New Late Cretaceous fruit and its seeds from the Ingersoll Shale (eastern Alabama, U.S.A.) indicate affinity with Ranunculaceae (Ranunculales)

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ABSTRACT. We describe a new ranunculacean fruit from Ingersoll Shale sediments (Santonian, 85.5 to 83.5 Ma), a part of the Eutaw Formation as it occurs in eastern Alabama. The Ranunculales/Ranunculaceae are basal eudicots but their fossil record is not well documented which is most likely due to their taxa being predominantly herbaceous and therefore lacking a propensity for fossilization. Two fruits are in evidence, one is a mature fruit in the process of dehiscence and in which several seeds are describable, and the other is interpreted as a less mature fruit. From these fruits, we describe a new genus, *Costellifructus* Axsmith, Stults, Wang, et Boucher gen. nov., and species, *Costellifructus alabamensis* Axsmith, Stults, Wang et Boucher sp. nov. Both fruits are urceolate and display follicles that are fused at the base and maintain this fusion through the length of the main body of the fruit thus forming a capsule. The fusion of follicles is denoted by areas of depression on the fruit. Especially observable in the large fruit are follicular ridges which continue into long stylar extensions. Interestingly, this is a character which is also very recognizable on extant ranunculacean genera such as *Aquilegia* L. and *Delphinium* Tourn. ex L. Seeds are characterized as small ($2.5 \times 2 \text{ mm}$), rugose, ridged, obovate longitudinally, and trigonal in cross-section profile, properties fitting within some ranunculacean taxa.

KEYWORDS: Costellifructus alabamensis, Cretaceous, Ingersoll Shale, ranunculacean fossils

INTRODUCTION

Although the order Ranunculales (Juss. ex Bercht. et J. Presl 1820) and family Ranunculaceae (Juss. 1789) are considered basal eudicots, their Cretaceous record is not well documented. The fact that most of the taxa within Ranunculales/Ranunculaceae are herbaceous, contributes to this problem as herbaceous species produce fewer vegetative and reproductive organs than woody plants and these organs are also often constructed of material with lesser fossilization potential (Friis et al., 2011). Furthermore, the variability of characters within Ranunculales/Ranunculaceae makes the ability to recognize its synapomorphies challenging, leading to difficulty in assigning a potential fossil as Ranunculalean or Ranunculacean (Shi and Li, 2003; Anderson et al., 2005).

Apparently the ranunculalean stem group existed as far back as 120 Ma during the Early Cretaceous, and stem groups of all

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families within it (i.e. Berberidaceae Juss., Circaeasteraceae Kuntz ex. Hutch., Eupteleaceae K. Wilh., Lardizabalaceae R. Br., Menispermaceae Juss., Papaveraceae Juss., and Ranunculaceae) diverged by the latter portion of the Early Cretaceous or beginning of the Late Cretaceous (Hoot, 1991; Anderson et al., 2005; Jud et al., 2018). Fossil fruit records that are possibly ranunculaceaen have been recovered in Lower Cretaceous deposits in South America (Gobo et al., 2022; but see argument in Pessoa et al., 2023). The review by Pigg and DeVore (2005), and references within that publication, places the first reliable fruit records of the family Ranunculaceae with an extinct Thalictrum-like achene (Friis et al., 1994) from the Early Cretaceous (early Barremian-Aptian), follicles of Hyrcantha Krassilov, Shilin et Vachrameev during the middle Albian (Krassilov et al., 1983), and seeds of *Eocaltha* Rodriguez-De La Rosa, Cevallos-Ferriz et Silva-Pineda during the Late Cretaceous (Campian) (Rodriguez-de la Rosa et al., 1998). Records of an extinct ranunculacean genus describe Paleoactaea Pigg et Devore fruit from the Late Paleocene and Early Eocene (Reid and Chandler, 1933; Crane et al., 1990; Collinson and Cleal, 2001; Pigg and Devore, 2005). Records of fruit corresponding to several extant ranunculacean genera (as listed in Pigg and Devore, 2005) begin within the Oligocene (i.e. Clematis L., Glaucidium Siebold et Zucc., Hydrastis L., Myosurus L., Ranunculus L., Trautvetteria Fischer et C. Meyer) and continue into the Pliocene (i.e. Caltha L., Anemone L.) (Reid and Reid, 1915; Weyland, 1937; Li, 1952; Andreánszky, 1961; Takhtajan, 1974; Mai and Walther, 1978; Łańcucka-Środoniowa, 1979; Mai, 1985, 2001; Tiffney, 1985; Mathews, 1987; Matthews and Ovenden, 1990; Collinson et al., 1993; Martinetto, 2001).

Here we describe a recently discovered fruit with seeds from the Upper Cretaceous Ingersoll Shale (Santonian, 85.5 to 83.5 Ma) of eastern central Alabama, U.S.A. as most probably ranunculaceaen. This is an important contribution to the fossil history of Ranunculales/ Ranunculaceae.

MATERIALS AND METHODS

GEOLOGICAL SETTING OF THE INGERSOLL SHALE

The Upper Cretaceous Ingersoll Shale is part of the Eutaw Formation (85.5 to 80.6 Ma, Santonian to Campanian), a marine/marginal marine formation occurring along the eastern edge of the Western Interior Seaway (Fig. 1). In its entirety, the Eutaw Formation is a belt running from southwestern Tennessee, through northeastern Mississippi and northwestern central Alabama, into central western Georgia. It unconformably overlies the Tuscaloosa Formation, and is disconformably overlain by the Mooreville Chalk in its western region, and by the Blufftown Formation in its eastern portion (Savrda and Nanson, 2003). The Ingersoll Shale (85.5 to 83.5 Ma) occurs along the eastern border of central Alabama (Fig. 1), in Phenix City in Russell County, 32.5°N, 85.0°W, approximately 1 m above the contact between the Tuscaloosa and the Eutaw formations (Knight, 2007; Bingham et al., 2008; Knight et al., 2010). It is a thin clay lens (<1 m) interpreted as a small, shallow tidal channel deposit potentially filled in less than one year (Bingham et al., 2008). The rich fossil floral assemblage of the Ingersoll Shale includes ferns, horsetails, conifers (including Araucaria Juss.) and angiosperms (Knight 2007;



Figure 1. Paleogeographic map of a portion of North America during the late Santionian (~84 Ma) designating the Western Interior Seaway and Appalachia. The Eutaw Formation is in black overlying the darker green. Ingersoll Shale site is located at white block. Modified from R. Blakey, Colorado Plateau Geosystems, Inc. https://deeptimemaps.com/westerninterior-seaway/ and also from Bingham et al., 2008

Stults and Axsmith, 2012). Its faunal record consists of bivalves, insects and other terrestrial arthropods (some in amber), fish scales and the most abundant collection of feathers from a North American Mesozoic deposit (Bingham et al., 2008).

PREPARATION OF FOSSILS

Fruit fossils of the Ingersoll Shale are partly compression and partly impression fossils. The compressed material is thick with a lot of organic texture preserved. Portions of the fruit material are loosely affixed to the matrix, requiring caution to prevent disruption during transport and study. Examination incorporated a dissection microscope (Nikon SMZ 1500) (Tokyo, Japan) and epifluorescent microscopy (Nikon Eclipse E400; Nikon Intensilight GHGF1). Fossils were examined and photographed on a light table with a Pentax digital camera (Tokyo, Japan). Smaller image photographs and measurements were obtained using Nikon Elements and Adobe Photoshop software (San Jose, California, U.S.A).

COMPARISONS WITHIN BASAL EUDICOT TAXA

Initial observations, showing a fossil fruit with fused follicles, long, stylar extensions, and numerous seeds dehiscing from its upper portion, suggested that it was some sort of Ranunculales/Ranunculaceae. However, other basal eudicot orders, i.e. Buxales Takht. ex Reveal, Proteales J. ex Bercht et J. Presl. and Trochodendrales Takht. ex Cronquist, share some of the same morphological/reproductive characteristics (including being syncarpous and dehiscent) with the Ranunculales, and, it is recognized that these four orders form a morphological (but paraphyletic) evolutionary transition between basal angiosperms and core eudicots (Anderson et al., 2005; Wang et al., 2009; APG IV, 2016). Therefore, we first performed comparisons of the fruits (and, if necessary to rule out a taxon, the seeds) of families and/or genera contained within Buxales, Proteales and Trochodendrales. After that, we considered the genera listed for the basal Ranunculales (including Eupteleaceae and Papaveraceae) and the core Ranunculales (including Berberidaceae, Circaeasteraceae, Lardizabalaceae, Menispermaceae and Ranunculaceae).

In a taxonomic search, genera listed as accepted in the World Flora Online (at http://www.worldfloraonline.org) were used. This database is described as a collaborative, international project initiated with the involvement of the Missouri Botanical Garden. New York Botanical Garden, Royal Botanic Garden Edinburgh, and Royal Botanic Gardens Kew. Data from this source was accessed over several days in January, 2023. Taxa included in these comparisons are listed in Table 1, each with a reference source which included information about the fruit and/or seeds. However, comprehensive literature sources and online databases were especially necessary as a beginning point for deriving information and were also subsequently helpful in providing additional descriptors and/or diagrams or pictures of taxa under consideration in order to delineate differences more conclusively. These resourses are listed in Table 2 and when attributed

further in this manuscript, will be referenced in the shortened format from Table 2. Several of these literature sources also contained the individual reports listed per taxon in Table 1. For example, Kadereit, 1993 (in Tab. 1) described several genera of Papaveraceae in 'The families and genera of vascular plants. V.2: Flowering Plants, Dicotyledons: Magnoliid, Hamamelid and Caryophyllid families'. A note to consider with respect to the taxa listed in Table 1 is that some of these references shown may list and describe the genera under different families than are currently indicated via recent phylogenetic revision. However, the listing of taxa within Table 1 follows the current phylogeny of APG IV (2016). An example of this is that the genus Corydalis DC. is currently considered within Papaveraceae (APG IV, 2016), but the reference with the description of this genus (Lidén, 1993a) listed it under Fumariaceae Marquis.

PHYLOGENETIC ANALYSIS

Eight characters from these fossils were coded according to criteria from a 66-character data matrix (Wang et al., 2009, 2016). The characters coded for include: carpel number (more than 3); carpel form (ascidiate up to stigma); carpel fusion (syncarpous); ovule number (more than 2); integument number (bitegmic, inferred rather than directly observed as this is a basic character of an angiosperm ovule (Endress, 2011), and because a sclerotic layer can be seen in the fossil which is usually the outer integument); fruit wall (dry); fruit dehiscence (dehiscent); and beak (present). Maximum parsimony (MP) and Bayesian inference (BI) analyses were carried out in PAUP* v.4.0b10 (Swofford, 2003) and MrBayes v.3.0b4 (Ronquist and Huelsenbeck, 2003), respectively. Two separate analyses were performed. However, one only contains the fossil Costellisfructus alabamensis and the other further added the fossil Leefructus mirus Sun, Dilcher, Wang et Chen with characters outlined by Wang et al. (2016).

RESULTS

COMPARISONS AMONG BASAL EUDICOT TAXA FRUITS (AND SEEDS, WHEN NECESSARY)

Buxales Takht. ex Reveal, Proteales Juss. ex Bercht. et J. Presl., and Trochodendrales Takht. ex Cronquist are considered basal eudicots (along with Ranunculales) and their fruits share somewhat similar morphologies to the fossil fruits under consideration in this study. Fortunately, the comparisons within these orders did not include an inordinately large number of genera to regard. For example, Buxales contains the one family (Buxaceae Dumort.) with six genera: Buxus L., Didymeles Thouars, Haptanthus Goldberg et C. Nelson, Pachysandra Michx., Sarcococca Lindl., and Styloceras Kunth ex A. Juss.

Order	Family	Genus/Genera	Reference	
Oruci	Buxaceae	Buxus L.	Köhler, 2007	
tuxales akht. ex Reveal	Dumort.	Didymeles Thouars	von Balthazar et al., 2003	
		Haptanthus Goldbery et C. Nelson	Shipunova and Shipunova 2011	
ЧĘ		Pachysandra Michx., Sarcocca Lindl., Styloceras Kunth ex A. Juss.	Köhler 2007	
	Nelumbonaceae		Williamson and Schnei-	
	A. Rich		der, 1993	
	Platanaceae T. Lestib.		Kubitzki, 1993	
-T	Proteaceae Juss.	Acidonia L.A.S. Johnson et B.G. Briggs, Adenanthos Labill., Agastachys R.Br., Alloxylon P.H. Weston et Crisp, Athertonia L.A.S. Johnson et B.G. Briggs, Aulax P.J. Berguis, Austromuellera C.T. White, Banksia L.f., Beauprea Brongn. et Gris, Beaupreopsis Virot, Bellendena R.Br., Bleas- dalea F. Muell. ex Domin, Brabejum L., Buckinghamia F. Muell., Card- wellia F. Muell., Carnarvonia F.Muell., Catalepidea, P.H.Weston, Cenar- rhenes Labill., Conospermum Sm., Darlingia F. Muell., Diastella Salisb. ex Knight, Eidothea A.W. Douglas et B. Hyland, Embothrium J.R. Forst. et G. Forst., Euplassa Salisb. ex Knight, Faurea Harv.	Weston, 2007	
Pre		Finschia Warb.	Catling, 2010	
rcht et J. I		Floydia L.A.S. Johnson et B.G. Briggs, Franklandia R.Br., Garnieria Brongn., Grevillea R. Br. ex Knight, Hakea Schrad., Helicia Lour., Hicks- beachia F. Muell., Hollandaea F.Muell., Isopogon R.Br. ex Knight, Kerma- decia Brongn. et Gris, Knightia R. Br., Lambertia Sm.	Weston, 2007	
x B(Lasjia P.H. Weston et A.R. Mast	Gross and Hyland, 1993	
les J. ex		Leucadendron R. Br., Leucospermum R.Br., Macadamia F.Muell., Mala- gasia L.A.S. Johnson et B.F. Briggs, Megahertzia A.S. George et B. Hyland, Mimetes Salisb., Musgravea F. Muell., Neorites L.S. Sm.	Weston, 2007	
tea		Nothorites P.H. Weston et A.R. Mast	George and Hyland, 1995	
\Pr		Opisthiolepis L.S. Sm., Orites R. Br., Orothamnus Pappe ex Hook., Panopsis Salisb. ex Knight	Weston, 2007	
		Oreocallis R. Br.	Prance et al., 2007	
		Paranomus Salisb., Persoonia, Sm., Petrophile R.Br. ex Knight, Placosper- mum C.T. White et W.D. Francis, Protea L., Roupala Aubl., Scolymocepha- lus Kuntze, Serruria Salisb., Sleumerodenndron Virot, orocephalus R.Br., Spatalla Salisb., Sphalmium B.G. Briggs, B. Hyland et L.A.S. Johnson, Stenocarpus R.Br., Stirlingia Endl., Strangea Meisn., Symphionema R.Br., Synaphea R.Br., Telopea Sol. ex Baill., Toronia L.A.S. Johnson et B.G. Briggs, Triunia L.A.S. Johnson et B.G. Briggs, Turrillia A.S.Sm., Vexa- torella Rourke, Virotia L.A.S. Johnson et B.G. Briggs, Xylomelum Sm.	Weston, 2007	
	Sabiaceae Blume	Meliosma Blume, Ophiocaryon Endl., Sabia Colebr.	Kubitzki, 2007	
Trochodendrales Takht. ex Cronquist	Trochoden- draceae Eichler		Watson and Dallwitz, 1992+	
	Berberidacaee Juss.	Achlys DC	Whetstone et al., 1997a	
		Berberis L.	Whittemore, 1997a	
resl.		Bongardia C.A. Mey, Caulophyllum Michx., Epimedium Tourn ex L., Gymnospermium Spach	Loconte, 1993	
s J. F		Jeffersonia Bart.	O'Rourke, 1997a	
ale et e		Leontice L.	Loconte, 1993	
ht.		Nandina Thunb.	Whetstone et al., 1997b	
nur terc		Plagiorhegma Maxim.	Loconte, 1993	
Rar Juss. ex B		Podophyllum L.	O'Rourke, 1997b	
		Ranzania T.Itô	Stearn et al., 2002	
	a .	Vancouveria C. Morren et Decne	Whetstone et al., 1997c	
	Cırcaeaster- aceae Kuntz ex. Hutch.		Cheng-Yih and Kubitzki, 1993a	
	Eupteleaceae K. Wilh.		Endress, 1993	

 $\textbf{Table 1. List of basal eudicot taxa investigated for fruit comparison^{a,b}$

Table 1. Continued

Order	Family	Conuc/Conoro	Deferrer ee
Order	Family	Genus/Genera	Reference
	Lardizabal-	Akebia Decne., Boquila, Decaisna Hook. F. et Thomson, Lardizabala	Cheng-Yih and Kubitzki,
	aceae R. Br.	Ruiz, Sargentoaoxa Render et E.H. Wilson	1993b
		Sinofranchetia (Diels) Hemsl., Stauntonia DC.	
	Menisper-		Rhodes, 1997
	Papavoraçoao	Adlumia Raf ex DC	Lidán 1003a
	Juss.	Aretamagan Torr, at Frám	Moyor 1007
	0 uss.		Meyer, 1997
		Argemone L.	Ownbey, 1997
		Bocconia Plum. ex L.	Kadereit, 1993
		Canbya Parry ex A.Gray	Kiger, 1997a
		Capnoides Mill.	Lidén, 1993a
		Cathcartia Hook.f.	Grierson and Long, 1984
		Ceratocapnos Durieu	Lidén, 1993a
		Chelidonium L.	Kiger, 1997b
		Coreanomecon Nakai	Yun and Oh, 2018
		Corydalis DC, Cryptocapnos Rech., Cysticapnos Mill.	Lidén, 1993a
		Dendromecon Benth.	Kiger, 1997c
		Dicentra Barkh, ex Bernh.	Lidén, 1993a
		Dicranostigma Hook f. et Thomson	Kadereit 1993
		Discocannos Cham et Schltdl	Lidón 1993a
		Ebrandorfaria Fukubara at Lidán	Storp 1061
			Zhong and Cross Wilson
		Lomecon Hance	2008a
ssl.		Eschscholzia Cham.	Clark, 1997a
Pre		Fumaria Tourn. ex L., Fumariola Korsch.	Lidén, 1993a
J.		Glaucium Mill.	Kiger, 1997d
et		Hunnemannia Sweet, Hylomecon Maxim.	Kadereit, 1993
ht.		Hypecoum Tourn. ex L.	Lidén, 1993a
erc		Ichtvoselmis Lidén et T.Fukuhara	Yao, 2008
хB		Lamprocapnos Endl.	Zhang and Lidén, 2008
e.		Macleava B. Br.	Kiger 1997e
nsa		Meconella Nutt	Hannan 1997a
s J		Macononsis Vig	Kadaroit 1993
lale		Panavar I	Kigor and Murray 1997
Icu		Platucannos (DC) Bornh	Lidón 1002a
JUL		Distustemen Ponth	Liden, 1995a
Raı		Pratystemon Dentil.	
		Pseudojumaria Medik.	Liden, 1993a
			Liden, 1993b
		Romneya Harv.	Clark, 1997b
		Rupicapnos Pomel	Lidén, 1993a
		Sanguinaria Dill ex L.	Kiger, 1997f
		Sarcocapnos DC.	Lidén, 1993a
		Stylophorum Nutt.	Kiger, 1997g
		Trigonocapnos Schltr.	Lidén, 1993a
	Ranunculaceae Juss.	Aconitum L.	Brink and Woods, 1997
		Actaea L.	Ford, 1997a
		Adonis L.	Parfitt, 1997a
		Anemoclema (Franch.) W.T. Wang	Dezhi and Robinson, 2008
		Anemonastrum Holum	Mosyakin, 2016
		Anemone L.	Dutten et al., 1997a
		Anemonella Spach	Gleason and Cronquist,
		Anemonoides Mill.	Dutton et al 1997h
		Anemonopsis Siebold et Zucc	Tamura 1993
		Aquilegia L	Whittemore 1007h
		Arctaranthic Grann Actoronymum IR Drymm at Unteh Dassin Dalff	Tamura 1009
		et W.W. Sm., <i>Calathodes</i> Hook.f. et Thomson, <i>Callianthemoides</i> Tamura, <i>Callianthemum</i> C.A.Mey	1aiiiuia, 1990
		Caltha L., Coptis Salisb.	Ford, 1997b
		· •	

Order	Family	Genus/Genera	Reference	
	Ranunculaceae	Clematis L.	Pringle, 1997	
	Juss.	Cyrtorhyncha Nutt.	Tamura, 1993	
		Delphinium Tourn. ex L.	Warnock, 1997	
		Dichocarpum W.T.Wang et P.K.Hsiao	Tamura, 1993	
		Enemion Raf.	Ford, 1997c	
		Eranthis Salisb.	Parfitt, 1997b	
		Eriocapitella Nakai	Wencai et al., 2008	
		Glaucidium Siebold et Zucc.	Huxley, 1992	
Presl.		Gymnaconitum (Stapf) Wei Wang et Z.D.Chen	Liangqian and Kadota, 2008	
		Halerpestes Greene, Hamadryas Comm. ex Juss.	Tamura, 1993	
J.		Helleborus Gueldnst	Ford, 1997d	
Ranunculales Juss. ex Bercht. et		Hepatica Mill.	Whittemore and Parfitt, 1997	
		Hydrastis J.Ellis ex L.	Ford, 1997e	
		Isopyrum L., Kingdonia Balf.f. et W.W.Sm., Knowltonia Salisb., Lepto- pyrum Raf.	Tamura, 1993	
		Leucocoma Ehrh.	Nieuwland, 1914	
		Megaleranthis Ohwi, Metanemone W.T.Wang	Tamura, 1993	
		Nigella L.	Ford, 1997f	
		Oxygraphis Bunge, Paraquilegia J.R. Drumm et Hutch., Paroxygraphis W.W.Sm., Peltocalathos Tamura	Tamura, 1993	
		Pseudodelphinium H.Duman, Vural, Aytaç et Adigüzel	Vural et al., 2012	
		Psychrophila (DC.) Bercht. et J.Presl.	Messina, 2015	
		Pulsatilla Mill.	Tamura, 1993	
		Ranunculus L.	Whittemore, 1997c	
		Semiaquilegia Makino	Tamura, 1993	
		Thacla Spach	Ford, 1997g	
		Thalictrum Tourn. ex L.	Park and Festerling, 1997	
		Trautvetteria Fisch. et C.A.Mey, Trollius L.	Parfitt, 1997c, d	
		Urophysa Ulbr.	Tamura, 1993	
		Xanthorhiza Marshall	Parfitt, 1997e	

Table 1. Continued

^a Did not list the genus if family only contains one genus. Also did not list individual genera if the family as a whole can be ruled out. For example, all fruits in Menispermaceae genera can be categorized as drupes, so no need to list individual genera.

^b Description at times initially described under different name than what appears in list. For example, *Eriocapitella* described under *Anemone*, *Gymnaconitum* under *Aconitum*, *Anemoides* under *Anemone*, *Thacla* synonim to *Caltha*, and *Leucocoma* synonym for a *Thalictrum*.

(APG IV, 2016). Within Buxales (Buxaceae), only Buxus had a fruit considered a capsule, but its loculicidal dehiscence is described as spreading into 3 two-horned valves (Watson and Dallwitz, 1992 +; Köhler, 2007; Department of Horticulture, College of Agricultural Sciences, Oregon State University, Plant-Systematics.org). Didymeles, Pachysandra, and Sarcocca are drupaceous (Watson and Dallwitz, 1992 +; Brickell, 2008; Department of Horticulture, College of Agricultural Sciences, Oregon State University), Styloceras is subdrupaceous with dry mesocarp (Köhler, 2007; Royal Botanic Gardens Kew,) and the fruits of Haptanthus are unknown (Shipunov and Shipunova, 2011). Proteales includes the single genus families Nelumbonaceae A. Rich and Platanaceae T. Lestib., the few genera

family Sabiaceae Blume, and the many genera family Proteaceae Juss. (APG IV, 2016). The single genus within Nelumbonaceae (Nelumbo Adans.) has fruits which are an aggregate of nuts (Williamson and Schneider, 1993; USAM). The single genus within Platanaceae (Platanus L.) has fruits which are aggregates of achenes and hairs on a fruithead (Kubitski, 1993; USAM). Sabiaceae is a three-genus family (including Meliosma Blume, Ophiocaryon Endl., and Sabia Colebr.) whose fruits are either drupes or schizocarps (Kubitski, 2007). Proteaceae has 84 genera (World Flora Online) with fruits described as achenes, drupes, follicles, nuts or nutlets (Simpson, 2010). However, our investigation noticed that particular features of the follicular proteacous fruits rule them out as the

likely nearest relative of the fossil (we here describe) as many of these proteaceous genera have winged seeds (such as Alloxylon P.H. Weston et Crisp, Buckinghamia F. Muell., Embothrium J.R. Forst. et G.Forst, Grevillea R. Br. ex Knight, Hakea Schrad., Megahertzia A.S. George et B. Hyland, Neorites L.S. Sm., Nothorites P.H. Weston et A.R. Mast, Oreocallis R.Br., Orites R.Br., Sphalmium B.G. Briggs, B. Hyland et L.A.S. Johnson, Stenocarpus R.Br., Strangea Meisn), or woody follicles (such as Cardwellia F. Muell., Lomatia R.Br., Xylomelum Sm.), or woody follicles and winged seeds such as *Knightia* R.Br. (George and Hyland, 1995; Prance et al., 2007; Weston, 2007). Interestingly, although Watson and Dallwitz (1992+) mention gynoecia of adjoining flowers forming a multiple fruit, we could not find any genus that described a follicular Proteaceae having follicles that display syncarpy as has occurred often in Ranunculales/Ranunculaceae (Dilcher et al., 2007; Bravi

et al., 2010; Friis et al., 2011; Sun et al., 2011). Trochodendrales consists of a single family (Trochodendraceae Eichler) with a single genus (Trochodendron Siebold et Zucc.) (APG IV, 2016) whose fruits are loculicidal capsules with outwardly curved persistent short styles and winged seeds and whose fossil record indicates it was much more widely distributed in the past than today (Watson and Dallwitz, 1992+; Pigg et al., 2007; Manchester et al., 2018a). Our comparisons with these other basal eudicot orders allowed us to rule them out as containing the most likely candidate for nearest relative for our fossil.

Within the Ranunculales, Eupteleaceae and Papaveraceae are sister to the remainder of the group (Yi et al., 2007). Eupteleaceae fruits are samaras (Endress, 1993). Papaveraceae fruits are capsular and mostly recognized by the poricidal dehiscence of *Papaver* L., although valvate or transverse dehiscence also occurs in the family (Watson

Table 2. Comprehensive Plant Literature Sources and Online Plant Databases

Online Database or Literature Source	Author(s) or Editor(s) or Web Address	Taxa Searched	
The families of flowering plants: descriptions, illus- trations, identification, and information retrieval	Watson, L., Dallwitz, M.J. (1992+)	Buxales Takht. ex Reveal Papaveraceae Juss. Ranunculaceae Juss. Trochodendraceae Eichler	
Flora of North America, North of Mexico	Flora of North America Editorial Com- mittee (1993+)	Ranunculaceae	
The families and genera of vascular plants V. 2: Flowering plants, Dicotyledons, Magnoliid, Hama- melid, and Caryophylliid families	Kubitzki, K., Rohwer, J.G., Bittrich, V. (eds) (1993)	Papaveraceae Ranunculaceeae	
Family guide for fruits, seeds: descriptions, illustra- tion, and information retrieval.	Kirkbride, J.H., Jr., Gunn, C.R., Dall- witz. M.J. (2000+)	Papaveraceae	
Flowering Plants Eudiicots. The Families and Genera of Vascular Plants, vol. 9.	Kubitzki, K. (ed.) (2007)	Papaveraceae	
Flora of Australia online	ecobits.net.au/flora-of-australia-online	Proteaceae Juss. Ranunculaceae	
Flora of China	www.efloras.org	Circaeasteraceae Kuntz ex. Hutch.	
Flora of Zimbabwe	www.zimbabweflora.co.zw	Proteaceae	
International Dendrology Society, Trees and Shrubs online	www.dendrology.org/trees-and-shrubs- online	Proteaceae	
Misfud, MaltaWildPlants.com by Stephen Misfud	www.maltawildplants.com	Papaveraceae	
Oregon State University College of Agricultural Sci- ences Department of Horticulture	landscapeplants.oregonstate.edu/plants	Buxaceae Dumort	
Plant Resources of Tropical Africa	prota4u.org	Proteaceae	
PlantSystematics.org	www.plantsystematics.org	Berberidaceae Juss. Buxaceae	
PlantZAfrica.com	www.plantzafrica.com	Proteaceae	
Royal Botanic Gardens Kew	powo.science.kew.org	Buxaceae Ranunculaceae	
World Flora online	www.worldfloraonline.org	Papaveraceae	

All of these sources were accessed January 2023 except PlantSystematics.org which was accessed December 2023.

and Dallwitz, 1992+; Kadereit, 1993; Lidén, 1993a; Kiger, 1997a-g; J.H. Kirkbride, Jr., C.R. Gunn, and M.J. Dallwitz, 2000+; Zhang and Grey-Wilson, 2008a, b; Misfud, MaltaWildPlants.com by Stephen Mifsud; World Flora Online). Capsular genera (other than Papaver) within Papaveraceae include Cory*dalis* with a long, slender, often torulose capsule, Dicentra Barkh. ex Bernh. with an elongate two-valved capsule, Discocapnos Cham. and Schltdl. with only one persistent style, and Hylomecon Maxim. which is two-valvate, narrowly terete, and has carunculate seeds. Hypecoum Tourn. ex L. has an arcuate, ellipsoid capsule usually pinched at internodes. Macleaya R.Br., and Pteridophyllym Siebold et Zucc. are bivalvular, as is Sanguinaria Dill. ex. L., which is also ellipsoidal-elongate and dehisces from the base. Meconopsis Vig. has a short style that expands basally to cover top of ovary. Examples of seeds for some genera in Papaveraceae include *Chelidonium* L. that has arillate seeds, Cryptocapnos Rech. has a one-seeded nutlet, Fumaria Tourn. ex L. and Fumariola Korsch. are also one-seeded and Sarcocapnos DC is one-or-two-seeded. Analysis reveals that within the genera of Papaveraceae, the mode of dehiscence, the shape of the capsules, the short styles, the fact that only one or two seeds may result per capsule, and characteristics of some of the seeds themselves indicate that it is not the most likely family for the fossil described here (Grierson and Long, 1984; Kadereit, 1993; Lidén, 1993a, b; Kiger, 1997a-g; Yun and Oh, 2018; World Flora Online).

The core Ranunculales consists of Ber-Circaeasteraceae, Lardizabalberidaceae, aceae, Meninspermaceae and Ranunculaceae. Berberidaceae genera have capsules, follicles, berries, or utricles (Whetstone et al., 1997a-c; PlantsSystematics.org). The genera of Berberidaceae which have follicles are: Achlys DC. whose follicles have transverse dehiscence, Vancouveria C.Morren et Decne whose follicles are not aggregated, Bongardia C.A.Mey. which has a dry, thin, papery capsule with grooves or folds in its walls and seeds often with a dusty coating, Plagiorhegma Maxim. characterized by a leathery capsule with oblique longitudinal dehiscence, and *Jeffersonia* Bart. whose capsule has a reflexed lid (Loconte, 1993; O'Rourke, 1997a, b; Whetstone et al., 1997, World Flora

Online). Circaeasteraceae is endemic to China and Japan (Cheng-Yih and Kubitzki, 1993a; Dezhi and Bartholomew, 2001) and currently has only two species, both of which fruits are indehiscent achenes. Lardizabalaceae fruits are aggregates of berries or fleshy follicles that may be eaten, such as Akebia Decne. Decaisnea Hook.f. et Thomson, Lardizabala Ruiz, and Stauntonia DC. (Cheng-Yih and Kubitzki, 1993b). Menispermaceae fruits are drupes (Rhodes, 1997). Within Ranunculaceae are many genera whose fruits are achenes, berries, or utricles (Whittemore and Parfitt, 1997). However, genera that produce follicles include Aconitum L., Aquilegia, Beesia Balf. f. et W.W. Sm., Calathodes Hook. F. et Thomson, Caltha, Consolida Gray, Coptis Salisb., Delphinium, Dichocarpum W.T. Wang et P.K. Hsiao, Enamion Raf., Eranthis Salisb., Glaucidium, Gymnaconitum Wei Wang et Z.D. Chen, Helleborus Gueldenst., Isopyrum L., Leptopyrum Raf., Megaleranthis Ohwi, Nigella L., Paraquilegia J.R. Drumm et Hutch., Semiaquilegia Makino, Trollius L., Urophysa Ulbr., and Xanthorhiza Marshall (Huxley, 1992; Tamura, 1993; Ford, 1997a-g; Brink and Woods, 1997; Parfitt, 1997a-e; Warnock, 1997; Whittemore, 1997a-c; Whittemore and Parfitt, 1997; Liangqian and Kadota, 2008). Some of these ranunculacean genera have follicles in clusters or aggregates (e.g. Aconitum, Aquilegia, Caltha, Coptis, Delphinium), some are radially fused (such as Ena*mion*, *Megaleranthis*, *Trollius*), and some have follicles with prominent veins (e.g. Aconitum, Aquilegia, Eranthis, Helleborus, Trollius). The Ranunculaceae genera whose follicles are more than simple clusters or aggregates and instead somewhat fused include only Helleborus and Nigella (Whittemore and Parfitt, 1997). Those Helleborus species which have follicles connate at the base of the fruit may be somewhat capsular however the genus' follicles/capsules also have prominent transverse veins. Nigella fruits are unique in that they can be considered capsular as their follicles are partially connate and it is the only ranunculacean genus with a truly syncarpous gynoecium (Whittemore and Parfitt, 1997; Rohweder, 1976; Heiss et al., 2011). Unlike Helleborus there are no noticeable transverse veins on Nigella capsules. Thus, our following description of this fossil suggests that it may be a close relative to Nigella.

SYSTEMATICS

Class MAGNOLIOPSIDA Cronquist, Takhtajan et Zimmerman 1966

Order RANUNCULALES Jussieu ex Berchtold et J. Presl 1820

> Family RANUNCULACEAE Jussieu 1789

Genus *Costellifructus* Axsmith, Stults, Wang et Boucher, **gen. nov**.

Costellifructus alabamensis Axsmith, Stults, Wang, et Boucher, gen. et sp. nov.

Holotype here designated. UF19310-84718 at the Florida Museum of Natural History, Gainesville, FL (Figs 2A, B, 3 A-D).

Etymology. The genus name *Costellifructus* joins *costella* (derived from the catalonian language of northeastern Spain referring to a rib) with *fructus* (meaning fruit). The specific epithet *alabamensis* references the location where this fruit was found.

Type locality. Phenix City, Russell County, Alabama, U.S.A. 32.5°N, 85.0°W (Bingham et al., 2008).

Type Stratum. Clay lens of the Ingersoll Shale of the Eutaw Formation.

Collected by Terrell Knight and P. Sean Bingham.

Age. Santonian (83.5 to 85.5 Ma).

Material. Two specimens are preserved as compression/impression fossils on dark gray claystone (UF 19310-84718, UF 19310-84719).

Combined generic and species diagnosis: Urceolate fruit with basally fused follicles and long stylar extensions (Fig. 2A). Follicles maintain fusion through length of main body of fruit to form a capsule. Fusion discontinues at apical region; area of fusion is thickened, but depressed (Fig. 2B blue dots). Raised ridges within each follicle (Fig. 2B, purple dots) start basally and extend apically into the stylar extensions (Fig. 2B). The upper portion of the main fruit body curves towards the center (Fig. 2A). Aside from stylar extensions, the apical portion of the fruit gives evidence of valvate dehiscence due to a breakup and release of seeds, of which many are in evidence. Ovary is superior. Fruit wall is thickened. Pedicel has raised area directly below fruit body (Fig. 2A). Dehisced seeds are small, rugose, ridged along perimeter, pointed tip, obovate in longitudinal view and trigonal in cross-sectional profile (Fig. 3A). Thickened cell walls, characteristic of sclerenchyma in seed coats are in evidence under epiflourescence (Fig. 3B).

Combined generic and species description. Both the large and small fruits are urceolate (shape better seen in smaller, undehisced fruit) composed of basally fused follicles that maintain fusion through the length of the main body of the fruit (forming a capsule). Four fused follicles are observed in a dehiscing fruit specimen, three, possibly four fused follicles are observed in an undehisced fruit (Figs 2A, 3C).

Large, dehisced fruit: 4.3 cm long (excluding stylar extensions) and 1.7 cm wide; longest stylar extension is 2 cm long and 0.3 mm wide (Fig. 2A). Fusion discontinues at apical region; area of fusion is thickened, but depressed (Fig. 2B blue dots). Four fused follicles observed but is likely that originally consisted of at least five fused follicles based on presence of five stylar extensions at apices of fused follicles; follicles approximately 1.5 cm long and 3.5 mm wide; raised ridges within each follicle (Fig. 2B, purple dots) start basally and extend apically into the stylar extensions (Fig. 2B). This ridge was likely central within each follicle but shifted during the burial process as the follicle is compressed. The upper portion of the main fruit body curves towards the center and appears to have been a closed fruit prior to dehiscence (Fig. 2A). Aside from stylar extensions, the apical portion of the mature fruit is amorphous apparently due to breakup during valvate dehiscence. Ovary is superior. Relatively thickened fruit wall (measured at 155 µm). Pedicel on mature fruit is approximately 1.8 mm wide and has raised area directly below the fruit body (2 mm wide) interpreted as flattened receptacle (Fig. 2A). Epidermal cells of the fruit wall cuticle (Fig. 3D) are polygonal with straight anticlinal walls, as found in some species of Ranunculaceae (Shi and Li, 2003).



Figure 2. A. *Costellifructus alabamensis* large, dehisced fruit UF19310-84718, receptacle at black arrow, small light blue dots delineate the outline of the urceolate shape of the fruit. Larger white arrow indicates a line of depression on the fruit, smaller white arrow indicates a ridge on the fruit, scale bar = 0.5 cm. This was originally described as flower morphotype 1 (Knight, 2007); **B**. Portion of same large, dehisced fruit, blue dots designate depressed lines where follicles were fused. Purple dots indicate ridges on the fused follicles which continue into the stylar extensions. A couple of additional stylar extensions also indicated, sclae bar = 0.5 cm

Seeds from large fruit: six seeds of dehisced fruit are in evidence and are small (approximately 2.5×2 mm) and rugose (Fig. 3A); ridge displayed along perimeter of several seeds; pointed tip in evidence on one seed (Fig. 3A); obovate in longitudinal view; trigonal in a cross-sectional profile (Fig. 3A). Thickened cell walls, characteristic of sclerenchyma in seed coats are in evidence under epifluorescence (Fig. 3B). No raphe or hilum can be discerned, although shape suggests they are anatropous as expected in ranunculacean seeds (Wiegand, 1895; Leng and Friis, 2003). Although only six seeds are obvious, undeniably many more were contained in the whole fruit as partial seeds appear to be in evidence (Fig. 3A).

Small fruit, undehisced: urceolate shape (Fig. 3C); 1.5 cm long and 0.9 cm wide. Width dimensions change over course of fruit body and are approximately 3 mm basally, expanding centrally to 6 mm, narrowing to 5 mm near apex, and once again expanding to 7 mm near the apex before a collar of stylar extensions begins. Stylar extensions are not well preserved so their length is not measured. Three, possibly four fused follicles are observed; follicles are 2 mm wide. The fusion characteristics are easier to discern in the smaller fruit as it is more intact than the larger specimen.



Figure 3. A. Apical portion of large, dehisced fruit displaying several seeds amid stylar extensions, best represented seed at larger black arrow, additional seeds indicated with smaller black arrows, scale bar = 0.1 cm; **B**. Enlarged, epifluorescent picture of seed coat of seed seen in A, with thickened cell walls characteristic of sclerenchyma in seeds coats, scale bar = 100μ ; **C**. Smaller, un-dehisced fruit UF19310-84719, scale bar = 0.5 cm. This was originally described as flower morphotype 3 (Knight, 2007); **D**. Fruit cuticle from smaller, undehisced fruit showing straight anticlinal epidermal cell walls, scale bar = 50μ

No seeds are discerned in the smaller fruit so this is interpreted as an inflated fruit prior to dehiscence. Epidermal cells of the fruit wall cuticle (Fig. 3D) are polygonal with straight anticlinal walls.

Remarks. Two fruits are in evidence, a larger fruit in the process of expelling seeds apically via valvate dehiscence and a smaller, probably less mature fruit. Both fruits are urceolate; basally fused follicles maintain fusion through the length of the main body of the fruit to form a capsule. Several important characters of the fossil strongly suggest a ranunculacean type of fruit such as the follicular size and shape, the stylar extensions forming a characteristic ranunculacean 'beak' (Fig. 4A), the receptacle on the pedicel, the shapes and surfaces of the seeds, and the straight anticlinal walls of the cuticle epidermis. Aside from the stylar extensions and details that suggest a closed capsule prior to dehiscence, the apical portion of the mature fruit is difficult to further describe. The flattened disk, basal to the mature fruit, is interpreted as a receptacle and area of attachment for many floral parts, a character commonly associated in basal eudicot taxa. Based upon our deduction that the fossil is capsular we suggest it may be related to Nigella (Fig. 4B), which is usually designated as capsular with species' carpels often united 34 to all the length of the fruit (otherwise referred to as fused follicles), is often (but not always) an inflated fruit, and has stylar extensions (Zohary, 1983; Whittemore and Parfitt, 1997). We discussed several other ranunculacean fruits with follicles in the previous Results Section, "Comparisons among basal eudicot taxa fruits and seeds, when necessary", however, for purposes of further consideration, we offer a closer inspection of two genera within Ranunculcaceae. Although the general shape of the fossil looks similar to the ranunculacean genera Aquilegia L. or Delphinium L. (Fig. 4C, D), we point out some differences. The five follicles of Aquilegia are aggregated, not fused, but the genus has similar stylar extensions (Fig. 4C). It also seems that *Delphinium* L. (Fig. 4D) usually has three aggregated, but unfused, follicles although again with similar stylar extensions. While Tamura (1993) indicated that Delphinium (with approximately 320 species) sometimes has five follicles, we could not find a picture or drawing of any *Delphinium* with five follicles. Pictures of fruits for 32 species of the genus (of which 22 were found in listing of Flora of North America and which is one third of the *Delphinium* species listed in that publication) all had only three follicles (e.g. D. alabamicum Kral, D. carolinianum Walter, D. geyeri Greene, D. hansenii Greene, D. nudicaule Torr. et A. Gray, D. tricorne Michx., etc.) so it would appear that *Delphinium* is not a good candidate for comparison of a fruit with five fused follicles. Importantly, the probable area of follicle fusion in our fossil to form a capsule is actually a thickened depression and an area such as this is demonstrable on extant Nigella (Fig. 4B), but not on Aquilegia or *Delphinium* (Fig. 4C, D). The raised ridge on each follicle extends into the stylar extension, a character which is similar to Aquilegia and Delphinium. At least six seeds are in evidence and it is extremely likely that more were contained in the fruit during life. Several of these seeds display a ridge along their perimeter. The best-displayed seed has a pointed, ridged tip and we assume this is

a common character of these seeds. Seed surfaces within genus Nigella share some characters with our fossil as Nigella seeds may be granulate to reticulate (as opposed to Aquilegia which only has smooth seeds; Eranthis and *Xanthorhiza* have only smooth seeds also), have ridges, pointed tips, and be triquetrous (Zohary, 1983; Whittemore and Parfitt, 1997). For example, seeds of Nigella arvensis Pall. ex M. Bieb., N. fumariifolia Kotschy, N. integrifolia Regel, N. sativa L. and N. turcica Dönmez et Mutlu share these characters (Heiss et al., 2011). For our illustration here, we point out that Wang et al. (2009) updated the classification of Ranunculales/Ranunculaceae such that Aquilegia is in subfamily Thalictroideae Raf., while *Delphinium* and *Nigella* are within subfamily Ranunculoideae Arn., but separate tribes – *Delphinium* being in tribe Delphineae Schröd. and Nigella in tribe Nigelleae Schröd.

PHYLOGENETIC ANALYSIS WITH COSTELLIFRUCTUS

The phylogenetic analyses (Fig. 5) with Costellifructus indicate that Ranunculales and its seven families are monophyletic, and Costellifructus and the extant Ranunculaceae united together. Costellifructus and ten extant Ranunculaceae lineages formed a polytomy based on MP analysis (strict consensus tree shown in Fig. 5A), whereas BI analysis (Fig. 5B) shows that within Ranunculaceae, Glaucidioidae, Hydrastidoideae, Coptidoideae are successive sister taxa to the clade containing the other extant Ranunculaceae and Costel*lifructus*. These analyses generated congruent results about the position of Costellifructus. The phylogenetic analyses that included the fossil *Leefructus* generated similar results and weakly supports the sister relationship between Costellifructus and Leefructus.

DISCUSSION

COMPARISONS WITH PROBABLE FOSSIL RANUNCULACEAEN FRUITS

The fruit we describe is a syncarpous follicle (capsule) with characteristics suggestive of Ranunculales, particularly Ranunculaceae. Two fruits are in evidence; one is mature, already dehisced, but with several seeds



Figure 4. A. Drawing interpretation for *Costellifructus alabamensis*; **B.** *Nigella sativa* modified from Heba et al., (2009). Arrows denote depressed areas of fusion and raised area continuing into stylar extension; **C.** USAM 000013337 *Aquilegia canadensis* with aggregate of five follicles (they are not fused) and apparent transverse venation. Note raised area (at arrow) centralized on follicle continuing into stylar extension, scale = 0.5 cm; **D.** USAM 000013384 *Delphinium carolinianum* with three aggregate follicles (they are not fused). Note raised area (at arrow) centralized on each follicle continuing into stylar extension, scale = 0.1 cm

remaining in evidence; the other has not yet dehisced and we interpret it as less mature.

Ranunculaleans that display apocarpy, pseudosyncarpy, and syncarpy have been described from the earliest records (Friis et al., 2011), thus their fossil record (as it exists at this point) does not show any stratigraphic order to the appearance of more derived forms (e.g. fused follicles) from ancestral forms (e.g. free follicles) (Leng and Friis, 2003). Table 3 compares ranunculalean follicular fruit fossils and aspects of age, degree of follicle fusion, and follicle size. The putative ranunculacean fruits found in Lower Cretaceous deposits, *Santaniella lobata* Gobo et al., and *S. acuta* Gobo et al., from Brazil are aggregate follicles. *Leefructus mirus* (late Aptian to early Albian) has loosely fused carpels, *Ternaricarpites floribundus* Krassilov *et* Volynets (early to middle Albian) is described with free follicles, middle Albian species *Hyrcantha karatscheensis* (Vachrameev) Krassilov *et* Vachrameev is described as a mixture of apocarpy or with basal syncarpy, while *H. decussata* (Leng



Figure 5. Phylogenetic results with *Costellifructus alabamensis*. **A**. Strict consensus tree of 14,352 MPTs based on morphological data under the backbone constraint. Numbers above are bootstrap percentages. Fossil taxon (†) highlighted with a gray shaded box; **B**. Phylogram obtained from Bayesian inference analysis of the combined molecular and morphological data. Numbers above are Bayesian posterior probabilities (>0.65). Fossil taxon (†) highlighted with a gray shaded box

et Friis) Dilcher et al., has follicles fused about half the length from the base, *Ranunculaecarpus quinquecarpellatus* Samylina (Albian to Cenomanian) has free carpels, and *Sagaria cilentana* Bravi et al., (Albian to Cenomanian) has follicles fused for approximately ¾ of their lengths (Samylina, 1960; Krassilov et al., 1983; Leng and Friis, 2003; Dilcher et al., 2007; Krassilov and Volynets, 2008; Bravi et al., 2010; Sun et al., 2011; Gobo et al., 2022) (Note approximate date ranges from Table 3 footnote). From an evolutionary standpoint, it therefore appears that the fusion of follicles occurred early on within the Ranunculaceae, such that its refinement observed with *Sagaria cilentana* and more profoundly seen in *Costellifructus alabamensis* is not much of a stretch. Currently, within the family, a mix of ancestral and derived features are still recognized, although it is apparent that the younger fossils from Table 3, *Sagaria cilentana* and *Costellifructus alabamensis*, have a commonality with

Fossil fruit follicles	Age	Description	Size	Seeds	References
Santaniella lobata, Gobo, Coiffard, Bachelier, L.Kunzmann et Iannuzzi (cf. Ranunculaceae)	Early Cretaceous	Aggregate, pendulous Apocarpous	23–30 mm × 11–12 mm	3–5 mm × 2 mm; ellipti- cal, symmetri- cal, papillate, punctate	Gobo et al., 2022
Santaniella acuta Gobo, Coiffard, Bachelier, L.Kunzmann et Iannuzzi (cf. Ranunculaceae)	Early Cretaceous	Aggregate	21–25 mm × 12 mm	3–5 mm × 2 mm; ellipti- cal, symmetri- cal	Gobo et al., 2022
<i>Leefructus mirus</i> Sun, Dilcher, Wang et Chen ^a (Ranunculaceae)	late Aptian to early Albian	5 narrow, pseudosyncarpous carpels on flattened receptacle; loosely fused 2/3 of basal end; long stigmatic tips	6 mm × 4 mm		Sun et al., 2011
Ternaricarpites floribundus Krassilov et Volynets	early to mid- dle Albian	3 follicles, free to base. Cleft at tip	6–8 mm long		Krassilov and Volynets, 2008
Hyrcantha Krassilov et Vachrameev sp. [H. decus- sata (Leng et Friis) Dilcher, Sun, Ji et Li ^b , H. karat- scheensis Krassilov et Vach- rameev] (Ranunculaceae?)	middle Albian	2–4 carpels fused for about half their length from base or adherent only at the base. Mucronate apices. Cone- shaped receptacle	7–12.5 mm × 3 mm	Ovate, Smooth, flat- tened 2 mm × 1 mm	Krassilov et al., 1983; Leng and Friis, 2003, 2006; Dilcher et al., 2007
Ranunculaecarpus quinquecarpellatus Samylina	Albian to Cenomanian	5 free carpels		Reticulate	Samylina, 1960; Manchester et al., 2018b
Sagaria cilentana Bravi, Barone Lumaga et Mickle (aff. Ranunculaceae)	Albian to Cenomanian	3 follicles syncarpous fused to about ¾ from base. Mucronate tip. Cup-shaped receptacle; Dehiscent slits on follicles?	11 mm × 3 mm		Bravi et al., 2010
Costellifructus alabamensis sp. nov.	Santonian	3–4 follicles fused through ¾ of length from base	43 mm long (exclusive of stigmatic extensions) × 17 mm wide	Obovate retic- ulate, ridged, trigonal in x,s, hardened	This article

Table 3. Follicular fruit fossils of possible/probable ranunculalean/ranunculacean affinity

* Notes. Table does not include achenoid fossils with affinity to Ranunculales/Ranunculaceae. Table includes seeds for comparison if described for fruit. Aptian 125–113 Ma; Albian 113–100.5 Ma; Cenomanian 100.5–93.9 Ma; Santonian 86.3–83.6 Ma. ^a Name refers to a whole plant, however, the comparison in this table refers to only the fruit described.

^b Synonym: Sinocarpus decussatus Leng et Friis.

advanced degrees of follicle fusion. Follicles of Costellifructus alabamensis are about twice the size of those of Sagaria cilentana and Hyrcantha decussata, and much larger than those of Leefructus mirus, and Ternaricarpites floribundus. The stylar extensions of Costellifructus alabamensis, seen in members of the Delphinium clade of Ranunculaceae (i.e. Nigella species) are also suggested to have occurred in Leefructus mirus (Sun et al., 2011). The 'ribs' of Costellifructus alabamensis are unique from the other fruits of Table 3. Sagaria cilentana is specifically described as without ribbed character, while the carpel thickening of Hyrcantha decussata along the contact areas (Leng and Friis, 2003) was suggested as ribbed due to a thickened area of follicle fusion. In contrast, the ribs of Costellifructus alabamensis appear as thickened areas centralized on each style and proceeding into the stylar extensions, whereas the probable area of follicle fusion is actually a thickened depression (Fig. 2A, B).

The trait of centralized, raised, thickened areas on the follicles proceeding into stylar extensions is similar to that seen in fruits within the *Delphinium* clade (Fig. 4B–D).

In longitudinal view, the seeds of Costel*lifructus alabamensis* are asymmetrical in their curvature, but overall shape is obovate with a reticulate surface. The seed presented in the uppermost portion of the fruit displays a pointed apex, which we presume to be a common feature. From a cross-sectional perspective, the seeds are trigonal, appear firm, and ridges are in evidence. No raphé or hilum can be discerned, although their shape may suggest they are anatropous as expected in a ranunculacean fruit (Wiegand, 1895; Leng and Friis, 2003). The ridges and reticulate surface are features in common with Ranunculaecarpus quinquecarpellatus; while the firm, trigonal shape is dissimilar to the flattened seeds of Hyrcantha decussata and the elliptical, symmetrical seeds of Santaniella species



Figure 6. Phylogenetic results including *Costellifructus alabamensis* and *Leefructus*. Phylogram obtained from Bayesian inference analysis of the combined molecular and morphological data. Numbers above are Bayesian posterior probabilities (>0.65). Fossil taxa (†) highlighted with a gray shaded box

(Samylina, 1960; Leng and Friis, 2003; Manchester et al., 2018b; Gobo et al., 2022).

CONSIDERATIONS OF THE INGERSOLL SHALE

The Ingersoll Shale accumulated steadily during a period of estuarine transgression, hastily infilling a shallow, narrow tidal channel with fine sediment under a low-energy regime. This resulted in a rapidly-accumulating anoxic environment that suffered little bioturbation after deposition (Bingham et al., 2008; Savrda et al., 2009; Knight et al., 2010). Fossil impact of this condition is that large leaves and articulated branches did not undergo damage during transport and transport was limited. Therefore, the Ingersoll Shale floral components are assumed to have been part of the shoreline community in the immediate area. Original investigation of the Ingersoll Shale flora listed 41 different angiosperm leaf morphotypes (Knight, 2007). Our current opinion is that this gives an exaggerated measure of the floral diversity, as it appears in some instances the same taxon is represented by multiple morphotypes and that the plant biodiversity is somewhat limited. Most angiosperm taxa in this assemblage

are represented by only one or two leaves. Importantly, however, in terms of number of specimens, Manihotites georgiana Berry (1910, 1914, 1919a, b, 1925) is the primary angiosperm contributor while 'Sassafras-appearing morphotypes' is the secondary angiosperm contributor to the Ingersoll Shale flora. It must also be emphasized that gymnosperms, such as Araucariaceae Henkel et W.Hochst., Cheirolepidiaceae Tahktajan and Cupressaceae Gray (Taxodiaceae) are equally numerous contributors to this flora. The significant proportion of the *M. georgiana* input to the floral numbers may suggest that it is possibly the vegetative component to the original plant of this fruit. We have noted commonality of polygonal epidermal cells with straight anticlinal walls in both M. georgiana (from specimens of the Ingersoll Shale, as well as the Blackhawk Formation in Utah) and Costellifructus alabamensis. Interestingly, Berry (1914) considered the possibility of *M. georgiana* as possibly ranunculacean in his initial assessment because of the deeplydissected, multiply-lobed leaf lamina. Manihotites georgiana has basally palinactinodromous primary venation but its subsequent higher order venation does not fit into any standard categorization pattern (Ellis et al., 2009). It has

also been noted that the high diversity of leaf venation and leaf dissection patterns found in ranunculalean/ranunculacean leaves does not indicate separation into categories fitting into any phylogenic pattern for the group, (Hickey and Wolfe, 1975; Avita et al., 1981; Gleissberg and Kadereit, 1999).

EVOLUTIONARY SIGNIFICANCE

Using character trait categories from the phylogenetic analysis of Ranunculales (Wang et al., 2009, 2016) for available morphological characters of this fossil fruit supports a close relationship to extant Ranunculaceae. The uncanny resemblance of Costellifructus to Nigella fruits would indicate a strong relationship and infer that crown taxa of Ranunculaceae were established at least by the Santonian. Anderson et al. (2005) estimated an age of approximately 120 Ma for the stem group of Ranunculales based on a molecular clock model. However, the assertion that *Leefructus* is Ranunculaceae (125 Ma) along with the probability that Hyrcantha is also ranunculacean would push that date back further (Dilcher et al., 2007; Sun et al., 2011). Differences in statistical analysis led Anderson et al. (2005) to consider that the crown groups of Ranunculaceae occurred around either 87 Ma or 73 Ma. Based upon the presence of Costel*lifructus alabamensis* in Santonian soil, it is apparent the the older age is more likely. The remarkable similarity of Costellifructus alaba*mensis* with its fused follicles to the syncarpous fruits of Nigella (Nigelleae) may also clear up some of the phylogenetic confusion within the family Ranunculaceae (Heiss et al., 2011). Plastid phylogenomic analyses support Nigelleae Langlet ex Tamura as sister to Delphinieae Schrödinger (Zhai et al., 2019), whereas nuclear phylogenomic analyses suggest Nigelleae, Delphineae, Cimicifugeae Torr. et A. Gray and Caltheae Bercht. et J. Presl. formed a clade (He et al., 2022). Molecular dating estimation indicates that these four tribes, the other five tribes of Ranunculoideae Arn., and Thalictroideae Raf. diverged within a narrow time span (Wang et al., 2016). Our interpretation of this fossil is consistent with that hypothesis.

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