

Morphology, affinities and phytogeographic history of *Porosia* Hickey in the Cretaceous and Paleocene of North America and Asia

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Received 3 January 2014; accepted for publication 10 March 2014

ABSTRACT. Morphology and anatomy of the extinct angiosperm fruit, *Porosia verrucosa* (Lesqueruex) Hickey, are documented in detail based on various modes of preservation including molds, casts, and permineralizations from more than seventy localities in the late Cretaceous and Paleocene. The fruits are schizocarpic with paired unilocular, single-seeded mericarps seated on a prominent gynophore with an hypogynous perianth borne on a long pedicel. The most distinctive feature of these fruits is the regularly spaced cylindrical intrusions over the surface of the endocarp. These are interpreted to represent oil cavities similar to those common in the fruits of extant Rutaceae. The oldest known occurrences of *P. verrucosa* are from the Late Cretaceous (Campanian to Maastrichtian) of western North America, but the genus traversed Beringia and became widespread in the Paleocene both in Asia (Kazakhstan, Amur Region, and Koryak Highlands), and North America (Montana, North Dakota, Wyoming, Colorado, Oregon, Washington, Alberta, Saskatchewan). It extended to the late Paleocene in the Rocky Mountain and Great Plains region, and appears to have become extinct near the Paleocene-Eocene boundary.

KEYWORDS: Fossil fruits, Rutaceae, Campanian, Maastrichtian, Paleocene

INTRODUCTION

Fossil plant remains known as *Porosia verrucosa* (Lesquereux) Hickey from the Late Cretaceous and Paleocene of North America and Asia have been elusive as to their morphological structure and taxonomic relationships. The distinctive reniform bodies, typically 1 to 2 cm in diameter and a few mm thick, are usually preserved as impressions with prominent closely spaced protuberances. They were regarded as float leaves of an aquatic plant by some authors (Brown 1962, Krassilov 1973, 1976, Hickey 1977, Crane et al. 1990), and as fruits or seeds by others (Lesquereux 1878, McIver & Basinger 1993, Serbet 1997).

Porosia verrucosa fossils were considered by several investigators (Dorf 1942, Hantke 1954, Brown 1962, Krassilov 1973, 1976)

to be specialized float leaves congeneric and conspecific with leaves of the extinct aquatic araceous plant, *Limnobiophyllum scutatum* (Dawson) Krassilov (1973) – “*Lemna*” *scutata* of Dawson 1875. However, *Porosia* specimens were never found in direct attachment with *Limnobiophyllum* leaves and the two entities are only rarely found together at the same site. Whereas *Porosia* apparently was restricted to Asia and North America, *Limnobiophyllum* also extended into the Neogene of southern Europe (Kvaček 1995) where *Porosia* is lacking. Complete specimens of *Limnobiophyllum scutatum*, with roots, stolons, leaves, and flowers with stamens containing spinose pollen, have proven that *L. scutatum* belongs to the Araceae-Lemnaceae clade (Stockey et al.

1997). In contrast, the systematic affinities of *Porosia* have remained elusive.

Unequivocal proof that the *Porosia* structures represent fruits rather than leaves is provided by permineralized specimens. A silicified *Porosia verrucosa* specimen from the Horseshoe Canyon Formation of Drumheller, Alberta, Canada (ca 71 Ma) was sectioned by Serbet (1997), showing a seed inside the locule, surrounded by pericarp containing regularly spaced cavities. Those cavities, commonly filled with sediment during clastic deposition, correspond with the verrucae, or tubercles, commonly observed in impression and compression fossils. Additional permineralized specimens presented herein from the Paleocene of North Dakota, USA, also show important morphological and anatomical characters confirming that *P. verrucosa* represent unilocular fruits.

The purpose of this article is to compile available information on the morphological and anatomical structure of *Porosia* and consider its systematic affinity relative to extant angiosperms, and to compile geographic and stratigraphic data on its distribution. Characters of fruit morphology and anatomy indicate likely affinities to the Rutaceae. Although leaves have not been found in direct attachment to twigs bearing these fruits, we infer the most probable leaf candidate from those found in co-occurrence at numerous localities. A compilation of all localities known to possess *P. verrucosa* is provided to document the geographic and stratigraphic range.

MATERIAL AND METHODS

Specimens collected from western North America during the 1980s through 2013 by S.R. Manchester with students and colleagues from sites in Wyoming, Montana, North Dakota, Oregon are deposited at the Florida Museum of Natural History. Other North American impression specimens were observed and photographed in museum collections including the Smithsonian (collections of Leo Lesquereux, Frank H. Knowlton, Roland Brown, Leo Hickey, and Scott Wing), the Field Museum, Chicago (collections of Patrick Herendeen and Peter Crane), the University of California Museum of Paleontology (collections of Erling Dorf), the University of Washington, Burke Museum (collections of Donald Hopkins), the Denver Museum of Nature and Science (collections of Regan Dunn, Richard Barclay, and Kirk Johnson), and the Tyrrell Museum, Drumheller, Alberta (Aulenback & Braman 1991).

Asian specimens were collected from the Amur region by V. Krassilov, M.A. Akhmetiev, T.M. Kodrul,

and S.R. Manchester; from the Koryak region by L.B. Golovneva; and from the Zaisan Basin in Kazakhstan by E.V. Romanova. The collections studied are deposited at the Institute of Biology and Pedology of the Far Eastern Branch of the Russian Academy of Sciences, Vladivostok (Krassilov collection), the Geological Institute of the Russian Academy of Sciences, Moscow (collections of Akhmetiev and Kodrul), the Komarov Botanical Institute of the Russian Academy of Sciences, St. Petersburg (collections of Golovneva), and the Institute of Botany and Phytointroduction, of the Committee of Science and Education of the Republic of Kazakhstan, Almaty, Kazakhstan (Romanova collection).

Prefixes used for the designations of specimens and localities cited herein are BIN (Komarov Botanical Institute, St. Petersburg), DMNH (Denver Museum of Nature and Science), FMNH (Field Museum of Natural History, Chicago), GIN (Geological Institute, Moscow), IBP (Institute of Botany and Phytointroduction, Almaty, Kazakhstan), TMP (Tyrrell Museum, Drumheller), UCMP (University of California Museum of Paleontology, Berkeley), UF (Florida Museum of Natural History, University of Florida, Gainesville), UWBM (Burke Museum, University of Washington, Seattle), USNM (United States Natural History Museum, Smithsonian Institution), and USGS (US Geological Survey – specimens now deposited at USNM).

Locality data are provided as precisely as possible from published sources, field notes, and museum records (Tab. 1). Latitude and longitude coordinates are presented in relation to the WGS 84 datum, derived from direct GPS, by conversion from the traditional township and range coordinate systems (website for conversion: <http://www.earthpoint.us/TownshipsSearchByDescription.aspx>), or by “revisiting” the sites via Google Earth. Localities were plotted on geographic maps (Fig. 1) using the websites: <http://woodshole.er.usgs.gov/mapit/> and http://www.odsni.de/odsni/services/paleomap/adv_map.html.

Impression specimens were found by breaking sediment along bedding planes of siltstone and shale with a hammer and chisel. Both halves (counterparts) were retained whenever possible, so that opposite surfaces of the same fruits could be observed. Details obscured by covering sediment were exposed in the laboratory by precision chipping or grinding with a diamond-tipped drill while observing through a dissecting microscope. Details of cuticle and individual cell layers on compression specimens from Belaya Gora and Arkhara Hill were observed using a Zeiss Axiostar Plus light microscope (LM) and TESCAN and CAMSCAN scanning electron microscopes (SEM). Naturally macerated cuticles were cleaned with HF for 19 hours, washed with distilled water, then treated briefly with 5% KOH, washed and embedded in glycerin jelly to prepare slides for LM study. For SEM observation, cuticles were mounted on stubs and coated with gold.

Permineralized, anatomically preserved specimens from the Almont, and Beicegal Creek localities of North Dakota were photographed in their initial fracture plane, then reassembled with cyanoacrylate glue and sectioned transversely with a Microslice II annular diamond saw to reveal internal anatomy.

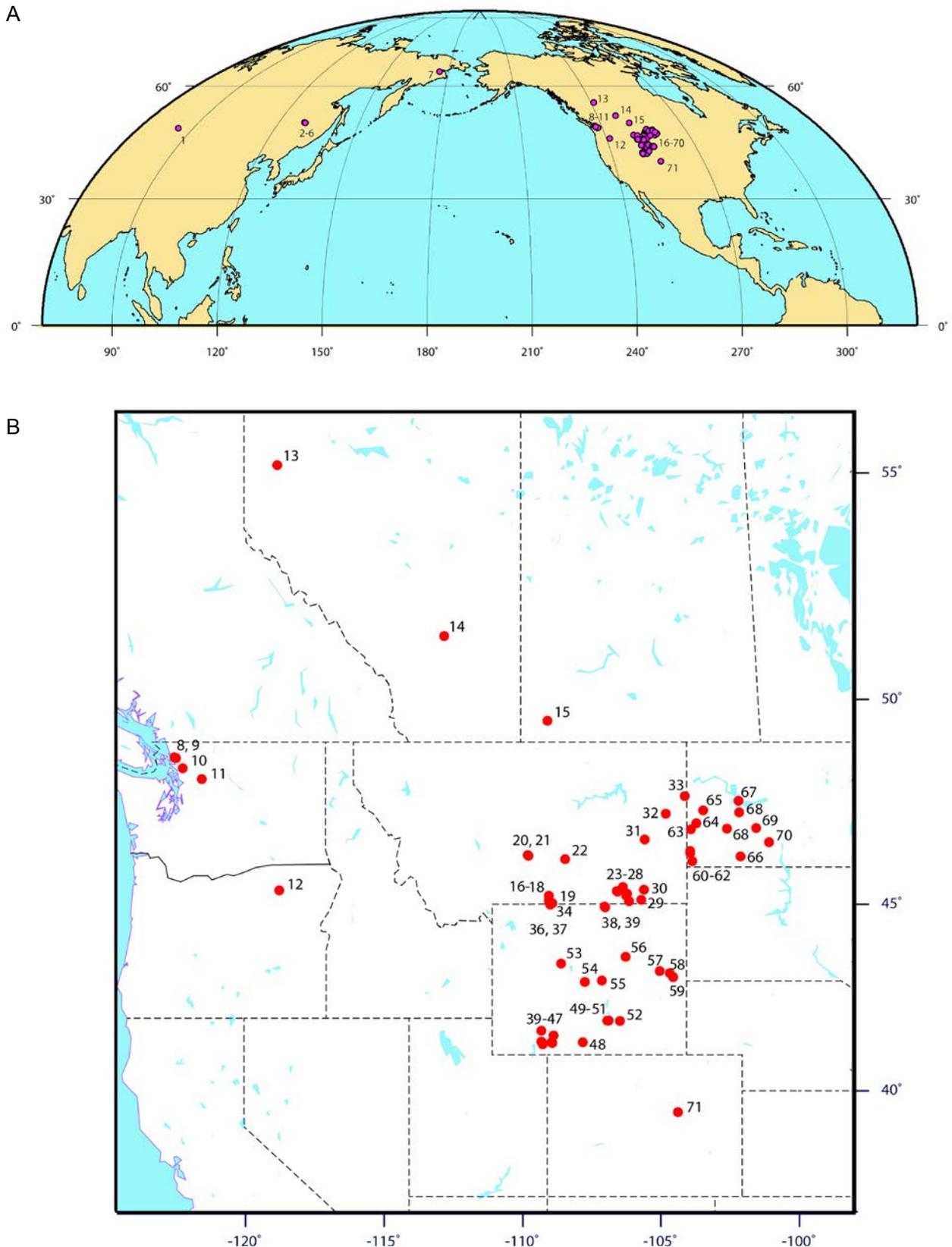


Fig. 1. A. Map of Asia and North America showing distribution of *Porosia verrucosa* fruits. B. Detail of North American distribution. Numerical labels coincide with the source, age, and collection data provided in Table 1

High resolution depth of focus was obtained with successive images taken with a Pentax K7 camera fitted with a Zeiss luminar lens with maximum aperture setting, using a Cognisis Stack Shot camera focusing rail. Successive images were composited with Helicon focus

software. Anatomical images of the sectioned permineralized fruits were obtained with sections immersed in liquid (xylene in some instances, water in others), with a Canon Rebel camera mounted on a Zeiss photomicroscope.

Table 1. Localities from which *Porosia* is known in Asia (1–7) and North America (8–71), plotted in Fig. 1

Locality	Map no.	Age, Formation	Coordinates	Collection number	Notes, example specimens
Karabiryuk, Zaisan Basin, Kazakhstan	1	Early Paleocene (Danian)	48°34.436'N, 84°26.556'E	KB324, 325	Akhmetiev & Shevyreva 1989, Golovneva 2008 (coll. E.V. Romanova, IBP)
Bureya River Island, Amur Region	2	Early Paleocene (Danian) Upper Tsagayan Fm	49°34.656'N, 129°36.338'E	Krassilov 575	Krassilov 1976, 25–30 m above flood plain
Darmakan Valley 2, Amur Region	3	Early Paleocene (Danian) Upper Tsagayan Fm	49°35.860'N, 129°36.532'E	Krassilov 571, 574	Krassilov 1976, 100 m upstream from 566, 12 m above floodplain
Darmakan Valley 1, Amur Region	4	Early Paleocene (Danian) Upper Tsagayan Fm	49°35.860'N, 129°36.532'E	Krassilov 566	Krassilov 1976, 100 m from the mouth 5 m above floodplain
Belaya Gora Amur Region	5	Early Paleocene (Danian) Upper Tsagayan Fm	49°36.127' N, 129°36.078'E	UF 18650	Krassilov 1976; Akhmetiev et al. 2002; UF30344, 30350, 30486, 33741, 60662, 60663
Arkharo Hill, quarry, lower unit, Amur Region	6	Early Paleocene (Danian) Upper Tsagayan Fm	49°25.494'N, 130°05.062'E	Krassilov 570	Akhmetiev et al. 2002, Krassilov 1976
Ovrazhniy River, Koryak Highlands	7	Early Paleocene (Danian) Rarytkin Fm	64°29.856'N, 175°36.756'E	Golovneva 72	Pl. 27, figs 4–6 in Golovneva 1994b
Chuckanut Drive, Washington	8	Paleocene/Early Eocene Chuckanut Formation	48°37.481'N, 122°27.2645'W	UWBM B6206	UWBM PB 22530, Coll. Don Hopkins
Clayton Beach, Washington	9	Paleocene/Early Eocene Chuckanut Formation	48°38.478' N, 122°28.834'W	UWBM B4590	UWBM PB 93331, 93333, Coll. Don Hopkins
Walker Valley, Washington	10	Eocene Padden Member, Chuckanut Fm	48°22.620'N, 122°11.280'W	UWBM B7691	UWBM PB16900, 23887
Coal Lake Rd, Washington	11	Paleocene Chuckanut Fm	48°06.7215' N, 121°31.28117'W	UWBM B6200	UWBM PB 9533, 92941, Coll. Don Hopkins
Denning Spring near Pilot Rock, Oregon	12	Paleocene or early Eocene "Herren" Fm.	45°20.923'N, 118°43.486'W	UF 271	Fig. 3 in Gordon 1985, Fig 17d in Manchester 1999
Grande Prairie, Alberta	13	Upper Cretaceous (Campanian)	55°9.912'N, 118°47.973'W	TMP	Fig. 666 in Aulenback 2009
Drumheller, Alberta	14	Upper Cretaceous (Campanian) Horseshoe Canyon Fm	51°28.339'N, 112°46.070'W	TMP	Kents Knoll; Serbet 1997
Ravenscrag Butte, Saskatchewan	15	Early Paleocene Ravenscrag Fm	49°30.4'N, 109°1.2'W	US32	Mclver & Basinger 1993
SW of Bridger, Montana	16	Fort Union Fm	45°13.010'N, 108°58.604'W	USGS 9402	Brown 1962
Silver Tip, Montana	17	Paleocene (Tiffanian) Fort Union Fm	45°6.248'N, 108°58.767'W	LJH7866	Hickey 1980
Foster Mine, Montana	18	Paleocene Fort Union Fm	45°8.141'N, 109°10.774'W	USNM 14164	Hickey 1980
Serendipity Summit, Montana	19	Early Paleocene (Torrejonian) Fort Union Fm	45°01.89'N, 108°51.86'W	UF 18912 = USNM 14191	Hickey 1980, UF 65000
Fish Cr., Montana	20	Paleocene	46°14.73'N, 109°44.88'W	UF 19028	UF 39295
Melville, Montana	21	Paleocene Lebo Mbr, Fort Union Fm	46°13.561'N, 109°43.626'W	USGS 8563	Sandstone capping Bear Butte
East Fork Razor Cr., Montana	22	Paleocene Fort Union Fm	46°8.278'N, 108°23.739'W	UF 18163	UF 25934; coll. Gary Eichhorn
Birney road cut, Montana	23	Paleocene Tongue River Mbr, Fort Union Fm	45°19.534'N, 106°30.506'W	UF 18968	UF 34511, 38354, 49681–83, 50912, 50914–20, 52149, 52150, 53384–86, 60413
Brown Gulch, Montana	24	Paleocene Tongue River Mbr, Fort Union Fm	45°20.491'N, 106°32.303'W	UF 19166	UF 51015
O'Dell Cr., Montana	25	Paleocene Tongue River Mbr, Fort Union	45°26.088'N, 106°18.772'W	UF 19165	UF 52184–52189
Horse Cr., Montana	26	Paleocene Tongue River Mbr, Fort Union	45°15.87'N, 106°09.62'W	UF 18969	UF 34526, 34528, 50985
Tooley Cr., Montana	27	Paleocene Tongue River Mbr, Fort Union	45°12.794'N, 106°11.321'W	UF 18745	UF 65001
Sayle Road, Montana	28	Paleocene Tongue River Mbr, Fort Union	45°5.238'N, 106°4.926'W	USGS 8887	Brown 1962

Table 1. Continued

Locality	Map no.	Age, Formation	Coordinates	Collection number	Notes, example specimens
Traub Ranch, Montana	29	Paleocene Tongue River Mbr, Fort Union	45°06.75'N, 105°39.48'W	UF 18133	UF 33735
SW of Broadus, Montana	30	Paleocene Tongue River Mbr, Fort Union	45°21.956'N, 105°32.451'W	USGS 8786	Brown 1962
Shirley Canal, Montana	31	Paleocene Lebo Mbr, Fort Union Fm	46°38.173' N, 105°31.282' W	UF 19380 =USGS 8519	UF 60221
Stipek, Montana	32	Paleocene Fort Union Fm	47°16.453'N, 104°45.705'W	USGS 8196	Brown 1962
East of Sidney, Montana	33	Paleocene Fort Union Fm	47°42.841'N, 104°5.211'W	USGS 8195	Hance 1912, Brown 1962
Elk Basin, Wyoming	34	Paleocene Fort Union Fm	44°59.769'N, 108°55.412'W	USGS 9404	Brown 1962
Northeast of Parkman, Wyoming	35	Paleocene Fort Union Fm	44°59.304'N, 107°11.966'W	USGS 5512	Pl. 16, fig. 10 in Brown 1962. 7 mi NE of Parkman
Bighorn Basin, Wyoming	36	Late Paleocene (Clarkforkian) Fort Union Fm	44.2°N, 107.9°W	USNM 37558 S.L. Wing 868	Low resolution coordinates
West side Tongue River, Wyoming	37	Paleocene Fort Union Fm	44°56.368'N, 106°57.789'W	USGS 4897	Pl. 16, fig. 1 in Brown 1962
Carneyville I, Wyoming	38	Paleocene Fort Union Fm	44°55.786'N, 106°56.458'W	USGS 4898	Brown 1962
Carneyville II, Wyoming	39	Paleocene Fort Union Fm	41°17.182'N, 106°56.741'W	UF 19382	UF 60493
Little Bitter Cr., Wyoming	40	Paleocene Fort Union Fm	44°50.130'N, 106°56.524'W	USGS 8920	Brown 1962
East side Little Bitter Cr., Wyoming	41	Paleocene Fort Union Fm	41°20.279'N, 109°12.454'W	USGS 8922	Brown 1962
W side Little Bitter Cr., Wyoming	42	Paleocene Fort Union Fm	41°19.56'N, 109°14.28'W	UF 18202	UF 28825, Wilf 2002
W of Earnest Butte, Wyoming	43	Paleocene Fort Union Fm	41°22.034'N, 109°14.748'W	USGS 5321	Brown 1962
Black Buttes, Wyoming	44	Late Cretaceous (Maastrichtian) Lance Fm	~41°31.635'N; 108°48.590'W	USNM	Hickey 1977, pl. 54, fig. 3, Lesquereux (Locality info from Breithaupt 1982)
Big Flat Draw I, Wyoming	45	Paleocene Fort Union Fm	41°20.457'N 108°51.673'W	UF 15778	UF 10457
Big Flat Draw II, Wyoming	46	Paleocene Fort Union Fm	41°20.62'N 108°52.45'W	UF 18199	UF 21792
NW of Rock Springs, Wyoming	47	Paleocene Fort Union Fm	41°39.854'N, 109°15.878'W	USGS 9403	5 miles NW Rock Springs, N Side of Highway Brown 1962
Mexican Flats, Wyoming	48	Paleocene Fort Union Fm	41°21.328'N, 107°44.828'W	UF 18540	UF 33732, 33733, 33742
Saddle Back Hills, Wyoming	49	Paleocene Fort Union Fm	41°56.285'N, 106°52.363'W	USGS 6985	Brown 1962
Big Ditch, Wyoming	50	Paleocene Fort Union Fm	41°56.588'N, 106°49.834'W	USGS 6417	Brown 1962
Hanna Basin, Wyoming	51	Paleocene (Tiffanian) Ferris Fm.	41°56.317'N, 106°50.233'W	DMNH 2629	DMNH 23597 Coll. Regan Dunn
Como, Wyoming	52	Paleocene (Tiffanian) Ferris Fm.	41°56.010'N, 106°24.950'W	USGS 8424	3.3 mi NW of Como, USNM cabinet 239 d4,
Shotgun Butte Area, Wyoming	53	Paleocene Fort Union Fm	43°27.109'N, 108°32.787'W	USGS 9405	Brown 1962
Gas Hills, Wyoming	54	Paleocene Fort Union Fm	42°58.164'N, 107°41.477'W	USGS 9129	Brown, 1962
Hells Half Acre Wyoming	55	Paleocene Fort Union Fm	43°1.056', N, 107°4.775'W	UF 15740-e	UF 33743–33745
Linch, Wyoming	56	Paleocene Fort Union Fm	43°37.807'N, 106°12.366'W	UF 18260	UF 16022, 16023, 16025
Cow Cr., Wyoming	57	Paleocene Fort Union Fm	43°15.83'N, 104°59.72'W	UF 18132	UF 33736–33738
Lance Cr., Wyoming	58	Late Cretaceous (Maastrichtian) Lance Fm	43°12.461'N, 104°37.383'W	UCMP P3651	Dorf 1942

Table 1. Continued

Locality	Map no.	Age, Formation	Coordinates	Collection number	Notes, example specimens
Lance Cr. 2, Wyoming	59	Late Cretaceous (Maastriichtian) Lance Fm	43°5.941'N, 104°30.254'W	UCMP P3859	Dorf 1942
Bowman County, N. Dakota	60	Early Paleocene (Puercan) Ludlow Mbr, Fort Union Fm	46.1°N, 103.8°W:	KJ87140	8.3 m above K-T boundary, Johnson 2002
Bobcat HCIII, N. Dakota	61	Late Cretaceous (Lancian) Hell Creek Fm	46°17.717'N, 103°52.700'W	DMNH 1.573	2.14 m below K-T boundary, Johnson 2002
Hastata Heaven, N. Dakota	62	Late Cretaceous (Lancian) Hell Creek Fm	46°20.767'N, 103°52.900'W	DMNH 2099	17.075 m below K-T boundary, Johnson 2002
Sentinel Butte, N. Dakota	63	Paleocene	46°53.100'N, 103°50.984'W	USGS 8913	Brown 1962
Wannagan Cr., N. Dakota	64	Paleocene (Tiffanian) Tongue River Fm	47°2.074'N, 103°39.684'W		Erickson 1999, Melchior & Hall 1983
Beicegel Cr, N. Dakota	65	Paleocene Sentinel Butte Fm	47°21.98'N, 103°25.02'W	UF 18796	UF 34634, 34637
10 miles south of Bentley, N. Dakota	66	Paleocene Bear Den Mbr, Golden Valley Fm	46°12.530'N, 102°3.958'W	USGS 6376	Hickey 1977
N of Gladstone, N. Dakota	66	Paleocene Bear Den Mbr, Golden Valley Fm.	46°54.188'N, 102°33.534'W	USNM 14083	Pl 54, fig. 4 in Hickey 1977
Elbowoods, N. Dakota	67	Paleocene Ft. Union Group	47°5.083692'N, 102°9.193710'W	USGS 8212	Pl. 16, fig. 3 in Brown 1962
Goodman Cr. Bluffs, N. Dakota	68	Bear Den Mbr, Golden Valley Fm, Paleocene	47°18.772' N, 102°6.566' W	UF 18750= USNM 14059	Hickey 1977
Almont, N. Dakota	69	Late Paleocene (Tiffanian) Sentinel Butte Fm,	46°55.214'N, 101°30.290'W	UF 15722	UF 30579, 53389
E. Morton County, N. Dakota	70	Bear Den Mbr, Golden Valley Fm, Paleocene	46°34.211'N, 101°2.011'W	USGS 6652	Hickey 1977
Comanche Cr. Rd., Colorado	71	Early Paleocene (Puercan) Denver Fm	39°24.763'N, 104°20.021'W	DMNH 2360	Coll. R. Barclay

SYSTEMATIC POSITION

ANGIOSPERMAE

SAPINDALES

Rutaceae

Porosia Hickey 1977 emend.
Manchester & Kodrul

Emended diagnosis. Suborbicular to reniform fruit bodies, lenticular in cross section, borne in pairs on a gynophore, subtended by a narrow hypogynous perianth scar and an elongate pedicel. Each mericarp unilocular, single-seeded, composed of a fibrous, woody endocarp, beset with numerous closely spaced cylindrical tubules oriented at right angles to the surface, penetrating nearly to the locule. Endocarp covered by soft mesocarp tissue, and well-cutinized exocarp. A set of ramified, flabellate veins radiates through the mesocarp from the ventral margin of each mericarp, and is faintly impressed on the mesocarp surface.

Comment. Hickey's diagnosis used the term "body" for these structures because of the prior disagreements as to whether they represented leaves or fruits. Our emended diagnosis treats the organs as "fruit bodies", because the earlier controversy has been resolved. The observation that these fruits were borne in pairs on a gynophore with a hypogynous perianth have also been added, and the original wording in Hickey's diagnosis referring to carbonaceous ground mass has been replaced with text on the sclerenchymatous anatomy now confirmed from permineralized specimens.

Porosia verrucosa (Lesquereux) Hickey
1977 emend. Manchester & Kodrul

Basionym. *Carpites verrucosus* Lesquereux 1878; p. 305, Pl. 10, fig. 9.

Synonymy.

1962 *Hydromystria expansa* (Heer) Hantke in Brown 1962 (part); p. 52, Pl. 16, figs 1, 3, 10, only

1973 *Limnobiophyllum scutatatum* (Dawson) Krassilov (nontypes); p. 110, Pl. 23, figs 46–61;

1976 *Limnobiophyllum scutatatum* (Dawson) Krassilov (nontypes); p. 52, Pl. 12, figs 1–12.

Emended diagnosis. Fruit schizocarpic, with two mericarps, typically bisymmetrical, but sometimes asymmetrical with one of the mericarps remaining small and less developed. Mericarps lenticular in cross section, suborbicular to reniform in face view with convex dorsal surface, the ventral edges straight, parallel with the pedicel in lower half, convex in apical half. Mature, fully developed endocarps 8 to 20 mm high, 7 to 16 mm wide, and 1.8 to 2.2 mm thick; smaller, incompletely developed mericarps (possibly abortive), similar in shape to mature mericarps, 2–4 mm high, 2–3 mm wide. Pedicel 8 to 20 mm long, 1 to 1.5 mm thick, abruptly expanded at the junction with fruit. Pedicel appears to be articulate at intervals of 6 to 12 mm below the fruit. Mericarps together ensheathed by fleshy mesocarp and cuticle-covered exocarp. Stamens not seen. Possible remnants of a narrow style situated in the axis of symmetry between the two mericarps. Each endocarp unilocular, with apparently one seed developed, lensoidal in cross section with a pair of planar cotyledons. Endocarp wall 500–600 μm thick, composed of fibers 30 to 64 μm in diameter and 300–400 μm long, and penetrated by numerous cylindrical intrusions (tubercles open to the surface of endocarp, extending almost to the locule). These tubercles are evenly spaced across both faces of the endocarp. Epidermal layer composed of polygonal cells, 30–35 μm in diameter, with straight anticlinal walls. Stomata distributed about 10 per mm^2 , irregularly oriented with anomocytic to cyclocytically arranged subsidiary cells similar in size and shape to surrounding cells.

Neotype. In establishing *Porosia* as a new genus, Hickey (1977) adopted *Carpolithus verrucosus* of Lesquereux (1878) as the type. Because Lesquereux' original specimen was missing, Hickey designated a neotype from the same locality and museum collection (Black Buttes, Wyoming, USNM 948; refigured here, Pl. 2, fig. 17).

Additional specimens. UF 15722-6176 (Crane et al. 1990), 30579, 53389, UF 15740D-33743-33745, 15740E-23179, UF 15776-33734, UF 15778-14057, UF 18132-33736-33738, UF 18133-33735, UF 18163-25934 (Manchester 1999), UF 18199-21792, UF 18202-28825, UF 18260-16022, 16023, 16025, UF 18331-16020, UF 18540-33732, 33733, 33742, UF 18650-27771,

30344, 30350, 30486, 33741, 60662, 60663, UF 18650-27771, UF 18745-65001, UF 18750-33739, 33740, UF 18796-34634, 34637, UF 18912-65000, UF 18968-38354, 49681-49683, 50912, 50914-50920, 52149, 52150, 53384-53386, 60413, UF 18969-34511, 34520, 34526, 34528, 50985, UF 19165-52184-52189, UF 19166-51015, UF 19380-60221, UF 19382-60493 [Digits before hyphen indicates locality; dash (-) indicates a consecutive numerical series of specimens], FMNH-PP34481 (Crane et al. 1990, fig. 29g), PP 34483 (Crane et al. 1990, fig. 29c), PP 45561.

Description. Our reconstruction diagram (Fig. 2) combines information from impression, permineralization and compression specimens to depict the fruit as it looked when ripe. Complete pedicellate specimens indicate that the fruits developed from paired ovaries, with their ventral margins coalesced in their basal half (Pl. 1, figs 1-7); hence they appear to be schizocarpic. A prominent thickening at the junction of the pedicel and the fruit (Pl. 1, figs 5-10) indicates the position of a gynophore and hypogynous perianth. Each mericarp is elliptical to reniform, more or less D-shaped in face view (Pl. 1, 2), and lenticular in cross section (Pl. 3, fig. 12; Pl. 4, fig. 7). A ventral placental bulge is commonly visible on each mericarp (e.g., Pl. 1,

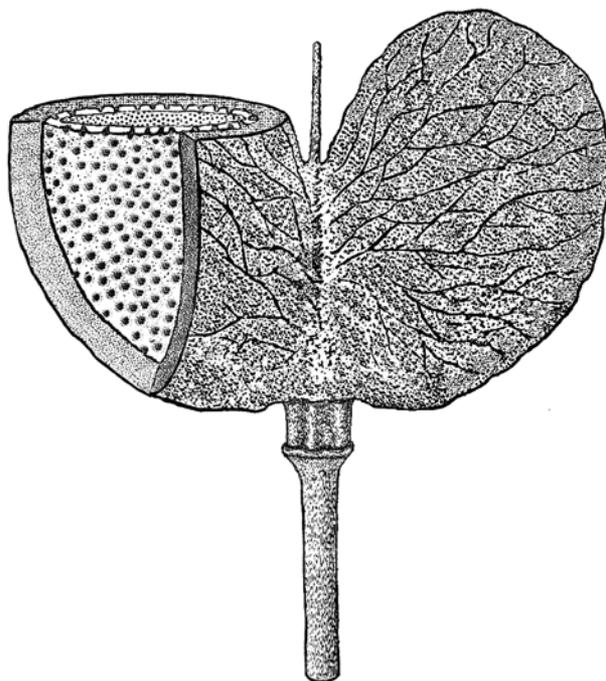


Fig. 2. Reconstruction of a mature *Porosia verrucosa* fruit. Apical portion of left mericarp cut away to reveal wall structure. This represents a slightly dried fruit, showing the reticulate venation; probably the venation would be less obvious at the surface of the ripe fleshy mericarps

figs 1, 2). Fully developed mericarps range from 0.8 to 2.0 cm in length, 0.6 to 1.6 cm in width, and 1.3–2.2 mm in thickness. Frequently, however, only one of the pair develops fully while the other remains small, only a few mm in length and width (Pl. 1, fig. 8; Pl. 2, figs 7, 8, 10–13). Well-preserved specimens show a layer of mesocarp and exocarp with cuticle surrounding the exocarp (Pl. 1, figs 5, 6, 9). There is no indication of styler protrusions on the fruit bodies, so we infer that there was a single nonpersistent style in median position arising between the ovaries. One specimen shows remnants of what we interpret to be a single style in the expected position (Pl. 3, fig. 2).

The prominent “collar” at the junction of the pedicel with the fruit is 1.5–2 mm wide, and 1 mm high (Pl. 3, figs 1, 3, 7, 8). It is thicker and more conspicuous than the scars that would be expected simply from the shedding of perianth; we interpret it to represent the gynophore. It bears five longitudinal grooves and appears to have been pentagonal in transverse view. The surface was finely papillate (Pl. 3, figs 3, 9) and might have been nectariferous. The pentagonal, longitudinally grooved morphology may have been due to the influence of five stamens during development, as documented in extant *Cneorum* of Rutaceae (Caris et al. 2006), but stamens have not been preserved. The gynophore is seen in some specimens to be immediately subtended by a narrower transverse rim representing the hypogynous detached perianth (Pl. 3, fig. 2, 8).

The outer surface of the fruit is mostly smooth, enveloped by cuticle that is well preserved in compression specimens at some localities (e.g., Pl. 1, figs 6, 9), with the faint expression of an underlying network of veins radiating from the ventral attachment (Pl. 2 figs 1, 9). The mesocarp was apparently fleshy and parenchymatous. Although cells of that tissue usually are not preserved, the thickness of the mesocarp can be inferred from the distance between preserved outer cuticle of exocarp and the underlying indurated endocarp tissue to have been 1–1.5 mm, or as much as 3 mm (Pl. 1, figs 6, 9). Prominent reticulate venation of the mericarps is best seen in some of the impression and compression specimens that are exposed at the surface of the exocarp or mesocarp (Pl. 2, figs 1, 9), but such specimens are much more rare than those showing the punctate endocarp surface (Pl. 2, figs

2, 3, 7, 8, 14–17). In some specimens, a stair step fracturing of the fossil has revealed both the endocarp surface, and the veiny surface of mesocarp (Pl. 2, figs 4–6, 13).

The most distinctive feature of these fruits is the prominently verrucate surface referred to in the species designation, consisting of numerous more or less evenly spaced tubercles (Pl. 1, 2; Pl. 3, fig. 4; Pl. 4, figs 1–5). Under the former interpretation that *Porosia* represented float leaves, Krassilov (1976) reported that only one surface, presumed to be the lower, was densely covered with cylindrical tubercles, and that the other surface (interpreted as top) was smooth or indistinctly pitted. Krassilov thus disagreed with Brown (1962) and Hickey (1977) who interpreted the tubercles as sedimentary infillings of cylindrical air chambers on both surfaces. Permineralized specimens, e.g. figs 123–130 in Serbet (1997) and Pl. 4, herein, now prove that both faces of the structure had externally pitted endocarp walls. In permineralizations the tubercles are filled with translucent silica, indicating that they lacked cellular tissue and were either empty or fluid-filled. The cavities vary from 100–200 μm in diameter and extend from the mesocarp boundary almost to the locule (Pl. 3, figs 12–14; Pl. 4, figs 5–7).

The endocarp wall is about 0.3 mm thick, and composed mainly of fibers. The fibers run parallel to the outer surface, and are concentrically arranged around the tubercles (Pl. 4, fig. 8). At the edges of the fruit, tubercles are lacking and the fibers run in a more uniform course paralleling the margin. The spacing and size of tubercles varies according to size of the mericarp. In specimens with asymmetrical mericarp development, the smaller mericarp has correspondingly smaller tubercles than the large one (e.g., Pl. 2, figs 7, 8, 10–13), suggesting that the cavities initiated early in ontogeny and enlarged proportionally with growth of the fruit, as occurs in the oil cells of extant *Citrus* (Knight et al. 2001). The locule lining is smooth (Pl. 3, figs 12–14). Only one seed developed per locule. As illustrated and described by Serbet (1997), the seed coat is uniseriate, composed of cuboidal cells ca 30 μm thick (seen also here in Pl. 3, fig. 14). The embryo bore a pair of cotyledons flattened in the same plane as the fruit (Pl. 3, fig. 13).

Epidermal anatomy was described based on compression specimens from Darmakan in the Amur Region by Krassilov (1973, 1976);

we also investigated additional specimens from the same vicinity by SEM and transmitted light microscopy (Pl. 5, figs 1–15). Epidermal anatomy is uniform over costal and intercostal areas of the mesocarp. Cells are polygonal, about 25–35 μm in diameter with straight, strongly delineated anticlinal walls. Stomata are distributed about 10 per mm^2 , and are irregularly oriented. The stomatal pit is oval, up to 50 μm long, encircled by 8 to 12 subsidiary cells that are similar in shape and size to the ordinary epidermal cells. The anticlinal walls of the subsidiary cells are weakly cutinized in proximity with the guard cells. The pattern is anomocytic to cyclocytic. We did not observe the modified polar subsidiary cells mentioned by Krassilov (1973).

Maceration of tissues beneath the exocarp yielded an internal cuticular layer that we interpret to represent the locule lining bearing the impressions of polygonal isodiametric to somewhat elongate cells (Pl. 5, figs 12–17). Under the former foliar interpretation, Krassilov (1973) referred to this layer as the lower epidermis: “Lower cuticle delicate. Cells elongated, pointed, forming files, intercostal cells broader than costal. Stomata absent. Druses (glands in Krassilov 1976) fairly frequent, spheroid, diameters 29–35 μm , filled with dark granular contents, leaving round spots when lost” (Krassilov 1973, p. 111). We observed various globose bodies, but consider them to be fungal in nature, rather than glands.

The mericarps were apparently the ultimate dispersal unit for these fruits. The fruits recovered appear to be complete, rather than isolated valves, and we have not found corresponding isolated seeds. Thus, the mericarps were apparently indehiscent. Two specimens are seen to have ruptured along the plane of bisymmetry (Pl. 4, fig. 3; and Crane et al. 1990, fig. 29g) and could be interpreted to indicate that the mericarps were secondarily dehiscent, or it might have opened upon germination.

Botanical affinity. Some of the new observations presented here, ie., that the fruits are borne consistently in pairs and probably schizocarpic, the hypogynous position of perianth, the long pedicel, a single shared central style, a prominent gynophore, and endocarp tissue composed of fibers, along with confirmation of other distinctive characters including cylindrical endocarp cavities, and a single seed per

locule, provide a set of characters useful in evaluating affinities of this extinct genus. The divorce from *Limnobiophyllum* can be finalized because of irreconcilable differences.

In some respects, *Porosia* fruits resemble those of the extant southeast Asian genus *Sabia* (Sabiaceae), which can produce both schizocarpic and solitary fruits. *Sabia* endocarps correspond in reniform shape and lenticular cross section, may have one or a pair of single-seeded endocarps developing per flower, and a sclerenchymatous fruit wall. However, sections of *Sabia* endocarps reveal a different anatomy, with wall lacking prominent tubercles and composed of isodiametric sclereids rather than fibers. In addition, the endocarp is reticulately ridged in *Sabia*, but smooth surfaced in *Porosia*. Therefore, we believe the similarities with *Sabia* are due to morphological convergence, and do not consider these to be related taxa.

The organization of paired fruit bodies on the receptacle is rather distinctive and informative as to possible systematic position. Although there are clearly two ovaries per receptacle, they are joined only partially in the ventral part, with a shared style between them (Fig. 2). The development of apocarpous ovaries around the floral axis occurs in some Sapindales, especially Simaroubaceae (e.g., *Ailanthus*, *Picrasma*, *Chaneya*) and in the related family, Rutaceae (e.g., *Andreadoxa*, *Conchocarpus*).

The prominent, closely spaced cylindrical cavities in the endocarp wall provide an important clue to the affinities of this taxon. Visible with the naked eye, these cavities are much larger than those found in most angiosperm families. These intrusions in the fruit wall appear to represent oil glands characteristic of many Rutaceae. In addition, the pattern of cells surrounding the stomata of *Porosia* fruit cuticle corresponds closely to the actinocytic or cyclocytic condition documented for fruits of extant Rutaceae including *Dictamnus*, *Ptelea*, *Ruta*, and *Zanthoxylum* (Brückner 1991). That anatomical similarity, along with the schizocarpic fruits, indicates that *Porosia* may best be attributed to the Rutaceae. The prominent collar below the fruit corresponds in morphology to the gynophore present in Rutaceae, but it is larger than usually seen in extant genera of this family. Rutaceae fruits develop from 1–5 carpels that can be distinct or proximally connate, and form a variety of different fruit types

ranging from syncarpous to apocarpous, including capsules, berries, samaras, and schizocarps (Kubitzki et al. 2011). Although the Rutaceae are monophyletic, the traditional infrafamilial classification, based largely on fruit type (Engler 1931) included subfamilies and tribes that are largely non-monophyletic as assessed from molecular characters (Chase et al. 1999).

Dr. Jacquelyn Kallunki (New York Botanical Garden) advised us that many of the extant genera of the Rutaceae with dehiscent fruits (e.g., the *Euodia*, *Esenbeckia*, and *Angostura* Alliances in the Rutoideae, cf. Kubitzki 2011) have a bony endocarp that twists on drying and thus ejects the seeds. This endocarp falls separately and would be expected to be readily preserved and identifiable among the fossil remains at the numerous localities where *Porosia* has been collected, yet such bits have not been observed at any of these places. The fact that *Porosia* is represented primarily by undehiscent fruits strongly suggests that they were naturally indehiscent. That is, they are better interpreted as drupes, which in some Rutaceae have a hard indehiscent endocarp with more or less fleshy mesocarp.

There are some differences from extant Rutaceae, however, that indicate this assignment should be regarded as tentative. The usual condition in Rutaceae is to have five carpels per fruit. Extant genera with grossly similar fruits, e.g., *Andreadoxa*, *Conchocarpus*, have dehiscent fruits, and the tubercles are mainly confined to the mesocarp rather than entering the endocarp. In addition, leaves of Rutaceae are typically compound, or unifoliolate. The petiolules (or petiole, when described as simple) have a prominent pulvinis at junction with the lamina. Such leaves would be readily recognized in association with *Porosia*, but have not been found.

Associated leaves. Our attempt to identify probable leaves of *Porosia* considered all angiosperm leaves co-occurring at localities with the fruits. Some leaves could be eliminated from consideration as candidates for *Porosia* foliage because they could be identified confidently on the basis of leaf architecture to other genera with morphologically distinct fruit types such as *Davidia*, *Beringiaphyllum*, *Browniea*, *Juglandiphyllites*, *Corylites*, *Cornus*, *Aesculus*, *Zizyphoides*, *Trochodendroides*, *Celtis*, *Platanus*, *Macginitiea*, and *Dyrana* (Akhmetiev et al.

2002, Golovneva 1994b, Pigg & De Vore 2010). The remaining subset of unidentified leaves were considered as likely candidates for the leaves of *Porosia*. At some sites, like Almont, North Dakota, the diversity of unidentified leaves and fruits is high, so that the association of a particular leaf type with *Porosia* would be difficult to confirm. At many sites, however, the diversity is relatively low (ten or fewer angiosperm genera), so that by the process of elimination, only a few unidentified leaf types remain, once the easily identified taxa (above list) are excluded. Leaves borne by the *Porosia* plant should co-occur with the fruits at many different sites of different age, geography and depositional environment. One of the foliage types that occasionally co-occurs with *Porosia* fruits, both in Asia and North America, is the pinnately compound leaf of *Averrhoites* affinis (Newberry) Hickey. However, this foliage type continues into Eocene strata that lack *Porosia* fruits, and has a more consistent co-occurrence with the extinct flower type, *Pistillipolianthus* (Scott Wing, pers. comm; and pers. obs.). If *Averrhoites* is eliminated from consideration, the primary candidates are simple, entire-margined leaves that co-occur with the fruits at many different sites. The leaves have a long slender petiole, and rounded to slightly cordate lamina base. This leaf type, commonly attributed to *Nyssa*, is prevalent at sites where *Porosia* are also abundant, e.g. Birney road cut, Montana. Similar leaves have been called *Phyllites demoresi* Brown (1962) and were included partly in the concept of *Nyssa alata* (Ward) Brown (1962).

Leaves called *Nyssa bureica* Krassilov occur in association with *Porosia* fruits both at the Tsagan area of Amur region (Krassilov 1976, Akhmetiev et al. 2002) and at the Zaisan Basin, Kazakhstan (Akhmetiev & Shevyreva 1989). All three sites from which Krassilov collected leaves of *N. bureica* also yielded fruits of *Porosia* (sites 570, 574, 575). Other candidates include *Nyssa tshucotica* Golovneva (Golovneva & Herman 1992) = *Amaamia tshucotica* (Golovneva) Moiseeva (Moiseeva 2008). Despite similarity of these leaves to those of extant *Nyssa*, no fruits of that genus have been observed in any of the studied Paleocene sites. *Nyssa* has woody fruit stones that should preserve readily, and would be recognizable by the characteristic germination valves as known from Eocene and younger sites (Eyde 1997).

We must note, however, that the fossil *Nyssa*-like leaves under discussion have long narrow petioles with no indication of the pulvinate thickening that would be expected in the compound or unifoliolate leaves of most Rutaceae. Under the hypothesis that the *Porosia* fruits are Rutaceae, we expect that the leaves would be compound or unifoliolate, but such foliage has not been recovered. This may indicate that *Porosia* fruits do not belong to Rutaceae, or that these leaves were not produced by *Porosia* plants.

Distribution. The oldest occurrences of *Porosia verrucosa* are from the Late Cretaceous of North America (Tab. 1), for example from the Campanian Horseshoe Canyon Formation dinosaur beds of Alberta, Canada (Pl. 2, fig. 16) and from the Maastrichtian Lance Formation of Wyoming in the USA (Pl. 2, fig. 17). In Asia, *Porosia* has not yet been confirmed from pre-Tertiary occurrences. The Amur region occurrences of *Porosia* (treated as *Limnobiophyllum*) of Krassilov (1973, 1976) were at first considered to be Maastrichtian, but later revised as Paleocene (Danian; Akhmetiev et al. 2002). *Limnobiophyllum* (sensu lato) was reported from Maastrichtian deposits of the Koryak Highland, North-eastern Russia (Gornorechenskaya flora; Golovneva 1994a, b), but poor preservation of available specimens precludes determining with certainty whether they represent *Limnobiophyllum* (sensu stricto), or *Porosia* (Golovneva pers. comm., 2013). Although *Limnobiophyllum* was also reported from the Campanian of Kundur, Amur Region, Russia (Bugdaeva et al. 2001), the single known specimen does not appear to represent *Porosia* (pers. obs.).

Currently, the oldest known Asian occurrences of *Porosia* are early Paleocene (Danian) (Tab. 1, sites 1–7). During this time, the genus was widely distributed (Fig. 1) with occurrences in the Zaisan Basin in Kazakhstan (Fig. 1.5 in Akhmetiev & Shevyreva 1989, Golovneva 2008), the Amur region (Krassilov 1973, 1976, Akhmetiev et al. 2002), and the Koryak Highlands (Golovneva 1994a, b) in the Russian Far East. In North America, *Porosia* occurs at numerous localities in the Paleocene of the Rocky Mountains and Great Plains (Tab. 1, sites 8–71; Brown 1962, Hickey 1977, Crane et al. 1990, McIver & Basinger 1993) ranging from Early Paleocene (Puercan), to

late Paleocene (Clarkforkian III land mammal age; Wing 1998, Wing et al. 1995). In the Bighorn Basin of Wyoming, Wing (1998) recorded *Porosia* from 13 stratigraphic levels of the late Paleocene, extending from the Tiffanian and throughout the Clarkforkian, but not into the Eocene. More to the west, the species is found in the Paleocene or early Eocene Pilot Rock flora of Oregon (Gordon 1985, Manchester 1999), and the Paleocene and Eocene of the Chuckanut Formation (Tab. 1). The extinction of *Porosia* apparently occurred near the Paleocene-Eocene boundary. We exclude from our concept of the genus, an early Eocene specimen figured by Hickey (1977) from White Butte, North Dakota, because closer examination of the specimen showed that it had external protuberances rather than cavities and appears to be a crushed globose infructescence with numerous protruding styles. *Porosia* is unknown from Europe and thus seems to be a good example of a taxon that dispersed across Beringia during the Late Cretaceous or early Paleocene.

Porosia verrucosa, along with *Nordenskiöldia borealis* (Crane et al. 1991), was among the Late Cretaceous angiosperms able to survive the Cretaceous-Tertiary extinction event despite loss of a large proportion of other taxa in the Rocky Mountain region (Johnson 2002). It flourished in floras of relatively low diversity in the early and middle Paleocene, and in higher diversity floras of the late Paleocene (Clarkforkian). During the Clarkforkian, *Porosia* occurred in floras estimated to have had a mean annual temperature of about 19°C and annual rainfall of 130–150 cm (Wilf 2002). However, *Porosia* is not known from Eocene sites in the Rocky Mountain region nor in Asia, and may have been decimated by the abrupt climatic warming of the basal Eocene (Wing et al. 2005, Wing & Currano 2013). The youngest known occurrences are those from late Paleocene to early Eocene sites of Washington and Oregon (Tab. 1, sites 8–12; Fig. 1B).

ACKNOWLEDGEMENTS

We thank Mikhail A. Akhmetiev, Kevin Aulenback, Richard Barclay, Reagan Dunn, Ronald Eng, Diane Erwin, Lena Golovneva, Ian Gordon, Donald Hopkins, Kirk Johnson, Hongshan Wang, Scott Wing, for access to specimens and/or providing images, Terry Lott for invaluable technical assistance, Roman Rakitov for assistance with SEM and Liliya Kuzmina for

help with drawing. Samples of extant *Sabia dielsii* Levl. fruit from Vietnam were collected and provided for comparative study by Chen Zhiduan, Zhang Jinbo, and Lu Limin. Helpful review comments were provided by Lena Golovneva, Jacquelyn Kallunki, and Kathleen Pigg. This research was supported by the Russian Foundation for Basic Research, grant 14-04-00800 and US National Science Foundation grant EAR 9220079.

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PLATES

Plate 1

Complete fruits of *Porosia verrucosa* from Paleocene of North America and Asia

1. Fully developed schizocarpic fruit with two mericarps on long pedicel. Mesocarp and exocarp (brown color) surrounds the two endocarps. Clayton Beach, Washington, Chuckanut Formation, UWBM9333/B4590
2. Pedicellate schizocarp with fully developed mericarps showing typical verrucate endocarp casts. Mexican Fats, Wyoming, UF 18540-33742
3. Pair of basally fused mericarps on pedicel. Note expanded gynophore junction of pedicel with base of fruit. East Fork, Razor Creek, Montana, UF 18163-25934
4. Pair of mericarps, Belaya Gora, Amur Region, Russia, UF 18650-27771
5. Pedicellate schizocarp with softer tissue of fruit preserved, surrounding the pair of endocarps. Karabiryuk, Zaisan Basin, Kazakhstan. Image courtesy Lena Golovneva, IBP Kb-5
6. Pedicellate schizocarp with intact cuticular sheath, and prominent collar at junction of pedicel and fruit. Belaya Gora, Amur Region, Russia, GIN 4867-BG-2269
7. Pedicellate schizocarp with two equally developed mericarps. Archara Hill, GIN 4867-A1-4a
8. Pedicellate schizocarp with one mericarp enlarged, the other (arrow) remaining small. Belaya Gora, GIN 4867-BG-2279
9. Single fruit specimen. Image courtesy Lena Golovneva, IBP Kb325-254
10. Pedicel bearing one mericarp. Birney road cut, Montana, UF 18968-049681

Scale bars: 1 cm in 1–10

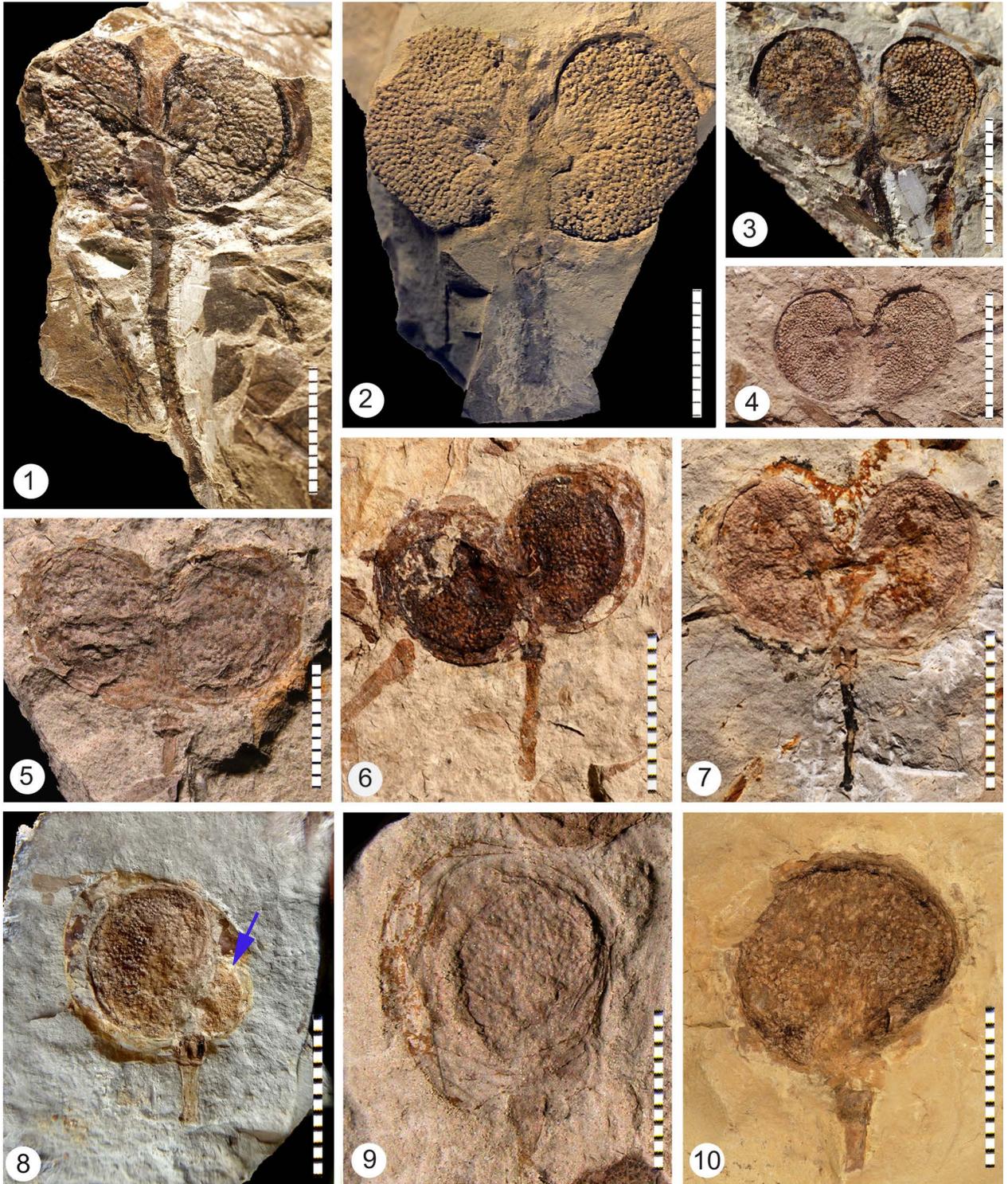


Plate 2

Isolated mericarps and asymmetrically developed schizocarps from North America and Asia

1. Pair of mericarps, the one on left with part of the reticulately veined outer wall broken away to expose tuberculae of the endocarp. O'Dell Creek, Montana, UF 19165-52189
2. Single large mericarp showing marginal rim (contracted mesocarp), and tuberculate endocarp cast. Horse Creek, Montana, UF 18968-50915
3. Smaller isolated mericarp. O'Dell Creek, Montana, UF 18968-53386
4. Mericarp with portion of veiny mesocarp remaining intact in upper half, but broken away in lower and right sides exposing the tubercled endocarp cast. O'Dell Creek, Montana, UF 19165-52184
- 5, 6. Same specimen, successively degaged. 5. with tuberculate endocarp cast remaining in place over lower 2/3 of fruit, reticulate venation of outer layer partially exposed. 6. Endocarp cast completely removed to show surface venation. Horse Creek, Montana, UF 18969-34526
7. Two connected mericarps, one enlarged, one small (arrow). Mexican Flats, Wyoming, UF 18540-33732
8. Two connected mericarps (one of them smaller, arrow). O'Dell Creek, Montana, UF 19165-52185
9. Isolated mericarp with surface venation preserved. Horse Creek, Montana, UF 18969-034520a'
10. Pair of connected mericarps, one smaller (arrow). Belaya Gora, GIN 4867-BG-836a
11. Detail of the smaller mericarp from 7
12. Detail of the smaller mericarp from 13
13. Broken fruit showing external venation and internal tuberculae. Goodman Cr. Bluffs, North Dakota, UF 18750-33739
14. Denver Formation, Colorado, Puercan. DMNH 23497 (DMNH loc 2360)
15. Lance Creek, Wyoming, Maastrichtian. Original of Dorf, (1942), UCMP 2578
16. Campanian of Kents Knoll, Drumheller, Alberta, photo courtesy K. Aulenback, TMP 88.232.1286
17. Neotype of Hickey (1977), Maastrichtian of Black Buttes, Wyoming, USNM 948

Scale bars: 1 cm in 1–10, 13–17; 3 mm in 11, 12

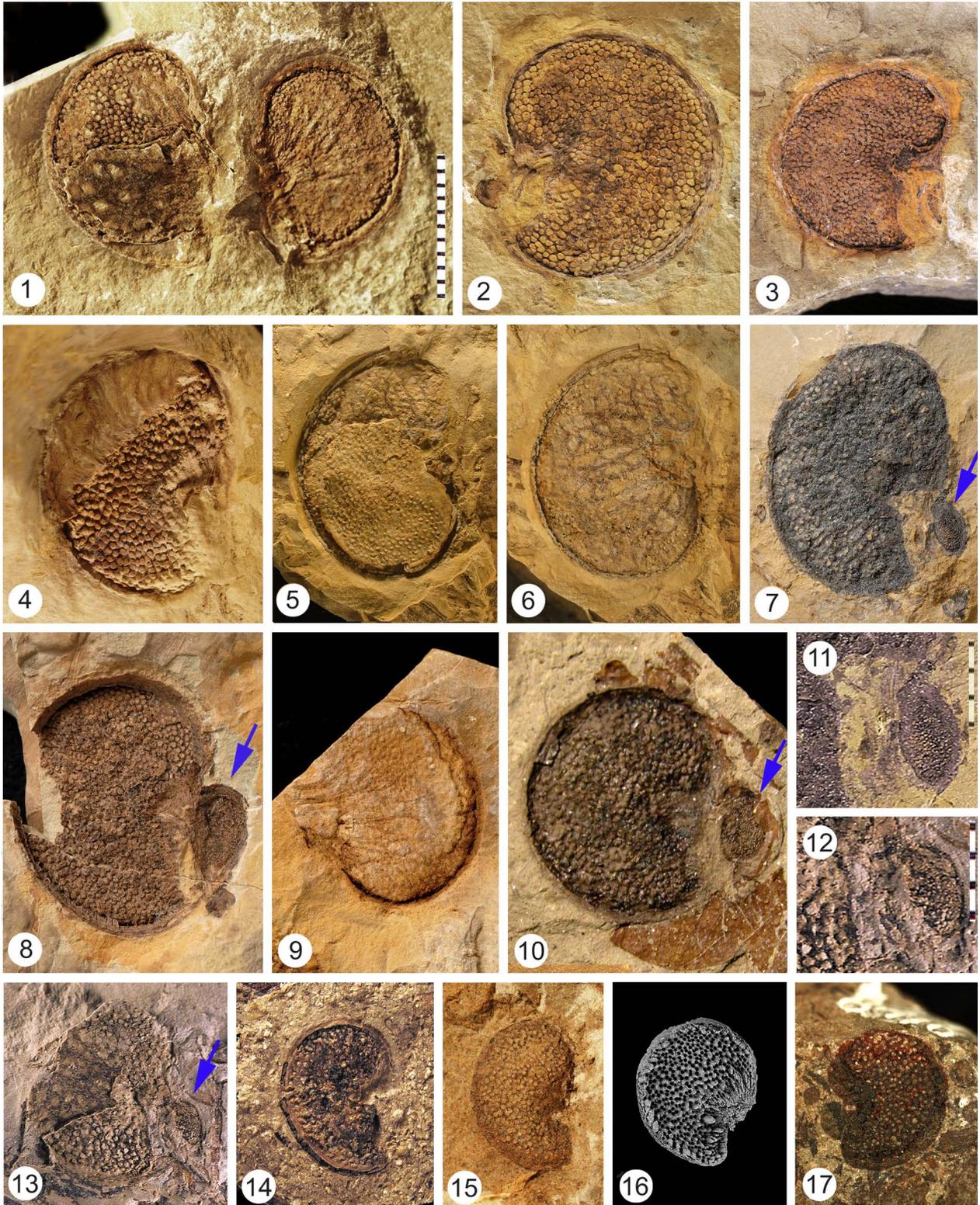


Plate 3

1–5. Sedimentary impression of a complete fruit with two fully developed mericarps.
Counterpart of the specimen in Plate 1, fig. 7. Archara Hill, GIN 4867-A1-4b

1. Equally developed mericarps
2. Enlargement of sinus between the mericarps, showing trace of median style (arrow)
3. Junction between pedicel and fruit. Note the collar-like gynophore (this side shows 3 angles), subtended by a thickened rim of perianth scar (arrows)
4. Surface of impression fossil, showing sedimentary infillings of the endocarp cavities (tubercles), and polygonal outlines of sclereids
5. Margin of endocarp, showing anatomy of fibers, and lack of tubercles
6. Compressed pedicellate fruit with two mericarps, Belaya Gora, GIN 4867-BG-2269
7. Enlargement of specimen from Plate 1, fig. 8, showing pedicel and gynophore
8. Enlargement from 7, showing perianth scar, SEM
9. Detail from surface of gynophore in fig. 8
10. Enlargement from fig. 6, showing cuticle of fruit margin, and impression of underlying mesocarp cells

11–14. Permineralized mericarp. Almont, North Dakota, FMNH PP45561

11. View of mericarp as exposed in natural fracture
12. Transverse section of mericarp after reassembling both counterparts, showing single locule and thick endocarp with scattered tubercular indentations
13. Detail of locule containing an embryo with two cotyledons
14. Detail of endocarp wall and locule, with thin locule lining partially separated from endocarp

Scale bars: 5 mm in 1, 6, 9, 12; 1 mm in 2–5, 8, 13; 3 mm in 7; 10 mm in 9, 11; 200 μm in 10; 500 μm in 14

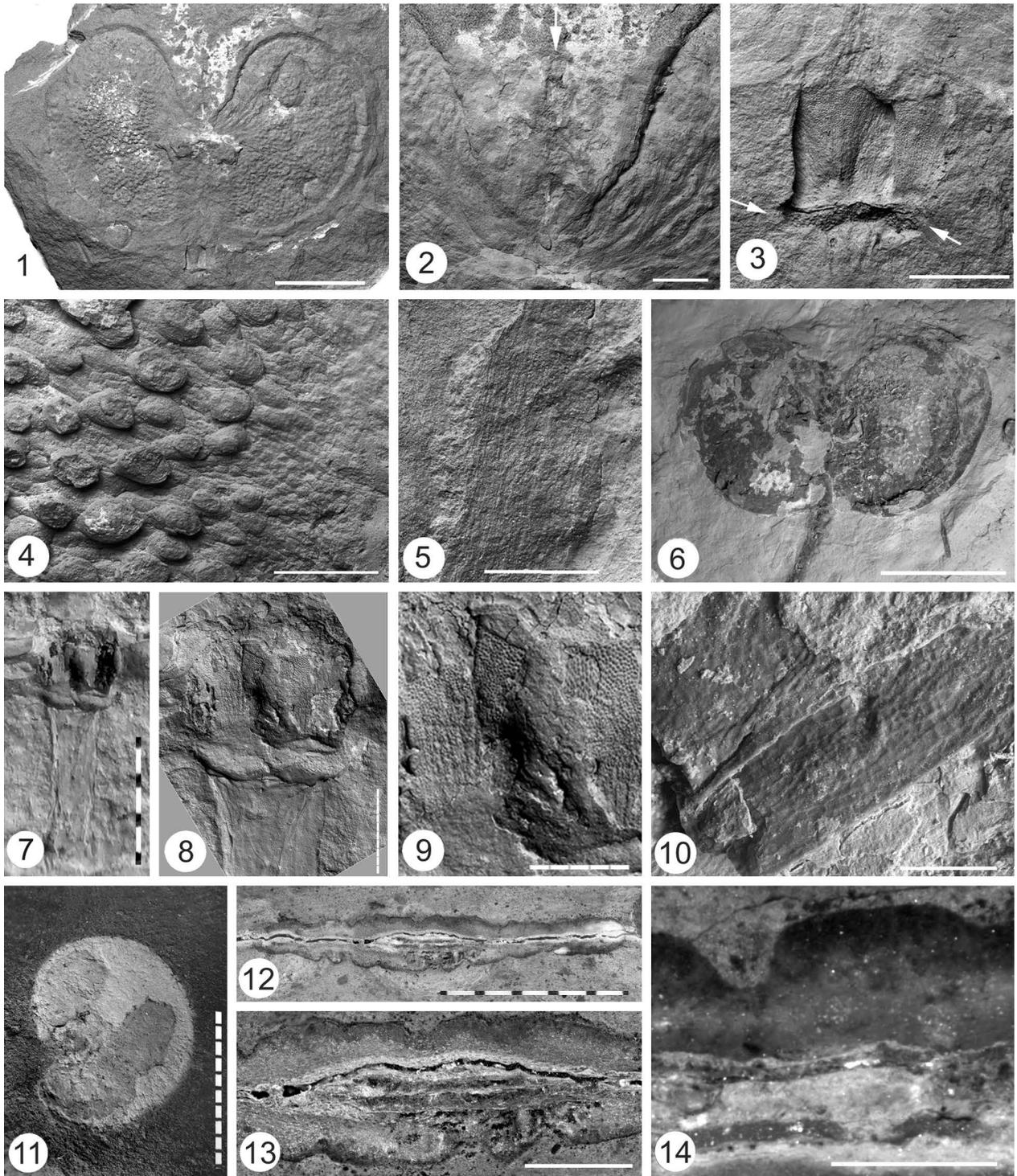


Plate 4

Permineralized *Porosia verrucosa* fruits from Paleocene of North Dakota, USA

1. Mericarp from Beicegal Creek, UF 18796-34637
2. Mericarp from Almont, UF 15722-30579
3. A fragmented (dehiscent or germinated?) mericarp. Almont, UF 15722-53389
4. Fragmentary mericarp, Beicegal Creek, UF 18796-34634
5. Oblique edge view of tilted specimen from fig. 4, showing part of the endocarp walls, and the exposed locule surface. Brown sediment intrudes the cavities in endocarp wall. (locule surface facing upwards)
6. Detail of endocarp wall, transverse section of the specimen in 2, intercepting two endocarp cavities
7. Transverse section of the specimen in 2, showing flattened outline, crushed locule, and the presence of tubercles on both upper and lower surface
8. Detail from 3, showing aligned fibers of endocarp margin (upper left) and sclereids encircling the tubercles. Immersed in water
9. Detail from 7, showing endocarp fibers in transverse section
10. Enlargement of endocarp wall between two tubercles, showing fibers in transverse section

Scale bars: 10 mm in 1–4; 5 mm in 5, 7; 0.5 mm in 6, 9; 1 mm in 8; 0.25 mm in 10

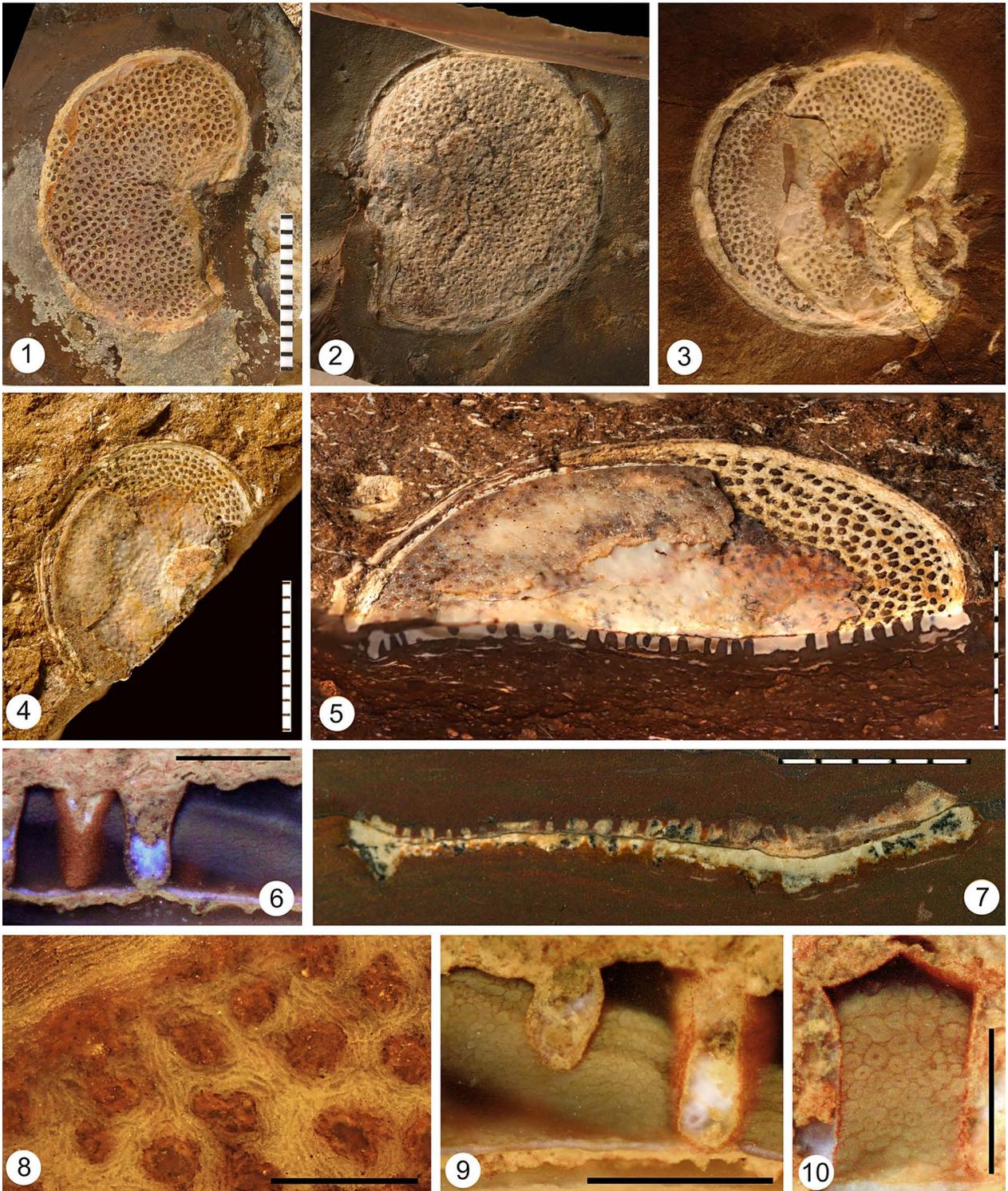


Plate 5

Isolated tissue and cuticle from Pl. 1, fig. 6. Belaya Gora, GIN 4867-BG-2269

- 1–3. Exocarp cuticle, inner side showing polygonal epidermal cell outlines, and stomata SEM
- 4–6. Exocarp cuticle, showing showing indentations accommodating the tubercles, and scattered stomata
Transmitted light microscopy
- 7–11. Stomata
- 2–15. Locule lining, SEM
- 16, 17. Locule lining, LM

Scale bars: 0.5 mm in 1, 200 μm in 2–6, 13, 14; 100 μm in 7–11, 15–17; 500 μm in 12

