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Cornalean affinities, phylogenetic significance, and biogeographic implications of *Operculifructus* infructescences from the Late Cretaceous (Campanian) of Mexico

Reilly F. Hayes^{1,4}, Selena Y. Smith², Marisol Montellano-Ballesteros³, Gerardo Álvarez-Reyes³, René Hernández-Rivera³, and David E. Fastovsky¹

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¹ Department of Geosciences, University of Rhode Island, Kingston, Rhode Island 02881, USA

² Department of Earth & Environmental Sciences and Museum of Paleontology, University of Michigan, Ann Arbor, Michigan 48109, USA

³ Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Coyoacán, México, CDMX 04510, Mexico

⁴ Author for correspondence (e-mail: reilly_hayes@uri.edu); ORCID id 0000-0002-2021-5151

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PREMISE OF THE STUDY: Cretaceous Cornales provide a crucial record of the early history of asterids. Most lineages of the order are well represented in the fossil record, but South African families of Curtisiaceae and Grubbiaceae remain poorly understood. Seventy-three specimens of a fossil infructescence belonging to the genus *Operculifructus* Estrada-Ruiz & Cevallos-Ferriz from the Late Cretaceous (Campanian) El Gallo Formation, Baja California, Mexico bear previously undescribed characters that suggest a relationship to Grubbiaceae.

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METHODS: Microstructures of the fossils were examined through light microscopy and x-ray microcomputed tomography (microCT) scanning. Modern *Grubbia tomentosa* (Thunb.) Harms fruits were scanned for comparison to the fossil material. Phylogenetic analyses using the 77 fruit characters of Atkinson (2018) were performed to test relationships of the fossil to major lineages of the order. Several analyses applied topological constraints to the extant taxa, based on various genetically supported hypotheses of relationship within Cornales.

KEY RESULTS: Novel structures of *Operculifructus* newly observed here include (1) anatropous ovules, (2) drupaceous fruits, (3) an epigynous disc, (4) and a styler canal in the center of the disc aligned with the micropylar protrusion of the seed. Phylogenetic analysis consistently resolves *Operculifructus* as sister to Grubbiaceae.

CONCLUSIONS: *Operculifructus* provides direct evidence for the occurrence of Grubbiaceae in the Late Cretaceous, much older than previous Eocene evidence. The phylogeny of Atkinson (2018) indicates that the new phylogenetic position recovered for *Operculifructus* also establishes the presence of the most basal drupaceous cornalean fruits in North America by the Campanian.

HIPÓTESIS DE LA INVESTIGACIÓN: Cornales cretácicos representan un registro esencial en la historia de los astéridos. Casi todos los linajes del orden están bien representados en el registro fósil, pero las familias africanas sureñas Curtisiaceae y Grubbiaceae permanecen pobremente entendidas. Setenta y tres ejemplares de una infrutescencia fósil perteneciente al género *Operculifructus* Estrada-Ruiz & Cevallos-Ferriz de la formación campaniana (Cretácico Tardío) El Gallo, Baja California, México, poseen caracteres no descritos previamente y sugieren una relación con Grubbiaceae.

METODOLOGÍA: Microestructuras de los fósiles fueron examinadas con microscopio de luz y microtomografía computarizada (micro-CT) de rayos X. Frutos actuales de *Grubbia tomentosa* (Thunb.) Harms fueron escaneados para su comparación con el material fósil. Se realizaron análisis filogenéticos usando los 77 caracteres de frutos de Atkinson (2018) para probar las relaciones de los fósiles con los linajes principales del orden. En algunos análisis se aplicaron restricciones topológicas a los taxa actuales basándose en varias hipótesis, soportadas genéticamente, de las relaciones dentro de Cornales.

RESULTADOS CENTRALES (CRUCIALES): Las estructuras novedosas de *Operculifructus*, recientemente observadas aquí, incluyen (1) óvulos anátropos; (2) frutos drupáceos; (3) disco epígino; y (4) un canal estilar en el centro del disco alineado con la protuberancia micropilar de la semilla. Los análisis filogenéticos consistentemente dan como resultado que *Operculifructus* es hermano de Grubbiaceae.

CONCLUSIONES: *Operculifructus* proporciona evidencia directa de la presencia de Grubbiaceae en el Cretácico Tardío, mucho antes que la previa evidencia en el Eoceno. La filogenia de Atkinson (2018) indica que la nueva posición filogenética recuperada para *Operculifructus* también resalta la presencia de frutos drupáceos cornaleanos más basales en Norteamérica durante el Campaniano.

KEY WORDS: asterids; Cornales; Cretaceous; Curtisiaceae; drupaceous fruits; Grubbiaceae; *Operculifructus*; phylogeny.

Grubbiaceae are an enigmatic southern African family of evergreen shrubs comprised of three species of a single genus, *Grubbia* Berg. (Carlquist, 1977; Plant List, 2013). Once referred alternatively to Santalales (Schultze-Motel, 1964), Bruniales (Dahlgren, 1989; Thorne, 1992a, b), and Ericales (Takhtajan, 1987; Cronquist, 1988), molecular-based phylogenies have resolved them firmly within the Cornales (Xiang, 1999; Xiang et al., 2002, 2011; Fan and Xiang, 2003). Alongside Curtisiaceae, another enigmatic, monogeneric South African family, Grubbiaceae constitute one of five major cornalean clades, following the scheme of Xiang et al. (2011): (1) (Cornaceae-Alangiaceae) [CA], (2) (Curtisiaceae-Grubbiaceae) [CG], (3) ((Nyssaceae-Davidiaceae)-Mastixiaceae) [NMD], (4) (Hydrangeaceae-Loasaceae) [HL], and (5) (Hydrostachyaceae). Although each clade is well supported, relationships at the deepest nodes of the phylogeny remain unstable, with analyses based on varying combinations of nuclear and chloroplast molecular data producing a broad array of topologies (Xiang, 1999; Xiang et al., 2002, 2011; Fan and Xiang, 2003). This instability has been widely attributed to a rapid initial Cretaceous radiation (Xiang et al., 2002, 2011; Fan and Xiang, 2003; Atkinson, 2016). Indeed, the topology recovered by the recent morphological analysis of Atkinson (2018) differs widely from those produced by molecular analyses, and contests the reality of a CG clade. Fossil

Cornales therefore provide an important resource for elucidating patterns of character evolution and relationship within the order.

The fossil record of Cornales is extensive (Atkinson, 2016; Atkinson et al., 2016, 2017, 2018; Stockey et al., 2016; for review, see Manchester et al., 2015), but very few of those Cretaceous fossils that are known constitute crown members of any extant lineage (Atkinson, 2018). The records of Grubbiaceae and Curtisiaceae are exceptionally poor compared to others of the order, the former containing no more than three extant species, and the latter one extant and one fossil species (Carlquist, 1977; Yembaturova, 2009). The Eocene-aged *Curtisia quadrilocularis* (Reid & Chandler) Manch., Q-Y Xiang, & Q-P Xiang (Manchester et al., 2007) hints at a historically broader range for at least this family. Although *C. quadrilocularis* sets a minimum age for a CG clade, molecular estimates date its origination to anywhere between the Late Cretaceous and late Paleogene (Xiang et al., 2011; Magallón et al., 2015). By contrast, the time-scaled phylogeny of Atkinson (2018) indicates that Grubbiaceae appeared by the Turonian, and Curtisiaceae by the Campanian.

We here report a new occurrence of infructescences belonging to the genus *Operculifructus* Estrada-Ruiz & Cevallos-Ferriz from the late Campanian El Gallo Formation, Baja California, Mexico. First recovered and described from the Campanian-Maastrichtian Cerro del Pueblo Formation (Coahuila, Mexico), the genus was initially described as an aggregate or multiple infructescence comprised of many unilocular and operculate fruits with orthotropous seeds with distal projections of the integuments (Estrada-Ruiz and Cevallos-Ferriz, 2007). El Gallo fossils preserve several features unobserved in the Cerro del Pueblo material and prompt modification to the generic diagnosis. These characters also suggest a markedly different phylogenetic position for *Operculifructus*: contrary to the previous assignment to Alismatales (family *incertae sedis*), our study indicates that it belongs within Cornales, sister to Grubbiaceae.

<h1>LOCALITY, STRATIGRAPHY, AND PALEOENVIRONMENT

El Gallo Formation occurs in an extensive sequence of northeast dipping exposures north and west of the town of El Rosario, Baja California, Mexico (Fig. 1). There, an estuary (“La Bocana”) cuts into and exposes a >3000 m Cretaceous-to-Paleogene, broadly conformable sequence of marine and terrestrial sedimentary rocks, ~1300 m of which consist of El Gallo

Formation. Kilmer (1963) recognized three members in El Gallo Formation, the lowest of which, “El Disecado Member,” is the source of the fossils described here.

El Disecado Member consists of 1150 m of interbedded medium-to-coarse sandstones interbedded with fine to very fine sandy siltstones. Fulford and Busby-Spera (1993) reconstructed the unit as representing a low-sinuosity fluvial system, grading into a marginal marine setting. It has been dated, using $^{40}\text{Ar}/^{39}\text{Ar}$ analysis of sanidine crystals from tuffs within the unit, at 74.87 ± 0.05 to 73.59 ± 0.09 mya (Renne et al., 1991), recently corrected to 75.84 ± 0.05 to 74.55 ± 0.09 mya (Peacock et al., 2014); these dates place it in the late Campanian.

The entire El Disecado Member is fossiliferous, producing a suite of vertebrate fossils ranging from fish to tetrapods (including dinosaurs and mammals; see Romo de Vivar-Martínez, 2011; Prieto-Márquez et al., 2012; Fastovsky et al., 2014; Peacock et al., 2014; García-Alcántara, 2016; Romo de Vivar-Martínez et al., 2016). The fossils are distributed among some 100+ localities, are generally disarticulated and commonly fragmentary, and appear to occur exclusively as clasts in what was evidently a very active fluvial system.

Plant macrofossil preservation in El Disecado Member contrasts with the vertebrate preservation. Plant macrofossils are generally found in siltstone—very fine sandstone deposits, representing floodplain settings that preserve considerable organic material and plant fragments. They are commonly associated with carbonate nodule-bearing, ferric oxyhydroxide-mottled paleosols (Fricke et al., 2015) suggesting sufficient landscape stability for pedogenesis. Extensive mottling in the paleosols, along with the nodules, indicates wet/dry cyclicity and associated redox fluctuations in the soil subsurface, likely attributable to climate. Regardless, the plant remains are largely in situ, while those of the vertebrates are allochthonous. A more detailed description of the contrasting taphonomies of plants and vertebrates, as well as the paleoenvironments, preserved in El Disecado Member, is currently in progress.

The preponderance of the plant macrofossils described here were found in three closely spaced localities: “Granito de mostaza,” “Víbora,” and “La esquina de la frutería de Gerry” (Fig. 2). The fossils are permanently housed in the Museo de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México, D.F., Mexico.

<h1>MATERIALS AND METHODS

Seventy-three partial and complete fossil infructescences assignable to *Operculifructus* constitute the material studied here; these represent the overwhelming proportion (89%) of plant material collected in El Gallo Formation between the 2013 and 2016 field seasons. Other, more poorly preserved material of unknown affinity is also present in this collection, including petrified wood, cone fragments, roots, and stems. Three-dimensional, iron-oxide permineralization preserves the reproductive structures, while compression fossils represent the few vegetative structures present. Notably, we found no material referable to the taxa reported by Morris (1973) during the initial exploration of El Gallo Formation by the Los Angeles County Natural History Museum.

All material was examined petrographically in the Department of Geosciences, University of Rhode Island. The infructescences were first observed at low magnification with a Meiji EMZ (Meiji Techno, Saitama, Japan) dissecting microscope, before six were selected to be examined in thin section at high magnification with an Olympus BH-2 (Olympus, Shinjuku, Japan) petrographic microscope. These sections were cut from the fossils along planes that would yield cross and longitudinal sections of multiple individual fruits on the structure, and photographed in reflected light with an Olympus DP73 camera attachment.

Modern and fossil representatives of fruits were scanned using x-ray microcomputed tomography (microCT) on a Nikon XT H 225ST CT system with a tungsten reflection system at the University of Michigan CTEES facility. Scans of fossils were performed at 135 kV, 195 μ A, with 2.5 mm Cu filter to reduce strong artifacts in reconstructed images and 2.83 s exposure. Voxel size was 13.92 μ m. Extant *Grubbia tomentosa* (Thunb.) Harms (Schlechter 1093 South Africa (BRU)) was scanned at 45 Kv, 100 μ A, with 1.42 s exposure and no filter. Resulting voxel size was 5.13 μ m. The series of two-dimensional projection images were acquired by the x-ray detector using Inspect-X and reconstructed in CT Pro 3D (Nikon Metrology, Brighton, Michigan, USA) using a Feldkamp-Davis-Kress (FDK) type algorithm. Reconstructed data sets were analyzed in Avizo 9 Lite 3D software (FEI, Hillsboro, Oregon, USA). These data are publicly available under project no. 564 on MorphoSource (Duke University; https://www.morphosource.org/Detail/ProjectDetail/Show/project_id/564).

To test the affinity of *Operculifructus* to various cornalean clades, the genus was incorporated into the matrix of 77 morphological characters and 58 fossil and extant cornalean taxa of Atkinson (2018). Four phylogenetic analyses were performed in PAUP* version 4.0a162

(Swofford, 2002) through full heuristic searches under standard settings, saving 10,000 trees in each analysis. In each analysis, we deactivated the seven characters reported by Atkinson (2018) to decrease phylogenetic resolution. In three of these analyses, alternate hypotheses of relationship within Cornales, supported by the genetic data of Xiang et al. (2011), were set as backbone topological constraints applied to the extant taxa. We concatenated all three forms of *Operculifructus* (*O. lopezii*, *O. latomatensis*, and El Gallo fossils described here) into *Operculifructus* spp., because while early iterations of these analyses strongly supported monophyly of the genus, they could not resolve relationships among these forms with the character data presently available. We employ *Grubbia rosmarinifolia* Berg. in the phylogenetic analysis for consistency with Atkinson (2018), and because the syncarp characters diagnostic of different *Grubbia* species (i.e. size, color, hirsute vs. tomentose sulci between fruits; Carlquist, 1977) are not coded in the character matrix of Atkinson (2018) and potentially require reevaluation; the specimen of *G. tomentosa* we examined showed a suite of characters intermediate to those described by Carlquist (1977) for *G. tomentosa* and *G. rourkei*. Bootstrap support was estimated for these clades through a heuristic search of 1000 replicates, with all other search parameters on standard settings. The Trace Character Over Trees command in Mesquite version 3.51 (Maddison and Maddison, 2018) was used to reconstruct character state changes at nodes of interest throughout each tree. The morphological character matrix and molecularly based topological constraints are available under project no. 3238 on MorphoBank (O’Leary and Kaufman, 2012; <http://morphobank.org/permalink/?P3238>).

<h1>RESULTS

<h2>Systematic paleobotany

<h3>Order

Cornales Link. *sensu* Xiang et al. 2011

<h3>Family

Incertae sedis

<h3>Genus

Operculifructus Estrada-Ruiz and Cevallos-Ferriz emend. Hayes and Smith

<h3>Emended generic diagnosis

Polyhedral, cone-like syncarpous infructescences; 6–27 fruits per infructescence; fruits drupaceous, obpyramidal, unilocular, one-seeded; seeds subtend pulvinate, disc-like operculum; pericarp comprised of well-differentiated layers with thin exocarp, fleshy mesocarp comprised of relatively large, isodiametric cells, transition sclereids between mesocarp and endocarp, and one- to three-layered endocarp; channel in fruit from operculum to proximal zone; ovules anatropous, cylindrical to pyriform.

<h3>Type species

Operculifructus lopezii Estrada-Ruiz et Cevallos-Ferriz

<h3>Basionym

Operculifruetus lopezii Estrada-Ruiz and Cevallos-Ferriz, Int. J. Plant Sci. 168: 509.

<h3>Holotype

Colección Nacional de Paleontología, Instituto de Geología, UNAM. Catalog no. LPB 410.

<h3>Type locality, stratigraphy, and age

La Tomatera, Coahuila, Mexico; Cerro del Pueblo Formation; late Campanian.

<h3>Description

Infructescences are polyhedral, and diagenetic compression perhaps produced a roughly oblate spheroid shape in fossil specimens (Fig. 3A—C). They range from 0.8–2.5 cm and 0.7–0.9 cm along their major and minor axes, respectively. Between 9 and 18 obpyramidal fruits comprise each infructescence, and vary from pentagonal to hexagonal in surficial expression. A thin peduncle was observed on the three-dimensional volume reconstruction of one specimen, extending distally from the proximal zone of the infructescence to the nexus of four fruits on the surface (Fig. 3D).

Fruits are unilocular with a single, apparently marginally attached seed. On one specimen, a funiculus still attached to the base of a seed recurves from the proximal zone of the infructescence and plunges distally into the locule (Figs. 3C and 4). This arrangement suggests that each seed developed from an anatropous ovule, contrary to their previous description as orthotropous (Estrada-Ruiz and Cevallos-Ferriz, 2007).

Each seed subtends a pulvinate, disc-shaped operculum comprised of three well-differentiated layers of cells, and bound by sclerenchymatous, distal projections of the endocarp (Fig. 5A). An apical protrusion occupies the center of the operculum and contains a canal that runs through it to the seed below (Figs. 3E and 5B, C). A corresponding protrusion is present on the distal face of the seed and bears the micropyle (Fig. 3F). These features suggest a single stylar canal. The irregular absence of the operculum exposes the distal face of the seed below (Fig. 3A, F), perhaps due to abrasion. Tissues of the operculum display a similar pattern of differentiation to the pericarp elsewhere in the fruit, though the cells are relatively larger. Here, epidermal cells average 49 (29–77) μm by 39 (26–65) μm by 24 (12–32) μm , and those comprising the rest of the operculum measure 39 (29–61) μm by 61 (36–88) μm by 49 (39–73) μm (Fig. 6A).

The pericarp is tripartite: an exocarp, mesocarp, and endocarp are distinct. Three or four layers of rectangular, brick-shaped cells with average measurements of 14 (7–19) μm by 15 (8–25) μm by 15 (11–23) μm form an exocarp, while the mesocarp is comprised of isodiametric to ovoid cells that average 17 (14–25) μm by 23 (15–41) μm by 24 (15–42) μm (Fig. 6B). Small rectangular cells delineate adjacent fruits in the infructescence (Fig. 6C). We interpret the mesocarp as fleshy because it is composed of larger, more parenchymatous cells that contrast strongly in form and density to the endocarp (Fig. 3D). A one- or two-layer palisade of rectangular transition sclereids lies between the mesocarp and endocarp (Fig. 6D); these sclereids average 13 (9–16) μm by 25 (17–29) μm by 30 (26–35) μm (Fig. 6E). The endocarp consists of several layers of cells, averaging 41 (30–56) μm by 11 (7–17) μm by 13 (9–24) μm , that envelop the seed in a cylindrical jacket. Cells of the endocarp are oblong in cross section (Fig. 6D), and polyhedral to circular in longitudinal section (Fig. 6E). These tissues were previously interpreted as integuments (Estrada-Ruiz and Cevallos-Ferriz, 2007), but some El Gallo fossils missing seeds nevertheless still feature the distal projections that line the periphery of the operculum

(Fig. 3B). Consequently, we interpret them as transition sclereids and a stony endocarp, part of the pericarp proper, rather than a component of the seed.

Many fruit locules are often infilled with crystalline minerals (Fig. 5A—C). A vertical channel runs parallel to the locule, through the pericarp (Fig. 5A). Most seeds are inversely pyriform, with a slender, tapering base in the basal zone of each fruit and a broad, flat distal surface (Figs. 3D and 5A). They frequently appear laterally compressed, or even faintly crescent-like distally. The seed coat consists of a minute layer of polyhedral cells and is difficult to distinguish from surrounding tissues (Fig. 6E). Given this homogenous structure, we interpret the seed coat as unitegmic.

Structure of Grubbia tomentosa (Thunb.) Harms infructescence

The infructescence is a polyhedral syncarp of 18 fused drupaceous fruits (Fig. 7A, B) and is 6.5 mm and 4 mm along its respective major and minor axes. The distal face of each fruit is approximately pentagonal and adjoins to adjacent fruits along a raised, hirsute margin. A thin peduncle occurs at the base of the syncarp (Fig. 7A).

Each carpel is bilocular, with a single, anatropous ovule in each locule. Placentation is axile. Only one ovule matures to seed in each syncarp and apparently crushes the second locule and ovule within the carpel as it develops (Fig. 7B–D). The mature seed occupies much of the total volume of the syncarp and subtends an apical, pulvinate disc with a central scar denoting the position of the style. A long stylar canal runs from the micropyle at the apical end of the seed to this stylar scar on the disc (Fig. 7C). The seed is roughly ovoid in the proximal zone of the fruit and tapers to a point along the course of this canal (Fig. 7B).

Three distinct layers are evident in the pericarp (Fig. 7D). A thin exocarp constitutes the outermost layer, consisting of an epidermis comprised of a palisade of approximately rectangular cells and a hypodermis of spongy tissue with many air cavities. Tissues of the mesocarp appear fleshy, becoming spongy near the borders of adjacent fruits on the syncarp. Roughly isodiametric sclereids comprise a thick, dense endocarp that encloses the seed. Locules with immature ovules feature large, apical concentrations of sclereids that grow progressively more diffuse toward the proximal zone of the fruit. In the mature fruit, the endocarp replaces the spongy tissue at the periphery of immature fruits and there delineates channels along boundaries between adjoining fruits (Fig. 7D).

Vascular tissue is difficult to distinguish but appears to run through the endocarp into the septum between the two locules of each fruit and into the funiculi (Fig. 7D).

<h2>Phylogenetic analysis

Phylogenetic analysis under no topological constraint produced 1188 equally parsimonious trees of 197 steps (consistency index [CI] = 0.406, retention index [RI] = 0.750). Strict consensus of these trees (Fig. 8) recovers *Operculifructus* as sister to *Grubbia*, with the same topology of deeper cornalean relationships reported by Atkinson (2018). Character tracings performed across these trees identify the acquisition of drupaceous fruits with a thick and woody endocarp, one ovule per locule, and a smooth seed coat as synapomorphies for the node uniting a *Grubbia-Operculifructus* [GO] clade and all more derived cornalean taxa. Fused fruits represent the only unequivocal synapomorphy for the GO clade under this topology, though a funnel-shaped endocarp and a lack of germination valves may also be derived there. These tracings also indicate as derived in *Operculifructus* transition sclereids and the presence of elongate rather than isodiametric endocarp sclereids.

By contrast, in a second analysis under a topological constraint specifying no branching order among the major cornalean lineages recovered by the genetic analysis of Xiang et al. (2011) (i.e., the monophyly of CA, CG, NMD, HL, and Hydrostachyaceae), we obtained 10,000 equally parsimonious trees of 202 steps (CI = 0.396, RI = 0.739). *Operculifructus* groups within a (Curtisiaceae-(Grubbiaceae-*Operculifructus*) [C-GO] clade under strict consensus of these trees (Fig. 9A). The C-GO clade here lies in a large polyphyletic clade comprised of CA, NMD, and those fossil taxa designated by Atkinson (2018) as the stem NMD group.

A third analysis (Fig. 9B), performed under a topological constraint as before but also specifying the monophyly of a CA-CG clade, retrieved with high support by all analyses of Xiang et al. (2011), produced 10,000 equally parsimonious trees of 202 steps (CI = 0.396, RI = 0.739). Strict consensus of these trees (Fig. 9B) recovers the C-GO clade as sister to a polyphyletic clade comprising the stem NMD group, and these clades as a monophyletic sister to the CA group.

A fourth analysis specifying the monophyly of a NMD-(HL-Hydrostachyaceae) clade, in addition to the CA-CG clade and major lineages, produced 10,000 equally parsimonious trees of 209 steps (CI = 0.383, RI = 0.724). The topology of this constraint was highly supported by

many but not all analyses of Xiang et al. (2011). Strict consensus of these trees (Fig. 9C) produces a poorly resolved phylogeny, with a monophyletic C-GO clade falling within a large polyphyletic group containing all cornalean lineages.

Character tracings performed on trees produced by the three constrained analyses all recover fused fruits and the secondary loss of germination valves as synapomorphies for a GO clade. Whether a funnel-shaped endocarp is derived for the GO clade is equivocal, as in the analysis performed under no topological constraints (Fig. 8). Elongate sclereids are reconstructed as derived in *Operculifructus*, as before, but the presence of transition sclereids is here plesiomorphic, rather than derived. Synapomorphies for a C-GO clade are largely equivocal across these analyses, with vasculature in the fruit axis only definitively reconstructed as derived for the clade in the analysis specifying only monophyly of a CA-CG clade in addition to that of major lineages (Fig. 9B).

DISCUSSION

Comparisons with previously described fossils

Several features firmly situate El Gallo fossils in *Operculifructus* (operculate unilocular infructescence; thin, disc-like operculum; 9–18 fruits per infructescence; rectangular transition sclereids; thick endocarp with oblong sclereids), and we therefore assign the fossils to the genus. Two species have been described, *O. lopezii* and *O. latomatensis* of the late Campanian to Maastrichtian Cerro del Pueblo Formation, Coahuila, Mexico (Estrada-Ruiz and Cevallos-Ferriz, 2007). Magnetostratigraphic correlation of the Cerro del Pueblo to the Horseshoe Canyon Formation (Eberth et al., 2004; southeastern Alberta, Canada) places it within the *Baculites reesidei* and *B. jenseni* ammonite zones, the former dated to a maximum age of 72.5 Ma. More recent work updates the maximum age of this zone to 72.94 ± 0.45 Ma (Cobban et al., 2006); *Operculifructus*, then, appears in Baja California 3.4–1.07 Ma earlier than in the Mexican mainland. The genus may persist later in this record as well: Estrada-Ruiz and Cevallos-Ferriz (2007: fig. 6) also report a similar infructescence from the Oligocene-Miocene El Cien Formation of Baja California Sur, though a lack of microstructural data precludes a confident diagnosis and full comparison with El Gallo specimens described here. Moreover, it remains possible that this fossil is reworked from older Cretaceous sediments.

El Gallo *Operculifructus* exhibits characters previously unique to *O. lopezii* and *O. latomatensis* (Table 1). It bears 9–18 fruits per infructescence, a range that encompasses that of El Cien infructescence (12) and resembles that of *O. lopezii* (6–15) more closely than *O. latomatensis* (21–27). Like *O. lopezii* and *O. latomatensis*, El Gallo infructescences feature a pulvinate operculum bound by distal projections of the endocarp. The relatively shallow operculum of El Gallo *Operculifructus* much more closely resembles that of *O. lopezii* (both ~1.5 mm thick) than the deeper operculum (~12 mm thick) of *O. latomatensis*. The protrusions of the distal face of the seed and opercular tissue noted on El Gallo *Operculifructus* were not observed macroscopically in either *O. lopezii* or *O. latomatensis*. This is perhaps attributable to preservational constraints, as these features are also absent from more poorly preserved fossils among El Gallo infructescences. One specimen of *O. lopezii* did nevertheless feature “an orifice toward [the] geometric center [of the operculum] that is surrounded by radially arranged cells, as seen in cross section” (Estrada-Ruiz and Cevallos-Ferriz, 2007: fig. 2J). This structure may represent the styler canal observed among El Gallo fossils.

As in *O. latomatensis* and *O. lopezii*, El Gallo *Operculifructus* features a zone of rectangular transition sclereids between the mesocarp and endocarp, and a thick endocarp of stratified oblong cells. The morphology of these transition sclereids is shared among all three *Operculifructus* taxa in which it is known. More noteworthy is the structure of the endocarp: variation in cell shape and cell wall thickness here form three zones in *O. lopezii*, but cells are homogeneous in *O. latomatensis* and El Gallo fossils.

El Gallo *Operculifructus* possesses diagnostic characters of both *O. lopezii* and *O. latomatensis*. This coincidence, alongside the geographic distance and older age (ca. 1–3 Ma older) of El Gallo material, suggests that these features might represent a distinct species. Alternatively, because *O. lopezii* and *O. latomatensis* co-occur (Estrada-Ruiz and Cevallos-Ferriz, 2007), these features could indicate morphological plasticity within the genus. It would therefore be prudent to examine intraspecific and interspecific morphological variation within these species, alongside their closest living relatives, to determine whether the morphological variations we see warrant erection of a new species. For this reason, while we are confident these fossils belong in *Operculifructus*, we conservatively designate them as *Operculifructus* sp.

<h2>Phylogenetic affinity of *Operculifructus*

Estrada-Ruiz and Cevallos-Ferriz (2007) described *Operculifructus* as *incertae sedis* within the monocot order Alismatales, based on a mosaic of characters present in some taxa distributed throughout the order. These included spherical aggregate or multiple infructescences, unilocular berries, and orthotropous ovules. However, these characters do not diagnose the crown Alismatales node. Conventionally recognized morphological synapomorphies of Alismatales include scale- or stem-like trichomes within the leaf bases at the nodes, extrorse anthers, and a large green embryo (Judd et al., 2008), none of which is observable in *Operculifructus*. Because the fossil taxon also lacks characters diagnostic of any family or smaller clade within Alismatales, no known synapomorphies support placement of *Operculifructus* in the order.

By contrast, *Operculifructus* bears a striking resemblance to compound fruits of Cornales, such as those of big-bracted dogwoods (i.e., *Cornus kousa* Bürger), *Grubbia*, and, to some extent, *Camptotheca* Decne. Moreover, features recognized in El Gallo *Operculifructus* are consistent with the suite of characters generally considered diagnostic of this order. These characters include (1) drupaceous fruit with woody endocarp; (2) apical germination valves; (3) one seed per locule; (4) anatropous ovules; (5) the absence of a central vascular bundle; and (6) an epigynous, disc-like region of nectariferous tissue persistent on fruits (Stockey et al., 1998; Manchester et al., 1999; Takahasi et al., 2002; Atkinson, 2016; Atkinson et al., 2016, 2017, 2018; Stockey et al., 2016). Almost half of the cornalean families bear all six of these characters, but one or more can be absent, as in Davidiaceae (lacking nectariferous disc; Manchester et al., 1999), Curtisiaceae (possessing centralized vasculature; Manchester et al., 2007), Grubbiaceae (lacking apical germination valves and possessing centralized vasculature; Smith and Smith, 1942; Carlquist, 1977), Hydrangeaceae (capsular, multiseeded fruits; Morozowska et al., 2012), Loasaceae (capsular, multiseeded fruits; Weigend et al., 2004), and Hydrostachyaceae (capsular, multiseeded fruits; Albach et al., 2001). How different lineages acquired or lost these characters remains unclear, however, because uncertainty in deep-node relationships in the cornalean phylogeny obscures patterns of character evolution within it. It is possible that these characters are synapomorphic (or perhaps plesiomorphic, in the case of anatropous ovules) for the crown Cornales node, and therefore lost secondarily in clades that do not possess them, or acquired at sequential nodes within the phylogeny, with lineages missing them being sister to successively more derived clades.

The topology reported by Atkinson (2018) supports this latter hypothesis, with capsular, multiseeded fruits with centralized vasculature ancestral to Cornales; drupaceous, single-seeded fruits uniting Grubbiaceae and all more derived lineages; germination valves uniting a (*Hironoia-Amersinia*) clade and all more derived lineages; and decentralized vasculature uniting a monophyletic core cornalean group containing CA and stem and crown NMD lineages. By contrast, Xiang et al. (2011) note that the strongly supported monophyly of an NMD-(HL-Hydrostachyaceae) clade in many of their analyses suggests that drupaceous fruits, germination valves, and the absence of a central vascular bundle are derived at the crown Cornales node, rather than acquired in a hypothesized Cornaceae-NMD lineage, though they caution that this topology was not well supported by total-evidence analysis. The actual diagnostic power of these broadly “cornalean” characters within the order is relevant to this discussion because *Operculifructus* lacks germination valves and the diffuse fruit vasculature of some cornalean families. In short, whether these character states are independently derived within or ancestral to Cornales has significant implications for their utility in assessing the position of *Operculifructis*.

Other characters provide more direct evidence about the relationships of *Operculifructus*. Unique morphologies present nowhere else in Cornales distinguish fruits of the HL, Hydrostachyaceae, and NMD lineages. Fruits of HL and Hydrostachyaceae are typically capsules with multiple seeds per locule (Cronquist, 1988; Albach et al., 2001; Weigend et al., 2004; Morozowska et al., 2012) and bear little resemblance to the single-seeded, drupaceous fossil infructescences. A fibrous endocarp distinguishes NMD and contrasts strongly with the elongate isodiametric cells that constitute this tissue elsewhere in the order (Eyde, 1963; Stockey et al., 2016). This endocarp morphology is easily recognized in fossils (Manchester et al., 1999; Takahashi et al., 2002; Noll, 2013) but appears not at all like that of *Operculifructus*.

The CA clade possesses the most extensive fossil record of any major cornalean lineage (Eyde, 1988; Feng et al., 2009; Manchester et al., 2009, 2010; Atkinson et al., 2016), and traits that diagnose it unequivocally are well understood. Following Eyde (1988) and Manchester et al. (2015), fruits of Cornaceae (*Cornus* L.) can be recognized by their transseptal vascular strands, multiple locules per fruit, inferior ovaries, dorsal (elongate) germination valves, and endocarps comprised of isodiametric cells. Some species also feature transition sclereids between the mesocarp and endocarp, as in *C. mas* L. and *C. officinalis* Siebold & Zucc. (Morozowska et al., 2013). Fruits of Alangiaceae (*Alangium*) possess similar characters but differ in the structure of

the septal vasculature and the presence of laticifers around vascular bundles (Eyde, 1968). Although the syncarps present among the big-bracted dogwoods of Cornaceae (Eyde, 1988; Xiang et al., 2006) resemble the *Operculifructus* fossils, this similarity is limited by the diffuse vasculature, germination valves, and bilocular fruits that are unlike *Operculifructus*.

Although a CG clade is consistently retrieved in molecular analyses of Cornales (Xiang, 1999; Xiang et al., 2002, 2011; Fan and Xiang, 2003), few morphological characters unite fruits of the group apart from plesiomorphic cornalean traits. This is perhaps unsurprising, as the morphological analysis of Atkinson (2018) does not support the existence of the clade. Diagnostic characters of Curtisiaceae (*Curtisia* Aiton) include the consistent presence of four locules, an absence of ribbing or vasculature along the surface of the stone, faint grooves delimiting the location of the germination valves, locule lining comprised of a single stratum of transversely arranged digitate cells, and transition sclereids between the mesocarp and endocarp (Manchester et al., 2007; Yembaturova et al., 2009). *Grubbia* fruits, by contrast, are hirsute, cone-like syncarps that feature a scarious disc crowning a single seed, a small, distally protruding scar left by the style in the center of each disc, and two locules per fruit that unite to form one through the disintegration of the septum as the ovary matures (Harvey and Sonder, 1859–60; Smith and Smith, 1942; Carlquist, 1977; Kubitzki, 2004).

MicroCT scans of the extant *Grubbia tomentosa* (Fig. 7) reveal characters shared with *Operculifructus*. In both taxa, the single seed of each fruit immediately subtends the epigynous disc, with a protrusion at the location of the micropyle thrust into its overlying tissue and contiguous with a long stylar canal (Fig. 7B–D). The epigynous disc is internally fleshy or spongy, with an outermost layer comprised of box-like cells, and bears a prominent stylar scar on its surface. The occasional absence of this disc in some *Operculifructus* fossils (Fig. 3B, F) raises the possibility that it served a similar role in seed dispersal to the germination valves of all drupaceous cornalean taxa apart from *Grubbia*, but such an interpretation is speculative. Moreover, the presence of distinct tissue layers in the disc of *Operculifructus* presents a clear structural difference to true cornalean germination valves. We therefore consider germination valves absent in both taxa. *Grubbia* and El Gallo *Operculifructus* also share an absence of diffuse endocarp vasculature and, perhaps, the gross likeness both bear to cypress cones, in addition to anatropous ovules, a single ovule per locule, a smooth seed coat, a thick, woody endocarp, and the drupaceous nature of the individual fruits.

These similarities in gross morphology are not exact, however. Only one ovule belonging to a single fruit on each *Grubbia* infructescence matures into a seed, whereas every ovule appears to have matured to seed in *Operculifructus*. Additionally, *Grubbia* lacks the distal projections of the endocarp that delimit the circumference of the overlying disc in *Operculifructus*, but it appears to have channels approximately corresponding to the periphery of the disc (Fig. 7C), as well as a similarly structured apical funnel of the endocarp (Fig. 7D). A lack of immature ovaries among the fossils frustrates comparison to the initially bilocular ovaries of *Grubbia*, though they both appear unilocular at maturity. This also complicates interpretation of placentation in the fossils, as the apparently marginal attachment of their seeds resembles the attachment of seeds in mature *Grubbia* fruits, in which placentation is axile but the second locule is crushed. For these reasons, we code both the number of locules per fruit and placentation as uncertain for *Operculifructus* in our phylogenetic analyses. Nevertheless, *Operculifructus* appears to bear the greatest similarity to Grubbiaceae among Cornales.

In the four phylogenetic analyses we performed, *Operculifructus* was consistently recovered as sister to Grubbiaceae (Figs. 8 and 9). Character tracings performed for all analyses reconstruct syncarpous fruits as an unambiguous synapomorphy for the clade, and secondary loss of germination valves and a funnel-shaped endocarp as potentially derived there. Alternatively, analyses performed under constraints defined by relationships recovered by Xiang et al. (2011) identify the secondary loss of germination valves as an unequivocal synapomorphy for the clade, and axial placentation as plausibly derived there, though the state of this second character could not be confidently reconstructed. The discrepancy between these reconstructions reflect discordance in hypotheses of relationship between the GO clade and other cornalean lineages. If the phylogeny of Atkinson (2018) is correct, the GO clade represents an intermediate form between a capsular-fruited ancestral grade and its sister clade of all other drupaceous-fruited lineages, with relatively few unique morphological innovations. Alternatively, per the topologies of Xiang et al. (2011), the GO clade may constitute a morphologically derived clade within a lineage sister to CA. Intriguingly, our second constrained analysis (Fig. 9B) recovers those taxa Atkinson (2018) designates as the stem NMD lineage as sister to a C-GO clade within this lineage. This suggests the possibility that the four extant species within Curtisiaceae and Grubbiaceae constitute a relict assemblage of a lineage otherwise restricted to the Late Cretaceous, but bootstrap support for this relationship is not high.

Based on comparative morphology and phylogenetic analyses, we propose to transfer *Operculifructus* from Alismatales, family *incertae sedis*, to Cornales, as sister to Grubbiaceae. The analyses reported here quantitatively establish this relationship, though the position of this GO clade within Cornales appears to depend on the robustness of our current molecularly (Xiang et al., 2011) or morphologically (Atkinson, 2018) based understanding of relationships among the major cornalean lineages. Additionally, it remains unclear whether *Operculifructus* might be considered a crown member, or even stem member, of Grubbiaceae. The most recent circumscription of the family (Carlquist, 1977) is based only on the extant *Grubbia*, and although it includes some evidently derived characters at the GO node, such as syncarpous fruits, it also describes many embryo, endosperm, floral, and vegetative characters unobservable in the fossil. This precludes determination of whether Grubbiaceae might encompass both genera. Nevertheless, our analyses affirm a close relationship between *Grubbia* and *Operculifructus*.

<h2>Cretaceous cornalean phytogeography

Operculifructus documents the presence of the currently South African GO clade across northern Mexico during the Campanian. This age predates previous fossil-constrained molecular estimates for the origin of the family, although it falls within the 95% credibility (Xiang et al., 2011) and posterior density intervals (Magallón et al., 2015) constructed around those dates, and is consistent with the time-scaled phylogeny of Atkinson (2018). It puts into question a previously hypothesized Eurasian origin for a CG lineage based on the recognition of fossil *Curtisia quadrilocularis* from the early Eocene of southern England (Manchester et al., 2007) and highlights the difficulty of inferring biogeographic histories for lineages with an extreme paucity of fossils (see also Atkinson et al., 2016). Despite the spatial and temporal distance of *Operculifructus* from the Cenozoic fossil *Curtisia*, the global distribution of fossil Cornales suggests that the incidence of the GO clade in Mexico during the Cretaceous—and perhaps later, if the Oligocene-Miocene El Cien fossil is not reworked—is not entirely surprising.

The Late Cretaceous of North America likely represents an important time and place for the diversification of Cornales. *Tylerianthus crossmanensis* Gandolfo, Nixon, & Crepet (1998), a charcoalified flower of the Turonian Raritan Formation of New Jersey, arguably provides the oldest evidence of the order globally. The flower was described as possessing a strong morphological affinity to the Hydrangeaceae (Cornales) and Saxifragaceae (Saxifragales), and

Gandolfo et al. (1998) reported that preliminary phylogenetic analysis using the character matrix of Hufford (1992) consistently resolved it as sister to the former; however, due to concerns about the original matrix, they neither figured these results nor reported the coding of characters for the fossil. Thus, whether this analysis sufficed to assign the fossil to the Hydrangeaceae is disputed (Crepet et al., 2004; Martínez-Millán, 2010; Friis et al., 2011; Manchester et al., 2015; Atkinson et al., 2018), and some data suggest a younger, Coniacian-Campanian age for the fossil (for discussion, see Massoni et al., 2015).

More definitive evidence establishes the presence of a core group (Fig. 8; Atkinson, 2018) of Cornales in Late Cretaceous North America. The Coniacian *Obamacarpa* Atkinson, Stockey, & Rothwell; *Edencarpa* Atkinson, Stockey, & Rothwell; and *Eydeia vancouverensis* Atkinson, Stockey, & Rothwell (2018) of Vancouver Island, Canada, all bear characters known today only in these clades, though not consistent with any one family. The Campanian *Suciacarpa* Atkinson (2016) and *Sheltercarpa* Atkinson, Stockey, & Rothwell (2017) display similar characters, and all five taxa fall within the stem NMD group recovered by Atkinson (2018) and here (Fig. 8; but see also Fig. 9B). Moreover, *Suciacarpa* and *Sheltercarpa* co-occur with fossils referable to the extant *Cornus* (Atkinson et al., 2016); this provides the earliest record of coexistence between probable stem members of the NMD group and crown members of CA. Evidence for crown members of the NMD clade is apparently absent from Cretaceous North America, as phylogenetic analysis of fruits previously referred to *Nyssa* L. and *Davidia* Baill. from the Campanian of Alberta (Manchester et al., 2015: fig. 5) recovers them within the stem NMD group (Atkinson, 2018).

Only Asia bears a record of Cornales comparable in age to that of North America. The Coniacian *Hironoia fusiformis* Takahashi, Crane, & Manchester (2002) and Coniacian-Santonian *Eydeia hokkaidoensis* Stockey, Nishida, & Atkinson (2016) of Japan are at least coeval with *Obamacarpa*, *Edencarpa*, and *Eydeia vancouverensis*, and phylogenetic analysis recovers the former fossil as sister to *Amersinia obrullata* Manchester, Crane, & Glovneva, and the latter within the stem NMD group (Atkinson, 2018). Evidence for the CA clade emerges somewhat later in Asia than in North America with Paleocene leaves of *Cornus krassilovi* Manchester et al. (2009) from Russia. However, the record is such that it remains unclear whether this apparent lag reflects a real phytogeographic pattern or sparse sampling of Asian deposits of the appropriate age. We do know that members of the crown NMD clade appear roughly synchronously in Asia

and North America with leaf impressions of *Davidia antiqua* (Newberry) Manchester (2002), reported from early Paleocene deposits of the Kamchatka Peninsula, Russia, and western North America.

An ancestral region for Cornales cannot be confidently identified with present data. Nevertheless, if the relationships within Cornales recovered by Atkinson (2018) and here (Fig. 8) are correct, recognition of *Operculifructus* establishes North America as the only continent presently known to possess the most basal drupaceous cornalean fruits by the Campanian. Additionally, both the early Eocene *Curtisia quadrilocularis* and Cretaceous *Operculifructus* provide evidence for European and North American biogeographic connections to Africa. More fossils, especially from Africa, will be important to deciphering the extent and directionality of these relationships. While an accurate account of the early dispersal of Cornales must likely await the recovery of more (and older) material, referral of *Operculifructus* in or sister to Grubbiaceae hints at a deep and complex phytogeographic history for this enigmatic lineage.

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<h1>AUTHOR CONTRIBUTIONS

R.F.H. interpreted the fossils, performed the phylogenetic analyses, and drafted the manuscript. S.Y.S. produced all microCT data and provided critical revisions of the manuscript. M.M.-B. supervised the fieldwork in Baja California. G.Á.-R. and R.H.-R. collected the studied fossils. D.E.F. supervised analysis and interpretation of the fossils, reconstructed the depositional environments of the localities, and provided comments on the manuscript.

<h1>DATA ACCESSIBILITY

Raw microCT data are available on MorphoSource

(https://www.morphosource.org/Detail/ProjectDetail/Show/project_id/564) under project no. 564 (title: Late Cretaceous infructescences of *Operculifructus* (Cornales) from Mexico). Phylogenetic data, including a morphological character matrix, molecularly based topological constraints, and diagnostics for character reconstructions, are available under project no. 3238 on MorphoBank (<http://morphobank.org/permalink/?P3238>).

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FIGURE 1. Location of study area near El Rosario, Baja California, Mexico. El Disecado Member of El Gallo Formation is indicated by gray fill; the band of fossiliferous localities is indicated by circles. Also indicated are the key localities for El Gallo flora assemblage and the

approximate position of the type locality of *Operculifructus* in the Cerro del Pueblo Formation, Coahuila, Mexico.

FIGURE 2. Stratigraphic sections measured in the three localities yielding the preponderance of floral material: (A) Víbora (N30.04772, W115.75540), (B) Granito de mostaza (N30.04760, W115.75904), and (C) La esquina de la frutería de Gerry (N30.05237, W115.75889). In each case, the floral material is found associated with finer-grained deposits, interpreted as paleosols, suggesting landscape stability and autochthonous preservation of the floral material. Note scale differences.

FIGURE 3. El Gallo *Operculifructus* sp. (A) Overview of two infructescences. Note distal protrusions (Prt) of seed and operculum on the two frontmost fruits of the right infructescence. Scale bar = 0.25 cm. IGM-PB 1357 left, IGM-PB 1355 right. (B) An infructescence missing seeds but still bearing the distal projections of tissue (End) that would delimit the circumference of the operculum. Scale bar = 0.25 cm. IGM-PB 1358. (C) Cross section through fractured infructescence—note the funiculus (Fun) attached to the centermost seed. Scale bar = 0.25 cm. IGM-PB 1359. (D) Volume rendering of an infructescence illustrating density contrast between epicarp and mesocarp (green) and endocarp (yellow). Note peduncle (Ped) present on right side of structure. Scale bar = 1.25 mm. IGM-PB 1355. (E) Distal protrusion of the opercular tissue (Prt) and associated canal. Scale bar = 0.425 mm. IGM-PB 1355. (F) Distal protrusion of the seed with a central orifice (Prt), probably micropyle. This protrusion corresponds to that of the operculum above. Scale bar = 0.425 mm. IGM-PB 1355.

FIGURE 4. Detailed view of funiculus (Fun) attached to seed (See) shown in Fig. 3C. Note curvature away from the plane of section in the proximal zone of infructescence, and ascension into locule toward surface of fruit. Inset: sketch of relationship between funiculus (Fun) and seed (See). Scale bar = 1.25 mm. IGM-PB 1359.

FIGURE 5. MicroCT digital sections of El Gallo *Operculifructus*. (A) Section of a complete infructescence. Note positions of operculum (Opr), endocarp projections (Prj), endocarp (End), and mesocarp (Mes) of a single fruit, and vertical channel (Cha) running through the pericarp,

parallel to the seed. Scale bar = 0.625 mm. IGM-PB 1355. (B) Section of one fruit displaying protrusion of seed (Prt), and corresponding protrusion of operculum (Scr) above, perhaps representing stylar scar; compare to Fig. 3E, F. Scale bar = 0.25 mm. IGM-PB 1355. (C) Section of one fruit illustrating probable stylar canal (Can) running through operculum to seed protrusion. Scale bar = 0.625 mm. IGM-PB 1355.

FIGURE 6. Microstructures of El Gallo *Operculifructus*. Individual cell dimensions are indicated by dotted outlines. (A) Longitudinal section of one infructescence, with seed crowned by operculum (Opr) bound by distal projections of the endocarp (Prj). Relative positions of Fig. 4B, C, E are denoted by boxes, and Fig. 4D by dashed line. Scale bar = 500 μm . IGM-PB 1360. (B) Longitudinal section comparing of the boxy cells of exocarp (Exo) and irregular, polyhedral cells of mesocarp (Mes). Scale bar = 100 μm . IGM-PB 1360. (C) Longitudinal section illustrating rectangular cells (Mar) at the marginal contact between two fruits in an infructescence. Scale bar = 100 μm . IGM-PB 1360. (D) Cross section illustrating mesocarp (Mes), uniseriate palisade of transition sclerids (Tsc), many layers of orthogonally oriented cells in endocarp (End), and seed (See). Scale bar = 100 μm . IGM-PB 1360. (E) Longitudinal section displaying differentiation between mesocarp (Mes), transition sclerids (Tsc), endocarp (End), and seed (See). Scale bar = 100 μm . IGM-PB 1361.

FIGURE 7. Fruits of *Grubbia tomentosa* (Thunb.) Harms [BRU: Schlechter 1093, South Africa]. (A) Overview of single syncarp. Note prominent stylar scar in the center of each disc on the structure, and peduncle (Ped) protruding from the bottom of the syncarp. Scale bar = 1.25 mm. (B) Three-dimensional volume reconstruction of syncarp. Only one ovule per syncarp matures into seed; note long stylar canal running from stylar scar atop the disc (Dis) to distal protrusion (Prt) of the seed. Scale bar = 1.25 mm. (C) MicroCT digital section of syncarp. Note oblique section through immature ovary with two locules (Loc), and the close relationship between the disc (Dis), apical protrusion (Prt) of the seed, stylar scar (Scr), and canal (Can). The channel (Cha) corresponds to the periphery of the seeded fruit. Scale bar = 1.25 mm. (D) Different plane of digital section of same syncarp as in C, illustrating tissue differentiation between the epidermal (Epi) and hypodermal (Hyp) layers of the exocarp, the mesocarp (Mes),

and the endocarp (End). Note presence of apical sclerids above locules bearing immature ovules, and note embryo (Emb). Scale bar = 1.25 mm.

FIGURE 8. Strict consensus of 1188 equally parsimonious trees recovered under no topological constraint, with reconstructed evolution of select characters mapped onto the phylogeny. Unequivocal apomorphies were reconstructed as derived for marked clades in all 1188 trees. Equivocal apomorphies were reconstructed for marked clades in all 1188 trees, but uncertainty in reconstructions at deeper nodes prevents determination of whether they are derived or primitive for those clades. Equivocal reconstructions are marked at clades for which a single character state could not be reconstructed across all 1188 trees. Labeling of major groups redrawn from Atkinson (2018). Dagger denotes *Operculifructus*-Grubbiaceae clade. Numbers above branches denote bootstrap support.

FIGURE 9. Strict consensus trees recovered under topological constraints defined by major clades recovered by molecular analyses of Xiang et al. (2011), with reconstructed evolution of select characters mapped onto the phylogenies. (A) Strict consensus of 10,000 equally parsimonious trees, under a constraint specifying the monophyly of CA, CG, NMD, HL, and Hydrostachyaceae. (B) Strict consensus of 10,000 equally parsimonious trees, under a constraint specifying monophyly of CA-CG in addition to those clades in A. (C) Strict consensus of 10,000 equally parsimonious trees, under a constraint specifying the monophyly of CA-CG and NMD-(Hydrostachyaceae-HL) in addition to those clades in A. Definitions of unequivocal apomorphies, equivocal apomorphies, and equivocal character state reconstructions are as in Fig. 8. Dagger denotes *Operculifructus*-Grubbiaceae clade. Numbers above branches denote bootstrap support. Versions of A–C with full tip labels and support values for clades below the family level are available in Appendix S1 as Figs. S1, S2, and S3, respectively (see Supplemental Data with this article).

TABLE 1. Morphological features apparent in infructescences from Cerro del Pueblo, El Gallo, and El Cien formations. In the case of El Cien, no microstructural data are yet available on the infructescence. Modified from Estrada-Ruiz and Cevallos-Ferriz (2007).

Feature	<i>Operculifructus</i>	<i>Operculifructus</i>	El Cien	El Gallo
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	<i>lopezii</i>	<i>latomatensis</i>	infructescence	<i>Operculifructus</i>
Infructescence form	Polyhedral	Polyhedral	Polyhedral	Polyhedral
Type of infructescence	Aggregate or multiple	Aggregate or multiple	Aggregate or multiple	Aggregate or multiple
Operculate fruit	Yes	Yes	Yes	Yes
Number of fruits per infructescence	6–15	21–27	12	9–18
Vertical channel in fruit	Present	Present	?	Present
Seed shape	Cylindrical to pyriform	Cylindrical	?	Pyriform
Endocarp differentiation	Three layers	One layer	?	One layer
Transition sclereids	Present	Present	?	Present
Number of locules per carpel	1	1	?	1
Number of ovules per carpel	1	1	?	1
Ovule orientation	Anatropous	Anatropous	?	Anatropous
Diameter of infructescence (cm)	0.6–1.7	1.8–2.3	1.3	0.8–2.5 (major axis) 0.7–0.9 (minor axis)
Distal protrusion of seed	?	?	?	Yes
Orifice on operculum face	?	?	?	Yes

“La esquina
de la frutería
de Gerry”

“Víbora”

“Granito de mostaza”

Cerro del
Pueblo Fm.

México

30°03'58"

30°01'59"

115°46'07"

115°44'08"

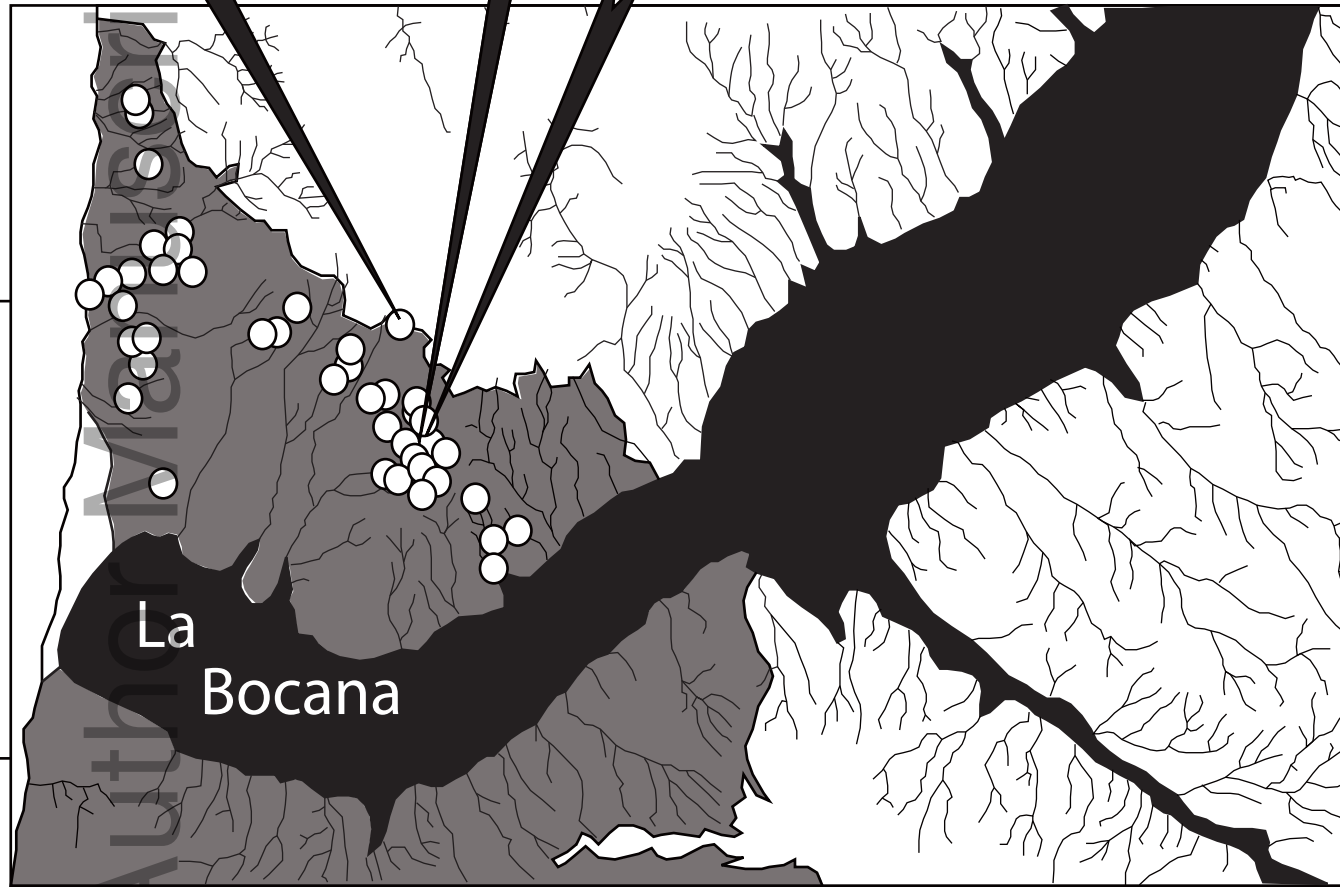
115°42'09"

La
Bocana

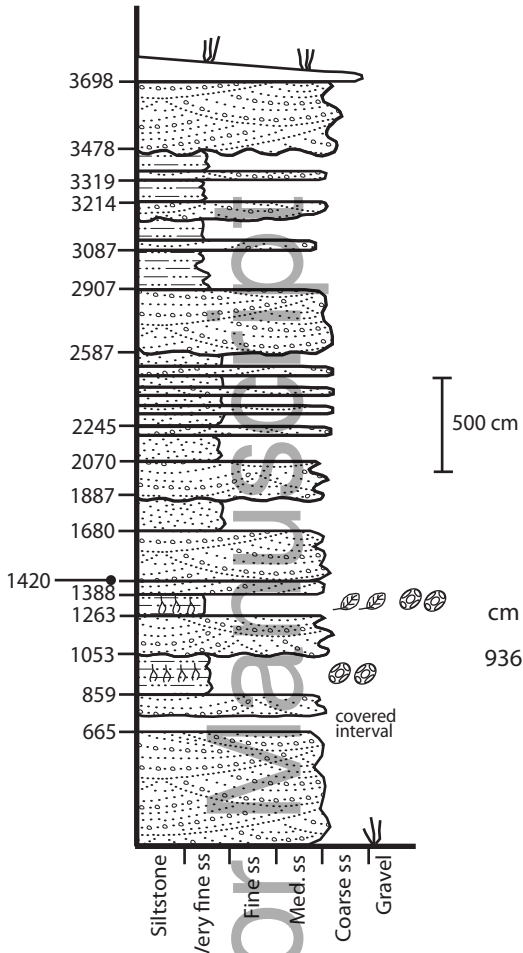
0

3

6 km

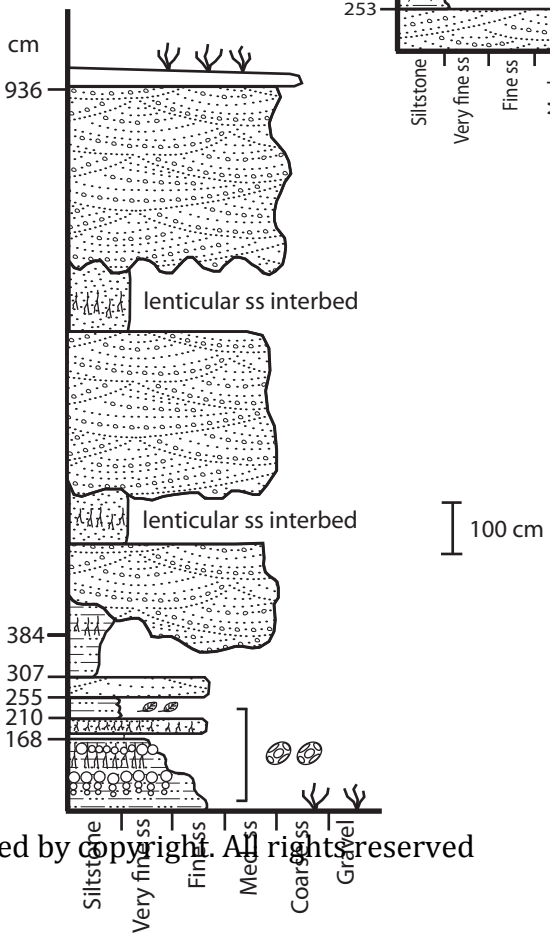


A. "Víbora"



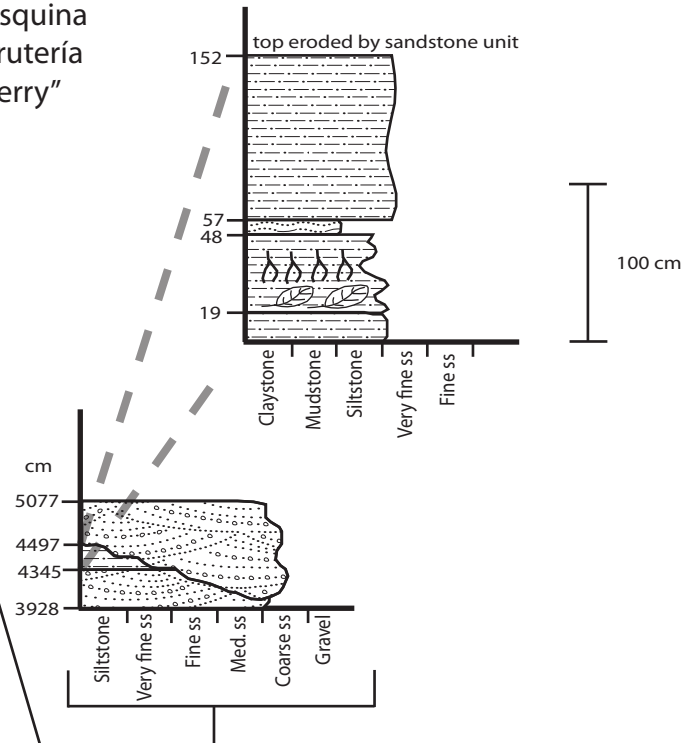
500 cm

B. "Granito de mostaza"



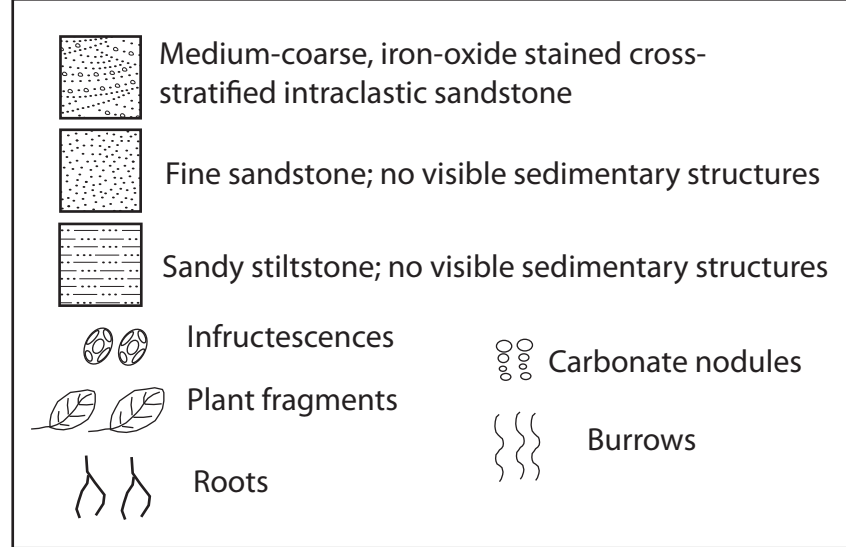
100 cm

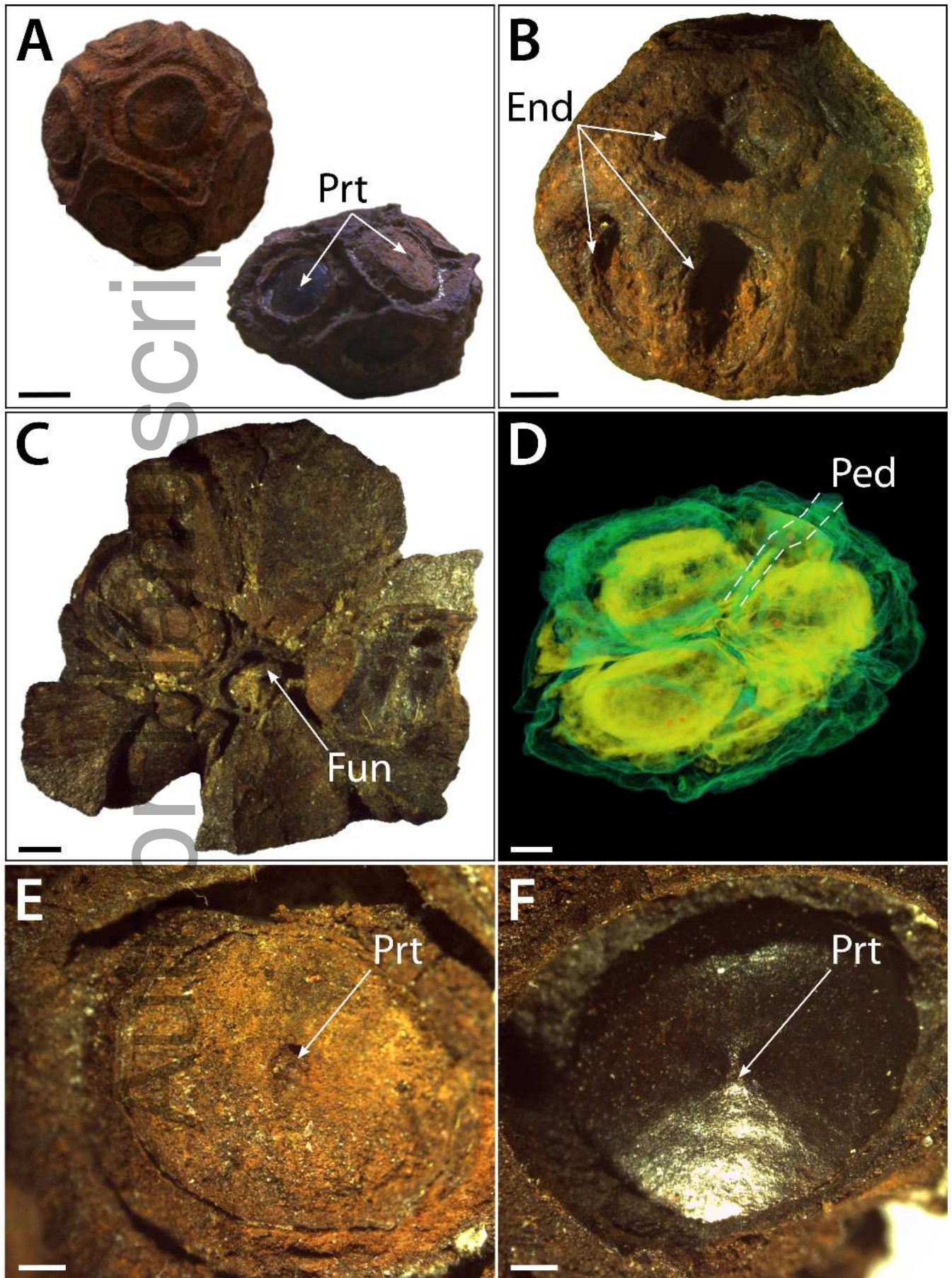
C. "La Esquina de la Frutería de Gerry"

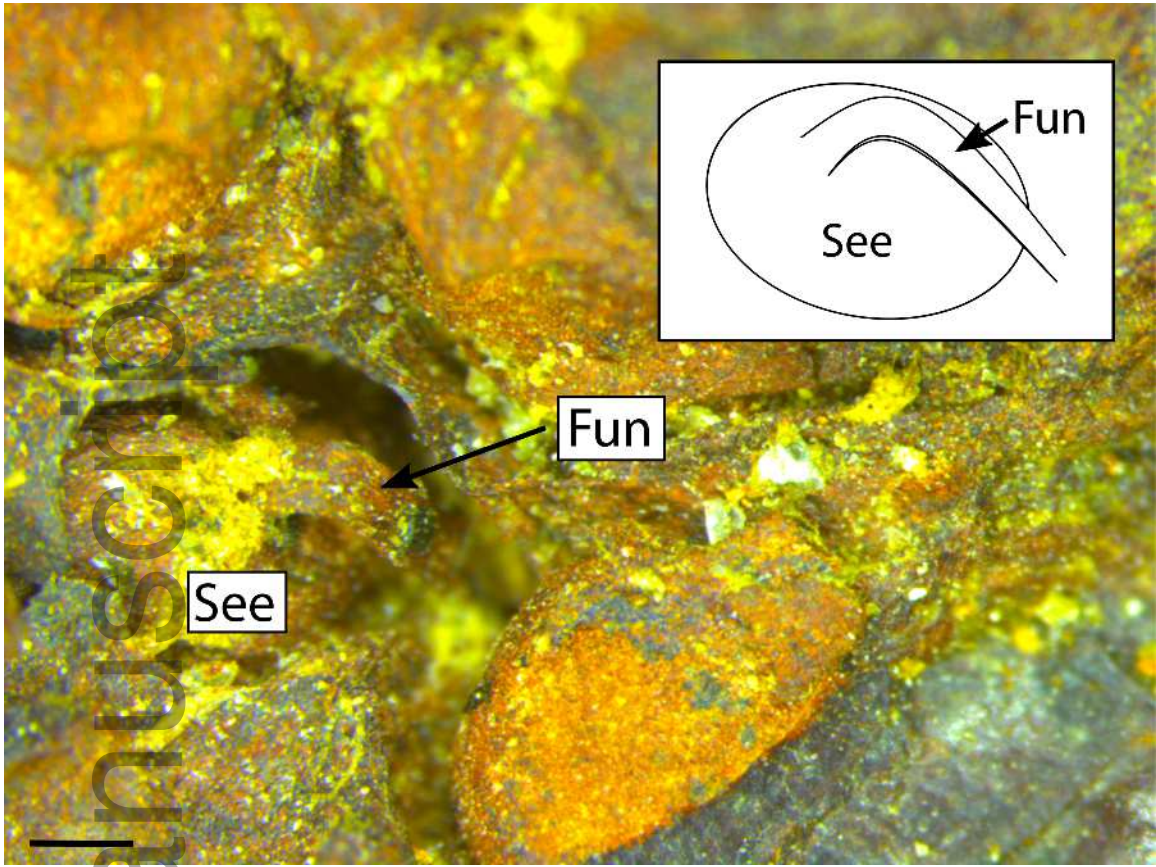


100 cm

Key

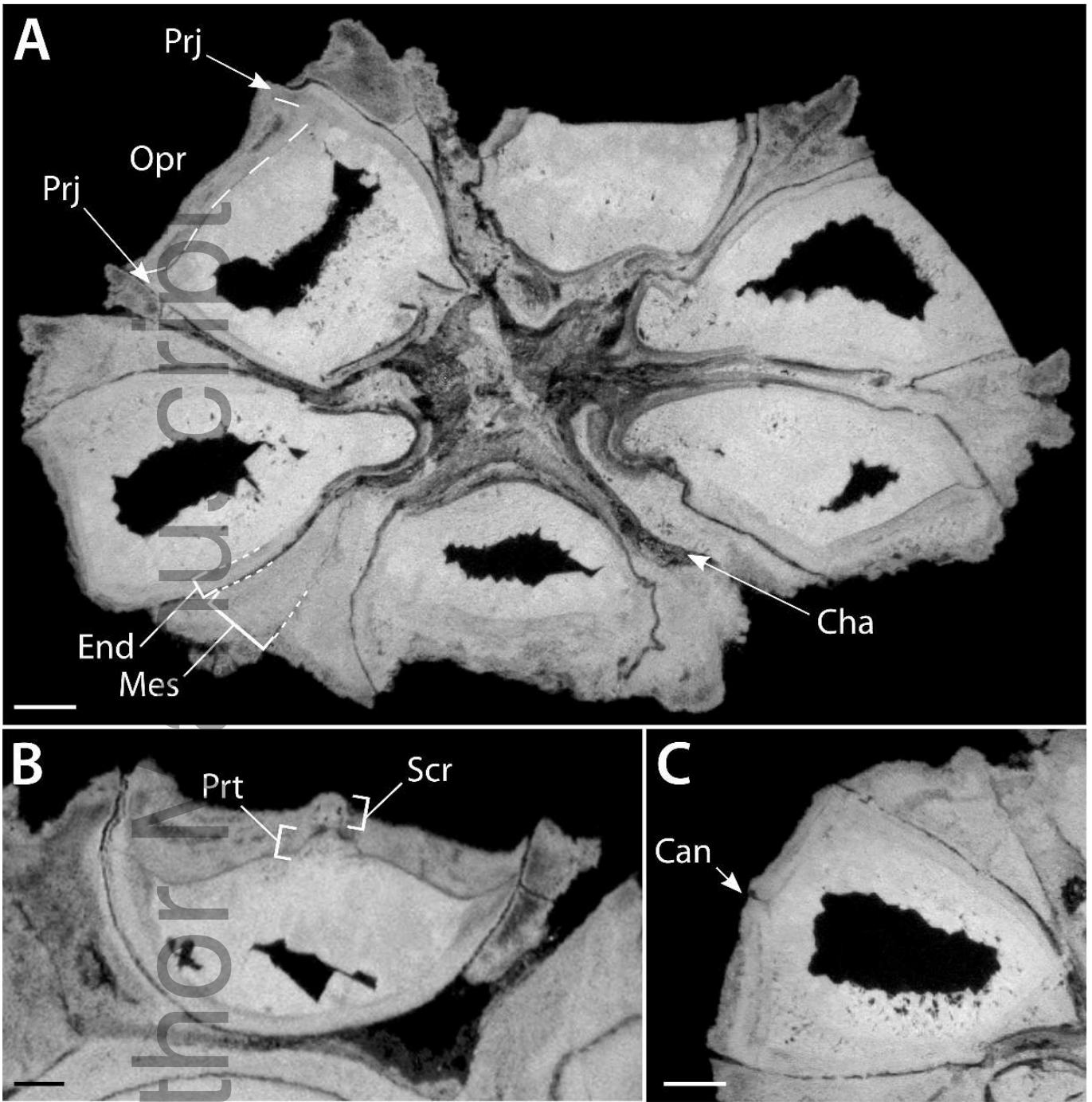




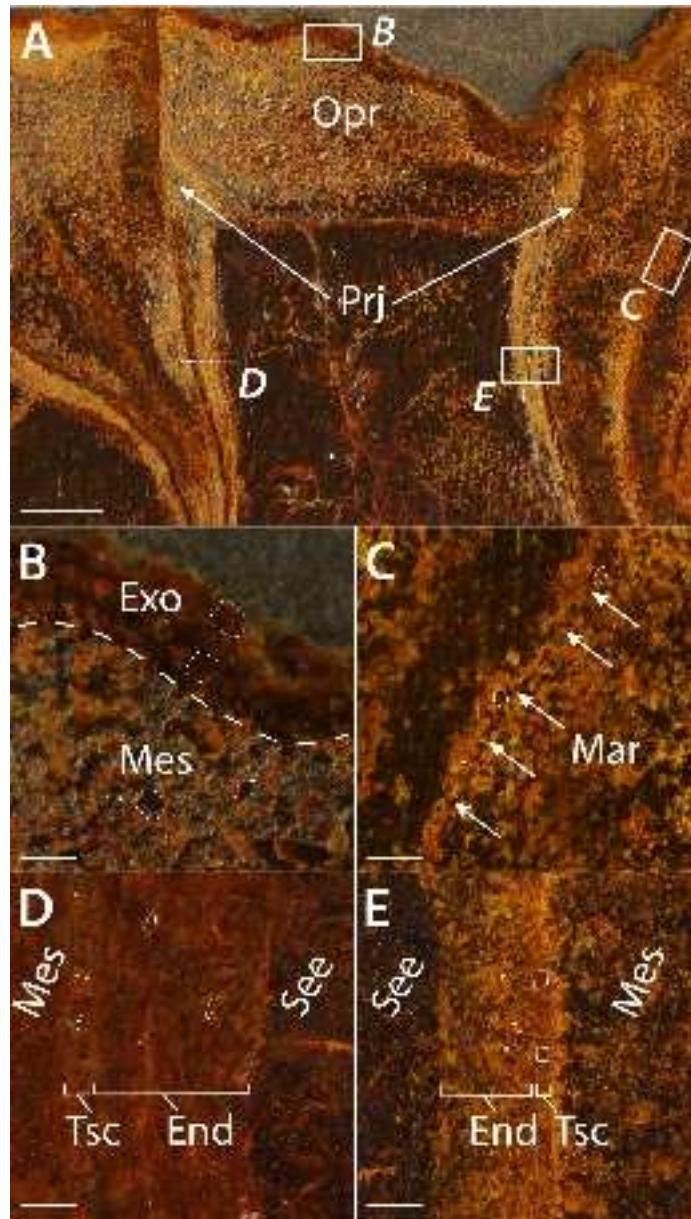


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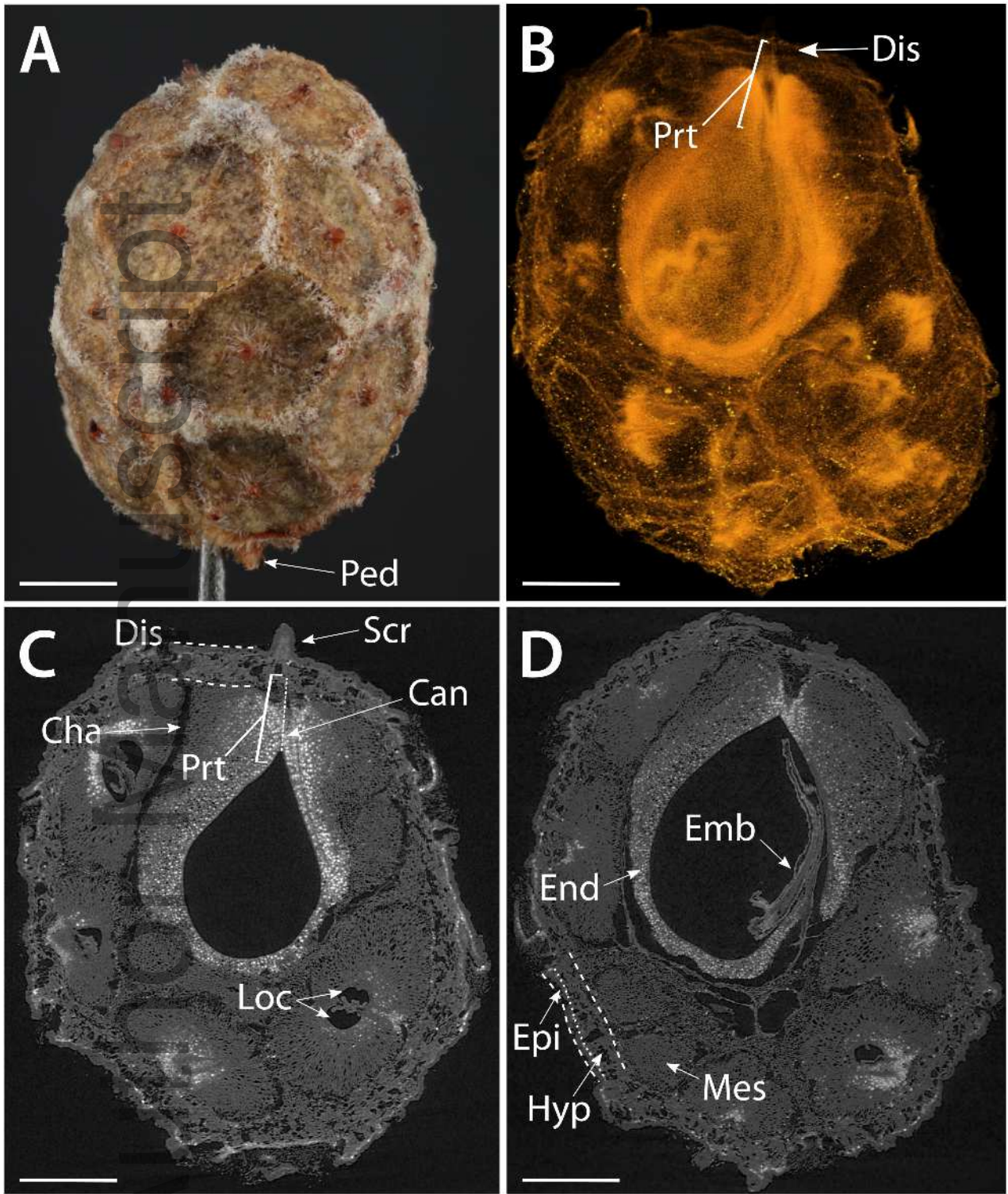
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ajb2_1179_f6.png

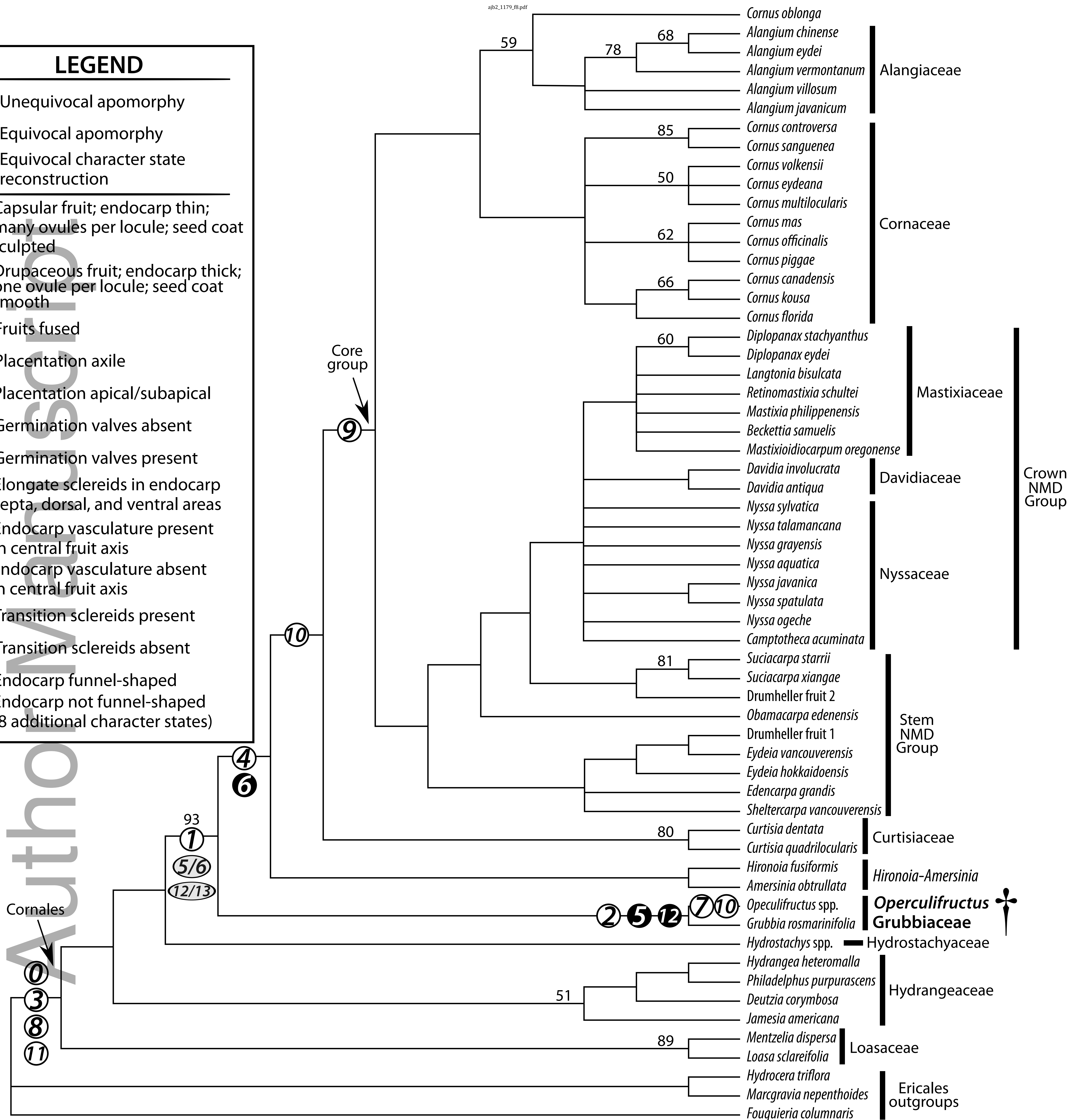


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LEGEND

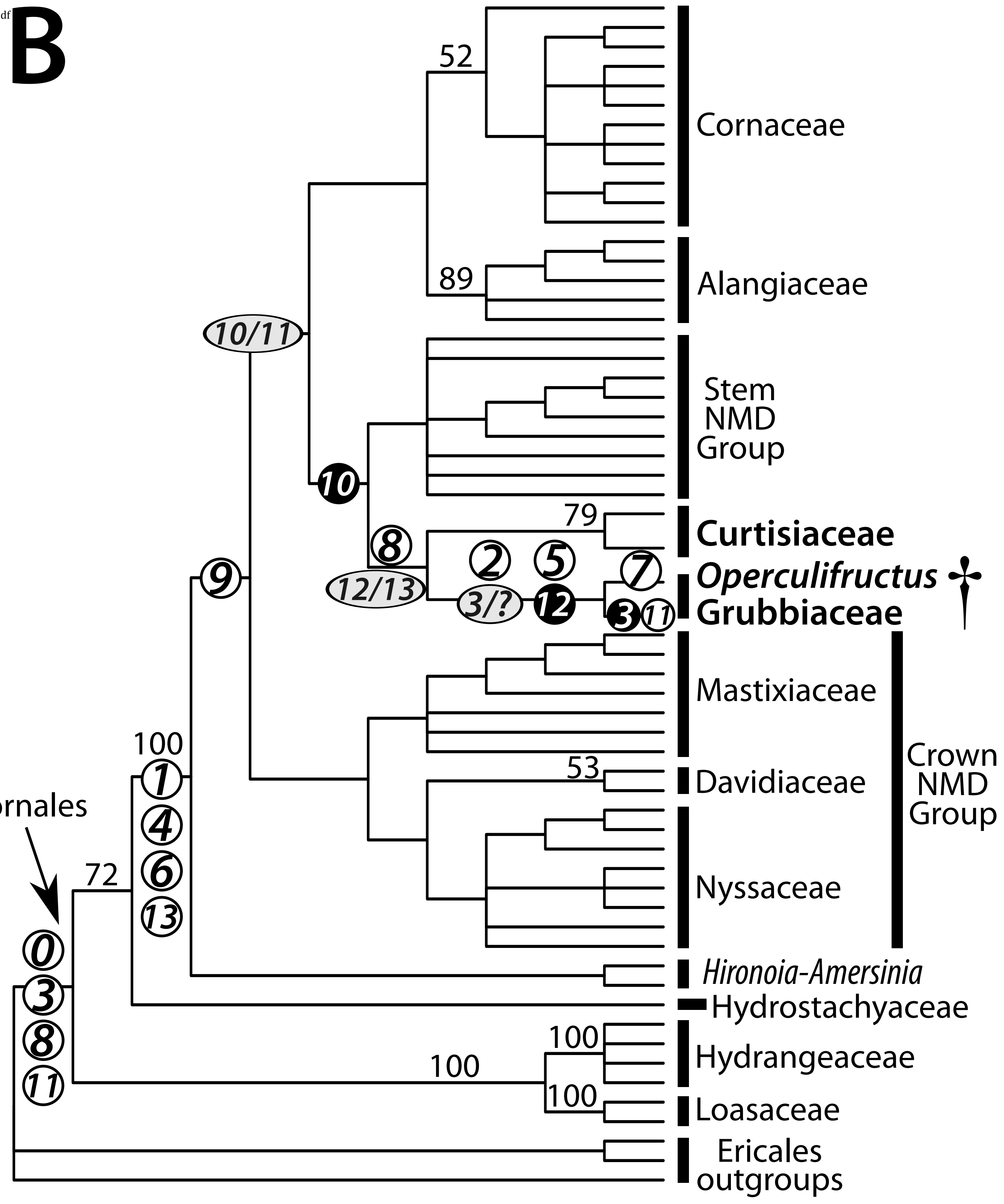
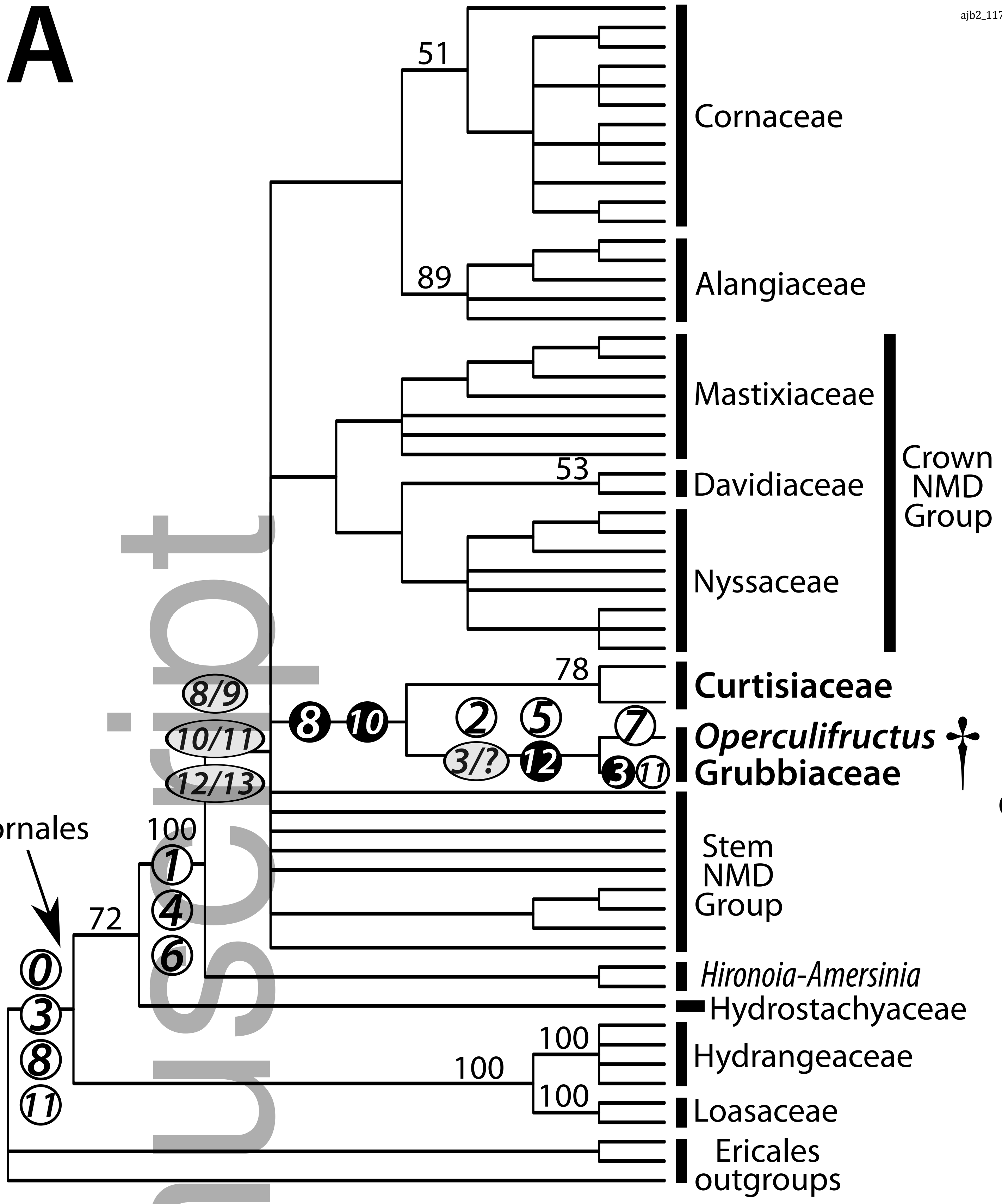
- X** Unequivocal apomorphy
- X** Equivocal apomorphy
- X/Y** Equivocal character state reconstruction

- 0** Capsular fruit; endocarp thin; many ovules per locule; seed coat sculpted
- 1** Drupaceous fruit; endocarp thick; one ovule per locule; seed coat smooth
- 2** Fruits fused
- 3** Placentation axile
- 4** Placentation apical/subapical
- 5** Germination valves absent
- 6** Germination valves present
- 7** Elongate sclereids in endocarp septa, dorsal, and ventral areas
- 8** Endocarp vasculature present in central fruit axis
- 9** Endocarp vasculature absent in central fruit axis
- 10** Transition sclereids present
- 11** Transition sclereids absent
- 12** Endocarp funnel-shaped
- 13** Endocarp not funnel-shaped (8 additional character states)



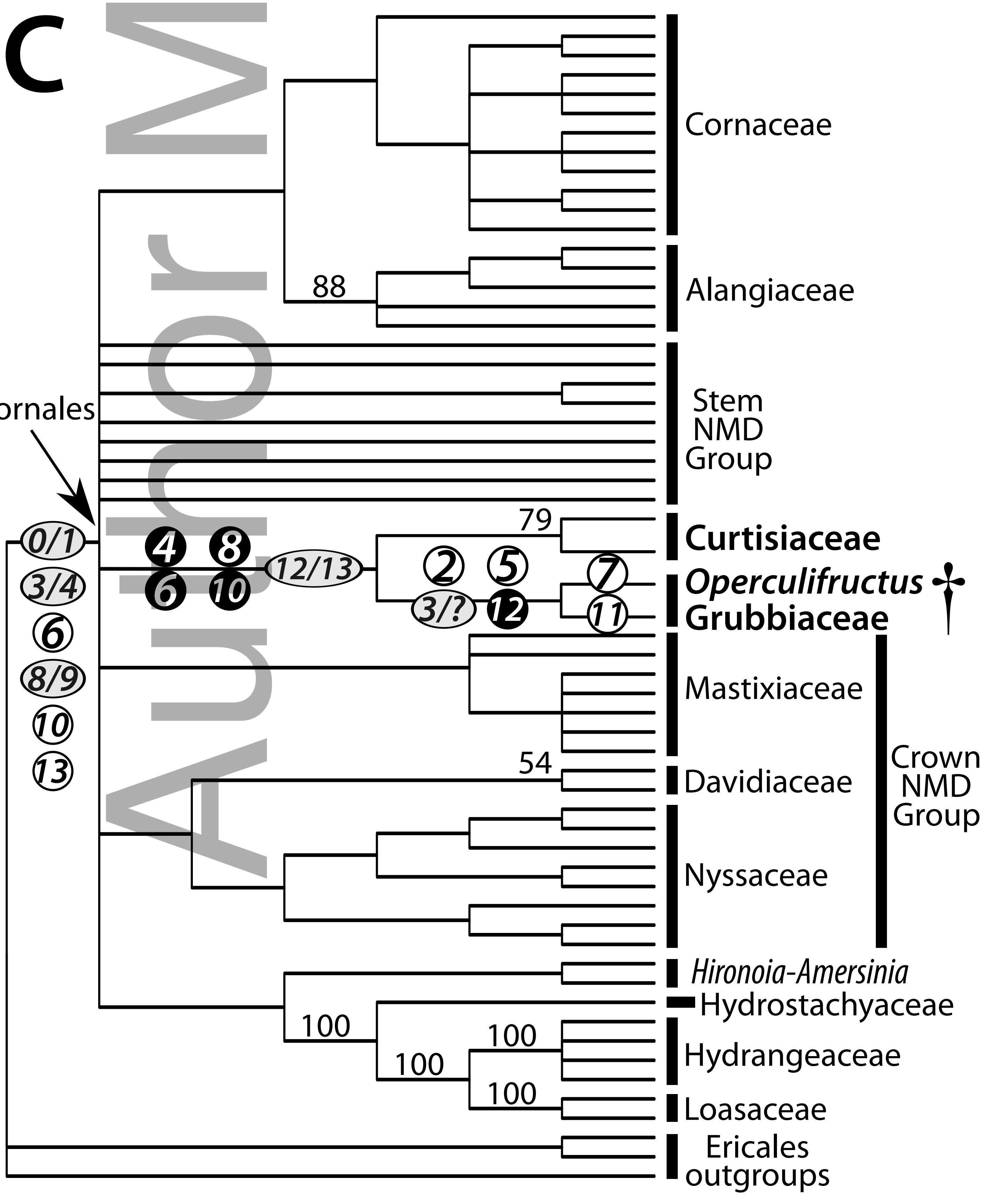
Morphological analysis under no constraint

After Atkinson (2018)



Molecularly based constraint
Monophyly of major lineages sensu Xiang et al. 2011

Molecularly based constraint
Monophyly of major lineages sensu Xiang et al. 2011 & CA-CG



Molecularly based constraint
Monophyly of major lineages, sensu Xiang et al. 2011, CA-CG, & NMD-(HL-Hydrostachyaceae)

LEGEND

- X** Unequivocal apomorphy
- X** Equivocal apomorphy
- X/Y** Equivocal character state reconstruction

- 0** Capsular fruit; endocarp thin; many ovules per locule; seed coat sculpted
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