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NEW SOCIAL INSECT NESTS FROM THE UPPER JURASSIC MORRISON FORMATION OF UTAH

Elliott Armour Smith, Mark A. Loewen, and James I. Kirkland

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The Emerging Complexities of the Morrison Formation
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Cover

Overturned boulder composed of a floodplain paleosol, revealing the underside of a fossil social insect nest. The boulder is from a locality in the Brushy Basin Member of the Upper Jurassic Morrison Formation, near Green River, Utah.

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New Social Insect Nests from the Upper Jurassic Morrison Formation of Utah

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ABSTRACT

This paper reports a new assemblage of social insect ichnofossils from the Brushy Basin Member of the Upper Jurassic Morrison Formation near Green River, Utah. At least seven distinct nests are visible in the locality horizon, identifiable at the outcrop scale by loci of anastomosing, and orthogonally connected horizontal burrows and vertical shafts. A boulder-sized block from the in situ horizon has eroded and rolled downhill, revealing the ventral aspect of the nest, showing a view of the overall nest architecture. Burrow and shaft clusters are organized into mega-galleries which have branching arms and ovate, bulbous chambers. The organization of distinct trace morphologies is consistent with ethological complexity of the social insects. A small sample was collected and analyzed by serial sectioning and petrographic thin sectioning to observe small-scale morphological features. Centimeter-scale analysis shows chamber, gallery, and burrow walls have complex topography. Pebble-sized, hollow, ellipsoid features are distributed throughout the uppermost facies of the nest and have undergone complete silicification of their outer surfaces. The ellipsoids share similarity with pellet structures made of mud or carton produced by modern termites. This trace fossil assemblage suggests it is possible that termites had acquired subterranean nesting behavior, and mud or carton utilization in nest construction in seasonally arid habitats by the Late Jurassic.

INTRODUCTION

Despite their individual cognitive simplicity, eusocial insects (termites, ants, bees, and wasps) are responsible for building some of the most complex structures in the animal kingdom (Theraulaz and others, 1998). Eusociality, the highest degree of animal sociality, is a remarkable biological phenomenon where members of a species are differentiated into reproductive castes and provide alloparental care (Crespi and Yanega, 1995). Eusocial insects that create the most complex structures are ants and termites, which are some of the most ecologically successful groups of organisms on Earth. Ants and termites are found on all continents except Antarctica and include over 12,000 living species and 3000 fossil species (Ward, 2007; Krishna and others, 2013).

Social insects can create structures that are spectacularly more complex than other solitary and subsocial arthropods because of stigmergy and self-organization (Theraulaz and others, 1998). Stigmergy is the transmission of information via the environment, rather than direct organismal communication (Theraulaz and Bonabeau, 1999). The nest itself serves as a template for

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the individuals in the colony to respond to stimuli, and their cumulative responses create a complex product in absence of individuals with cognitive complexity (Perna and Theraulaz, 2017). The nests of social termites are constructed to regulate temperature, moisture, and gas exchange (Ocko and others, 2019). The nests of ants have readily observable effects on the chemistry and physical properties of the soil they inhabit (Nkem and others, 2000). Aside from their ecological dominance and taxonomic diversity, the eusocial insects serve as complex and nuanced models for how selection operates at the group level (Fewell, 2003). Since Wilson's (1971) groundbreaking book *The Insect Societies* was published, social insects were brought to the center of an extensive debate amongst evolutionary scholars on the nature of natural selection, with opinions representing a multi-level selection, and gene selection views (Van Veleen, 2009).

Genomic evidence and body fossil continues to shed light on the once obscure origins of these ecologically important and evolutionarily successful groups of animal life. Brady and others (2006) estimated the common ancestor of extant ants evolved between 115 to 135 Ma, with a fossil-calibrated, molecular phylogenetic analysis. The authors concluded that a Jurassic origin of eusocial ants is unlikely. Cretaceous amber deposits from Burma (99 Ma) have yielded a morphologically specialized, stem-group ant taxon that appears to be eusocial (Barden and Grimaldi, 2016). Fossil distribution analysis and molecular phylogenetics have supported the hypothesis that the evolutionary radiation of crown-group ants coincided with the rise of angiosperms (Moreau and others, 2006; Perrichot and others, 2008).

Termites (Isoptera) are a monophyletic clade of eusocial insects that are now understood to be derived from cockroaches (Blattodea) (Inward and others, 2007), with the most recent common ancestor of termites and cockroaches likely evolving in the Permian (Legendre and others, 2015). Termites are the sister group to *Cryptocerus* roaches, with an estimated divergence time in the Early Jurassic (~195 Ma), and crown-group diversification occurring in the Late Jurassic (~150 Ma) (Bourguignon and others, 2014). In the Mesozoic, termites were not speciose, and represent a small fraction of insect diversity in fossil deposits (Engel and others, 2009). The first definitive termite fossils date back to the Early Cretaceous, with the oldest winged, stem-group termite fossils from Siberia dated to 135 Ma (Krishna and others, 2013). Despite their rarity, the body fossil record of termites indicates they were cosmopolitan and relatively diverse by the Late Cretaceous (Engel and Delcòs, 2010). Early Cretaceous (99 Ma) amber deposits from Myanmar reveal a speciose termite fauna with morphs belonging to reproductive castes, a diagnostic feature of eusociality (Engel and others, 2016).

The most basal living termite species, *Mastotermes darwiniensis* is the only member of the Mastotermitidae, and is only found on the continent of Australia (Krishna and others, 2013). The fossil history of this group has a cosmopolitan distribution, with fossil mastotermitids reported from the Lower Cretaceous Wealden Clay of England and Eocene amber deposits from the Baltic region (Engel, 2008; Krishna and others, 2013). The fossil history of termite species and their modern distribution indicate that their evolution predated Gondwanan rifting and thus did not initially coincide with the rise of angiosperms (Engel and others, 2009). Genomic and fossil evidence suggest that the the Late Jurassic was likely a key time in the radiation of crown isoptera (Legendre and others, 2015).

Genomic and body fossils provide only a partial picture of the evolution of social insects. Ichnofossils are the only direct evidence of the evolution of nest architecture and nesting behavior. Many reported social insect ichnofossils have been controversial (Genise, 2016). However, some reported ichnotaxa have been referred to living clades of ants and termites (Smith and others, 2011; Roberts and others, 2016), but these ichnotaxa are almost exclusively Cenozoic (Genise and others, 2000). Ichnofossils record notable events in termite evolution including the development of fungal agriculture dating back to the Miocene (25 Ma) of Africa (Duringer and others, 2006; Roberts and others, 2016).

Ant and termite nests have many similar elements, and nest architecture has been suggested to be of limited phylogenetic utility (Hasiotis, 2003; Genise, 2016). However, ant and termite nests have both homoplastic and autapomorphic characteristics. In modern ant nests, cylindrical galleries connect oblate to elliptical, expanded chambers, connected by vertical descending, cylindrical shafts (Tschinkel, 2004). Extant ant nest morphologies display diagonal central shafts, and variation in the clustering of chambers either near the top or the bottom of the nest (Tschinkel, 2015).

The ichnologic record of social insects from the Mesozoic is sparse and more taxonomically ambiguous than the Cenozoic record; however, it contains localities that inform science about the early evolution of social insects. Xing and others (2013) reported insect traces on a dinosaur skeleton from the Lower Jurassic Lufeng Formation of China. Xing and others (2013) noted the morphological similarity between these traces and the foraging galleries of modern termites, which are constructed with mud or carton (fecal matter mixed with saliva). The authors could not rule out a coleopteran as the trace-maker, they suggest the possibility that traces may be attributed to either a stem or crown-group termite.

Roberts and Tapanila (2006) reported social insect nests housed in the sand infilled casts of tree stumps from the Late Cretaceous Kaiparowits Formation of southern Utah. However, the Kaiparowits social insect nests were not definitively concluded to belong to either ants or termites. Termite ichnofossils have been reported from the Early Jurassic Clarens Formation of South Africa (Bordy and others, 2004). The hypothesis of a social insect tracemaker in both reported ichnofossil localities was supported by the occurrence of multiple bioturbation centers. However, the South African Early Jurassic termite mounds reported by Bordy and others (2004) were disputed, with a countering opinion citing a lack of clear morphology overlap between extant termites and failing to eliminate root traces as an origin (Genise and others, 2005).

The North American ichnofossil record of the terrestrial Jurassic has been reported by Hasiotis (2004) in a survey of the Upper Jurassic Morrison Formation ichnofacies. The author reports a diverse ichnofauna with a variety of ethologies adapted to conditions of channel, floodplain, lacustrine, and marginal-marine environments. In this survey, ichnofossils with ants and termites as interpreted tracemakers are reported. These termite and ant ichnofossils have been contested by Bromley and others (2007), who regard these reports as lacking ichnotaxonomic treatment, modern comparative morphology, and a nonsynchronous body fossil record. The new ichnofossil assemblage presented in this paper will add to the diversity of the Morrison ichnofauna, and provide previously reported Morrison social insect ichnofossils with additional context.

GEOLOGIC SETTING

The trace fossil assemblage in the Morrison Formation lies 12.4 km southeast of Green River, Utah, near the Crystal Geyser area (figure 1) and occurs within the upper Brushy Basin Member of the Morrison Formation (Bell, 1986). Deposition of the Morrison Formation occurred concurrently with the commencement of Cordilleran Highlands uplift, which provided a source of northeast-travelling clastic sediment (Dickinson and Gehrels, 2008). The Brushy Basin Member is an approximately 100 ± 30 m succession of mostly fine-grained, smectitic mudstones (Dickinson and Gehrels, 2008). The upper Brushy Basin Member is characterized by smectitic mudstones attributed to volcanic ash sourced from calderas to the southwest of the depositional basin (Turner and Peterson, 2004). The depositional environments of the Brushy Basin are low-gradient stream channels, floodplains, and playa lakes (Dickinson and Gehrels, 2008).

The upper Brushy Basin Member of the Morrison was deposited in the continental interior, bordered by a subduction zone to the west, and more proximal to a transcontinental rift zone. This zone was the setting for igneous complexes that provided the source for the volcanic ash seen in the "clay change" between the upper and lower Brushy Basin Member (Turner and Peterson, 2004). The locality is 8 m below the uppermost Jurassic unconformity (figure 2) and lies above the "clay change," which is described as the presence of extensive bentonitic volcanic ash that contain altered zeolites giving the upper Brushy Basin Member its array of color (Turner and Peterson, 2004).

Radiometric dates for the Brushy Basin Member are reported by several groups of authors and are largely in congruence. The top of the Brushy Basin has been reported by two U-Pb dates from near Hanksville, Utah, at 149.0 + 2.5/-2.2 Ma and 149.3 ± 0.5 Ma (Kowallis and

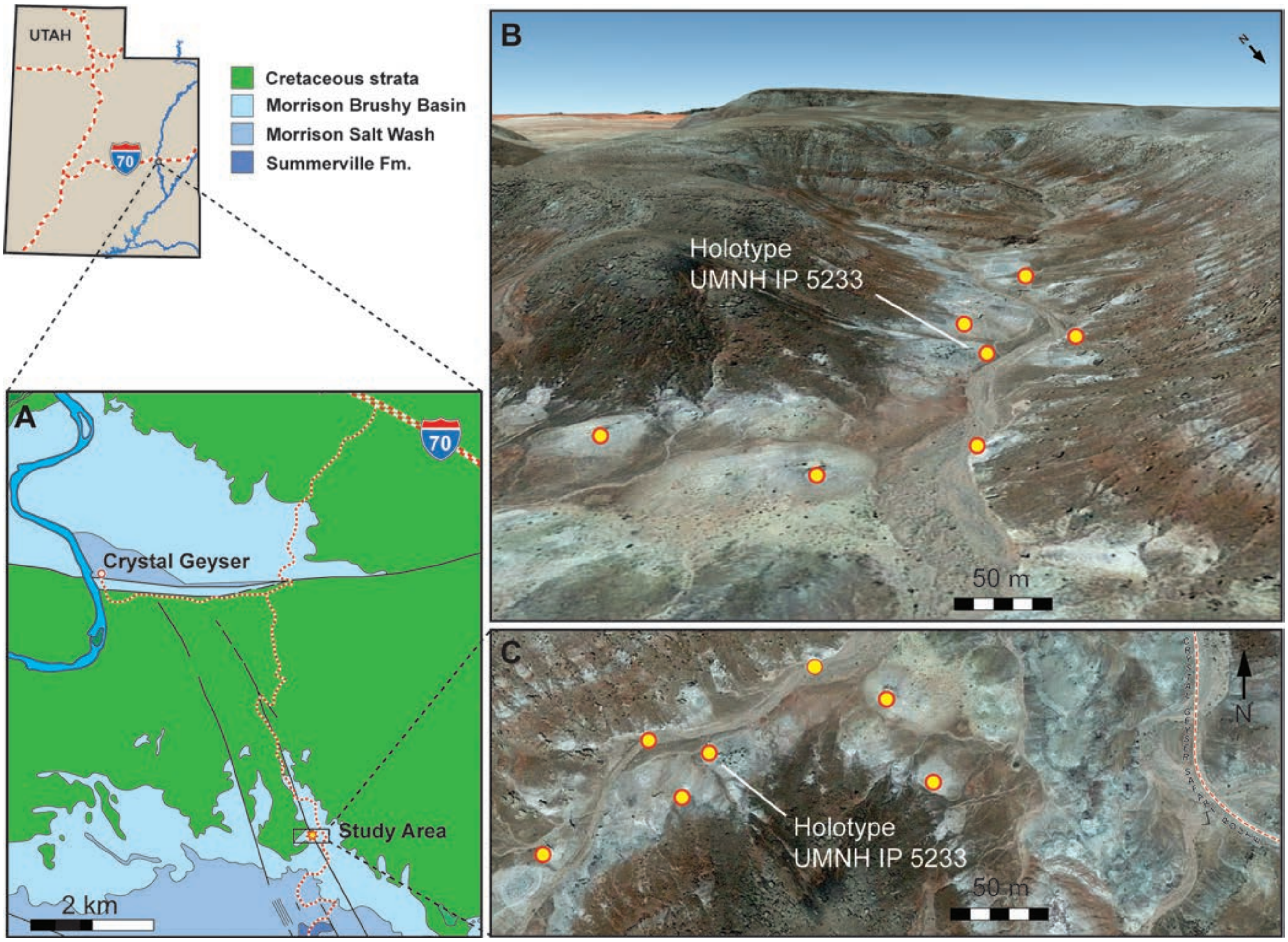


Figure 1. Geologic map of the Crystal Geyser area (A), near Green River, Utah (modified from Sable, 1955). A profile satellite image of the locality (B), with yellow dots indicating nest sites. An overhead satellite image of the locality (C), showing the exposure of the nest horizon. Satellite images from Google Earth, full citation in references.

others, 2007). Trujillo and others (2014) reported an age for the Mygatt-Moore Quarry of Mesa County, Colorado. The Mygatt-Moore Quarry is reported to be 64 m above the base of the Brushy Basin Member, and these authors report a U-Pb age date from a zircon sample, collected from a smectitic mudstone from the quarry, at 152.18 ± 0.29 Ma.

A recalibrated ^{40}Ar/^{39}Ar radiometric date from Little Cedar Mountain, Emery County, Utah, dates the top of the Brushy Basin Member to 150.00 ± 0.52 Ma (Trujillo and Kowallis, 2015). These authors also suggest a congruence between dates occurring in the Middle to Upper Brushy Basin across known stratigraphic sections that is approximately 151 Ma. Galli and others (2018) report U-Pb dates ranging from 150.208 ± 0.094 Ma in the middle of the Brushy Basin Member, and 149.43 ± 0.059 Ma, 2 m from the top of the member. However, the date from the middle of the member may not be as low stratigraphically as these authors report (J. Foster, Utah Field House of Natural History State Park Museum, personal communication, 2019).

The new trace fossil locality, which is 8 m below the top of the Brushy Basin Member is stratigraphically higher than the Mygatt-Moore dinosaur quarry, so the radiometric age date of 152.18 ± 0.29 Ma can be confidently placed as a maximum age for the new locality (Trujillo and others, 2014). The recalibrated ^{40}Ar/^{39}Ar radiometric date from Little Cedar Mountain serves as

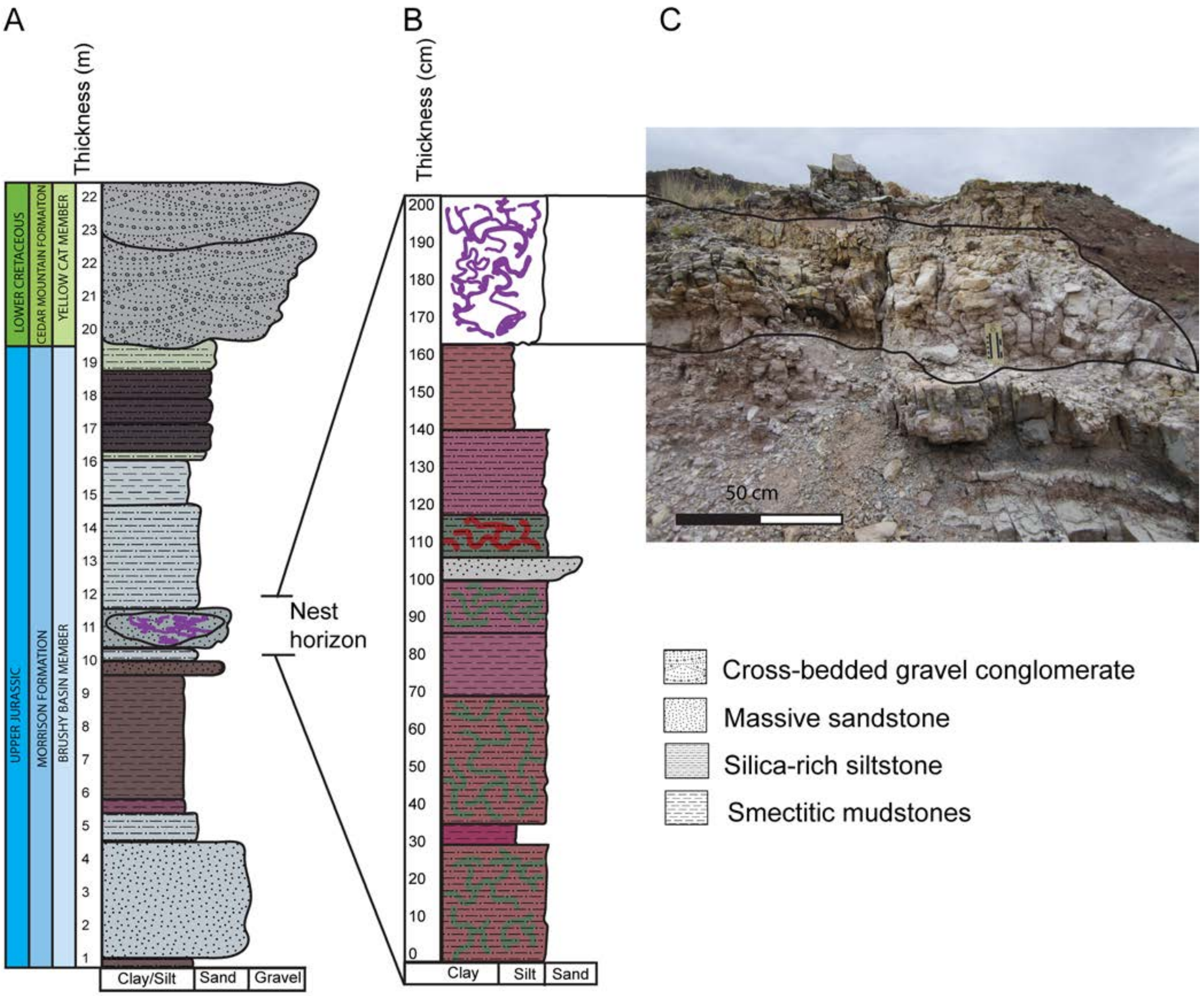


Figure 2. Stratigraphy of the type locality of *Eopolis ekdalei* (UMNH IP 5233), note the Jurassic-Cretaceous boundary (A). Elaborated detail at the nest horizon shows lateral variation in grain size and color (B). An annotated photograph shows the stratigraphic horizon where UMNH IP 5233, the type specimen of *Eopolis ekdalei*, was extracted (C).

an appropriate upper age limit for the new Morrison trace fossil locality, at 150.00 ± 0.52 Ma (Trujillo and Kowallis, 2015).

The paleoenvironment of the Morrison Formation has been characterized as dry, with high evaporation and transpiration relative to precipitation (Turner and Peterson, 2004). The flora is most accurately characterized as herbaceous-dominant, with a relative lack of woody plant fossils (Parrish, 2004). The upper Brushy Basin Member was deposited as a low gradient alluvial plain with wetlands and inwardly draining alkaline lakes. The water supply to the Morrison Basin was likely fed by meteoric water in the highlands that fed losing streams that intercepted the surface down gradient (Turner and Peterson, 2004).

The locality horizon can be considered a paleosol due to several lithologic observations (figure 2). The locality horizon lacks clear horizontal bedding features and contains rhizoliths. Mudstones and siltstones are mottled and contain discolorations consistent with oxidization. Paleosol formation at the uppermost Morrison Formation unconformity reflects decreasing deposition and/or accommodation and consequently greater longevity of sediments on the depositional surface (Demko and others, 2004).

METHODS

The ichnofossils in this report were named using a morphology based approach outlined by Bertling and others (2006). Analysis of these ichnofossils was conducted at a range of visual scales from outcrop to millimeter-scale. Eight centers of intense bioturbation eroding in relief were photographed and observed (figure 1). The spatial distribution and elevation of the mounds were recorded with Universal Transverse Mercator (UTM) coordinates, and plotted on a 1:24,000 scale U.S. Geological Survey map (figure 1). A geologic map of Tidwell-1 quadrangle was used to construct the locality map (Sable, 1955) (figure 1).

The stratigraphy of the ichnofossil assemblage was described by utilizing a drainage that eroded through the stratigraphic horizon of the ichnofossil assemblage (figure 2). The lithology and mineralogy of the ichnofossils were described with transmitted light photographs of petrographic thin sections. The photographs were supplemented with a Quantitative Evaluation of Materials by Scanning Electron Microscopy (QEMSCAN) analysis, which produces a quantitatively descriptive image of mineral fabrics by assigning a mineral identity to each pixel based on spectral data. The QEMSCAN analysis was performed at the Advanced Rock Characterization Laboratory at the University of Utah, which consists of a Carl Zeiss EVO 50 Scanning Electron Microscope running the QEMSCAN proprietary software. A 27 mm^2 area of a petrographic thin section was imaged with a 20-micrometer spot for 11 minutes.

Individual mounds were preserved with pervasive cracks and weathering surfaces. This preservation made approaches to collecting the specimen difficult. Ultimately, we decided that leaving the nests at the locality in situ would be the best immediate approach for preserving them, and smaller samples for serial sectioning would be most ideal for describing interior burrow morphology.

To assess the internal stratinomy of the uppermost facies in each mound, a ~30 cm in diameter sample was cut into nine serial sections and photographed with consistent parameters. Sharp contrast in burrow lining (contact between pale purple and white silt/clay) was accentuated using Adobe Illustrator (figure 3). The thin sections and serial sections of the ichnofossil sample are reposited at the Natural History Museum of Utah in Salt Lake City (UMNH).

SYSTEMATIC ICHNOLOGY

Eopolis – New Ichnogenus

Etymology

Eo- (Greek), dawn, origin. Polis- (Greek), city. The name refers to the interpreted nature of the trace as a structure built by a social insect, animals that are renowned for the complexity of the structures they build. The name also refers to the early occurrence of the trace, near the evolutionary origin of the earliest social insects.

Type Specimen

Holotype, UMNH IP 5233.

Material

Sample is composed of nine serial sections, and two petrographic thin sections.

Horizon, Age, Locality

Holotype specimen collected near the top of the Brushy Basin Member of the Upper Jurassic Morrison Formation. The locality is approximately 12.4 km southeast of Green River, Utah. The nest horizon is approximately 20 m below the unconformable contact with the Yellow Cat Member of the Cretaceous Cedar Mountain Formation.

Diagnosis

This trace is defined as a densely clustered burrow network, composed of cylindrical horizontal galleries and vertical shafts, punctuated by expanded, ovate to spherical chambers. Clusters of orthogonally and obliquely intersecting cylindrical burrows are contained

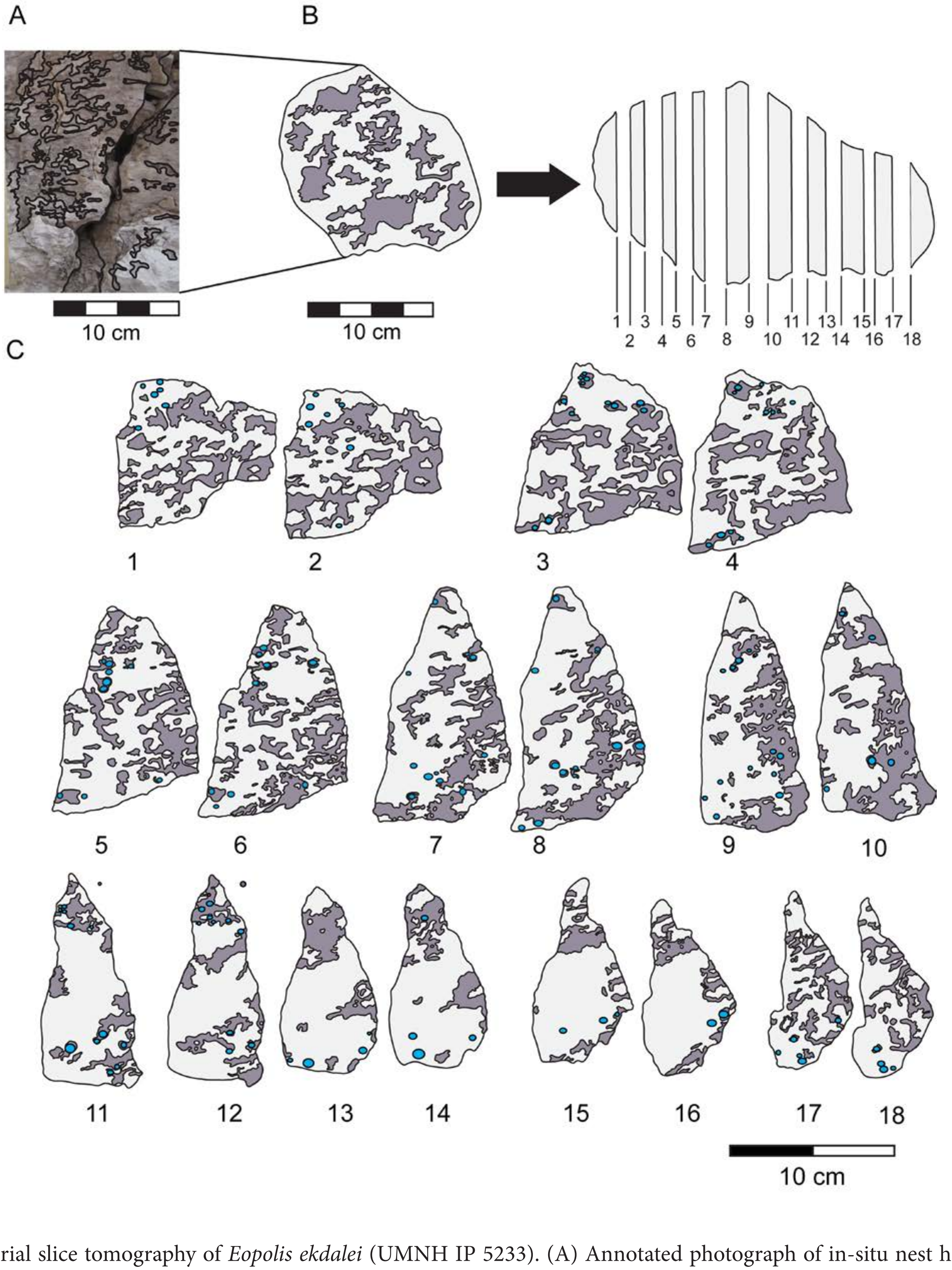


Figure 3. Serial slice tomography of *Eopolis ekdalei* (UMNH IP 5233). (A) Annotated photograph of in-situ nest horizon. (B) A diagram illustrating dimensions of macrosample and slice numbers. (C) Small scale burrow morphology interpreted from serial section photographs. Pale-purple clayey silt is the matrix and white clayey silt is the infill. Slice numbers indicate sequence, as shown in (B). Ellipsoids are marked in blue for contrast.

within a larger, also unlined network with anastomosing morphology. Chamber walls are unlined, but have a cellular or honeycomb-like morphology.

Horizontally oriented, or obliquely oriented galleries have cylindrical morphology, with an average diameter of 0.49 cm (n = 13), ranging from 0.32 to 0.79 cm. Vertically oriented shafts have similar dimensions, with an average diameter of 0.49 cm (n = 16), ranging from 0.30 to 0.79 cm. Chambers are sub-spherical or sub-ovate to amorphous, with undulating, rugose margins. Chamber diameter ranges from 5 to 20 cm at their greatest width. The mounds are approximately 0.5 m in vertical relief, and 0.75 to 1 m in horizontal diameter, and possess a cylindrical shape with the vertical axis being the shortest.

Eopolis ekdalei – New Ichnospecies

Etymology

Specific epithet for Tony Ekdale, Ph.D., paleontologist and professor in the Department of Geology and Geophysics at the University of Utah, for his outstanding contributions to the field of ichnology.

Diagnosis

As the genus.

Differential Diagnosis

At this locality, the ichnospecies is represented by at least seven nests that are flat and cylindrical in gross morphology. *Eopolis* has clustered, anastomosing burrow networks like *Termitichnus* (Bown, 1982) and *Socialites* (Roberts and Tapanila, 2006). The highest density of burrows does occur in a central location, however, there is no indication that a spherical pericicie exists as in *Termitichnus* (Bown, 1982). There is also no indication that chambers are stacks of oblate discs as in *Krausichnus* (Genise and Bown, 1994) or *Daimoniobarax* (Smith and others, 2011). The small-scale (hand sample) morphology of the trace has roughly horizontal burrow orientation, but there does not appear to be tightly clustered connections of passages by ramps, and distinct partition walls as in *Coatonichnus* (Duringer and others, 2007).

RESULTS

Lithology and Stratigraphy of Nest Horizon

The nest horizon can be described as an approximately 0.5-m-thick layer of tuffaceous, bentonitic siltstone, lying immediately above mudstone-claystone layers with diffuse bioturbation (figure 2). Approximately 2 m of outcrop at the horizon of the trace fossil assemblage reveal mostly bioturbated red siltstone with green-gray mottles. The bioturbated siltstones are punctuated by non-bioturbated, red-purple siltstone and mudstone. Additionally, green mudstone and sandstone are observed punctuating the red-purple mudstone beds. All eight mounds are topped by a purple and white, bioturbated clay-rich siltstone with pebble-sized, hollow, purple ellipsoid structures.

Eight mounds of silicified mudstone and siltstone crop out in approximately 0.5 to 1 m of relief (figure 1). Burrow concentration and complexity increases generally towards the center of each mound, so each mound is a center of bioturbation. The core of each mound displays a silicified texture with an orange hue, and the surrounding mudstone and sandstone beds appear to deform in a concave-up fashion in relation to the peak of each mound. The deformation of the beds adjacent to the mounds is likely the result of soft-sediment deformation.

Description

Anastomosing masses of purple sediment are punctuated with gaps of white sediment approximately 2 to 3 cm in length (figure 4). Purple and white sediments in uppermost facies reveal boundary of burrows (figure 3). Typically, the white appears as infill, and purple appears as matrix. However, the white sediment is much more abundant, and the purple coloration revealing the matrix is limited through these layers. It is likely much of the matrix is composed of white sediment as well, which obscures the differentiation between burrow and matrix in some places (figure 4A). The matrix-burrow boundaries are gradational, but occasionally display sharp contrast. Ovate, columnar structures occasionally transect purple sediment, both directly and obliquely. Smaller circular features, white sediment within purple

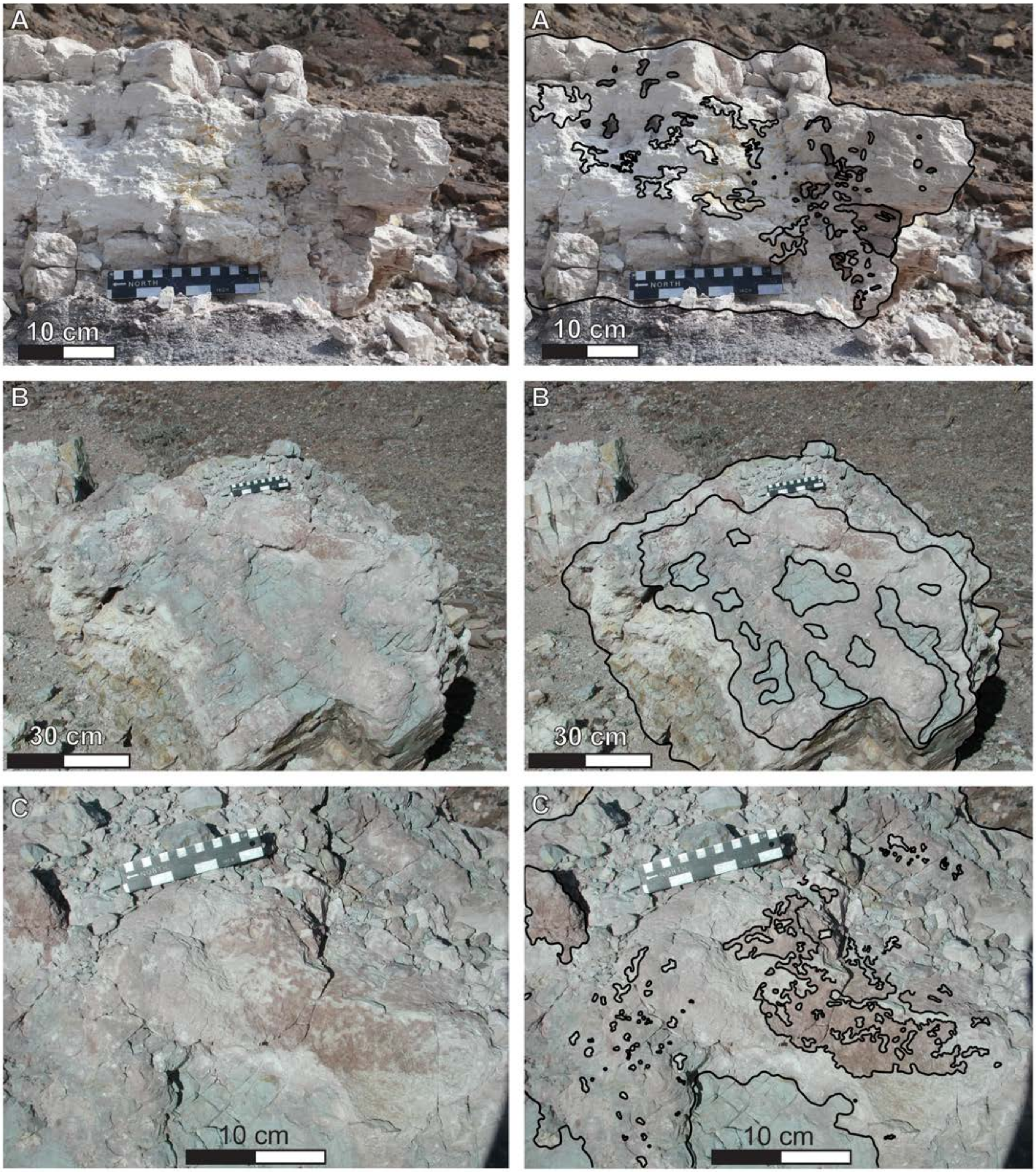


Figure 4. Photographs (left) and interpretations (right) of the type locality of *Eopolis ekdalei* (UMNH IP 5233). (A) This view shows an in situ nest with burrows in cross section from lateral view. (B) This view shows a nest block fallen out of place, exposing a transverse planar view underneath a nest. (C) This view shows a close-up photo and interpretation of an extended branch of the mega-gallery.

sediment, are 2 to 5 mm in diameter.

An approximately 25-cm-thick deposit of white siltstone with purple mottles lies directly on top of an unbioturbated gray mudstone (figure 4A). The mound contains a network of vertically and horizontally oriented tunnels, with an average diameter of 0.49 cm (n = 13). The burrows appear in vertical and horizontal relief, with semicircular portions of the cylindrical tunnels exposed in cross section, vertically and horizontally. The vertical and horizontal tunnel join in an approximately orthogonal fashion. The tunnels are unlined but have a rugose texture. The second distinct morphology that can be seen on figure 4A are vertical shafts. Shafts are exposed vertically and have an average diameter of 0.49 cm (n = 16). Some of the shafts are adjacent to more open galleries with are undulating margins. These are more difficult to see as the sediment lacks the pale purple color.

A large boulder-sized block that has fallen from the outcrop above revealed the ventral surface of a nest (figure 4B). An anastomosing gallery is visible on a distinctly larger scale than the tunnel lattice and vertical, undulating galleries seen on figure 4A. This feature is a mega-gallery. The arms or branches of the mega gallery are approximately 25 to 30 cm thick and are composed of the tunnel lattice and smaller vertical galleries. A 1.5-cm-wide, 25-cm-long horizontal tunnel is exposed on the underside of the block (figure 4C). The lining to the tunnel, and adjacent small galleries, is not composed of a distinct substrate, but has an anastomosing, or undulating lining. Three to five sinuous waves in the lining occur on a 5 cm horizontal line. Vertical and horizontal tunnels 0.5 to 2 cm in diameter, with unlined walls, are visible in the arm of the mega-gallery.

Vertical galleries with an undulating or sinuous lining are visible from the periphery of a nest location (figure 3). A series of horizontally oriented, ribbon-like striations are visible between tunnel and gallery openings. An open gallery shows a bulb hanging down into the gallery; the bulb is approximately 1.5 cm in diameter. Figure 3 shows the tunnel lattice, and how small-scale galleries change in three-dimensional space. Slices are approximately 10 to 15 cm in the longest direction, and 2 cm thick. Gaps between slices are approximately 1 cm (width of rock saw blade). Anastomosing or sinuous vertical gallery walls are crossed by a lattice of vertical and horizontal tunnels. Ellipsoid features (figures 5 and 6) are pervasive throughout this horizon, with a mean diameter of 0.31 cm (n = 128) through the short axis.

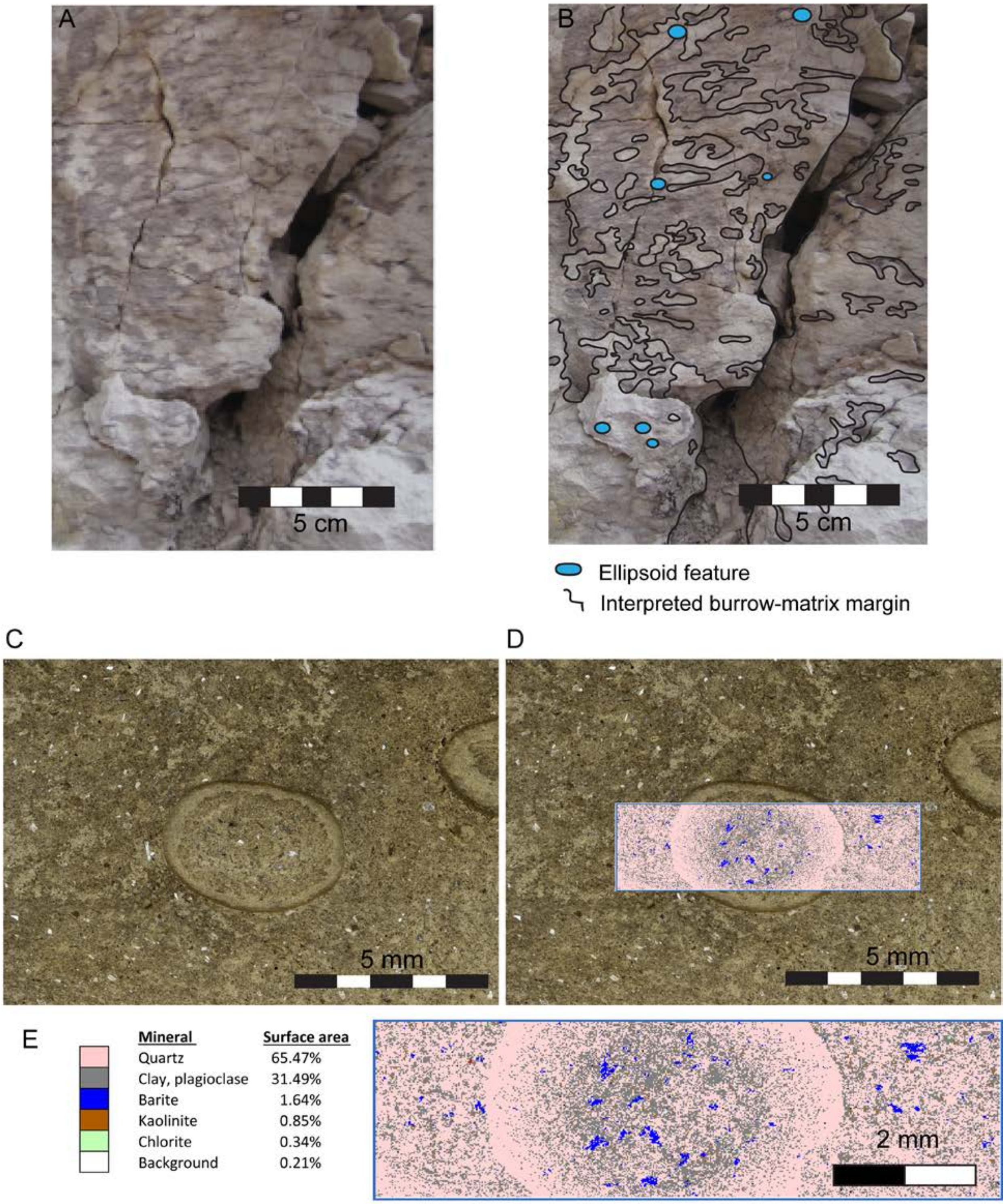
These ellipsoid features can be ruled out as continuous burrows in cross section (figure 3). Cross sections of ellipsoids are seen on either side of cuts, (cross sections 3 and 4), but are not horizontally continuous through multiple slices (figure 3). For instance, on figure 3, the cross sections on either side of a cut, numbers 5 and 6, go through a group of ellipsoids. The next pair of cross sections (7 and 8) also cut through a group of ellipsoids that are below the group on cross sections 5 and 6. If these were horizontally continuous burrows, the ellipsoids higher on cross sections 5 and 6 would persist through cross sections 7 and 8 (figure 3). The lining of these ellipsoid features is pale-purple, with white sediment internally. These ellipsoids generally occur at the contact between the pale-purple and white sediment, but are also found isolated within white sediment.

QEMSCAN Analysis

Ellipsoid features are ubiquitous through the white and pale-purple siltstone facies (figure 5). The ellipsoids are hollow and vertically compressed. The lining of ellipsoids is approximately 10 to 20 microns thick. The outermost layer these of ellipsoid features is silica. The rock fabric of the purple and white siltstone facies is a groundmass of quartz and clay minerals, along with and barite and feldspar crystals that are larger than the groundmass (figure 5C). Ellipsoid structures are composed entirely of silica. Feldspar crystals seen in petrographic thin section (figure 5C) are white and elongate (~100 μm length). Clay mineral and silt-size quartz grains are likely too small to see in petrographic thin section at the magnification displayed in figure 5. Barite crystals appear opaque and dark (figure 5C). The QEMSCAN analysis is unable to differentiate the composition of the clay minerals (figures 5D and 5E) versus the plagioclase crystals, and are all identified as gray pixels.

Interpretation of Locality

Our study has observed this trace fossil assemblage at outcrop scale (figures 1 to 3), centimeter scale (figure



	Mineral	Surface area
🟥	Quartz	65.47%
⬛	Clay, plagioclase	31.49%
🟦	Barite	1.64%
🟫	Kaolinite	0.85%
🟩	Chlorite	0.34%
⬜	Background	0.21%

Figure 5. A close-up photograph of the type locality nest horizon of *Eopolis ekdalei*, where UMNH IP 5233 was extracted. Some matrix is gray-purple and silica rich, with infill composed of bentonitic clay (A). The field photograph of nest horizon with interpreted burrow linings (B). A petrographic thin section photograph of a silicified ellipsoid feature (C) with an overlain QEMSCAN analysis (D). A visual representation of the QEMSCAN analysis with surface area of mineral content reported as a percentage (E).

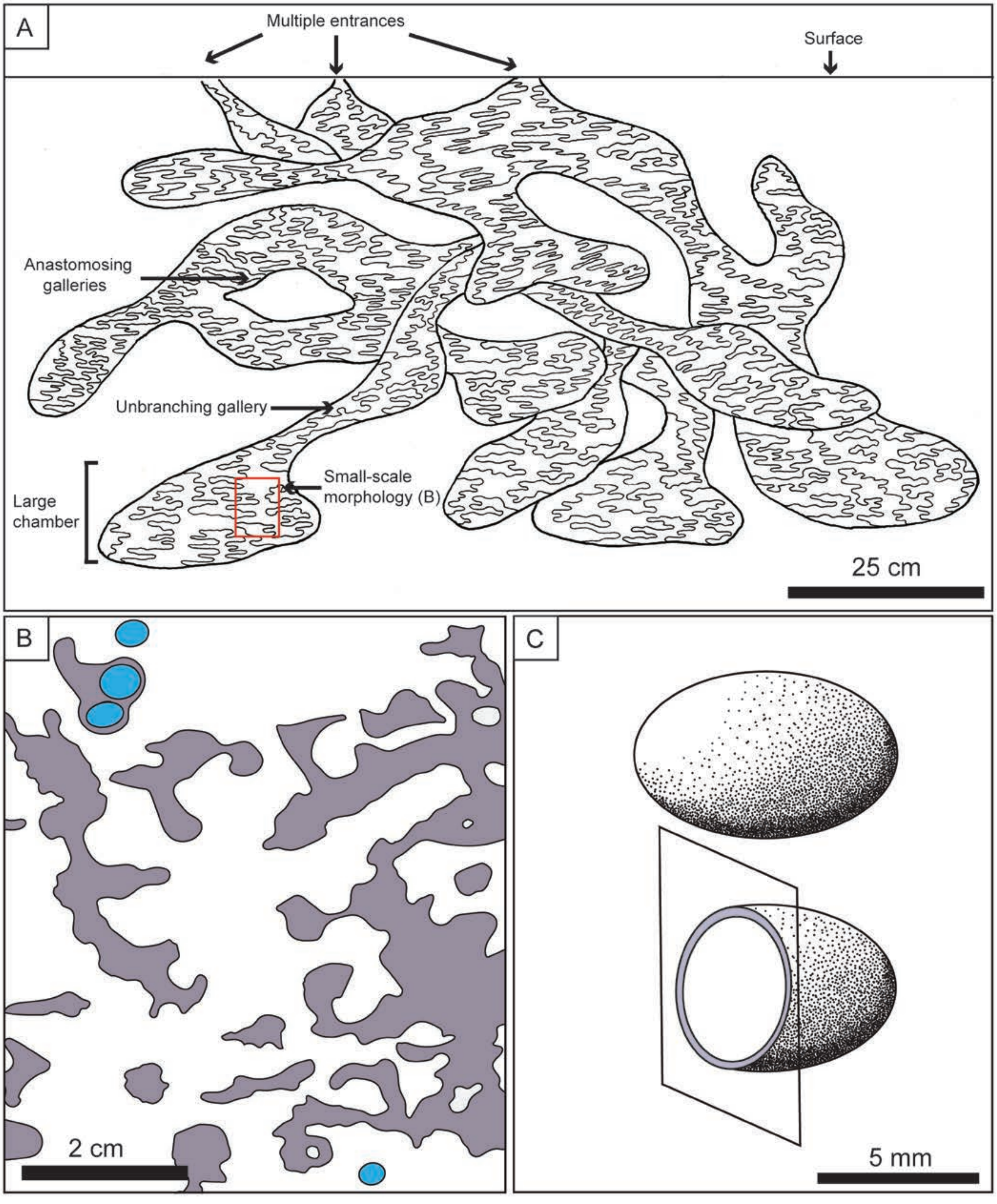


Figure 6. An interpretation of the new Morrison Formation trace fossil site at outcrop scale (A). Trace fossil interpretation at close-up scale (slice 5, UMNH 5233, figure 4), noting embedding of ellipsoids (blue for contrast) (B). A schematic drawing of a single ellipsoid, with appearance in cross section (C).

3), and microscopic scale (figure 5). We can use these observations to support an overall interpretation of its reconstruction. Large chambers, anastomosing galleries, and single, unbranching galleries are visible in the ventral view of the displaced block (figures 3B and 6A). At the hand-sample scale, purple silt matrix can be differentiated from the white silt infill. Silicified ellipsoids occur with an apparently random distribution at the hand-sample scale (figure 6B). Burrows are roughly horizontally oriented, but also intersect cross sections vertically, and at oblique angles. Walls of the burrows have intensely folded and complex surfaces (figure 6C). Individual ellipsoids appear as circles in cross section (figure 6C).

DISCUSSION

These findings demonstrate a new occurrence of social insect nest ichnofossils from the Morrison Formation, morphologically distinct from reported social insect ichnofossils both within and outside of the Morrison. These traces show a high degree of ethologic complexity, consistent with the architecture of modern and fossil social insect nests. Features that indicate multiple, synchronous behaviors are reported in these nests including burrow excavation, gallery/chamber construction, and ellipsoid producing behavior. These ichnofossils predate the first body fossil occurrences of social insects by 15 million years (Krishna and others, 2013).

Several alternative hypotheses will be addressed here. Ichnofossils created by the activity of plant roots are known as rhizoliths, and they are cited as an alternative tracemaker to reported fossil social insect nests (Genise, 2016). Rhizolith horizons have a superficial resemblance to social insect burrow networks. Rhizolith horizons have cylindrical infillings that are densely clustered and may cross each other in a woven appearance (Badawy, 2018). In general, rhizolith horizons are defined by vertically oriented casts, with horizontally extending mats that may appear anastomosing in planar view (Owen and others, 2008). Often, plant root traces and social insect nests are reported in association with insect burrow networks woven into rhizolith fabrics (Roberts and Tapanila, 2006; Genise and others, 2010). Discrete rhizolith horizons can be identified immediately below and above the nest horizon (figure 2), but they are either not as dominant, or are completely obscured by the nest horizon.

Another alternative hypothesis to explain the origin of these traces is that the nests are a composite product of other solitary to subsocial soil infauna that create a structure that appears complex from their individual burrowing activities. A diversity of modern animal life has soil habitat, creating traces that are the result of resting, breeding, and locomotion behaviors (Hasiotis, 2007). Neoichnological experiments have demonstrated that individual beetle larvae produce backfilled, meniscate burrows (Counts and Hasiotis, 2009). Cicada larvae have been demonstrated to create similar this type of burrow as well (Smith and Hasiotis, 2008). A diversity of arthropods create trace fossils with both unique and similar features (Hasiotis, 2002). Ratcliffe and Fagerstrom (1980) demonstrated that beetles (Coeloptera) were responsible for creating both single-chambered, branching, and anastomosing burrows in Holocene sediments. The brood traces of dung beetles, bee cells, and wasp cocoons are common ichnofossils in the Cenozoic record of South America, grouped together as the *Coprinisphaera* ichnofacies (Genise and others, 2000). Although Hasiotis (2004) has reported a diversity of trace fossils attributed to the behaviors of insects in the Morrison Formation, several lines of evidence do not support a soil insect infauna origin for this assemblage. *Eopolis*, with its anastomosing mega-galleries, appears to be much larger and more complex than nests attributed to termites from the Late Triassic Chinle Formation, *Archaeoentomichnus* (Hasiostis and Dubiel, 1995). However, unlike *Archeoentomichnus*, *Eopolis* lacks a distinct periecie and spiral-shaped ramp (Hasiostis and Dubiel, 1995). First, the isolated occurrence of any of these trace features (including horizontal shafts, vertical shafts, sinuous walls, ellipsoidal features) can be reasonably attributed to other, non-social taxonomic groups of insects. Second, the anastomosing burrows that are contained within a larger gallery apparatus suggest a distinct hierarchy and ethological complexity (figure 4). The similar morphology amongst each mound or locus in this ichnofossil assemblage suggests that the trace-maker is monospecific (figure 2).

Despite their size and complexity of their nests, ants can effectively be ruled out as a trace-maker for these new Morrison ichnofossils. There is a clear morphological discrepancy between this trace fossil assemblage and the traces of modern and fossil ant nests. In modern ant nests it has been observed that a positive correlation between colony size and nest size exists, in addition to decreasing nest volume with depth (Mikheyev and Tschinkel, 2004). Ant nests have been described as having a single entrance (Tschinkel, 2004) or multiple entrances (Guimaraes and others, 2018). Despite variation in shaft or gallery density and orientation, fossil ant nests and modern ant nests possess distinctively oblate, disk-like chambers (Smith and others, 2011). The genomic and body fossils evidence for the evolution of ants is also incongruent with a Late Jurassic origin (Brady and others, 2006; LaPolla and others, 2013). Moreau and others (2006) suggest a divergence date for the node of extant ants (Formicidae) between the Middle Jurassic (168 Ma) and Early Cretaceous (140 Ma). However, Tschinkel (2015) suggested that the earliest ant nests likely resembled ground-nesting wasps and bees, with simple descending shafts and single to few expanded brooding chambers. The first unanimously accepted ant nest ichnogenus, *Parowanichnus*, was described by Bown and others (1997) from the Eocene Claron Formation of Utah. *Parowanichnus* is consistent with the modern ant nest morphology and other Cenozoic ant traces (Smith, 2011). Despite reported ichnofossils with ants as suggested tracemakers from the Early Cretaceous (Genise and others, 2010), the morphology of these new ichnofossils does bear resemblance to those created by ants.

Another hypothesis for the origin of these ichnofossils is that they were created by a non-formicid, hymenopteran architect. Wasps and bees have a trace fossil record extending back to approximately 85 Ma to the Late Cretaceous, at the terrestrial Conacian-Santonian boundary of Argentina (Genise and others, 2007). Despite the similarity in the ellipsoid features from the Brushy Basin nests to reported hymenopteran pupal chambers, these features are too far removed from the hypothesized origin of wasps and bees to be considered of wasp or bee origin. The most recent genetic phylogeny of hymenoptera places their initial major radiation in the Paleozoic (281 Ma), the first appearance of eusocial bees (Apidae) in the Cenozoic (approximately 60 Ma), and eusocial wasp (Vespidae) families (approximately 100 Ma) (Peters and others, 2017). Although additional phylogenetic work does place the major radiation of Aculeata (the clade containing ants, bees, and wasps) in the Middle Jurassic (170 Ma) (Brady and others, 2009), the first clear evidence of wasp and bee eusocial behavior in the trace fossil record is from the Cretaceous (Genise and others, 2007). Vespid wasps are one of the only eusocial, non-formicid hymenopteran clades that excavate nests in the soil. Vespid wasps likely evolved eusociality twice independently (Johnson and others, 2013), and the earliest claimed fossil vespid is from the Early Cretaceous (Barremian) of Spain (Rasnitsyn and Martínez-Delclòs, 2000). The trace morphology of wasp and bee traces are also not consistent with the *Eopolis ekdali*. The morphology and dimensions of *Celliforma* (hymenopteryan pupation chamber) are consistent in shape, size, and dimension with the ellipsoids in *Eopolis*. However, in *Celliforma*, the cells are clustered around a vertical descending shaft (Hasiostis, 2002). In *Eopolis*, the ellipsoidal features are generally found at matrix-infill boundaries but are otherwise random within the burrow complex (figure 3).

The ichnofossils presented in this paper support the hypothesis that termites evolved eusocial behavior by the Late Jurassic, preceding not only the rise of angiosperms, but the rifting of Gondwana. Termite nests exhibit a significant amount of intraspecific, interspecific, and ontogenetic variation (Hasiotis, 2003). Termite nests can be characterized as diffuse, or concentrated, depending on the arrangement and geometry of galleries and chambers (Genise, 2016). Concentrated nests have a central arrangement of cavities referred to as the endocie, and a peripheral boxwork of galleries referred to as the perecie (Genise, 2016). The concentrated endocie-perecie morphology is generally restricted the Termitidae (Korb, 2010), the most derived family of Isoptera (Engel and others, 2009). The nest morphology displayed in these ichnofossils is more characteristic of the diffuse arrangement, which is best seen in the ventral view of the block (figure 4C). Termite mounds exhibit a hierarchy of organization, with the smallest components centrally located underground (Korb, 2010). Although the nests presented in this paper are not consistent with the morphology the higher Termitidae, they are likely representative of a termite trace-maker that creates nests in association with a detrital or high-cellulose food source (Genise, 2016).

These trace fossils occur in a key evolutionary interval for termites, as genomic and fossil studies have highlighted the Late Jurassic as a period of radiation for crown Isoptera (Engel and others, 2009; Legendre and others, 2015). The fossil record of insects from the Late Jurassic is poorly sampled, and roaches (Blattodea) are a relatively uncommon component of known faunas (Grimaldi and Engel, 2005). Phylogenetic analyses placed the split between termites and their sister group, the wood-feeding cryptocerid roaches, in the Triassic, with estimates of 241 Ma (Ware and others, 2010) and 228 Ma (Brandl and others, 2007). The understanding of the evolutionary transition of wood-feeding, sub-social cryptocerid roaches (Blattodea) to the eusocial termites (Isoptera) is highly speculative. These trace fossils suggest it is possible that termites had undergone an initial radiation, and lineages representative of the range of life habit, including wood-restricted lineages (lower termites) and ground-nesting lineages (higher termites), had occurred at a minimum by the Late Jurassic.

The presence of the ellipsoid features (figure 5) have intriguing ethological implications. The QEMSCAN results indicate that the ellipsoid features have a silica rind, or outer layer, that are completely silicified (figure 5). It can be ruled out with near certainty that these ellipsoid features (figure 5) were transported to the depositional site, given that there is a paleosol (figure 2) and the rock is dominated by silt-sized grains or smaller. These purple-rind features do not appear to be continuous burrows, as they would be observed continuing through the sequence of slices of UMNH IP 5233 (figure 3). Rather, these features appear to have discrete boundaries (figure 6C). It is possible that these pellets vary in porosity to the groundmass and have thus been preferentially silicified.

Modern termites are observed to incorporate organic matter into their nests in the form of pellets, which can be fecal material mixed with saliva (Sarcinelli and others, 2009). There is an extensive record of fossilized termite coprolites in the published literature beginning in the Early Cretaceous (Colin and others, 2011). These ellipsoid structures (figure 6C) share a resemblance in shape to the pellet structures of modern and fossil termites (Colin and others, 2011), but are notably larger. Average diameter of the ellipsoids reported here is 3.1 mm, whereas termite pellets are in the range of 0.5 to 1 mm in diameter (Colin and others, 2011).

Cosarinsky and others (2005) did not identify pellets in fossil nests in their comparison of modern and fossil termite nest micromorphology. However, these authors did attribute the lack of pellets in reported termite ichnofossils as the result of unfavorable preservation conditions. Some of the silicified particles observed in the petrographic thin sections of UMNH IP 5233 are not fully enclosed ellipsoids, but rather crescent-shaped fragments of ellipsoids (Fig. 5). Cosarinsky and others (2005) attributed similarly shaped structures in modern termite nests as possible cuticle fragments. The current consensus regarding the evolution of termites places the expansion of their ecology from obligate wood feeding to ground nesting in the Late Cretaceous (Engel and others, 2009). Termites were already quite diverse by the mid-Cretaceous (Engel and others, 2009). Though these nests may not be directly attributable to the higher termites (Neoisoptera), they call into question the reported emergence of Neoisoptera in the Late Cretaceous as postulated by molecular phylogenies (Bourguignon and others, 2014). These ichnofossils are within the chronologic range of emergence of Neoisoptera as suggested by fossil-calibrated phylogenies (Ware and others, 2010). Despite their low abundance as indicated by the body fossil record, termites may have expanded into ground-feeding niches by the Late Jurassic.

The findings in this paper illustrate the opportunity for palaeoentomology and ichnology to expand its knowledge of the timing and details of social insect evolution. Future areas of research include investigating the phylogenetic signal in social insect nest morphology and linking body fossil deposits to contemporaneous nest horizons. A promising avenue of future research with social insects is using three-dimensional digital imaging, which can produce quantitative structure models (Varoudis and others, 2018). Three-dimensional imaging has great potential for neoichnological experiments because development of burrow morphology can be visualized and measured in real time, enhancing the understanding of ethology and trace geometry (Himmi and others, 2018).

CONCLUSIONS

In this paper we present new social insect nest ichnogenus and ichnospecies, *Eopolis ekdalei*, from the Brushy Basin Member of the Upper Jurassic Morrison Formation of Utah. At least seven nests are observed at the locality horizon, and they display complex ethology at multiple scales. The organization of anastomosing burrow networks in a diffuse, bulbous arrangement, is consistent with social insect architecture having hierarchical organization. The morphology of these traces does not resemble an ant (Formicidae) trace maker. Also, the body fossil and molecular evidence does not support a Late Jurassic origin for ants. The nests are more morphologically consistent with termites, which have a body fossils record indicating a Jurassic, Gondwanan origin. The large, subterranean nests presented here, if in fact created by termites, suggest it is possible that termites had undergone a transition into soil habitats in seasonally arid climates by the Late Jurassic. Identification and description of contemporaneous social insect trace fossils will shed greater light on the origin of social insects, one of the most ecologically successful groups of organisms on the planet.

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REFERENCES

Badawy, H.S., 2018, Termite nests, rhizoliths and pedotypes of the Oligocene fluviomarine rock sequence in northern Egypt—proxies for Tethyan tropical palaeoclimates: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 492, p. 161–176.

Barden, P., and Grimaldi, D.A., 2016, Adaptive radiation in socially advanced stem-group ants from the Cretaceous: Current Biology, v. 26, no. 4, p. 515–521.

Bell, T.E., 1986, Deposition and diagenesis of the Brushy Basin Member and upper part of the Westwater Canyon Member of the Morrison Formation, San Juan Basin, New Mexico, *in* Turner-Peterson, C.E., Santos, E.S., and Fishman, N.S., editors, A basin analysis case study—the Morrison Formation Grants uranium region: American Association of Petroleum Geologists Studies in Geology 22, p. 77–91.

Bertling, M., Braddy, S.J., Bromley, R.G., Demathieu, G.R., Genise, J., Mikuláš, R., Nielsen, J.K., Nielsen, K.S., Rindsberg, A.K., Schlirf, M., and Uchman, A., 2006, Names for trace fossils—a uniform approach: Lethaia, v. 39, no. 3, p. 265–286.

Bordy, E.M., Bumby, A.J., Catuneanu, O., and Eriksson, P.G., 2004, Advanced Early Jurassic termite (Insecta: Isoptera) nests—evidence from the Clarens Formation in the Tuli Basin, southern Africa: Palaios, v. 19, no. 1, p. 68–78.

Bourguignon, T., Lo, N., Cameron, S.L., Šobotník, J., Hayashi, Y., Shigenobu, S., Watanabe, D., Roisin, Y., Miura, T., and Evans, T.A., 2014, The evolutionary history of termites as inferred from 66 mitochondrial genomes: Molecular Biology and Evolution, v. 32, no. 2, p. 406–421.

Bown, T.M., 1982, Ichnofossils and rhizoliths of the nearshore fluvial Jebel Qatrani Formation (Oligocene), Fayum Province, Egypt: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 40, no. 4, p. 255–309.

Bown, T.M., Hasiotis, S.T., Genise, J.F., Maldonado, F., and Brouwers, E.M., 1997, Trace fossils of Hymenoptera and other insects, and paleoenvironments of the Claron Formation (Paleocene and Eocene), southwestern Utah: U.S. Geological Survey Bulletin 2153, p. 41–58.

Brady, S.G., Larkin, L., and Danforth, B.N., 2009, Bees, ants, and stinging wasps (Aculeata), *in* Hedges, S.B., and Kumar, S., editors, The timetree of life: United Kingdom, Oxford University Press, p. 264–269.

Brady, S.G., Schultz, T.R., Fisher, B.L., and Ward, P.S., 2006, Evaluating alternative hypotheses for the early evolution and diversification of ants: Proceedings of the National Academy of Sciences, v. 103, no. 48, p. 18,172–18,177.

Brandl, R., Hyodo, F., von Korff-Schmising, M., Maekawa, K., Miura, T., Takematsu, Y., Matsumoto, T., Abe, T., Bagine, R., and Kaib, M., 2007, Divergence times in the termite genus *Macrotermes* (Isoptera: Termitidae): Molecular Phylogenetics and Evolution, v. 45, no. 1, p. 239–250.

Bromley, R.G., Buatois, L.A., Genise, J.F., Labandeira, C.C., Mngano, M.G., Melchor, R.N., Schlirf, M. and Uchman, A., 2007, Comments on the paper, Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA—paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses, by Stephen T. Hasiotis: Sedimentary Geology, v. 200, p. 141–150.

Colin, J.P., Néraudeau, D., Nel, A., and Perrichot, V., 2011, Termite coprolites (Insecta: Isoptera) from the Cretaceous of western France—a palaeoecological insight: Revue de Micropaléontologie, v. 54, no. 3, p. 129–139.

Cosarinsky, M.I., Bellosi, E.S., and Genise, J.F., 2005, Micromorphology of modern epigean termite nests and possible termite ichnofossils—a comparative analysis (Isoptera): Sociobiology, v. 45, no. 3, p. 745–778.

Counts, J.W., and Hasiotis, S.T., 2009, Neoichnological experiments with masked chafer beetles (Coleoptera: Scarabaeidae)—implications for backfilled continental trace fossils: Palaios, v. 24, no. 2, p. 74–91.

Crespi, B.J., and Yanega, D., 1995, The definition of eusociality: Behavioral Ecology, v. 6, no. 1, p. 109–115.

Demko, T.M., Currie, B.S., and Nicoll, K.A., 2004, Regional paleoclimatic and stratigraphic implications of paleosols and fluvial/overbank architecture in the Morrison Formation (Upper Jurassic), Western Interior, USA: Sedimentary Geology, v. 167, p. 115–135.

Dickinson, W.R., and Gehrels, G.E., 2008, Sediment delivery to the Cordilleran foreland basin—insights from U-Pb ages of detrital zircons in Upper Jurassic and Cretaceous strata of the Colorado Plateau: American Journal of Science, v. 308, no. 10, p. 1041–1082.

Duringer, P., Schuster, M., Genise, J.F., Likius, A., Mackaye, H.T., Vignaud, P., and Brunet, M., 2006, The first fossil fungus gardens of Isoptera—oldest evidence of symbiotic termite fungiculture (Miocene, Chad basin): Naturwissenschaften, v. 93, no. 12, p. 610–615.

Duringer, P., Schuster, M., Genise, J.F., Mackaye, H.T., Vignaud, P., and Brunet, M., 2007, New termite trace fossils—galleries, nests and fungus combs from the Chad basin of Africa (Upper Miocene–Lower Pliocene): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 251, no. 3–4, p. 323–353.

Engel, M.S., 2008, Two new termites in Baltic amber (Isoptera): Journal of the Kansas Entomological Society, v. 81, no. 3, p. 194–203.

Engel, M.S., Barden, P., Riccio, M.L., and Grimaldi, D.A., 2016, Morphologically specialized termite castes and advanced sociality in the Early Cretaceous: Current Biology, v. 26, no. 4, p. 522–530.

Engel, M.S., and Delclòs, X., 2010, Primitive termites in Cretaceous amber from Spain and Canada (Isoptera): Journal of the Kansas Entomological Society, v. 83, no. 2, p. 111–128.

Engel, M.S., Grimaldi, D.A., and Krishna, K., 2009, Termites (Isoptera)—their phylogeny, classification, and rise to ecological dominance: American Museum Novitates, no. 3650, p. 1–27.

Fewell, J.H., 2003, Social insect networks: Science, v. 301, no. 5641, p. 1867–1870.

Galli, K.G., Buchwaldt, R., Lucas, S.G., and Tanner, L., 2018, New chemical abrasion thermal ionization mass spectrometry dates from the Brushy Basin Member, Morrison Formation, western Colorado—implications for dinosaur evolution: Journal of Geology, v. 126, no. 5, p. 473–486.

Genise, J.F., 2016, Ichnoentomology—insect traces in soils and paleosols: Springer, Topics in Geobiology, v. 37, 689 p.

Genise, J.F., Alonso-Zarza, A.M., Krause, J.M., Sánchez, M.V., Sarzetti, L., Farina, J.L., González, M.G., Cosarinsky, M., and Bellosi, E.S., 2010, Rhizolith balls from the Lower Cretaceous of Patagonia—just roots or the oldest evidence of insect agriculture?: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 287, no. 1–4, p. 128–142.

Genise, J.F., Bellosi, E.S., Melchor, R.N., and Cosarinsky, M.I., 2005, Comment – Advanced Early Jurassic termite (Insecta: Isoptera) nests—evidence from the Clarens Formation in the Tuli Basin, Southern Africa: Palaios, v. 20, no. 3, p. 303–308.

Genise, J.F., and Bown, T.M., 1994, New trace fossils of termites (Insecta: Isoptera) from the late Eocene-early Miocene of Egypt, and the reconstruction of ancient isopteran social behavior: Ichnos: An International Journal of Plant & Animal, v. 3, no. 3, p. 155–183.

Genise, J.F., Mangano, M.G., Buatois, L.A., Laza, J.H., and Verde, M., 2000, Insect trace fossil associations in paleosols—the *Coprinisphaera* ichnofacies: Palaios, v. 15, no. 1, p. 49–64.

Genise, J.F., Melchor, R.N., Bellosi, E.S., González, M.G., and Krause, M., 2007, New insect pupation chambers (Pupichnia) from the Upper Cretaceous of Patagonia, Argentina: Cretaceous Research, v. 28, p. 547–559.

Grimaldi, D., and Engel, M.S., 2005, Evolution of the insects: United Kingdom, Cambridge University Press, 755 p.

Guimarães, I.D.C., Pereira, M.C., Batista, N.R., Rodrigues, C.A.P., and Antonialli-Junior, W.F., 2018, The complex nest architecture of the Ponerinae ant Odontomachus chelifer: PLOS One, v. 13, no. 1, p. e0189896.

Hasiotis, S.T., 2002, Continental trace fossils: Society for Sedimentary Geology (SEPM) Short Course Notes, no. 51, 134 p.

Hasiotis, S.T., 2003, Complex ichnofossils of solitary and social soil organisms—understanding their evolution and roles in terrestrial paleoecosystems: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 192, no. 1–4, p. 259–320.

Hasiotis, S.T., 2004, Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain region, USA—paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses: Sedimentary Geology, v. 167, no. 3–4, p. 177–268.

Hasiotis, S.T., 2007, Continental ichnology—fundamental processes and controls on trace fossil distribution, *in* Miller, W., III, editor, Trace fossils—concepts, problems, prospects: Amsterdam, The Netherlands, Elsevier, p. 268–284.

Hasiotis, S.T., and Dubiel, R.F., 1995, Termite (Insecta: Isoptera) nest ichnofossils from the Upper Triassic Chinle Formation, Petrified Forest National Park, Arizona: Ichnos, v. 4, p. 119–130.

Himmi, S.K., Yoshimura, T., Yanase, Y., Torigoe, T., Akada, M., Ikeda, M., and Imazu, S., 2018, Volume visualization of hidden gallery system of drywood termite using computed tomography—a new approach on monitoring of termite infestation, *in* McLellan, B., editor, Sustainable future for human security—society, cities, and governance: Singapore, Springer Nature, p. 61–68.

Inward, D., Beccaloni, G., and Eggleton, P., 2007, Death of an order—a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches: Biology Letters, v. 3, no. 3, p. 331–335.

Johnson, B.R., Borowiec, M.L., Chiu, J.C., Lee, E.K., Atallah, J., and Ward, P.S., 2013, Phylogenomics resolves evolutionary relationships among ants, bees, and wasps: Current Biology, v. 23, no. 20, p. 2058–2062.

Korb, J., 2010, Termite mound architecture, from function to construction, *in* Bignell, D.E., Roisin, Y., and Lo, N., editors, Biology of termites—a modern synthesis: Dordrecht, The Netherlands, Springer, p. 349–373.

Kowallis, B.J., Britt, B.B., Greenhalgh, B.W., and Sprinkel, D.A., 2007, New U-Pb zircon ages from an ash bed in the Brushy Basin Member of the Morrison Formation near Hanksville, Utah, *in* Willis, G.C., Hylland, M.D., Clark, D.L., and Chidsey, T.C., Jr., editors, Central Utah—diverse geology of a dynamic landscap: Utah Geological Association Publication 36, p. 75–80.

Krishna, K., Grimaldi, D.A., Krishna, V., and Engel, M.S., 2013, Treatise on the Isoptera of the world: Bulletin of the American Museum of Natural History, no. 377, p. 1–200.

La Polla, J.S., Dlussky, G.M., Perrichot, V., 2013, Ants and the fossil record: Annual Review of Entomology, v. 58, no. 1, p. 609–630.

Legendre, F., Nel, A., Svenson, G.J., Robillard, T., Pellens, R., and Grandcolas, P., 2015, Phylogeny of Dictyoptera—dating the origin of cockroaches, praying mantises and termites with molecular data and controlled fossil evidence: PLOS One, v. 10, no. 7, p. e0130127.

Mikheyev, A.S., and Tschinkel, W.R., 2004, Nest architecture of the ant Formica pallidefulva—structure, costs and rules of excavation: Insectes Sociaux, v. 51, no. 1, p. 30–36.

Moreau, C.S., Bell, C.D., Vila, R., Archibald, S.B., and Pierce, N.E., 2006, Phylogeny of the ants—diversification in the age of angiosperms: Science, v. 312, no. 5770, p. 101–104.

Nkem, J.N., de Bruyn, L.L., Grant, C.D., and Hulugalle, N.R., 2000, The impact of ant bioturbation and foraging activities on surrounding soil properties: Pedobiologia, v. 44, no. 5, p. 609–621.

Ocko, S.A., Heyde, A., and Mahadevan, L., 2019, Morphogenesis of termite mounds: Proceedings of the National Academy of Sciences, v. 116, no. 9, p. 3379–3384.

Owen, R.A., Owen, R.B., Renaut, R.W., Scott, J.J., Jones, B., and Ashley, G.M., 2008, Mineralogy and origin of rhizoliths on the margins of saline, alkaline Lake Bogoria, Kenya Rift Valley: Sedimentary Geology, v. 203, no. 1–2, p. 143–163.

Parrish, J.T., Peterson, F., and Turner, C.E., 2004. Jurassic "savannah"—plant taphonomy and climate of the Morrison Formation (Upper Jurassic, Western USA): Sedimentary Geology, v. 167, no. 3–4, p. 137–162.

Perna, A., and Theraulaz, G., 2017, When social behaviour is moulded in clay—on growth and form of social insect nests: Journal of Experimental Biology, v. 220, no. 1, p. 83–91.

Perrichot, V., Lacau, S., Néraudeau, D., and Nel, A., 2008, Fossil evidence for the early ant evolution: Naturwissenschaften, v. 95, no. 2, p. 85.

Peters, R.S., Krogmann, L., Mayer, C., Donath, A., Gunkel, S., Meusemann, K., Kozlov, A., Podsiadlowski, L., Petersen, M., Lanfear, R., and Diez, P.A., 2017, Evolutionary history of the Hymenoptera: Current Biology, v. 27, no. 7, p. 1013–1018.

Rasnitsyn, A.P., and Martínez-Delclòs, X., 2000, Wasps (Insecta: Vespida = Hymenoptera) from the Early Cretaceous of Spain: Acta Geologica Hispanica, v. 35, no. 1, p. 65–96.

Ratcliffe, B.C., and Fagerstrom, J.A., 1980, Invertebrate lebensspuren of Holocene floodplains—their morphology, origin and paleoecological significance: Journal of Paleontology, v.

54, no. 3, p. 614–630.

Roberts, E.M., Todd, C.N., Aanen, D.K., Nobre, T., Hilbert-Wolf, H.L., O'Connor, P.M., Tapanila, L., Mtelela, C., and Stevens, N.J., 2016, Oligocene termite nests with in situ fungus gardens from the Rukwa Rift Basin, Tanzania—support a Paleogene African origin for insect agriculture: PLOS One, v. 11, no. 6, p. e0156847.

Roberts, E.M., and Tapanila, L., 2006, A new social insect nest from the Upper Cretaceous Kaiparowits Formation of southern Utah: Journal of Paleontology, v. 80, no. 4, p. 768–774.

Sable, V.H., 1955, Photogeologic map of the Tidwell-1 quadrangle, Grand County, Utah: U.S. Geological Survey Miscellaneous Geologic Investigations Map I–87, 1 plate, scale 1:24,000.

Sarcinelli, T.S., Schaefer, C.E.G., de Souza Lynch, L., Arato, H.D., Viana, J.H.M., de Albuquerque Filho, M.R., and Gonçalves, T.T., 2009, Chemical, physical and micromorphological properties of termite mounds and adjacent soils along a toposequence in Zona da Mata, Minas Gerais State, Brazil: Catena, v. 76, no. 2, p. 107–113.

Smith, J.J., and Hasiotis, S.T., 2008, Traces and burrowing behaviors of the cicada nymph Cicadetta calliope—neoichnology and paleoecological significance of extant soil-dwelling insects: Palaios, v. 23, no. 8, p. 503–513.

Smith, J.J., Platt, B.F., Ludvigson, G.A., and Thomasson, J.R., 2011, Ant-nest ichnofossils in honeycomb calcretes, Neogene Ogallala Formation, High Plains region of western Kansas, USA: Palaeogeography, Palaeoclimatology, Palaeoecology: v. 308, no. 3–4, p. 383–394.

Theraulaz, G., and Bonabeau, E., 1999, A brief history of stigmergy: Artificial Life, v. 5, no. 2, p. 97–116.

Theraulaz, G., Bonabeau, E., and Deneubourg, J.L., 1998, The origin of nest complexity in social insects: Complexity, v. 3, no. 6, p. 15–25.

Trujillo, K.C., Foster, J.R., Hunt-Foster, R.K., and Chamberlain, K.R., 2014, A U/Pb age for the Mygatt-Moore Quarry, Upper Jurassic Morrison Formation, Mesa County, Colorado: Volumina Jurassica, v. 12, no. 2, p. 107–114.

Trujillo, K.C., and Kowallis, B.J., 2015, Recalibrated legacy ^{40}Ar/^{39}Ar ages for the Upper Jurassic Morrison Formation, Western Interior, U.S.A.: Geology of the Intermountain West, v. 2, p. 1–8.

Tschinkel, W.R., 2004, The nest architecture of the Florida harvester ant, *Pogonomyrmex badius*: Journal of Insect Science, v. 4, no. 1, p. 21.

Tschinkel, W.R., 2015, The architecture of subterranean ant nests—beauty and mystery underfoot: Journal of Bioeconomics, v. 17, no. 3, p. 271–291.

Turner, C.E., and Peterson, F., 2004, Reconstruction of the Upper Jurassic Morrison Formation extinct ecosystem—a synthesis: Sedimentary Geology, v. 167, no. 3–4, p. 309–355.

Van Veleen, M., 2009, Group selection, kin selection, altruism, and cooperation—when inclusive fitness is right and when it can be wrong: Journal of Theoretical Biology, v. 259, p. 589–600.

Varoudis, T., Swenson, A.G., Kirkton, S.D., and Waters, J.S., 2018, Exploring nest structures of acorn dwelling ants with X-ray microtomography and surface-based three-dimensional visibility graph analysis: Philosophical Transactions of the Royal Society B, v. 373:20170237, p. 1–10, http://doi.org/10.1098/rstb.2017.0237.

Ward, P.S., 2007, Phylogeny, classification, and species-level taxonomy of ants (Hymenoptera: Formicidae): Zootaxa, v. 1668, p. 549–563.

Ware, J.L., Grimaldi, D.A., and Engel, M.S., 2010, The effects of fossil placement and calibration on divergence times and rates—an example from the termites (Insecta: Isoptera): Arthropod Structure and Development, v. 39, no. 2–3, p. 204–219.

Wilson, E.O., 1971, The insect societies: Cambridge, Massachusetts, Harvard University Press, 548 p.

Xing, L., Roberts, E.M., Harris, J.D., Gingras, M.K., Ran, H., Zhang, J., Xu, X., Burns, M.E., and Dong, Z., 2013, Novel insect traces on a dinosaur skeleton from the Lower Jurassic Lufeng Formation of China: Palaeogeography, Palaeoclimatology, Palaeoecology. v. 388, p. 58–68.