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Microtomography of an enigmatic fossil egg clutch from the Oligocene John Day Formation, Oregon, USA, reveals an exquisitely preserved 29-million-year-old fossil grasshopper ootheca

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ABSTRACT

Eggs are one of the least understood life stages of insects, and are poorly represented in the fossil record. Using microtomography, we studied an enigmatic fossil egg clutch of a presumed entomological affinity from the Oligocene Turtle Cove Member, John Day Formation, from the National Park Service-administered lands of John Day Fossil Beds National Monument, Oregon. A highly organized egg mass comprising a large clutch size of approximately 50 slightly curved ellipsoidal eggs arranged radially in several planes is preserved, enclosed in a disc-shaped layer of cemented and compacted soil particles. Based on the morphology of the overall structure and the eggs, we conclude that the specimen represents a fossilized underground ootheca of the grasshoppers and locusts (Orthoptera: Caelifera), also known as an egg pod. This likely represents the oldest and the first unambiguous fossil evidence of a grasshopper egg pod. We describe *Subterroothecichnus radialis* igen. et isp. nov. and *Curvellipsoentomoolithus laddi* oogen. et oosp. nov., representing the egg pod and the eggs, respectively. We advocate for adopting ootaxonomy in studying fossil eggs of entomological affinities, as widely practiced with fossil amniotic eggs. An additional 26 individual and clustered *C. laddi* collected throughout the A–H subunits of the Turtle Cove Member suggest the stable presence of grasshoppers in the Turtle Cove fauna, and we discuss the paleoecological implications. Oothecae have convergently evolved several times in several insect groups; this ovipositional strategy likely contributed to the fossilization of this lesser-known ontogenetic stage, enriching our understanding of past insect life.

Abbreviations. In this paper, "JODA" is used both as an abbreviation for John Day Fossil Beds National Monument (per National Park Service convention) and as the repository prefix code for museum specimen identifying numbers (per National Park Service policy). "JDNM" is the locality number identifier for John Day Fossil Beds National Monument.

INTRODUCTION

Insects are one of the most successful groups of eukaryotes, representing more than half of all described eukaryotic species, and estimates suggest 5.5 million species of insects exist (Stork et al. 2015; Stork 2018). Several life history traits, including evolution of flight and holometaboly, have greatly impacted the evolutionary success of insects (Misof et al. 2014; Truman 2019). Eggs, the first stage of the insect life cycle, are immobile, and thus cannot actively escape from unfavorable environmental or predation risks, unlike insects in their subsequent mobile stages. Nonetheless, an array of protective strategies exists against biotic and abiotic stresses, including temperature, drought,

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exposure to ultraviolet radiation, predation, pathogens, and parasitoids (Jacobs et al. 2013; Winters et al. 2014; Abram et al. 2015; Eisner et al. 2020; Hilker et al. 2023).

Ovipositional strategies, such as site, clutch size, clutch interval, egg size, and phenology, are crucial to reproductive success and survival and fitness of the offspring. Insects lay eggs individually or in groups, and oviposition in clusters is commonly found in various insect taxa. Advantages to oviposition in clusters include protection from predators and/or environmental conditions, and more efficient resource use (Young 1983; Prokopy and Roitberg 2001; Desurmont and Weston 2011). Several groups of insects produce an additional hardened layer surrounding the egg clusters known as an ootheca, egg capsule, egg pod, egg sac, or egg case (Du et al. 2022). This concentrated and protected form of oviposition may protect eggs from desiccation, predators, and parasitoids (Fatouros et al. 2020). The majority of oothecae-producing taxa are members of the Polyneoptera, particularly the Dictyoptera (mantids and cockroaches) and the Orthoptera (grasshoppers and crickets; Du et al. 2022), as well as the Mantophasmatodea (Roth et al. 2014) and a stick insect (Goldberg et al. 2015), but examples are also found in the cassidine tortoise beetles (Chrysomelidae; Hinton 1981; Flowers and Chaboo 2015) and, in addition, include a lanternfly (Malek et al. 2019). Among the termites—the once distinct order Isoptera but now understood to be eusocial cockroaches—ootheca production is lost in most taxa but retained in the earliest diverging monotypic family, Mastotermitidae (Courrent et al. 2008). Grasshoppers and locusts (Orthoptera: Caelifera) produce hardened subterranean egg pods (Chapman and Robertson 1958; Chernyakhovskii 2006; Sultana et al. 2020; Du et al. 2022). According to Du et al. (2022), morphology of orthopteran oothecae/egg pods differs from dictyopteran oothecae, and among the two suborders of Orthoptera, egg pods are found in the suborder Caelifera but unknown from Ensifera (crickets and katydids). Both dictyopteran and caeliferan oothecae are made of various oothecal structural proteins that become sclerotized and melanized, forming a hardened or leathery protective layer (Du et al. 2022).

The insect fossil record is heavily influenced by taphonomy and various ecological factors. Mobility—especially the ability to fly—greatly enhances the likelihood of fossilization. For instance, fossils of ecologically abundant flightless hexapods, such as immature terrestrial nymphs and larvae, worker ants, and apterygote hexapods, are scarcely represented in the sedimentary rocks but are relatively common in ambers (Rasnitsyn 2002). Sometimes both adults and immature nymphs/larvae of a wide variety of insects are preserved in fine-grained sedimentary rocks, such as the paper shales of the Eocene Florissant Formation at Florissant Fossil Beds National Monument in Colorado (Meyer 2003: 258). Non-mobile stages, such as eggs and pupae, are relatively poorly represented in the fossil record. Few fossils exist of insect eggs preserved in sedimentary rocks (Gall and Tiffney 1983; Sellick 1994; Heřmanová and Kvaček 2010; Heřmanová et al. 2013; Fisher and Watson 2015), although a much more extensive trace fossil record exists from endo-or exophytic oviposition preserved with fossil plants (van Konijnenburg-van Cittert and Schmeißner 1999; Krassilov et al. 2007; Laaß and Hauschke 2019; Meng et al. 2019; Romero-Lebrón et al. 2022), with the earliest record extended back to the Pennsylvanian (323.2–298.9 Ma; Laaß and Hauschke 2019). Fossil oothecae are also known (Anisyutkin et al. 2008; Poinar 2010; Hörnig et al. 2013; Gao et al. 2019; Li and Huang 2019; Cariglino et al. 2020), and there are rare examples of eggs preserved inside an adult female (Huang et al. 2008) or on the surface of an adult body representing brood care (e.g., Wang et al. 2015; Fu et al. 2022).

Here we describe an enigmatic fossil insect egg clutch (JODA 17384) from the Turtle Cove Member of the Oligocene John Day Formation, from John Day Fossil Beds National Monument (JODA), which is administered by the National Park Service (NPS). The exposed surface of the specimen shows 28 slightly curved ellipsoidal eggs that are 4.48–4.65 mm long and 1.63–1.84 mm wide. The eggs are radially arranged within a hemilenticular, green zeolitized sandy

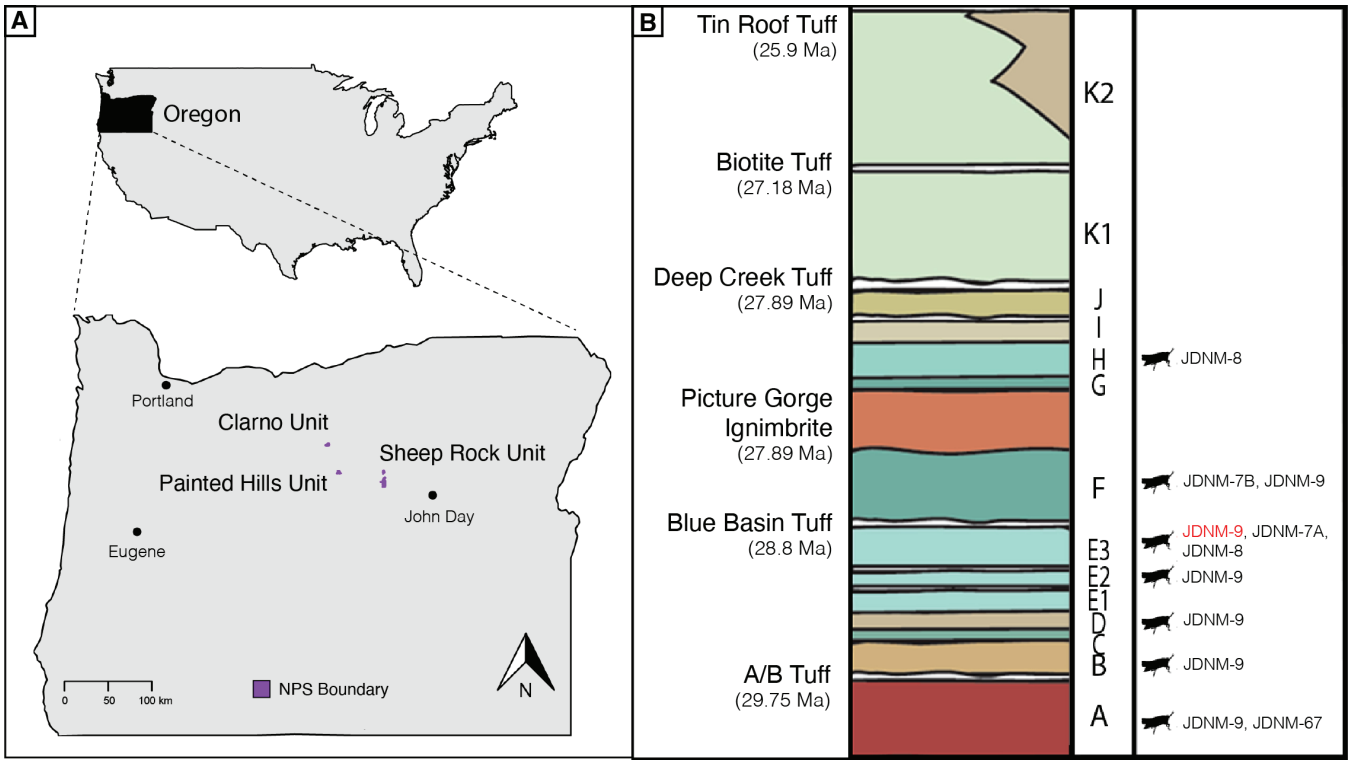
claystone that macroscopically differs from the surrounding sedimentary matrix. Twenty-six additional specimens of individual and clustered eggs of the same morphology have been collected throughout the A–H informal units of the Turtle Cove Member. To better understand the structure embedded within the matrix, we studied JODA 17384 and two additional specimens (JODA 8754 and JODA 14423) in further detail using microtomography.

GEOLOGIC SETTING

The John Day Basin of central and eastern Oregon preserves remarkably complete and well-dated terrestrial sedimentary sequences from the middle Eocene to upper Miocene (ca. 47–7 Ma), divided into the middle Eocene Clarno Formation; the upper Eocene to lower Miocene John Day Formation; the lower–middle Miocene Picture Gorge Basalts, Dayville Basalts, and Camas Creek Member of the Monument Mountain Basalt (part of the Columbia River Basalt Group); the middle–upper Miocene Mascall Formation; and the upper Miocene Rattlesnake Formation, in successive order (Waters 1961; Bailey 1989; Albright et al. 2008; Dillhoff et al. 2009). The John Day Formation (39–18 Ma; Albright et al. 2008) is distributed across eastern and central Oregon and is currently subdivided into seven members: Big Basin, Turtle Cove, Kimberly, Haystack Valley, Balm Creek, Johnson Canyon, and Rose Creek (Retallack et al. 1999; Hunt and Stepleton 2004; Albright et al. 2008). The John Day Formation consists of volcaniclastic sedimentary rocks and airfall tuffs, deposited in a backarc landscape of low hills and interspersed lakes, that was covered periodically by voluminous ashfalls from the Western Cascades (Robinson et al. 1984; Albright et al. 2008; Dillhoff et al. 2009; McClaughry et al. 2009).

The specimens described in this study are from the Turtle Cove Member (31.45–26.6 Ma; Figure 1). The Turtle Cove Member consists of about 400 m of section that Albright et al. (2008) divided into 14 lithostratigraphic subunits (A–K2) with 10 recently dated or re-dated tuffs. These subunits are sandy to silty claystone with some layers zeolitized (green), and others non-zeolitized (Albright et al. 2008). Paleosols have been identified in the lower Turtle Cove Member (Retallack and Samuels 2020). Specifically, deep calcic (Xaxus and Yapas) and shallow calcic (Xaxuspa and Yapaspa) pedotypes, formerly vitrand soils (grass-shard-rich andisols), have been identified (Retallack and Samuels

FIGURE 1. Locality map and the composite stratigraphy of the Turtle Cove Member, John Day Formation. (A) Locality map showing the NPS boundaries of the three units of John Day Fossil Beds National Monument, Oregon. (B) Composite stratigraphy of the Turtle Cove Member. Black caeliferan silhouettes indicate horizons with the egg fossils. Locality numbers are indicated to the right of the silhouette. Red lettering indicates type locality and horizon. Dated tuffs are indicated to the left of the section. Color of layers indicates approximate color of the horizon in the field. Section courtesy of NPS and based on Albright et al. (2008) and Fremd (2010). PhyloPic image available for reuse under the Universal (CC0 1.0) Public Domain Dedication license, https://creativecommons.org/publicdomain/zero/1.0/.



2020). These paleosols suggest a wooded grassland environment with bunch grasses (Retallack 2004). The Turtle Cove Member contains several dated tuffs and the Picture Gorge ignimbrite (PGI), a super-volcanic event related to the Yellowstone Hotspot (Seligman et al. 2014). The PGI is between subunits F and G. The Turtle Cove fauna is assigned to the Whitneyan (Wh2) and Arikareean (Ar1 and Ar2) North American Land Mammal Ages.

METHODS

Specimens were all surface-collected from outcrops of the Turtle Cove Member of the John Day Formation through inventory and monitoring practices of JODA originally established in the 1980s and continued to the present (Kort and Famoso 2020). Many isolated specimens were likely separated from egg clusters through erosion of the bedrock. Specimens studied herein have been collected between 1996 and 2021, and the holotype specimen (JODA 17384) was collected in July 2012.

Microcomputed tomography (microtomography)

Specimens were carefully packaged within cylindrical containers using low-radiodensity packing materials to stabilize. Containers were mounted on autoloader sample holders for scanning with a Zeiss Xradia 620 Versa X-ray Microscope (Carl Zeiss X-ray Microscopy, Dublin, California, USA). All scans were performed with the 0.4X objective. Source and detector positions were independently set for each sample for maximizing voxel size while retaining reasonable scan times to achieve good image quality, as assessed by intensity and transmission outputs during scan setup. Scan parameters determined for each sample are summarized in Table 1. Resulting image datasets were reviewed, representative 2D slice and 3D rendering images captured, and full image datasets converted to dicom format with Dragonfly Pro (Object Research Systems, Montreal, Canada).

Data visualization

The resulting dicom files were visualized using 3D Slicer v. 5.0.3 (https://www.slicer.org/). The segmentation was done on the resulting tomography of JODA 17384 to better understand the internal structure using the Segment Editor module (Pinter et al. 2019). In addition to the eggs, three distinctive zones are recognized from microtomography: the matrix in which the eggs are embedded, the bow-shaped layer surrounding the egg mass (Figure 2D–F, white arrows), and the surrounding sandy matrix. The bow-shaped layer has greater compaction/cementation compared to the other two. In addition, multiple cracks can be seen around the layer (Figure 3), suggesting differences in density between adjacent matrices. Therefore, we focused on the eggs and the bow-shaped layer surrounding the egg mass. Threshold was adjusted to separate the egg pod and the eggs preserved inside from the surrounding matrix; many sediment particles that had density similar to that of the structures of interest were manually erased. Due to the eggs being embedded in the green claystone, the manual segmentation was done to a level that did not erase the eggshell.

Repository information

All specimens herein are reposited at John Day Fossil Beds National Monument, Kimberly, OR, 97848, USA.

RESULTS

The raw microCT data for the following specimens are available on MorphoSource: JODA 17384 (https://doi.org/10.17602/M2/M517891), JODA 8754 (https://doi.org/10.17602/M2/M527567), and JODA 14423 (https://doi.org/10.17602/M2/M527767). The 3D mesh created for JODA 17384 is also available on MorphoSource (https://doi.org/10.17602/M2/M532603).

TABLE 1. Microtomography parameters for Zeiss Xradia 620 Versa scans of three separate specimens: A well-preserved egg clutch (JODA 17384), a partial egg cluster (JODA 8754), and three isolated eggs (JODA 14423).

Sample	kV	W	Filter	Exposure (s)	Voxel size (µm)	Field of View diameter (mm)	Binning	Projections	Scan time
JODA 17384	80	10	LE6	5	30.274	31.0	2	2401	4h 59m
JODA 8754	70	8.5	LE4	2	12.796	13.1	2	2401	2h 19m
JODA 14423	40	3	LE1	6	7.2688	14.9	1	2401	5h 41m

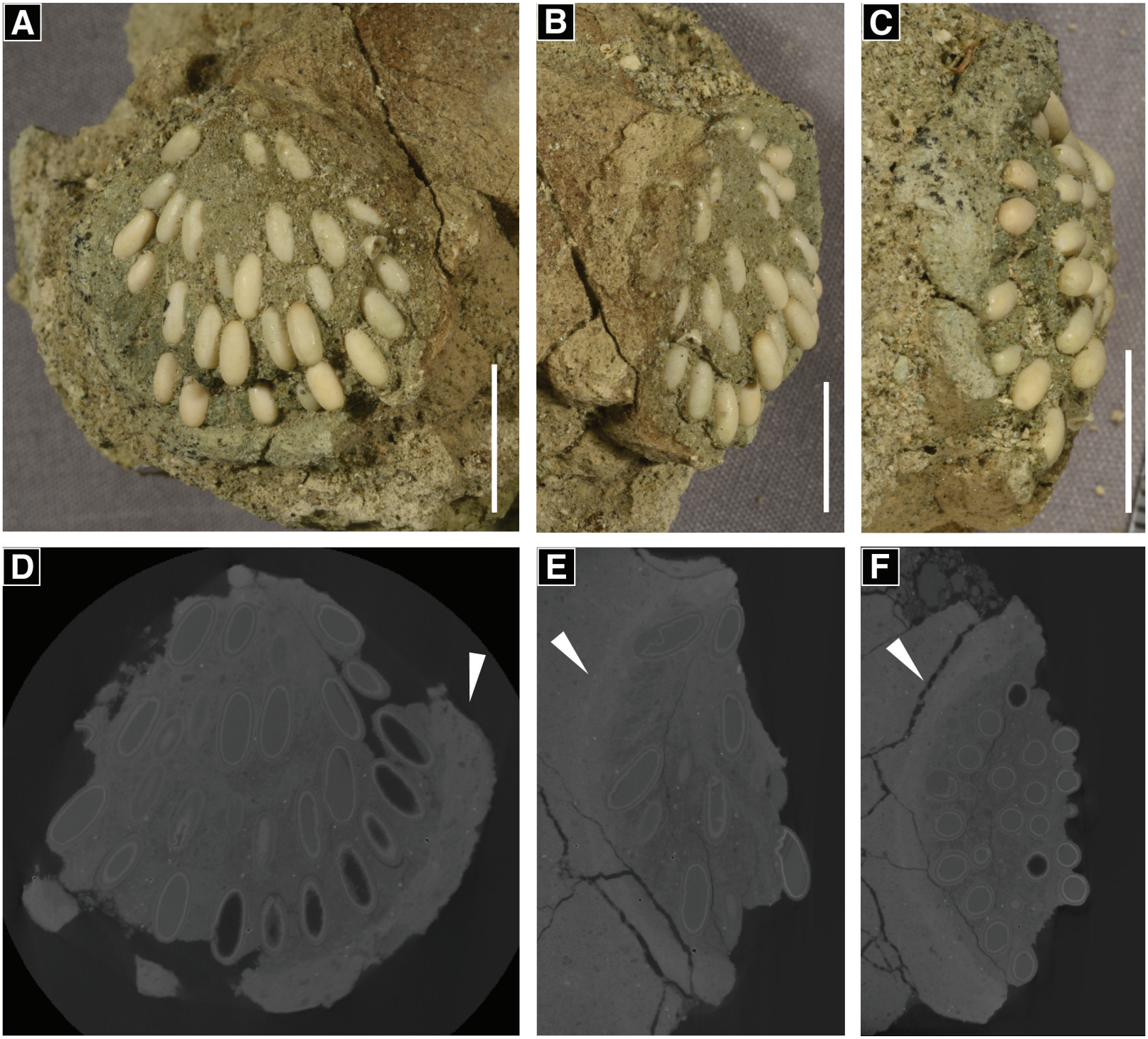


FIGURE 2. Macroscopic and microtomograph images of the holotype specimen (JODA 17384) of *Subterroothecichnus radialis* igen. et isp. nov., and *Curvellipsoentomoolithus laddi* oogen. et oosp. nov. from the Turtle Cove Member, John Day Formation, Oregon, USA, preserving a caeliferan subterranean ootheca/egg pod and the eggs within it. (A–C) Macroscopic image of the exposed portion of the ootheca. (D–F) Microtomography images of the same specimen. White arrows indicate the more cemented ootheca wall. From left to right: X-Y, Y-Z, and X-Z planar view, respectively. Scale bar is 1 cm.

JODA 17384 comprises a hemilenticular layer preserved as green zeolitized sandy claystone that is macroscopically distinguished from the surrounding sedimentary matrix, and approximately 28 slightly curved eggs embedded within this layer in a radial arrangement on the exposed surface (Figure 2A–C). Microtomography revealed in total approximately 50 eggs laid in four or five planes, in a radial arrangement within each plane in four or five concentric arcs (central angle of approximately 100–115°; Figure 3A). The 3D segmentation shows that the more cemented bow-shaped layer, identified from individual cross-sectional images, continuously surrounds the egg mass, forming a disc-shape layer consisting of more cemented soil particles. The resulting segmentation of the specimen also shows that

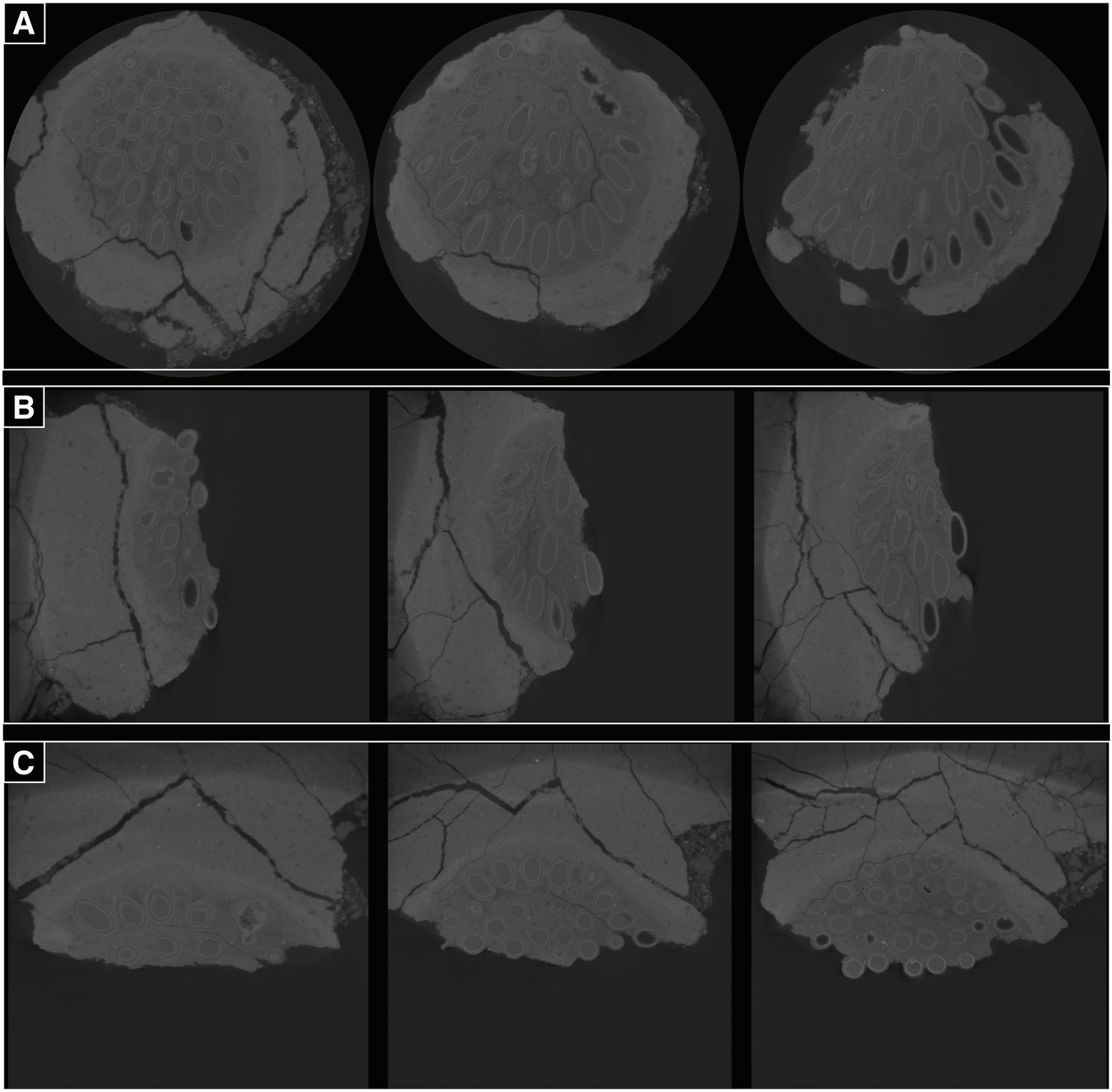


FIGURE 3. Microtomography of JODA 17384 showing the structure of *Subterroothecichnus radialis* isp. nov. and the arrangement of *Curvellipsoentomoolithus laddi* oosp. nov. from the three perpendicularly crossing planes. (A) X-Y cross-section, left to right moving from closer to farther from the pod wall. (B) Y-Z cross-section, left to right laterally through the pod, displaying eggs tending to the slope of the pod wall at approximately 45°. (C) X-Z cross section, left to right moving from anterior to posterior end of the pod.

the disc-shaped structure apically transitions into a thick and short cylindrical area (Figure 4E, white arrow). Based on an extensive morphological comparison between the studied specimens and oothecae, as well as eggs of extant insects, we interpreted that the specimen represents a fossilized subterranean ootheca, commonly known as the

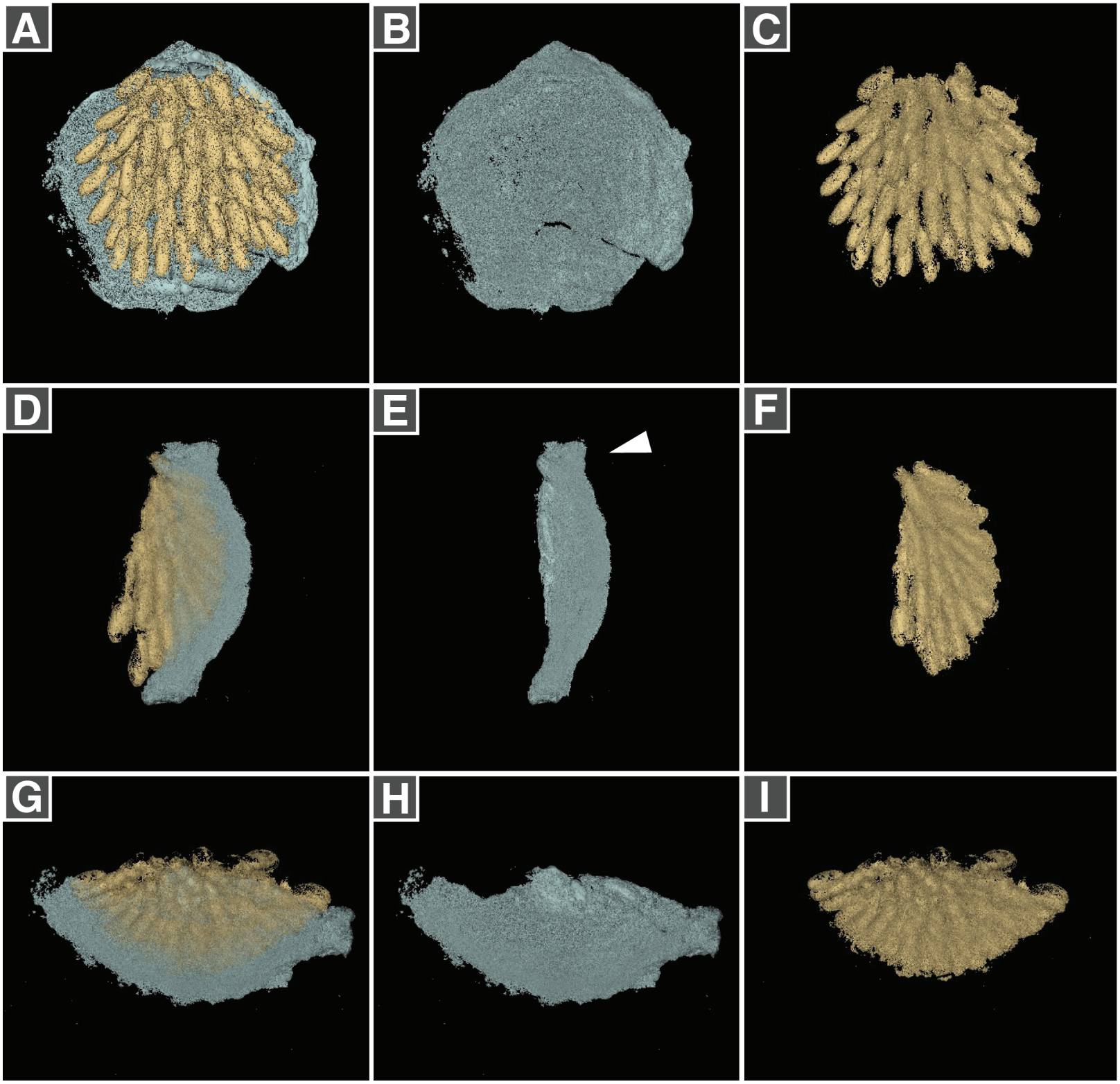


FIGURE 4. 3D segmentation of the microtomography of JODA 17384, revealing the structural arrangement of *Curvellipsoentomoolithus laddi* oosp. nov. within the ootheca *Subterroothecichnus radialis* isp. nov. Left, middle, and right columns show the egg pod, pod wall, and egg mass, respectively. (A–C) X-Y planar view of the specimen. (D–F) Y-Z planar view of the specimen. (G–I) X-Z planar view of the specimen, viewed from the posterior end.

egg pod, of the kind produced by grasshopper and locusts (Orthoptera: Caelifera). The more cemented disc-shaped layer represents the oothecal wall, the product of mixing of the female oothecal secretion with the surrounding soil particles, which subsequently became hardened, and the apical cylindrical transitional area is the preserved basal parts of the plug, which is a frothy oothecal secretion filling the cylindrical ovipositor trace above the egg mass

(Chapman and Robertson 1958). We followed Chapman and Robertson's (1958) descriptive terminology of the ootheca/egg pod , and Church et al.'s (2019a, 2019b) of the eggs.

Systematic paleontology

A systematic approach to fossil insect eggs is challenging due to the infinitesimal likelihood of affiliating eggs with specific parent insect species, with the rare exceptions where eggs are preserved with the imago—inside the female abdomen, during oviposition, or through parental brooding (e.g., Hörnig et al. 2013; Wang et al. 2015; Chen 2022; Chen and Xu 2022; Fu et al. 2022). In some cases, certain morphological characters of the preserved eggs can suggest their systematic affinities (e.g., Gall and Tiffney 1983; Sellick 1994), but these characteristics seldom allow generic or specific identification. Fisher and Watson (2015) compared the problem of the systematics of the fossil insect eggs to the organ- and morphotaxa of fossil plants and some animal fossils, such as conodont elements. However, organ- and morphotaxa represent different parts of the same organisms, whereas eggs represent a different life history stage, and morphotaxa have a greater chance of being correlated to different organ taxa by finding organically articulated fossils or using epidermal morphology, at least in fossil plants. A more comparable system would be the fossilized eggs of other animals—which are systematically studied and described using ootaxonomy—a parataxonomic system for describing fossilized amniotic eggs (Mikhailov et al. 1996). We advocate for applying ootaxonomy to studying fossilized eggs of entomological affinities to allow more systematic approach in making comparisons across a broader spatial and temporal scale and correlating certain taxonomic affinities (see Discussion, below). Additionally, JODA 17384 not only preserves fossilized insect eggs but also the subterranean ootheca/egg pod as well, which is a trace fossil. Therefore, we described JODA 17384 and other materials using two parataxonomic systems—ichnotaxonomy and ootaxonomy—and suggest its caeliferan affinity (Orthoptera) based on the combined ichnological and oological evidence.

Entomoothecichnidae ifam. nov. Lee, Famoso, and Lin

Diagnosis. The new ichnofamily is proposed for fossilized insect oothecae, also referred to as egg cases, egg pods, egg sacs, and egg capsules.

Remarks. Two ichnogenera, *Oothecichnus* Anisyutkin et Rasnitsyn 2008 and *Blattoothecichnus* Hinkelman 2019, have been erected to accommodate the dictyopteran (roachioid) and more specifically blattodean oothecae, respectively (Anisyutkin et al. 2008; Hinkelman 2019). Neither ichnogenus is appropriate for the subterranean ootheca described herein (see below), thus the erection of a new fossil ootheca ichnogenus was needed. The diversity and number of described fossil insect ootheca have increased dramatically in the past two decades. For a better systematic approach, we propose the new ichnofamily Entomoothecichnidae, and that the two previously described ichnogenera and the *Subterroothecichnus* igen. nov. be placed under the new ichnofamily. The ichnofamily is designated for fossil insect oothecae, and does not include other protective structures produced by various invertebrates and vertebrates, such as gastropods, cephalopods, and cartilaginous fishes, that are commonly referred to as *oothecae, egg cases, egg sacs,* and *egg capsules.*

Subterroothecichnus igen. nov. Lee, Famoso, and Lin

Diagnosis. The new ichnogenus is proposed for fossil subterranean oothecae, also referred to as *egg pods,* that incorporate surrounding soil particles into the ootheca wall by mixing with oothecal secretion during their production.

Etymology. The genus name is a combination of *subterra* (Latin for underground), *ootheca* (Greek

for eggcase), and *ichnos* (Greek for trace), referring to the subterranean ootheca, also known as egg pods.

Comparisons and Remarks. *Oothecichnus* Anisyutkin et Rasnitsyn 2008 was erected for fossil oothecae of roachioid insects, particularly of cockroaches and mantids (Anisyutkin et al. 2008). A few species of *Oothecichnus* have been described, including the Late Triassic *O. pensilis* and *O. duraznensis* from Argentina (Cariglino et al. 2020), and Late Cretaceous *O. negevianus* from Israel (Anisyutkin et al. 2008). A separate ichnogenus *Blattoothecichnus* Hinkelman 2019 was erected more specifically for fossilized blattodean oothecae (Hinkelman 2019). There are several other unnamed fossil oothecae described as well (see Cariglino et al. 2020), all of which have dictyopteran affinities. Dictyopteran oothecae are characterized by an aligned arrangement of eggs and not having external particles incorporated into the structure (Li and Huang 2019; Cariglino et al. 2020), which differs from caeliferan oothecae and the specimen described herein. Thus, we propose a new ichnogenus *Subterroothecichnus* for subterranean fossil oothecae/egg pods that incorporate surrounding soil particles into their ootheca wall during their production as they mix with the oothecal secretion.

Type species. *Subterroothecichnus radialis* isp. nov.

Subterroothecichnus radialis isp. nov. Lee, Famoso, and Lin

Holotype. Specimen JODA 17384 (Figures 2–4).

Type locality. JDNM-9, Blue Basin, Sheep Rock Unit, John Day Fossil Beds National Monument, Grant County, Oregon, USA. Precise locality data available from the repository for qualified researchers on request.

Type horizon. Likely from a slump of unit E3 over E2 informal subunits of the Turtle Cove Member, John Day Formation (Oligocene). Specimen is stratigraphically below the Blue Basin Tuff (28.8 Ma) and above the A/B Tuff (29.75 Ma).

Diagnosis. Overall ootheca disc-shaped. Ootheca wall consisting of cemented soil particles; the portion of the ootheca surrounding the egg mass circularly lenticular to oblately spheroidal; ootheca wall apically transitioning into a cylindrical plug, which may be preserved in various lengths or completely absent; ootheca wall thicker at the anterior and posterior end of the pod. Eggs, when preserved, are ellipsoidal with slight curvature and arranged in several planes, in a radial arrangement within each plane in concentric arcs (Figure 4). Eggs tending to the egg pod wall at an angle of approximately 45°.

Etymology. The specific epithet *radialis* refers to the radial arrangement of the eggs within the ootheca.

Other materials studied. From JDNM-9, Blue Basin, Turtle Cove Member unit B, JODA 4777—unit E2, JODA 8754—unit E3, JODA 14423.

Descriptions. The ootheca wall is 1.4–2.1 mm thick in the middle portion; the anterior and posterior parts are thicker with 2.5–3.3 mm thickness. Approximately 50 eggs are preserved, 4.48–4.65 mm long and 1.63–1.84 mm wide. See below for more details of the preserved eggs. Eggs are laid in four to five planes (Figure 4F). Within each plane, eggs are in a radial arrangement, in four to five concentric arcs centering the plug. Ovipositional arc in each plane is approximately 100–115° (Figure 3A). Eggs on the plane most proximal to the ootheca wall tend to the slope of the wall at an

angle of approximately 45°, and the successive planes tend to the preceding one (Figure 4F). Eggs are spaced with a 0.2–0.5 mm gap between them.

Intra- and interspecific variations exist in extant grasshopper oothecae. The thickness of the ootheca wall, the morphology and the extent of development of the plug, the insertional angle of the ovipositor, and the number and arrangement of eggs can vary among species, but also within species depending on the ovipositional environment and the local population density (Katiyar 1957; Chapman and Robertson 1958; Thompson 1986; Maeno et al. 2020). The plug, made of frothy oothecal secretion filling the cylindrical trace of the ovipositor, not only shows plasticity in the degree of formation, but is also known to be easily broken off during collection (Chapman and Robertson 1958; Sultana et al. 2017, 2020). Therefore, such characters with known intraspecific variations in extant species are described here but are not strictly diagnostic to the new ichnotaxon.

Remarks. Extant female grasshoppers are known to insert their ovipositor at varying angles. ranging from oblique to a right angle (Chapman and Robertson 1958; Thompson 1986). The arrangement of the eggs with *S. radialis* suggest that the ootheca was likely deposited with the ovipositor inserted in soil at a shallow oblique angle.

Entomoolithidae oofam. nov. Lee, Famoso, and Lin

Diagnosis. The new oofamily is proposed for fossil eggs of entomological affinities.

Remarks. Insect egg morphologies are extremely diverse, yet eggs of distant lineages can be easily compared using quantitative traits (Church et al. 2019a). We have relatively few records of fossil insect eggs through the Phanerozoic compared to amniotic eggs (see Discussion, below). Many records are without proper nomenclature, nor are they described using a uniform descriptive language for further comparisons. In addition, several specimens have been presumed to be of botanical and/or other origins (see Discussion for more). In comparison, various amniotic ootaxa have been described based on the root "oolithus, " meaning "stone egg," as suggested by Mikhailov et al. (1996). Applying ootaxonomy to fossilized eggs of entomological affinities would provide a more organized system that can help make temporal and spatial comparisons, as well as taxonomic correlations. Thanks to the recent progress in understanding the evolution of insect eggs (Church et al. 2019a; Donoughe 2022) based on a large dataset incorporating eggs of more than 6,700 extant insect species (Church et al. 2019b), we are now better equipped for potentially making taxonomic and parataxonomic correlations—at least with the extant insect groups. This more systematic approach may also bring more awareness of fossil eggs of entomological affinities that are diverse and abundant in extant terrestrial ecosystems, which could aid in their identifications and reinterpretations. We propose a single family Entomoolithidae oofam. nov. to accommodate fossil eggs of entomological affinities. We suggest that the diagnoses of fossil entomological eggs include some of the defining egg traits from Church et al. (2019a, 2019b), when possible: length, width and breadth, aspect ratio, asymmetry, and angle of curvature. Additionally, chorion ultrastructure, ornamentation, and other diagnostic surficial morphology should be described, when preserved, as they may provide taxonomic affinities (Hinton 1981; Fisher and Watson 2015) (see Discussion for more).

Curvellipsoentomoolithus oogen. nov. Lee, Famoso, and Lin

Diagnosis. The new oogenus is proposed for fossil eggs of entomological affinities with an overall ellipsoidal shape with curvature.

Remarks. Unlike the amniote eggs, insect eggs are frequently curved along the longitudinal axis

of the egg. High degrees of curvature have evolved in the orders Orthoptera, Hemiptera, Hymenoptera, and Diptera (Church et al. 2019a). Therefore, *Curvellipsoentomoolithus* may be attributed to such groups. However, other groups of insects are also known to produce eggs with minor curvature. In addition, the existence of novel ovipositional strategies that are unknown from extant members of a specific clade has been suggested based on the preserved ovipositor morphology of fossil insets (Chen et al. 2021), which may affect the egg morphology as well. Thus, caution is needed when making taxonomic and ootaxonomic correlations based on egg morphology alone, especially in the deeper geologic past.

Type species. *Curvellipsoentomoolithus laddi* oosp. nov. Lee, Famoso, and Lin

Curvellipsoentomoolithus laddi oosp. nov. Lee, Famoso, and Lin

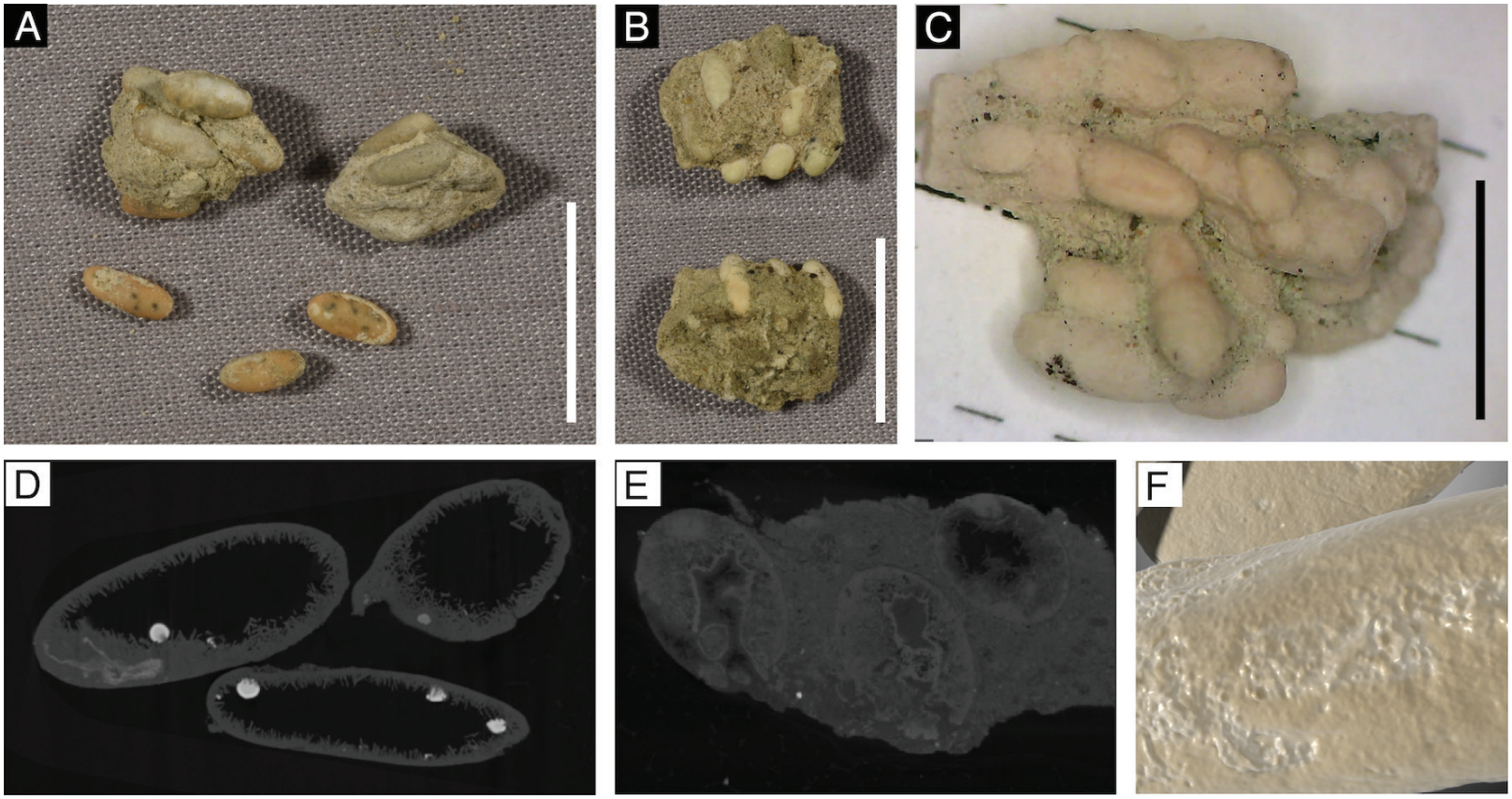
Holotype. Specimen JODA 17384 (Figures 2–4).

Type locality. JDNM-9, Blue Basin, Sheep Rock Unit, John Day Fossil Beds National Monument, Grant County, Oregon, USA. Precise locality data available from the repository for qualified researchers on request.

Type horizon. Likely from a slump of unit E3 over E2 informal units of the Turtle Cove Member, John Day Formation (Oligocene). Specimen is stratigraphically below the Blue Basin Tuff (28.8 Ma) and above the A/B Tuff (29.75 Ma).

Diagnosis. Relatively large insect eggs in overall ellipsoidal shape with slight curvature. Eggs 4.48–4.65 mm long, 1.63–1.84 mm wide; aspect ratio (length/width) 2.5–3; asymmetry 0–0.15, indicating the overall symmetrical shape; angle of curvature θ=10–25°. Eggs frequently preserved in cluster with individual eggs in a (sub)parallel arrangement. Small oval chorionic protrusions present on the chorion surface (Figure 5F; video available at https://doi.org/10.17602/M2/M532694).

FIGURE 5. Additional specimens of *Curvellipsoentomoolithus laddi* oosp. nov., showing clusters of eggs in a (sub)parallel orientation (A–C; scale = 1 cm), internal mineralization of the eggs (D–E), and the chorionic characters (F). (A, D, F): JODA 14423. (B, E): JODA 8754. (C): JODA 4777.



Etymology. Named posthumously after Benjamin Ladd, first NPS Superintendent of John Day Fossil Beds National Monument, who began the protection and resource management and science programs at the park that study and protect these specimens, which are currently only known from within NPS boundaries.

Other materials studied. From JDNM-67, Deer Gulch—Turtle Cove Member unit A, JODA 10179; from JDNM-7A South Foree—Turtle Cove Member unit E3, JODA 18153; from JDNM-7B, North Foree—Turtle Cove Member unit E3, JODA 18958—unit F, JODA 7210; from JDNM-8, Sheep Rock—Turtle Cove Member unit H, JODA 7291; from JDNM-9, Blue Basin—Turtle Cove Member unknown bed, JODA 12936, 12942—unit A, JODA 17921—unit B, JODA 4777—unit D, JODA 17698, 17725—unit E2, JODA 10198, 10218, 10223, 10245, 10252, 10356, 10359, 17560, 8754—unit E3, 10241, 10243, 14423, 18962—unit F, JODA 8771, 18960.

Remarks. Dimensions are known to change during embryonic development in living insect eggs due to water exchange, typically <20% in length (Chaves et al. 2003; Rezende et al. 2016; Church et al. 2019a). In addition, certain locusts are known to manipulate their egg size according to the local population density during the gregarious phases (Maeno et al. 2020). Considering the potential plasticity in egg size, in addition to potential taphonomic change, the egg dimensions are given as a range. The specimens studied herein do not show a strong sign of taphonomic shrinkage, as many partial egg clusters are tightly embedded in the matrix without a gap or recognizable morphological distortion. The chorion surface has small oval protrusions, representing the chorion sculpture. Chorion sculpturing of the extant grasshopper eggs is known to vary from smooth to highly arranged pentagonal, hexagonal, or oval tubercles or cells (Chapman and Robertson 1958; Ganguly et al. 2008). See "Taxonomic and parataxonomic correlations" below for additional details on comparisons with other eggs.

The heavily mineralized nature of the eggs and abundance of isolated and clustered eggs represented by the 26 additional JODA specimens that have been collected throughout the A–H subunits of the Turtle Cove Member support an Oligocene age of the studied materials, not Recent. Microtomography of the JODA 8754 specimen (Figure 5E) shows an unusual internal structure inside the egg cavity, which may represent embryos. Further study and data visualization of the specimen is to follow.

Taxonomic and parataxonomic correlations and the proposed caeliferan affinity

Despite the difficulties making systematic correlations of ichno- and ootaxa to specific biological groups, we propose a caeliferan affinity (Orthopetra: Caelifera) for *Subterroothecichnus radialis* isp. nov. and *Curvellipsoentomoolithus laddi* oosp. nov., based on three morphological features: (1) subterranean ootheca/egg pod deposition; (2) morphology of the ootheca; and (3) the arrangement, number, and morphology of the eggs within the ootheca.

As noted above, we interpreted the disc-shaped, more cemented layer surrounding the egg mass as the ootheca wall. The subterranean ootheca/egg pod wall of the insect is a cemented layer of oothecal secretion and surrounding soil particles, which is apparent in the holotype specimen. Among the handful of insects that are known to produce oothecae, only a subset of them is known to lay oothecae underground: the grasshoppers and locusts (Orthoptera: Caelifera) and the hillwalkers (Mantophasmatodea). Some cockroach and praying mantis species are known to deposit their oothecae underground; however, this represents the dictyopteran oothecae being deposited onto a pre-dug depression or dropped on the soil surface, then covered up, resulting in their burial and the soil particles and other substrate material sticking to the fresh oothecal membrane (Roth 1968; Ehrmann 2011; Brannoch et al. 2017). This is fundamentally different from the caeliferan and the mantophasmatodean subterranean oothecae/egg pod production, which are produced underground from the abdomen that is inserted into soil, with the walls

of these oothecae/egg pods consisting of cemented soil particles and oothecal secretion that become sclerotized and melanized (Chapman and Robertson 1958; Eisner et al. 1966). The newly proposed ichnogenus *Subterroothecichnus* is to accommodate fossils of the latter category.

Among the two known groups of subterranean ootheca/egg pod producers, the Mantophasmatodea is known to produce elongated egg pods. Per Roth et al. (2014), the ellipsoidal and curved mantophasmatodean eggs are arranged vertically in regular rows within the elongated egg pods, and the clutch size can vary from 8–30, depending on the species (Tojo et al. 2004; Roth et al. 2014; Küpper et al. 2019). The caeliferan oothecae are typically known to be cylindrically elongated, with eggs arranged in row(s) with little to no space between and around them (e.g., Waloff 1950; Katiyar 1957; Chapman and Robertson 1958; Sultana et al. 2020; Ubero-Pascal et al. 2020); some of these oothecae could bear superficial resemblance to mantophasmatodean oothecae. This overall cylindrical shape reflects the morphology of female grasshopper ovipositors and their ovipositional behavior: during oviposition, two pairs of shovel-shaped ovipositor valves in the last abdominal segments repeatedly open and close, extending the ovipositor further into soil (Thompson 1986). The cylindrical ovipositor can extend up to tenfold in length, allowed by intersegmental soft cuticles and are flexible (Jorgensen and Rice 1983). In addition to the more common cylindrical shapes, grasshopper oothecae also include pyriform shapes and, in some cases, more broadly expanded forms resembling *S. radialis*, as well as the variations in arrangements of the eggs (Waloff 1950; Katiyar 1957; Chapman and Robertson 1958; Chernyakhovskii 2006). Per Chapman and Robertson (1958), species belonging to the family Pyrgomorphidae as well as most of the subfamily Catantopinae (family Acrididae) that they studied have radially symmetrical pods, whereas other species belonging to various subfamilies of Acrididae have bilaterally symmetrical pods with eggs arranged in parallel rows. This broad taxonomic pattern is congruent with other descriptive studies, although an array of intraspecific variation exists as well (Waloff 1950; Katiyar 1957; Sultana et al. 2017, 2020; Ubero-Pascal et al. 2020). Among the records we found, *S. radialis* isp. nov. described herein has the highest overall morphological resemblance to the egg pod of *Hieroglyphus concolor* (Katiyar 1957; Figure 5D); unfortunately, the arrangement of eggs within it is not described. Due to intraspecific variation as well as the sparse taxonomic coverage of caeliferan ootheca morphology, their phylogenetic significance, if any, within the suborder is yet to be understood. On the other hand, an egg pod similar in shape to *S. radialis* is unknown in Mantophasmatodea to date. Thus, the known examples of extant caeliferan egg pods that are similar to the new ichnotaxon, which differs from hitherto described mantophasmatodean egg pods, strengthen the proposed caeliferan affinity.

The nature of *S. radialis*, including its probable subterranean production and the overall morphology, support its caeliferan affinity. Additionally, the relatively large clutch size of approximately 50 eggs, representing the minimum clutch size, also strengthens the proposed affinity. The combination of large clutch size and relatively large egg size is mostly known from grasshopper species, and relatively rare outside orthopterans. The known clutch size from a single grasshopper egg pod can range from two to over 200 eggs, varying between species (Okelo 1979; Dysart 2000; Ingrisch and Rentz 2009).

To find other potential producers of eggs similar to *Curvellipsoentomoolithus laddi* oosp. nov., we compared its morphology to a recently developed dataset of global insect egg size and shape, including more than 6,700 extant species (Church et al. 2019a, 2019b). The size and length-to-width aspect ratio of our specimens lie within the morphospace that is mainly occupied by Polyneoptera, Neuropteroidea, and Hymenoptera. We then reviewed approximately 800 taxa from Church et al.'s dataset (2019b) that have the egg lengths of 4 mm or more. Although strongly curved eggs are known of have evolved in the Orthoptera, Hemiptera, Hymenoptera, and Diptera (Church et al. 2019a), the curvature is not heavily pronounced in *C. laddi* and therefore all species that have eggs 4 mm or longer have been reviewed. The majority are crickets, katydids, and grasshoppers (Orthoptera) and leaf and stick insects (Phasmatodea), followed by bees and wasps (Hymenoptera)

and beetles (Coleoptera), with the orders Blattodea, Mantodea, Hemiptera, Lepidoptera, and Diptera each being represented by a single family.

Phasmatid eggs are easily distinguished from those of *C. laddi:* in addition to their unique phasmatid egg morphology with an operculum and the micropylar plate that resemble plant diaspores, their ovipositional strategies include single eggs dropped or flicked to the ground, eggs glued to a substrate, eggs laid in cracks or crevices on the ground (Bedford 1978; Robertson et al. 2018). In a single known Phasmatid species, oothecae are attached to vegetation (Goldberg et al. 2015). Among the hymenopterans that produce large eggs comparable in characters to those of *C. laddi*, several taxa build brood chambers made of mud that could resemble the egg pods in overall shape, but are frequently divided into cells (digger bees and orchid bees in the family Apidae; subfamilies Eumeninae and Zethinae, family Vestidae) and/or provisioned with paralyzed prey (families Crabronidae, Sphecidae, Pompiliidae, Scoliidae), which is distinct from *S. radialis* and the arrangement of *C. laddi* within it. Additionally, the eggs do not occur in such a large clutch size.

Most large beetle eggs have an aspect ratio (length-to-width ratio) of less than 2; several longhorn beetles (family Cerambycidae) have an aspect ratio of 2–3, but their eggs are laid endophytically. Some carabids and tenebrionids also lay large eggs in soil, either singularly or in clutches, but the clutch size is smaller, and an egg pod structure is unknown from these groups. The other groups are represented by a single family each: the mantids (Family Mantidae) and the giant cockroaches (Family Blaberidae) either produce dictyopteran oothecae or are viviparous; Hemiptera is represented by a few species of giant water bugs (family Belostomatidae), which provide parental brood care by attaching eggs to male bodies; Lepidoptepra is represented by a single species of castniid palm borer (Family Castniidae; Monteys and Aguilar 2005); and Diptera is represented by a single genus *Mesembrina* (Family Muscidae), which lay a single egg in animal dung (Hinton 1960).

The remainder of species with eggs that are 4 mm or longer belong to the order Orthoptera. Members of both suborders Caelifera (grasshoppers and locusts) and Ensifera (crickets and katydids) produce large eggs; however, deposition of underground egg pods is so far known only from the Caelifera (Du et al. 2022; Ubero-Pascal et al. 2020). Hence, multiple lines of evidence from modern groups—including the underground deposition of the ootheca/egg pod, morphology of the ootheca, and the arrangement, number, and morphology of the eggs within it—support a caeliferan affinity (order Orthoptera) of the parataxa *Subterroothecichnus radialis* ichnosp. nov. and *Curvellipsoentomoolithus laddi* oosp. nov.

DISCUSSION

Ootheca: Different types and convergent evolution

An ootheca, a type of egg mass surrounded by a protective layer consisting of hardened oothecal structural proteins (OSPs), independently evolved in multiple insect lineages (Du et al. 2022). Most species of the praying mantises and cockroaches (Dictyoptera: orders Mantodea and Blattodea), the grasshoppers and locusts (order Orthoeptra, suborder Caelifera), and the hillwalkers (order Mantophasmatodea) are known to produce oothecae, as well as the cassidine tortoise beetles, a stick insect, and a plant hopper (see Introduction). Among the three better-understood polyneopteran groups of ootheca producers—the mantises (order Mantodea), the cockroaches (order Blattodea), and the grasshoppers and locusts (order Orthoptera, suborder Caelifera)—significant morphological variation exists.

The mantodean oothecae are known to exhibit extensive architectural and cryptic variation, with the external wall mostly made of protein and calcium-based compounds, which can range from smooth and flexible to textured and hardened (Brannoch et al. 2017). Their oothecae consist of one or more egg chambers with each containing a single egg, and an emergent area known as

the keel, which where the opening of the individual egg chambers, through which the hatchlings emerge, are dorsally aligned in two parallel rows that are usually alternating, with some known variations (Brannoch et al. 2017; Cariglino et al. 2020). In blattodean oothecae, two rows of lateral egg chambers flank a conspicuous linear dorsal keel that splits open when hatchlings arise, with some variations known in termites and some ovovivi- and viviparous taxa (Roth 1968; see Cariglino et al. 2020 for more on dictyopteran oothecae). Chemically, dictyopteran oothecae are usually known to contain quinone, a dark tannin that helps with sclerotization and melanization of the oothecae but also functions as a sex pheromone, and calcium oxalate crystals, which add structural rigidity (Brunet 1951; Hackman and Goldberg 1960; Roth 1968; Courrent et al. 2008). Recently, Du et al. (2022) suggested that—based on the proteomic and metabolomic evidence—the two dictyopteran oothecae share proline-rich proteins (PRPs) as the most abundant OSPs, but mantids and cockroaches developed glycine-rich proteins (GRPs) and fibroins as distinct OSPs, respectively, suggesting their functional convergence. It is notable that PRPs and GRPs are also abundant structural proteins in plant cell walls (Josè and Puigdomènech 1993).

On the other hand, the subterranean caeliferan oothecae, also known as egg pods, differ significantly in their morphology from the dictyopteran ones. Instead of producing structurally intricate oothecae in an aerial environment, grasshoppers insert their abdomen into soil using two pairs of shovel-shaped valves, and produce oothecal secretions that mix with the surrounding soil particles, which become sclerotized and melanized (Eisner et al. 1966; Thompson 1986). Their oothecae frequently have cylindrically elongated shapes with varying degrees of curvature, reflecting the ovipositor morphology. However, some known variations exist in the shapes of caeliferan ootheca, including laterally expanded lenticular ones, which resemble *S. radialis* isp. nov. described herein. The eggs are laid within the oothecae, most commonly in regular parallel rows, with some known variations ranging from irregular to radially symmetrical arrangements (Waloff 1950; Katiyar 1957; Chapman and Robertson 1958; Chernyakhovskii 2006). As the oviposition proceeds, the cavities between the eggs, those between the egg and the egg pod wall, and the void plug region above the egg mass are filled with frothy oothecal secretions, which become hardened (Chapman and Robertson 1958). In the holotype specimen (JODA 17384), such frothy oothecal secretions, dating from ca. 29 Ma, are preserved as green zeolitized sandy claystone. Chemically, only some OSPs are shared between the dictyopteran and caeliferan oothecae, namely the vitellogenins and apolipoproteins, which strongly suggests the convergent evolution of OSPs and the sclerotization and melanization processes in the two groups (Du et al. 2022). Specifically, the caeliferan oothecae lack the PRPs and GRPs found in the dictyopteran ones, and therefore are structurally less rigid (Du et al. 2022).

Such OSPs are produced in the colleterial glands (CGs) in Dictyoptera, which are a type of female accessory reproductive gland in various insects that primarily produce substances for egg packaging, adhering eggs to a surface, and protective egg coating (Baccetti 1967; Hoffmann 1995; Gillott 2003; Du et al. 2022). The dictyopteran CGs, two in number, are asymmetrical, with the much larger left CG producing many of the OSPs and the smaller right CG producing tanning substances (Brunet 1951; Du et al. 2022). In contrast, a different pair of glands is involved in the production of caeliferan ootheca. While Du et al. (2022) referred to these as *symmetrical CGs,* Hoffmann (1995) and Baccetti (1967) referred to such glands as the *mesodermal accessory glands* and the *pseudocolleterial glands,* respectively. Unlike the CGs that develop as evaginations of the common oviduct or from the imaginal discs, and that are nearly always ectodermal when present, the orthopteran pseudocolleterial glands are extensions of the lateral oviducts and thus mesodermal (Baccetti 1967; Gillott 2003). The CGs are found in female Thysanura, in many hemi- and holometabolous groups, but are unknown in the orders Ephemeroptera, Orthoptera, Plecoptera, Psocodea, suborder Heteroptera (order Hemiptera), and most Coleoptera (Matsuda 1976). The differences in organs responsible for OSPs production in the dictyopterans and caeliferans further support the convergent evolution of ootheca in the groups, using different

glands and chemicals. Additionally, such accessory glands are unknown in the hillwalkers (Mantophasmatodea), the other polyneopteran group that produces subterranean oothecae/egg pods (Klass et al. 2003; Küpper et al. 2019); instead, a newly identified type of glands secrete oothecal secretion, termed the *ventrovaginal glands* (Küpper et al. 2019). This supports multiple independent origins of ootheca in distant insect lineages, using different glands and chemicals. Future studies on proteomic and metabolomic analyses of the oothecae, as well as anatomical studies of female glandular structures responsible for production of OSPs in other known ootheca-producing insects, will help us better understand the evolution of oothecae in insects.

Subterroothecichnus and the subterranean ootheca/egg pod

Two groups of insects are known to produce subterranean oothecae/egg pods that incorporate surrounding soil particles into the structure: the grasshoppers and locusts (order Orthoptera, suborder Caelifera) and the hillwalkers (order Mantophasmatodea). Much more is known about the caeliferan egg pods, considering the interest in their agroeconomic significance and in methods to control many grasshoppers and especially the locusts—that is, in the various species of acridid grasshoppers that have a swarming phase (e.g., Lomer et al. 1999). In contrast, ootheca production in the hillwalkers is less known, as the order is the most recently described of all insects (Klass et al. 2002, 2003; Zompro et al. 2002). The mantophasmatodean eggs lack a defined operculum and a micropylar plate, which are characteristics of the phasmatid eggs (Klass et al. 2002; Zompro et al. 2002), although scanning electron microscopy reveals an anteriorly located circular ridge representing the hatching line, probably marking an operculum that is detached when the nymph hatches (Zompro et al. 2002). The eggs are approximately 2.75 mm long and 0.95 mm wide, with an overall oblong-oval shape with curvature (Roth et al. 2014; Zompro et al. 2002) resembling some grasshopper eggs. The surface of the chorion below the hatching line consists of a network of hexagonal plates interconnected by traberculae (Zompro et al. 2002). Without a well-preserved circular hatching line, a hypothetical fossil mantophasmatodean egg would likely be placed under *Curveelipsoentomoolithus* oogen. nov.

There is a large difference in mantophasmatodean and the caeliferan ootheca production, resulting from their anatomical differences. The elongated and curved mantophasmatodean eggs are in a regular vertical arrangement within the egg pods (Tojo et al. 2004; Roth et al. 2014; Küpper et al. 2019). It is unclear what the processes of the oviposition and ootheca production look like; judging from the descriptions and accompanied figures in Roth et al. 2014 and Küpper et al.2019), it appears that the female hillwalkers produce ootheca by horizontally adding eggs. Caeliferan eggs are vertically added within the ootheca as the expanded ovipositor retracts during the progress of oviposition. Such flexible ovipositors and the two pairs of shovel-shaped appendages are unknown from the hillwalkers: while they insert their abdomen into soil to lay oothecae, vertically cylindrical forms would not be produced without the digging ovipositor. The mantophasmatodean ootheca seem to lack a structure similar to the plug of caeliferan ootheca, which is congruent with this anatomical difference. However, the caeliferan and the mantophasmatodean ootheca can resemble each other when they are not in an *in situ* oviposition. In the most common and the simplest forms of caeliferan egg pods, cylindrical elongated egg pods with varying degrees of curvature contain eggs arranged in parallel vertical rows at an angle of approximately 45° to the longitudinal axis of the pod, with some variations in the angle, ranging from 0° (parallel to the longitudinal axis) to 90° in some species (Waloff 1950; Chapman and Robertson 1958). When portions of the cylindrical caeliferan oothecae with eggs laid perpendicularly to the ootheca wall are broken off, they can bear high morphological resemblance to the mantophasmatodean ones.

Contrary to their current relictual distribution, confined to Namibia, South Africa, and Tanzania (Adis et al. 2002; Klass et al. 2002; 2003; Picker et al. 2002; Zompro et al. 2002; Roth et al. 2014; Wipfler et al. 2017), the mantophasmatids had a wider geographic distribution in the geologic

past, with their fossils known from the Middle Jurassic of China (Huang et al. 2008) and Eocene Baltic amber (Zompro 2001). Thus, it is possible that the morphology of the mantophasmatodean oothecae was more diverse in the geologic past. However, a remarkable morphological stasis in their eggs has been recorded in the fossilized abdomen of the *Juramantophasma sinica* (Huang et al. 2008). The abdomen of the holotype specimen from the Middle Jurassic (165 Ma) of Daohugou, Inner Mongolia, China—representing a nearly complete adult female in compression—preserves 28 visible eggs (approximately 3.3 mm long, 1.6 mm wide) in parallel rows, with eggs showing the circular hatching ridge and small spots on the chorion (Huang et al. 2008) that are also known from extant species. It appears that the individual died shortly before the ootheca production and oviposition, and became rapidly fossilized. Although the specimen does not include a deposited egg pod, the clutch size, and the morphology of the eggs and their arrangements, are remarkably similar to extant mantophasmatodean oothecae, suggesting a remarkable stasis in the species' ovipositional strategy over a long period of time.

Within the suborder Caelifera (Orthoptera), understanding the origin of oothecae requires further study. Among its nine superfamilies (Acridoidea, Pyrgomorphoidea, Pneumoroidea, Trigonopteygoidea, Tanaoceroidea, Eumastacoidea, Proscopioidea, Tetrigoidea, and Tridactyloidea; Song et al. 2015), we found descriptions of egg pods or mention of their presence in many species belonging to the clade comprising the Acridoidea, Pyrgomorphoidea, Pneumoroidea, and Trigonopterygoidea (Donelson et al. 2008; Kekeunou et al. 2015, 2020; Sultana et al. 2017, 2020; Shaikh and Sultana 2018)—although we were unable to find information regarding ootheca production in the small superfamily Trigonopterygoidea, containing 21 species. This clade represents nearly 75% of caeliferan species. In contrast, the remaining earlier-branching superfamilies do not lay their eggs in cemented oothecae, or else insufficient information exists to make meaningful inferences. Eggs in the superfamily Tetrigoidea—the second-most-specious caeliferan superfamily—are laid in clusters but not in cemented pods, and eggs possess an anterior chorionic horn or filament (Paranjape 1985; Ingrisch and Rentz 2009). The serrated ovipositor valves in the Tetrigoidea also differ from the smooth acridoidean ones (Paranjape 1985). Some studies refer to Tetrigoidean egg clutches as egg pods (Forsman 2001; Steenman et al. 2015), but these studies lack structural descriptions to determine if the clutches are deposited in cemented pods. Morabine grasshoppers, belonging to the superfamily Eumastacoidea, also lay their eggs in a coherent cluster but not in an egg pod (Blackith and Blackith 1966, 1969), and they lack CGs that produce OSPs, per Blackith and Blackith (1966). We were unable to find information on the presence of oothecae in the superfamilies Tanaoceroidea, Proscopoidea, and Tridactyloidea, which collectively account for less than 5% of caeliferan species. Based on the existing information, ootheca production within Caelifera appears to be a derived character that evolved along the lineage leading to the speciose clade comprising Acridoidea, Pyrgomorphoidea, Pneumoroidea, and Trigonopterygoidea; however, poor taxonomic resolution, especially for species besides the agroeconomically significant Acridoidea and Pyrgomorphoidea, hinders our understanding of the evolution of caeliferan ootheca. Additionally, endo- and exophytic oviposition independently evolved several times among acridoid taxa that inhabit marsh and wet tropical forest environments; in these taxa, ovipositor morphology also differs significantly from that of the soil-ovipositing relatives (Braker 1989). Future studies on the origin of caeliferan ootheca production and its potential ecological significance will enrich our understanding of this reproductive strategy.

In summary, multiple lines of evidence preserved in the exquisite holotype specimen JODA 17384 and the additional 26 egg clusters reported here support the proposed caeliferan affinity of *Subterroothecichnus radialis* isp. nov. and *Curvellipsoentomoolithus laddi* oosp. nov. This likely represents the first and oldest unequivocal fossil evidence of underground grasshopper ootheca (see below). The new ichnogenus *Subterroothecichnus* may have taxonomic correlations with the grasshoppers and locusts (suborder Caelifera, order Orthoptera) as well as the hillwalkers

(order Mantophasmatodea), although it is possible that other insect taxa may have produced underground egg pods in the past.

It has been suggested that one of the original roles of the dictyopteran ootheca was to prevent eggs from desiccation (Cariglino et al. 2020; Du et al. 2022), as disturbance in the sclerotization and melanization processes of the OSPs significantly increased water loss from the cockroach ootheca, leading to their distortion (Du et al. 2022). Interestingly, most of the mantis species that are known to bury their oothecae underground (see Taxonomic and Parataxonomic Correlations, above) are from arid regions (Ehrmann 2011; Shcherbakov and Savitsky 2015), many belonging to the families Eremiaphilidae and Rivetinidae (superfamily Eremiaphiloidea). It has been speculated that burial of oothecae in soil prevents their desiccation and thus enable species of *Rivetina* to occupy more arid areas compared to other mantids (Lindt 1993). Similarly, Küpper et al. (2019) noted that mantodean underground egg pods are highly resistant to heat and desiccation, protecting the eggs from hot and dry summers.

In comparison, the adaptive functions of underground deposition of egg pods by caeliferans are not yet fully understood. It is likely that they function in controlling water availability around the eggs, at least in some capacity, although it is possible that their initial function wasn't to protect the eggs from aridity, as suggested for other underground insect oothecae. Eisner et al. (1966) reported that the acridid oothecal secretion also tanned the eggs, and suggested that the sclerotization and melanization processes may protect the eggs against water loss or water intake. They further speculated that the plug region, made of the hardened oothecal froth and intermixed airspaces, may provide a respiratory system when submerged by floods, similar to the plastron respiration seen in some aquatic insects, or insulation against extreme temperatures. Hunter-Jones and Lambert (1961) similarly noted that the frothy oothecal secretion protected the eggs from excessive water. Braker (1989) even speculated that the evolution of oviposition on host plants in some acridoid taxa that usually inhabit mesic environments may provide (together with their depositional depth) an adaptive advantage against flooding because grasshopper eggs are sensitive to water balance. There are some other lines of evidence suggesting their potential function in protection from desiccation. According to Katiyar (1957), acridids lay their eggs in xerophilic, mesophilic, or hygrophilic soils, with thicker and more rigid pod walls found in drier sediments. As noted, the depositional depth of oothecae may also provide an adaptive advantage. Stauffer and Whitman (2007) noted that xeric taxa tend to lay their egg pods at a greater depth, whereas species from hydric habitats tend to lay shallow or even above-ground pods, suggesting that ovipositional depth is another potential adaptive strategy against extreme temperatures and/or desiccation. Deep deposition of the egg pods would protect them from desiccation, extreme temperature fluctuations, egg predators and parasites, wind or flash-flood erosion, and/or wildfire (Branson and Vermeire 2007; Stauffer and Whitman 2007). However, other factors, such as the adult female body size, soil texture, and the surrounding vegetation, are known to affect the ovipositional depth (Inglis et al. 1998; Herrmann et al. 2010).

Lastly, we found one other fossil record, possibly representing another example of fossilized underground grasshopper oothecae, that could potentially be placed under the new ichnogenus *Subterroothecichnus*. Meco et al. (2010, 2011) studied the numerous tubular concretions found in the late Pliocene to Quaternary sediments in the Canary Islands Archipelago. These concretions are 2–3 cm long and 1 cm wide, closed at one end and open at the other, occurring in extremely high densities exclusively within areas approximately 10 cm from the paleosol layers. They interpreted such tubular concretions, repeatedly occurring in association with paleosol layers, to be acridian egg pods, specifically resembling egg pods of *Dociostaurus maroccanus*, an extant temperate locust species ranging across North Africa, southern and eastern Europe, and western and central Asia. Meco et al. (2011) interpreted that the fluctuation in their abundance over time, coinciding with interglacial or interstadial periods, represents repeated locust infestations. Interestingly, egg

pods of some locusts are known to contain pheromones that attract other females and facilitate their synchronous oviposition in high densities (Saini et al. 1995; Mccaffery et al. 1998; Ferenz and Seidelmann 2003), which may have contributed to the high abundance and density of fossilized caeliferan egg pods found in the Canary Islands.

Importantly, Meco et al.'s (2010, 2011) egg pod concretions had previously been interpreted as hymenopteran brood chambers (Ellis and Ellis-Adam 1993; Edwards and Meco 2000; Alonso-Zarza and Silva 2002; Ortiz et al. 2006) or coleopteran pupal chambers (Genise and Edwards 2003; Ortiz et al. 2006), because their roughly tubular, but more ellipsoidal, overall morphology, along with smooth and regular cell walls and nearly circular exit holes, also closely resembles the hymenopteran brood chamber ichnogenera *Celliforma* or *Palmiraichnus* and the coleopteran pupal chamber *Rebuffoichnus*. With these uncertainties, Genise et al. (2013) proposed a new ichnotaxon *Rebuffoichnus guanche* to accommodate all specimens with the proposed orthopteran, hymenopteran, or coleopteran affinities, and reinstated the coleopteran interpretation of the structures. Many of them are in horizontal positions in soil, which aligns more with a coleopteran interpretation than the proposed orthopteran affinity. However, La Roche et al. (2014) found some hymenopteran cells belonging to the ichnospecies *Palmiraichnus castellanosi* among such concretions, and it is currently unknown whether there are at least some concretions that can be definitively identified as acridian egg pods. According to Meco et al. (2010), some of the preserved concretions contained fossilized eggs, which they suggested support an acridian oothecae interpretation. Microtomography of such specimens with preserved eggs within them would clarify the proposed egg pod identity. Despite the close resemblance of the supposed fossil acridian egg pods from the Canary Islands to those of the extant *D. maroccanus*, such egg pod morphology is quite rare among the grasshoppers and locusts (Meco et al. 2011). This demonstrates the complexity of interpreting biological affinities of ichnofossils, and suggests that recognizing *Subterroothecichnus* could be challenging without preserved eggs inside. As the taxonomic and functional interpretations of these Pleistocene specimens remain unresolved, our holotype specimen studied herein, JODA 17384, represents the oldest and likely the first unequivocal fossil evidence of a grasshopper ootheca.

Fossil insect eggs and ootaxonomy

Insect egg morphologies are extremely diverse, which is unsurprising considering the immense taxonomic diversity and ecological success of insects, occupying an array of terrestrial environments. Many insect eggs are laid without parental care; thus, protection of this immobile stage relies on the eggshell layers to cope with biotic and abiotic stresses, such as desiccation, flooding, pathogens, and predation (Rezende et al. 2016). At the same time, the eggshell needs to allow gas exchange and sperm entry, which are performed by structurally specific regions of the eggshells known as the aeropyles and the micropyles, respectively (Hinton 1981; Chapman 1998; Rezende et al. 2016). Insect eggshells are highly organized and multilayered proteinaceous composite structures, which can primarily be divided into the inner vitelline membrane and the outer chorion, both produced by the ovarian follicular epithelial cells (Rezende et al. 2016). The vitelline membrane contains a variety of proteins and is known to play a key role in water retention and gas exchange, in addition to its protective function (Zhai et al. 2022). The chorion plays a pivotal role in the protection of the embryo and in gas exchange, and in some insects also contains proteins essential for egg maturation (Lou et al. 2018). The chorion is often subdivided into the endochorion, which is largely proteinaceous, and the fibrous exochorion, composed mainly of polysaccharides (Trougakos and Margaritis 2002). Chorion proteins are rich in glycine, tyrosine, and proline, with the abundance of these amino acids associated with structural functions (Irles and Piulachs 2011). Proline- and glycine-rich proteins are also abundant in dictyopteran oothecae. Further subdivisions and additions of the layers are also known (see Rezende et al. 2016 for more).

The chorion hardens at maturity and frequently has characteristic surface patterns. Chorionic surface characters can be grouped into three categories: chorionic sculpturing, micropyle, and attachment structures (Sierra et al. 1995). Many insect chorions have microscopic hexagonal patterns which, per Mendonça et al. (2008), reflect the impressions of the follicular epithelial cells in the ovaries that produce them. In fossilized insect eggs, external features of this layer become preserved in compression/impression, cast/mold, and fossils preserved in ambers. In rare cases where eggs are structurally preserved, features of the internal surface (Heřmanová et al. 2013), and even the anatomical structures of the layered chorion (Fisher and Watson 2015), are visible, showing a remarkable conservation in insect eggshell structure. An extensive amount of research has been conducted on eggs of extant insects and their chorion characters, including Southwood 1956, Hinton 1981, and Margaritis 1985. Consequently, ootaxonomy of extant insects and comparative morphological studies of different groups are well advanced, in order to distinguish insect taxa based on egg chorionic characters, especially for taxa of agroeconomic, forensic, or public health interest (Mendonça et al. 2008; Al-Dosary et al. 2010). In addition to this rich record of chorion ultrastructure, our understanding of the evolution and ecology of insect egg morphology has improved significantly using more sophisticated statistical and systematic approaches, owing to the recently developed large dataset of the egg morphology (Church et al. 2019a, 2019b; Donoughe 2022). For instance, oblately ellipsoidal insect eggs (aspect ratio <1) are only found within Plecoptera and Lepidoptera; extreme asymmetry of eggs is found in Condylognatha and Hymenoptera; and a high degree of egg curvature is found in Orthoptera, Hemiptera, Hymenoptera, and Diptera, among extant insects (Church et al. 2019a).

Insect eggs are scarcely known from the fossil record, and those with ultrastructural preservation are even rarer (Fisher and Watson 2015). Nonetheless, descriptions of fossil insect eggs with chorionic characters preserved from the Mesozoic and Cenozoic sediments have grown in number in recent years, necessitating a more uniform descriptive and comparative system describing them. Egg morphology and chorionic characters can sometimes provide their taxonomic affinities. For instance, Gall and Tiffney (1983) described a fossil moth egg of the family Noctuidae from the Late Cretaceous of Massachusetts based on the chorion sculpturing, and Sellick (1994) described three species of phasmatodean eggs (Pseudophasmatidae: tribe Anisomorphini) from the Eocene Clarno Nut Beds of Oregon (also within JODA), based on the presence of a detachable anterior operculum and dorsal micropylar plate. More frequently, however, understanding the taxonomic affinities of these phasmatodean eggs calls for careful assessment using the macromorphology, ultrastructure (chorionic characters), and other associated trace fossils preserving ovipositional behaviors. Although not all fossil insect eggs can be attributed to living groups of insects based on their morphology, especially those from a deeper geologic past, comparisons with extant insect eggs are necessary for a systematic understanding. The recent advancements in our understanding of insect egg morphology using quantitative traits, as well as the extensive literature on extant insect ootaxonomy using chorionic characters, can help us compare fossil insect eggs with extant ones more easily for taxonomic correlations.

Many of the described fossil insect eggs are without a proper name orcertain taxonomic correlations (Feng et al. 2022); rather, they are described simply on the basis of suggested taxonomic affinities based on morphological features (Gall and Tiffney 1983; Heřmanová and Kvaček 2010) or by virtue of being preserved in association with the parent or larval insect and therefore having a definitive taxonomic position (Huang et al. 2008; Wang et al. 2015; Chen 2022; Pérez-de la Fuente et al. 2019; Chen and Xu 2022; Fu et al. 2022). Others are described with binomial names—though without being attributed to any certain groups (Krassilov 2008)—or with certain taxonomic affinities (Sellick 1994; Heřmanová et al. 2013; Fisher and Watson 2015) when their preserved morphology provides sufficient characters for taxonomic correlations. A summary of selected occurrences of fossil insect eggs preserving morphological details is provided in Table 2.

TABLE 2. Selected examples of fossil insect eggs preserving key egg morphological traits and chorionic characters.

Ootaxon	Systematic affinity	shape	length (mm)	width (mm)	Aspect ratio	asymmetry	Angle of curvature (°)	Egg shell characters	Age and locality	Preservation	Reference
N/A	Basal Hymenoptera / Coleoptera	ovoid	0.28–0.31	0.15–0.18	1.62–1.96*	0.08–0.23*	0*	Crenulate lateral rim with intercalary septae	L. Triassic. Luntz Fm., Austria	Attached to bennettitalean leaf cuticle	Pott et al. 2008
N/A	N/A	Spheroid-ovoid to ellipsoid	0.10–0.28	0.08–0.26	1.0–2.4	0.08–0.11*	0–0.21*	Pyramidal micropylar projection; gelatinous exochorion with spheroidal bodies	L. Triassic. Xuijahe Fm., Sichuan, China	Numerous endophitic oviposition in ginkgoalean leaves	Feng et al. 2022
N/A	Mantophasmatodea: Mantophasmatidae: *Juramantophasma sinica*	Curved ellipsoid	3.3	1.6	2.06*	N/A	N/A	Small chorionic spots; a circular hatching ridge	M. Jurassic. Daohugou Fm., Inner Mongolia, China	Compression; inside female abdomen	Huang et al. 2008
N/A	Hemiptera: Corixoidea: *Karataviella popovi*	Elogately ovoid	max. 1.28	max. 0.61	2.1–2.2	N/A	0*	Flat micropylar area; smooth chorionic surface; borne on short stalk	M.–L. Jurassic. Haifanggou Fm., China	Compression; egg clutch preserved on female left mesotibia	Fu et al. 2022
Merangia horricomis	Hemiptera: Heteroptera	Cylindrical to barrel-shaped	<0.5	0.6	0.83*	0*	0*	Lateral surface spinose; layered anterior pole; basal plate	E. Cretaceous. Wealden, Germany	Attached to conifer leaf cuticle, structurally preserved	Fisher and Watson 2015
N/A	Neuroptera: Chrysopoidea: *Tragichrysa ovoruptora*	Half ellipsoid (incomplete)	0.6 (incomplete)	0.42	3.25*	0.14*	0*	Finely granulate with short anterior process; egg bursters present	E. Cretaceous. Lebanese amber, Lebanon	Preserved in amber with hatchlings	Pérez-de la Fuente et al. 2019
N/A	Hemiptera: Ortheziidae: *Wathondara kotejai*	Ellipsoid	0.3	0.2	1.5*	N/A	0*	N/A	Mid-Cretaceous. Burmese amber, Myanmar	Approx. 60 eggs preserved within a wax ovisac, preserved on an adult body	Wang et al. 2015
N/A	Plecoptera: Perspicuusoperlidae: *Perspicuusoperla lata*	Cylindrical	ca. 0.75	0.2*	3.05*	0*	0*	Chorion entirely membranous, transparent and smooth; with an anterior collar	Mid-Cretaceous. Burmese amber, Myanmar	Dozens of eggs preserved in amber, near an adult	Chen 2022
N/A	Plecoptera: Petroperlidae: *Ovaloperla staniczeki*	Ovoid	ca. 0.3	ca. 0.2	1.5*	0.22*	0*	Chorion sclerotized; circular membranous area on one pole; gelatinous coat present	Mid-Cretaceous. Burmese amber, Myanmar	Preserved in amber, with an adult	Chen and Xu 2022

TABLE 2 (cont'd). Selected examples of fossil insect eggs preserving key egg morphological traits and chorionic characters.

Ootaxon	Systematic affinity	shape	length (mm)	width (mm)	Aspect ratio	asymmetry	Angle of curvature (°)	Egg shell characters	Age and locality	Preservation	Reference
N/A	unknown	Ellipsoid	0.9–1.7	0.4–0.8	1.64–2.68		0*	No discernible pores, micropyles, or opercula	Mid-Cretaceous. Burmese amber, Myanmar	Egg clutches preserved in amber; clutch size 18–28	Xing et al. 2021
Transpiroveon polygonatum	unknown	ellipsoid	ca. 1	0.45–0.71*	1.44–2.22*	0*	0*	Chorion surface with polygonal meshwork; simple intrachorionic transpiration meshwork present	Mid-Cretaceous. Hatira and Ora Fms. Israel	Attached to dicot leaf	Krassilov 2008
N/A (formerly known as *Palaeoaldrovanda splendens*)	Unknown; likely Phasmatodea / Lepidoptera	Ovoid	0.4–1.6	0.7–1.4	1.35*	0.05–0.13*	0*	Chorion sculptures with rectangular cells in rows; apical conical projection; basal cap-like projection	Late Cretaceous. Klikov Fm., Czech Republic	Charcoalified; structurally preserved	Hermanová and Kvaček 2010
Knoblochia cretacea	Unknown; likely Phasmatodea / Lepidoptera	Spheroid/ovoid	1	0.75	1.33*	0*	0*	Longitudinally ridged; chorion sculptures with large cells apical conical projection and coronal rim; basal round collar	Late Cretaceous, central Europe	Structurally preserved in the flysch-type sediments	Hermanová et al. 2013
N/A	Lepidoptera: Noctuidae	Spheroid/ovoid	0.6	0.5–0.6	1.09*	0.40*	0*	18–20 longitudinal ridges, adjacent ones connected by latitudinal ridges	Late Cretaceous. Magothy Fm., MA, USA	Structurally preserved	Gall and Tiffney 1983
Eophasma oregonense, and two other similar phasmatid eggs	Phasmatodea: Pseudophasmatidae: tribe Anisomorphini	Ellipsoid	3.30–4.20	2.25–2.50	1.37–1.68	0.15*	0*	Rhomboidal micropylar plate & operculum	Eocene. Clarno Fm., OR, USA	Cast and mold	Sellick 1994
Curvellipsoentomoolithus laddi	Orthoptera: Caelifera	Curved ellipsoid	4.48–4.65	1.63–1.84	2.5–3	0–0.15	10–20	Small chorionic spots	Oligocene. John Day Fm., OR, USA	Frequently preserved in clusters or in an egg pod	Present study

The records known so far are geographically and stratigraphically restricted, although some are known from more than one locality (e.g., Heřmanová et al. 2013). It is possible that the hitherto known records may be isolated occurrences without further spatial or temporal correlations. However, descriptions of well-preserved fossil insect eggs have been rapidly increasing in recent years: 11 out of 16 examples have been described from 2010 onward (including the present study; Table 2). The examples that we were able to locate demonstrate that fossilization of insect eggs is not random but highly dependent on taphonomy, as well as on the insects' ecology and ovipositional strategy. Five occurrences are known from amber inclusion and the other 11 are from sedimentary rocks. Six occurrences represent eggs preserved either inside a female abdomen, on an adult body representing brood care, or in close association with adult/larvae body fossils, thus providing a direct taxonomic link to the species level; four are preserved within or attached to leaves, representing endo- or exophytic oviposition; two are found in an organized egg clutch (including the present study); and only four represent isolated findings of individual eggs in sedimentary rocks.

It is likely that the scarcity of the findings of isolated small eggs is largely due to their size. However, taxonomic misidentification can also play a role. Two out of the four records of isolated eggs represent reinterpretation of specimens previously described as plant diaspores. *Palaeoaldrovanda splendens*, originally described as a seed of a freshwater carnivorous plant in the sundew family (Droseraceae) from the Late Cretaceous of the Czech Republic, has recently been reinterpreted as an insect egg (Heřmanová and Kvaček 2010). Similarly, *Knoblochia cretacea*, a Late Cretaceous insect egg taxon from central Europe, was originally described as *Spirellea kvacekii*, belonging to the monocot family Stemonaceae (Pandanales; Heřmanová et al. 2013). There is a large number of diverse insect eggs that resemble plant diaspores (Heřmanová et al. 2013). In particular, eggs of the stick insects are known to have high morphological resemblance to plant diaspores, and also a possible ecological convergence in dispersal (Hughes and Westoby 1992; O'Hanlon et al. 2020). We speculate that many fossil insect eggs may have been misidentified as plant diaspore mesofossils. Historically, misidentification of paleoentomological structures as fossilized plant diaspores hasn't been uncommon: for instance, the type species of the organ genus *Microcarpolithes*, erected for small diaspores of angiospermous affinities, has turned out to be an insect coprolite (Knobloch 1977; Tiffney 1984). Careful re-examinations of paleocarpological specimens and other mesofossils using scanning electron microscopy (SEM) and/or microtomography may reveal additional diversity of insect eggs from the geologic past.

Considering the close relationship between plants and insects throughout the Phanerozoic, it is not surprising that a much richer fossil record exists for impressions of insect eggs preserved with plant tissues, representing endo- and exophytic oviposition. The earliest record of insect egg impressions preserved on plant tissues extends back to the Pennsylvanian (see Introduction). Such records have primarily been treated as trace fossils. Numerous traces of plant–insect interactions, including oviposition, have been studied and classified into functional groups according to morphological and topological characteristics (e.g., Labandeira et al. 2007). Systematically, Vasilenko (2005) erected the ichnofamily Paleoovoididae to accommodate fossil formations interpreted as invertebrate egg batches preserved on different parts of plants, under the group Phagophytichnidea (fossil plant damages). Recently, the existing classification system of fossilized insect traces on plants has been revised in accordance with the International Code of Zoological Nomenclature, with a new subfamily Paleoexoovoidinae proposed for exophytic ovipositions (Enushchenko and Frolov 2020). Krassilov (2008) used a different approach in describing fossilized insect traces (which the author referred to as *phyllostigmas*) and applied plant morphotaxa and the botanical nomenclatorial system in describing the traces. Between the two systematic approaches, the ichnotaxonomic descriptions are more widely applied and also more suitable for the insect traces than the botanical morphotaxa approach.

The rich trace fossil record of egg impressions on plant materials provides us with more information about insect eggs from the geologic past, in addition to the structurally preserved fossils. When well preserved, the egg dimensions as well as the overall shape can be extracted from such traces, in addition to their ovipositional pattern. Chorionic characters would hardly be recognizable in such impressions because plant tissues overlie the eggs and obscure the ultrastructure in endophytic oviposition, as well as some exophytic oviposition, if the eggs are laid on the opposite side of the exposed leaf surface. However, in rare cases of exceptional preservation, chorions are structurally preserved in association with plant fossils: attached to plant surface or cuticle (Krassilov 2008; Pott et al. 2008; Fisher and Watson 2015) or in between the adaxial and abaxial cuticle (Feng et al. 2022). Such examples not only preserve impressions of eggs and their ovipositional patterns, but also the fine chorionic details, which are important in studying and classifying extant insect eggs. Currently, there is no uniform approach in differentiating the structurally preserved egg remains from their impressions left on fossil plants. Structurally preserved chorions are sometimes described using organ- or morphotaxonomic practices (e.g., Krassilov 2008; Fisher and Watson 2015), but ichnotaxonomy is also used (e.g., Enushchenko and Frolov 2020). In the latter, the ultrastructure of the preserved eggs can be overlooked as the ichnological approach tends to focus more on the traces of eggs and their arrangement. For example, the recently described ichnospecies *Paleoovidus vasilenkoi* preserves fragments of two closely spaced eggs, which appear to preserve chorionic ultrastructure (Enushchenko and Frolov 2020, Figure 2). However, such microscopic details are not included in the descriptions.

Establishing an organizational system of fossil insect eggs that preserve distinct morphological characters and/or chorion ultrastructure would aid researchers in making geographic, stratigraphic, and taxonomic comparisons more easily. A similar problem has been addressed in vertebrate paleontology by using a parataxonomic system, namely ootaxonomy. According to Mikhailov et al. (1996), binomial nomenclature of fossil vertebrate eggs has been widely practiced beginning in the 1950s by Chinese paleontologists, followed by other researchers in the 1990s. However, due to the varying methodologies and criteria for egg identification and description, challenges arose regarding taxonomic, geographic, and stratigraphic correlations, as well as paleobiological interpretations. Thus, a more uniform parataxonomic approach, ootaxonomy, has been practiced starting in the late 1980s, which enabled geographic and stratigraphic correlations of fossil eggs, as well as improved our understanding of their paleobiological and paleoecological inmplications. Ootaxa are described based on their morphology, including the shape, pore systems, and sculpturing of the shell's outer surface, and the root *oolithus*—meaning *stone egg*—is included in the oofamily and oogenus of egg parataxa to distinguish them from animal taxa (Mikhailov et al. 1996). Mikhailov and colleagues noted that structural differences in the eggshells reflect systematic relations in their producers; thus, fossil egg parataxa are not arbitrary, but instead closely reflect phylogenetic relationships.

This approach has yet to be adopted for describing fossilized invertebrate eggs. In addition to their small size, their compositions make them much less likely to be fossilized (Zatoń et al. 2009) compared to the calcareous shells of the amniotic eggs. However, many insect eggs, similar to amniote eggs, have successfully adapted to their terrestrial environments, with a more structurally rigid and protective eggshell. Additional ovipositional strategies may also improve the structural rigidity of these insect eggs, thus increasing the likelihood of their fossilization (see below). A tremendous morphological diversity exists among insect eggs, yet they can readily be compared across distant lineages using quantitative traits (Church et al. 2019a, 2019b), which is comparable to the ootaxaonomic system of fossil amniote eggs. The number of known occurrences of fossil insect eggs with fine preservation has grown rapidly, and the number will likely continue to increase. Thus, we advocate for adopting ootaxonomy in describing fossil insect eggs, including a more uniform descriptive language, similar to the

practice already followed in studying amniotic eggs. The potential application of ootaxonomy in fossil eggs of invertebrate origin has already been noted by Mikhailov et al. (1996: 763).

We propose a single oofamily Entomoolithidae for fossilized insect eggs with preserved distinctive morphological characters and/or ultrastructure. The 16 examples summarized in Table 2 including *C. laddi*, as well as other similar examples with better chorionic descriptions, including the exophytically preserved *P. vasilenkoi* (Enushchenko and Frolov 2020), would fit into the new oofamily. We suggest including the root *entomoolithus* in the oogenus names, to distinguish them from animal taxa as well as other amniotic ootaxa. Although the number of known fossil insect eggs has increased rapidly and likely will continue to grow, the eggs are less likely to be fossilized than amniotic ones. Considering the taphonomy and the number of known occurrences thus far, we propose a single oofamily for now, but the number may grow in the future with more discoveries. This is also comparable to the family-level classification of the ichnofamily Paleoovoididae, representing impressions of invertebrate egg clutches preserved on various plant parts (Vasilenko 2005; Enushchenko and Frolov 2020). The largest known living insect egg is approximately 16.5 mm long and 3 mm wide, belonging to a xylocopine carpenter bee (Church et al. 2019a, 2019b), which provides a rough upper boundary of consideration.

We suggest that diagnoses of fossil insect ootaxa include the following defining egg traits when preserved, as defined by Church et al. (2019a, 2019b): length, width and/or breadth, aspect ratio, asymmetry, and angle of curvature. The egg volume is also a defining trait in Church et al. (2019a, 2019b), but it can readily be calculated from the length and width. Such quantitative traits measured from fossil eggs can readily be compared to the large dataset of extant insect egg morphology, encompassing over 6,700 species. The key trait values of the selected occurrences that would be placed under Entomoolithidae are provided in Table 2. Values with asterisk signs indicate that they were not provided in the written descriptions and are calculated from accompanied figures. "N/A" is used when there was no given value and figures cannot provide sufficient details for measurement. Many written descriptions are missing the aspect ratio, asymmetry, and degree of curvature. We also suggest providing detailed measurements of length and width in a range, as the current descriptive languages vary in their precision, and many are given as approximations. Describing fossil insects using a set of qualitative characters and uniform descriptive language, in accordance with the extant insect egg descriptions, will allow us to quantitatively compare them to the eggs of living groups for taxonomic correlations. Additionally, chorion characters, such as the chorion sculpture, micropyles, attachment structures, and other ultrastructures should be described, when preserved, using descriptive terminology similar to that as reviewed and practiced in Fisher and Watson (2015).

The key traits used for identifying insect eggs differ from the amniotic eggs. In amniotic eggshells, differences in the structural organizations of biocrystalline materials are distinctive among different groups, providing an important key for taxonomic correlations (Mikhailov et al. 1996). Therefore, making histological examinations is important in identifying vertebrate eggs. In contrast, extant insect ootaxonomy is mostly based on the chorionic ultrastructure, which is externally available for examination. Thus, not all the 16 selected occurrences of fossil insect eggs presented in Table 2 that would fit under the newly proposed oofamily Entomoolithidae have structurally preserved eggshells showing distinct eggshell layers. Instead, these occurrences preserve the overall egg morphology, from which most of the defining egg traits *sensu* Church et al. (2019a, 2019b) can be measured, as well as distinctive morphological and/or chorionic characters, which are important in identifying and classifying insect eggs. Therefore, the selected examples include some structurally preserved specimens, but also casts preserving identifiable morphological details as well as compressions preserving fine morphological details. Rare cases of preserved chorions from endo- or exophytic ovipositions are also included, as they represent the actual egg. Such chorionic ultrastructures wouldn't be preserved in most ovipositional impressions in the ichnofamily Paleoovoididae

because the plant tissues usually overlie the eggs and their chorionic ultrastructure. However, their morphology, when distinctive enough, can also help making taxonomic correlations to the ichnotaxa as well; thus, we recommend that the descriptions of the traces of endo- and exophytic oviposition also include the quantitative measures of the defining egg traits *sensu* Church et al. (2019a, 2019b). Taxonomic identification of fossil insect eggs can significantly improve when ichnological evidence is preserved together, such as the arrangement of egg clutch, ovipositional patterns, or the presence of oothecae. Examining the specimen of interest using both oological and ichnological evidence may be needed to better understand their taxonomic affinities, as in the present study.

Lastly, it is worth noting that certain ovipositional strategies may increase the likelihood of fossilization of the laid eggs. Grasshopper oothecal secretions not only provide the structural rigidity of the protective oothecae through sclerotization and melanization, but also result in the tanning of the eggs, which further sclerotize them and make them more impermeable (Eisner et al. 1966). This may have contributed to the preservation of *C. laddi* described herein, which are frequently found in clusters with (sub)parallel orientations. Additionally, in other groups of insects the colleterial glands, responsible for the production of oothecal structural proteins in the dictyopterans, as well as other reproductive glands, also produce a viscous adhesive secretion that coats eggs, helping them stick to various substrates. Such secretions are also known to become hardened upon contact with the air (Berry 1968), which can increase the structural rigidity and thus the likelihood of fossilization. The four previously described fossil insect eggs that are found as isolated specimens (Gall and Tiffney 1983; Sellick 1994; Heřmanová and Kvaček 2010; Heřmanová et al. 2013) have a phasmatodean or lepidopteran affinity or have morphological resemblance to both groups. Their extant members are known to coat their eggs with adhesive secretions (Berry 1968; Büscher et al. 2020), which may have aided their fossilization. Studying the ovipositional behavior and ecology of extant insects may help us better understand the preservational biases in fossil insect eggs.

An unusual preservation in a cooling and drying environment

The John Day Basin of eastern and central Oregon preserves remarkably complete terrestrial sedimentary sequences from the middle Eocene to upper Miocene (ca. 47–7 Ma). The upper Eocene to lower Miocene John Day Formation is subdivided into seven members—Big Basin, Turtle Cove, Kimberly, Haystack Valley, Balm Creek, Johnson Canyon, and Rose Creek—in successive order (Albright et al. 2008). Abundant plant fossils are known from the early Oligocene Bridge Creek flora of the Big Basin Member, but few vertebrate remains are known from it (Samuels et al. 2016; Jacisin and Hopkins 2018). In contrast, the overlying Turtle Cove and Kimberly members yield few fossil plants but preserve an exceptional collection of Oligocene fauna (Fremd 2010; Graham 2014). The Bridge Creek flora, preserving at least 125 species that inhabited a lake margin environment, includes mostly broad-leaved deciduous trees, several conifer species, with *Metasequoia* being the most common, as well as ferns and horsetails, and is taxonomically and physiognomically comparable to the mixed mesophytic forests of the mesic region in East Asia today (Meyer and Manchester 1997). This flora marks the transition from a warmer Eocene (sub)tropical climate, exemplified by the boreotropical Clarno Nut Bed flora from the underlying Eocene Clarno Formation (Dillhoff et al. 2009), to a cooler, more temperate climate in the early Oligocene (Manchester and Meyer 1987; Meyer and Manchester 1997; Manchester 2000; Dillhoff et al. 2009). The Eocene–Oligocene transition (ca. 34 Ma) represents a climatic shift from a largely ice-free greenhouse to an icehouse climate, involving global cooling and the first major glaciation of Antarctica (Hutchinson et al. 2021), during which the exceptionally preserved floras and faunas of the John Day Formation were deposited. However, it has been suggested that global vegetation change across this transition was spatially and temporally heterogeneous in both hemispheres and does not represent a single response to rapid cooling (Pound and Salzmann 2017).

A significant portion of JODA's fossil specimens comes from the highly fossiliferous Turtle Cove Member (ca. 31.45–26.6 Ma), yielding approximately 6,800–13,800 catalogued paleontological specimens (Kort and Famoso 2020). It consists of interbedded soft claystone, siltstone, and blue-green zeolitized tuffaceous claystones (Fremd 2010). Remains of fossil plants are poorly known, although vegetative and reproductive remains belonging to Ulmaceae, Cannabaceae, and Rosaceae have been recovered (JODA 13070: Chaney 1925; Fremd 2010; Graham 2014; Retallack and Samuels 2020). The exceptional Oligocene Turtle Cove fauna includes about 82 vertebrate genera representing reptiles (tortoise, snake, and worm lizards), birds, and almost 74 species of mammals, ranging from marsupials to various carnivorans, ungulates, rodents, and lagomorphs (Leidy 1871; Cope 1873, 1884; Marsh 1874; Hay 1908; Shufeldt 1915; Stock and Furlong 1922; Stirton and Rensberger 1964; Berman 1976; Dingus 1990; Fremd 2010; Korth and Samuels 2015; Prothero 2015; Samuels et al. 2015; Famoso et al. 2016; Korth and Cavin 2016; Famoso 2017; Jewell 2019; Paterson et al. 2020; Samuels 2021; Famoso and Orcutt 2022). Famous elements include *Miohippus*, an important early horse species that advanced understanding of the evolution of horses (Marsh 1874; Famoso 2017), the false saber-toothed feliforms of the family Nimravidae (Albright et al. 2008; Barrett et al. 2021), and the last known North American primate *Ekgmowechashala* until the arrival of humans ca. 25 million years later (Samuels et al. 2015).

Many of the paleoenvironmental interpretations of the John Day Formation come from the analyses of paleosols. Paleosols from the Clarno Formation and the Big Basin and Turtle Cove Members of the John Day Formation display a stepwise change from ultisol- to alfisol- to inceptisole-like paleosols, representing the climatic and biotic shifts from the humid subtropical Eocene to the subhumid or dry and temperate Oligocene conditions (Bestland et al. 1997; Retallack 2004; Retallack and Samuels 2020). The transition from the non-calcareous alfisol- and inceptisol-like paleosols to calcareous inceptisol- andandisol-like paleosols occurring around the boundary between the Big Basin and the Turtle Cove Members (ca. 30 Ma) is thought to reflect the mid-Oligocene global cooling (Bestland et al. 1997). Specifically, the occurrences of shallow calcic (Xaxuspa and Yapaspa) and deep calcic (Xaxus and Yapas) pedotypes, formerly vitrand soils (grass-shard-rich andisols), in the lower Turtle Cove Member suggest a wooded grassland environment (Retallack 2004; Retallack and Samuels 2020).

The gradual environmental shift towards cool and dry conditions throughout the Turtle Cove Member, transitioning from a woodland to an open forest environment, similar to the underlying Bridge Creek flora, fostered browsers, like three-toed horses, mouse-deer, burrowing beavers, and oreodonts; grazers, like the two species of the rhino *Diceratherium*; carnivores, including many species of canids, bear-dogs, and nimravids; as well as some arboreal animals, including tree squirrels and a primate (Albright et al. 2008; Fremd 2010; Korth and Samuels 2015). Remarkably, the Turtle Cove Member has 13 described species of dogs (Canidae), representing the most diverse canid assemblage known to date (Tedford et al. 2009; Fremd 2010). Its gradual transition into more open vegetation also provided more habitats for an array of fossorial animals: the burrowing beavers *Palaeocastor peninsulatus* and *Capacikala gradatus* that used scratch-digging behavior and/or flattened incisors represent the first appearance of burrowing mammals in Oregon (Korth and Samuels 2015). Soon after, gophers diversified and the specialized tooth-digging beaver *Palaeocastor fossor* appeared (Samuels and Valkenburgh 2009; Korth and Samuels 2015). The small entoptychine gophers and the larger burrowing beaver *P. fossor* likely partitioned their niche by preferring different soil depth and consistency, as seen in extant rodents (Nevo 1999: 413). Additionally, trace fossils belonging to ichnogenera *Edaphichnium* and *Taenidium*, representing earthworm chimneys and cicada burrows, respectively, are known from the Turtle Cove Member (Retallack 2004; Retallack and Samuels 2020). *Subterroothecichnus radialis* igen. et isp. nov. and *Curvellipsoentomoolithus laddi* oogen. et oosp. nov., newly described herein, further support that the Turtle Cove Member had complex and thriving underground communities, in addition to diverse and heterogenous above-ground landscapes.

It is likely that the oviposition and the formation of the egg pods occurred in a riparian environment. The holotype JODA 17384 as well as several other partial egg clutch specimens are preserved in a more sandy matrix, which would represent fluvial channel deposits. The underground deposition of the egg pods near the banks would have helped their preservation when a flood further buried them and created an anoxic environment for their fossilization. Extant female grasshoppers lay their eggs in xero-, meso-, and hygrophilic soils (Katiyar 1957), although some species are known to prefer moist sand over all other soil types of different moisture levels, and to avoid completely dry soil (Edwards and Epp 1965). Additionally, several grasshopper taxa have radiated into freshwater environments globally, including floating aquatic vegetation, plants adapted to flooded zones, and vegetation on floodplains and shores of running rivers (Amédégnato and Devriese 2008). *Hieroglyphus concolor*, the aforementioned grasshopper species whose egg pod bears a close resemblance to those of *S. radialis* (Katiyar 1957; Figure 5D), is known to inhabit marshy environments, wet ditches, and grassy banks, although it is unknown yet whether there is any correlation between *H. concolor* habitat preference and egg pod morphology. We speculate that the JODA 17384 specimen, as well as other 26 isolated egg clutches, were laid near the banks and subsequently buried by floods.

Grasshoppers play a pivotal role in extant ecosystems. For instance, grasshopper species have the largest faunal populations in grassland ecosystems (Guo et al. 2006). As primary consumers, they can accelerate nutrient cycling, influence soil microbial and mycorrhizal symbiont communities, and increase primary productivity in the long term (Belovsky 2000; Kula et al. 2005; Ibanez et al. 2023). Also, grasshoppers support communities of secondary or higher-level consumers, such as predaceous and parasitoid insects, spiders, amphibians, reptiles, birds, and various mammals, including mice, rats, shrews, gophers, and badgers (Belovsky and Slade 1993; Hostetter 2000). Grasshopper egg pods are also consumed by several animals: larvae of several species of ground beetles (Coleoptera: Carabidae), blister beetles (Coleoptera: Meloidae), bee flies (Diptera: Bombyliidae), as well as many burrowing and non-burrowing, omnivorous and insectivorous mammals (Hostetter 2000). Several *Scelio* species of the large and cosmopolitan egg parasitoid wasp family Scelionidae are known parasitoids of grasshopper eggs (Dysart 1995; Baker et al. 1996). Although the occurrences of *Curvellipsoentomoolithus laddi* oosp. nov. throughout subunits A–H of the Turtle Cove Member are not conclusive evidence of the grasshopper's presence throughout the member, it is likely that such isolated or clustered specimens of *C. laddi*, frequently in (sub)parallel orientations, come from grasshopper egg pods and represent a relatively stable caeliferan presence in the Turtle Cove fauna. Grasshoppers and their eggs could have been preyed upon by various insectivores known from the Turtle Cove Member, including shrews, moles, and the Oligocene insectivore *Micropternodus* (Russell 1960; Albright et al. 2008; Fremd 2010; Famoso et al. 2016), as well as an array of rodents (Fremd 2010; Korth and Samuels 2015). Overall, *Subterroothecichnus radialis* igen. et isp. nov. and *Curvellipsoentomoolithus laddi* oogen. et oosp. nov., newly described from the exquisitely preserved caeliferan ootheca in John Day Fossil Beds National Monument, enrich our understanding of the ecology and environment of the Turtle Cove Member, as well as the diversity of past life.

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REFERENCES

Abram, P.K., E. Guerra-Grenier, M.L. Després-Einspenner, S. Ito, K. Wakamatsu, G. Boivin, and J. Brodeur. 2015. An insect with selective control of egg coloration. *Current Biology* 25(15): 2007–2011. https://doi.org/10.1016/j.cub.2015.06.010

Adis, J., O. Zompro, E. Moombolah-Goagoses, and E. Marais. 2002. Gladiators: A new order of insect. *Scientific American* 287(5): 60–65. https://doi.org/10.1038/scientificamerican1102-60

Albright, L.B. III, M.O. Woodburne, T.J. Fremd, C.C. Swisher III, B.J. MacFadden, and G.R. Scott. 2008. Revised chronostratigraphy and biostratigraphy of the John Day Formation (Turtle Cove and Kimberly Members), Oregon, with implications for updated calibration of the Arikareean North American Land Mammal Age. *The Journal of Geology* 116(3): 211–237. https://doi.org/10.1086/587650

Al-Dosary, M.M., A.M. Al-Bekairi, and E.B. Moursy. 2010. Morphology of the egg shell and the developing embryo of the red palm weevil, *Rhynchophorus ferrugineus* (Oliver). *Saudi Journal of Biological Sciences* 17(2): 177–183. https://doi.org/10.1016/j.sjbs.2010.02.012

Alonso-Zarza, A.M., and P.G. Silva. 2002. Quaternary laminar calcretes with bee nests: Evidences of small-scale climatic fluctuations, Eastern Canary Islands, Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 178(1–2): 119–135. https://doi.org/10.1016/S0031-0182(01)00405-9

Amédégnato, C., and H. Devriese. 2008. Global diversity of true and pygmy grasshoppers (Acridomorpha, Orthoptera) in freshwater. *Hydrobiologia* 595(1): 535–543. https://doi.org/10.1007/s10750-007-9132-z

Anisyutkin, L.D., V.G. Grachev, A.G. Ponomarenko, A.P. Rasnitsyn, and P. Vršanský. 2008. Fossil insects in the Cretaceous mangrove facies of Southern Negev, Israel. In *Plant-Arthropod Interactions in the Early Angiosperm History: Evidence from the Cretaceous of Israel* V. Krassilov and A.P. Rasnitsyn, eds. Leiden: Brill, 189–224. https://doi.org/10.1163/ej.9789004170711.1-229

Baccetti, B. 1967. L'ultrastruttura delle ghiandole della ooteca in Ortotteri Acridoidei, Blattoidei e Mantoidei. *Zeitschrift für Zellforschung* 77: 64–79. https://doi.org/10.1007/BF00336699

Bailey, M.M. 1989. Revisions to stratigraphic nomenclature of the Picture Gorge Basalt Subgroup, Columbia River Basalt Group. In *Volcanism and Tectonism in the Columbia River Flood-Basalt Province*/ S.P. Reidel and P.R. Hooper, eds. Special Paper 239. Boulder, CO: Geological Society of America, 67–84. https://doi.org/10.1130/SPE239-p67

Baker, G.L., R.J. Dysart, and R.G. Pigott. 1996. Parasitism of grasshopper and locust eggs (Orthoptera: Acrididae) by *Scelio* species (Hymenoptera: Scelionidae) in southern Australia. *Australian Journal of Zoology* 44(4): 427. https://doi.org/10.1071/ZO9960427

Barrett, P.Z., S.S.B. Hopkins, and S.A. Price. 2021. How many sabertooths? Reevaluating the number of carnivoran sabretooth lineages with total-evidence Bayesian techniques and a novel origin of the Miocene Nimravidae. *Journal of Vertebrate Paleontology* 41(1): e1923523. https://doi.org/10.1080/02724634.2021.1923523

Bedford, G.O. 1978. Biology and ecology of the Phasmatodea. *Annual Review of Entomology* 23: 125–149.

Belovsky, G.E. 2000. Do grasshoppers diminish grassland productivity? A new perspective for control based on conservation. In *Grasshoppers and Grassland Health*. J.A. Lockwood, A.V. Latchininsky, and M.G. Sergeev, eds.

Dordrecht: Springer Netherlands, 7–29. https://doi.org/10.1007/978-94-011-4337-0_2

Belovsky, G.E., and J.B. Slade. 1993. The role of vertebrate and invertebrate predators in a grasshopper community. *Oikos* 68(2): 193–201.

Berman, D.S. 1976. A new Amphisbaenian (Reptilia: Amphisbaenia) from the Oligocene-Miocene John Day Formation, Oregon. *Journal of Paleontology* 50(1): 165–174.

Berry, S.J. 1968. The fine structure of the colleterial glands of *Hyalophora cecropia* (Lepidoptera). *Journal of Morphology* 125(3): 259–279. https://doi.org/10.1002/jmor.1051250302

Bestland, E.A., G.J. Retallack, and C.C. Swisher. 1997. Stepwise climate change recorded in Eocene-Oligocene paleosol sequences from central Oregon. *Journal of Geology* 105(2): 153–172. https://doi.org/10.1086/515906

Blackith, R.E., and R.M. Blackith. 1966. The anatomy and physiology of the Morabine grasshoppers I. Digestive and reproductive systems. *Australian Journal of Zoology* 14(1): 31–48. https://doi.org/10.1071/ZO9660031

Blackith, R.E., and R.M. Blackith. 1969. Observations on the biology of some Morabine grasshoppers. *Australian Journal of Zoology* 17(1): 1–12. https://doi.org/10.1071/ZO9690001

Braker, H.E. 1989. Evolution and ecology of oviposition on host plants by Acridoid grasshoppers. *Biological Journal of the Linnean Society* 38: 389–406.

Brannoch, S.K., F. Wieland, J. Rivera, K.D. Klass, O. Béthoux, and G.J. Svenson. 2017. Manual of praying mantis morphology, nomenclature, and practices (Insecta, Mantodea). *ZooKeys* 696: 1–100. https://doi.org/10.3897/zookeys.696.12542

Branson, D.H., and L.T. Vermeire. 2007. Grasshopper egg mortality mediated by oviposition tactics and fire intensity. *Ecological Entomology* 32(1): 128–134. https://doi.org/10.1111/j.1365-2311.2006.00847.x

Brunet, P.C.J. 1951. The formation of the ootheca by *Periplaneta americana*. *Journal of Cell Science* 3(18): 113–127.

Büscher, T.H., E. Quigley, and S.N. Gorb. 2020. Adhesion performance in the eggs of the Philippine leaf insect *Phyllium philippinicum* (Phasmatodea: Phylliidae). *Insects* 11(7): 1–20. https://doi.org/10.3390/insects11070400

Cariglino, B., M.B. Lara, and A.M. Zavattieri. 2020. Earliest record of fossil insect oothecae confirms the presence of Crown-Dictyopteran Taxa in the Late Triassic. *Systematic Entomology* 45(4): 935–947. https://doi.org/10.1111/syen.12442

Chaney, R.W. 1925. Notes on two fossil hackberries from the Tertiary of the western United States. Publication 349. Washington, DC: Carnegie Institution of Washington, 51–56.

Chapman, R.F. 1998. *The Insects: Structure and Function*. London: Cambridge University Press.

Chapman, R.F., and I.A.D. Robertson. 1958. The egg pods of some tropical African grasshoppers. *Journal of the Entomological Society of South Africa* 21(1): 85–112.

Chaves, L.F., P. Ramoni-Perazzi, E. Lizano, and N. Añez. 2003. Morphometrical changes in eggs of *Rhodnius Prolixus* (Heteroptera: Reduviidae) during development. *Entomotropica* 18(2): 83–88.

Chen, L., J.-J. Gu, Q. Yang, D. Ren, A. Blanke, and O. Béthoux. 2021. Ovipositor and mouthparts in a fossil insect support a novel ecological role for early Orthopterans in 300 million years old forests. *eLife* 10: e71006. https://doi.org/10.7554/eLife.71006

Chen, Z.T. 2022. Bizarre egg structure uncovers a new family of Plecoptera (Insecta) from Mid-Cretaceous Burmese amber. *Fossil Record* 25(1): 75–82. https://doi.org/10.3897/fr.25.81862

Chen, Z.T., and C.P. Xu. 2022. A new stonefly of Petroperlidae (Insecta: Plecoptera) and its eggs from Mid-Cretaceous Kachin Amber. *Cretaceous Research* 138: 105272. https://doi.org/10.1016/j.cretres.2022.105272

Chernyakhovskii, M.E. 2006. New and little known egg-pods of Acridids (Orthoptera, Acrididae) of the fauna of Russia and adjacent countries. *Entomological Review* 86(6): 635–637. https://doi.org/10.1134/s0013873806060030

Church, S.H., S. Donoughe, B.A.S. de Medeiros, and C.G. Extavour. 2019a. Insect egg size and shape evolve with ecology but not developmental rate. *Nature* 571(7763): 58–62. https://doi.org/10.1038/s41586-019-1302-4

Church, S.H., S. Donoughe, B.A.S. de Medeiros, and C.G. Extavour. 2019b. A dataset of egg size and shape from more than 6,700 insect species. *Scientific Data* 6(1). https://doi.org/10.1038/s41597-019-0049-y

Cope, E.D. 1873. Third notice of extinct Vertebrata from the Tertiary of the Plains. *Paleontological Bulletin* 16: 1–8.

Cope, E.D. 1884. *The Vertebrata of the Tertiary Formations of the West, Book 1*." US Geological Survey of the Territories Report 3. Washington, DC: US Geological Survey.

Courrent, A., A. Quennedey, C.A. Nalepa, A. Robert, M. Lenz, and C. Bordereau. 2008. The fine structure of colleterial glands in two cockroaches and three termites, including a detailed study of *Cryptocercus punctulatus* (Blattaria, Cryptocercidae) and *Mastotermes darwiniensis* (Isoptera, Mastotermitidae). *Arthropod Structure & Development* 37(1): 55–66. https://doi.org/10.1016/j.asd.2007.03.004

Desurmont, G.A., and P.A. Weston. 2011. Aggregative oviposition of a phytophagous beetle overcomes egg-crushing plant defences. *Ecological Entomology* 36(3): 335–343. https://doi.org/10.1111/j.1365-2311.2011.01277.x

Dillhoff, R.M., T.A. Dillhoff, R.E. Dunn, J.A. Myers, and C.A.E. Strömberg. 2009. Cenozoic paleobotany of the John Day Basin, Central Oregon. In *Volcanoes to Vineyards: Geologic Field Trips through the Dynamic Landscape of the Pacific Northwest*. J.E.O'Connor, R.J. Dorsey, and I.P. Madin, eds. Geological Society of America Field Guide 15. Boulder, CO: Geological Society of America, 135–164.

Dingus, L. 1990. Systematics, stratigraphy, and chronology for mammalian fossils (Late Arikareean to Hemingfordian) from the uppermost John Day Formation, Warm Springs, Oregon. *PaleoBios* 12: 1–24.

Donelson, N.C., A.R. Smith, and M.J. Van Staaden. 2008. Variation in adult longevity in a polymorphic grasshopper species. *Journal of Orthoptera Research* 17(2): 279–282. https://doi.org/10.1665/1082-6467-17.2.279

Donoughe, S. 2022. Insect egg morphology: Evolution, development, and ecology. *Current Opinion in Insect Science* 50: 100868. https://doi.org/10.1016/j.cois.2021.12.008

Du, E., S. Wang, Y.X. Luan, C. Zhou, Z. Li, N. Li, S. Zhou, et al. 2022. Convergent adaptation of ootheca formation as a reproductive strategy in Polyneoptera. *Molecular Biology and Evolution* 39(3). https://doi.org/10.1093/molbev/msac042

Dysart, R.J. 1995. New host records for North American *Scelio* (Hymenoptera: Scelionidae), parasitic on grasshopper eggs (Orthoptera: Acrididae). *Journal of the Kansas Entomological Society* 68(1): 74–79.

Dysart, R.J. 2000. Insect predators and parasites of grasshopper eggs. In *Grasshopper Integrated Pest Management User Handbook*. G.L. Cunningham and M.W. Sampson, eds. Technical Bulletin 1809. Washington DC: US Department of Agriculture, Animal and Plant Health Inspection Service.

Edwards, N., and J. Meco. 2000. Morphology and palaeoenvironment of brood cells of quaternary ground-nesting solitary bees (Hymenoptera, Apidae) from Fuerteventura, Canary Islands, Spain. *Proceedings of the Geologists' Association* 111(2): 173–183. https://doi.org/10.1016/S0016-7878(00)80007-3

Edwards, R.L., and H.T. Epp. 1965. The influence of soil moisture and soil type on the oviposition behaviour of the migratory grasshopper, *Melanoplus sanguinipes* (Fabricius). *The Canadian Entomologist* 97(4): 401–409. https://doi.org/10.4039/Ent97401-4

Ehrmann, R. 2011. Mantodea from Turkey and Cyprus (Dictyoptera: Mantodea). *Articulata* 26(1): 1–42.

Eisner, T., M. Eisner, C. Rossini, V.K. Iyengar, B.L. Roach, E. Benedikt, and J. Meinwald. 2020. Chemical defense against predation in an insect egg. *Proceedings of the National Academy of Sciences* 97(4): 1634–1639.

Eisner, T., J. Shepherd, and G.M. Happ. 1966. Tanning of grasshopper eggs by an exocrine secretion. *Science* 152: 95–97. https://doi.org/10.1126/science.152.3718.95

Ellis, W.N., and A.C. Ellis-Adam. 1993. Fossil brood cells of solitary bees on Fuerteventura and Lanzarote, Canary Islands (Hymenoptera: Apoidea). *Entomologische Berichten Amsterdam* 53(12): 161–173.

Enushchenko, I.V., and A.O. Frolov. 2020. Revision of existing classification of fossil insect feeding traces and description of new ichnotaxa from Middle Jurassic sediments of eastern Siberia (Russia). *Zootaxa* 4758(2): 347–359. https://doi.org/10.11646/zootaxa.4758.2.8

Famoso, N.A. 2017. Statistical analysis of dental Variation in the Oligocene equid *Miohippus* (Mammalia, Perissodactyla) of Oregon. *Journal of Paleontology* 91(5): 1060–1068. https://doi.org/10.1017/jpa.2017.42

Famoso, N.A., and J.D. Orcutt. 2022. First occurrences of *Palaeogale* von Meyer, 1846 in the Pacific Northwest, United States. *Geodiversitas* 44(14): 427–436. https://doi.org/10.5252/geodiversitas2022v44a14

Famoso, N.A., J.X. Samuels, S.S.B. Hopkins, E.B. Davis, and M.M. Emery. 2016. Updated biostratigraphy of the Turtle Cove Member (John Day Formation) in the John Day Basin, Oregon. Society of Vertebrate Paleontology Meeting Abstract*s*.

Fatouros, N.E., A. Cusumano, F. Bin, A. Polaszek, and J.C. Van Lenteren. 2020. How to escape from insect egg parasitoids: A review of potential factors explaining parasitoid absence across the Insecta. *Proceedings of the Royal Society B: Biological Sciences* 287(1931). https://doi.org/10.1098/rspb.2020.0344

Feng, Z., S. Wan, Q. Sui, C. Labandeira, Y. Guo, and J. Chen. 2022. A Triassic tritrophic triad documents an early food-web cascade. *Current Biology* 32(23): 5165–5171.e2. https://doi.org/10.1016/j.cub.2022.10.031

Ferenz, H.G., and K. Seidelmann. 2003. Pheromones in relation to aggregation and reproduction in desert locusts. *Physiological Entomology* 28(1): 11–18. https://doi.org/10.1046/j.1365-3032.2003.00318.x

Fisher, H.L., and J. Watson. 2015. A fossil insect egg on an Early Cretaceous conifer shoot from the Wealden of Germany. *Cretaceous Research* 53: 38–47. https://doi.org/10.1016/j.cretres.2014.10.013

Flowers, R.W., and C.S. Chaboo. 2015. Natural history of the tortoise beetle, *Discomorpha* (*Discomorpha*) *Biplagiata* (Guérin) (Chrysomelidae: Cassidinae: Omocerini). *Insecta Mundi* 439: 1–10.

Forsman, A. 2001. Clutch size versus clutch interval: Life history strategies in the colour-polymorphic pygmy grasshopper *Tetrix subulata*. *Oecologia* 129(3): 357–366. https://doi.org/10.1007/s004420100743

Fremd, T.J. 2010. *Guidebook—SVP Field Symposium 2010 John Day Basin Field Conference, John Day Fossil Beds National Monument (and Surrounding Basin), Oregon, USA*. Society of Vertebrate Paleontology.

Fu, Y., C. Cai, P. Chen, and D. Huang. 2022. The earliest known brood care in insects. *Proceedings of the Royal Society B* 289: 20220447. https://doi.org/10.1098/rspb.2022.044

Gall, L.F., and B.H. Tiffney. 1983. A fossil noctuid moth egg from the Late Cretaceous of eastern North America. *Science* 219(4584): 507–509. https://doi.org/10.1126/science.219.4584.507

Ganguly, A., C. Malakar, H. Anand, S. Das, A. Das, and P. Haldar. 2008. Scanning electron microscopy of egg-surface sculpturing of two common Indian short-horn grasshoppers (Orthoptera, Acrididae). *Journal of Orthoptera Research* 17(1): 97–100.

Gao, T., C. Shih, C.C. Labandeira, X. Liu, Z. Wang, Y. Che, X. Yin, and D. Ren. 2019. Maternal care by Early Cretaceous cockroaches. *Journal of Systematic Palaeontology* 17(5): 379–391. https://doi.org/10.1080/14772019.2018.1426059

Genise, J.F., A.M. Alonso-Zarza, M. Verde, and A. Meléndez. 2013. Insect trace fossils in Aeolian deposits and calcretes from the Canary Islands: Their ichnotaxonomy, producers, and palaeoenvironmental significance. *Palaeogeography, Palaeoclimatology, Palaeoecology* 377: 110–124. https://doi.org/10.1016/j.palaeo.2013.03.005.

Genise, J.F., and N. Edwards. 2003. Ichnotaxonomy, origin, and paleoenvironment of Quaternary insect cells from Fuerteventura, Canary Islands, Spain. *Journal of the Kansas Entomological Society* 76(2): 320–327.

Gillott, C. 2003. Insect accessory reproductive glands: Key players in production and protection of eggs. In *Chemoecology of Insect Eggs and Egg Deposition*. M. Hilker and T. Meiners, eds. Berlin and Vienna: Blackwell, 37–59. https://doi.org/10.1002/9780470760253.ch2

Goldberg, J., J. Bresseel, J. Constant, B. Kneubühler, F. Leubner, P. Michalik, and S. Bradler. 2015. Extreme convergence in egg-laying strategy across insect orders. *Scientific Reports* 5: 7825. https://doi.org/10.1038/srep07825

Graham, J.P. 2014. *John Day Fossil Beds National Monument Geologic Resources Inventory Report*. Natural Resource Stewardship and Science Natural Resource Report NPS/NRSS/GRD/NRR—2014/846. Washington, DC: National Park Service.

Guo, Z.-W., H.-C. Li, and Y.-L. Gan. 2006. Grasshopper (Orthoptera: Acrididae) biodiversity and grassland ecosystems. *Insect Science* 13(3): 221–227. https://doi.org/10.1111/j.1744-7917.2006.00086.x

Hackman, R.H., and M. Goldberg. 1960. Composition of the Oothecae of three orthoptera. *Journal of Insect Physiology* 5(1): 73–78. https://doi.org/10.1016/0022-1910(60)90024-X

Hay, O.P. 1908. *The Fossil Turtles of North America*. Publication 75. Washington, DC: Carnegie Institution of Washington.

Heřmanová, Z., E. Bodor, and J. Kvaček. 2013. *Knoblochia cretacea*, Late Cretaceous insect eggs from Central Europe. *Cretaceous Research* 45: 7–15. https://doi.org/10.1016/j.cretres.2013.07.001

Heřmanová, Z., and J. Kvaček. 2010. Late Cretaceous Palaeoaldrovanda, not seeds of a carnivorous plant, but eggs of an insect. *Journal of the National Museum (Prague)*, Natural History Series 179(9): 105–118.

Herrmann, D.L., A.E. Ko, S. Bhatt, J.E. Jannot, and S.A. Juliano. 2010. Geographic variation in size and oviposition depths of *Romalea microptera* (Orthoptera: Acrididae) is associated with different soil conditions. *Annals of the Entomological Society of America* 103(2): 227–235. https://doi.org/10.1603/AN09131

Hilker, M., H. Salem, and N.E. Fatouros. 2023. Adaptive plasticity of insect eggs in response to environmental challenges. *Annual Review of Entomology* 68: 451–469. https://doi.org/10.1146/annurev-ento-120120

Hinkelman, J. 2019. *Spinaeblattina myanmarensis* gen. et sp. nov. and *Blattoothecichnus argenteus* ichnogen. et ichnosp. nov. (both Mesoblattinidae) from Mid-Cretaceous Myanmar amber. *Cretaceous Research* 99: 229–239. https://doi.org/10.1016/j.cretres.2019.02.026

Hinton, H.E. 1960. The chorionic plastron and its role in the eggs of the Muscinae (Díptera). *Journal of Cell Science* S3-101(55): 313–332. https://doi.org/10.1242/jcs.s3-101.55.313

Hinton, H.E. 1981. *Biology of Insect Eggs*. Vols. I–III. Oxford: Pergamon Press.

Hoffmann, K.H. 1995. Oogenesis and the female reproductive system. In *Insect Reproduction*. S.R. Leather, ed. Boca Raton, FL: CRC Press, 1–32. https://doi.org/10.1201/9781351073608-1

Hörnig, M.K., J.T. Haug, and C. Haug. 2013. New details of *Santanmantis axelrodi* and the evolution of the Mantodean morphotype. *Palaeodiversity* 6: 157–168.

Hostetter, D.L. 2000. Natural enemies attacking grasshopper nymphs and adults. In *Grasshopper Integrated Pest Management User Handbook*. G.L. Cunningham and M.W. Sampson, eds. Technical Bulletin 1809. Washington, DC: US Department of Agriculture, Animal and Plant Health Inspection Service.

Huang, D., A. Nel, O. Zompro, and A. Waller. 2008. Mantophasmatodea now in the Jurassic. *Naturwissenschaften* 95(10): 947–952. https://doi.org/10.1007/s00114-008-0412-x

Hughes, L., and M. Westoby. 1992. Capitula on stick insect eggs and elaiosomes on Seeds: Convergent adaptations for burial by ants. *Functional Ecology* 6(6): 642–648. https://doi.org/10.2307/2389958

Hunt, R.M., Jr., and E. Stepleton. 2004. Geology and paleontology of the Upper John Day beds. John Day River Valley, Oregon: Lithographic and biochronologic revision in the Haystack Valley and Kimberly Areas (Kimberly and Mt. Misery Quadrangles). *Bulletin of the American Museum of Natural History* 282: 1–90. https://doi.org/10.1206/0003-0090(2004)282<0001:GAPOTU>2.0.CO;2

Hunter-Jones, P., and J.G. Lambert. 1961. Egg development of *Humbe tenuicornis* Schaum (Orthoptera: Acrididae) in relation to availability of water. *Proceedings of the Royal Entomological Society of London. Series A, General Entomology* 36(4–6): 75–80. https://doi.org/10.1111/j.1365-3032.1961.tb00271.x

Hutchinson, D.K., H.K. Coxall, D.J. Lunt, M. Steinthorsdottir, A.M. de Boer, M. Baatsen, A. von der Heydt, et al. 2021. The Eocene–Oligocene transition: A review of marine and terrestrial proxy data, models and model–data comparisons. *Climate of the Past* 17(1): 269–315. https://doi.org/10.5194/cp-17-269-2021

Ibanez, S., A. Foulquier, C. Brun, M.-P. Colace, G. Piton, L. Bernard, C. Gallet, and J.-C. Clément. 2023. The contrasted impacts of grasshoppers on soil microbial activities in function of primary production and herbivore diet. *Peer Community Journal* 3: e12. https://doi.org/10.24072/pcjournal.229

Inglis, G., D.L. Johnson, L.M. Kawchuk, and M.S. Goettel. 1998. Effect of soil texture and soil sterilization on susceptibility of ovipositing grasshoppers to *Beauveria bassiana*. *Journal of Invertebrate Pathology* 71(1): 73–81. https://doi.org/10.1006/jipa.1997.4698

Ingrisch, S., and D.C.F. Rentz. 2009. Orthoptera: Grasshoppers, locusts, katydids, crickets. In *Encyclopedia of Insects*. 2nd ed. V.H. Resh and R.T. Cardé, eds. Amsterdam: Elsevier, 732–743. https://doi.org/10.1016/B978-0-12-374144-8.00196-X

Irles, P., and M.-D. Piulachs. 2011. Citrus, a key insect eggshell protein. *Insect Biochemistry and Molecular Biology* 41(2): 101–108. https://doi.org/10.1016/j.ibmb.2010.11.001

Jacisin, J.J., and S.S.B. Hopkins. 2018. A redescription and phylogenetic analysis based on new material of the fossil newts *Taricha oligocenica* Van Frank, 1955 and *Taricha lindoei* Naylor, 1979 (Amphibia, Salamandridae) from the Oligocene of Oregon. *Journal of Paleontology* 92(4): 713–733. https://doi.org/10.1017/jpa.2017.85

Jacobs, C.G.C., G.L. Rezende, G.E.M. Lamers, and M. van der Zee. 2013. The extraembryonic serosa protects the insect egg against desiccation. *Proceedings of the Royal Society B: Biological Sciences* 280(1764). https://doi.org/10.1098/rspb.2013.1082

Jewell, L.K. 2019. Species diversity in the Hypertragulid (Mammalia: Artiodactyla) population of the John Day Basin, Oregon. University Honors Theses Paper 718, Portland State University.

Jorgensen, W.K., and M.J. Rice. 1983. Superextension and supercontraction in locust ovipositor muscles. *Journal of Insect Physiology* 29(5): 437–448.

Josè, M., and P. Puigdomènech. 1993. Structure and expression of genes coding for structural proteins of the plant cell wall. *New Phytologist* 125(2): 259–282. https://doi.org/10.1111/j.1469-8137.1993.tb03881.x

Katiyar, K.N. 1957. Ecology of oviposition and the structure of egg-pods and eggs in some Indian Acrididae. *Records of the Indian Museum* 55: 29–68.

Kekeunou, S., M. Mbadjoun-Nziké, A.C. Wandji, S.B. Soh-Baleba, A.L. Djomnang-Nkwala, A. Simeu-Noutchom, C. Oumarou-Ngoute, P.C.A. Um-Nyobe, L.G. Guiadem-Simo, and P.N. Akono. 2020. Morphology, development and reproduction of *Atractomorpha acutipennis* (Guérin-Méneville, 1844) (Orthoptera: Pyrgomorphidae). *Tropical Zoology* 33(3): 97–112. https://doi.org/10.4081/tz.2020.81

Kekeunou, S., D. Mbeng, C. Oumarou-Ngoute, and A.C. Wandji. 2015. Morphology, development and reproduction of *Pyrgomorpha vignaudii* (Orthoptera: Pyrgomorphidae). *Entomological Research* 45(2): 58–70. https://doi.org/10.1111/1748-5967.12097

Klass, K.-D., M.D. Picker, J. Damgaard, S. van Noort, and K. Tojo. 2003. The taxonomy, genitalic morphology, and phylogenetic relationships of southern African Mantophasmatodea (Insecta). *Entomologische Abhandlungen* 61(1): 3–67.

Klass, K.-D., O. Zompro, N.P. Kristensen, and J. Adis. 2002. Mantophasmatodea: A new insect order with extant members in the Afrotropics. *Science* 296(5572): 1456–1459.

Knobloch, E. 1977. Paläokarpologische Charakteristik der Flyschzone der mährischen Karpaten. *Sbornik Geologickych vēd Paleontologie* 19: 79–137.

Kort, A.E., and N.A. Famoso. 2020. Novel analysis of locality data can inform better inventory and monitoring practices for paleontological resources at John Day Fossil Beds National Monument Oregon, USA. *Palaeontologia Electronica* 23(1): 1–17. https://doi.org/10.26879/1053

Korth, W.W., and J. Cavin. 2016. New material of the marsupial (Mammalia, Metatheria) *Herpetotherium Merriami* (Stock and Furlong) from the John Day Formation, Late Oligocene, Oregon, USA. *Journal of Paleontology* 90(6): 1225–1232. https://doi.org/10.1017/jpa.2016.117

Korth, W.W., and J.X. Samuels. 2015. New rodent material from the John Day Formation (Arikareean, Middle Oligocene to Early Miocene) of Oregon. *Annals of Carnegie Museum* 83(1): 19–84. https://doi.org/10.2992/007.083.0102

Krassilov, V. 2008. Traumas on fossil leaves from the Cretaceous of Israel. In *Plant–Arthropod Interactions in the Early Angiosperm History: Evidence from the Cretaceous of Israel*. V. Krassilov and A. Rasnitsyn, eds. Leiden, Netherlands: Brill, 7–187. https://doi.org/10.1163/ej.9789004170711.1-229.

Krassilov, V., N. Silantieva, M. Hellmund, and W. Hellmund. 2007. Insect egg sets on angiosperm leaves from the Lower Cretaceous of Negev, Israel. *Cretaceous Research* 28(5): 803–811. https://doi.org/10.1016/j.cretres.2006.11.004

Kula, A. A.R., D.C. Hartnett, and G.W.T. Wilson. 2005. Effects of mycorrhizal symbiosis on tallgrass prairie plant–herbivore interactions. *Ecology Letters* 8(1): 61–69. https://doi.org/10.1111/j.1461-0248.2004.00690.x

Küpper, S.C., K.-D. Klass, G. Uhl, and M.J.B. Eberhard. 2019. Comparative morphology of the internal female genitalia in two species of Mantophasmatodea. *Zoomorphology* 138(1): 73–83. https://doi.org/10.1007/s00435-018-0421-z

La Roche, F., J.F. Genise, C. Castillo, M.L. Quesada, C.M. García-Gotera, and J. de la Nuez. 2014. Fossil bee cells from the Canary Islands. Ichnotaxonomy, palaeobiology and palaeoenvironments of *Palmiraichnus castellanosi*. *Palaeogeography, Palaeoclimatology, Palaeoecology* 409(1): 249–264. https://doi.org/10.1016/j.palaeo.2014.05.012

Laaß, M., and N. Hauschke. 2019. Earliest record of exophytic insect oviposition on plant material from the Latest Pennsylvanian (Gzhelian, Stephanian C) of the Saale Basin, Germany. *Palaeogeography, Palaeoclimatology, Palaeoecology* 534: 109337. https://doi.org/10.1016/j.palaeo.2019.109337

Labandeira, C.C., P. Wilf, K. Johnson, and F. Marsh. 2007. Guide to insect (and other) damage types on compressed plant fossils. Washington, DC: Smithsonian Institution. https://www.researchgate.net/publication/271076149

Leidy, J. 1871. Notice of some extinct rodents. *Proceedings of the Academy of Natural Sciences of Philadelphia* 22: 230–232.

Li, X.R., and D. Huang. 2019. A mantis-type ootheca from Mid-Cretaceous Burmese Amber (Insecta: Dictyoptera). *Cretaceous Research* 100: 134–137. https://doi.org/10.1016/j.cretres.2019.04.002

Lindt, I.I. 1993. On the speciation in Mantodea. In *Proceedings of the 10th Congress of the All-Union Entomological Society*. St. Petersburg: Zoological Institute, Academy of Sciences, 89–91.

Lomer, C.J., R.P. Bateman, D. Dent, H. de Groote, O.K. Douro-Kpindou, C. Kooyman, J. Langewald, Z. Ouambam, R. Peveling, and M. Thomas. 1999. Development of strategies for the incorporation of biological pesticides into the integrated management of locusts and grasshoppers. *Agricultural and Forest Entomology* 1(1): 71–88. https://doi.org/10.1111/j.1461-9563.1999.tb00001.x

Lou, Y.H., P.L. Pan, Y.X. Ye, C. Cheng, H.J. Xu, and C.X. Zhang. 2018. Identification and functional analysis of a novel chorion protein essential for egg maturation in the brown planthopper. *Insect Molecular Biology* 27(3): 393–403. https://doi.org/10.1111/imb.12380

Maeno, K.O., C. Piou, and S. Ghaout. 2020. The desert locust, *Schistocerca gregaria*, Plastically manipulates egg size by regulating both egg numbers and production rate according to population density. *Journal of Insect Physiology* 122: 104020. https://doi.org/10.1016/j.jinsphys.2020.104020

Malek, R., J.M. Kaser, H.J. Broadley, J. Gould, M. Ciolli, G. Anfora, K.A. Hoelmer, and Z. Szendrei. 2019. Footprints and ootheca of *Lycorma delicatula* influence host-searching and-acceptance of the egg-parasitoid *Anastatus orientalis*. *Environmental Entomology* 48(6): 1270–76. https://doi.org/10.1093/ee/nvz110

Manchester, S.R. 2000. Late Eocene fossil plants of the John Day Formation, Wheeler County, Oregon. *Oregon Geology* 62(3): 51–63.

Manchester, S.R., and H.W. Meyer. 1987. Oligocene fossil plants of the John Day Formation, Fossil, Oregon. *Oregon Geology* 49(12): 115–127.

Margaritis, L.H. 1985. Structure and physiology of the eggshell. In *Comprehensive Insect Physiology, Biochemistry and Pharmacology*. Vol. 1. G.A. Kerkut and L.I. Gilbert, eds. Oxford: Pergamon Press, 153–230.

Marsh, O.C. 1874. Fossil horses in America. *The American Naturalist* 8(5): 288–294. https://doi.org/10.1086/271317

Matsuda, R. 1976. *Morphology and Evolution of the Insect Abdomen: With Special Reference to Developmental Patterns and Their Bearings upon Systematics*. 1st ed. International Series in Pure and Applied Biology ; Zoology Division, Vol. 56. Oxford and New York: Pergamon Press.

McCaffery, A.R., S.J. Simpson, M.S. Islam, and P. Roessingh. 1998. A gregarizing factor present in the egg pod foam of the desert locust *Schistocerca gregaria*. *The Journal of Experimental Biology* 201: 347–363.

McClaughry, J.D., M.L. Ferns, M.J. Streck, K.A. Patridge, and C.L. Gordon. 2009. Paleogene calderas of central and eastern Oregon: Eruptive sources of widespread tuffs in the John Day and Clarno Formations. In *Volcanoes to Vineyards: Geologic Field Trips through the Dynamic Landscape of the Pacific Northwest.* J.E.O'Connor, R.J. Dorsey, and I.P. Madin, eds. Geological Society of America Field Guide 15. Boulder, CO: Geological Society of America, 407–434. https://doi.org/10.1130/2009.fld015(20)

Meco, J., D.R. Muhs, M. Fontugne, A.J.G. Ramos, A. Lomoschitz, and D. Patterson. 2011. Late Pliocene and Quaternary Eurasian locust infestations in the Canary Archipelago. *Lethaia* 44(4): 440–454. https://doi.org/10.1111/j.1502-3931.2010.00255.x

Meco, J., N. Petit-Maire, J. Ballester, J.F. Betancort, and A.J.G. Ramos. 2010. The Acridian plagues, a New Holocene and Pleistocene palaeoclimatic indicator. *Global and Planetary Change* 72(4): 318–320. https://doi.org/10.1016/j.gloplacha.2010.01.007

Mendonça, P.M., J.R. dos Santos-Mallet, R.P. de Mello, L. Gomes, and M.M. de Carvalho Queiroz. 2008. Identification of fly eggs using scanning electron microscopy for forensic investigations. *Micron* 39(7): 802–807. https://doi.org/10.1016/j.micron.2008.01.014

Meng, Q.M., C.C. Labandeira, Q.L. Ding, and D. Ren. 2019. The natural history of oviposition on a ginkgophyte fruit from the Middle Jurassic of northeastern China. *Insect Science* 26(1): 171–179. https://doi.org/10.1111/1744-7917.12506

Meyer, H.W. 2003. *The Fossils of Florissant*. Washington, DC: Smithsonian Books.

Meyer, H.W, and S.R. Manchester. 1997. *The Oligocene Bridge Creek Flora of the John Day Formation, Oregon*. University of California Publications in Geological Sciences, Vol. 141. Berkeley and Los Angeles: University of California Press.

Mikhailov, K.E., E.S. Bray, and K.E. Hirsch. 1996. Parataxonomy of fossil egg remains (Veterovata): Principles and applications. *Journal of Vertebrate Paleontology* 16(4): 763–769.

Misof, B., S. Liu, K. Meusemann, R.S. Peters, A. Donath, C. Mayer, P.B. Frandsen, et al. 2014. Phylogenomics resolves the timing and pattern of insect evolution. *Science* 346(6210): 763–767. https://doi.org/10.1126/science.1257570

Monteys, V.S.I, and L. Aguilar. 2005. The Castniid palm borer, *Paysandisia archon* (Burmeister, 1880), in Europe: Comparative biology, pest status and possible control methods (Lepidoptera: Castniidae). *Nachrichten Des Entomologischen Vereins Apollo* 26(1/2): 61–94.

Nevo, E. 1999. *Mosaic Evolution of Subterranean Mammals: Regression, Progression and Global Convergence*. New York: Oxford University Press.

O'Hanlon, J.C., B.R. Jones, and M.W. Bulbert. 2020. The dynamic eggs of the Phasmatodea and their apparent convergence with plants. *The Science of Nature* 107: 34. https://doi.org/10.1007/s00114-020-01690-1/Published

Okelo, O. 1979. Influence of male presence on clutch size in *Schistocerca vaga* Scudder (Orthoptera: Acrididae). *International Journal of Invertebrate Reproduction* 1(5): 317–121. https://doi.org/10.1080/01651269.1979.10553329

Ortiz, J.E., T. Torres, Y. Yanes, C. Castillo, J. de la Nuez, M. Ibáñez, and M.R. Alonso. 2006. Climatic cycles inferred from the aminostratigraphy and aminochronology of Quaternary dunes and palaeosols from the eastern islands of the Canary Archipelago. *Journal of Quaternary Science* 21(3): 287–306. https://doi.org/10.1002/jqs.962

Paranjape, S.Y. 1985. Behavioural analysis of feeding and breeding in Orthopteran insects. *Proceedings: Animal Sciences* 94(3): 265–282. https://doi.org/10.1007/BF03186268

Paterson, R., J.X. Samuels, N. Rybczynski, M.J. Ryan, and H.C. Maddin. 2020. The earliest mustelid in North America. *Zoological Journal of the Linnean Society* 188: 1318–1339. https://doi.org/10.1093/zoolinnean/zlz091

Pérez-de la Fuente, R., M.S. Engel, D. Azar, and E. Peñalver. 2019. The hatching mechanism of 130-million-year-old insects: An association of neonates, egg shells and egg bursters in Lebanese amber. *Palaeontology* 62(4): 547–59. https://doi.org/10.1111/pala.12414

Picker, M.D., J.F. Colville, and S. van Noort. 2002. Mantophasmatodea now in South Africa. *Science* 297(5586): 1475. https://doi.org/10.1126/science.297.5586.1475b

Pinter, C., A. Lasso, and G. Fichtinger. 2019. Polymorph segmentation representation for medical image computing. *Computer Methods and Programs in Biomedicine* 171: 19–26. https://doi.org/10.1016/j.cmpb.2019.02.011

Poinar, G. 2010. Palaeoecological perspectives in Dominican amber. *Annales de La Societe Entomologique de France* 46(1–2): 23–52. https://doi.org/10.1080/00379271.2010.10697637

Pott, C., C.C. Labandeira, M. Krings, and H. Kerp. 2008. Fossil insect eggs and ovipositional damage on Bennettitalean leaf cuticles from the Carnian (Upper Triassic) of Austria. *Journal of Paleontology* 82(4): 778–789. https://doi.org/10.1666/06-094.1

Pound, M.J., and U. Salzmann. 2017. Heterogeneity in global vegetation and terrestrial climate change during the Late Eocene to Early Oligocene Transition. *Scientific Reports* 7(1): 43386. https://doi.org/10.1038/srep43386

Prokopy, R.J, and B.D. Roitberg. 2001. Joining and avoidance behavior in nonsocial insects. *Annual Review of Entomology* 46: 631–665. https://doi.org/10.1146/annurev.ento.46.1.631

Prothero, D.R. 2015. Evolution of the Early Miocene hesperhyine peccaries. *New Mexico Museum of Natural History and Science Bulletin* 67: 235–256.

Rasnitsyn, A.P. 2002. Introduction to palaeoentomology. In *History of Insects*. A.P. Rasnitsyn and D.L.J. Quicke, eds. Dordrecht, Netherlands: Kluwer, 1–63.

Retallack, G.J. 2004. Late Oligocene bunch grassland and Early Miocene sod grassland paleosols from central Oregon, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 207(3–4): 203–237. https://doi.org/10.1016/j.palaeo.2003.09.027

Retallack, G.J., E.A. Bestland, and T.J. Fremd. 1999. Eocene and Oligocene paleosols of central Oregon. *Geological Society of America Special Paper* 344: 1–192. https://doi.org/10.1130/SPE344

Retallack, G.J., and J.X. Samuels. 2020. Paleosol-based inference of niches for Oligocene and Early Miocene fossils from the John Day Formation of Oregon. *Journal of Vertebrate Paleontology* 40(1): e1761823. https://doi.org/10.1080/02724634.2019.1761823

Rezende, G.L., H.C.M. Vargas, B. Moussian, and E. Cohen. 2016. Composite eggshell matrices: Chorionic layers and sub-chorionic cuticular envelopes. In *Extracellular Composite Matrices in Arthropods*. E. Cohen and B. Moussian, eds. New York: Springer International, 325–66. https://doi.org/10.1007/978-3-319-40740-1_9

Robertson, J.A., S. Bradler, and M.F. Whiting. 2018. Evolution of oviposition techniques in stick and leaf insects (Phasmatodea). *Frontiers in Ecology and Evolution* 6: 216. https://doi.org/10.3389/fevo.2018.00216

Robinson, P.T., G.F. Brem, and E.H. Mckee. 1984. John Day Formation of Oregon: A distal record of early Cascade volcanism. *Geology* 12(4): 229–232. https://doi.org/10.1130/0091-7613(1984)12<229:JDFOOA>2.0.CO;2

Romero-Lebrón, E., J.M. Robledo, X. Delclòs, J.F. Petrulevičius, and R.M. Gleiser. 2022. Endophytic insect oviposition traces in deep time. *Palaeogeography, Palaeoclimatology, Palaeoecology* 590: 110855. https://doi.org/10.1016/j.palaeo.2022.110855

Roth, L.M. 1968. Oöthecae of the Blattaria. *Annals of the Entomological Society of America* 61(1): 83–111. https://doi.org/10.1093/aesa/61.1.83

Roth, S., J. Molina, and R. Predel. 2014. Biodiversity, ecology, and behavior of the recently discovered insect order Mantophasmatodea. *Frontiers in Zoology* 11(1): 70. https://doi.org/10.1186/s12983-014-0070-0

Russell, D.A. 1960. A review of the Oligocene insectivore *Micropternodus borealis*. *Journal of Paleontology* 34(5): 940–949.

Saini, R.K., M.M. Rai, A. Hassanali, J. Wawiye, and H. Odongo. 1995. Semiochemicals from froth of egg pods attract ovipositing female *Schistocerca gregaria*. *Journal of Insect Physiology* 41(8): 711–716. https://doi.org/10.1016/0022-1910(95)00016-N

Samuels, J.X. 2021. The first records of *Sinclairella* (Apatemyidae) from the Pacific Northwest, USA. *PaleoBios* 38(1). https://doi.org/10.5070/P9381053299

Samuels, J.X., L.B. Albright, and T.J. Fremd. 2015. The last fossil primate in North America, new material of the enigmatic *Ekgmowechashala* from the Arikareean of Oregon. *American Journal of Physical Anthropology* 158(1): 43–54. https://doi.org/10.1002/ajpa.22769

Samuels, J.X., M.C. Mihlbachler, W.W. Korth, L. Holbrook, K.E. Bredehoeft, and T.J. Fremd. 2016. The first Late Eocene and earliest Oligocene faunas from the John Day Basin of Oregon: Filling gaps in the most complete record of mammal evolution in North America. Society of Vertebrate Paleontology Annual Meeting Abstracts.

Samuels, J.X., and B. van Valkenburgh. 2009. Craniodental adaptations for digging in extinct burrowing beavers. *Journal of Vertebrate Paleontology* 29(1): 254–268. https://doi.org/10.1080/02724634.2009.10010376.

Seligman, A.N., I.N. Bindeman, J. McClaughry, R.A. Stern, and C. Fisher. 2014. The earliest low and high δ18O caldera-forming eruptions of the Yellowstone Plume: Implications for the 30–40 Ma Oregon calderas and speculations on plume-triggered delaminations. *Frontiers in Earth Science* 2: 34. https://doi.org/10.3389/feart.2014.00034

Sellick, J.T.C. 1994. Phasmida (stick insect) eggs from the Eocene of Oregon. *Palaeontology* 37(4): 913–921.

Shaikh, N., and R. Sultana. 2018. Comparative study on the morphometric characteristics of egg-pods in various sub-families of Acrididae. *Journal of Entomology and Zoology Studies* 6:1423–1426.

Shcherbakov, E.O., and V.Y. Savitsky. 2015. New data on the fauna, taxonomy and ecology of praying mantises (Dictyoptera, Mantodea) from Russia. *Entomological Review* 95(2): 181–199. https://doi.org/10.1134/S0013873815020049

Shufeldt, R.W. 1915. Fossil birds in the Marsh Collection of Yale University. *Transactions of the Connecticut Academy of Arts and Sciences* 19: 1–110.

Sierra, D., I.D. Velez, and S.I. Uribe. 1995. Electronic microscopy of eggs as a taxonomic parameter. *Bol Dir Malariol San Amb* 30: 327–336.

Song, H., C. Amédégnato, M.M. Cigliano, L. Desutter-Grandcolas, S.W. Heads, Y. Huang, D. Otte, and M.F. Whiting. 2015. 300 million years of diversification: Elucidating the patterns of Orthopteran evolution based on comprehensive taxon and gene sampling. *Cladistics* 31(6): 621–651. https://doi.org/10.1111/cla.12116

Southwood, T.R.E. 1956. The structure of the eggs of the terrestrial heteroptera and its relationship to the classification of the group. *Transactions of the Royal Entomological Society of London* 108(6): 163–221. https://doi.org/10.1111/j.1365-2311.1956.tb02269.x

Stauffer, T.W., and D.W. Whitman. 2007. Divergent oviposition behaviors in a desert vs a marsh grasshopper. *Journal of Orthoptera Research* 16(1): 103–114. https://doi.org/10.1665/1082-6467(2007)16[103:dobiad]2.0.co;2

Steenman, A., A.W. Lehmann, and G.U.C. Lehmann. 2015. Life-history trade-off between macroptery and reproduction in the wing-dimorphic pygmy grasshopper *Tetrix Subulata* (Orthoptera Tetrigidae). *Ethology Ecology & Evolution* 27(1): 93–100. https://doi.org/10.1080/03949370.2014.885466

Stirton, R.A., and J.M. Rensberger. 1964. Occurrence of the insectivore genus *Micropternodus* in the John Day Formation of Central Oregon. *Bulletin of the Southern California Academy of Sciences* 63(2): 57–80.

Stock, C., and E.L. Furlong. 1922. A marsupial from the John Day Oligocene of Logan Butte, eastern Oregon. *Bulletin of the Department of Geological Sciences of the University of California* 13: 311–317.

Stork, N.E. 2018. How many species of insects and other terrestrial arthropods are there on earth? *Annual Review of Entomology* 63: 31–45. https://doi.org/10.1146/annurev-ento-020117-043348

Stork, N.E., J. McBroom, C. Gely, and A.J. Hamilton. 2015. New approaches narrow global species estimates for beetles, insects, and terrestrial arthropods. *Proceedings of the National Academy of Sciences of the United States of America* 112(24): 7519–7523. https://doi.org/10.1073/pnas.1502408112

Sultana, R., S. Kumar, and I.A. Soomro. 2017. Study on morphology and development of egg-pod and eggs of *Poekilocerus pictus* (Orthoptera: Pyrgomorphidae). *Journal of Entomology and Zoology Studies* 5(3): 537–540.

Sultana, R., N. Soomro, S. Kumar, A.A. Samejo, and S. Soomro. 2020. Comparative study of egg-pod morphology in two genera of Oxyinae (Acrididae: Orthoptera). *Pakistan Journal of Zoology* 52(4): 1327–1332. https://doi.org/10.17582/journal.pjz/20190523070550

Tedford, R.H., X. Wang, and B.E. Taylor. 2009. Phylogenetic systematics of the North American fossil Caninae (Carnivora: Canidae). *Bulletin of the American Museum of Natural History* 325: 1–218. https://doi.org/10.1206/574.1

Thompson, K.J. 1986. Oviposition digging in the grasshopper. 1. Functional anatomy and the motor programme. *Journal of Experimental Biology* 122: 387–411.

Tiffney, B.H. 1984. Seed size, dispersal syndromes, and the rise of the angiosperms: Evidence and hypothesis. *Annals of the Missouri Botanical Garden* 71: 551–576.

Tojo, K., R. Machida, K.-D. Klass, and M.D. Picker. 2004. Biology of South African heel-walkers, with special reference to reproductive biology (Insecta: Mantophasmatodea). *Proceedings of the Arthoropodan Embryological Society of Japan* 39: 15–21.

Trougakos, I.P., and L.H. Margaritis. 2002. Novel morphological and physiological aspects of insect eggs. In *Chemo-ecology of Insect Eggs and Egg Deposition*. M. Hilker and T. Meiners, eds. Oxford and Malden, MA: Blackwell, 3–36.

Truman, J.W. 2019. The evolution of insect metamorphosis. *Current Biology* 29(23): R1252–68. https://doi.org/10.1016/j.cub.2019.10.009

Ubero-Pascal, N., M.D. García, E. Clemente, and J.J. Presa. 2020. Discriminating two sympatric species of Acinipe (Orthoptera: Pamphagidae) on the basis of egg-pod and egg morphologies. *Zoologischer Anzeiger* 289: 67–76. https://doi.org/10.1016/j.jcz.2020.09.005

Van Konijnenburg-Van Cittert, J.H.A, and S. Schmeißner. 1999. Fossil insect eggs on Lower Jurassic plant remains from Bavaria (Germany). *Palaeogeography, Palaeoclimatology, Palaeoecology* 152: 215–223. https://doi.org/10.1016/S0031-0182(99)00059-0

Vasilenko, D.V. 2005. Damages on Mesozoic Plants from the Transbaikalian Locality Chernovskie Kopi. *Paleontological Journal* 39(6): 628–633.

Waloff, N. 1950. The egg pods of British short-horned grasshoppers (Acrididae). *Proceedings of the Royal Entomological Society of London. Series A, General Entomology* 25(10–12): 115–126. https://doi.org/10.1111/j.1365-3032.1950.tb00088.x

Wang, B., F. Xia, T. Wappler, E. Simon, H. Zhang, E.A. Jarzembowski, and J. Szwedo. 2015. Brood care in a 100-million-year-old scale insect. *eLife* 4: e05447. https://doi.org/10.7554/eLife.05447

Waters, A.C. 1961. Stratigraphic and lithologic variations in the Columbia River Basalt. *American Journal of Science* 259(8): 583–611. https://doi.org/10.2475/ajs.259.8.583

Winters, A.E., M. Stevens, C. Mitchell, S.P. Blomberg, and J.D. Blount. 2014. Maternal effects and warning signal honesty in eggs and offspring of an aposematic ladybird beetle. *Functional Ecology* 28(5): 1187–96. https://doi.org/10.1111/1365-2435.12266

Wipfler, B., T. Theska, and R. Predel. 2017. Mantophasmatodea from the Richtersveld in South Africa with description of two new genera and species. *ZooKeys* 746: 137–160. https://doi.org/10.3897/zookeys.746.14885

Young, A.M. 1983. On the evolution of egg placement and gregariousness of caterpillars in the Lepidoptera. *Acta Biotheoretica* 32: 43–60. https://doi.org/10.1007/BF00047974

Zatoń, M., G. Niedźwiedzki, and G. Pieńkowski. 2009. Gastropod egg capsules preserved on bivalve shells from the Lower Jurassic (Hettangian) of Poland. *Palaios* 24(9): 568–577. https://doi.org/10.2110/palo.2009.p09-005r

Zhai, Y.-L., S.-J. Dong, M.-M. Zou, Y.-D. Qin, L.-L. Liu, M.-H. Cao, M.-Q. Huang, L. Vasseur, M.-S. You, and L. Peng. 2022. Vitelline membrane protein 26 mutagenesis, using CRISPR/Cas9, results in egg collapse in *Plutella xylostella*. *International Journal of Molecular Sciences* 23(17): 9538. https://doi.org/10.3390/ijms23179538

Zompro, O. 2001. The Phasmatodea and *Raptophasma* n. gen., Orthoptera incertae sedis, in Baltic amber (Insecta: Orthoptera). *Mitteilungen Des Geologisch-Paläontologischen Institutes Der Universität Hamburg* 85: 229–261.

Zompro, O., J. Adis, and W. Weitschat. 2002. A review of the order Mantophasmatodea (Insecta). *Zoologischer Anzeiger* 241(3): 269–279.