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Celliforma rozeni, a new ichnospecies of bee (Hymenoptera: Anthophila) brood cell from the Eocene of Wyoming

Richard J. Knecht[1–4*] & Stephen L. Buchmann[5]

Abstract. Trace fossils of bee brood cells provide direct evidence of nesting behavior in deep time and are particularly valuable where body fossils of bees are rare or absent. The ichnogenus *Celliforma* Brown represents the principal ichnotaxonomic framework for interpreting fossil brood cells of solitary ground-nesting bees, yet ichnotaxonomic resolution within this group depends critically on the recognition of discrete, behaviorally meaningful constructional characters rather than preservational variation. Here we describe ***Celliforma rozeni*** Knecht & Buchmann, isp. nov., from the Early Eocene Wagon Bed Formation of Wyoming, USA. This new ichnospecies is diagnosed by a consistently expressed dextral spiral apical closure composed of seven to eight turns, a feature that exceeds the four to five turns characteristic of the type ichnospecies *C. spirifer* and falls outside the known range of variation for previously described taxa. The description is based on a holotype and multiple paratypes housed in the Museum of Comparative Zoology, Harvard University, and examined alongside more than 100 additional specimens from the Jerome Rozen Bee Nests Collection (American Museum of Natural History) and private collections. Comparisons of spiral turn number and cell dimensions (apex-base height, maximum width), alongside comparative ichnotaxonomic analysis, support the recognition of *C. rozeni* as a distinct ichnospecies. A revised key to all five valid ichnospecies of *Celliforma* is provided. In extant solitary bees, brood-cell closure architecture, including spiral turn number, reflects species-specific and inherited motor programs rather than ontogenetic or environmental variation. Accordingly, *C. rozeni* is interpreted as a distinct behavioral ichnotaxon, likely representing a separate tracemaker lineage within early Cenozoic ground-nesting bees. The recognition of *C. rozeni* expands the documented behavioral diversity of Eocene solitary bees and adds resolution to the fossil record of pollinators. The coexistence of multiple *Celliforma* ichnospecies within Wagon Bed paleosols suggests behavioral differentiation and niche partitioning among ground-nesting bees by the early Cenozoic, underscoring the utility of fine-scale brood-cell architecture for reconstructing pollinator community structure in deep time.

[1] Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109, USA
[2] Museum of Paleontology, University of Michigan, Ann Arbor, MI 48109, USA
[3] Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA
[4] Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA (rknecht@fas.harvard.edu)
[5] Departments of Ecology and Evolutionary Biology, and Entomology, University of Arizona, Tucson, AZ 85721, USA (buchmann.stephen@gmail.com)

*Corresponding author

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INTRODUCTION

Bees (Anthophila) represent one of the most ecologically and evolutionarily successful radiation among insects, marked by their distinctive transition from predatory wasp ancestors to primarily pollen- and nectar-feeding forms (Michener, 2007; Cardinal & Danforth, 2013). This trophic transformation, from carnivorous wasps to fully herbivorous "protobees", appears to have taken place during the early Cretaceous, around 124 million years ago (Branstetter *et al*., 2017; Sann *et al*., 2018). Modern bees comprise seven families and approximately 500 genera, but their origins lie within minute apoid wasps (likely members of the Ammoplanidae) that preyed on hemipterans such as pollen-coated thrips (Sann *et al*., 2018; Danforth *et al*., 2019). The current hypotheses (Sann *et al*., 2018) propose that these early wasps initially consumed thrips incidentally covered in pollen, before ultimately abandoning animal prey altogether and shifting to the exclusive collection of floral pollen and nectar for both adult nutrition and larval provisioning. Phylogenetic analyses combining molecular and morphological data further indicate that the major lineages of solitary bees diversified early in their evolutionary history, irrespective of their sparse representation in the body-fossil record (Danforth *et al*., 2006). Despite this deep origin, the oldest confirmed bee fossil is the stingless bee *Cretotrigona prisca* Michener & Grimaldi, 1988 (Apidae, Apinae, Meliponini), preserved in Cretaceous amber dated between ~96 and 74 million years ago (Michener & Grimaldi, 1988; Engel, 2000; Engel *et al*., 2023). With a gap of approximately 28–50 million years between their inferred Cretaceous origin and the oldest confirmed body fossil, the earliest solitary bees remain conspicuously absent from the fossil record. Today, roughly 10% of the ~20,000 described extant bee species (Ascher & Pickering, 2024) are cleptoparasites, exploiting the brood cells and pollen provisions of host bees. An additional noteworthy deviation from strict pollinivory occurs in three Neotropical species of "vulture bees" (*Trigona* spp.), which supplement nectar feeding with carrion consumption (Figueroa *et al*., 2021).

Nesting behavior further reflects the remarkable ecological heterogeneity of modern bees. Female bees occupy a wide range of environments (many of them seasonally or persistently arid) and construct nests using an equally diverse suite of substrates (Michener, 1979, 2007). Documented nesting sites include soft decayed wood, pith-filled twigs, abandoned beetle burrows, mammal bones, rock surfaces and crevices, mud, leaf fragments, snail shells, loose sand, plant resins, and exposed banks, cliffsides, or bare ground (Michener, 2007; Viñola-López *et al*., 2025). Approximately 20–30% of species are cavity nesters, whereas the majority (roughly 70–75%) are ground nesters (Michener, 2007). Most ground-nesting taxa excavate tunnels in sandy or loamy soils, with andrenid and halictid bees often producing elaborate vertical shafts bearing lateral brood cells. These cells are commonly lined with waterproof, antimicrobial secretions derived from exocrine glands, which help protect developing larvae from fungal attack and other microbial hazards (Hefetz *et al*., 1979; Cane, 1981). Other lineages specialize in above-ground nesting. Megachilidae, including leafcutter and mason bees, frequently occupy hollow stems and beetle borings, constructing brood cells from leaf discs, petals, mud, sand, resin, or plant trichomes (Krombein, 1967; Michener, 2007). Stingless bees (Meliponini) can nest below ground but more typically inhabit hollow trees, rock crevices, or even active termite nests; their nest architecture is supplemented with cerumen, a composite material of beeswax blended with plant resins, gums, and saps (Roubik, 2006).

Solitary bees are among the most behaviorally diverse and ecologically influential groups of insects (Klein *et al*., 2007; Danforth *et al*., 2019), yet their body fossils are rare and often fragmentary. In contrast, their subterranean brood cells, constructed in soil or other substrates, preserve distinctive architectural features that make them

exceptionally informative trace fossils. These structures record behaviors such as cell excavation, lining secretion, and closure construction, offering a unique window into the nesting biology of bees that otherwise leave little direct evidence in the fossil record (Genise, 2017; Genise *et al*., 2020). Because many solitary bees produce brood cells with diagnostic shapes, textures, and terminal caps, fossilized brood chambers can be interpreted with high confidence and used to reconstruct aspects of past ecosystems, soil conditions, and angiosperm-associated pollinator communities (Bown & Kraus, 1983; Grimaldi & Engel, 2005). Spiral inner closures are widely treated as a bee-associated construction trait in brood cells and are not commonly reported from solitary wasp cells, supporting a bee affinity for *Celliforma* (*e.g*., Krombein, 1967; Michener, 2007).

The ichnogenus *Celliforma* Brown, 1934 first recognized in the early twentieth century, remains the principal trace fossil attributed to solitary ground-nesting bees. Brown's pioneering work in Eocene and Oligocene paleosols of western North America (Brown, 1934, 1935) demonstrated that these flask- to ovoid-shaped chambers, often with smooth linings and occasionally with spiral terminal closures, closely parallel the brood cells of modern andrenid, halictid, and apid bees. These criteria (cell geometry, wall microtexture, lining composition, and cell cap closure morphology) continue to anchor the ichnotaxonomic framework for interpreting fossil bee nests (Genise, 2017). Subsequent discoveries across North and South America have expanded the morphological range of *Celliforma* (Bown *et al*., 1997; Genise *et al*., 2000; Sarzetti *et al*., 2008), confirming that solitary bees with diverse nest architectures were well established by the early Cenozoic.

Despite this growing record, the ichnodiversity of fossil bee cells remains incompletely resolved, and many specimens have been historically assigned to broad morphotypes or left in open nomenclature. Early ichnotaxonomic work already demonstrated that subtle but repeatable differences in brood-cell architecture can reflect distinct trace makers and paleoenvironmental contexts, even within broadly similar nest morphotypes (Genise & Bown, 1994). Variation in neck curvature, chamber proportions, lining characteristics, and closure construction suggests greater behavioral and taxonomic diversity among early bees than presently reflected in named ichnospecies. Furthermore, new discoveries from underexplored formations and paleosols continue to reveal previously undocumented nest morphologies, underscoring the need for careful ichnotaxonomic revision and addition of new ichnospecies where appropriate (Elliott & Nations, 1998; Genise, 2017).

In this study, we describe *Celliforma rozeni* isp. nov., from the Eocene Wagon Bed Formation of central Wyoming, USA (Fig. 1). We provide a detailed morphological characterization of these fossil brood cells, compare them with established ichnospecies of *Celliforma*, and discuss their implications for interpreting solitary bee nesting behavior and paleoenvironments during the Eocene. This new material expands the recognized diversity of *Celliforma* and highlights the continued utility of ichnofossils in documenting the evolutionary history and ecological roles of ancient bees.

Geologic Setting

The Wagon Bed Formation is exposed primarily in Wyoming's Wind River Basin, where it sits stratigraphically between the Paleocene Fort Union Formation below and the Eocene Wasatch Formation above (Keefer, 1965). This early Eocene unit records the initial phase of basin infilling after the Laramide uplift had raised the Wind River Range and Owl Creek Mountains to the west and north. Regionally, the Wagon Bed Formation is broadly coeval with early phases of Green River Formation deposition, which are well constrained by high-precision $^{40}Ar/^{39}Ar$ geochronology (Smith *et al*., 2003).

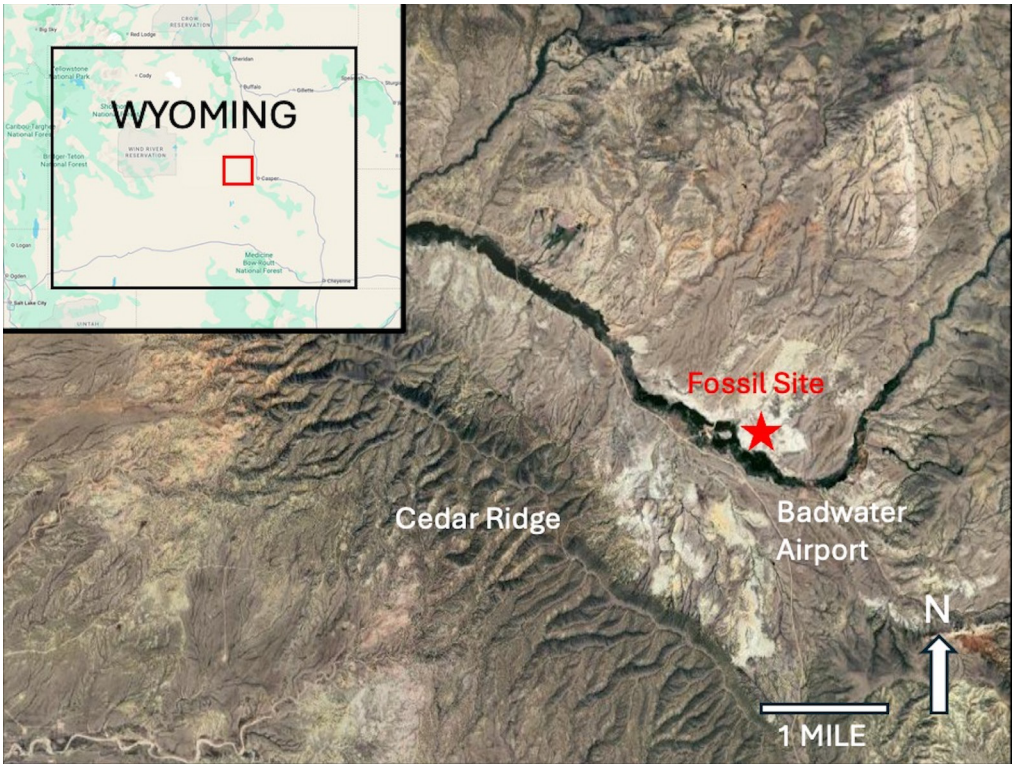


Figure 1. Map indicating approximate location of fossil locality from which the *Celliforma* specimens in this study were collected. The location is approximate to protect the privacy of the landowners.

The formation accumulated under greenhouse conditions (Wilf, 2000; Zachos *et al*., 2001; Wing & Currano, 2013). Rapid subsidence combined with high sediment supply to produce a heterogeneous mix: fluvial channel sandstones, floodplain mudstones and siltstones, carbonaceous shales, and scattered thin coal seams (Keefer, 1965). These lithologies mark a shift from the Fort Union's extensive peat swamps toward the more integrated, oxidized fluvial systems that dominate the overlying Wasatch (Gingerich, 1983; Bown, 1980).

Most deposits formed in low-gradient alluvial and lacustrine settings typical of humid subtropical environments. Overbank fines are abundant. Paleosols, root traces, and occasional lacustrine intervals point to prolonged floodplain stability and poor drainage (Wing *et al*., 2005). Channel sandstones show ripple lamination and trough cross-bedding consistent with low to moderate flow energy, while carbonaceous horizons record episodic swamp development.

All of this accumulated under early Eocene greenhouse conditions, when elevated temperatures and an intensified hydrological cycle sustained dense forest cover across western North America (Wilf, 2000; Wing & Currano, 2013). High rates of chemical weathering are evident in the clay mineralogy and paleosol development (Smith *et al*., 2008). The Wagon Bed Formation thus preserves a critical snapshot: the landscape stabilizing after Laramide deformation, ecosystems responding to peak greenhouse warmth, and fluvial architecture transitioning toward the Wasatch pattern (Kraus & Riggins, 2007).

The nesting horizon occurs in tuffaceous sediment consistent with regional Eocene volcanism; volcanic ash and volcaniclastic detritus derived from the Absaroka volcanic field were incorporated into Eocene basin fills, including units in the Wind River Basin (Keefer, 1965; Smith *et al*., 2008); the ash may represent primary airfall and/or reworked tephra. The specific eruptive source of the ash at the nesting horizon remains to be tested with tephra geochemistry and/or zircon geochronology (Smith *et al*., 2003).

MATERIAL AND METHODS

All *Celliforma* specimens examined in this study were recovered from the Early Eocene Wagon Bed Formation of Lysite, Wyoming and are housed in the paleoentomology collection of Harvard's Museum of Comparative Zoology (MCZ, Cambridge, MA, USA) and the Rozen Collection within the entomological department of the American Museum of Natural History (AMNH, New York City, NY, USA). Other specimens from this locality are deposited in the University of Arizona Entomology Department insect collection, and others privately held in the collection of S. Buchmann. Specimens were collected in situ from an exposed and extensive paleosol horizon on a private parcel of land, using hand tools and standard field techniques. The first solo expedition was by Dr. Jerome G. Rozen (AMNH, Entomology) in 1978. These sealed brood cells, burrow casts and fossils representative of other smaller bees and/or wasps are deposited in the Rozen bee nest holdings at AMNH and also now in the MCZ holdings at Harvard. Two additional expeditions were made by S.L. Buchmann (UA and USDA-ARS) in the summers of 1983 and 1989. These materials are now dispersed between MCZ (holotype and paratypes) along with other specimens in the University of Arizona Entomology Insect Collection and some materials remaining in the private collection of S.L. Buchmann. Locality names used here (*e.g*., Badwater, Lysite, and Lost Cabin) refer to the same general field area in the central Wind River Basin and are included as nearby geographic reference points for the nesting horizon and locality rather than as distinct fossil sites (Fig. 1).

Specimens were studied under a binocular microscope and Keyence digital microscope VHX-7000 and photographed using a Nikon D3X digital camera equipped with a Micro-Nikkor AF-S 60 mm f/2.8G ED macro lens. Photos were then focus-stacked using Adobe Photoshop (v.27.1) to create high-resolution images. Specimens were measured using ImageJ (1.53t) and a Mitutoyo 500-197-30 Electronic Digital Caliper.

RESULTS

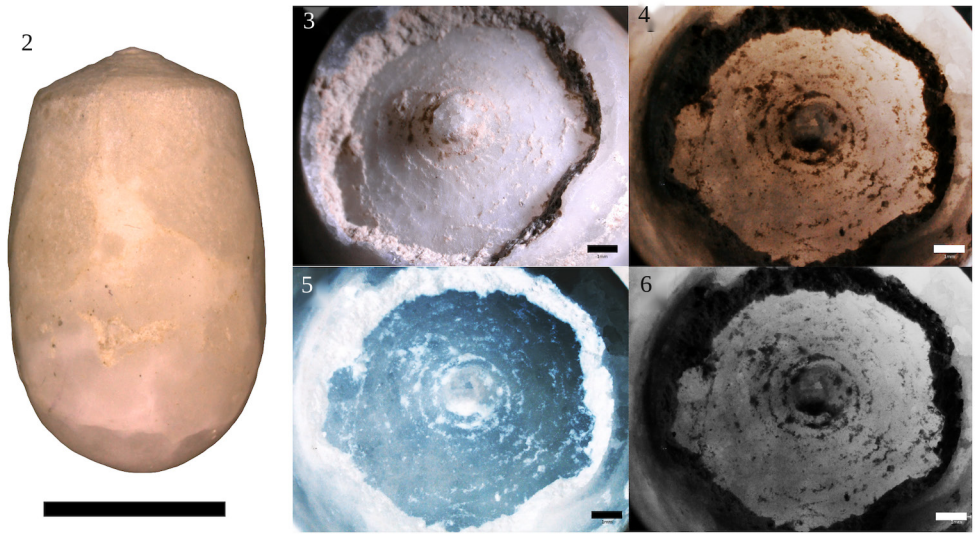
Systematic Paleoichnology

Ichnofamily Celliformidae Genise, 2000

Ichnogenus *Celliforma* Brown, 1934

Type ichnospecies: *Celliforma spirifer* Brown, 1934

Diagnosis: Solitary brood cells or internal molds of solitary brood cells, flask- to ovoid-shaped, with a smooth or finely textured inner lining. Cells typically exhibit a rounded end and a tapered posterior end with a distinct apical closure, which may be planar or spirally constructed. Neck region variably expressed, from straight to moderately constricted or curved. Chambers are commonly arranged singly or in loose clusters and not enclosed within a discrete external wall (Genise, 2000).



Figures 2–6. Holotype of *Celliforma rozeni* (MCZ:ENT:PALE-45901). **2.** Entire cell. **3.** Inverted cap seen in *C. rozeni* paratype showing characteristic dextral spiral of 7–8 turns (MCZ:ENT:PALE-45899) with light from above. **4–6.** Inverted cap with light coming from below, with inverted colors, and in black and white to enhance visualization of spirals, respectively. Scale bar = 1 mm except 1 cm in Fig. 1.

Celliforma rozeni Knecht & Buchmann, isp. nov.
(Figs. 2–6)

Zoobank: urn:lsid:zoobank.org:act:992E85E6-2C33-4270-97D5-E46677D27AA8

ETYMOLOGY: In honor of Dr. Jerome Rozen, former Senior Curator of Entomology, of the American Museum of Natural History, for his lifetime contributions to our knowledge of larval bees (Anthophila), cleptoparasites, and bee nesting architecture.

HOLOTYPE: MCZ:ENT:PALE-45901 from the Wagon Bed Formation of Lost Cabin, Wyoming, USA. The holotype is housed in the paleoentomology collection within the Department of Entomology at Harvard's Museum of Comparative Zoology (Cambridge, MA, USA).

PARATYPES: MCZ:ENT:PALE-45899, and MCZ:ENT:PALE-45900, all from the Wagon Bed Formation of Lost Cabin, Wyoming, USA. The paratypes are housed in the paleoentomology collection within the Department of Entomology at Harvard's Museum of Comparative Zoology (Cambridge, MA, USA) and also distributed to the University of Arizona Entomology Dept. Insect Collection, and some retained in the private collection of S.L. Buchmann in Tucson, AZ.

EXAMINED MATERIAL: Harvard University, Museum of Comparative Zoology, Department of Entomology Specimens MCZ:ENT:PALE-45899 - MCZ:ENT:PALE-45931; American Museum of Natural History, Division of Invertebrate Zoology, Dr. Jerome Rozen Collection, n >100 unnumbered specimens (some specimens had assigned field numbers but not accession numbers).

DIAGNOSIS: *Celliforma* exhibiting a rounded end and a tapered posterior end with a distinct apical closure, spirally constructed, with a dextral spiral of 7–8 turns. Apex is slightly elevated.

Description: Cells commonly arranged singly or in loose clusters, occasionally in a linear series, and not enclosed within a discrete external wall. *Celliforma rozeni* specimens have an average (n=40) apex-base height of ~2.3 cm and width (at greatest point) of ~1.4 cm. Holotype (MCZ:ENT:PALE-45901) has an apex-base height of 2.38 cm, width (at greatest point) of 1.42 cm, and rim-base measurement of 2.10 cm. Spiral width on paratype (MCZ:ENT:PALE-45899) averages ~0.7 mm. Spiral turn number is consistently 7–8 across all examined specimens, with no intermediate forms linking *C. rozeni* to the 4–5 turns characteristic of *C. spirifer*; both 7- and 8-turn configurations occur and are treated as within-ichnospecies variation. A thick apical cell cap overlies the inner spiral closure in most specimens, occasionally bearing a protruding nipple-like structure of variable prominence (Figs. 2–6). In a small proportion of specimens, the cap is preserved inverted (rotated approximately 180° from its original orientation), a taphonomic condition that nonetheless permits full documentation of spiral morphology (Figs. 3–6).

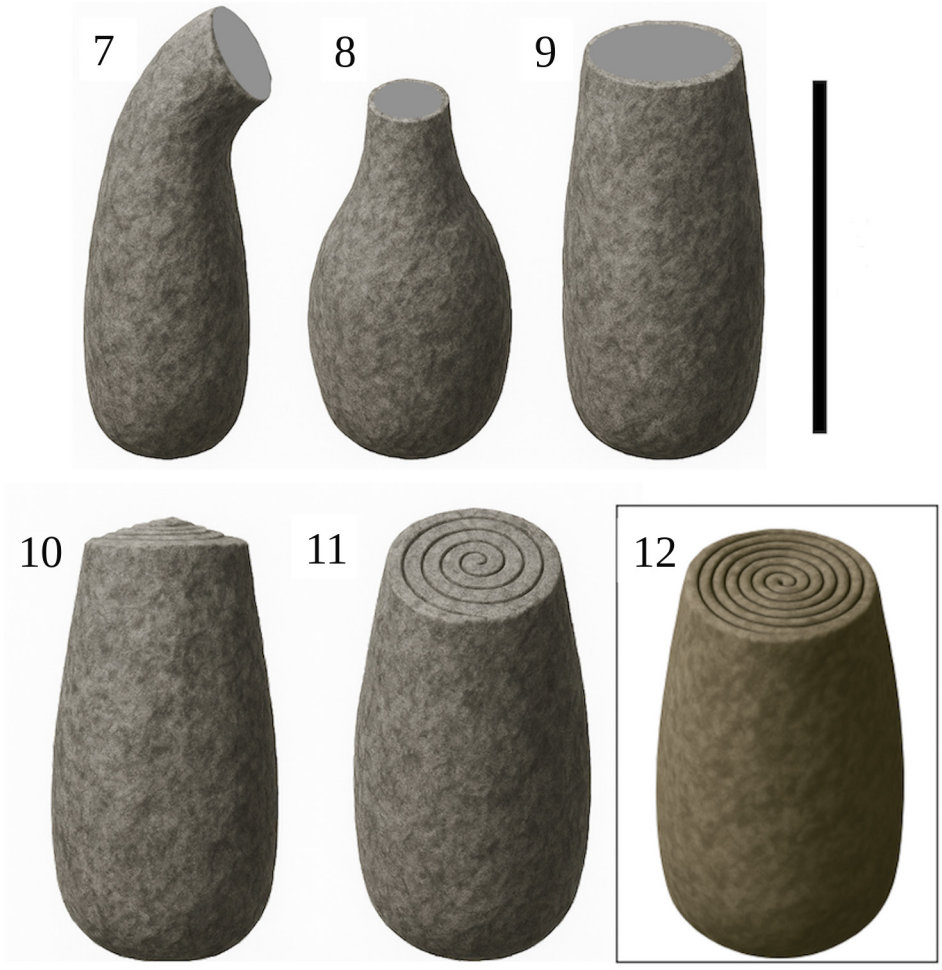
Revised Key to Ichnogenus *Celliforma*
(Modified from Genise, 2017)

The following is a key to the ichnogenus *Celliforma*, modified from Genise (2017), to incorporate all five valid ichnospecies: *C. spirifer* Brown (1934), *C. germanica* Brown (1935), *C. rosellii* Genise & Bown (1994), *C. curvata* Sarzetti *et al*. (2014), and *C. rozeni* Knecht & Buchmann (this study).

1. Curved longitudinal axis ……
.....*C. curvata* Sarzetti *et al*. (2014); Fig. 7
—. Straight longitudinal axis……..... 2
2(1). Specimens with a spiral closure ……..... 3
—. Specimens with no spiral closure ...….....….....…..……...…..... 4
3(2). Specimens with a dextral spiral of 4–5 turns …….....
.....*C. spirifer* Brown (1934); Figs. 10, 11
—. Specimens with a dextral spiral of 7–8 turns …….
...……..*C. rozeni* Knecht & Buchmann (this volume); Fig. 12
4(2). Specimens with a constriction or neck before the flat extreme ……
..….....*C. germanica* Brown (1935); Fig. 8
—. Specimens without constriction .....…*C. rosellii* Genise & Bown (1994); Fig. 9

DISCUSSION

The ichnotaxonomy of *Celliforma* has long been shaped by efforts to distinguish biologically meaningful behavioral variation from preservational or constructional noise, particularly with respect to spiral apical closures. In his original description of *C. spirifer*, Brown (1934) explicitly documented variability in spiral expression, noting that spirals could be well developed, faint, or nearly absent, and he did not initially recognize multiple ichnospecies within this material (Brown, 1935). Only subsequently did Brown (1935) erect *C. nuda* (Figs. 13–21) for material from the Florida "silex beds," a decision motivated primarily by differences in provenance, mineral composition, proportions, and depositional setting rather than by a discrete behavioral character or a consistently absent spiral closure (Brown, 1935). Brown himself emphasized the circumstantial nature of the evidence and the uncertainty of tracemaker identity. Later revisionary work demonstrated that the characters used to distinguish *C. nuda* fall within the morphological and preservational range of *C. spirifer*, and the taxon was therefore rejected as lacking an independent ichnotaxobase and treated as a junior synonym of *C. spirifer* (Genise, 2000, 2017).



Figures 7–12. *Celliforma* ichnospecies. **7.** *C. curvata.* **8.** *C. germanica.* **9.** *C. rosellii.* **10.** Lateral view showing slightly elevated apex seen in *C. spirifer* and *C. rozeni*. **11.** *C. spirifer* showing characteristic dextral spiral with 4–5 turns. **12.** *C. rozeni* showing characteristic dextral spiral with 7–8 turns. Both Figs. 11 and 12 models are flattened at the apex for ease of seeing spirals but would have similar topology to that seen in Fig. 10. Modified after Genise (2017). Scale bar = 2 cm.

In contrast, *C. rozeni* exhibits a tightly constrained and repeatable apical architecture characterized by a dextral spiral of seven to eight turns (Fig. 12), a feature not documented in any previously described ichnospecies of *Celliforma*. This exceeds the four to five turns typical of *C. spirifer* (Fig. 11; Brown, 1934; Genise, 2000, 2017) and falls outside the known morphological envelope of spiral variability recognized for that ichnospecies. Importantly, the number of spiral turns is not a trivial geometric byproduct but a behaviorally regulated construction trait. Studies of extant solitary bees demonstrate that brood cell closure architecture (including spiral tightness, number of rotations, and cap thickness) is often species-specific and remarkably consistent within taxa, reflecting inherited motor programs rather than environmental contingency (Krombein, 1967; Michener, 2007; Danforth *et al*., 2019). As illustrated in Figures 10–12, the spiral cap of *C. rozeni* (Fig. 12) occupies a non-overlapping morphospace relative to *C. spirifer* (Fig. 11), with spiral turn counts consistently exceeding the documented

range of the latter and showing no intermediate forms. It should be noted that these spirals are made as the final inner cell cap closure behavior by the nesting female bee. There is often a thick cell cap atop these inner cap spirals, sometimes with a protruding "nipple" like structure that may be for gaseous exchange (*e.g.*, as in modern centridine bees; Sabino *et al.*, 2021). Many of the *C. rozeni* brood cells show this characteristic nipple-like structure (Figs. 2–6). Inner spiral cap closures are widespread in brood-cell architecture of many extant solitary bees (*e.g.*, Krombein, 1967; Michener, 2007). Comparable spiral cap structures are not commonly reported from solitary wasp brood cells, supporting a bee affinity for *Celliforma* (*e.g.*, Krombein, 1967; Michener, 2007). Surprisingly, in a small percentage of the sealed *C. rozeni* brood cells, the entire cell cap is flipped 180 degrees and preserved upside down (Figs. 3–6).

Figures 13–20. Specimens previously assigned to *Celliforma nuda* (Brown, 1935) but now considered to be a junior synonym of *C. spirifer* (Genise, 2000). Collected by Dall (1915), specimens are housed in the collections of the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution (USNM PAL 340879). Photos by Matthew T. Miller (USNM). Scale bar = 1cm.

Accordingly, the erection of *C. rozeni* is justified not merely on structural grounds but as a behavioral ichnotaxon that likely reflects a distinct trace maker lineage or clade-level nesting program. The observed spiral turn counts in *C. rozeni* cannot be attributed to ontogenetic stage or taphonomic modification, as brood cell closures are constructed at a fixed point in the nesting sequence and the spiral architecture is preserved with uniform geometry across multiple specimens and preservational states (Figs. 2–12), rather than showing progressive truncation, distortion, or collapse. The visual contrast between *C. spirifer*/*C. nuda* material (Figs. 13–21) and *C. rozeni* (Figs. 2–6, 12) illustrates that spiral turn number constitutes a discrete, repeatable, and non-overlapping character state rather than a preservational variant. Recognizing spiral turn number as a valid ichnotaxobase increases the behavioral resolution of the fossil bee record and aligns ichnotaxonomic practice with ethological criteria used in modern bee biology. This refinement carries broader implications for paleoecological reconstruction: differentiating ichnospecies that encode distinct nesting behaviors

allows more precise inference of bee diversity, nesting strategies, and pollinator community structure in deep time. In Eocene paleosols such as those of the Wagon Bed Formation, where body fossils of bees remain rare, this added resolution enhances our ability to reconstruct terrestrial ecosystem dynamics, including soil stability, floral resource availability, and the partitioning of nesting niches among early Cenozoic pollinators.

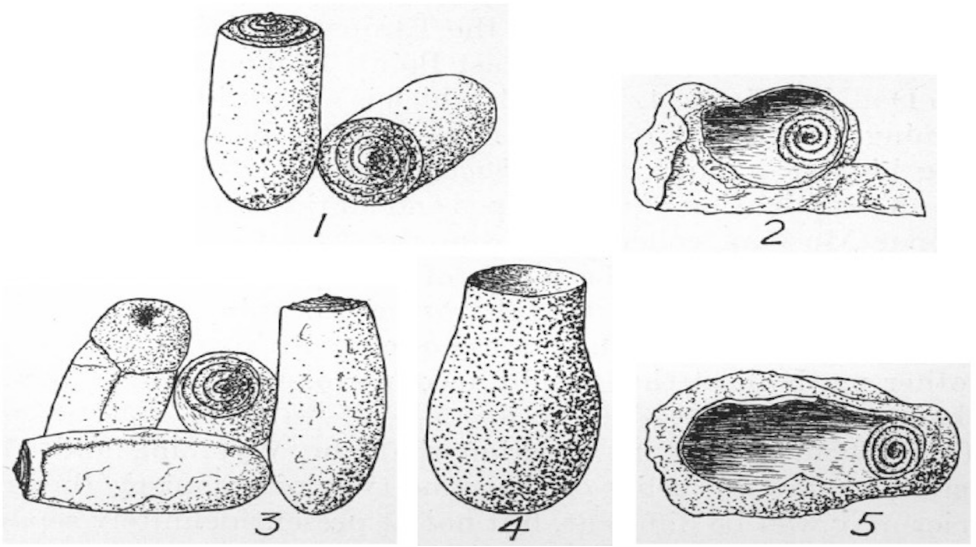


Figure 21. Original illustration reproduced from Brown (1934) figuring *Celliforma* specimens from Florida and Wyoming. The original publication is believed to be in the public domain because no copyright renewal has been identified. Brown (1935) later went on to name specimens from Florida, *C. nuda* and those from Wyoming, *C. spirifer*. *C. nuda* is now considered a junior synonym of *C. spirifer* (Genise, 2000).

CONCLUSION

Celliforma rozeni isp. nov. expands the documented behavioral diversity of fossil bees and demonstrates that spiral brood-cell architecture encodes taxonomically informative construction programs rather than preservational or incidental variation. The consistent expression of a dextral spiral cap composed of seven to eight turns distinguishes *C. rozeni* from all previously described ichnospecies of *Celliforma* and supports the interpretation that fine-scale closure morphology can serve as a robust ichnotaxobase (Brown, 1934; Genise, 2000, 2017). This finding reinforces the value of behavioral characters, particularly those tied to fixed points in the nesting sequence, for resolving ichnodiversity in groups with sparse body-fossil records (Krombein, 1967; Michener, 2007; Genise *et al*., 2013).

From a paleobiological perspective, the recognition of *C. rozeni* adds resolution to our understanding of Eocene bee communities. The presence of multiple *Celliforma* ichnospecies with distinct brood-cell architectures within early Cenozoic paleosols implies behavioral differentiation among ground-nesting bees and suggests niche partitioning in nesting strategies, substrates, or microhabitats (Bown & Kraus, 1983; Genise *et al*., 2000; Genise, 2017). For example, *C. curvata*, *C. rosellii*, and *C. germanica* co-occur in late Eocene paleosols of Oaxaca, Mexico (Guerrero-Arenas *et al*., 2018). Within the Wagon Bed Formation itself, *C. rozeni* occurs alongside additional undescribed

solitary bee and wasp brood cells (Knecht & Buchmann, pers. obs.), suggesting that niche partitioning among hymenopteran nest builders was already established at this locality by the early Eocene. Such differentiation is consistent with the establishment of modern-style solitary bee guilds by the early Cenozoic, in which multiple lineages coexist through fine-scale segregation of nesting behaviors despite overlapping floral resources (Potts *et al*., 2003; Danforth *et al*., 2019).

The occurrence of *C. rozeni* in the Wagon Bed Formation further highlights the potential of this unit to preserve additional, currently unrecognized ichnodiversity. Paleosols formed under conditions of prolonged floodplain stability, such as those documented in the Wagon Bed Formation, are well known to preserve diverse insect trace fossil assemblages (Bown *et al*., 1997; Elliott & Nations, 1998; Genise, 2017). Systematic survey and targeted sampling of Eocene paleosols are therefore likely to yield further distinct nest morphologies and provide critical insight into the early radiation and ecological structuring of solitary bees during greenhouse climates (Wilf, 2000; Wing *et al*., 2005; Wing & Currano, 2013).

Finally, the revised key to *Celliforma* presented here now permits identification of five valid ichnospecies, enhancing the practical utility of fossil bee brood cells for paleoecological and paleoenvironmental reconstruction. Improved ichnotaxonomic resolution strengthens the use of bee trace fossils as indicators of soil development, landscape stability, and pollinator community structure in deep time (Bown & Kraus, 1983; Genise *et al*., 2013; Genise, 2017).

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