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; Pickering, 2004) 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.](image-url)
GEOLÓGICO Y PALEONTOLOGICO

El material evaluado para este escrito proviene del Acueducto de Deerfield de Sudoriental New England, que está ubicado en el noreste de los Estados Unidos de América (Fig. 2). El rifting que formó el acueducto, que finalmente resultó en el desarme de Pangea, comenzó hacia el Triásico Medio y terminó en el Jurásico Medio (Manspeizer y Cousminer, 1988; Olsen et al., 1992). Durante el rifting, las condiciones paleoclimáticas regionales eran monzónicas (Parrish, 1993), y había una larga estación seca (Hubert, 1978).

El rifting y la subsistencia de la meseta fueron lentos en el Triásico Medio, dando lugar a la acumulación de sedimentos fluviales, que formaron conglomerados arkósicos de la Formación Sugarloaf del Acueducto de Deerfield (vea Wems et al., 2016 para nombres alternativos de formaciones debido a una extensa sinónimia en las formaciones de Newark Supergroup). La extensión crustal se aceleró en el Jurásico Temprano, causando pequeños desplazamientos normales en la borda este del acueducto para coalescer en half grabens asimétricos, con su borde oriental sechina (Schlische y Olsen, 1990). Debido a la asimetría del Acueducto de Deerfield, las capas inclinan y se aplanan hacia el este. Concurrente con el aumento de la extensión y la subsistencia se produjo un cambio de condiciones fluviales a lacustres. Las capas lacustres representan depósitos en lagos en el Jurásico Temprano (Cornet et al., 1973). Las capas lacustres exhiben patrones que alternan de gris a negro, formados en aguas permanentes profunda, separadas por capas de arcilla y areniscas formadas en lagos temporales. Olsen (1986) argumentó que la cíclicidad en las capas lacustres resultó de cambios climáticos influenciados por Milankovitch, pero recientemente se ha sugerido que esta hipótesis ha sido cuestionada por Tanner y Lucas (2015). Existe un intervalo volcánico de 600 ka llamado Provincia Magmática del Cuadrante Central Atlántico que produjo volcánios basálticos (Olsen et al., 1996) que se asociaron con el rápido rifting y la subsistencia en el Jurásico. Algunos de estos lavas volcánicas que se depositaron en el rifting final han sido implicados en el evento de extinción del Triásico Medio (Blackburn et al., 2013).

Los nombres exactos de los lugares de los que Edward Hitchcock coleccionó el tipo de pata de Grammepus erismatus y Lithographus hieroglyphicus no se han especificado. En 1858 indicó que ambos eran del terraplén de un granjero (“Field’s Farm”), mientras que en el catálogo descriptivo del siglo 18, los especímenes se indican de un lugar en el oeste de la localidad de la Lily Pond. El nombre de la localidad en la Lily Pond y el nombre de la localidad de Newfield están vinculados con el río Connecticut, al este de la localidad de “Field Farm”. La coloración marrón de las placas de los especímenes de los que se han conservado las pistas terrestres indica que los sedimentos de los que se originó fueron depositados en aguas superiores con un grado de humedad bajo, pero al que se ha expuesto subacuáticamente.

MATERIALES Y MÉTODOS

Para los fósiles

El material que Edward Hitchcock coleccionó se encuentra en el Museo Beneski de Historia Natural en Amherst College. Las placas en las que se produjeron se han conservado en el identificador de acrónimo de la colección de las localidades, ACM ICH 9/13, 12/2, 26/21, 36/37, 36/39, 47/12, 47/14, 47/18, y 55/36. ACM ICH 36/37 se ha perdido de la colección, por lo que no se pueden analizar. Grammepus erismatus no se ha encontrado en ACM ICH 9/13, 12/2, y 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 $\geq 4\phi$, with minor amounts that were $\leq 3.75\phi$. 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.
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. 11, J) do not exhibit any joined tracks. Indeed, ACM ICH 47/18 (Fig. 11, 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.

**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 tarsi 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 (Dytidae), 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

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**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 synonyms 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.

**Acknowledgments**

PRG appreciates the hospitality of Hayley Singleton, of the Beneski Museum of Natural History, and Kate Wellspring, formerly of the Beneski Museum of Natural History, for granting him permission to examine the specimens in the Hitchcock Ichnology Collection. PRG also thanks Jessica Cundiff of the Museum of Comparative Zoology at Harvard University for permission to view specimens there. We thank Neal Alexandrowicz and Donna Cain, both of Collin College, for serving as secondary faculty advisors for Matthew Ward and Jack Simon. We are grateful to Ethan Vasquez for helping us make a tertarium for the crickets. Finally, this paper benefited from thorough reviews by Nicholas Minter and Lothar Vallon.

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