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GRAMMEPUS HITCHCOCK, 1858: A SEDIMENTARY VARIANT OF THE FOSSIL INSECT TRACKWAY *LITHOGRAPHUS*

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Abstract: The ichnogenus *Grammepus,* which is inferred to have been made by a winged (pterygote) insect, was differentiated from other ichnotaxa because its largest tracks were nearly continuous, forming two furrows. Otherwise, it strongly resembles the ichnogenus *Lithographus.* Examination of both ichnogenera indicate that the largest tracks in *Lithographus* can be very close together, that some specimens of *Grammepus* lack furrow-like tracks, and that the type specimen of the type species *Grammepus erismatus* has separate tracks in some places, and furrow-like ones in others. Given the lack of a feature that can consistently differentiate *Lithographus* and *Grammepus*, the latter is synonymized with the former. Experiments with the modern cricket *Acheta domesticus* in sediment of different saturation levels indicate that a single pterygote producer could produce both *"Grammepus-"* and *Lithographus*-like morphologies, with the former being formed in wet, soft sediment wherein the legs drag, and the latter being formed in firmer, drier sediment wherein the legs do not drag.

Key words: Ichnology, arthropod ichnotaxonomy, intergrading trace fossils, morphological variability, sediment saturation.

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INTRODUCTION

In a previous issue of this journal, Rindsberg (2018) argued that ichnotaxonomy was still an immature science because different names are sometimes applied to the same trace fossil. He noted that, in part, this problem arises from the different choices that researchers make when considering distinctive morphological characters (i.e., ichnotaxobases) to define ichnotaxa. The problem of what to consider an important characteristic was especially prevalent in previous centuries, before ichnotaxonomists began to develop standards for the naming of trace fossils. During those times, the decision about what was an important feature of a particular trace was entirely at the discretion of individual researchers, some of whom worked alone at a time when ichnology was in its infancy. Recalling some of the more recent discussions by ichnotaxonomists (e.g., Bertling *et al.,* 2006; Rindsberg, 2018) suggested that researchers use ichnotaxobases that reflect anatomy and behaviour and avoid the use of ichnotaxobases that reflect the trace fossil taphonomy.

Among the ichnotaxobases that Bertling *et al.* (2006) considered useful were overall shape, orientation, ornamentation, and internal structure of the trace. They argued that size, taphonomy, preservation, and sediment consistency (not to be confused with substrate type) should not be used. Following these guidelines has the potential to reduce the number of ichnotaxa established in the future, and will therefore help to avoid subsequent instances of different names being created for the same trace morphology. What it will not do, however, is declutter the literature of the many synonymous ichnotaxa (e.g., see Häntzschel, 1975; Pickerill, 1994) that were named before calls for standardization began. Minter *et al.* (2007) proposed guidelines for synonymizing already existing ichnotaxa in order to deal with the problem of multiple names for similar traces.

Among these guidelines were that ichnotaxa should be synonymized when the differences are minor ones caused by slight changes in trace maker behaviour or in sediment consistency.

In the nineteenth century, Edward Hitchcock, who worked in New England, established 31 ichnogenera and 60 ichnospecies for invertebrate trace fossils that he discovered (Hitchcock, 1858, 1865). Some of these ichnotaxa (e.g., *Lithographus*) are widely used, whereas others (e.g., *Grammepus*) rarely are. Hitchcock is known as a taxonomic splitter who used even minute differences to establish ichnotaxa (Olsen *et al.,* 1992; Keighley and Pickerill, 1998; Rainforth, 2005; Minter and Braddy, 2009). Not only did his excessive splitting result in a plethora of trace fossil names, but his poor drawings sometimes caused later researchers to establish a new name for similar trace fossils found elsewhere (e.g., see Goldstein *et al.,* 2017). Work has begun to address the large number of objective and subjective synonyms that Hitchcock named (e.g., Rainforth, 2005; Minter *et al.,* 2012; Lucas *et al.,* 2013; Dalman and Lucas, 2015; Getty, 2016, 2017, 2018; Getty and Burnette, 2019), but more work is needed. This paper is part of that additional work, and compares two of the ichnogenera that Hitchcock attributed to insects: *Lithographus* and *Grammepus* (Fig. 1).

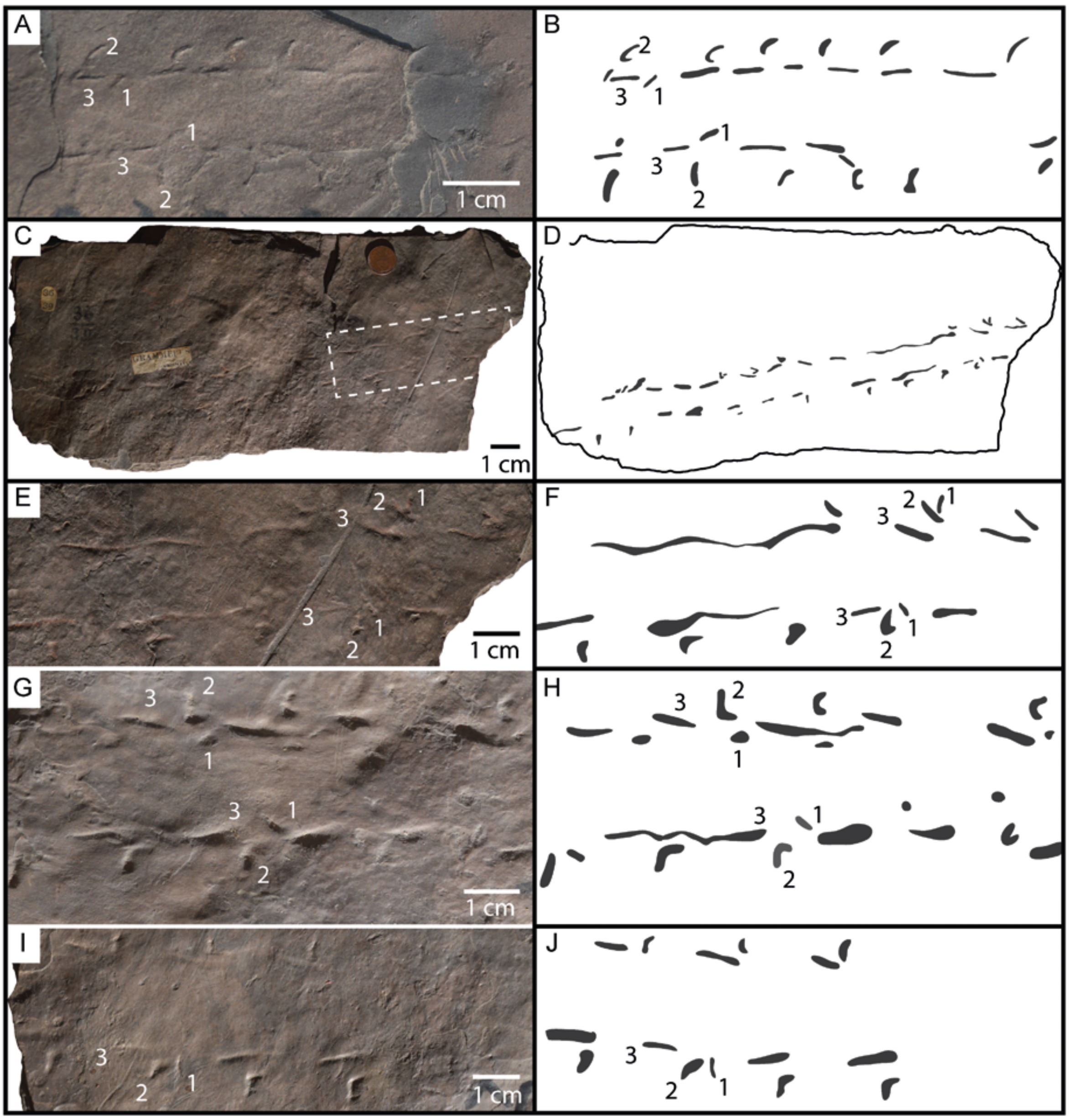

Fig. 1. *Lithographus hieroglyphicus* and its junior subjective synonym *Grammepus erismatus*. Numbers refer to tracks interpreted to have been made by the first, second, and third legs on each side of the insect. Direction of locomotion is from left to right in all cases. **A, B.** Photograph and interpretive drawing of a portion of the *Lithographus hieroglyphicus* lectotype, which is preserved on ACM ICH 36/26. **C, D.** Photograph and interpretive sketch of ACM ICH 36/39, on which the *Grammepus erismatus* holotype is preserved. **E, F.** Photograph and interpretive sketch of a portion of the holotype delineated in C by the white, dashed box. **G, H.** Photograph and interpretive drawing of a portion of the *G. erismatus* preserved on ACM ICH 47/12. **I, J.** Photograph and interpretive drawing of a portion of the *G. erismatus* preserved on ACM ICH 47/18.

GEOLOGICAL AND PALEONTOLOGICAL CONTEXT

The specimens evaluated for this paper are from the Deerfield Basin of southern New England, which is located in the north-eastern part of the United States of America (Fig. 2). The rifting that formed the basin, which ultimately resulted in the breakup of Pangea, began by the late Triassic and ended in the middle Jurassic (Manspeizer and Cousminer, 1988; Olsen *et al.,* 1992). Throughout the phase of rifting, the Deerfield Basin filled with sediments and igneous rocks that are part of the Newark Supergroup (Olsen, 1978, 1997). During rifting, regional paleoclimate conditions were primarily monsoonal (Parrish, 1993), and there was a long dry season (Hubert, 1978).

Rifting and basin subsidence were slow in the late Triassic, resulting in the deposition of mostly fluvial sediments, which formed arkosic conglomerates of the Sugarloaf Formation of the Deerfield Basin (but see Weems *et al.*, 2016 for alternative formation names due to an extensive synonymy across the Newark Supergroup basins). Crustal extension sped up in the early Jurassic, causing small normal faults on the eastern basin boundary to coalesce to form asymmetrical, east-dipping half grabens (Schlische and Olsen, 1990). Due to the asymmetry of the Deerfield Basin, the beds tilt and thicken eastward. Concurrent with the increase in extension rate and basin subsidence was a shift from fluvial to lacustrine conditions. The Fall River beds and the Turners Falls Formation of the Deerfield Basin represent deposition in lakes in the early Jurassic (Cornet *et al.,* 1973). The lake deposits exhibit regularly repeating patterns of grey to black shale formed in deep, permanent water that are separated by red mudstone and sandstone formed in shallow, ephemeral lakes. Olsen (1986) argued that cyclicity in the lacustrine strata resulted from Milankovitch cycle-influenced climate changes, but recently this hypothesis has been called into question by Tanner and Lucas (2015). There was a 600-ka volcanic interval called the Central Atlantic Magmatic Province that produced basaltic lava flows (Olsen *et al.,* 1996) that occurred in association with the rapid extension and subsidence in the Jurassic. The earliest of these lava flows has been implicated in the end-Triassic extinction event (Blackburn *et al.,* 2013).

The exact locations from which Edward Hitchcock collected the type specimens of *Grammepus erismatus* and *Lithographus hieroglyphicus* are unclear. In 1858 he indicated that both were from the land of a local farmer (‘Field’s Farm’), whereas in the 1865 descriptive catalogue the specimens are said to have come from a location called the Lily Pond. He later collected additional specimens from the Lily Pond and potentially even a stretch of the Connecticut River to the east of the other locations that was once called the ‘Horse Race’. All three of these localities, however, are within 10 km of each other and expose lacustrine beds of the Turners Falls Formation. The brownish colour of the fossil-bearing slabs and the presence of terrestrial insect trackways on them indicate that the sediments that formed them were deposited in shallow water that was later subaerially exposed.

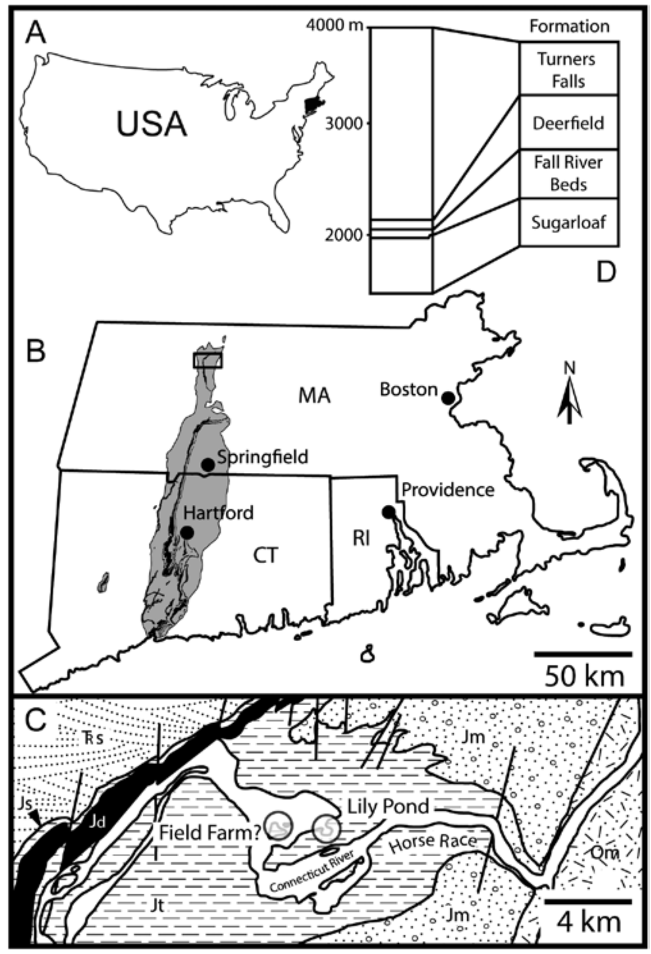

Fig. 2. Geological and geographical context. **A.** Map of the contiguous United States with southern New England shaded black. **B.** Map of southern New England showing the distribution of Mesozoic Newark Supergroup rocks. Grey shading indicates sedimentary rocks and black represents igneous ones. **C.** Close-up map, modified from Zen et al. (1983), of the boxed region in B, showing the distribution of rock formations and the localities from which Hitchcock collected trackways that he called *Grammepus*. **D.** Simplified stratigraphic column of the Deerfield Basin with traditional formation names used.

MATERIALS AND METHODS

For the fossils

The trackways that Edward Hitchcock collected are housed at the Beneski Museum of Natural History at Amherst College. The slabs on which they occur have the institutional abbreviation ACM ICH followed by a fractional identification number. Those trackways that he named *Grammepus erismatus* (herein *Lithographus hieroglyphicus*) were identified using the descriptive catalogue of specimens edited by his son, C. H. Hitchcock, in 1865. According to the catalogue, they occur on ACM ICH 9/13, 12/2, 26/21, 36/37, 36/39, 47/12, 47/14, 47/18, and 55/36. ACM ICH 36/37 is missing from the museum, so any trackways on it could not be analyzed. *Grammepus erismatus* could not be found on ACM ICH 9/13, 12/2, and 26/21, although the latter two specimens were mounted to the wall in the museum in such a way as to prevent one side from being inspected, so trackways could occur on the unseen side. Trackways were identified and examined on 36/39, 47/12, 47/14, 47/18, and 55/36. The fossil-bearing slabs were illuminated with low-angle light from different angles to accentuate trackway details, and they were then photographed. Interpretive drawings of the trackways were produced from the photographs. Trackway terminology follows Trewin (1994) where possible.

For the experiments

In order to test the hypothesis that *Grammepus erismatus* is a sedimentological variant of *Lithographus hieroglyphicus,* experiments were conducted with the house cricket *Acheta domesticus* Linnaeus, 1758 in sediment of varying saturation amounts (Fig. 3). The insects were purchased from a local pet store and were maintained in a small terrarium while experiments were ongoing. The experimental sediment consisted of mud with a grain size that was mostly ≥ 4ϕ, with minor amounts that were ≤ 3.75ϕ. The mud mixtures were produced, and the experiments conducted, in a manner similar to that employed by Getty *et al*. (2013) for experiments with wingless insects. The sediment was saturated by dripping water onto it with a pipette, and then the surface was smoothed in order to make a flat, featureless surface across which the animals could walk. The loss of water was recorded by weighing the sediment-filled pan at intervals as the experiments were conducted. The primary difference between the experiments conducted by Getty *et al*. (2013) and those reported herein was in the use of petri dishes in the experiments with the crickets, whereas a rectangular container was used with the wingless insects.

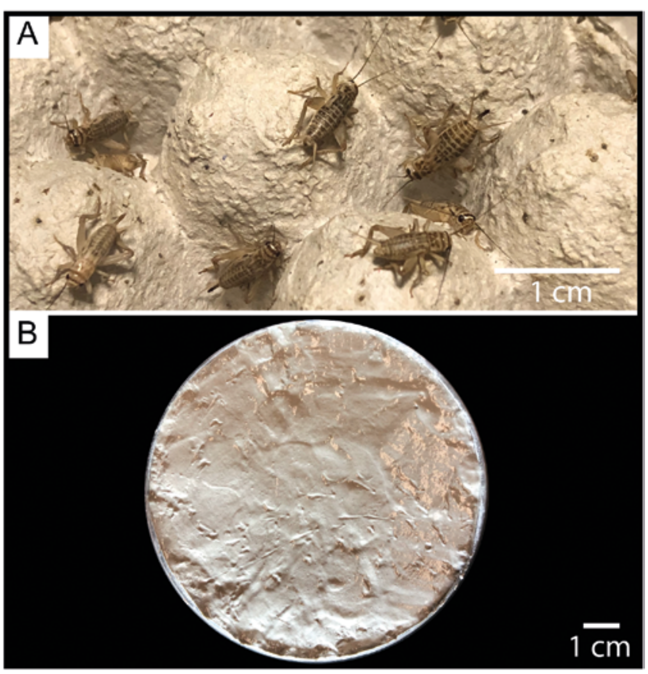

Fig. 3. Experimental animals and apparatus. **A.** The house cricket *Acheta domesticus*. **B.** A mud-filled petri dish in which trackways were produced.

SYSTEMATIC ICHNOLOGY

Ichnogenus *Lithographus*
Lithographus hieroglyphicus Hitchcock, 1858
Fig. 1

v 1858 *Grammepus erismatus* nov. sp. – E. Hitchcock, p. 155, plate 29, fig. 1.

v* 1858 *Lithographus hieroglyphicus* nov. sp. – E. Hitchcock, p. 156, pl. 29, fig. 3; pl. 37, fig. 2.

1858 *Lithographus cruscularis* nov. sp. – E. Hitchcock, p. 157, pl. 29, fig. 4; pl. 30, fig. 3.

1865 *Copeza propinquata* – E. Hitchcock, p. 15.

1865 *Copeza cruscularis* – E. Hitchcock, p. 16.

1865 *Copeza punctata* – E. Hitchcock, p. 16, pl. 6, fig. 14.

1865 *Grammepus erismatus* – E. Hitchcock, p. 16.

1915 *Grammepus erismatus* E. Hitchcock – Lull, p. 64.

1915 *Lithographus cruscularis* E. Hitchcock – Lull, p. 59.

1915 *Lithographus punctatus* (E. Hitchcock) – Lull, p. 59.

1953 *Grammepus erismatus* E. Hitchcock – Lull, p. 48.

1953 *Lithographus cruscularis* E. Hitchcock – Lull, p. 43.

1953 *Lithographus punctatus* (E. Hitchcock) – Lull, p. 44.

1975 *Grammepus erismatus* Hitchcock, 1858 – Häntzschel, p. W185.

2005 *Grammepus erismatus* E. Hitchcock, 1858 – Rainforth, p. 845, fig. 5.24.

2005 *Lithographus hieroglyphicus* E. Hitchcock, 1858 – Rainforth, p. 872, fig. 5.43.

2005 *Lithographus punctatus* (E. Hitchcock, 1865) Lull 1915 – Rainforth, p. 873, fig. 5.44.

non 2005 *Bifurculapes elachistotatus* E. Hitchcock, 1858 – Rainforth, p. 832, fig. 5.12.

2009 *Lithographus hieroglyphicus* Hitchcock, 1858 – Minter and Braddy, p. 28, figs. 16–17.

Material: ACM ICH 36/39, 47/12, 47/14, 47/18, and 55/36.
Emended diagnosis: Trackways composed of two track rows, occasionally with a straight to sinuous, single or double, medial impression. Track rows with sets of up to three morphologically different tracks (elongate, crescentic to comma-like or circular to ovate) of different sizes. The smallest track of each set is the inner or middle track in relation to the trackway axis. It is usually elongate but may be circular to ovate and oriented parallel to anterolaterally relative to the trackway axis. The mid-sized track is oriented perpendicular or slightly oblique to the trackway axis. It is usually crescentic with its concave side oriented in the

direction of movement. Most often, it is located between the other two tracks. The longest track, usually elongate and straight, is oriented parallel or posterolaterally relative to the trackway axis, and is either the middle or inner track. The longest tracks may be connected to form straight or zigzagging furrows. These sets of tracks are arranged in alternate to staggered symmetry (modified from Minter and Braddy, 2009 and Minter *et al.*, 2012).

Description: Preserved trackway segments are straight to gently curving, measure from 4.7 to 42.7 cm long, and are preserved as concave epireliefs and convex hyporeliefs. The tracks are arranged into two rows, within which the tracks are clustered into groups that have a stride measuring 0.3 to 2.8 cm. Each group consists of up to three tracks that are arranged in alternate symmetry. The external widths of the trackways range from 0.5 to 3.7 cm, and internal widths are between 0.3 and 1.9 cm. Individual tracks vary in shape and in position relative to the trackway axis. The smallest tracks, which measure 0.1 to 0.2 cm long, are typically elongate and straight, but can be punctate, and are positioned either closest to the midline or between the other tracks. The mid-length tracks are occasionally elongate and straight but more often strongly curved, measure 0.1 to 0.8 cm long, and are usually on the outside of the trackway. The longest tracks are 0.1 to 1.6 cm long, are elongate and straight or occasionally gently curving, and are usually closest to the trackway axis, although they sometimes occur between the other two tracks.

Remarks: Hitchcock (1858) differentiated *Grammepus* from other, similar ichnotaxa such as *Lithographus* because the largest tracks were nearly confluent, therefore forming elongate furrows. This characteristic is problematic for differentiating *Grammepus* from *Lithographus,* however, for several reasons. First, as can be seen in the *Lithographus hieroglyphicus* lectotype (Fig. 1A, B), the largest tracks are very close together. Second, as can be seen in the *Grammepus erismatus* holotype (Fig. 1C–F), the longest tracks are discrete in some places and joined in others. This is true of other specimens that Hitchcock identified as *G. erismatus* as well (e.g., Fig. 1G, H). Finally, some trackways that Hitchcock identified as *G. erismatus* (e.g., Fig. 1I, J) do not exhibit any joined tracks. Indeed, ACM ICH 47/18 (Fig. 1I, J) is indistinguishable from *Lithographus* despite being called *Grammepus*. Given the lack of a consistent characteristic to differentiate the two ichnotaxa, we propose that they should be synonymized. *Grammepus* and *Lithographus* were published in the same work and consequently neither has priority according to ICZN (1999) rules. *Lithographus,* however, is more widely used and to synonymize it with *Grammepus,* which has been used in only a handful of publications, would be disruptive to the literature. Hence, we synonymize *Grammepus* with *Lithographus* instead.

Hitchcock (1858) originally established two ichnospecies within *Grammepus, G. erismatus* and *G. unordinatus*. He considered *G. unordinatus* a 'doubtful' ichnospecies, however, because there was only one specimen and it consisted of a single row of tracks. He later removed *G. unordinatus* to the new ichnotaxon *Ampelichnus sulcatus* Hitchcock, 1865, again considering the specimen of doubtful origin. Lull (1915) treated *A. sulcatus* as a junior synonym of *G. erismatus* but in 1953, noting that the species name *unordinatus* had priority, treated the two ichnogenera as distinct. Rainforth (2005) followed Hitchcock (1865) and Lull (1953) in maintaining the separation of the ichnogenera, as we do here because *Ampelichnus* is unlike *Grammepus,* and might even represent a tool mark or other sedimentary structure. Consequently, *Grammepus* includes a single ichnospecies, *G. erismatus*.

Lithographus and its included ichnospecies have a more complex history. When Hitchcock (1858) established the ichnogenus, he named two ichnospecies: *L. hieroglyphicus* and *L. cruscularis*. In 1865, however, he synonymized *Lithographus* with the ichnogenus *Copeza* Hitchcock, 1858, the type species of which is *C. triremis*. He thus moved *L. hieroglyphicus* and *L. cruscularis* to *Copeza* as *C. propinquata* and *C. cruscularis,* respectively. He also established *C. punctata* at that time. In revising Hitchcock's work, Lull (1915) recognized *Copeza* and *Lithographus* as distinct because of differences in arrangement of the tracks, and he revived *L. hieroglyphicus* and *L. cruscularis* while also including the ichnospecies *punctata* (as *punctatus*) within *Lithographus*. Rainforth (2005) followed Lull with the exception that she synonymized *L. cruscularis* with *Bifurculapes elachistotatus,* leaving only the ichnospecies *hieroglyphicus* and *punctatus* within *Lithographus*. Not considering Rainforth (2005), Minter and Braddy (2009) synonymized *Lithographus cruscularis*, along with *L. punctatus,* with *L. hieroglyphicus*. We do not follow Rainforth (2005) in considering *L. cruscularis* synonymous with *Bifurculapes elachistotatus,* which she argued because she thought that they might be different segments of the same trackway. Based on our observations, the two trackways appear to converge, which would mean that they are not the same. Furthermore, the two ichnogenera appear to represent different behaviours (i.e., *Lithographus* represents walking; see Davis *et al.,* 2007, whereas *Bifurculapes* represents swimming, see Getty, 2020). Instead, we accept Minter and Braddy's (2009) synonymy of *L. cruscularis* and *L. punctatus* with *L. hieroglyphicus,* which makes the ichnogenus monotypic.

The question then becomes whether or not to retain the species *G. erismatus* within *Lithographus,* or to synonymize it with *L. hieroglyphus*. We opt for the latter, as Minter and Braddy (2009) had done, noting again that no consistent character differentiates the two.

Discussion: Hitchcock (1858, 1865) noted that the sets of three tracks on different sides of the trackway in both *Lithographus hieroglyphicus* and its junior subjective synonym *Grammepus erismatus* indicated that the maker had six legs and was therefore most likely an insect, although he was cautious to not rule out crustaceans. Lull (1915, 1953) considered *Lithographus hieroglyphicus* to be the trackway of an insect, but was unsure of *Grammepus erismatus*.

Exactly what kind of insect made these trackways is more difficult to determine. The wingless insects (the paraphyletic Apterygota) can be ruled out because these animals walk on the tips of their tarsi (the distalmost part of the leg), which usually leaves circular tracks (e.g., Getty *et al.*, 2013). By contrast, the winged insects (Pterygota) walk with the whole of their tarsus in contact with the ground, which results in elongate tracks (e.g., Davis *et al*., 2007, fig. 5) similar to those seen in the fossils. Although rare (McDonald, 1992), there are some pterygote insects known from fragmentary body fossils in the Hartford and Deerfield basins, including beetles, cockroaches, and possible grasshoppers/crickets (Huber *et al.*, 2003), but the Pterygota are by far the largest subclass of insects and determining which among them made the trackways would require significant additional work to evaluate possible differences in trackway morphology among the different groups of pterygotes. The few exceptions are aquatic pterygotes, such as water boatmen (Corixidae), backswimmers (Notonectidae), predaceous diving beetles (Dyticidae), giant water bugs (Belostomatidae), and whirligig beetles (Gyrinidae), which can be ruled out because their trackways are different from *Lithographus* (Getty and Loeb, 2018; Getty, 2020). Thus, the fossils are attributed to a terrestrial pterygote, with no attempt to identify them further.

Comparison of modern and fossil pterygote insect trackways indicate that the smaller, anterior tracks are made by the first (prothoracic) legs. The medium-sized track, which usually is oriented perpendicular to the trackway axis, is made by the second (mesothoracic) legs, and the largest, usually elongate track is made by the third (metathoracic) legs.

EXPERIMENTAL RESULTS AND IMPLICATIONS

As illustrated in Figure 4, trackways produced by *Acheta domesticus* varied in morphology depending on the amount of water in the sediment. At 33% saturation (Fig. 4A, B), the resultant trackway consisted only of tracks produced by the second and third set of legs. No imprints of the first set of legs were made due to the firmness of the sediment. The tracks produced by the third set of legs, which were oriented posteriorly relative to the direction of movement, were not connected to each other. At slightly higher saturation levels (e.g., 36.4%; Fig. 4C, D), tracks of all three

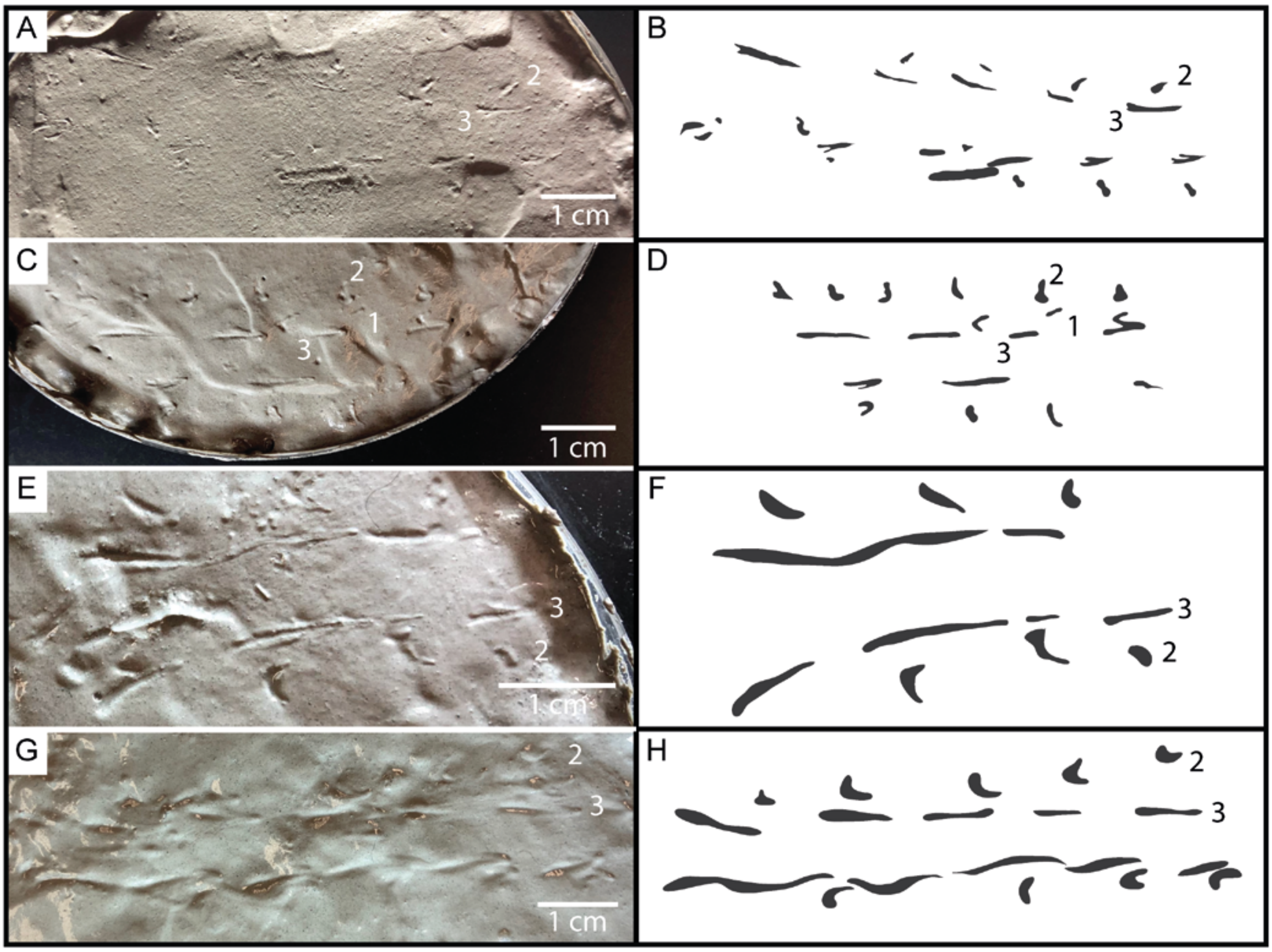

Fig. 4. Experimental trackways produced by *Acheta domesticus* in variably saturated mud. Numbers refer to tracks made by the first, second, and third legs of the insect. Direction of locomotion is from left to right in all cases. **A, B.** Photograph and interpretive sketch of a trackway produced in mud that was 33.0% water by weight. **C, D.** Photograph and interpretive sketch of a trackway produced in mud that was 36.4% water by weight. **E, F.** Photograph and interpretive sketch of a trackway produced in mud that was 37.8% water by weight. **G, H.** Photograph and interpretive sketch, respectively, of a trackway produced in mud that was 39.4% water by weight. Trackways in A and C are similar to those fossils that Hitchcock called *Lithographus,* whereas those in E and F are similar to those fossils that he differentiated as *Grammepus* because of the connected tracks made by the third legs.

leg sets were visible, and those of the third set remained separate from each other. At 37.8% saturation (Fig. 4E, F), imprints of the first set of legs were again missing, although those of the second and third set of legs were well developed. The tracks made by the third set of legs began to merge together and produce elongate, straight to zigzagging furrows. Finally, at the highest saturation levels (37.8%; Fig. 4G, H), the imprints made by the third set of legs were separate on the left side of the trackway but nearly confluent along the right side of the trackway. Again, leg sets two and three left imprints, but imprints of the first set of legs were not observed.

The trackways produced by *Acheta domesticus* in drier sediment (e.g., Fig. 4A–D) have a *Lithographus*-like morphology in that they have distinct tracks produced by the third leg set (Fig. 1A, B). Additionally, the modern trackways produced in wetter sediment (e.g., Fig. 4E–H) have a "*Grammepus"*-like morphology (Fig. 1C–H). Thus, the experimental results indicate that the same animal could have made both morphologies under different sediment saturation levels and that the primary difference between the two ichnotaxa is one of sediment consistency at the time of track formation. Fossil trackways that exhibit both morphologies were most likely produced on a surface that exhibited variable saturation levels at different locations.

CONCLUSIONS

As previous studies (e.g., Getty, 2016, 2018; Getty and Burnette, 2019) of Hitchcock's invertebrate traces have shown, the ichnotaxa are over split and synonymy is warranted in many cases for ichnotaxa that represent minor morphological variations of others. *Grammepus* is one such example of a minor morphological variant of a more well-known ichnogenus, *Lithographus*. Intergrading specimens, including the type specimen of *Grammepus erismatus,* indicate that there is no characteristic that consistently differentiates the two ichnogenera. *Grammepus* is consequently synonymized with *Lithographus*. Experiments with modern insects in sediment with different saturation levels show that the characteristic that was used to differentiate *Grammepus,* namely the elongate, nearly continuous medial tracks, are the result of a pterygote insect walking through wet, soft sediment. As more research is done on Hitchcock's invertebrate ichnotaxa, it is likely that more potential synonymies will be identified and that the rather large number of ichnotaxa will be reduced to a more manageable one that represents only a few recurring morphologies across sedimentary facies.

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