

Two-seeded cones of probable gnetalean affinity from the Morrison Formation (Late Jurassic) of Utah and Colorado, USA

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ABSTRACT. Three dimensional calcitic casts of a two-seeded compound cone are described from the Upper Jurassic Brushy Basin Member of the Morrison Formation based on specimens from Colorado and Utah. Cones of *Bassitheca hoodiorum* gen. et sp. nov. are broadly obovate in face view, ~3.5 mm high, ~2.6 mm wide, and viewed from above have two planes of symmetry. Micro-CT scanning of numerous specimens shows that each cone has two well-developed orthotropous seeds positioned opposite each other in the major plane and separated by a median longitudinal septum in the minor plane. At a higher level in the cone, a median apical septum in the major plane separates two depressions arranged opposite each other. The two well-developed seeds in the major plane are enclosed by bracts, but numerous incomplete cones, together with cones showing lines of dehiscence, indicate that each seed was shed by the abscission of a lateral valve. One specimen indicates that three vascular bundles entered the base of each well-developed seed and these are interpreted as the vascular supply to the envelope of a chlamydospermous ovule. The opposite and decussate arrangement of bracts at the base of the cone, the paired arrangement of the two well-developed seeds perpendicular to the two apical depressions, combined with the inferred seed envelope that was apparently shed with the seed, indicates a probable relationship to Gnetales and specifically to extant *Ephedra*. Along with *Dayvaultia tetragona* Manchester et Crane, also known from the Brushy Basin Member of the Morrison Formation, *Bassitheca hoodiorum* provides further evidence that the Gnetales were more significant in the Morrison vegetation than has been recognized previously.

KEYWORDS: Mesozoic, micro-CT scanning, gymnosperm cones, extended micropyles, calcitic casts

INTRODUCTION

Fossils of vertebrate animals from the Upper Jurassic Morrison Formation in western North America have played a pivotal role in developing our understanding of the anatomy and biology of dinosaurs and other Mesozoic

vertebrates since the late 1870s. Over the past 150 years more than one hundred species of fossil vertebrates have been described from the Morrison Formation, including lungfishes, ray-finned fishes, frogs, salamanders, lizards, crocodiles, pterosaurs and mammals, as well as diverse dinosaurs (Foster, 2020). The fossil

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record of plants in the Morrison Formation is also extensive based on macrofossils (Tidwell and Rushforth, 1970; Medlyn and Tidwell, 1975a, b; 1979; Tidwell, 1990a, b, 1994; Tidwell and Ash, 1990, 2006; Tidwell and Medlyn, 1992, 1993; Ash, 1994; Ash and Tidwell, 1998; Tidwell et al., 1998; Gee and Tidwell, 2010; Gee, 2011, 2013, 2016; Gee et al., 2014, 2019) as well as pollen and spores (Litwin et al., 1998; Hotton and Baghai-Riding, 2010, 2016), but so far the generally poor preservation of the plant megafossil, and the uncertain affinities of dispersed palynomorphs has hindered their contribution to understanding the structure and evolutionary biology of Jurassic plants.

Seed plants were abundant and diverse in the vegetation of Morrison times, as indicated by pollen grains in the palynoflora (Hotton and Baghai-Riding, 2010, 2016) as well as fossil leaves of Bennettitales, conifers, cycads, and ginkgophytes in the Morrison macroflora. However, reproductive structures of fossil plants are much less common, and because they are preserved mainly as impressions or thin compressions, they generally provide little structural information (Foster, 2020). Nevertheless, since the pioneering studies of Chandler (1966) it has been recognized that the Morrison Formation occasionally yields calcitic casts of small seed plant reproductive structures. These have promise for more detailed structural studies, and significant collections of these fossils have been made from several localities (Bass, 1964; Dayvault and Hatch, 2003, 2007; Tidwell and Medlyn, 1992). There are also occasional records of stems and cones with anatomical details preserved (Arnold, 1962; Gee, 2013; Gee et al., 2014, 2019). Interest in these fossils has been revived by new imaging techniques that allow detailed non-destructive examination of the structure of the most promising fossils as well as the continuing need to better understand the diversity of reproductive structures among Mesozoic seed plants (Gee, 2013; Gee et al., 2014; Manchester et al., 2021).

In this paper we describe a new kind of small cone that bore two seeds, based on numerous calcitic casts collected from the Brushy Basin Member of the Morrison Formation. Although these two-seeded cones are distinct from the co-occurring 6- to 8-seeded cones of *Dayvaultia tetragona* Manchester et Crane, described previously from similar calcitic material

(Manchester et al., 2021) and which are also organized on an opposite and decussate plan, the new fossils are also of probable gnetalean affinity. Such fossils contribute to understanding the fossil record of Gnetales prior to the Early Cretaceous, where the group is increasingly well-documented (Krassilov, 1986; Crane and Upchurch, 1987; Rydin et al., 2006a, b; Kunzman et al., 2011; Friis et al., 2007, 2009, 2011, 2013, 2014, 2019; Mendes et al., 2020; Rothwell and Stockey, 2013; Yang and Wang, 2013; Yang and Ferguson, 2015). The presence of *Bassitheca* at two Late Jurassic localities, in central Colorado and southern Utah, suggests that Gnetales were more prominent and more widespread in Late Jurassic vegetation than has been recognized by previous research.

MATERIALS AND METHODS

More than 300 specimens were studied from a site near Crescent Creek on the eastern flank of Mount Ellen in Garfield County, southeastern Utah (latitude 38.08042 N; longitude 110.64981 W; Fig. 1; Bass, 1964). The initial collections were made by Charles Bass, and subsequently by his daughter and son-in-law, Donna and Glen Hood, and the specimens are now part of the Bass and Hood collections housed at United States National Museum, Washington, DC (USNM). Numerous additional specimens were collected from the same site by Richard Dayvault and donated to the Florida Museum of Natural History (UF). Others, collected by William D. Tidwell, are deposited at the Brigham Young University Museum of Paleontology. Some of the specimens were picked from the surface of the outcrop, but most were recovered by careful screen washing of large amounts of clay carried out from the site by Glen and Donna Hood. Three additional specimens of the same species were located in the collections of the Denver Museum of Nature and Science (DMNH), from Valley of Death, Garden Park, Fremont County, Colorado (latitude 38.54777778 N, longitude 105.23111111 W; Fig. 1). These specimens were collected by Kenneth Carpenter during field work associated with his review of faunal remains near the base of the Brushy Basin Member (Carpenter, 1998). A radiometric date of 150.3 ± 0.26 Ma reported by Kowallis et al. (1998), subsequently recalibrated to 152.29 ± 0.30 Ma (Trujillo and Kowallis, 2015), was obtained from approximately the same stratigraphic level at the Valley of Death locality (Carpenter, 1998).

Specimens from both sites are preserved as calcitic casts that lack anatomical preservation of tissues and pollen. Nevertheless, surface detail and some limited internal structure are preserved quite faithfully and micro-CT scans also reveal differential preservation of the seed cavity. Micro-CT scans were performed at the University of Florida, College of Engineering Nanoscale Research Facility, with a GE Phoenix V|tome|x240 CT Scanner, using a Tungsten

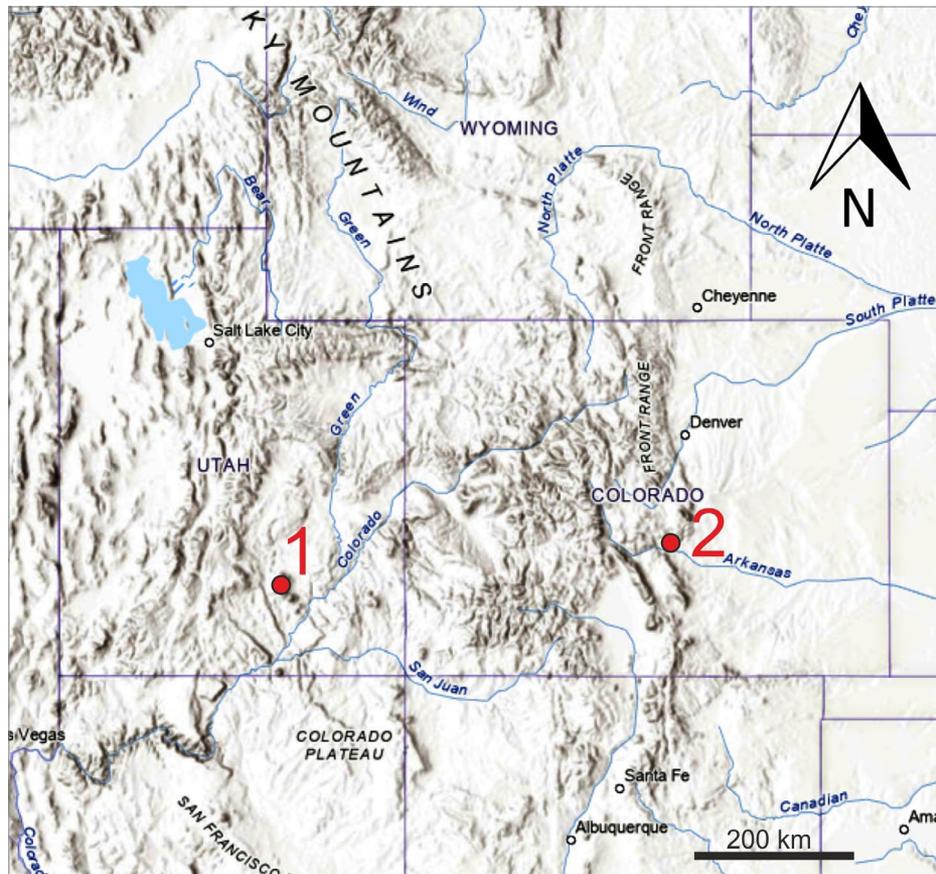


Figure 1. Locality map showing the Mt. Ellen locality, Utah (1), and Valley of Death, locality, Colorado (2), USA, which have both yielded *Bassitheca hoodiorum* gen. et sp. nov. from the Brushy Basin Member of the Morrison Formation. Basemap from Google maps

reflection target with a voltage of 80kV and current of 180 μ A with a voxel size of 17.6 μ m. We obtained 1800 images through a 360-degree rotation with 2-second exposures. The resulting datasets were processed with VG Studio Max 3.1, Avizo 9.0 Lite and Meshlab 2016.12 to obtain successive virtual sections, translucent volumes and surface renderings. Tiff stacks and interactive 3D meshes generated from the μ CT data are archived at morphosource.org (search string: *Bassitheca hoodiorum*).

SYSTEMATICS

Order: GNETALES?

Genus: *Bassitheca* Manchester et Crane
gen. nov.

Genus diagnosis. Cones broadly obovate in face view, convex and rounded basally, truncate apically, elliptical to narrowly ovate in lateral view, elliptical with two planes of symmetry in apical view. Cones borne on a short stout peduncle that is square to rounded in transverse section, containing four distinct vascular bundles. Cones comprised of two well-developed

orthotropous seeds positioned opposite each other in the major plane, separated by a distinct median longitudinal septum in the minor plane. Well-developed seeds surrounded by protective bracts and each seed released by shedding of a lateral valve. Each seed with an apical micropyle and supplied at the base by three vascular bundles. Above the level of the seeds a median apical septum in the major plane separates two well demarcated depressions arranged opposite each other in the minor plane.

Etymology. In honor of Charles Bass, discoverer of the locality that yielded the most specimens.

Plant Fossil Names registry. PFN002933 (for new genus).

Type species. *B. hoodiorum* sp. nov.

Species. *Bassitheca hoodiorum*
Manchester et Crane **sp. nov.**

Figs 2–6

Holotype. USNM 770225 (Fig. 2L–O).

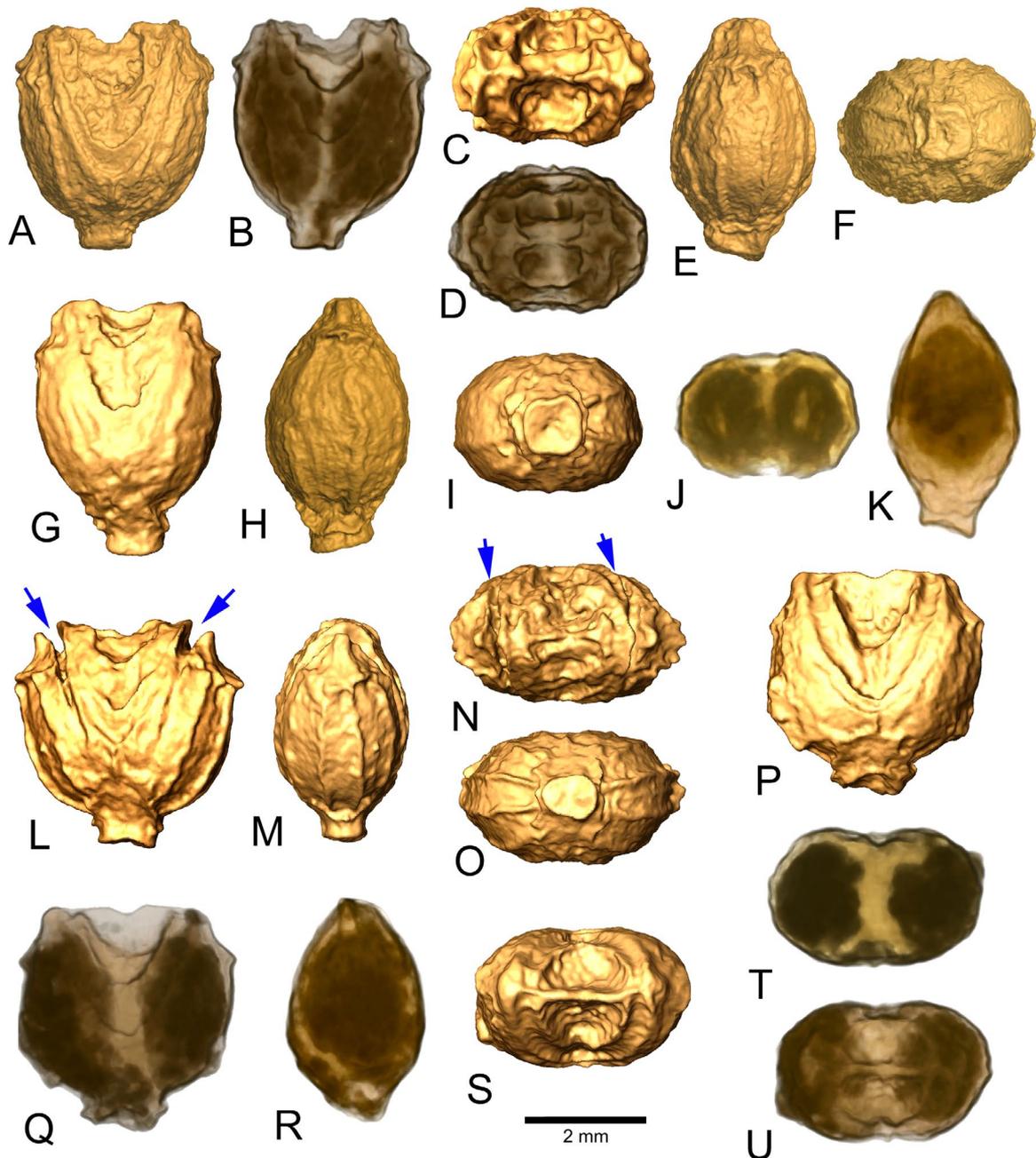


Figure 2. *Bassitheca hoodiorum* gen. et sp. nov. from the Morrison Formation, Mt. Ellen, Utah, USA. Micro-CT scan images. Reflective surface renderings (A, C, E–I, L–P, S), translucent volume renderings (B, D, J, K, Q, R, T, U). A–F. USNM 770219. Cone in face views (A, B), apical views (C, D), lateral view (E), basal view (F); note deep sinuses on broad faces (A), minor plane septum (B, D), longitudinal septum separating two apical depressions (C, D), distinct shoulder with apical micropylar projection (E), two pairs of lateral ribs arising from the base (F). G–K. USNM 770223. Cone in face view (G), lateral views (H, K), basal views (I, J); note distinct shoulder with apical micropylar projection (H), two pairs of lateral ribs arising from the base (I), transverse septum (J). L–O. USNM 770225. Holotype. Cone in face view (L), lateral view (M), apical view (N), basal view (O); note two lines of dehiscence (L, N arrows), distinct shoulder with apical micropylar projection (M), two pairs of lateral ribs arising from the base (O). P–U. USNM 770226. Cone in face view (P, Q), lateral view (R), apical views (S, U), basal view (T); note deep sinuses on broad faces (P), minor plane septum (Q, T, U), longitudinal septum separating two apical depressions (S)

Paratypes. UF 18537–84190, 84191, 84192, 84193; USNM 771463, 771464, 771467, 771506, 771523, 771527, 771528.

Other studied specimens. USNM 771461, 771462, 771465, 771466, 771468–771477, 771504, 771505, 771507–771522, 771524–771526, 771529–771539.

Species Diagnosis. As for the genus.

Etymology. In honor of Glen and Donna Hood, who collected and donated many of the specimens illustrated in this paper.

Plant Fossil Names registry. PFN002934 (for new species).

Description. Cones cordiform, 3.5 mm high, 2.6 mm wide and 2.0 mm deep, with two longitudinal planes of symmetry arranged at 90 degrees to one another. The major plane of symmetry reflecting a pair of broadly obovate faces that are convex and rounded basally, truncate apically, and usually with a broad, prominent, symmetrical central sinus on each face (Figs 2A, G, L, P; 3A, B, H, O; 4A, B, K, M; 6A, F). In lateral view, parallel to the minor plane of symmetry, cones elliptical to narrowly ovate (Figs 2E, H, M; 3C, D, I, R; 4C, D, N; 6B, C, G, H). Cones broadly to narrowly elliptical in apical (Figs 2C, N, S; 3F, P; 4H, S; 5F; 6D, I) and basal (Figs 2F, I, O; 3E, Q; 4G, R; 5H; 6E, J) views.

Longitudinal translucent silhouettes (Fig. 2B, Q), virtual sections in the major plane (Figs 3N; 4F, P; 5P), transverse translucent silhouettes (Fig. 2D, J, T, U) and virtual sections (Figs 3G, M; 4I; 5I) show two well-developed ellipsoidal seed cavities or seeds separated by a distinct median longitudinal septum in the minor plane. In longitudinal translucent silhouettes and in sections parallel to the minor plane the seed cavities or seeds are oval (Figs 2K, R; 4E, Q; 5R); in transverse view they are elliptical to almost circular, but they are flattened where they abut the septum (e.g. Figs 3G; 4I; 5I; 6K). The longitudinal axes of the seed cavities or seeds diverge from each other at about 35° so their micropyles are farther from each other than are their bases. In the apical portion of the cone a distinct median septum in the major plane separates two depressions arranged opposite each other in the minor plane (Figs 2C, N, S; 3F, K, P; 4H, S; 5F; 6D, I).

Cones borne on a distinct short stout peduncle ~0.3 mm long (Figs 2A, G, L, P; 3A, B, H, O; 4A, K, M; 5B, J, N; 6A, F). Seen from below, the peduncle is more-or-less square in well-preserved specimens (Figs 2I; 4L; 6E) to irregularly rounded in more weathered specimens (Figs 3E, L, Q; 4G), and ~1 mm in diameter. In some specimens the peduncle is slightly wider in the major (Fig. 2O) or minor (Figs 4R; 5H; 6E, J) plane. A pair of opposite, more-or-less triangular bracts, each with an acute apex, arises from the peduncle in the minor plane (Figs 2O; 3L; 4L, R; 5G, H). The apex of each bract is positioned between the two divergent seeds in the lower part of the cone. In some specimens there is a pair of opposite joints just below these bracts at the base of the cone. These joints are perpendicular to the opposite triangular bracts

above and probably indicate an original pair of bracts in the major plane (Figs 2A, L; 3A, B; 4A, B, K, M). In one specimen there are poorly preserved flaps of tissue attached to the pair of opposite joints (Fig. 3A, B, E).

Base of the peduncle sometimes with a central cross-shaped indentation, the four arms of which are offset by ~45° to the major and minor planes of the cone (Fig. 3L, R). Transverse sections of the peduncle show four symmetrically placed electron transparent canals in the same orientation as the tips of the central cross-shaped indentation (Fig. 4J, O). In longitudinal sections these electron transparent areas, which we interpret as vascular bundles, appear as strands in the peduncle that pass upwards and slightly diverge apically toward the base of the seeds (Fig. 4E, F, P, Q).

The two well-developed orthotropous seed cavities or seeds comprise the bulk of the cone and diverge only slightly from each other in the major plane (Figs 2B, Q; 3N; 4F, P; 5P). One specimen has three small holes entering the seed cavity from the base that we interpret as the positions of three vascular bundles (Fig. 5U, V). In the major plane at either end of the apical longitudinal septum each seed has a small apical protuberance that we interpret as indicating the position of the micropyle (Figs 2C, N, S; 3F, I, K, P; 4H, S; 5F; 6D, I). The tip of the protuberance sometimes preserves a small apical depression (Figs 3F, I, K; 6D, I). A fractured specimen shows a small projection from a central body in the seed cavity that extends to the outer surface in a position corresponding to the location of the presumed micropyle (Fig. 4C).

Externally the micropyle is located at the apex of a small protuberance with a smooth surface (Figs 3F, I, K; 4S; 6I, L). This protuberance gradually broadens below and connects to three poorly defined ribs (Figs 3F, K; 4S; 6I, L); one in the major plane that connects with the apical longitudinal septum (Fig 2C, D, N, S; 3F, K, P; 4H, S; 5F; 6D, I, L), and one laterally on either side of the seed more-or-less perpendicular to the major plane. These two lateral ribs extend downwards from the micropyle (Figs 2C, N, S; 3F, K, P; 4H, S; 5F; 6D, I, L). In the major plane, at either end, the cone expands into a distinct shoulder formed by a transverse flange of crumpled tissue about five sixths of the distance from the cone base. In most cases there is a distinct substantial conical extension

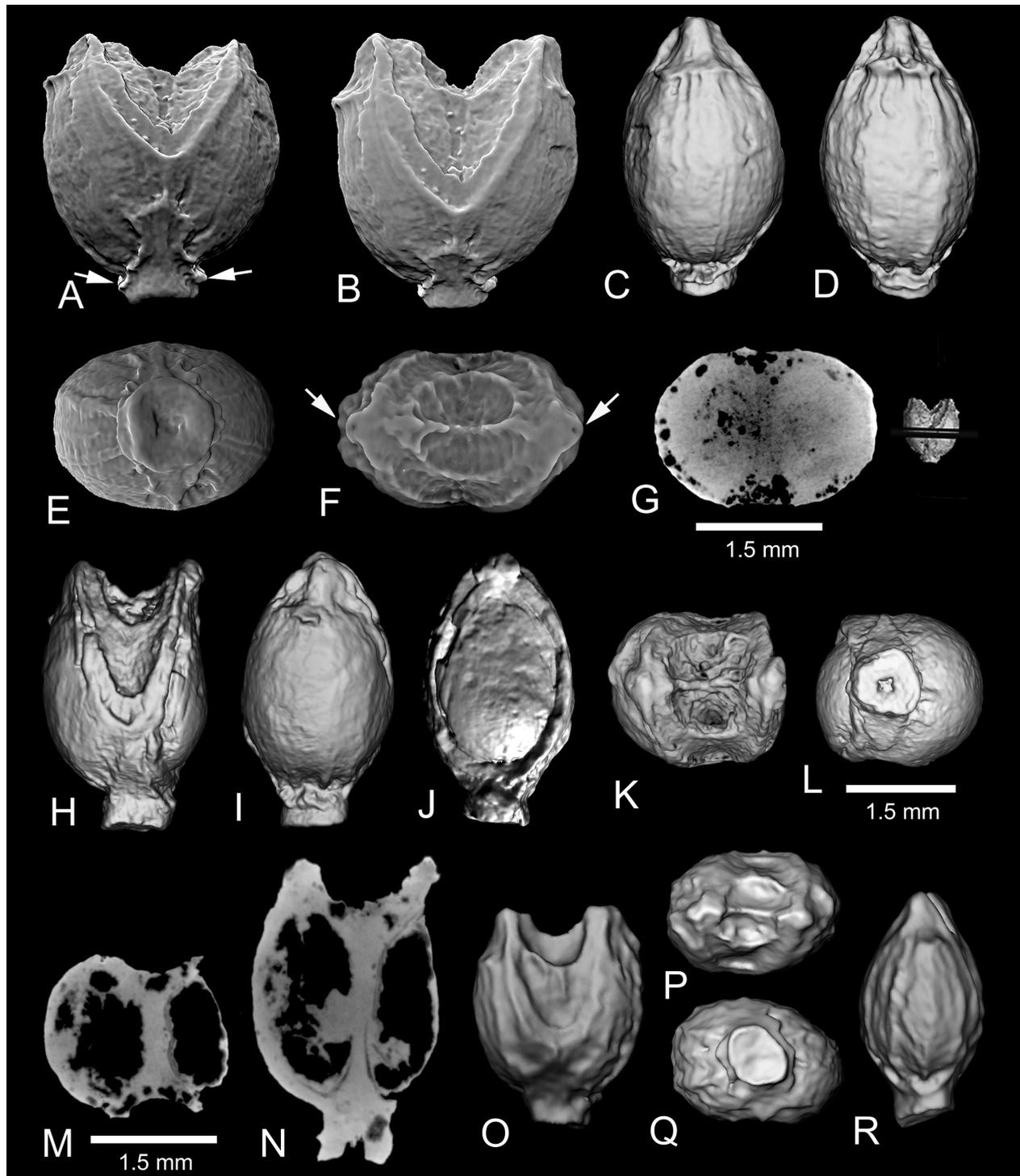


Figure 3. *Bassitheca hoodiorum* gen. et sp. nov. from the Morrison Formation, Mount Ellen, Utah, USA (A–N) and Valley of Death, Colorado, USA (O–R). Micro-CT scan image. Reflective surface renderings (A–E, H–K, O–R), depth map (F), virtual sections (G, M, N). A–G. USNM 77146. Cone in face views (base tilted forward to show basal in bract in A, orthogonal face view in B), opposing lateral views (C, D), basal view (E), apical view (F), transverse section near equator (G); note pair of opposite joints (arrows) below the cone base and two opposite poorly preserved bracts in the minor plane (A, B), deep sinuses on the broad face (A, B), distinct shoulder with apical micropylar projection (C, D), apical longitudinal septum separating two apical sunken areas and two micropylar openings (arrows, F), basal pair of opposite bracts in minor plane with two pairs of ribs on the lateral faces arising from the base (E), degraded cavities in the outer tissues of the cone (G). H–N. USNM 771506. Cone with one lateral valve detached exposing a seed (H), opposing lateral views (I, J), apical views (K), basal view (L), transverse section (M), longitudinal section in major plane (N); note pair of opposite joints below the cone base (H), septum in the minor plane (M, N), longitudinal septum separating two apical sunken areas with a pair of symmetrical micropylar projections placed centrally and two micropylar openings (K), basal cross connecting four basal vascular strands and a basal pair of opposite bracts in the minor plane (L), distinct shoulder with apical micropylar projection (I), absence of valve exposing the seed (J). O–R. DMNH EPI.49442a, DMNH locality 584. Cone in face view (O), apical view (P), basal view (Q), lateral view (R); note longitudinal septum separating two apical sunken areas (P), distinct shoulder with apical micropylar projection (R), deep sinuses on the broad face (O). Scale bar at G applies to A–G; bar at L applies to A–L and O–R; bar at M applies also to N

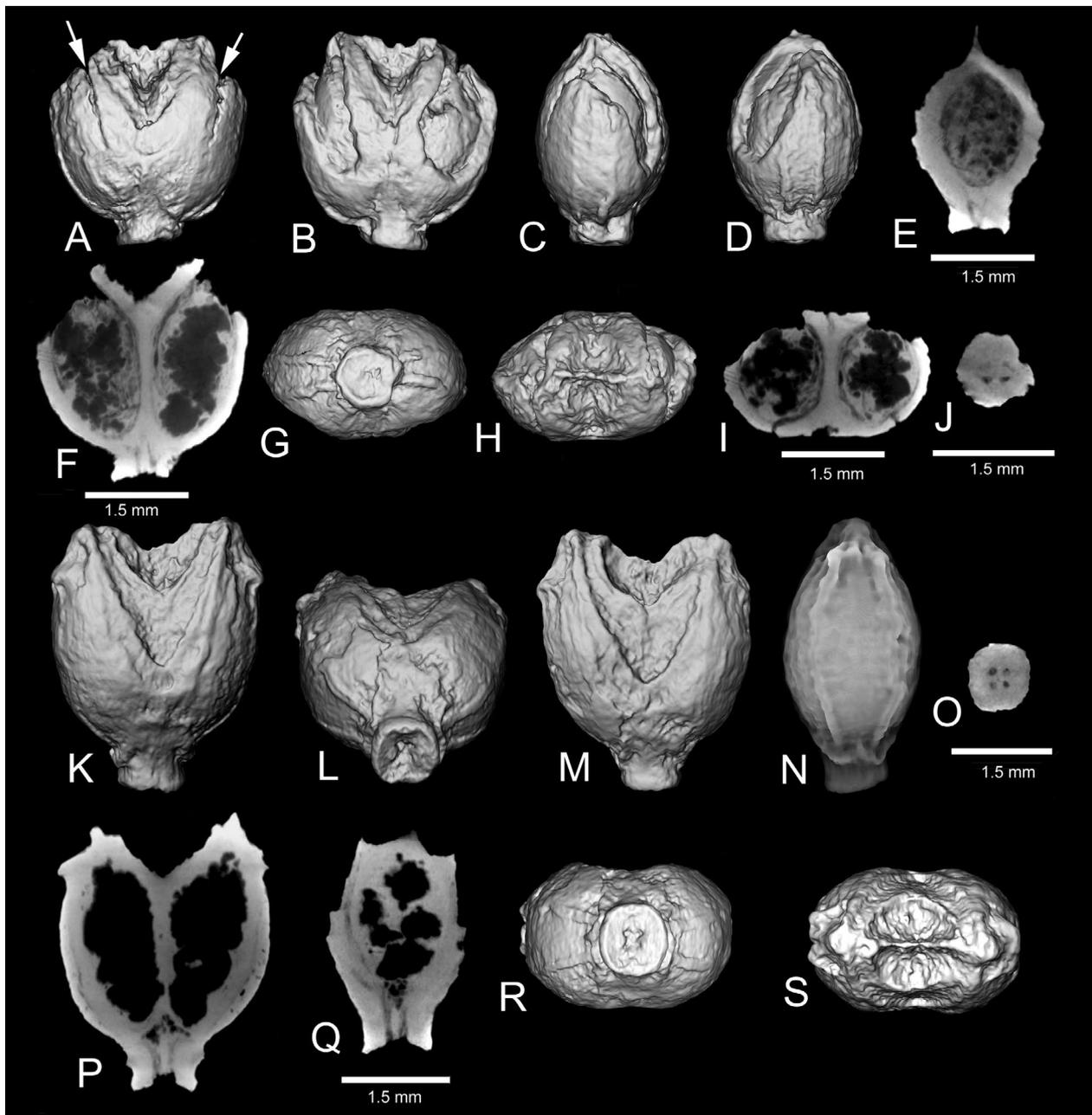


Figure 4. *Bassitheca hoodiorum* gen. et sp. nov. from the Morrison Formation, Mt Ellen, Utah, USA. Micro-CT scan images. Reflective surface renderings (A–D, G, H, K–M, R, S), depth map (N), virtual sections (E, F, I, J, O, P, Q). A–J. USNM 771504. Cone in opposing face views (A, B), in opposing lateral views (C, D), longitudinal section in the minor plane (E), longitudinal section in the major plane (F), basal view (G), apical view (H), transverse sections (I, J); note two lines of dehiscence (A, arrows), four vascular strands in transverse section through peduncle (J), minor plane septum (F, I), apical longitudinal septum (H), exposed seed body with apical projection (C), section and four vascular strands (J). K–S. USNM 771463. Cone in opposing face views (K, M), oblique basal view (L), lateral view (N), transverse section (O), longitudinal section in major plane (P), longitudinal section in minor plane (Q), basal view (R), apical view (S); note pair of opposite joints below the cone base (A, B, K), well-developed basal bract in the minor plane (L), four vascular strands in transverse section of peduncle (O), ascending vascular stands (Q), basal cross connecting four basal vascular strands and a basal pair of opposite bracts in the minor plane (R), pair of ribs and distinct shoulder with apical micropylar projection (N), deep sinuses on the broad face (K, M), pair of symmetrically micropylar projections placed centrally in the pair of opposite apical depressions (S). Scale bar at E applies to A–E, G, H; bar at O applies to K–O, R, S; bar at Q applies also to P

covering the presumed micropyle (Figs 2A–C, E, G, H, L–N; 3A–D, O, P, R; 4K, M, N; 5A, B; 6A–D, F–I).

In a few specimens a distinct fissure of dehiscence passes through the micropyle (Figs 2L, N; 3H, J, K, N; 5B, C, D, G) and along the

two flanking lateral ribs on either side (Figs 2C, N, S; 3F, K; 4H, S; 5F; 6I). A few specimens show partial dehiscence (Figs 2L; 4A–C). In other specimens the portion of the cone lateral to this line of dehiscence has detached as a complete valve (Figs 3H, J–N; 5B, C–E, G)

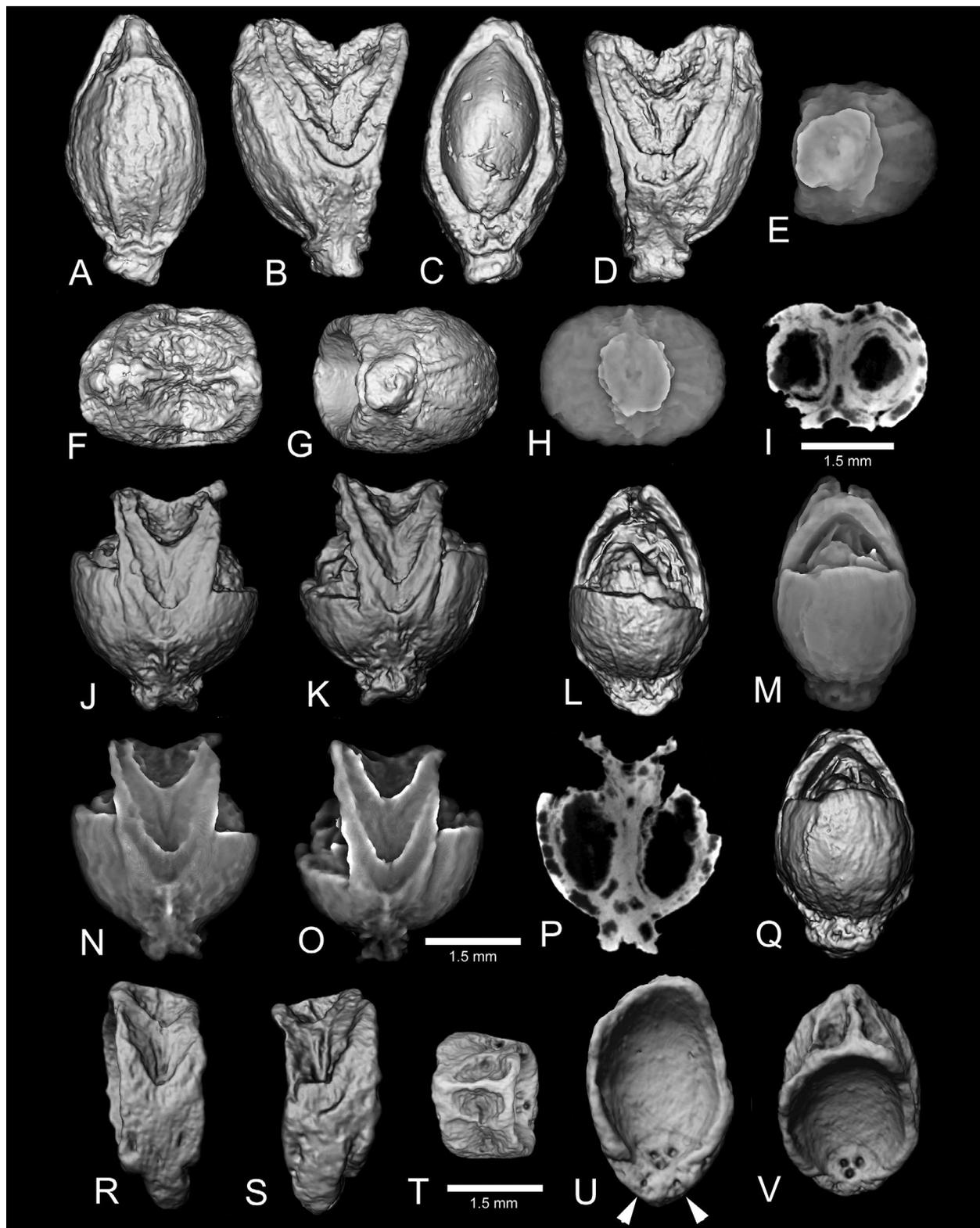


Figure 5. *Bassitheca hoodiorum* gen. et sp. nov. from the Morrison Formation, Mt Ellen, Utah, USA. Micro-CT scan images. Reflective surface renderings (A–D, F, G, J–L, Q, R–V), depth maps (E, H, M–O), virtual sections (I, P). A–G. USNM 771527. Cone with one lateral valve detached, in opposing lateral views (A, C), opposing face views (B, D), basal view (E, G), apical view (F); note deep lateral sinuses (B, D), pair of ribs and distinct shoulder with apical micropylar projection (A), lateral view of exposed seed locule (C), poorly preserved bracts in minor plane (G, H), pair of opposite joints below the cone base (B, D), longitudinal septum (F). H–Q. USNM 771531. Cone with two valves partially broken, in basal view (H), transverse section (I), opposing face views (J, K, N, O), opposing lateral views (L, M, Q), longitudinal section in major plane (P); note deep lateral sinuses (J, K), basal pair of opposite bracts in minor plane (H), minor plane septum (I, P), remains of seed body (Q), remains of seed body with apical projection (L). R–V. USNM 771528. Cone with both lateral valves detached, in opposing face views (R, S), apical view (T), lateral view of right side of S, T (U), oblique lateral view of left side of S, T (V); note deep lateral sinuses R, S), exposed concave surfaces of the seed locule with paired depressions of vascular supply to the valve (arrowheads) and three symmetrical depressions of vascular supply to the envelope at base of locule (U, V). Scale bar at I applies to A–I; bar at O applies to J–Q; bar at T applies to R–V

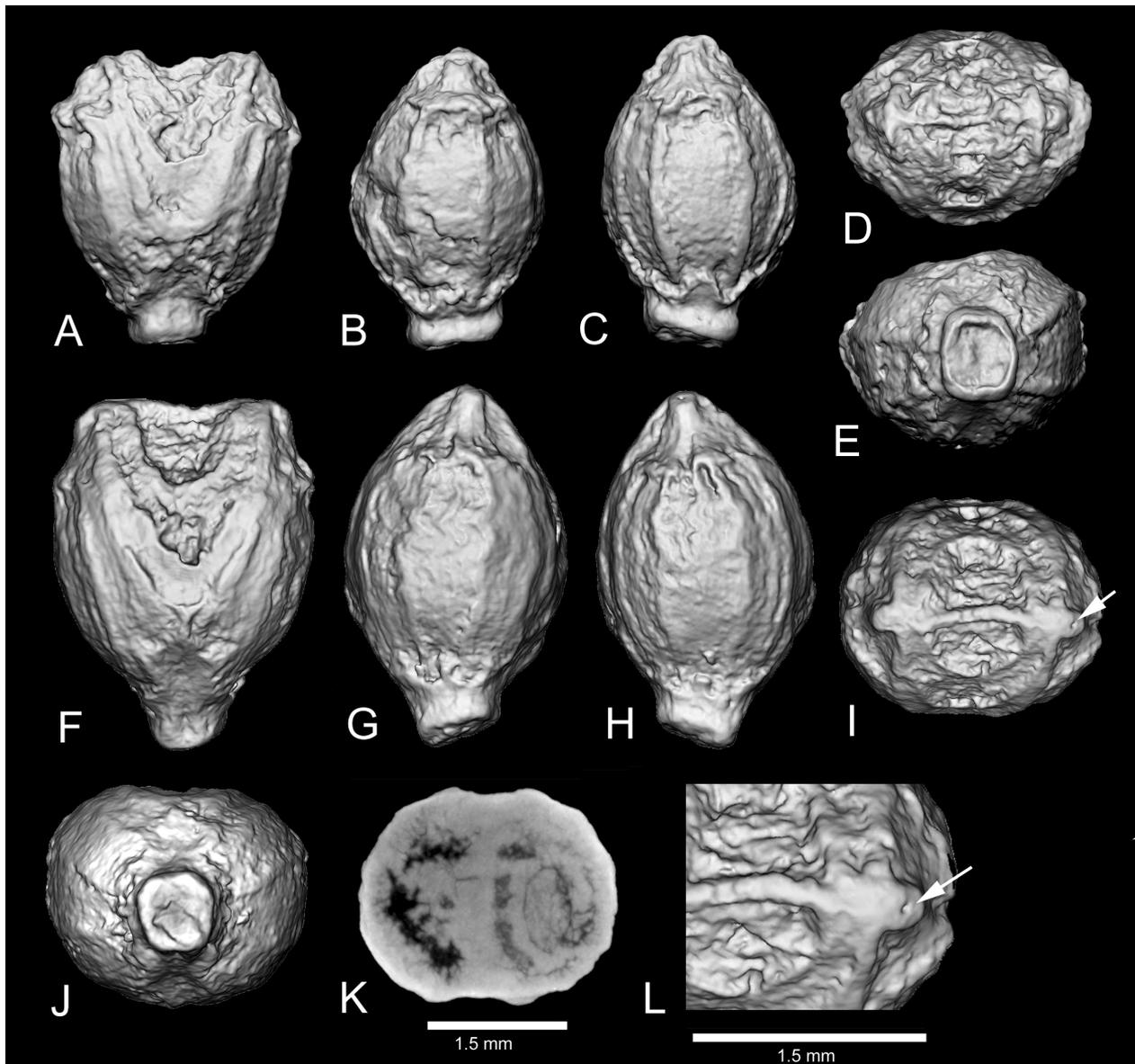


Figure 6. *Bassitheca hoodiorum* gen. et sp. nov. from the Morrison Formation, Mt Ellen, Utah, USA. Micro-CT scan images. Reflective surface renderings (A–J, L), virtual section (K). A–E. USNM 771523. Cone in face view (A), opposing lateral views (B, C), apical view (D), basal view (E); note deep lateral sinuses (A), pairs of ribs and distinct shoulder with apical micropylar projection (B, C). F–L. USNM 771464. Cone in face view (F), opposing lateral views (G, H), apical view (I, L), basal view (J), transverse section (K); note deep lateral sinuses (F), distinct shoulder with apical micropylar projection (G, H), minor plane septum (K), longitudinal septum (I), micropylar opening (I, L, arrows). Scale bar at K applies to A–K

exposing the surface of the seed (Fig. 3J, K, M, N) or revealing an empty locule from which the seed has been shed (Fig. 5B–E, G). In other specimens the cone is partly broken along the line of dehiscence (Figs 4A–D, F; 5J–Q). In some specimens both valves of the cone have been lost completely revealing two empty locules (e.g. Fig. 5R–V). At the base of one of the empty locules in this specimen there are two small cavities that suggest that two vascular bundles entered each valve from the base (Fig. 5U). These two bundles are positioned on either side of one of the three vascular bundles that enter the base of the seed (Fig. 5U, V).

On the lateral cone faces that form the two valves there are a pair of prominent ribs. These ribs are seen most clearly seen in views of the cone from the base. They appear to arise from the top of the peduncle, one on either side of the midline, and terminate in the transverse flange of crumpled tissue that forms the shoulder (Figs 2E, F, H, I, M, O; 3C–E; 4D, G, L, N, R; 5A, E, G, H; 6B, C, E, G, H). These ribs may reflect two vascular bundles that supply each valve. In a few specimens there is an additional pair of somewhat less prominent ribs, one on either side of the best developed pair of ribs (e.g. Figs 2F; 5E).

On each of the two broad faces of the cone there are two sinuses, the outer and deepest of which creates the appearance of a bisymmetrical cup in which the rest of the cone sits. The sinus is formed by two U- to V-shaped ridges that originate close to the micropyles of the two seeds and on both broad faces of the cone appear to be nested one inside the other (Figs 2A, G, L, P; 3A, B, H, O; 4A, K, M; 5B, D, J, K; 6A, F). The deeper of the two U- to V-shaped sinuses extends about one half or two-thirds of the way toward the base of the cone. It is typically clearly defined and appears to mark the free margin of another structure fused into the cone (Figs 2A, G, L, P; 3A, B, H, O; 4A, K, M; 5B, D, J, K; 6A, F). The shallower of the two sinuses also appears to be the free margin of a structure fused into the cone and it defines the outer edges of the two depressions on either side of the apical longitudinal septum (Figs 2A, C, P, S; 3A, B, F, H, K, O, P; 4M, S; 5B, D, F; 6F, I).

In some specimens there appears to be a third sinus, below and to the outside of the deepest of the two U- to V-shaped sinuses and running parallel to it. Like the deeper of the two well-defined sinuses this outermost sinus originates at or close to the micropyle. However, it has a different appearance than the other two sinuses, appearing not to be a free margin but rather a ridge created by an underlying structure. This ridge is sometimes reasonably clearly defined (Figs 2A; 3A, B, H; 5B, D, K), but in other specimens it is much less distinct (Figs 2G, L, P; 3O; 4A, K, M; 5J; 6A, F).

The two depressions on either side of the median apical septum are arranged opposite each other in the minor plane. They are at a higher level in the cone than the prominent pair of seed cavities or seeds in the major plane (Figs 2A, C, L, N, P, S; 3A, B, F, H, K, O, P; 4A, B, H, K, M, S; 5B, D, F; 6A, D, F, I). Usually these depressions are clearly delimited (Figs 2C, S; 3F, K, P; 4S; 6I), but they are sometimes less well defined (Figs 2N; 3K; 4H; 5F; 6D). Viewed from above, each depression is more-or-less elliptical, but they are often flattened along its inner margin where they abut the longitudinal septum (Figs 2C, S; 3F, P; 4H, S; 5F; 6I).

The internal surface of the two depressions varies among different specimens. In some specimens the depressions are prominently sunken with a floor that varies from smooth to somewhat rugulate (Figs 2C, S; 3F, K, P; 4H, S; 6I). In other specimens the depressions are

less pronounced with a floor that is more prominently folded (Figs 2N; 5F; 6D). In some specimens both depressions have a small projection positioned centrally and symmetrically (Fig. 4S). In other specimens there is a clear projection in only one of the depressions (Fig. 5F).

DISCUSSION

INTERPRETATION OF THE STRUCTURE OF THE *BASSITHECA* CONE

We interpret *Bassitheca* as a compound cone with a pair of well-developed orthotropic seeds positioned opposite each other in the major plane and separated by a longitudinal septum. Above, and fused into the same structure, is a mass of tissue that includes the pair of apical depressions. These depressions are opposite each other and separated by a median longitudinal septum that is perpendicular to the longitudinal septum between the well-developed seeds below. These two depressions may indicate the positions of a distal pair of aborted seeds and the central projections seen in some specimens could be the remains of micropyles (Figs 4S; 5F). However, the central projections are not a sufficiently consistent feature to be certain of this interpretation.

At the very base of the cone there appears to be a pair of bracts oriented in the major plane, the attachment scars of which are clearly visible (Fig. 3A, B, C, D, E). Above, and unequivocally present, is a pair of small triangular bracts in the minor plane immediately below the main part of the cone (Figs 3A, B, L; 4L, R; 5H). The opposite and decussate arrangement of these two pairs of bracts continues above in the arrangement of the two seeds.

The nature of the preservation makes interpreting the arrangement of the bracts associated with the seeds in the main body of the cone uncertain, but some inferences are possible. The main part of the cone appears to be formed by a pair of large, substantial bracts in the major plane. It is these bracts that form the bisymmetrical cup-shaped structure in which the rest of the cone sits. We interpret these two bracts as the outermost bracts of a single pair of opposite bracts associated with each seed. We think it likely that the two corresponding inner bracts, one from each pair, are fused back-to-back to form the longitudinal septum in the minor plane.

Other than the seed cavities or seeds themselves, the two outermost bracts are the most prominent feature of the *Bassitheca* cone. Each has two longitudinal ribs that originate at the base of the cone and pass upward on the lateral faces (Figs 2F, I, M, O; 3D, E; 4D, G, L, N, R; 5A, E, G, H; 6B, C, E, G, H). Frequently the two ribs are flanked by two additional ribs (e.g. Figs 2F; 5E). We interpret these ribs on the outermost bracts as indicating the position of vascular bundles. The two well-developed ribs may account for the pair of vascular bundles visible in specimen USNM 771528, which appear to supply the valve (Fig. 5U, V), and also the two pairs of vascular bundles seen in the peduncle (Fig. 4J, O) that diverge apically toward the base of the seeds (Fig. 4E, F, P, Q), and appear to correspond to the arms of the cross seen on the base of some specimens (Fig. 3L, R).

If our interpretation that each seed is enclosed by a pair of bracts in the major plane is correct then the inner margin of each pair of outer bracts may account for the deeper of the two U- to V-shaped sinuses seen on each flattened face of the cones. This putative bract margin appears internal to the line of dehiscence through which the valve is shed. A possible explanation for the inner, shallower U- to V-shaped sinuses is that it reflects the inner margins of two bracts, each of which is one of a pair associated with each seed in the minor plane. The outer margins of these same bracts beneath the two large outer bracts may define the line of dehiscence through which the valve is shed (Fig. 7). This would imply that the valve reflects that portion of the large outer bract that does not overlap with the pairs of bracts that are associated with each seed in the minor plane, but such interpretations must be regarded as very tentative in the absence of better internal detail.

Little information is preserved on the seeds of *Bassitheca*, but the micropyles seen on the cone surface (Figs 3F, I, K; 4H, S; 5F; 6D, I) along with the lack of an obvious raphe, indicate that the seeds were orthotropous and erect. The way in which the outer bract appears to have collapsed over the upper part of the seed in several specimens suggests that the main body of the seed formed a distinct shoulder above which there was a robust micropylar extension of resistant tissue (Figs 2E, H, M; 3C, D, I, R; 4N; 5B, C, G, H).

Also important for understanding the seeds of *Bassitheca* are the three vascular bundles

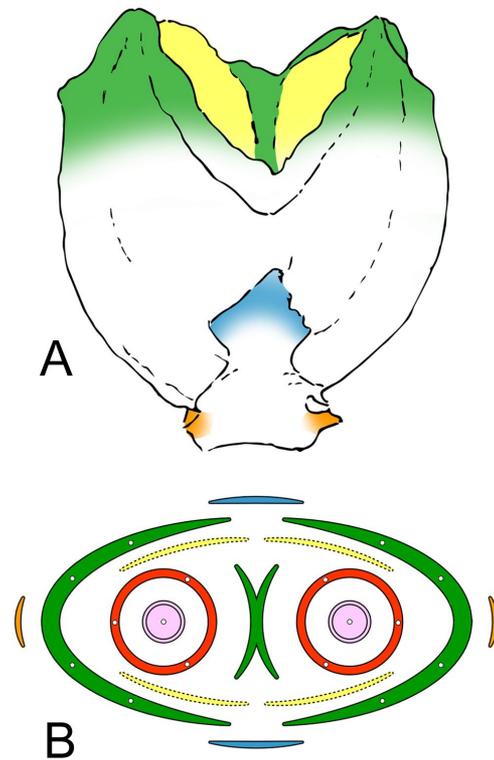


Figure 7. *Bassitheca hoodiorum* gen. et sp. nov. interpretation of cone structure. **A.** Simplified line drawing of specimen (Fig. 3A) colored to correlate with Fig. 7B. **B.** Interpretative diagram showing two seeds (pink), each with an apical micropyle surrounded by an envelope (red) supplied by three vascular bundles that correspond to the three holes seen in Fig. 5V. Each seed is tentatively interpreted as surrounded by a pair of bracts in the minor plane (yellow) and inferred to be surrounded by a pair of bracts in the major plane (green). The inner of the pair of bracts in the major plane are fused to form the median longitudinal septum in the minor plane and the outer of each pair forms the cup in which the rest of the structure sits. The two outer bracts each have four vascular bundles, of which the two inner correspond to the two holes seen in Fig. 5U. Beneath the two pairs of bracts (green) that enclose the two seeds is a pair of bracts in the minor plane (blue), beneath which are the two joints indicating the attachment of a further pair of bracts in the major plane (orange)

that enter the base of one of the well-developed seeds in specimen USNM 771528. These bundles alternate with the two vascular bundles that appear to supply the valve (Fig. 5U, V). The three vascular bundles could be the vascular supply to seed itself, but we know of no living gymnosperm in which the seeds are supplied by three vascular bundles in this way. More typically the seeds of living gymnosperms are supplied by a single vascular bundle, a more complex vascular supply, or have no vascular supply at all (Rodin and Kapil, 1969; Zumajo-Cardona et al., 2021). We think it more likely that these three bundles supplied an envelope with three vascular bundles rather than the seed directly. Precisely this situation occurs in some species of extant *Ephedra* (Rydin et al.,

2010). This key interpretation (Fig. 6) brings with it the implication that the envelope surrounding integument and nucellus would have been part of the dispersal unit and would have been shed with the seed. It also implies that the seeds of *Bassitheca* were chlamydospermous (see Friis et al., 2013).

In summary, our hypothesis, which remains to be tested by the discovery of better-preserved material, is that each of the two well-developed seeds of *Bassitheca* were surrounded and protected by an envelope that enclosed the nucellus and a thin integument. The envelope was supplied by three vascular bundles, which in turn may have been enclosed by a pair of modified bracts. The whole two-seeded structure was enclosed and protected by two pairs of large well-developed bracts around each seed in the major plane and an apical thickened hood as depicted in Fig. 7.

The outer bract of each pair of bracts surrounding the well-developed seeds contributed to the fused structure of the cone. The inner of the pair of bracts associated with each seed formed the septum. A portion of the outer of the pair of bracts associated with each seed formed the valve. The distinct line of dehiscence seen in several specimens (Figs 2L; 3H, I, J; 4B, C; 5J–O) suggests that release of the two seeds, each with a protective envelope, was accomplished by shedding of the valves. USNM 770500 (Fig. 5S, T), and similar specimens that are common in the collection, are the remains of a cone after both valves and both seeds had been shed. USNM 770527 (Fig. 5A–C) and USNM 770506 (Fig. 3H–N) are the remains of cones from which just one valve had been shed. In USNM 770506 (Fig. 3J, L) the remains of one seed, probably with its chlamydospermous outer envelope are still in place, whereas in USNM 770527 the seed has been lost (Fig. 5C, G).

RELATIONSHIP TO FOSSIL AND LIVING PLANTS

Assessing the relationships of *Bassitheca* to living and fossil plants is dependent on whether structural interpretations presented above are correct, of which the key features of importance for higher level systematics are: i) seeds that are orthotropous, erect and surrounded by an envelope, that is a shed, as part of the dispersal unit (chlamydospermous); ii) seeds borne in opposite pairs, each surrounded by a pair of bracts; iii) alternating pairs of bracts and seeds

borne perpendicular to each other in a decussate arrangement; and, iv) bracts associated with the seeds at least partially concrescent. This suite of features distinguishes the cones of *Bassitheca* from the ovulate reproductive structures of cycads and *Ginkgo*. The naked orthotropous seeds rule out a relationship to angiosperms and also to most conifers.

Among conifers, a small group of extant genera of Cupressaceae combine a highly reduced cone with opposite and decussate phyllotaxy of a small number of bracts. In some of these genera the cone is reduced to such an extent that the central cone axis does not extend beyond the seeds as is also the case in *Bassitheca*. Cones of this type occur in the ‘*Cupressus* group’ and the ‘*Libocedrus* group’ sensu Farjon (2008). However, the ovulate reproductive structures of both groups provide no obvious explanation for the three vascular bundles that entering the base of the seed cavity in *Bassitheca*. In addition, genera of both groups are relatively derived in the context of Cupressaceae as a whole, the early history of which is documented primarily by fossils from the Jurassic and Early Cretaceous related to genera assigned previously to Taxodiaceae, such as *Taiwania* and *Cunninghamia* (e.g. Herrera et al., 2017). It would be surprising to encounter close relatives of the ‘*Cupressus* group’ and the ‘*Libocedrus* group’ in the Jurassic.

The ‘*Cupressus* group’ comprises *Calocedrus*, *Chamaecyparis*, *Cupressus*, *Fokienia*, *Juniperus*, *Microbiota*, *Playcladus*, *Tetraclinis*, *Thuja*, *Thujopsis* and *Xanthocyparis* (Farjon, 2005). Cones of these conifers have an opposite and decussate organization and lack a remnant cone axis, but none resemble the cones of *Bassitheca*. In all cases, except *Juniperus* and *Microbiota*, the cones are woody with cone scales (bract-scale complexes) that typically have a prominent umbo or an extended tip (e.g. *Cupressus*). At maturity the cone scales are spreading and release seeds that are typically symmetrically or asymmetrically winged. In *Juniperus* the cones are modified into a globose succulent berry, and in *Microbiota* there is a single large seed at maturity. None of the ‘*Cupressus* group’ are a good morphological match for *Bassitheca* and none have two enclosed seeds each of which is released by shedding of a valve.

Similar considerations apply to the ‘*Libocedrus* group,’ which comprises *Austrocedrus*, *Libocedrus*, *Papuacedrus* and *Pilgerodendron*.

In all four genera the cones are very simple, but although they consist of just two pairs of decussate bract-scale complexes there is always a short remnant cone axis, although this is weakly developed in *Papuacedrus* (Farjon, 2005: pl. 14.1). Typically, only two of the four bract-scale complexes in each cone are fertile and each bract-scale complex has two seeds in its axil (e.g. *Austrocedrus*, Farjon, 2005: pl. 13.4). At maturity the cones are woody with spreading cone scales that have an acute subapical bract tip (*Austrocedrus*, Farjon, 2005: pl. 123.8, *Libocedrus*, Farjon, 2005: pl. 117.7-8, 118.6-7, 119.6-7, 120.6, 121.10, *Papuacedrus*, Farjon, 2005: pl. 116.7-8, *Pilgerodendron*, Farjon, 2005: 122.8-9). The seeds have two wings that are very unequally developed. There are no sterile apical cone scales, nothing resembling the tissue above the two seed cavities seen in *Bassitheca*, and no indication of seed shedding through two valves.

The most plausible candidates for the closest living relatives of *Bassitheca* are Gnetales; in particular, the ovulate structures of *Ephedra* provide a more straightforward basis for structural comparisons to *Bassitheca* than any other group of seed plants. Seed cones of *Ephedra* may be one, two or three seeded, and the paired, opposite and decussate arrangement of bracts of *Bassitheca*, along with two orthotropous seeds is not too different from the cones of many species of *Ephedra*. Chlamydospermous seeds are also characteristic of Gnetales and in extant *Ephedra* the envelope may be supplied by two, three or four vascular bundles. In several species of *Ephedra* the bracts associated with the seeds are also concrescent to varying extents.

In their comparative survey of the morphology of ovulate reproductive structures in extant *Ephedra* Rydin et al. (2010) note that the number of seeds per cone is typically two, more rarely three or one, and consistent with the two-seeded norm the bracts in the cone are arranged most often in opposite and decussate pairs. The two well-developed seeds, and the clear evidence of opposite and decussate bracts in *Bassitheca*, fit this pattern.

In extant *Ephedra* the number of bract pairs per cone varies within and among species, from two, to as many as nine, well within the range for what we interpret to have been the case in *Bassitheca*. Rydin et al. (2010) also record several species of *Ephedra*, for example *Ephedra*

foliata Boiss et C.A.Mey, *Ephedra viridis* Coville and *Ephedra americana* Humb. et Bonpl. Ex Willd., in which the cones contain two seeds, but the seed envelope has three vascular bundles, as we also envisage for *Bassitheca*. This is also the condition in *Ephedra foeminea*, which is resolved as the sister species to all other members of the genus based on phylogenetic analysis of molecular data (Rydin et al., 2010). A further point of similarity is that in extant *Ephedra* the bracts of the cone typically have two vascular bundles, as is also inferred for the valve through which the seed is shed in *Bassitheca* (Fig. 5V). Each of the two major bracts in *Bassitheca* appears to have two large vascular bundles flanked by two smaller bundles (Figs 2F, O; 3E; 4G; 5E, G).

While the similarities noted above provide reasonable support for the hypothesis that *Bassitheca* is closely related to extant Gnetales, specifically extant *Ephedra*, the fossils also exhibit specialized features that are not known in the extant genus. The protective cap above and perpendicular to the two well-developed seeds (perhaps derived from a pair of aborted seeds) is not known in extant *Ephedra*. A more complex modification is the shedding of seeds via the pair of lateral valves, for which we know of no modern analogue in extant Gnetales. While the bracts associated with the seeds in many species of *Ephedra* are concrescent to varying degrees, this is seen most obviously in those species that appear to be adapted for animal dispersal where the bracts are swollen, fleshy and red. We envisage that similar fusion of the bracts occurred in the cones of *Bassitheca*, but in connection with a different dispersal strategy in which the bracts provided protection, perhaps in a periodically arid environment. Rather than being fleshy, we suggest that the *Bassitheca* cone was hard and dried out at maturity, and that a specialized mechanism was required for the shedding of the seeds.

CONCLUSIONS

Notwithstanding the specializations exhibited by *Bassitheca* for the protection and shedding of the seeds, its relationships appear most likely to be with extant Gnetales. While the relationships of *Dayvaultia tetragona* Manchester et Crane, described previously from the Morrison Formation from similar calcitic

material, are likely to also be with Gnetales (Manchester et al., 2021), the structure of *Bassitheca* is more strikingly similar to that of extant *Ephedra*. Together, *Bassitheca* and *Dayvaultia* underscore the diversity among probable extinct Gnetales that were part of the Late Jurassic Morrison vegetation. Apart from their pollen grains, the presence of Gnetales in the fossil flora of the Morrison Formation has been largely unrecognized.

Dispersed pollen of the *Ephedra* type occurs sporadically throughout the Morrison Formation, albeit always in low numbers (usually less than 2% in a 300-point count). The recognition of at least two macrofossils of likely gnetalean affinity in the Morrison Formation adds support to the presumed ephedroid affinity of the dispersed pollen and demonstrates that Gnetales were at least locally abundant in the landscape. It also suggests that the Gnetales are likely under-represented in the palynoflora of the Morrison Formation due to distance from depositional sites, low stature, low pollen production associated with insect pollination, or a combination of these and other factors.

Also interesting is that just as chlamydospermous seeds are often abundant in Early Cretaceous mesofossil floras (Friis et al., 2019), both *Bassitheca* and *Dayvaultia* are represented by numerous specimens at some Morrison Formation sites in the Henry Mountains. In specimen counts from the late Barremian – early Aptian Torres Vedras mesofossil flora, in the Lusitanian Basin of Portugal (sample TV43) seeds of *Ephedrispermum lusitanicum* are known from 175 specimens and three other species of chlamydospermous seeds account for a further 132 specimens (Friis et al., 2019). Conifer seeds of various kinds are also common (168 specimens). Chlamydospermous seeds are much more common than angiosperm seeds or single-seeded fruits, which are known from 132 specimens.

Over the past three decades our understanding of the fossil record of the Gnetales has expanded dramatically. A major diversification of gnetalean pollen occurred during the Early and Mid-Cretaceous at low paleolatitudes (Crane and Lidgard, 1989) and fossil Gnetales are now known in Early Cretaceous macrofloras from Brazil (Kunzman et al., 2011), eastern Asia (Krassilov, 1986; Yang and Wang, 2013; Yang and Ferguson, 2015) and North America (Crane and Upchurch 1987), as well as in mesofossil floras from Asia, North America and

Europe (Rydin et al., 2006a, b; Friis et al., 2007, 2009, 2011, 2013, 2014, 2019; Mendes et al., 2020; Blickner et al., 2021). Gnetales are also present in Early Cretaceous fossil assemblages from western Canada where they are preserved as petrifications (Rothwell and Stockey, 2013). *Bassitheca* and *Dayvaultia* add new dimensions to this emerging and extensive record and extend it back into the Late Jurassic. Further efforts with the right search image will reveal more about the pre-Cretaceous fossil history of Gnetales, including from the Morrison Formation where other seed and cone types that are of probable gnetalean affinity are also present in collections from the Henry Mountains of Utah (Manchester and Crane, in progress). A critical issue is how extinct Gnetales from the Triassic and Jurassic relate structurally and ecologically to the later and better known forms from the Early Cretaceous.

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