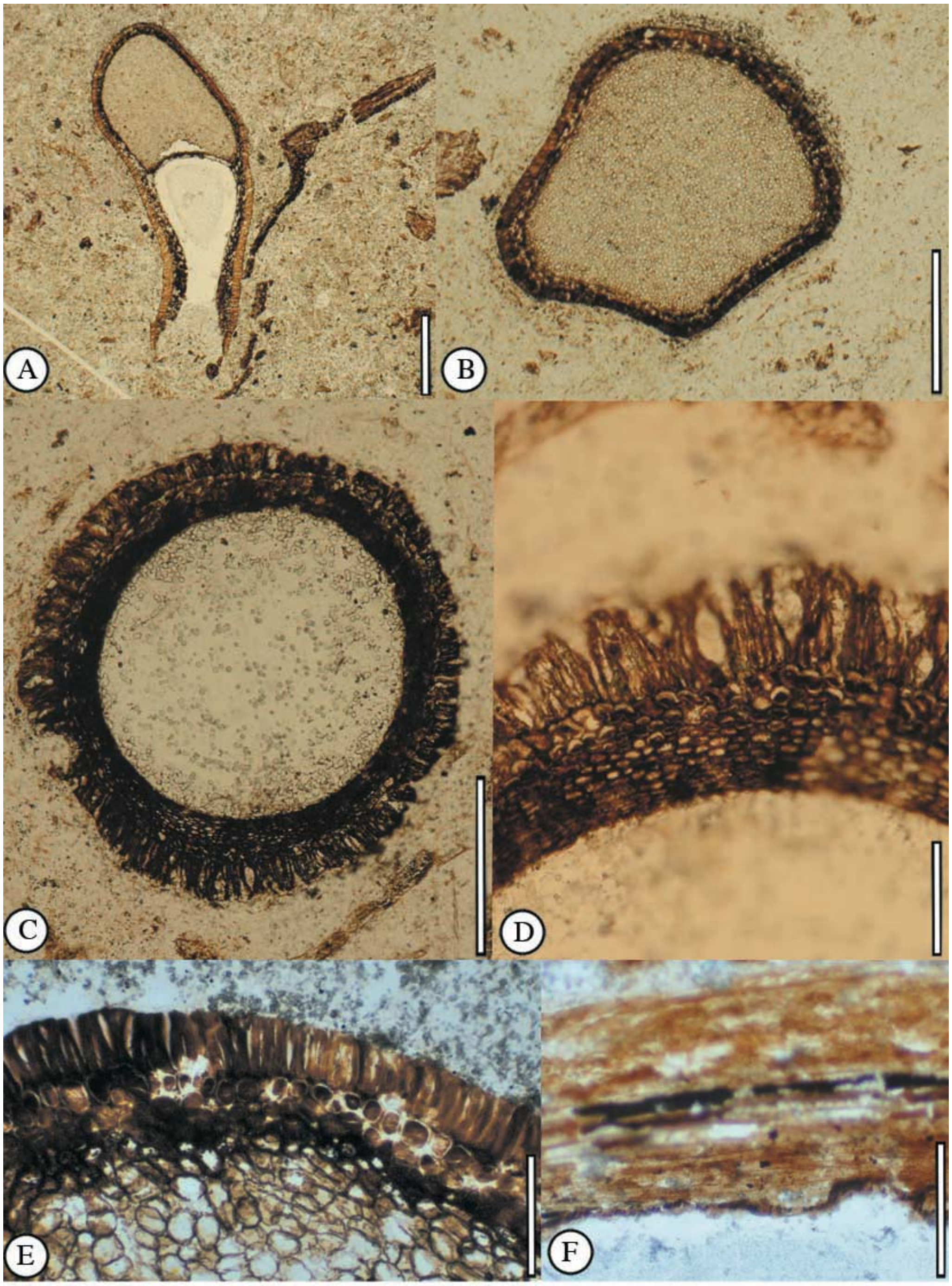

Fig. 22 Seed Coat Composition of *Kressia dakotensis.* A, Longitudinal section of the seed showing internal morphology. B, Cross section of the seed in the chalazal region through the parenchymatous chalazal cells. C, Cross section of

the seed showing the three layers of the seed coat near the micropylar region of the seed. D, Detail of the three layers of the seed coat with the outermost layer of palisade cells at the top of the image. E, Detail of the three layers of the seed coat within the chalazal region with the outermost layer of palisade cells at the top of the image. F, Detail of inner-most layer of the seed coat with the inner most layer on the bottom of the image and contain dark substances. A-C scale bar = 1 mm, D scale bar = 0.11 mm, E scale bar = 0.20, F scale bar = 0.25 mm.

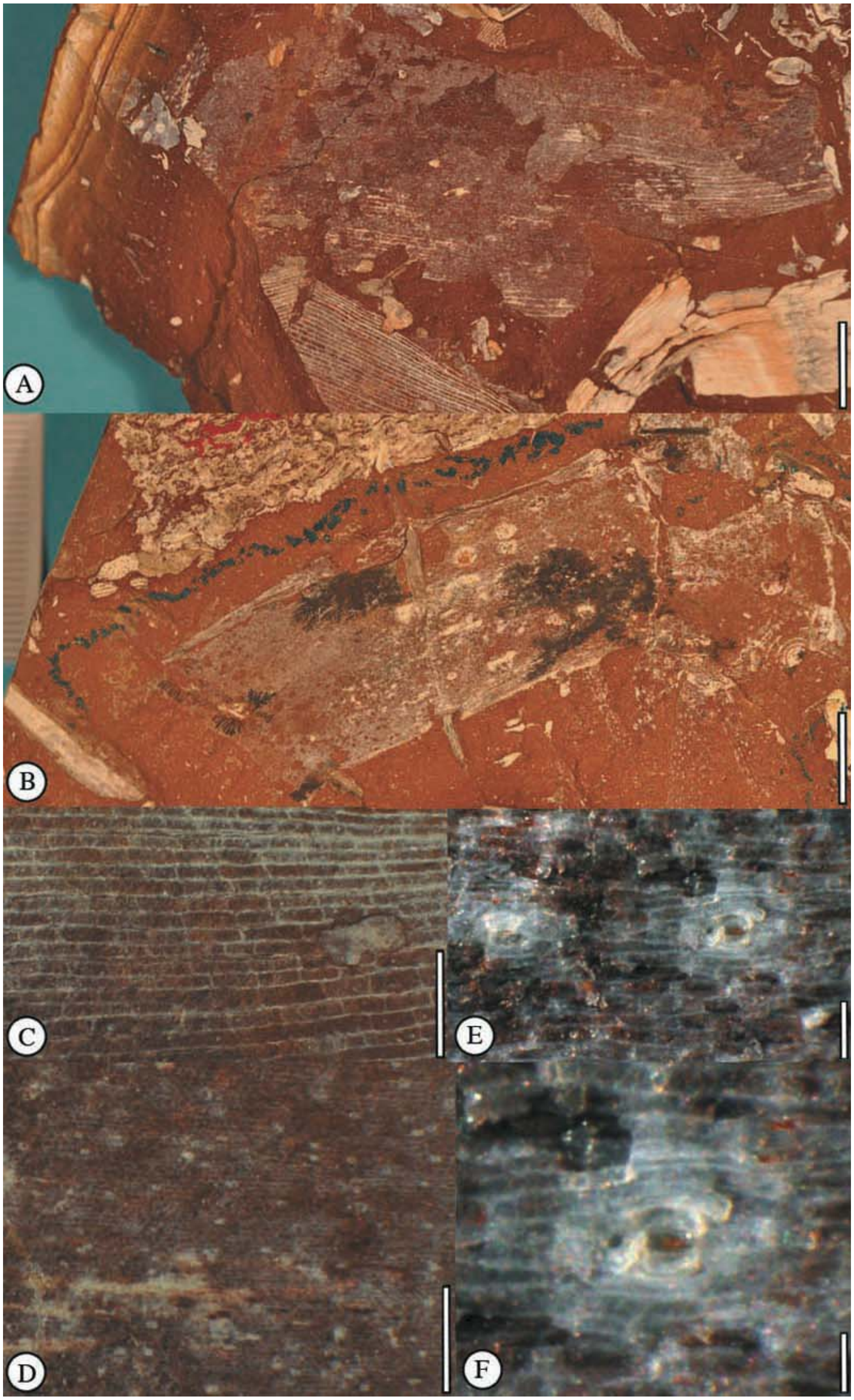
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Fig. 23 *Zingiberopsis hickeyi* leaf overview and stomata. A-B, Overview of leaf fragments from surface fractures. C, Detail of 23A showing characteristic parallel venation patterns of the leaf. D, Another close up of a different region of 23A showing rectangular epidermal cells and guard cells of the leaf. E, Details of the epidermal cells and two stomata of 23A. F, A single stoma showing the lip shaped guard cells and subsidiary cells. A and B scale bar = 10 mm, C and D scale bar = 1 mm, E scale bar 40 mm, F scale bar 0.20 mm.

CHAPTER 6

DISCUSSION

The fossil record of Zingiberales is well represented by both vegetative and reproductive material spanning the late Cretaceous to Neogene in both Americas as well as Eurasia (Fischer et al. 2009). Although these fossils are well documented, many have been attributed only to ordinal status, as a lack of complete sampling of extant members has limited the comparative material needed for strong correlations. In addition, the wide variation among authors in use of different terms for each of the various character states and anatomical descriptions has also increased the difficulty of relating these characters to those seen in well-preserved fossils. In order to address the relationships of the fossils with their extant relatives, a broad survey of extant zingiberalean fruits and seeds was undertaken and the resulting data were used to recognize trends within the extant groups as well as addressing the taxonomic affinities of the fossil Zingiberales fruits and seeds. Of these characters, the presence of an operculum, micropylar and chalazal thickenings and the composition of the integuments are the most reliable characters for determining the affinities of the fossil plants.

The Taxonomic Placement of *Kressia dakotensis*

The genus *Kressia dakotensis* Benedict gen. et sp. nov. is a distinct taxon that clearly belongs to the Zingiberales based on the presence of an operculum, the composition of the seed coat, details of the micropylar and chalazal regions and its close similarity with other fossil members of the order. These other fossils that have been assigned to the order are similar to one another in all being triloculate (e.g. *Spirematospermum*, *Striatornata*), however fruits have not been recovered for *Kressia*. Within the order, *Kressia dakotensis* is most closely allied to members of the family Zingiberaceae on the basis of seed coat characters, the presence of a hypostase, and shape of the embryo and operculum.

The Operculum. Operculate seeds are found in Musaceae, Lowiaceae, Costaceae, most Zingiberaceae and Marantaceae. (Within Zingiberaceae, some are nonfunctional or absent in some derived members of Zingiberoideae, e.g., *Hedychium*). The operculum of *Kressia dakotensis* is present and considered functional due to its full development in the seed and often is seen already dehisced in many of the seeds observed (figs. 21D, F, G). The operculum is basally flared, tapers apically, and is situated within the tube formed by the seed coat at the point where the seed coat is widest. The shape of the operculum, coupled with its relative sunken position within the seed coat are similar attributes to members of Costaceae and some members of Zingiberaceae (fig. 24). In contrast, opercula in Musaceae, Lowiaceae and Marantaceae tend to rest on the periphery of the seed coat and are not embedded in the seed (fig. 24).

The Chalazal Region. The variations of thickenings of the chalazal region in fossil Zingiberales is one of the largest points of contention with respect to the taxonomic placement of fossil Zingiberales within either the Musaceae or Zingiberaceae. Its development and composition have been carefully studied in order to understand the relationships of the fossils to living members. In

Marantaceae the chalazal region of the seed is characterized initially by a proliferation of cells, which then disintegrate to form the perisperm canal (fig. 12). During development the embryo folds in on itself and the seed becomes contorted, such that in mature seeds the perisperm canal is situated at the micropylar region of the seed (Grootjen 1981). In Musaceae the chalazal region is modified into a structure called the chalazal chamber, that is unique among the order by being formed multiple layers derived from both outer and inner integuments and raphe tissue (Bouharmont 1963; McGahan 1961a, fig. 12). It is a very robust structure in the seed that produces gelatinous cells or an acellular mass of tissue, which may be slightly bifurcated by a conspicuous invagination of sclerenchymatous cells of the mesotesta (fig. 12).

In the closely allied families Costaceae and Zingiberaceae, the chalazal modification, termed a hypostase, is derived from the proliferation of mesotestal cells to produce a uniform mass of cells (fig. 12). This structure can be either oriented symmetrically at the chalazal region or protruding out of one side of the seed, creating an asymmetrical shape to the seed coat in relatively few Zingiberaceae (e.g. *Alpinia boia,* fig. 11C-D). Symmetrically oriented hypostases can range from being disk shaped, to a disjointed group of cells (termed “trumpet shaped” in Liao and Wu 2000).

The chalazal structure in *K. dakotensis* is symmetric. It is characterized by a simple proliferation of isodiametric cells within the middle layer of the seed coat, creating a dome-shaped region (fig. 20). This structure is most similar to the symmetrical hypostase seen in Costaceae and Zingiberaceae, which are derived from a single layer of cells (the middle layer, presumably the mesotesta) at the chalazal region.

The Seed Coat. Within families with operculate seeds (Musaceae, Lowiaceae, Costaceae, Zingiberaceae and Marantaceae), the composition of the outer integument is quite variable. It ranges from highly reduced to a single layer (Heliconiaceae), to very thick and uniform (as in Musaceae), to a variety of other types of compositions (Zingiberaceae, figs. 26-29).

In Musaceae the seed coat is quite complex and derived from both the outer and inner integumentary layers to produce a tough seed coat more than 30 cells thick and comprised of three unique layers. In *Musa*, the exotesta comprises irregularly shaped sclereids that are disproportionately distributed along the seed coat, creating a warted or bumpy appearance in some members. In *Musa balbisiana* another layer occurs, comprising one or two cells and termed the “multiluminate sclereids”, though these were not seen in *M. textilis* or *M. peekelii* (figs. 7, 27). The mesotesta is the thickest layer of between 20 and 30 cells and comprises macrosclereids that are relatively uniform in shape. The endotesta is a single layer of square sclereids and is separated from the inner integument by a thin cuticle. The inner integument is composed of two layers of rectangular cell and surrounds the embryo cavity. In *Ensete*, the seed coat is of similar design to *Musa.* In both of these genera the bulk of the seed coat is made up of mestotesa (approximately 50+ cells thick), but the exotesta is seemingly reduced to a single layer of papillate cells (Jain 1961), an endotesta of a single layer of round macrosclereids, and an inner integument comprising two layers that are pigmented a faint brown and fill the central region of the septum that separates the chalazal chamber from the embryo. The layers of the cells described here for *Ensete* are preliminary as a developmental sequence of *Ensete* has not been observed and may have be misinterpreted by the author due to the lack of similarity with the seed coat in *Musa*.

The anatomy of the seed coats of Costaceae and Zingiberaceae differ significantly from Musaceae in being composed solely of the outer integument in mature seeds (fig. 27, 28). The two families can be distinguished easily from each other by the relative thickness of the outer integumentary layers, which function as the mechanical or protective layer of the seed coat. In Costaceae the mechanical layer is derived from both the endotesta and exotesta in all members examined to date, and the mesotesta in highly reduced in mature seeds (fig. 27H). The endotesta produces a conspicuous inner palisade, or rectangular layer of thick-walled macrosclereids adjacent to the embryo cavity (fig. 27H). These cells also comprise the inner layer of the hypostase, producing a very distinct boxy chalazal thickening. In Zingiberaceae, the exotesta, endotesta or a combination of both are responsible for forming the mechanical layer of the seed and are often thickened and palisade-like in many members (figs 27E-G, 28A-H).

In *Kressia dakotensis* the seed coat is composed of three distinct layers of which the outermost is thickest and palisade-like and provides the fossil with the characteristic spirally striate ornamentation unique to fossil seeds in this group (fig. 8). The middle layer of cells is smaller and is disjunctly distributed throughout the seed to create a seed coat that varies in different regions of the seed (fig. 22). Within the middle layer two distinct types of cells can be observed, one that macrosclereids that disjunctly cover the seed and the other of presumably parenchymatous cells that comprise the hypostase. The inner layer is composed of a single layer of small square sclerenchymatous cells that border the embryo cavity (fig. 22F). Based on the relative thickness and size of the inner layer it is reasonable to conclude that these cells are not responsible for forming a protective mechanical, and the sole protective layer is attributed to the palisade outermost layer.

The seed coat of *K. dakotensis* is most similar to those found within members of Zingiberaceae, including the palisade outer layer, a middle layer of two distinct cells and the inner layer of square cells (fig. 22D-E). Based on the similarity of operculum, hypostase, and seed coat composition, *K. dakotensis* should be considered a bona fide member of the Zingiberaceae. *Kressia* seeds differ from members of Musaceae by having a thickened palisade outer layer, an middle layer comprised of two distinct sets of cells, one sclerenchymatous the other presumably parenchymatous isodiametric cells, and a distinct inner layer of small, square macrosclereids (fig. 22F). This layer of small square macrosclereids in the innermost layer distinguish *Kressia* from members of Costaceae as all members of Costaceae studied to date have been shown to contain an inner layer of large rectangular macrosclereids, which function as the protective layer of the seed.

Seed Anatomy Variation within Zingiberaceae

The Zingiberaceae comprises four subfamilies, two of which, the Zingiberoideae (containing the tribes Globbeae, Zingibereae and the unplaced genus *Caulokaempferia*) and Alpiniodeae (including the tribes Alpinieae, Riedelieae and the unplaced genus *Siliquamomum*) have a significant amount of seed character data available and were available for study (See Taktajan 1985 and Liao and Wu 2000 for reviews). The seed coat anatomy of the family varies widely, especially in the mesotesta and endotesta layers. As noted by Liao and Wu (2000) in their preliminary study of the seed anatomy of Zingiberaceae, the two subfamilies have characteristic seeds that can be distinguished, at least in some part, by the composition of the seed coat. The members of Zingiberoideae have seeds with parenchymatous, circular to discoid endotestal cells, where in members of Alpiniodeae the endotesta is distinctly sclerenchymatous and can range from being small and square to elongate rectangular, macrosclereids (fig. 28). The small, rectangular macrosclereids observed in some members of Alpiniodeae look remarkably similar to those observed in *Kressia dakotensis* (fig. 28B, D).

The composition of the mesotesta also varies between the two subfamilies, where members of Zingiberaceae often have three distinct layers that comprise the mesotesta (termed hypodermis, translucent layer, and pigment cells by Liao and Wu 2000) and members of Alpiniodeae tend to have two layers to the mesotesta. The variation of mesotestal composition has been interpreted different ways by various authors and layering may vary within many genera (e.g., *Etlingera yunnanensis* and *E. lingiformis*), but as a generalization this distinction seems to correlate with the subfamilies, though not as strongly as the endotesal data.

The exotesta is another source of data delimiting the two groups and can be also compared with *Kressia dakotensis* when determining its affinities. The exotesta of all Alpiniodeae is a single layer thick and forms a uniform layer of palisade to square cells that often produce a spirally striate seed coat. The exotesta in some Zingiberoideae have a similar construction to Alpiniodeae, but members of the tribe Globbeae differ markedly by having multiple layers in the exotesta (e.g. *Globba,* fig. 28G) or fine hairs on their epidermis (e.g. *Hemiorchis*, *Globba,* and also seen in the unplaced genus *Caulokaempferia,* fig. 17). Based on the composition of the seed coat *K. dakotensis* is more closely related to the Alpiniodeae, but one character, the presence of a micropylar collar, is not seen in the fossil and must be addressed.

The micropylar collar is found in many members of the Zingiberales and is the result of a differential ingrowth of the seed coat into the nucellus and embryo cavity to create an “V” shaped collar that the operculum resides inside of (Groutan and Bouman 1981). It is presumably closely correlated with operculate seeds as a supporting structure or tunnel for which the operculum can initially jam and subsequently be freed upon germination of the seed. It has recently been shown that it is not a necessity and is absent in members of Lowiaceae and in *Cautleya gracilis* and *Caulokaempferia coenobialis* of Zingiberaceae (Liao and Wu 2000). The functionality of the operculum has yet to be determined, but it is interesting that it is secondarily lost in these two members of Zingiberaceae, which are relatively derived members of the family (see Liao and Wu 2000). It is this character that is most concerning when addressing the taxonomic affinity of *K. dakotensis* as the seed anatomy agree most closely with Alpiniodeae, but the absence of a micropylar collar, a structure that is quite uniform and notable in the seeds, counters this close relationship. If the development of the micropylar collar is not necessary for a functional operculum, maybe its absence is not too concerning when comparing *Kressia dakotensis* to members of Alpiniodeae. For now, *Kressia dakotensis* is described as a member of Zingiberaceae, but not formally described to any subfamily due to the lack on complete data of members within the family and subfamilies. If it is shown that a member of Alpiniodeae is lacking a micropylar collar, its affinity with this family will be substantiated.

Comparison of *Kressia dakotensis* with other fossil Zingiberales

Kressia dakotensis is a bona fide member of Zingiberaceae based on the characters mentioned above and is unique among previously described fossils of the order. To date, fossils described from the order include *Alpinia bivascularis, A. affine, Ensete oregonense, Musa cardiosperma, Striatornata sanantoniensis, Spirematospermum chandlerae, S. friedrichii, S. wetzleri*, and *Tricostatocarpon* *silvapinedae.* Of these, *Ensete oregonense, Musa cardiosperma, Striatornata sanantoniensis, Spirematospermum chandlerae, S. wetzleri* and *Tricostatocarpon silvapinedae* have cellular preservation and can be compared in detail.

Ensete oregonense conforms to the genus *Ensete* on the basis of the hilar cavity and hilar rim, two characters which are unique to the genus and differ greatly from *K. dakotensis* (Manchester and Kress 1993). The seed anatomy was not reported in detail, but is composed of a relatively homogenous layer of macrosclereids. It is possible that there are more layers to the seed, but the image provided by Manchester and Kress (1993), shows only the single layer, as the outer and inner layers of the seed coat are usually very subtle and difficult to capture.

Musa cardiosperma is known from triloculate fruits with a single layer of seeds per locule. Each seed is barrel-shaped and has a massively enlarged micropylar end (fig 29A-B). Jain (1961) described the seed coat as having three distinct layers, the outer, middle and inner regions, but Jain also included a hypodermis, making the seed coat effectively four unique cell types. The outer layer contains sclerified cells, of which every other cell formed an acute papillate tip and formed striations on the seed coat (Jain 1961, fig 29B). Just below the outer layer, the hypodermis as described by Jain (1961), is to be considered the middle layer, which is comprised of two distinct types of cells. This layer is highly sclerified towards the outer layer and transitions into a layer of parenchyma cells that ultimately proliferated to give rise to the large micropylar thickenings seen in LS. The inner layer is a single layer of sclerified cells that are rectangular in shape, but thickened laterally and not vertically as was the case with in the outer layer.

Musa cardiosperma is similar to *K. dakotensis* with respect to the striations of the seed coat and its composition of four distinct layers, the middle of which forming a transition from sclerenchymatous to parenchymatous cells. It is different in many regards as well. First, the outer layer of the seed coat in *M. cardiosperma* has alternating acute papillate cells, where *K. dakotensis* has a homogeneous layer of palisade cells in its outer layer. Second, the inner layer of cells is wider than tall in *M. cardiosperma*, while in *K. dakotensis* the cells are distinctly square. Third, and unique to this fossil, is the flaring of the micropylar region of the seed. Not only does *M. cardiosperma* appear to have a micropylar collar (though reported as rudimentary by Rodriguez-de la Rosa and Cevallos-Ferriz 1994), it also has a massive proliferation of parenchymatous cells to make a very large micropylar thickening, two structures not seen in *K. dakotensis*. These structures however, may be homologous with structures seen in the apical regions of some members of Zingiberaceae, where they have been described and carnucle-like or stalk-like structures (figs. 29C-D).

Striatornata sanantoniensis is the smallest-seeded genus of fossil described to date with pyramidal to pyriform seeds only 0.22 cm long on average and are tightly packed in poorly preserved fruits. Its seed coat comprises three layers, and the outer layer is a single layer of striately oriented cells, much like those of *K. dakotensis* (figs. 29E-G). The middle layer of cells are distributed in the same manner as *K. dakotensis* in being thicker in the micropylar region of the cell, and they surround what Rodriguez-de la Rosa and Cevallos-Ferriz (1994) interpret as a chalazal chamber of isodiametric cells. Due to its similarity in being derived simply from cells embedded in the middle layer of the seed coat, this probably not a chalazal chamber, but instead a hypostase similar to that seen in extant Zingiberaceae and *K. dakotensis*. Because this character is used to demonstrate the affinity of *S. sanantoniensis* to Musaceae it must be carefully analyzed and compared to the hypostase of Zingiberaceae and the chalazal chamber of Musaceae. The inner layer of the seed is also similar to *K. dakotensis,* in that it is a single layer or rectangular cells that surround the embryo cavity. Of the fossil genera described to Zingiberales to date, *S. sanantoniensis* is most similar to *K. dakotensis* in terms of seed coat anatomy, seed shape, and in having a dome-like structure of isodiametric cells at the chalazal region of the seed. Although the two differ markedly in their size and possibly fruit characters as the fruit of *K. dakotensis* is unknown at this time.

The genus *Spirematospermum* was the first seed of the order to be described for its internal anatomy and can be compared in great detail with *Kressia dakotensis*. *Spirematospermum chandlerae* and *S. wetzleri* have three distinct layers to their seed coats with the outermost layer of palisade cells forming the distinct spirally striate seed coat in the same manner as *K. dakotensis*. The middle layer of *S. chandlerae* is reported as being disproportionally thickened in both the chalazal and micropylar regions of the cell, although not figured, but likened to the figures of *S. wetzleri* in Koch and Friedrich 1971 (Friis 1988). In this layer of *S. wetzleri* a “chalazal chamber” has been reported, which has led to its recent assignment to Musaceae (Manchester and Kress 1993; Rodriguez-de la Rosa and Cevallos-Ferriz 1994; Fischer et al. 2009). However, this structure is not a chalazal chamber in the same sense as Musaceae, instead it contains a proliferation of parenchymatous cells within the middle layer of the seed coat. The “chamber” is simply a degradation of these cells during the fossilization process. This structure is instead interpreted as a hypostase, which supports its affinities with Zingiberaceae. More on the taxonomic affinity of *Spirematospermum* will be discussed later. In both species there is a single inner layer of rectangular cells that surround the embryo sac and are reported to contain silica bodies (Koch and Friedrich 1971; Friis 1988).

The composition of the seed coat of *Spirematospermum* as compared with *K. dakotensis* is quite similar with regards to having a single outer palisade layer, a middle layer of two distinct cells, one forming within the other and forming a disk of cells at the chalazal region, and an inner layer of square cells surrounding the embryo cavity. The most notable difference between the genus and *K. dakotensis* is the distinct proliferation of cells of the middle layer seen in the micropylar end of the seed (figs. 30A-I). These cells do not form a bulge or outgrowth as seen in *Musa cardiosperma*, but are significantly distinct from the cells of the micropylar region of *K. dakotensis*.

Tricostatocarpon silvapinedae seeds are pyriform with up to 90 seeds contained within one triloculate fruit. The morphology and anatomy of the seed is unique among the fossil seeds as it has been reported to contain no chalazal modification and in the seed coat layers of the seed coat (figs. 29H-I). The coat of *T. silvapinedae* comprises three layers, a single outer layer of thick-walled cells that are circular in XS, a middle layer 10-25 cells thick of isodiametric cells and an inner layer three to five cells thick, becoming up to nine cells thick at the micropylar region (Rodriguez-de la Rosa and Cevallos-Ferriz 1994). The outer layer of the seed coat is similar to *K. dakotensis* as it is a single cell thick, but differs in that its cells are cylindrical and not palisade as seen in *K. dakotensis*. The middle and inner layers are more numerous in *T. silvapinedae* than *K. dakotensis*, though both have a middle layer that are thicker at the micropylar and chalazal regions of the seed. It is clear from an in-depth analysis of the extant and extinct members of Zingiberales that *K. dakotensis* clearly belongs in the order as well as the family Zingiberaceae and is a taxon unique among the fossils.

Justification of a New Leaf Species *Zingiberopsis hickeyi*

Fossil leaves and leaf buds assigned to *Zingiberopsis hickeyi* Benedict sp. nov. clearly belongs to the genus *Zingiberopsis* of the family Zingiberaceae based on its characters of leaf venation and fiber spacing and is most closely allied to *Zingiberopsis isonervosa*. *Zingiberopsis* is characterized by large blades with acuminate tips, a long exligulate petiole, and a thick costa or midvein with secondaries diverging parallel to each other. Although *Z. hickeyi* is based on fragments of leaves with only a small portion of leaf material showing the details of venation, critical taxonomic features are available in sufficient detail to identify it (Hickey and Peterson 1978; Dr. Leo J. Hickey, Yale University, New Haven Connecticut, personal communication July, 2010).

Species of *Zingiberopsis* are identified by the pattern of venation and fibers seen in the leaves (Hickey and Peterson 1978). The venation and fiber pattern of *Z. hickeyi* is uniform and would be considered the "d" formula, differing from *Z. attenuata* (formula BdCdB), *Z. magnifolia* formula (AdCdBdCdBdCdBdCdBdA) and extant members of *Alpinia* (formula varies). The "d" formula is also seen in *Z. isonervosa* from the Early Eocene and Late Paleocene and shows a close relationship to *Z. hickeyi*. *Z. hickeyi* has a larger "d" vein size than either of the two forms published, and a large range in spacing of the veins, though a smaller spacing on average (Hickey and Peterson 1978). Epidermal cells and stomatal patterns are also preserved in *Z. hickeyi,* a feature previously unknown for the genus. Stomata are not well preserved, however they appear consistently tetracytic, which is a common stoma pattern for members of the Zingiberales (Tomlinson 1956, 1969; Hussin et al. 2000).

Revisions and New Findings in *Spirematospermum wetzleri*

The taxonomic placement of *Spirematospermum wetzleri* has been subject to much debate with its affinities in the order as either Musaceae (Manchester and Kress 1993; Rodriguez-de la Rosa and Cevallos-Ferriz 1994; Fischer et al. 2009) or Zingiberaceae (Chandler 1925; Koch and Friedrich 1971). The difficulty in assigning the fossil is based on the fact that the sampling within the order is scant as well as interpretation of the characters has been debated (Chandler 1925; Fischer et al. 2009). The most detailed study to date by Koch and Friedrich (1971) allied *S. wetzleri* with *Alpinia oxymitrum* based on triloculate fruits with axil placentation and the striate seed coat. Recently, Fischer et al. (2009) placed *S. wetzleri* into Musaceae based on the presence of a chalazal chamber and tapering of the base of the fruit, and into a fossil subfamily Parietimusoideae because *S. wetzleri* was interpreted to have parietal placentation.

In my analysis of *Kressia dakotensis* I have had the opportunity to study *S. wetzleri*, in detail, from both the Fasterholt material Koch and Friedrich (1971) studied and the Ponholz material Fisher et al. (2009) studied (figs. 16A-H). The three characters proposed by Fisher et al. that ally *S. wetzleri* with Musaceae will be addressed following a general interpretation of the gross morphology and anatomy of *S. wetzleri*. The ‘chalazal chamber’ as noted by Manchester and Kress (1993) and Rodriguez-de la Rosa and Cevallos-Ferriz (1994) was suggested to be homologous to the chalazal chamber found in Musaceae. However, as mentioned above, is not as complex as the chamber found in musacean members and because it is derived from a proliferation of cells within the middle layer of the seed coat it can be interpreted as a hypostase, which suggests its affinity to Zingiberaceae. Furthermore, the “chamber” itself is simply a degradation of cells of this middle layer and is simply a taphonomic artifact (fig. 29F).

The second and third characters used by Fischer et al. (2009) to help ally *Spirematospermum* to the Musaceae were those seen in the fruit. The tapering of the fruit into the pedicle was proposed to be most similar to Musaceae by Fisher et al. (2009), as many Musaceae have tapering fruits. While it is true that *A. oxymitrum* does not have a tapering fruit, other members of the Zingiberaceae due (e.g., *Aframomum*, fig. 19) though a general lack of information about fruit types limits the ability to infer much from subtleties of fruit type such as this. Parietal placentation was the other fruit character proposed by Fisher et al. (2009) to justify the Musaceae subfamily Parietimusoideae. The interpretation of *Spirematospermum* as having parietal placentation was suggested by Chandler (1925) when she first described the fossil genus and named the *S. wetzleri* species. It was subsequently reinterpreted as having axile placentation by Koch and Friedrich (1971), but again interpreted to have parietal placentation by Fischer et al. (2009). The difficulty in the interpretation of placentation is due, in part, because the seeds of Zingiberales are often densely packed into the fruit. In fact, many seeds are often contorted in shape because they have developed into and around the sibling seeds to the point of near fusion in adult fruits. To add to the difficulty, the fossils, in particular those of Ponholz are compressed quite severely along their main axis. This taphonomic artifact makes the confident deduction of the placentation weak as axially or parietally placentated fruits that have been so compressed would look very similar. Immature fruits of the fossil would need to be recovered and dissected to show unequivocal evidence of the taxon's placentation. These facts, coupled with the general lack of information about the fruits across the order makes the interpretation of the integumentary layer even more important with regards to addressing the taxonomic affinity of *Spirematospermum*.

The seed coat of *Spirematospermum* is separated into three layers, of which the outermost is spirally striated and is the character for which the form genus was named (Chandler 1925). This outermost layer is a single cell thick of palisade sclerenchymatous cells. The middle layer is composed of two distinct cell types, one of which contains circular sclerenchymatous cells that often contain dark contents and the other cell type is isodiametric and parenchymatous with distinctly thin walls (figs. 30H). It is this parenchymatous layer that divided differentially in the development of the seed to produce a thickened micropylar region and the hypostase at the chalazal region. The inner layer of the seed coat is a single layer of small, square cells that lines the embryo cavity. The three layers of the seed coat and the differential proliferation of the middle layer at the chalazal region is very similar to the seed coats of *Kressia dakotensis*, *Striatornata sanantoniensis,* and members of Alpiniodeae of Zingiberaceae, but differs from the two fossil genera and some members of Alpiniodeae with respect to the highly thickened micropylar region.

A thickening in the micropylar region is only present in some members of Zingiberaceae. There are two types of thickenings in the micropylar region in seeds of Zingiberaceae, and interestingly the type of micropylar thickening in

Zingiberaceae members seems to coincide with the currently recognized phylogenetic relationships within the subfamilies. Some members of Alpiniodeae have micropylar thickenings derived from a proliferation of mesotesta cells (fig. 25F), where many members of Zingiberoideae have an apical micropylar outgrowth that extends up above the seed and seems to be derived from the exotesta cells (e.g., *Globba, Hitchenia, Pyrgophyllum, Zingiber,* figs. 29C-D). The thickening observed in *Spirematospermum* is derived from the middle layer of cells and may be homologous the structure seen in Alpiniodeae members.

Though the micropylar thickening and seed coat composition of *Spirematospermum* is comparable to those seen in members of Alpiniodeae of the Zingiberaceae, the lack of a micropylar collar is conflicting as no members of the subfamily lack this character. As stated above some members of Zingiberaceae have been reported to lack a micropylar collar, which further supports *Spirematospermum* as being a bona fide member of the Zingiberaceae, though its exact taxonomic placement within the family is yet to be resolved.

Conclusions

The Zingiberales are a diverse group of monocotyledonous group of plants with a rich fossil record spanning much of the entire history of flowering plants. The fossil members described to the order, to date, have been an enigmatic group, of which, the systematic placement of *Spirematospermum* has been changed multiple times in the past hundred years. The difficulty of determining the taxonomic affinities of the fossils has been limited due to the lack of sampling of modern seeds. In this study I have surveyed all known literature describing the seed coats of extant Zingiberales as well as studied more than 80 fossil and extant specimens to understand the distribution of characters within the order. Integumentary anatomy is quite variant between families and within the subfamilies of Zingiberaceae the most significant characters in determining the taxonomic affinities of the fossils. *Kressia dakotensis* and *Spirematospermum wetzleri* are described as bona fide members of Zingiberaceae and show many similarities with members of Alpiniodeae. *Kressia, Spirematospermum* and *Striatornata sanantoniensis* are considered to be closely related on the basis of integumentary anatomy.

The statement by Rodriguez-de la Rosa and Cevallos-Ferriz (1994), "The seed structures of *Striatornata sanantoniensis, Tricostocarpon silvapinedae, Spirematospermum friedrichii, Spirematospermum chandlerae, Spirematospermum wetzleri, Musa cardiosperma* share more characters among themselves than with any group of plants in the Zingiberales" is still half true with the exact taxonomic affinities of many Zingiberales seeds yet to be revised and assigned.

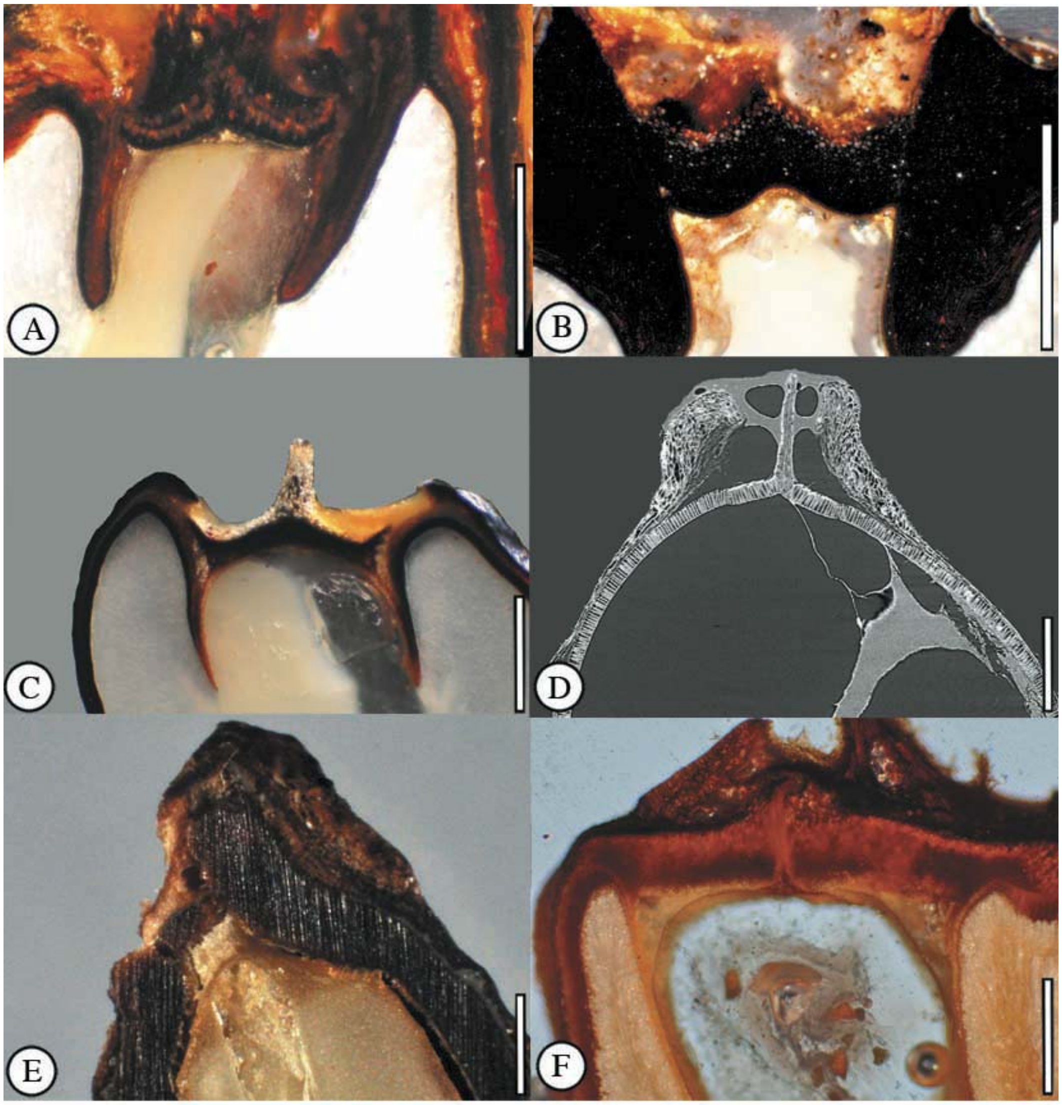

Fig. 24 Operculum variation in Zingiberales. A, *Alpinia bioa*, Zingiberaceae. B, *Musa sikkimensis*, Musaceae. C, *Dimerocostus argenteus,* Costaceae. D, *Orchidantha vietnamensis,* Lowiaceae. E, *Heliconia bihai,* Heliconiaceae. F, *Donax arundastrum,* Marantaceae. A-C scale bar = 0.5 mm, D scale bar = 1.25 mm, E scale bar = 1 mm, F scale bar = 0.5 mm.

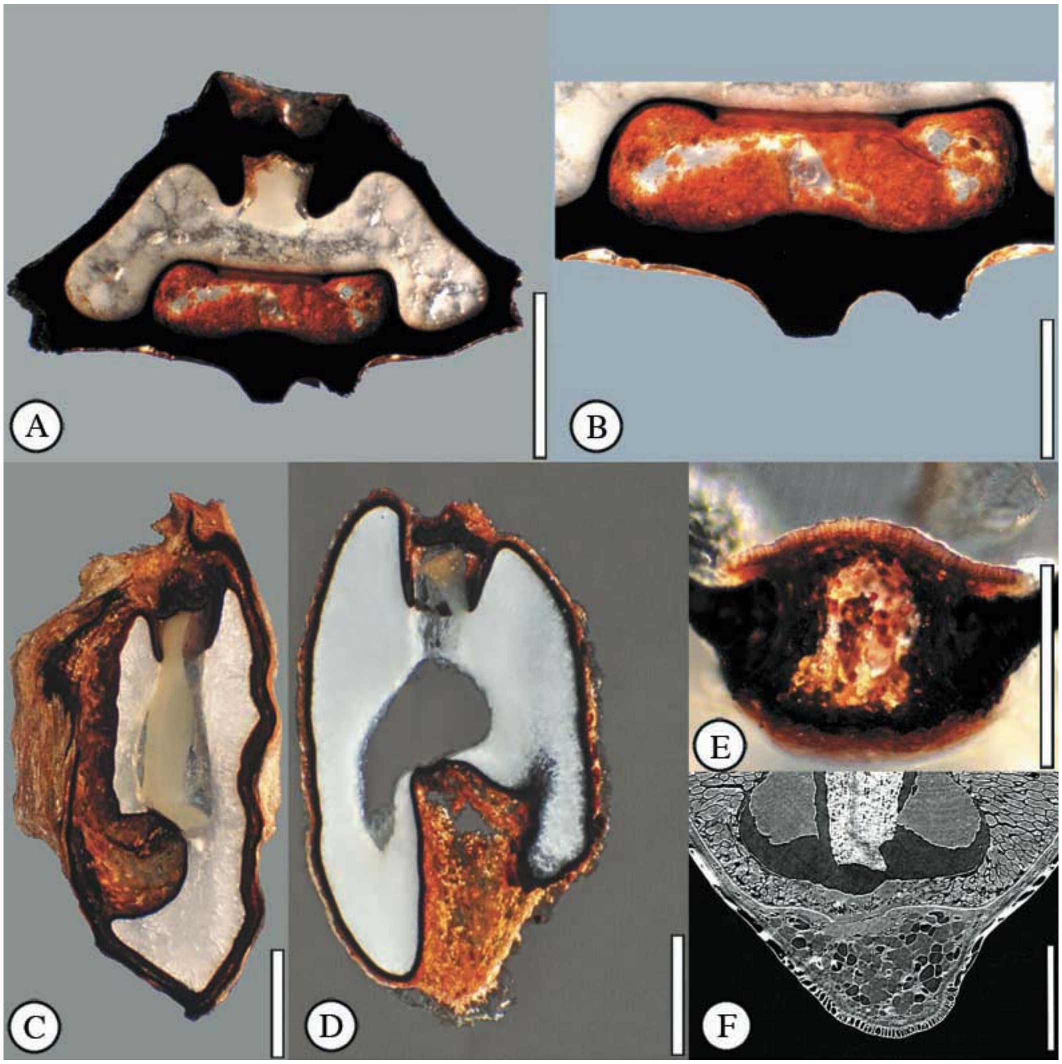

Fig. 25 Chalazal region variation in Zingiberales. A, *Musa* seed ls showing chalazal chamber. B, Detail of the *Musa* chalazal chamber (Musaceae). C, *Alpinia boia* asymmetrical hypostase (Zingiberaceae). D, *Alpinia oblongifolia* asymmetrical hypostase (Zingiberaceae). E, Detail of *Costus speciosus* hypostase composed of mesotesta cells and a thickened, palisade like inner testa (Costaceae). F, Detail of *Aframomum melegueta* hypostase composed of mesotesta cells (Zingiberaceae). A scale bar = 2 mm, B-D scale bar = 1 mm, E and F 0.5 mm,

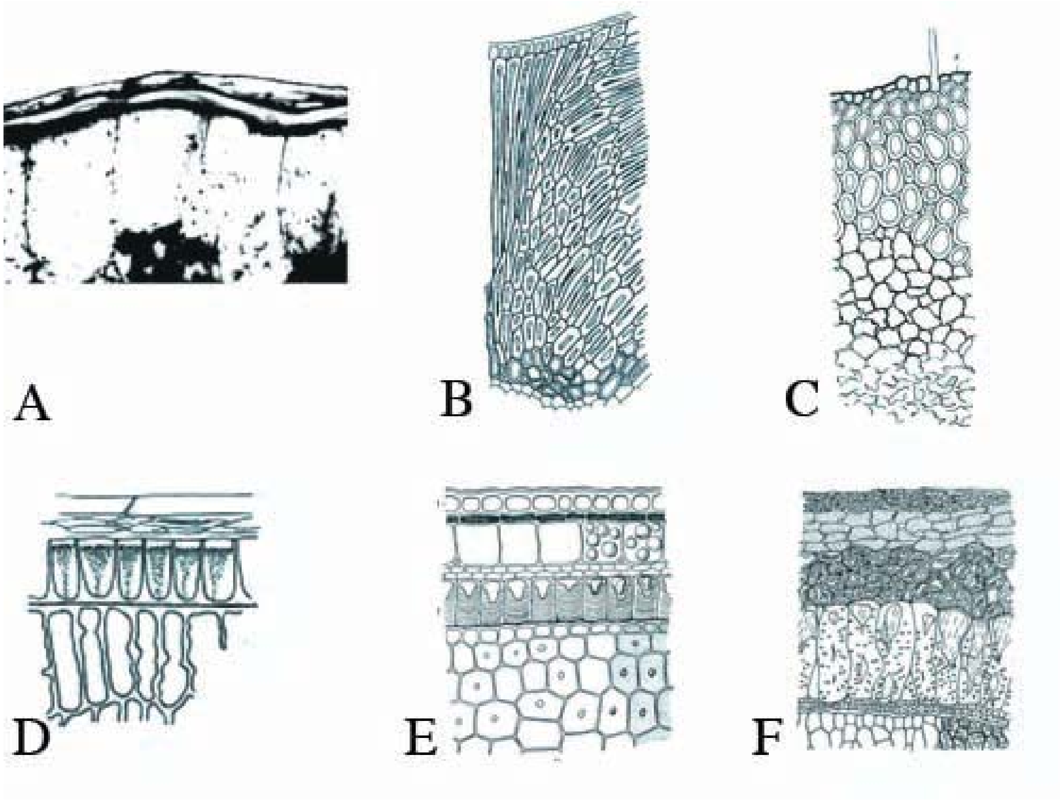

Fig. 26 Diagrams of seed coats in Zingiberales. A, Heliconiaceae seed coat. B, Musaceae seed coat. C, Lowiaceae seed coat. D, Costaceae seed coat. E, Zingiberaceae seed coat. F, Marantaceae seed coat. Image A modified from Simão et al. 2006 and B-F modified from Taktajan 1985.

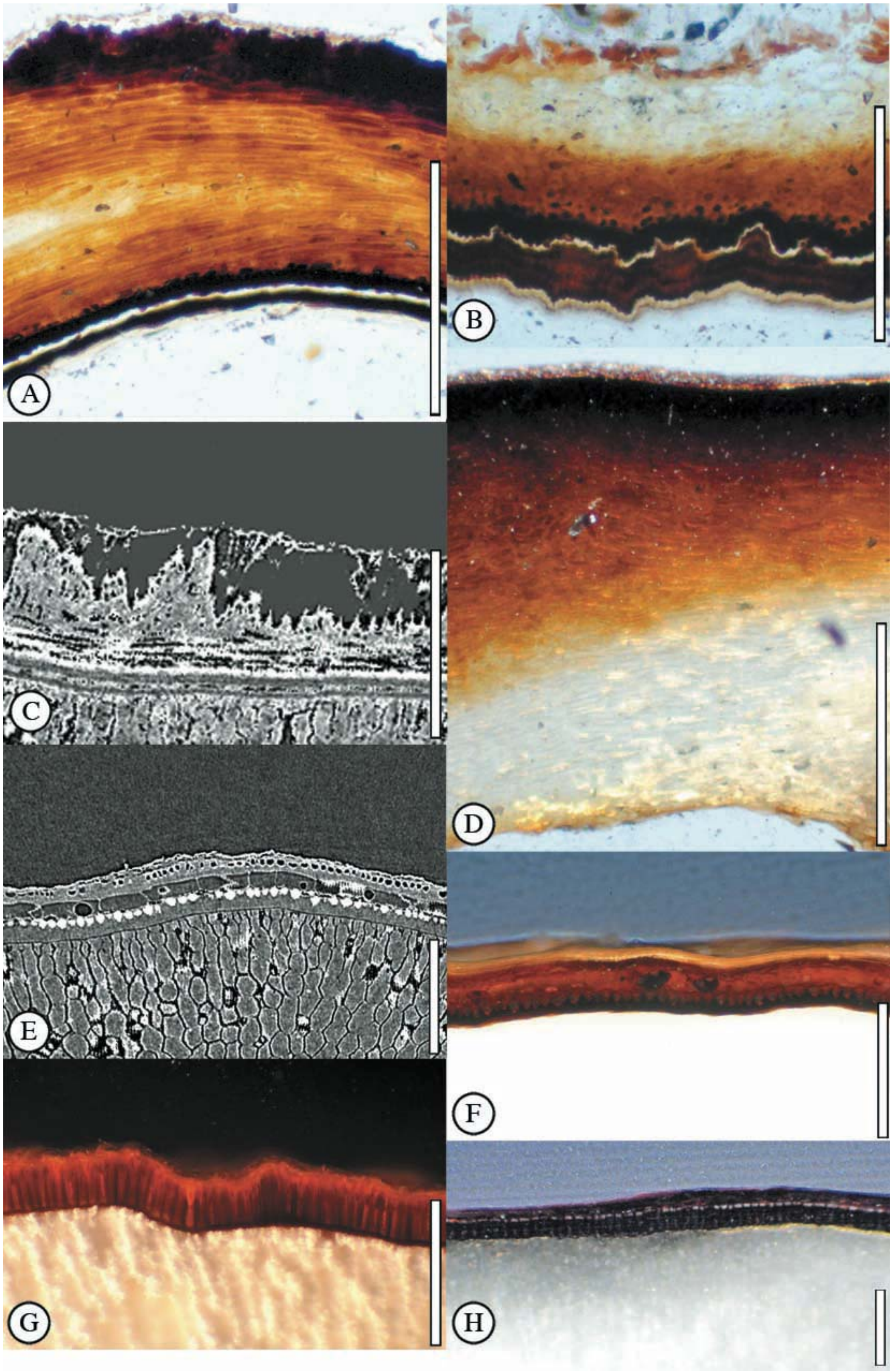
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Fig. 27 Seed coats of Musaceae, Zingiberaceae, and Costaceae. Exotesta is at the top of all images. A, Longitudinal section of a *Musa peekelii* seed coat composed of a darkened exotesta cells, a thick region of mesotestal cells and a single layer of endotestal cells. The separated layer in the image is the inner integument. B, Longitudinal section of *Musa peekelii* seed coat between the chalazal chamber and the embryo cavity. Note the inner integument is more pronounced and contains two layers of large sclerenchymatous cells. C, SRXTM image of *Musa textilis* seed coat Note the exotesta is fragmented and disproportionately distributed throughout the seed coat. D, *Ensete glucum* (Musaceae) seed coat showing homogenous sclerified testa. E, XRSTM image of the seed coat of *Alpinia fax* (Zingiberaceae) showing the proportions of the three layers of the testa. The exotesta is a single layer of circular cells, the mesotesta is a single layer of rectangular cells and the inner layer is a single layer of square sclerenchymatous cells. F, Longitudinal section of *Alpinia fax* seed coat containing the same layers as image E. G, *Etlingera linguiformis* (Zingiberaceae) seed coat showing large palisade endotesta cells. H, *Dimerocostus argenteus* (Costaceae) seed coat showing large palisade endotesta cells. A and B scale bar = 0.25 mm, C scale bar = 0.314 mm, D scale bar = 0.25 mm, E scale bar = 0.24 mm, F scale bar = 0.24 mm, G scale bar = 0.20 mm, H scale bar = 0.12.

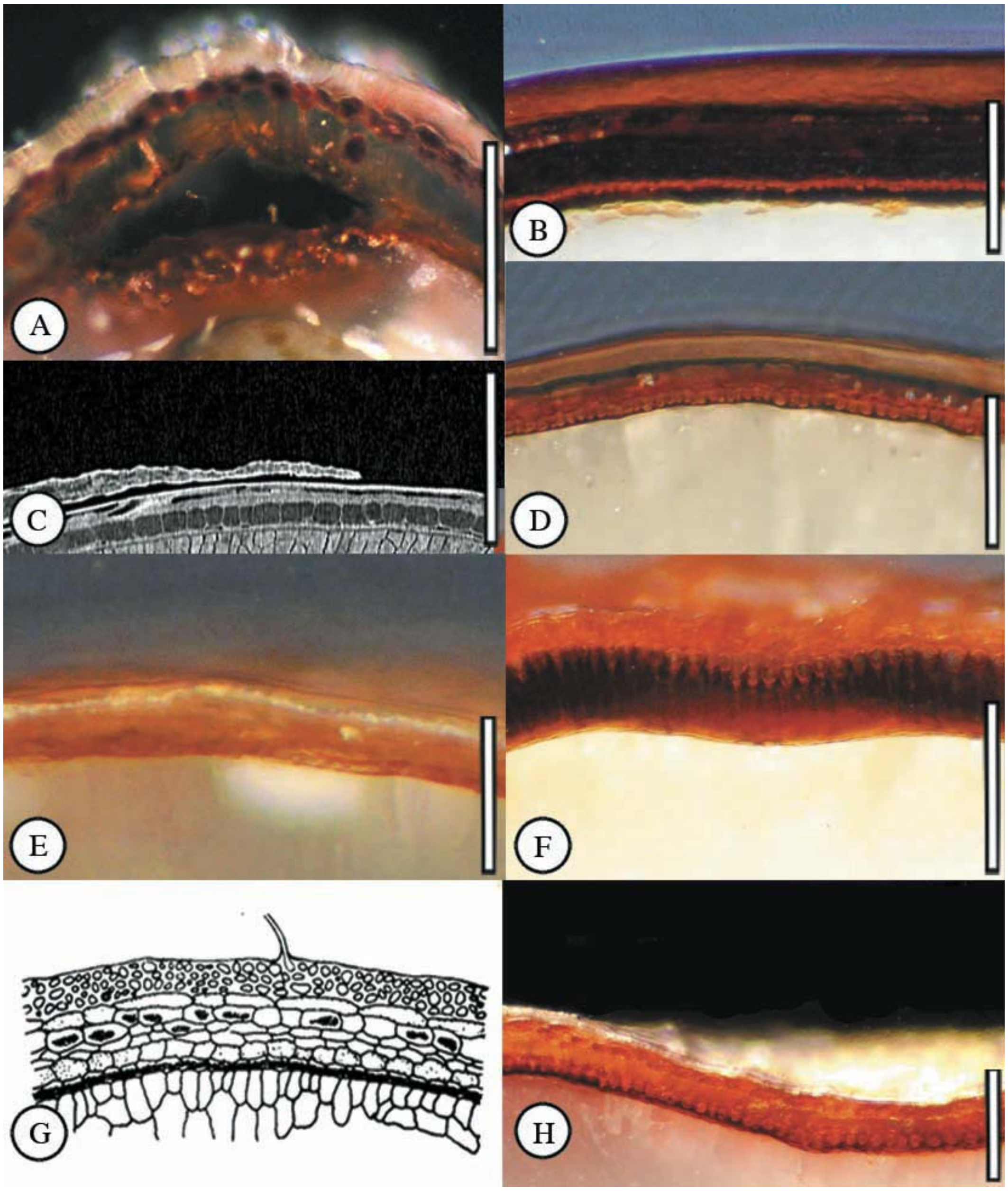

Fig. 28 Seed coat variation within Zingiberaceae. Exotesta is at the top of all images. A, *Hedychium borneensis* (Zingiberoideae). B, *Aframomum melegueta* (Alpinioideae). C, *Zingiber* sp. (Zingiberoideae). D, *Pleuranthodium* sp. (Reidelieae). E, *Hemiorchis* sp. (Globbeae). F, *Etlingera linguiformis*

(Alpinioideae). G, Line diagram of a *Globba* seed coat showing multicellular exotesta. H, *Vanoverbergia sepulcheri* (Alpiniodeae). G modified from Wu and Liao 1995 Figure 5. A scale bar = 0.25 mm, B scale bar = 0.1 mm, C scale bar = 0.5 mm, D scale bar = 0.25 mm, E scale bar = 0.4 mm, F scale bar = 0.125 mm, H scale bar = 0.14 mm.

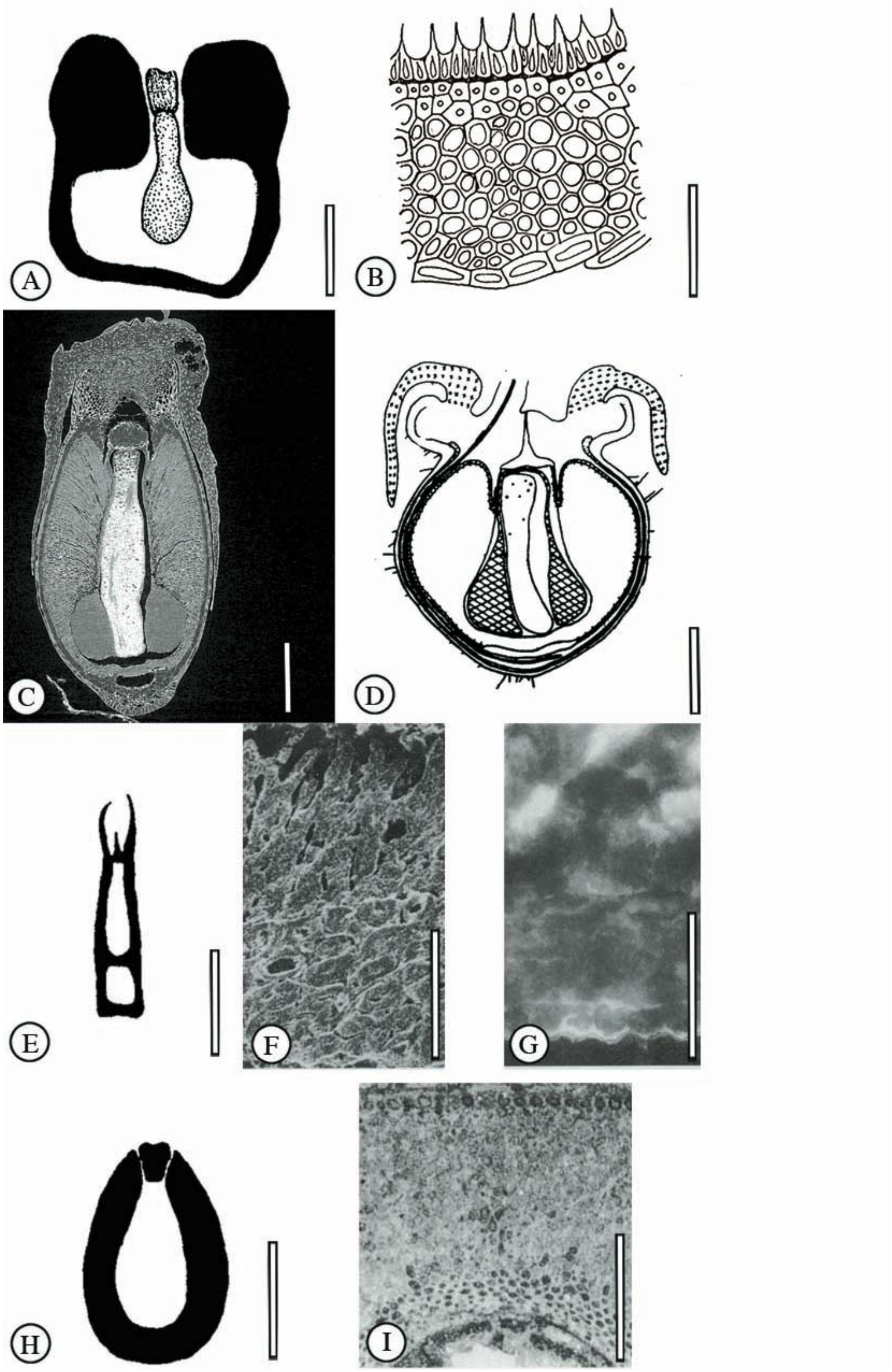
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Fig. 29 Fossil Zingiberales Diagrams and Seed Coat Anatomy. A, *Musa cardiosperma* line diagram. B, *Musa cardiosperma* seed coat line diagram. C, Synchrotron image of a *Zingiber sp.* seed showing an apical thickening. D, Diagram of *Globba* depicting the apical thickening. E, *Striatornata sanantoniensis* line diagram. F, Seed coat detail of *S. sanantoniensis* showing palisade outer and middle layers of the seed coat. G, *S. sanantoniensis* inner layer of the seed coat showing square cells. H, *Tricostocarpon silvapinedae* line diagram. I, Detail of *T. silvapinedae* seed coat showing three distinct layers. A scale bar = 2 mm, B scale bar = 0.6 mm, C-E scale bar = 1 mm, F scale bar = 0.05 mm, G scale bar = 0.12 mm, H scale bar = 3 mm, I scale bar = 0.10 mm. Figures 29F, 29G, and 29I modified from Rodriguez-de la Rosa and Cevallos-Ferriz (1994) 29D modified from Wu and Liao 1995. 29C courtesy of Dr. Selena Y. Smith of the University of Michigan, Margaret Collinson of the Royal Holloway University of London and the beamline staff Drs. Federica Marone and Julie Fife of the TOMCAT beamline, Swiss Light Source, Paul Scherrer Institute, Villigen, Switzerland.

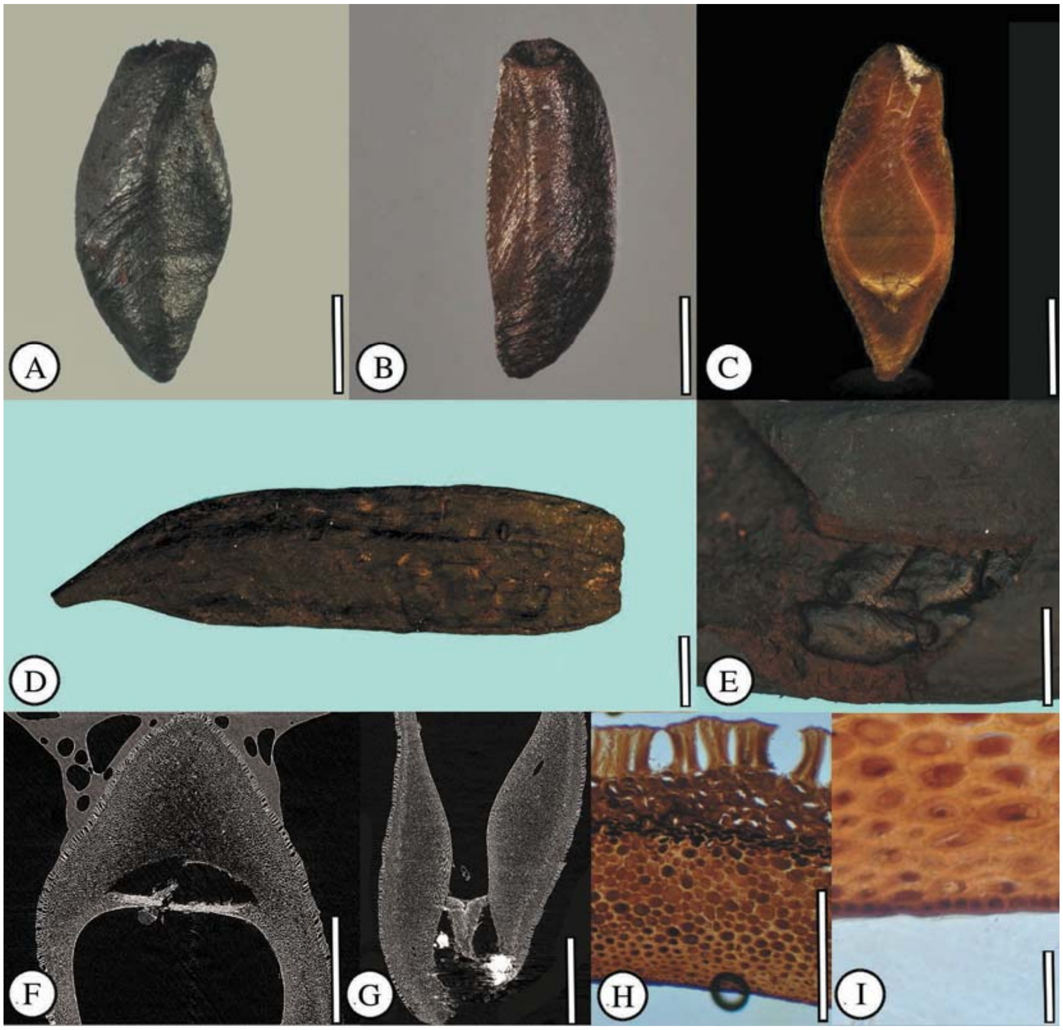

Fig. 30 *Spirematospermum wetzleri* fruit and seed detail. A, *Spirematospermum wetzleri* seed from Middle Miocene Ponholz, Germany. B, *S. wetzleri* seed from Miocene Fasterholt flora of Denmark. C, Synchrotron image of *S. wetzleri* from Fasterholt, Denmark showing embryo cavity and internal morphology of the seed. D, Fruit of *S. wetzleri* showing tapering of the fruit at the pedicle. E, General orientation of the seeds in the fruit. F, Synchrotron image showing chalazal region. G, Synchrotron image showing disjunct distribution of the middle layer of

the seed coat and operculum. H, Details of the seed coat that is composed of three distinct layers. I, Detail of the inner most layer of the seed with thick walled square cells. A-C scale bar = 2 mm, D scale bar = 10 mm, E scale bar = 5 mm, F and G scale bar = 1 mm, H scale bar = 0.2 mm, I scale bar = 0.05 mm.

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APPENDIX A

THE ALMONT AND BEICEGEL CREEK FLORAS

Family	Genus	Plant part	Almont	Beicegel Creek	References
PTERIDOPHYTES					
Blechnaceae	*Woodwardia* sp.	fronds	-	rare	Pigg, et al. 2006, fig. 4& 7
Ferns	Filicalean fern	frond, spores	-	rare	Matthews et al. 2006 (abstr)
Isoetaceae	*Isoetes* cf.. *horridus*	megaspores	-	rare	Matthews et al. 2007 (abstr)
GYMNOSPERMS					
Ginkgoaceae	*Ginkgo cranei*	leaves, seeds, ovulate stalks	abundant	common	Crane et al. 1990, fig. 2; Zhou et al. 2012
Cupressaceae	cf. *Parataxodium* sp.	leaves, ovulate & pollen cones seeds	abundant	abundant	Crane et al. 1990, fig.3&4
Cupressaceae	*Metasequoia*	seeds, cones, leaves	occasional	-	Manchester, pers. commun. Pigg unpubl data (UWSP)
Pinaceae	cf. *Pinus*	ovulate cone	-	rare	Manchester, pers. commun.
Taxaceae	*Diploporus*	seeds	occasional	occasional	Crane et al., 1990, fig. 25J; Manchester 1994
Taxaceae	*Torreya*	seeds	rare	-	Manchester, pers. commun.
ANGIOSPERMS					
Actinidiaceae	cf. *Saurura*	seeds and fruit	occasional	common (seeds)	Crane et al. 1990; fig. 24A-E; Pigg & DeVore 2003 (abstr)
Araliaceae	*Toricellia*	fruit	rare	-	Manchester, pers. commun.
Betulaceae	*Palaeocarpinus dakotensis*	infructescence, fruits, seeds, pollen catkins, pollen	abundant	abundant	Crane et al. 1990, fig.16,17; Manchester, et al. 2004

Betulaceae	*Corylites* sp.	leaves	abundant	abundant	Crane et al. 1990, fig.18A, B; Manchester, et al. 2004
Buxaceae?	genus	fruits	rare	rare	DeVore, Pigg pers. obs.
Cercidiphyllaceae	*Nyssidium arcticum*	fruits, seeds, leaves	occasional	-	Crane et al. 1990, fig.10
Cornales	*Amerisinia obtrullata*	fruits and seeds	common	abundant	Crane et al. 1990, fig. 24F-H; Manchester et al. 1999
Cornales	*Beringiaphyllum*	leaves	abundant	common	Crane et al. 1990, fig 30
Cornales	*Cornus* piggae	endocarps	rare	occasional	Crane et al. 1990, fig 20G-I; Xiang et al. 2003, fig.3H, Manchester et al. 2010
Cornales	*Davidia antiqua*	infructescence, fruit, leaves	common	rare	Crane et al. 1990; Manchester, 2002a
Cornales	cf. *Diplopanax*	endocarp	occasional	-	Manchester, pers commun.
Hamamelidaceae	*Hamawilsonia boglei*	infructesence with seeds	occasional	-	Crane et al., 1990 fig. 15; Benedict et al. 2008
Hamamelidaceae	genus	seeds	rare	-	Crane et al. 1990; fig. 27E-G Benedict et al. 2008
Hamamelidaceae	pollen catkins with in situ pollen	pollen catkins, pollen	rare	-	Crane et al. 1990; Benedict et al. 2008
Icacinaceae	*Icacinicarya dictyota*	endocarp	1 specimen	-	Pigg et al. 2008
Icacinaceae	*Icacinicarya collinsonae*	endocarp	-	1 specimen	Pigg et al. 2008
Icacinaceae	*Palaeophytocrene*	endocarps	rare	rare	Crane et al. 1990, fig 22A-C

Juglandaceae	*Cyclocarya brownii*	fruits, infructescences	common	common	Manchester & Dilcher 1982; Crane et al. 18 C, D, F, G; Taylor 2007 (abstr).; Taylor 2010
Juglandaceae	genus	leaves	rare	-	Crane et al. 1990, fig. 19
Meliosmaceae	*Meliosma rostellata*	fruits	common	common	Crane et al. 1990, fig. 21
Menispermaceae	cf. *Canticocculus*	fruits	rare	-	Crane et al. 1990, fig. 5
Menispermaceae	cf. *Tinomiscium*		rare	-	Manchester pers commun.
Myrtaceae	*Paleomyrtinea*	fruits and seeds	occasional	common	Crane et al. 1990, fig. 20A-E Pigg et al. 1993, fig. 18-22; 24
Nymphaeaceae	*Susiea newsalemae*	seeds	rare	-	Taylor et al. 2006
Nymphaeaceae	*Nuphar wutuensis*	seeds	1 specimen	-	Chen et al. 2004
Ochnaceae	*Ochna* sp.	fruits and isolated seeds	rare	rare	Crane et al. 1990, fig.26A-C Pigg et al. 2005 (abstr).
Platanaceae	*Macginicarpa* sp.	Infructesence	rare	-	Manchester pers commun.
Platanaceae	genus	pollen catkin	rare	-	Crane et al. 1990
Platanaceae	*Macginitiea*	leaves	occasional	occasional	Manchester pers commun.
Platanaceae	genus	leaf types a, b, c	rare	-	Crane et al. 1990 fig. 11
Polygalaceae	*Paleosecuridaca curtisii*	fruit	common	rare	Crane et al. 1990 fig. 23A-C Pigg et al. 2008
Polygonaceae	*Polygonocarpum curtisii*	fruits	occasional	-	Crane et al. 1990 fig. 23F-I; Manchester and O’ Leary 2010 fig 23A-G

Polygonaceae	*Podopteris antigua*	fruits	rare	-	Crane et al. 1990 fig. 23E; Manchester and O'Leary 2010 fig 23H-M
Ranunculaceae	*Paleoactaea nagelii*	fruit and seeds	rare	rare	Crane et al. 1990 fig. 25D-F; Pigg & DeVore 2005
Sapindaceae	cf. *Acer*	fruit	common	common	Crane et al. 1990 fig. 22B-D; Kittle et al. 2005 (abstr.) in prep
Sapindaceae	"	leaves	present?	present?	DeVore pers. observ.
Sapindaceae	*Aesculus hickeyi*	leaf	rare	-	Manchester, 2001
Sapindaceae	*Sapindus*	fruit	rare	-	Manchester pers.commun.
Trochodendraceae	*Nordenskioldia borealis*	fruit	common	common	Crane et al. 1990, 1991
Trochodendraceae	*Zizyphoides flabella*	leaf	abundant	common	Crane et al. 1990, 1991
Vitaceae	*Ampelocissus*	leaf	rare	-	Manchester pers. commun.
Zingiberaceae	*Kressia dakotensis*	Seed, embryo	occasional	abundant	Crane et al. 1990 fig. 26D-F; Benedict et al., 2007 (abstr). Benedict 2011 (abstr). This study
Zingiberaceae	*Zingiberopsis hickeyi*	Leaf with cuticle	occasional	occasional	This study
Incertae Sedis	*Averrhoites affinis*	leaf	occasional	occasional	Crane et al. 1990 fig. 31
Incertae Sedis	*Porosia verrucosa*	seed	occasional	occasional	Crane et al. 1990 fig. 29C,D Manchester 2002b
Incertae Sedis	Monocot remains	rhizomes	rare	abundant	Crane et al. 1990 fig. 29a,b DeVore et al. 2004 (abstr).

Incertae Sedis	Miscellaneous	Additional fruits, seeds, leaves	-	-	see: Crane et al. 1990

Table modified and updated from Pigg and DeVore 2010 and others referenced in the table.