Fruits of an "Old World" tribe (Phytocreneae; Icacinaceae) from the Paleogene of North and South America

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Abstract—The Phytocreneae (Icacinaceae) are a tribe of scrambling shrubs and lianas presently distributed in tropical Africa, Madagascar, and Indo-Malesia. We describe the oldest known fossils of this tribe and provide the first recognition of this group in the Neotropical fossil record based on distinctive fruit remains. *Palaeophytocrene piggae* sp. nov., from the late Paleocene of western North America, and *Palaeophytocrene hammenii* sp. nov. and cf. *Phytocrene* sp., from the middle-late Paleocene of Colombia, constitute the oldest confirmed records of this tribe. *Pyrenacantha austroamericana* sp. nov., from the Oligocene of Peru, represents an extant Old World genus known also from the Eocene fossil record of North America and Europe. Collectively, these fossils indicate that the Phytocreneae were previously established in the Neotropics, despite their current absence from the region, and may provide evidence for Paleogene floristic exchange between North and South America.

Keywords—Biogeography, fossil endocarps, Icacinaceae, Neotropics, Paleogene.

The Icacinaceae are a pantropical family within the *Lamiidae* (Soltis et al. 2011) consisting of trees, shrubs, and woody climbers. As currently circumscribed (Kårehed 2001; Lens et al. 2008), the family contains ~35 genera and 150 species divided among four informal groups: the *Icacina*, *Apodytes*, *Cassinopsis*, and *Emmotum* groups. Although these groups probably do not together form a monophyletic assemblage, the *Icacina* group itself is strongly supported in molecular and morphological phylogenetic analyses as monophyletic (Kårehed 2001; Lens et al. 2008). This clade, which is predominantly Paleotropical today, includes all of the genera of the traditional tribes Iodeae, Phytocreneae, and Sarcostigmateae, and some of the genera of the traditional tribe Icacineae (tribes sensu Engler 1893; Sleumer 1942). Relationships within the *Icacina* group remain poorly understood, but it appears that, of the tribes within this clade, perhaps only the Phytocreneae are monophyletic (Kårehed 2001; Lens et al. 2008).

The Phytocreneae (Engler 1893; Sleumer 1942), which consist of the lianescent genera *Chlamydocarya* Baill. (~five species), *Miquelia* Meisn. (~eight species), *Phytocrene* Wall. (~12 species), *Pyrenacantha* Wight (~30 species), and *Polycephalium* Engl. (~two species), occur today in lowland tropical forests of Africa, Madagascar, and Indo-Malesia (Sleumer 1971; Fig. 1). Fruits of this group are easily recognized and well documented in the fossil record (Fig. 1) due to the distinctive features of their endocarps, including deeply pitted outer surfaces formed by tuberculate indentations, which, in all genera except *Phytocrene*, penetrate into the locule, and transversely oriented, interlocking undulate to digitate cells making up the endocarp wall (Reid and Chandler 1933; Villiers 1973; Manchester 1994; Potgeiter and van Wyk 1994). Fossils of the Phytocreneae are well represented in the Paleogene of Europe (Reid and Chandler 1933) and North America (Crane et al. 1990; Manchester 1994; Rankin et al. 2008; Stull et al. 2011), suggesting that they were an important element of mid-latitude forests during the warm interval of the early Paleogene. Younger occurrences of Phytocreneae (*Pyrenacantha* and *Chlamydocarya*) are also known from the Oligocene Fayum flora of Egypt (Manchester and Tiffney 1993), indicating that this group has been present in tropical forests of Africa for at least 30 Ma. To date, the tribe has not been recognized in the fossil record of the Neotropics.

In this paper, we describe the oldest known fossils of this tribe and provide the first recognition of this group in the Neotropical fossil record. *Palaeophytocrene piggae* sp. nov., based on endocarps from the late Paleocene (~58 Ma) of western North America, and *Palaeophytocrene hammenii* sp. nov. and cf. *Phytocrene*, from the middle-late Paleocene of Colombia (~60–58 Ma), represent the oldest known fossil records of this tribe (Fig. 2). *Pyrenacantha austroamericana* sp. nov., a carbonate-permineralized endocarp from the late early Oligocene of Peru (~30–28.5 Ma), represents an extant genus also known from the Eocene fossil record of North America and Europe (Fig. 3). These fossils provide important information on the geographic history of this group, indicating that it was previously established in the Neotropics, despite its current absence from the region. The presence of *Palaeophytocrene* and *Pyrenacantha* in both North and South America may also reflect a broader pattern of floristic exchange between these regions during the Paleogene (Jaramillo and Dilcher 2001; Pennington and Dick 2004; Herrera et al. 2011).

Materials and Methods

Geological Settings—*Palaeophytocrene piggae* is based on endocarps from several localities in the Paleocene of the Great Plains of western North America. Two permineralized specimens were collected from the Almont locality, Morton County, North Dakota (Sentinel Butte Formation), which is considered late Paleocene (~58 Ma) in age (Crane et al. 1990; UF loc. 15722, 46°55′12.86″N, 101°30′17.40″W). Another permineralized specimen was recovered from Beicegel Creek, McKenzie County, North Dakota (UF loc.18907, 47°21.909′ N, 103°25.425′ W). The other specimens, which consist of endocarp impressions, casts, and molds, were collected from the Fort Union Formation in Montana and Wyoming. Brown (1962, pl. 67, Fig. 26) figured a specimen as "impression of a seed showing pits arranged in longitudinal rows" from Lebo Creek, Montana (USGS loc. 4618), and listed the same taxon from Sand Creek, 7 miles N. of Glenrock, Wyoming (USGS loc. 8551). Additional Fort Union Formation occurrences are Sand Draw (USGS loc. 9532, 42°48.049′N, 108°10.968′W), Hells Half Acre (UF loc. 15740D, 43°01.02′N, 107°04.66′W), Leffingwell Bluff (UF loc. 15776, 43°18.42′N, 105°02.09′W), and Linch (UF loc. 18255, 43°38.02′N, 106°12.32′W) in Wyoming, and Traub Ranch (USGS loc. 8910, ~45°9.344′N, 105°41.593′W) in southeastern Montana. These fossils are stored at the Florida Museum of Natural History (UF), the Field Museum (PP), and the Smithsonian Institution (USNM). Although Crane et al. (1990) previously reported several of these fossils, they did not formally name or describe the species; here we provide a full treatment of these stratigraphically significant records.
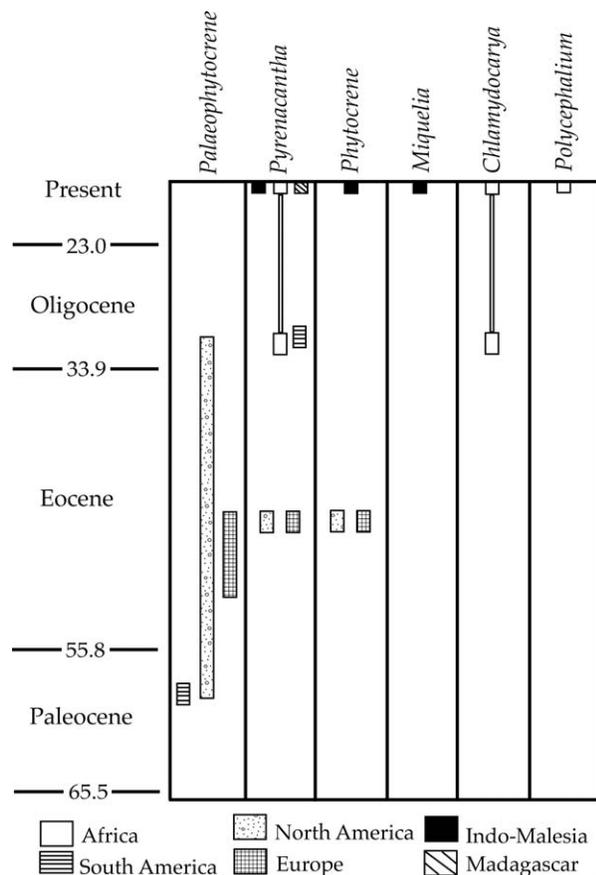
FIG. 1. Temporal and geographic distribution of Phytocreneae. Present distribution based on Sleumer (1942, 1971); fossil distribution based on Reid and Chandler (1933), Manchester and Meyer (1987), Crane et al. (1990), Manchester and Tiffney (1993), Manchester (1994), Rankin et al. (2008), Stull et al. (2011), Collinson et al. (2012), and this paper. Indo-Malesia is a biogeographic region including India, Indochina, and Malesia (with Malesia comprising the Malay Peninsula, the Malay Archipelago, New Guinea, and the Bismarck Archipelago). The genus *Phytocrene* might also be represented in the Paleocene of South America (based on cf. *Phytocrene* sp., informally described here).

Palaeophytocrene hammenii is based on single cast with an adhering carbonized wall, collected from the recently discovered middle-late Paleocene (~60–58 Ma) Bogotá flora of Colombia (Herrera et al. 2011). The locality outcrops in the Checua clay pit near the town of Nemocón in the state of Cundinamarca (STRI loc. FH0806, 5°0.8′14.5N, 73°50′80.2″W). Other plant remains found at this site include Annonaceae, Fabaceae, Malvaceae, and Menispermaceae. This fossil is stored in the paleontological collections of the Colombian Geological Institute (INGEOMINAS) in Bogotá, Colombia.

The species referred to as cf. *Phytocrene* sp. is based on an endocarp compression from the middle-late Paleocene (~60–58 Ma) Cerrejón Formation from northern Colombia (Wing et al. 2009; STRI loc. FH0322, Pit Tabaco, Cesar-Rancheria basin, Guajira peninsula, 11°1′N, 72°5′W). Other plant remains from this site include representatives of Araceae, Arecaceae, Fabaceae, Lauraceae, Malvaceae, and Menispermaceae (Doria et al. 2008; Herrera et al. 2008; Gomez-Navarro et al. 2009; Carvalho et al. 2011). This fossil is stored in the paleontological collections of the Colombian Geological Institute (INGEOMINAS) in Bogotá, Colombia.

Pyrenacantha austroamericana is described based on a single carbonate-permineralized endocarp recently collected from the Belén fruit and seed locality of northern coastal Peru. The Belén locality (UF loc. 603, 4°44.966′S, 81°14.219′W), which was first reported by Berry (1927, 1929), is located in the desert area of northwestern Peru, ~13 miles south of Talara, in the Piura Region. The locality contains an abundance of carbonate-permineralized fruits and seeds, representing taxa such as *Anonaspermum* (Annonaceae); *Leea, Cissus,* and *Ampelocissus* (Vitaceae); and *Duckesia* and *Vantanea* (Humiriaceae). Although formerly considered early Eocene in reviews of South American paleofloras (Romero 1986;

Burnham and Johnson 2004), a reassessment of the age based on diatom assemblages in the fossiliferous matrix (Manchester et al. in press) indicates that the site is late early Oligocene (~30–28.5 Ma). The specimen is housed at UF.

Systematic Comparisons—Other fossil and modern fruits of Phytocreneae were investigated to provide a context for comparative systematic evaluation (Table 1; Appendix 1). Modern species representing all extant genera of Phytocreneae were studied from the herbaria A, MO, UC, and WAG. The other fossil representatives studied include all of the four genera of the tribe currently known from the fossil record (*Chlamydocarya, Palaeophytocrene, Phytocrene,* and *Pyrenacantha*) (Table 1; Appendix 1). The major fruit morphological characters examined are listed in Table 1. The fossil and modern fruits were photographed with Nikon and Pentax SLR digital cameras. For higher magnification, specimens were imaged using a Zeiss STEMI SV8 dissecting microscope fitted with a Canon Powershot A640 camera.

Taxonomic Treatment

Palaeophytocrene piggae Stull, sp. nov.—TYPE: U. S. A. North Dakota: Sentinel Butte Formation (late Paleocene), Almont, 46°55′12.86″N, 101°30′17.40″W (holotype, here designated: UF 15722–22298).

Endocarp elliptic, unilocular, 7–10 mm long, 4–7 mm wide, with a slight bulge on one side at the apical end. Endocarp surface covered with numerous, evenly spaced pits arranged in five to seven longitudinal rows, with approximately six pits in each row. Pits formed by small, conical, tuberculate extensions into the locule. Tubercles ~0.15–0.25 mm long, ~0.25–0.5 mm in diameter, extending shallowly into the locule. Endocarp wall ~0.20 mm thick. Figure 2A–F.

Additional Specimens Studied—PP 33791 from Almont (UF loc. 15722), UF 53529 from Beicegel Creek (UF loc. 18907), UF 35281 from Leffingwell Bluff (UF loc. 15776), UF 23051 from Hell's Half Acre (UF loc. 15740D), UF 35282 from Linch (UF loc. 18255), USNM 545432 from Sand Draw (USGS loc. 9532), USNM 545703 from Traub Ranch (USGS loc. 8910), USNM 545704 from Lebo Creek (USGS loc. 4618), and USNM 545705 from Sand Creek (USGS loc. 8551).

Comments—This species is based on ten endocarps from several localities of the Fort Union and Sentinel Butte Formations (see Materials and Methods). Most of the fossils are compressions or impressions, revealing the pitting pattern on the endocarp surface and/or protrusions into the locule. Three specimens, from Almont and Beicegal Creek, North Dakota, are permineralized portions of endocarps, revealing the topography of the locule surface as well as the outer endocarp surface. On one of these permineralized specimens the tubercles are mostly broken, revealing sediment in-fillings of the tubercle channels, which correspond to the pits on the endocarp surface (Fig. 2A).

Etymology—The specific epithet, *piggae*, is established in honor of Kathleen B. Pigg, recognizing her contributions to paleobotany including the study of Icacinaceae in the Paleocene of North America.

Systematic Affinity—Endocarps of Phytocreneae show a suite of features consistent with the fossil specimen described here. They are unilocular, elliptic-ovoid, and possess pits on the outer surface created by the hollow core of tuberculate protrusions of the endocarp wall into the locule. These characters provide strong evidence for placement within the Phytocreneae. Although distinct from *Polycephalium, Pyrenacantha,* and *Chlamydocarya*, which possess cylindrical, spiny, or vertically elongate tubercles, and from *Phytocrene*, which has protrusions that terminate before the locule, these fossils show similarities with two genera of this tribe: the extant genus *Miquelia* (Fig. 4) and the fossil genus *Palaeophytocrene*. Endocarps of extant *Miquelia* show mound-like or sloping, rather
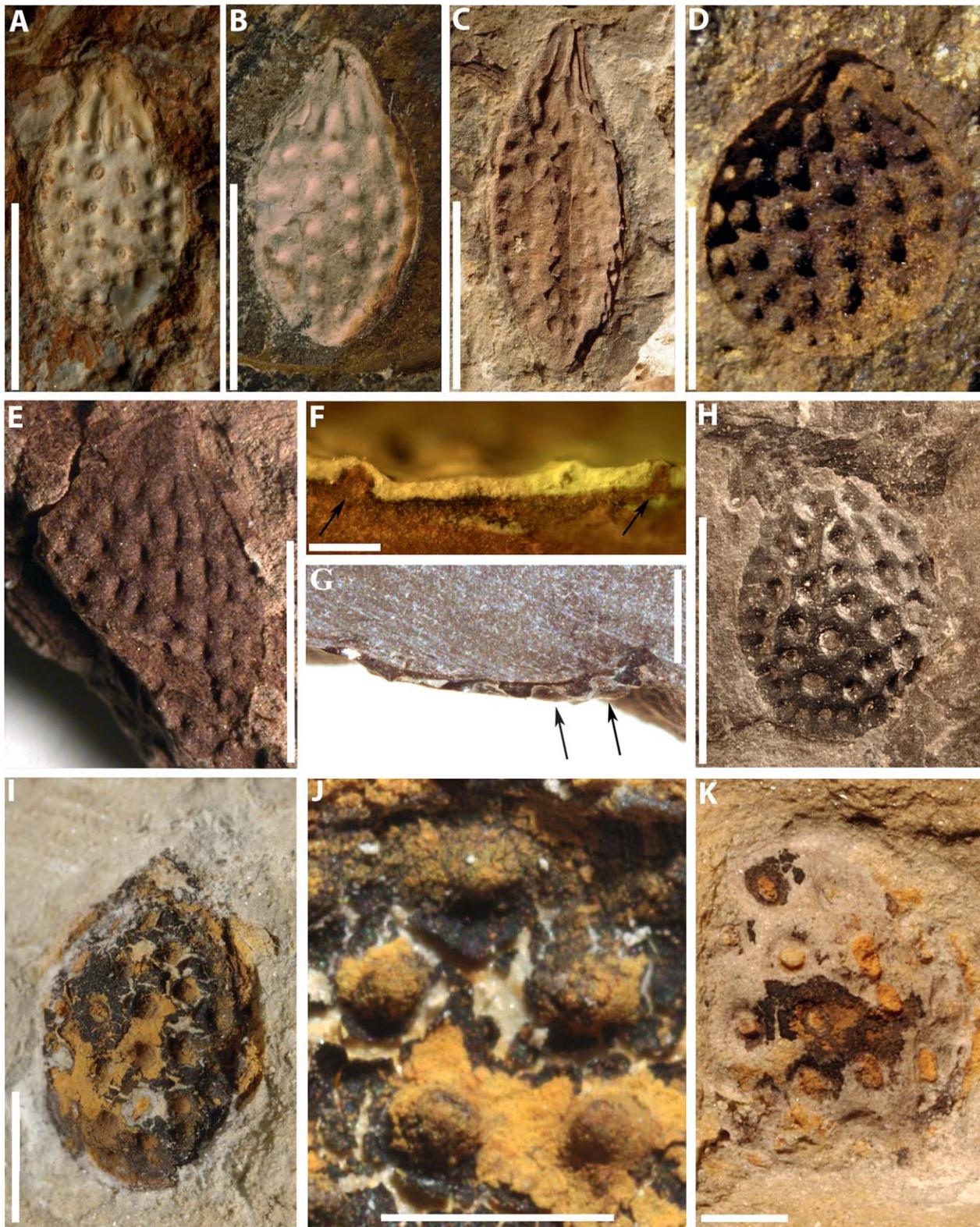
FIG. 2. Paleocene endocarps of Phytocreneae from western North America and Colombia. A–F. *Palaeophytocrene piggae* Stull, sp. nov. A. Permineralized endocarp showing the locular surface, UF 22298 holotype; UF loc. 15722. B. Same as A, PP 33791 (UF loc. 15722). C. Impression of the dorsal or ventral endocarp surface, USNM 545703 (USGS loc. 8910). D. Impression of endocarp surface, USNM 545432 (USGS loc. 9532). E. Endocarp compression, showing the pitted external surface, UF 23051 (UF loc. 15740D). F. Fossil from A in cross section, showing the endocarp wall and tubercluate extensions into the locule (indicated by arrows). G–H. cf. *Phytocrene* sp, STRI 9959 (STRI loc. FH0322). G. Transverse section of the fossil from H, showing the termination of the pits before the locule (indicated by arrows). H. Endocarp compression, showing the pitted external surface. I–K. *Palaeophytocrene hammenii* Stull, sp. nov., STRI 12832 holotype; STRI loc. FH0806. I. Fractured endocarp cast showing the morphology of the locule surface and remnant carbonized endocarp wall. J. Close-up view of the conical tubercules lining the locule surface. K. Counterpart of the endocarp cast shown in I. Scale bars: A–E, H = 5 mm; F = 0.5 mm; G, J = 1 mm; I, K = 2 mm.
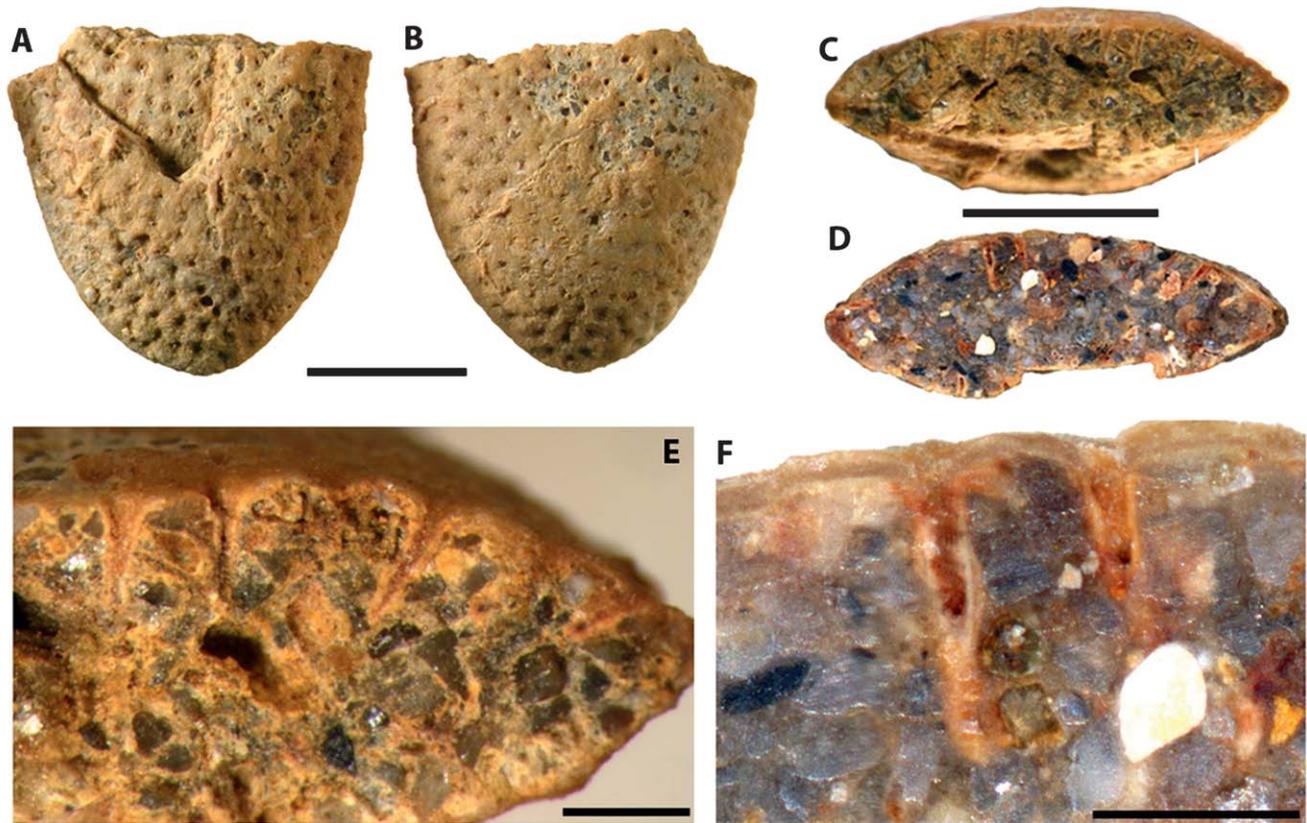
Fig. 3. *Pyrenacantha austroamericana* Stull, sp. nov., UF 54804 (holotype; UF loc. 603). A, B. Opposite lateral faces of the endocarp, showing the finely pitted surface. C, D. Transverse views of the endocarp, showing the spiny tuberculate extensions into the locule. E, F. Enlarged transverse views, showing hollow tubercle channels leading to pits on the endocarp surface. Scale bars: A, B, C, D = 5 mm; E, F = 1 mm.

than parallel-sided, tubercles (Reid and Chandler 1933; Rankin et al. 2008; Fig. 4F, L). Such conical tubercles, which are also shown in the fossils described here (Fig. 2F), have been considered an important feature for distinguishing between *Miquelia* and *Palaeophytocrene*, a genus established for fossil endocarps with pitted surfaces and broad, parallel-sided tubercles (Reid and Chandler 1933). However, numerous fossils placed in *Palaeophytocrene*, including *P. ambigua* described by Reid and Chandler (1933), show tubercle morphologies ranging from parallel-sided to conical. For example, *P. manchesteri* Rankin, Stockey & Beard (2008) was described as having conical tubercles, whereas *P. cf. pseudopersica* Scott (Rankin et al. 2008) has tubercles ranging from conical to parallel sided, and *P. hancockii* Scott (Scott 1954; Manchester 1994) has distinctly parallel-sided tubercles. In addition to this overlap in tubercle morphology, both *Palaeophytocrene* and at least some species of *Miquelia* appear to have micropapillate locule linings (Rankin et al. 2008; Fig. 4L). However, endocarps of *Palaeophytocrene* have relatively evenly spaced pits and usually lack reticulate ridging, whereas the fruits of *Miquelia* that we examined (Appendix 1) show more clustering of the pits, and have a reticulum of ridges on the endocarp surface (Fig. 4A, B, G, H). *Palaeophytocrene vancouverensis*, however, appears to possess a reticulum of ridges on its endocarp surface (Rankin et al. 2008). Clearly a re-evaluation of *Palaeophytocrene* with greater reference to modern fruits of *Miquelia*, as well as other genera of Phytocreneae, will be necessary to better delimit this fossil genus and understand its relation to modern taxa of this tribe. Because the fossils described here fit within the morpho-logical range of previously described fossils of *Palaeophytocrene*, it seems appropriate to place the species within *Palaeophytocrene*, as this genus has functioned as a general repository for pitted and shortly tuberculate endocarp fossils distinct from those of the modern genera. The approach is also adopted for the morphologically similar fossil from Colombia described below.

Palaeophytocrene piggae is distinct from other species of *Palaeophytocrene* in terms of size and number of surface pits; most previously described *Palaeophytocrene* species are larger than 10 mm in length and show a greater number of surface pits (e.g. 10–20 surface pits spanning the length vs. six pits in *P. piggae*). *Palaeophytocrene manchesteri* and *P. pseudopersica* (Rankin et al. 2008; Manchester 1994), which match the size range of *P. piggae* (Table 1), have a greater density of surface pits, and have larger tubercles than those of the fossil described here. *Palaeophytocrene piggae* differs from *P. hammenii* sp. nov., described below, in having considerably shorter tubercles and a more elongated apical end. *Palaeophytocrene piggae* differs from the Cerrejón fossil, cf. *Phytocrene* sp., described below, in having tubercles that extend into the locule; in the Cerrejón specimen, the pits or tubercles terminate before the locule cavity.

Palaeophytocrene hammenii Stull, sp. nov.—TYPE: COLOMBIA. Cundinamarca: Bogotá flora (middle-late Paleocene, Bogotá Formation), Checua clay pit, 5°0.8′14.5″N, 73°50′80.2″W (holotype, here designated: STRI 12832).

Endocarp elliptic, unilocular, ∼5 mm long, 3.25 mm wide. Inner surface of endocarp wall showing numerous tubercles, which are represented by pits on the external endocarp surface.

TABLE 1. Comparative morphology of modern and fossil Phytocreneae fruits. Data assembled from the following sources: Reid and Chandler (1933), Sleumer (1971), Manchester (1994), Rankin et al. (2008), and personal observations of the specimens listed in Appendix 1. All measurements are in millimeters. Authorities for binomials indicated in Appendix 1. Under the category Endocarp surface, "ridged" indicates the presence of an ornamentation of ridges on the endocarp surface, in addition to pits, whereas "smooth" refers to the absence of such surface ridging.

Taxon	Distribution or fossil locality	Endocarp surface (pitted/ridged or smooth	Endocarp length
1. *Chlamydocarya macrocarpa*	West Africa	Pitted/ridged	~20.25
2. *Chlamydocarya thomsoniana*	Central/West Africa	Pitted/ridged	~12
3. *Chlamydocarya* sp.	Oligocene Fayum flora, Egypt	Pitted/unknown	~27
4. *Miquelia caudata*	Malesia	Pitted/ridged	~17
5. *Miquelia celebica*	Malesia	Pitted/ridged	~16
6. *Polycephalium capitatum*	West Africa	Pitted/smooth	~9.5
7. *Pyrenacantha acuminata*	Central/West Africa	Pitted/smooth	~11.5
8. *Pyrenacantha kaurabasana*	East Africa	Pitted/smooth	~13.5
9. *Pyrenacantha occidentalis*	Eocene Clarno Nut Beds flora, Oregon	Pitted/smooth	25–33
10. *Pyrenacantha repanda*	Philippines	Pitted/smooth	~23.5
11. *Pyrenacantha austroamericana* sp. nov.	Oligocene Belen flora, Peru	Pitted/smooth	~20 (estimation)
12. *Pyrenacantha staudtii*	Central Africa	Pitted/smooth	~13.5
13. *Pyrenacantha sylvestris*	Central Africa	Pitted/smooth	~8.75
14. *Pyrenacantha* sp.	Oligocene Fayum flora, Egypt	Pitted/smooth	~30
15. *Palaeophytocrene ambigua*	Eocene London Clay flora, England	Pitted/smooth	~22
16. *Palaeophytocrene foveolata*	Eocene London Clay flora, England	Pitted/smooth	15–27
17. *Palaeophytocrene hammenii* sp. nov.	Paleocene Bogotá flora, Colombia	Pitted/unknown	~5
18. *Palaeophytocrene hancockii*	Eocene Clarno Nut Beds flora, Oregon	Pitted/smooth	38.5–85.0
19. *Palaeophytocrene manchesteri*	Eocene Appian Way, British Columbia	Pitted/smooth	~7.2
20. *Palaeophytocrene piggae* sp. nov.	Paleocene Fort Union Group, western North America	Pitted/smooth	7–8
21. *Palaeophytocrene* cf. *pseudopersica*	Eocene Appian Way, British Columbia	Pitted/smooth	At least 9.8
22. *Palaeophytocrene vancouverensis*	Eocene Appian Way, British Columbia	Pitted/ridged	~19.5
23. cf. *Phytocrene* sp.	Paleocene Cerrejón flora, Colombia	Pitted/ridged	~5.5

	Endocarp width	Endocarp thickness	Pit number (in length)	Pit number (in width)	Tubercle shape	Tubercle length	Tubercle diameter
1.	~15	~0.6	~8	~8	Elongate plates	~1.75	0.75–1.0
2.	7.5–10	~0.5	8–10	8–10	Elongate plates	~0.75	0.5–0.75
3.	~19	Unknown	Unknown	Unknown	Elongate plates	~1–2	1.0–1.5
4.	~11.25	0.25–0.5	~9	~6	Conical	0.5–0.75	1.0–1.25
5.	~7.25	0.25–0.5	~11	~7	Shallowly conical	~0.5	1.0–1.5
6.	~7	0.25–0.5	~12	~6	Peg-shaped	0.5–0.75	~0.25
7.	~8	~0.5	~15	~12	Thin, tapering	1.25–1.5	~0.25
8.	~10.25	~0.35	20–25	~15	Peg-shaped	0.5–0.75	~0.25
9.	~15.7	1.0	16–19	~12–14	Cylindrical	4.5–5.2	~1.0
10.	~30	0.25	20–25	~11–13	Spine-shaped	~0.75	0.15–0.25
11.	At least 11.5	0.25	At least 20	~11–13	Spine-shaped	~1.0	~0.25
12.	~9.5	0.25–0.5	~9	~6–7	Cylindrical to plate-like	1.5–2.0	0.5–0.75
13.	~9	0.25	~9	~9	Peg-shaped to plate-like	~1	~0.5
14.	~15	Unknown	20–25	~15	Cylindrical	Unknown	~0.8
15.	~14.5	1.0–1.2	8–9	~4–5	Conical	Unknown	0.3–0.5
16.	14–17	Unknown	~12	~8	Cylindrical	0.7–1.0	0.2–0.4
17.	~3.25	Unknown	~6	~5	Conical	0.5–0.75	~0.5
18.	26.9–50.0	2.0–2.3	~13–14	~9	Cylindrical	2.0–3.5	~2.2
19.	~5.3	0.1–0.3	~12	~9	Conical	0.5–0.75	~0.2–0.4
20.	4–5	0.25	~6	~5	Conical	0.15–0.25	0.25–0.5
21.	7.5–11.0	0.7–1.0	At least 8	~8	Cylindrical	1.4–1.8	0.6–1.0
22.	~12.5	1.5–2.1	~12	~6–7	Cylindrical-conical	2.0–2.7	0.8–1.4
23.	~4.0	~0.2	~7	~6	Absent	N/A	N/A

Tubercles more or less conical, 0.5–0.75 mm in length, ~0.5 mm in diameter, arranged in five longitudinal rows, with up to six tubercles per row. Figure 2I–K.

Comments—This species is based on a single carbonized endocarp retaining the three-dimensionality of the original fruit. The endocarp is fractured, showing tubercles lining the locule wall. Several tubercles are broken, revealing sediment-filled channels within that correspond to pits on the endocarp external surface.

Etymology—The specific epithet, *hammenii*, is established in honor of the late paleobotanist Thomas van der Hammen, who worked extensively toward the advancement of paleobotany in Colombia and the preservation of modern Andean forests.
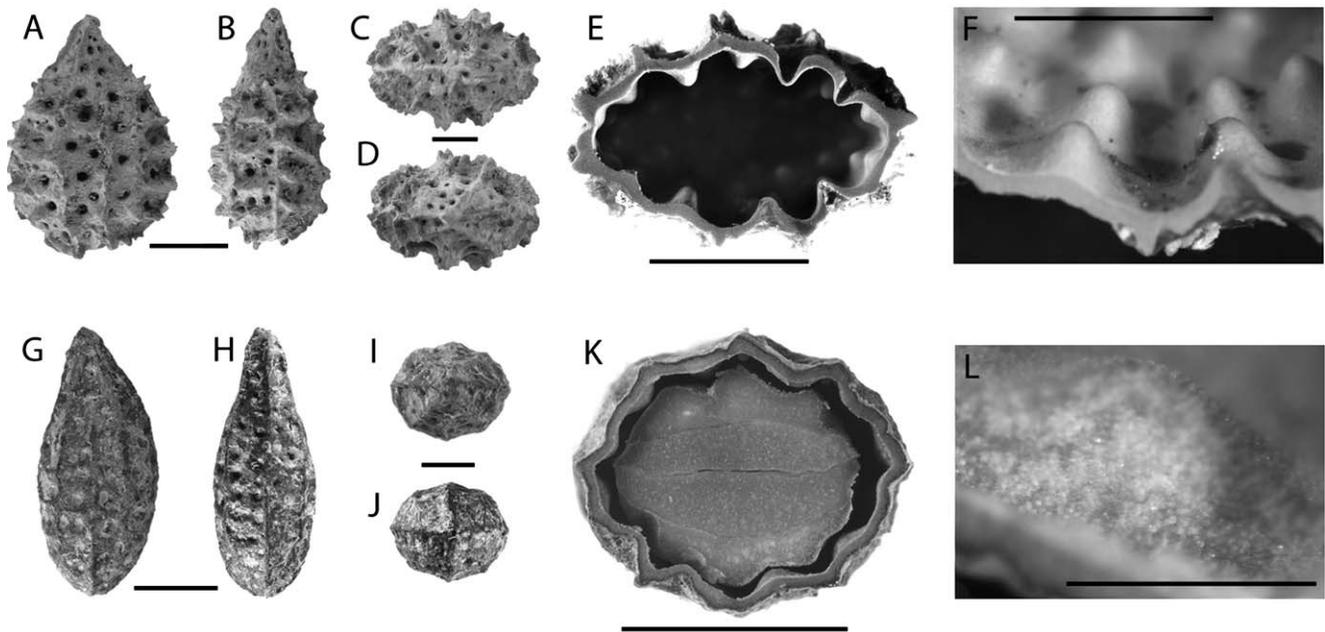
Fig. 4.   Modern endocarps of *Miquelia*. A–F. *Miquelia caudata* King (*King 7621*). A. Lateral view. B. Dorsal view. C. Basal view. D. Apical view. E. Transverse view. F. Close-up of the endocarp wall, showing the conical tubercles. G-L. *Miquelia celebica* Blume (*Ramos and Edano 49155*). G. Lateral view. H. Dorsal view. I. Apical view. J. Basal view. K. Transverse view. L. Close-up of a single, shallowly sloping tubercle covered in papillae. Scale bars: A, B, E, G, H, K = 5 mm; C, D, F, I, J = 3 mm; L = 1 mm.

Systematic Affinity—*Palaeophytocrene hammenii* is similar to *P. piggae* (described above). The endocarps of both species are relatively small (5–10 mm in length), and show surface pits arranged in longitudinal rows, with approximately five pits spanning the width of the endocarp and six pits spanning the length. *Palaeophytocrene hammenii* differs, however, in having longer tubercles that extend more deeply into the locule. Additionally, *P. piggae* has a more distinctly elongate apical end compared to this Colombian fossil. Therefore, despite morphological similarity with *P. piggae*, these differences support recognition of the Colombian fossil as a distinct species.

cf. Phytocrene sp. COLOMBIA. Guajira Peninsula: Cerrejón flora (middle-late Paleocene, Cerrejón Formation), Cesar-Rancheria basin, Pit Tabaco, 11°1′N, 72°5′W (ING 0857/STRI 9959).

Endocarp elliptic, unilocular, 5.5 mm long, 4.0 mm wide. Surface covered with numerous pits, ~7 pits in length and ~6 pits in width, that do not penetrate the locule. The pit diameters generally decrease toward the margin of the endocarp. Pits encircled by slight ridges. Endocarp wall ~0.2 mm thick. Figure 2G, H.

Comments—Only one fossil of this kind was recovered from the Cerrejón flora. It is a fragmentary, carbonized endocarp compression. The fossil represents a complete lateral endocarp half, suggesting that the original endocarp was bivalved; this is also suggested by the pitting pattern, which shows larger pits toward the center of the endocarp half and smaller pits along the margin. From the surface appearance (Fig. 2H), this fossil was first thought to represent *Palaeophytocrene hammenii*. However a transverse section (Fig. 2G) revealed that the tuberculate formations do not extend into the locule (Fig. 2G), an important difference from *P. hammenii* and *Palaeophytocrene* in general.

Systematic Affinity—*Phytocrene* is unique among the genera of Phytocreneae in having pits or tubercles that do not extend into the locule cavity. This character, which has proved useful in distinguishing fossils of *Phytocrene* from other members of this tribe (Stull et al. 2011), is also present in the fossil illustrated here, suggesting affinities between the Cerrejón specimen and this extant genus. However, the fossil is considerably smaller than the modern *Phytocrene* fruits we have examined. Additionally, unlike fruits of *Phytocrene*, the fossil illustrated here is possibly bivalved. Given these differences, and the limited number of modern *Phytocrene* fruits we have been able to study, we hesitate to place the fossil in this genus.

Pyrenacantha austroamericana Stull, sp. nov.—TYPE: PERU, Piura: Belén flora (late early Oligocene), 4°44.966′S, 81°14.219′W (holotype, here designated: UF 603–54804).

Endocarp unilocular, elliptical to ovoid overall (extrapolation from incomplete specimen), lenticular in transverse section, ~20 mm long (estimated based on the curvature of the of the incomplete specimen, which is ~10 mm in length), at least 11.5 mm wide, 4.25 mm thick; surface covered with small pits (0.15–0.25 mm in diameter), pits regularly spaced (0.75–1.0 mm apart, except near base, where they are more densely spaced). Width of endocarp spanned by ~12 pits (counted at the middle of the endocarp), length spanned by ~30 pits (twice the number counted from the partial specimen). The pits are the surface expression of elongate tubercles that penetrate the locule. Tubercles ~1 mm long, 0.25 mm in diameter at the base, and tapering distally to a point. Each tubercle possesses a hollow inner channel leading to a pit on the external endocarp surface. Endocarp wall relatively thin (~0.25 mm). Figure 3.

Comments—This species is based on a single, fragmentary carbonate-infiltrated endocarp lacking cellular preservation. Although the specimen represents only the basal half of the

fruit, the endocarp morphology is well preserved, showing the pitted external surface, the thickness of the endocarp wall, and the tuberculate extensions into the locule.

Etymology—The specific epithet, *austroamericana*, with the Latin derivation meaning literally "South America," emphasizes the geographic source, which is well outside the modern geographic range of the genus.

Systematic Affinity—The suite of features shown by this fossil is consistent with that of Phytocreneae endocarps in general (e.g. unilocular, elliptic, with pitted outer surfaces and tuberculate protrusions into the locule). Of the genera of Phytocreneae, the Peruvian fossil shows strongest similarity to *Pyrenacantha*. Most extant species of *Pyrenacantha* possess smooth endocarp surfaces covered with small, densely spaced pits of the kind seen in this fossil (e.g., Fig. 5B). Endocarp surface pits of other genera are wider in diameter (*Phytocrene*, *Miquelia*, and *Palaeophytocrene*), longitudinally oriented and encircled by ridge-like structures (*Chlamydocarya*; Fig. 5M), or irregularly spaced (*Polycephalium*; Fig. 5K). Also, like the Peruvian fossil, *Pyrenacantha* can have spiny or tapering tubercles, circular in transverse section, that extend into the locule cavity (Fig. 5D, E). This tubercle type is not found in any other genus of Phytocreneae. Tubercles of *Miquelia* are larger in diameter and shallowly conical (Reid and Chandler 1933; Rankin et al. 2008; Fig. 4F); those of *Phytocrene* do not

penetrate the locule or do so only slightly, appearing as low mounds (Reid and Chandler 1933; Rankin et al. 2008); those of *Chlamydocarya* are vertically elongate and plate-like (Fig. 5O); those of *Polycephalium* are peg-shaped (Fig. 5L); and those of *Palaeophytocrene* are typically much broader than the tubercles found in *Pyrenacantha* (Reid and Chandler 1933) and the other modern genera we have observed. Although a few species of *Pyrenacantha* show peg-shaped tubercles resembling those of *Polycephalium* (e.g. *Pyrenacantha kaurabassana*), no members of *Polycephalium* are known to possess the fine, densely spaced surface pits, corresponding to spiny tubercles, found in certain members *Pyrenacantha*. Therefore, we place the Peruvian fossil in the genus *Pyrenacantha*.

Among the modern species of *Pyrenacantha* examined, including specimens from Africa and Indo-Malesia, the Peruvian fossil is most morphologically similar to endocarps of *P. repanda*, of the Philippines (Sleumer 1971), and *P. volubilis*, which occurs in Cambodia, India, Sri Lanka, Vietnam, and the Hainan Province of China (Hua and Howard 2008). Endocarps of these species, like the fossil, possess small surface pits corresponding to spine-shaped tubercles that extend ~one mm into the locule (Hua and Howard 2008). The African species examined differ in having tubercles that are more elongate and cylindrical (*P. staudtii*), peg-shaped (*P. kaurabassana*), or thin and tapering to a hair-like apical strand (*P. vogeliana*, *P. acuminata*).
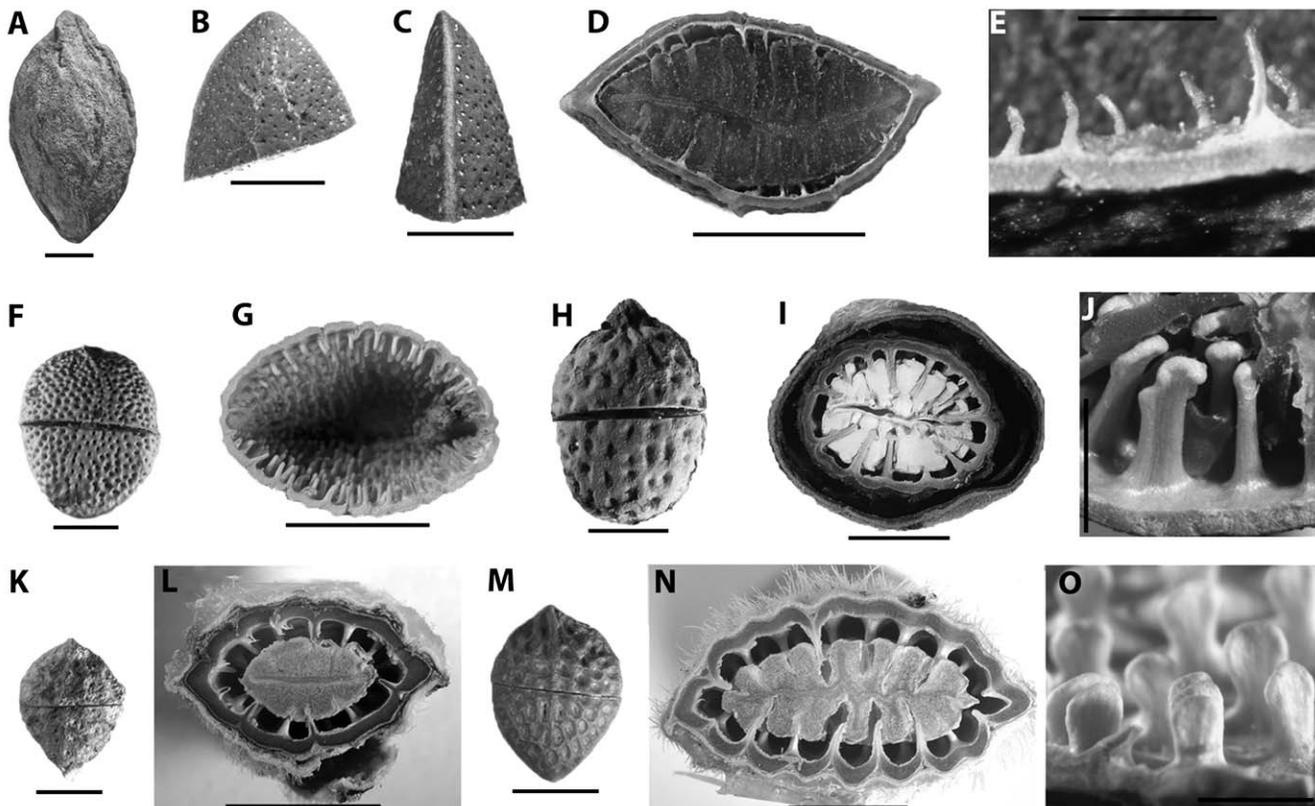

Fig. 5. Modern endocarps of *Pyrenacantha*, *Polycephalium*, and *Chlamydocarya*. A–E. *Pyrenacantha repanda* Merr. (*Elmer 17359*). A. Lateral view of fruit with exocarp remaining. B. Lateral view of sectioned endocarp (exocarp removed). C. Dorsal view. D. Transverse view. E. Close-up of the endocarp wall and the spiny tubercles. F–G. *Pyrenacantha kaurabasana* Baill. (*Reitsma 126*). F. Lateral view. G. Transverse view. H–J. *Pyrenacantha staudtii* (Engl.) Engl. (*Breteler 2968*). H. Lateral view. I. Transverse view. J. Close-up of the endocarp wall and tuberculate extensions (oblique lateral view). K–L. *Polycephalium lobatum* (Pierre) Pierre ex Engl. (*Bokdam 3062*). K. Laterial view. L. Transverse view. M–O. *Chlamydocarya macrocarpa* A. Chev. ex Hutch. (*Koning 1058*). M. Lateral view. N. Transverse view. O. Close-up of the vertically elongate tubercles (oblique lateral view). Scale bars: A–D, F–I, K, L, N = 5 mm; E = 1 mm; J, O = 2 mm; M = 10 mm.

Compared to other known fossils of *Pyrenacantha*, the Peruvian fossil is clearly distinct. *Pyrenacantha occidentalis* Manchester (1994), from the Eocene of Oregon, has cylindrical, rather than spiny, tubercles that extend much farther into the locule. Fossil endocarps of *Pyrenacantha* from the Oligocene of Fayum, Egypt, have peg-shaped tubercles (Manchester and Tiffney 1993; also examined for this study), similar to those of several modern African species (e.g. *P. kaurabassana* and *P. vitifolia*), but distinct from the spine-shaped tubercles of the species described here. Several specimens from the Eocene of Messel, Germany (e.g. SM.B Me 7150; Collinson et al. 2012) are similar in overall size and shape and in the size and density of their surface pits. However, the inner morphology of these Messel specimens has not yet been investigated, impeding more detailed comparison with the Peruvian fossil. Because the Peruvian fossil is geographically and temporally isolated from modern members of *Pyrenacantha*, and cannot be assigned to any previously described fossil species of this genus, it therefore warrants placement in a new species, *Pyrenacantha austroamericana*.

Discussion

Fossil Record of the Phytocreneae—The Phytocreneae are represented in the fossil record by three extant genera, *Chlamydocarya*, *Phytocrene*, and *Pyrenacantha*, and the extinct genus *Palaeophytocrene* (Fig. 1). Reid and Chandler (1933) also placed the fossil genus *Stizocarya*, from the Eocene London Clay Flora, in this tribe. *Stizocarya* was reported to have a tuberculate wall structure (Reid and Chandler 1933), like the other genera of this tribe, but there has been no subsequent work to further refine its placement. An endocarp similar to *Chlamydocarya* is known from the Oligocene of Egypt (Manchester and Tiffney 1993). This fossil shows the lamellate tubercles characteristic of the modern endocarps of this genus (Villiers 1973), but the lamellae are oriented at right angles to the long axis of the endocarp rather than parallel to it. *Phytocrene* is represented by two fossil species, *P. densipunctata* (Stull et al. 2011) and *P. punctilinearis* (Collinson et al. 2012), respectively from the Eocene of Tennessee, U. S. A., and the Eocene of Messel, Germany. Investigation of specimens previously attributed to *Phytocrene* by Scott and Barghoorn (1957) from the Cretaceous (Turonian) of New York revealed that these Cretaceous fossils do not represent this modern genus, or even the family Icacinaceae (Stull and Manchester, unpublished observations). Hence the specimens from Tennessee and Messel constitute the only confirmed fossil records for this genus. If the Cerrejón specimen, described here, does indeed represent *Phytocrene*, this would be the oldest record of this extant genus. The Cerrejón fossil is considerably smaller than *Phytocrene* fruits previously described from the Eocene of North America and Europe, and therefore, if it does represent *Phytocrene*, the Cerrejón fossil might not represent an immediate phylogenetic/biogeographic connection to these other fossil taxa.

Pyrenacantha and *Palaeophytocrene* are known from numerous Paleogene localities in various geographic regions. Fossil fruits of *Pyrenacantha* are known from the middle Eocene flora of Messel, Germany (Collinson et al. 2012), the middle Eocene Clarno Nut Beds of Oregon (Manchester 1994), and the Oligocene Fayum flora of Egypt (Manchester and Tiffney 1993). *Pyrenacantha austroamericana*, described here from the Oligocene of Peru, represents the first report of this genus from the Neotropics. As mentioned above, *P. austroamericana* is distinct from previously reported fossils of this genus and perhaps more morphologically similar to fruits of the modern Indo-Malesian species, e.g. *Pyrenacantha repanda*. Several specimens from Messel, Germany are at least superficially similar to *P. austroamericana* and deserve closer study, with focus on the internal structure, particularly the tubercle configuration.

Palaeophytocrene has the oldest and most extensive fossil record of the tribe, including reports from the early Eocene London Clay flora (Reid and Chandler 1933), the middle Eocene of Messel, Germany (Collinson et al. 2012), the middle Eocene of Oregon (Manchester 1994) and British Columbia (Rankin et al. 2008), the Eocene Roslyn Formation of Washington (Pigg and Wehr 2002), and the early Oligocene of Oregon (Manchester and Meyer 1987). The oldest fossils of *Palaeophytocrene*, and of tribe in general, are those described here from the middle-late Paleocene (~60–58 Ma) of western North America and Colombia.

Judging from the rarity of Paleocene specimens, even at well-collected sites, the Phytocreneae appear to have been a minor, yet widespread, constituent of Paleocene floras (Crane et al. 1990; and our observations); only a handful of fossils, representing two species of *Palaeophytocrene* (and potentially one species of *Phytocrene*), have been recognized from this epoch. In contrast, the tribe is an abundant, relatively diverse, and widespread constituent of Eocene floras (Reid and Chandler 1933; Manchester 1994; Stull et al. 2011; Collinson et al. i2012), including numerous species of *Palaeophytocrene* as well as representatives of several modern genera (*Phytocrene*, *Pyrenacantha*). This fossil record suggests that the tribe may have radiated in response to the expansion of warm biomes during the early Eocene, when global temperatures reached their Cenozoic maximum (Zachos et al. 2001; Wing et al. 2005). A similar pattern of diversification at this time is exhibited by members of the Iodeae (Pigg et al. 2008) as well as other, nonicacinaceous taxa, such as Menispermaceae (Jacques 2009), Sabiaceae (Reid and Chandler 1933; Crane et al. 1990; Manchester 1994), and Vitaceae (Chen 2009).

Biogeographic Implications—Today, the Phytocreneae occur in tropical Africa, Madagascar, and Indo-Malesia (Sleumer 1971). Although there have been numerous reports of this tribe from the Paleogene of North America and Europe (e.g. Reid and Chandler 1933; Manchester 1994; Rankin et al. 2008; Stull et al. 2011), suggesting that it was an important element of mid-latitude forests of these continents during times of warmer climate, previously there has been no indication that the Phytocreneae ever occurred in the Neotropics. *Pyrenacantha austroamericana*, *Palaeophytocrene hammenii*, and cf. *Phytocrene* sp. offer the first reliable paleobotanical evidence of this tribe in South America, expanding our understanding of the historical distribution of this group. These fossils, ranging in age from middle-late Paleocene to late early Oligocene (~60–30 Ma), also suggest that the Phytocreneae were present in the Neotropics throughout much of the Paleogene. The point at which the tribe was extirpated from South America is uncertain.

The presence of *Pyrenacantha* in northern Peru during the late early Oligocene (~30–28.5 Ma) suggests a drastic difference in climate compared with modern conditions, given that the genus occurs today mostly in humid tropical forest (Labat et al. 2006), whereas this part of Peru is currently extremely dry, a product of both the cool Humboldt current (Ravelo 2006) and the rain-shadow of the Andes. *Pyrenacantha austroamericana*, along with some other co-occurring fossils like *Ampelocissus*,

Duckesia, *Vantanea*, and *Leea* (Manchester et al. in press), suggest that the Belén area was much more humid during the early Oligocene, either because the Andes mountains still did not have a pronounced topographic relief (< 1,000 m) (Garzione et al. 2008), or because the Humboldt current was considerably reduced, or both. This paleobotanically inferred paleoclimate corroborates climate models predicting that a low topological relief for the Andes Mountains would significantly increase sea surface temperature and precipitation in northern coastal Peru (Sepulchre et al. 2009). This evidence challenges previous suggestions (Lamb and Davis 2003) that coastal northern Peru experienced an arid climate during the late Paleogene.

Although the Phytocreneae occur today exclusively in tropical Africa, Madagascar, and Indo-Malesia, there are several lines of evidence suggesting that these South American fossils represent a Paleogene floristic connection with North America, where the tribe was previously widespread and diverse (Manchester 1994; Stull et al. 2011). The morphological similarity of the roughly contemporaneous species *Palaeophytocrene piggae* and *P. hammenii* suggests that they might be closely related taxa that diverged following migration between these continents. The presence of *Pyrenacantha* in both North and South America during the Paleogene provides another potential floristic link between these regions (in addition to the Paleocene occurrences of *Palaeophytocrene*), and the observation that *Pyrenacantha austroamericana* is more similar morphologically to the extant Indo-Malesian species of this genus than to the extant African species also favors the hypothesis of exchange via North America. If the Paleocene fossil from Cerrejón, described here, does represent the genus *Phytocrene*, this would constitute another South American connection with a group distributed both in the fossil flora of North America and the modern flora of Indo-Malesia; however, the affinities of this fossil with other modern and fossil species of *Phytocrene* are ambiguous, limiting inferences of biogeographic patterns.

Although the directionality of this potential North-South America floristic connection is difficult to assess, the presence of *Palaeophytocrene* and *Pyrenacantha* in both North and South America requires that at least two dispersal events occurred between these continents during the Paleogene. This fits with growing evidence (e.g. Jaramillo and Dilcher 2001; Pennington and Dick 2004; Herrera et al. 2011) that floristic exchange between North and South America, particularly during the Paleogene, occurred more frequently than previously thought (Burnham and Graham 1999). This phytogeographic exchange could have been favored when a Caribbean volcanic arc briefly connected North and South America during the Paleocene (Cardona et al. 2010; Bayona et al. 2011), upon the first emergence of the Central American arch during the middle to late Eocene (Montes et al. 2012), or upon the emergence of the proto-Greater Antilles during the late Eocene (Iturralde-Vinent and MacPhee 1999). Other fossils supporting this floristic connection include fruits of *Palaeoluna* (Menispermaceae) shared between the Paleocene of Colombia and western North America (Herrera et al. 2011) and multiple pollen taxa shared between Colombia and the Gulf Coast of North America during the Paleocene-Eocene, e.g. *Bombacacidites nacimientoensis*, Malvaceae s. l. (Carvalho et al. 2011); *Ulmoideipites krempii*, Ulmaceae; *Syncolporites poricostatus*, Myrtaceae; and *Proxapertites operculatus*, Araceae (Jaramillo and Dilcher 2001).

While *Palaeophytocrene* may have migrated to or from South America before the late Paleocene, it is uncertain when *Pyrenacantha* arrived in South America. The oldest fossil records of *Pyrenacantha* are from the Middle Eocene of Europe (Collinson et al. 2012) and North America (Manchester 1994), suggesting that this genus may have originated in the Northern Hemisphere and then migrated to South America sometime between the Middle Eocene and Late Oligocene. However, it cannot be ruled out that *Pyrenacantha*, and possibly the tribe in general, originated in the Neotropics and then migrated northward during the early Paleogene. Future paleobotanical work on Paleocene-Eocene deposits in South America will be necessary to determine in more detail the history of *Pyrenacantha*, and the Phytocreneae in general, in the Neotropics.

The presence of a Paleogene floristic connection between North and South America also has important broader implications for tropical plant historical biogeography. Early Tertiary floras of North America (Manchester 1999) show strong taxonomic similarity with those of Europe (Reid and Chandler 1933; Collinson et al. 2012) and the modern flora of the Old World tropics, particularly Indo-Malesia, suggesting that migration between North America and the Old World tropics, via Europe, was frequent during the Paleogene (Tiffney 1985). If North America also had a floristic connection with South America during this period, even if relatively weak, this would have facilitated the exchange of taxa between the New and Old World tropics. This may explain the presence of "Old World" taxa in Paleogene floras of South America, such as Phytocreneae (Icacinaceae; this paper), *Leea* (Vitaceae; Manchester et al. in press), and *Stephania* (Menispermaceae; Herrera et al. 2011), and point to an important historical means by which tropical groups established pantropical distributions or New World-Old World disjunctions, as has been suggested in previous studies based on paleobotanical data (Herrera et al. 2011; Stull et al. 2011) and molecular dating analyses (e.g. Davis et al. 2002).

The new species described here provide important information on the age and geographic history of the Phytocreneae. Based on previous paleobotanical reports (e.g. Reid and Chandler 1933; Manchester 1994; Stull et al. 2011), the tribe was known to have extended into Europe and North America during the Paleogene, despite its present confinement to the Old World tropics. The fossils described here, which include the oldest records for the tribe, indicate that the Phytocreneae were present in South America as well as North America and Europe during the Paleogene. Several lines of evidence indicate that these South American fossils represent direct floristic exchange with North America during the Paleogene, offering important broader implications for the role of North America in shaping patterns of tropical plant distribution.

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APPENDIX 1. Modern and fossil fruits of Phytocreneae examined for this study. For the modern fruit specimens, voucher information is in the following sequence: taxon and authority, collector and number (herbarium acronym), country (number of fruit specimens examined). For the fossil fruit specimens, information is listed as follows: taxon and authority, museum acronym and specimen number(s), age, and locality. Fossil specimens not physically examined, but studied based on published descriptions and photographs, are noted with an asterisk. Acronyms of museums housing the fossil collections are as follows: UF (Florida Museum of Natural History), UM (University of Michigan Museum of Paleontology), NHM (Natural History Museum, London), UAPC-ALTA (University of Alberta Paleobotanical Collections).

Modern fruits: *Chlamydocarya macrocarpa* A. Chev. ex Hutch. et Dalziel, *Koning 4918* (WAG), Ivory Coast (1); *Chlamydocarya macrocarpa* A. Chev. ex Hutch. et Dalziel, *Koning 1058* (WAG), Ivory Coast (1); *Chlamydocarya thomsoniana* Baill., *Bos 5432* (WAG), Cameroon (1); *Chlamydocarya thomsoniana* Baill., *Koning 5275* (WAG), Ivory Coast (1); *Miquelia celebica* Blume, *Ramos and Edano 49155* (UC), Philippines (1); *Miquelia caudata* King, *King 7621* (UC), Malaysia (1); *Polycephalium lobatum* (Pierre) Pierre ex Engl., *Bokdam 3062* (WAG), Congo (2); *Pyrenacantha acuminata* Engl., *Wieringa 5017* (WAG), Gabon (1); *Pyrenacantha kaurabassana* Baill., *Reitsma 126* (WAG), Kenya (1); *Pyrenacantha kaurabassana* Baill., *Wilde 6359* (WAG), Ethiopia (1); *Pyrenacantha repanda* Merr., *Elmer 17359* (UC), Philippines (1); *Pyrenacantha staudtii* (Engl.) Engl., *Breteler 2968* (WAG), Cameroon (1); *Pyrenacantha sylvestris* S. Moore, *Breteler 11262* (WAG), Gabon (1).

Fossil fruits: **Chlamydocarya* sp., s. n., Oligocene, Fayum Flora, Egypt; **Palaeophytocrene ambigua* Reid et Chandler, NHM v22646, early Eocene, London Clay Flora, England; **Palaeophytocrene hancockii* Scott emend. Manchester, UM 29933 (and some UF and USNM specimens), middle Eocene, Clarno Nut Beds flora, Oregon; *Palaeophytocrene pseudopersica* Scott emend. Manchester, UF 8597, 8599, 8602, 8605-8610, middle Eocene, Nut Beds Flora, Oregon; **Palaeophytocrene* cf. *pseudopersica* Scott emend. Manchester, UAPC-ALTA AW112, AW118, AW118, Eocene, Appian Way, British Columbia; **Palaeophytocrene manchesteri* Rankin, Stockey et Beard, UAPC-ALTA AW301, Eocene, Appian Way, British Columbia; **Palaeophytocrene vancouverensis* Rankin, Stockey et Beard, UAPC-ALTA AW363, Eocene, Appian Way, British Columbia; *Phytocrene densipunctata* Stull, Moore et Manchester, UF 18927, middle Eocene, Cockfield Formation, Tennessee; *Pyrenacantha occidentalis* Manchester, UF 8617, middle Eocene, Nut Beds flora, Oregon; **Pyrenacantha* sp., s. n., Oligocene, Fayum Flora, Egypt.