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Authors: Patrick R. Getty, and Samuel B. Loeb

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Aquatic insect trackways from Jurassic playa lakes: Reinterpretation of *Lunulipes obscurus* (HITCHCOCK, 1865) based on neoichnological experiments

PATRICK R. GETTY & SAMUEL B. LOEB

Abstract

The ichnospecies *Lunulipes obscurus* is reevaluated and a new diagnosis provided. All samples from Early Jurassic lacustrine deposits of the Deerfield Basin in Massachusetts, USA that were previously determined to bear *Lunulipes* or *Lunulipes*-like traces were examined. This reevaluation revealed that the ichnospecies is restricted only to two slabs. The morphology of *Lunulipes obscurus* suggests that its arthropod maker beat a single pair of legs synchronously. This type of locomotion is used by aquatic insects such as backswimmers (Notonectidae), water boatmen (Corixidae), and predaceous diving beetles (Dytiscidae). Neoichnological experiments with these three taxa indicate that water boatmen produce trackways that are the most similar to the fossil, and hence we conclude that a water boatman or an unknown insect that employed a similar method of swimming produced the Early Jurassic traces. These trackways provide the first tentative evidence of water boatmen in the Deerfield Basin, and, if correctly identified, represent the first trace fossils of this aquatic insect group anywhere.

Keywords: Actuopaleontology, ichnology, Early Jurassic, Dytiscidae, Corixidae.

1. Introduction

In modern freshwater environments, aquatic insects perform numerous functions such as filtering water, aerating sediment, processing detritus, and serving as a food source for other organisms (e.g., HERSHEY & LAMBERTI 2001). As such, they are essential components of the ecosystems that they inhabit. A major step in the development of such ecosystems was the evolution of a lentic (still water) entomofauna in the Late Triassic and into the Early Jurassic (WOOTON 1988; PONOMARENKO 1996; MERRITT & WALLACE 2003; SINITSHEKOVA 2003). Three orders of insects, the Coleoptera (beetles), Diptera (flies), and Hemiptera (true bugs), contributed to the increase in aquatic insect diversity observed at this time (GRIMALDI & ENGEL 2005). Within each of these orders, various well-known families first appeared. Among the beetles, these include the Dytiscidae, or predaceous diving beetles. Among dipterans, the crane flies (Tipulidae) and various groups of midges (e.g., families Chaoboridae and Chironomidae) appeared. Finally, among the true bugs, numerous families such as the back swimmers (Notonectidae), creeping water bugs (Naucoridae), giant water bugs (Belostomatidae), water boatmen (Corixidae), and water scorpions (Nepidae) showed up.

The Late Triassic to Early Jurassic Newark Supergroup of eastern North America spans the timeframe during which these insect groups invaded still water (OLSEN & KENT 1999, 2000) and consists, in part, of lithified lacustrine sediments. Thus, one would expect to find aquatic insect fossils in the Newark Supergroup. Indeed, the ear-

liest known belostomatids and naucorids were recovered from Late Triassic rocks in the Dan River-Danville Basin, along the North Carolina-Virginia border in the USA (FRASER et al. 1996; FRASER & GRIMALDI 2003; CRISCIONE & GRIMALDI 2017). In other Newark Supergroup basins (e.g., the Hartford and Deerfield basins in Massachusetts) the insect fossil record is fragmentary and no unequivocal aquatic beetle or true bug body fossils have been identified (HUBER et al. 2003). Trace fossils of these insects, however, might have the potential to supplement the fragmentary body fossil record in these other basins, assuming that such traces can be identified.

The best place in the Newark Supergroup to search for aquatic insect traces is, arguably, not a field locality but the HITCHCOCK Ichnology Collection at the Beneski Museum at Amherst College. Its namesake, EDWARD HITCHCOCK, was a 19th century ichnological pioneer (HÄNTZSCHEL 1975; STEINBOCK 1989; PEMBERTON et al. 2007) who amassed the collection as he described traces from the Hartford and Deerfield basins. Among the many ichnogenera that HITCHCOCK (1865) established was *Lunula* (preoccupied name, replaced by *Lunulipes* GETTY, 2017), with the ichnospecies *obscurus*, for trackways that consist of small, lunate tracks (Fig. 1). HITCHCOCK considered *Lunula* a myriapod trackway, but admitted he could not be completely certain that it was not a plant imprint. LULL (1915, 1953) subsequently revised HITCHCOCK's work and initially considered *Lunula* an insect or crustacean trackway, only to later say that the trackway was made by an unknown arthropod. Thus, there is no consensus on what made *Lunulipes*. Morphological characteristics of the trackway,

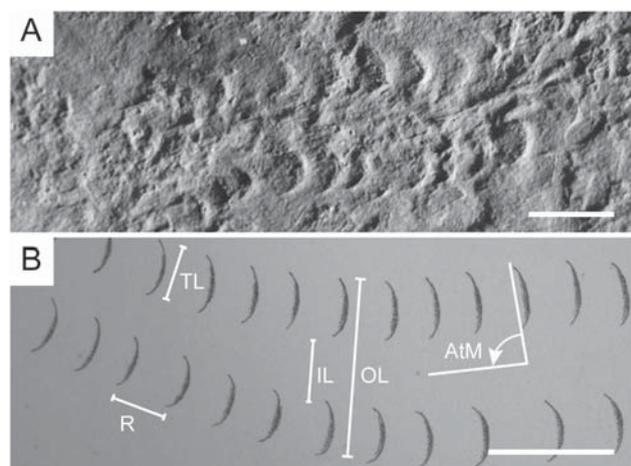


Fig. 1. *Lunulipes obscurus*; **A**: a portion of the lectotype, designated by RAINFORTH (2005), preserved on ACM ICH 52/14; **B**: portion of a trackway illustrated by HITCHCOCK (1865), with the measurements used in this study superimposed. – Scale: 10 mm.

such as the lack discernible track series (i.e., tracks made by multiple legs on a single side) suggest, however, that the trackway could have been made by an aquatic insect swimming by paddling with a single set of legs. In this paper, we present the results of neoichnological experiments to support the hypothesis that *Lunulipes* is most likely an aquatic insect trackway, and that as such it constitutes a valuable early record of these animals in a basin in which their body fossils have not been documented.

Abbreviations

Institutional: Beneski Museum of Natural History Ichthyology Collection (Amherst College, Amherst, Massachusetts, USA) = ACM ICH.

Trackway measurements (for Fig. 1) = AtM, angle to midline; IL, inner trackway length; OL, outer trackway length; TL, track length; R, repeat distance or stride.

Geographical and stratigraphic (for Fig. 2) = CT, Connecticut; MA, Massachusetts; RI, Rhode Island; Jdb, Jurassic Deerfield Basalt; Jm, Jurassic Mount Toby Formation; Js, Jurassic Fall River Beds; Jt, Jurassic Turners Falls Sandstone; Om, Ordovician Moretown Formation; Trs, Triassic Sugarloaf Formation.

Anatomical (for Fig. 4) = pro, prothoracic legs; mes, mesothoracic legs; met, metathoracic legs.

2. Geological context

Lunulipes obscurus has been found at only two sites, the Lily Pond quarry and Turners Falls, in the southern New England state of Massachusetts (HITCHCOCK 1865; Fig. 2). The Lily Pond quarry, which is now covered with water, is

located at approximately $42^{\circ}36'13.7''N$ $72^{\circ}32'05.7''W$. The exact location from which the Turners Falls specimen was collected is not known because HITCHCOCK did not record it in his published descriptions, and because he sometimes used the term Turners Falls for multiple outcrops along a 6.2 km stretch of river (OLSEN et al. 1992). The Lily Pond quarry and Turners Falls localities are within the Deerfield Basin, which spans the Late Triassic into the Early Jurassic and is one of a series of basins formed in the early Mesozoic in eastern North America known as the Newark Supergroup. The sediments and interposed igneous rocks in these basins accumulated as Pangea broke up in the Late Triassic through the Early Jurassic (VAN HOUTEN 1977; OLSEN 1978, 1997; OLSEN et al. 1992). Deposition within

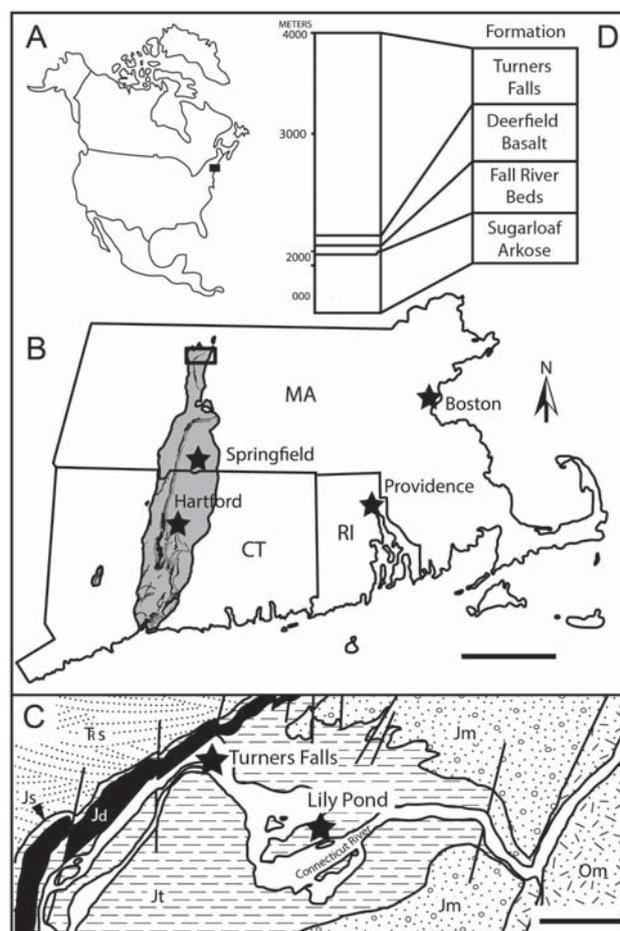


Fig. 2. *Lunulipes obscurus* geographic and stratigraphic context; **A**: map of North America with southern New England shaded by a black box; **B**: map of southern New England showing Newark Supergroup Mesozoic sedimentary rocks in gray and igneous rocks in black; **C**: bedrock geologic map of the boxed area in **B**. The stars indicate where the fossils were collected; **D**: simple stratigraphic column of the Deerfield Basin. – Scale: 50 km in **B** and 4 km in **C**.

the Deerfield Basin began in the Late Triassic with coarse fluvial sediments of the Sugarloaf Formation. Later, in the Early Jurassic, crustal extension rates increased and deposition shifted to fine-grained lacustrine sediments of the Fall River Beds and Turners Falls formations. This fundamental shift in depositional regimes coincided with the eruption of basaltic lava flows known as the Deerfield Basalt. Models indicate that the paleoclimate of the Deerfield Basin was monsoonal (PARRISH 1993), with a long dry season (HUBERT 1978).

Rocks exposed at the Turners Falls and Lily Pond localities belong to the Turners Falls Formation, which is 2 km thick and consists of playa and playa lake redbeds and gray to black lacustrine strata, along with minor fluvial strata (HUBERT & DUTCHER 2005). Cyclicality within the lake deposits, from red to gray and black shales, is attributed to Milankovich Cycle-influenced climate changes (OLSEN 1986). *Lunulipes* occurs on slabs of red shale, one of which preserves dinosaur tracks. The presence of dinosaur tracks, coupled with the red color of the shale, suggest that *Lunulipes* was produced in the shallow playa lake deposits of the formation. As noted by LULL (1953) and OLSEN et al. (1992), the two sites are among the most important of HITCHCOCK's collecting localities, with each yielding large numbers of well-defined vertebrate and invertebrate traces.

3. Materials and methods

Lunulipes obscurus trackways occur on two slabs, ACM ICH 52/12 and ACM ICH 52/14 (Fig. 3A, B). Eleven complete trackways (defined as two or more opposing track pairs) were identified, although additional isolated pairs of tracks or solitary tracks were also present on the slabs. Each trackway was photographed under low-angle light, with measurements later taken from the photographs using the public-domain image-processing and analysis program ImageJ (RASBAND 2014). The measurements (Fig. 1B) included outer trackway width, inner trackway width, track length, angle to midline for the track, and repeat distance (stride) between tracks. Outer trackway width is the greatest width of the trackway and was measured between the lateral tips of opposing tracks. Inner trackway width was measured between the two medial tips of opposing tracks. Angle to midline is defined as the angle constructed by a line running down the midline of the trackway and another line touching the medial and lateral tips of an individual track. Repeat distance was measured between successive tracks on the same side of the trackway (terminology according to TREWIN 1994).

To test the hypothesis that an aquatic insect made *Lunulipes*, three different types of insect were used in neoichnological experiments, including backswimmers (Notonectidae), water boatman (Corixidae), and preda-

cious diving beetles (Dytiscidae) (Fig. 4). These groups were chosen because each swims by beating a single pair of legs in unison (GITTELMAN 1974; BLAKE 1986; RIBERA et al. 1997; NGO & MCHENRY 2014), and this was deemed the most plausible way that *Lunulipes* was formed because the trackways lacked discernible track series (i.e., tracks made by multiple legs on a single side). The insects were identified to the family level using HAMMERSON (2004) in the field, and to the genus or species level in the lab using EVANS (2008). The backswimmers that were collected belong to the genus *Notonecta*, the water boatmen to the genus *Hesperocorixa*, and the predaceous diving beetles to the species *Graphoderus liberus*. The insects were collected at two different locations. The first location was a small, unnamed pond located in Storrs, Connecticut, on the University of Connecticut campus, at 41°49'02.26" N, 72°15'32.63" W. The second location was a marshy area along the side of the Fenton River, in Mansfield, Connecticut, located at 41°49'26.8"N 72°14'09.1"W.

Experiments were conducted using fine grained sediment in order to record the most detailed traces. Both clay and loess were tried in initial trials, but clay was used in later trials because the animals more easily left traces in it than in the loess. The sediment was placed into a container and shaken in order to produce a flat surface. Water was then added slowly in order to saturate the sediment without disturbing the surface. Once moistened, the surface was permitted to sit undisturbed until it compacted. Water was then added to the container until the sediment was covered with a shallow layer between 0.5 and 1.0 cm deep. The insects were placed into the container and allowed to swim; when the insects did not move on their own they were stimulated to do so by touching their abdomen with a blunt probe. Once the insects had produced a trackway, the insects were removed in order to prevent overprinting of the traces. Finally, photographs were taken of the traces for comparison with the trace fossils.

4. Systematic paleontology

Ichnogenus *Lunulipes* GETTY, 2017

non 1825 *Lunula* KOENIG.
1865 *Lunula* HITCHCOCK.

Type species: *Lunulipes obscurus* (HITCHCOCK, 1865), by monotypy.

Emended diagnosis: Concave epirelief trackway composed of two rows of crescent-shaped tracks, the long axes of which are oriented approximately perpendicular to the direction of locomotion. Within rows, tracks are arranged singly, one behind the other, such that no series are present.

Remarks: Originally called *Lunula* HITCHCOCK (1865), both HANTZSCHEL (1965, 1975) and ANDERSON (1981) noted that the original name was a junior homonym previously used by

KOENIG (1825, pl. 13, fig. 160) for a bryozoan. However, neither of these authors provided a replacement name for HITCHCOCK's ichnogenus, as is required by the International Code of Zoological Nomenclature (ICZN, 1999). Therefore, GETTY (2017) proposed the name *Lunulipes*. Whereas *Lunula* is feminine, *Lunulipes* is masculine, and the ending of the type species *obscura* had to be adjusted to *obscurus* in order to agree with the sex of the new ichnogenus name (GETTY 2017).

Lunulipes obscurus (HITCHCOCK, 1865)

Figs. 1, 3

v* 1865 *Lunula obscura*. – HITCHCOCK, p. 17, pl. 2, fig. 6.
 pt. 1865 *Lunula obscura*. – C. H. HITCHCOCK [non ACM ICH 33/36 (= *Cunicularius retrahens*); non ACM ICH 33/45 (= most likely fracture pattern)].

- 1871 *Lunula obscura*. – C. H. HITCHCOCK, p. 21.
 1889 *Lunula obscura*; C. H. HITCHCOCK, p. 119.
 1915 *Lunula obscura*. – LULL, p. 61.
 1953 *Lunula obscura*. – LULL, p. 46.
 1975 *Lunula obscura*. – HÄNTZSCHEL, p. W190.
 2005 *Lunula obscura*. – RAINFORTH, p. 874, fig. 5.45.
 2017 *Lunulipes obscurus*. – GETTY, p. 577, fig. 1.

Diagnosis: As for the ichnogenus.

Description: Trackways have an outer width of 1.0–1.8 cm and an inner width of 0.1–0.8 cm. The repeat distance between tracks, or stride, ranges from 0.5–2.0 cm. Individual tracks have a width of 0.3–0.8 cm and are oriented from 66–115° with respect to the trackway axis. Track shape is crescentic or apostrophe-form; in the latter either side of the track can be wider. Tracks are deepest on their convex side and become

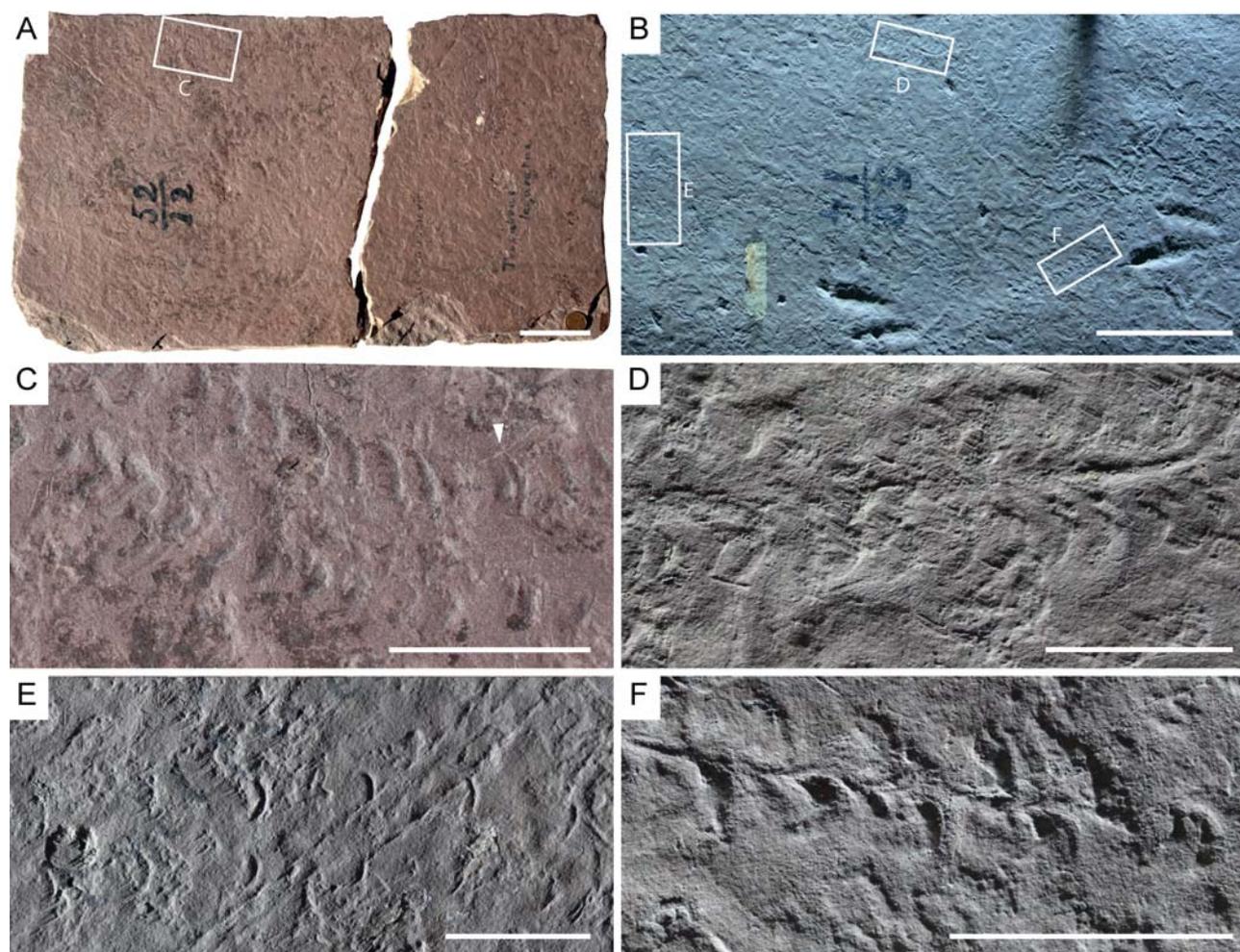


Fig. 3. *Lunulipes obscurus* from the Jurassic Turners Falls Formation of Massachusetts; **A:** ACM ICH 52/12, a slab of red shale from the Turners Falls locality preserving at least four trackways; **B:** ACM ICH 52/14, a slab of red shale (bluish color due to display lighting) from the Lily Pond preserving seven trackways; **C:** close-up of the boxed area in 3A, showing the lectotype; arrowhead points to what is either a bifid track or two very closely spaced tracks; **D:** close-up of the boxed region labeled D in panel 3B, showing an oppositely symmetric trackway with closely spaced tracks and a medial drag; **E:** close-up of the boxed region labeled E in panel 3B, showing an oppositely symmetric trackway with widely spaced tracks; **F:** close-up of the boxed region labeled F in panel 3B, showing portion of a trackway with alternate symmetry. – Scale: 6 cm in A and B, 2 cm elsewhere.



Fig. 4. Aquatic insects used in neoichnological experiments; **A:** the backswimmer *Notonecta* sp. (Notonectidae); **B:** the water boatman *Hesperocorixa* sp. (Corixidae); **C:** the predaceous diving beetle *Graphoderus liberus* (Dytiscidae). – Scale: 5 mm.

progressively shallower on their concave side; some exhibit sediment mounds adjacent to their convex side. Some tracks are possibly bifid, but it is also possible that what appear to be bifid tracks are simply two closely spaced tracks. Medial imprints are present in five of the 11 trackways; three are intermittently present whereas two are continuous. Trackways with the longest repeat distances lack medial imprints (e.g., Fig. 3E), whereas those with the shortest repeat distances have them (e.g., Fig. 3D). Ten of the trackways have exclusively opposite symmetry (e.g., Fig. 3C–E), whereas one trackway (Fig. 3F) exhibits both opposite and alternate symmetry at different points along its length.

Remarks: In addition to the trackways on ACM ICH 52/12 and ACM ICH 52/14, C. H. HITCHCOCK (1865) tentatively used *Lunula* in association with two other traces on other slabs. The first of these specimens is the burrow or deep surface trail *Cunicularius retrahens*, which is preserved on ACM ICH 33/36 (Fig. 5A, B). C. H. HITCHCOCK noted that there were crescentic imprints associated with the trace and said that these were reminiscent of *Lunulipes*. *Cunicularius retrahens*, however, is preserved in concave hyporelief on the underside of the slab and therefore the original surface topography is reversed. What appear as crescentic imprints in *C. retrahens* were actually mounds of sediment in the original trace. Thus, the similarity between the *L. obscurus* footprints and the crescentic elements in *C. retrahens* is merely a factor of preservation and indicates neither a relationship between the two ichnotaxa nor their makers.

The second of these other specimens is preserved on ACM ICH 33/45 (Fig. 5C, D). The number was given to part and

counterpart slabs that are held together by copper wire. The specimen, which C. H. HITCHCOCK (1865: 72) questionably attributed to *L. obscurus*, occurs on the stratigraphically upper surface of the top slab in convex epirelief. Considering that unquestionable *L. obscurus* specimens are preserved in concave epirelief on bed tops, it is unlikely that the structure is indeed a trackway. Rather, the two crescentic shapes that constitute the specimen most likely represent a fracture pattern in the rock.

5. Experimental results

Backswimmers, as their common name implies, swim upside down (Fig. 4A). Their padded metathoracic legs are held outward, away from the body, and project downward into the water column so that they can be used for swimming. The body itself is also held at an angle relative to the water surface, with the head projecting downward into the water column even farther than the metathoracic legs. They were only observed to right themselves at the water surface during attempts to fly away. Of the three groups of insects used in the experiments, they were deemed least likely to produce *Lunulipes*-like trackways because of their posture and only limited trials were conducted with them. A single backswimmer trackway (Fig. 6A) was produced in soft mud during experimental trials. The

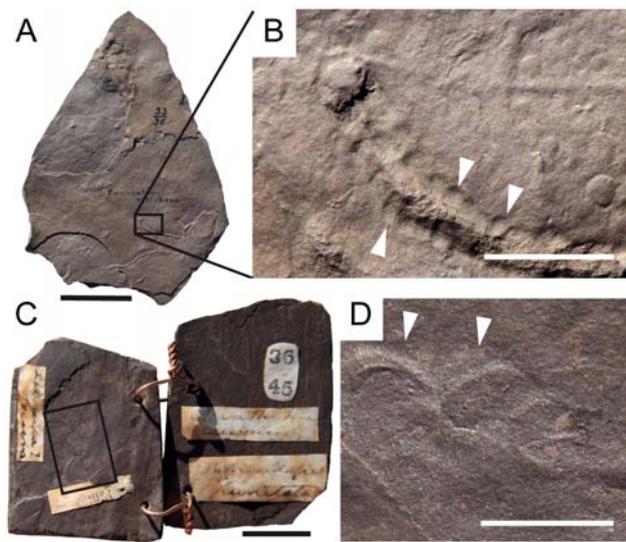


Fig. 5. Other specimens in the HITCHCOCK Collection listed as having *Lunulipes*, or *Lunulipes*-like traces on them; **A:** ACM ICH 33/36, underside of a shale slab showing the trail or burrow *Cunicularius retrahens*; **B:** close-up of the boxed area in 5A, showing the closely spaced depressions (arrowed) on either side of a central ridge. The specimen is preserved as a natural cast (concave hyporelief), so the structures were originally raised mounds; **C:** ACM ICH 36/45, two small shale slabs preserving multiple traces; **D:** close-up of the boxed region in panel 5C, showing two raised crescentic structures (arrowed) on the bed top which are likely fracture patterns on the rock. – Scale: 15 cm in A, 2 cm in B and C, 1 cm in D.

trackway consisted of a thick medial furrow produced by the dorsal surface of the body as it was dragged along the bottom, and it was segmented due to the jerking motion of the animal as it moved through the water. The left metathoracic leg scored the sediment surface as it was beat to propel the animal forward. The tracks left by this leg were long and thin to slightly ovate, and were oriented nearly parallel to the direction of locomotion. The right metathoracic leg did not touch the sediment and therefore did not leave any traces.

Water boatmen (Fig. 4B) produced six trackways during experimental trials. Four trackways were produced in firm loess, but these were poorly defined. Those produced in soft mud (Fig. 6B, C) were more defined. The trackways consisted of two rows of comma-shaped to lunate imprints produced by the metathoracic legs. The tracks exhibited opposite symmetry, were arranged singly (i.e., they lacked discrete series within the rows), and were oriented approximately perpendicular to the trackway midline. The tracks varied in thickness; the lateral part of the track was wider and straight-edged, whereas the medial part was narrower and tapered to a point. Medial furrows, produced by the ventral surface of the body, were present in five of the six

trackways produced, and occurred as intermittent grooves between the tracks (Fig. 6B) or continuous grooves running down the midline of the trackway (Fig. 6C).

Predaceous diving beetles (Fig. 4C) were used in 20 experimental trials, 17 of which yielded trackways (e.g., Fig. 6D, E). Fifteen of the trackways were similar to those produced by the water boatmen in consisting of two rows of lunate to comma-shaped tracks, produced by the metathoracic legs, arranged in opposite symmetry on either side of medial furrows. They differed from those produced by the water boatmen in that, in seven of the trackways, there were additional, smaller tracks (arrowed in Fig. 6D, E) produced by another set of legs. They further differed from the trackways produced by the water boatmen in that, in firm mud (Fig. 6D), the larger lunate tracks were bifid. In soft mud (Fig. 6E), the tracks were large, singular depressions. Medial grooves ranged from a series of thin, intermittent lines between the tracks and parallel to the midline in firm sediment (Fig. 6D) to wide and continuous furrows in soft sediment (Fig. 6E).

6. Discussion

As noted above, HITCHCOCK (1865) considered *Lunulipes obscurus* to be the work of a myriapod, and LULL (1915) considered it to be the work of a crustacean. A significant amount of neoichnological work has been done on myriapods and various aquatic crustaceans since HITCHCOCK and LULL conducted their studies (e.g., TRUSHEIM 1931; TASCH 1969; DAVIS et al. 2007; KNECHT et al. 2009; EISMAN & CHARNEY 2010). None of the trackways produced by the animals that were studied, however, strongly resembles *Lunulipes obscurus*.

Rather than myriapods or crustaceans, both of which use multiple appendages during locomotion, the presence of single tracks arranged one in front of the other on either side of the trackway suggests that the *Lunulipes obscurus* maker used only two legs during locomotion. Furthermore, the opposite symmetry observed in 10 of the 11 fossil trackways indicates that their maker used synchronous strokes of the legs. Water boatmen (Corixidae), predaceous diving beetles (Dytiscidae), and backswimmers (Notonectidae) swim in exactly such a fashion (GITTELMAN 1974; BLAKE 1986; RIBERA et al. 1997; NGO & MCHENRY 2014), and are thus better analogues for the *Lunulipes obscurus* trackmaker. (It is possible that the 11th specimen, which exhibits alternate symmetry, was produced by a different type of aquatic insect).

The results of the neoichnological experimentation that we conducted, however, indicate that water boatmen, predaceous diving beetles, and backswimmers are not equally likely to have been a maker for the fossils. For example, backswimmers swim upside down with their head deeper

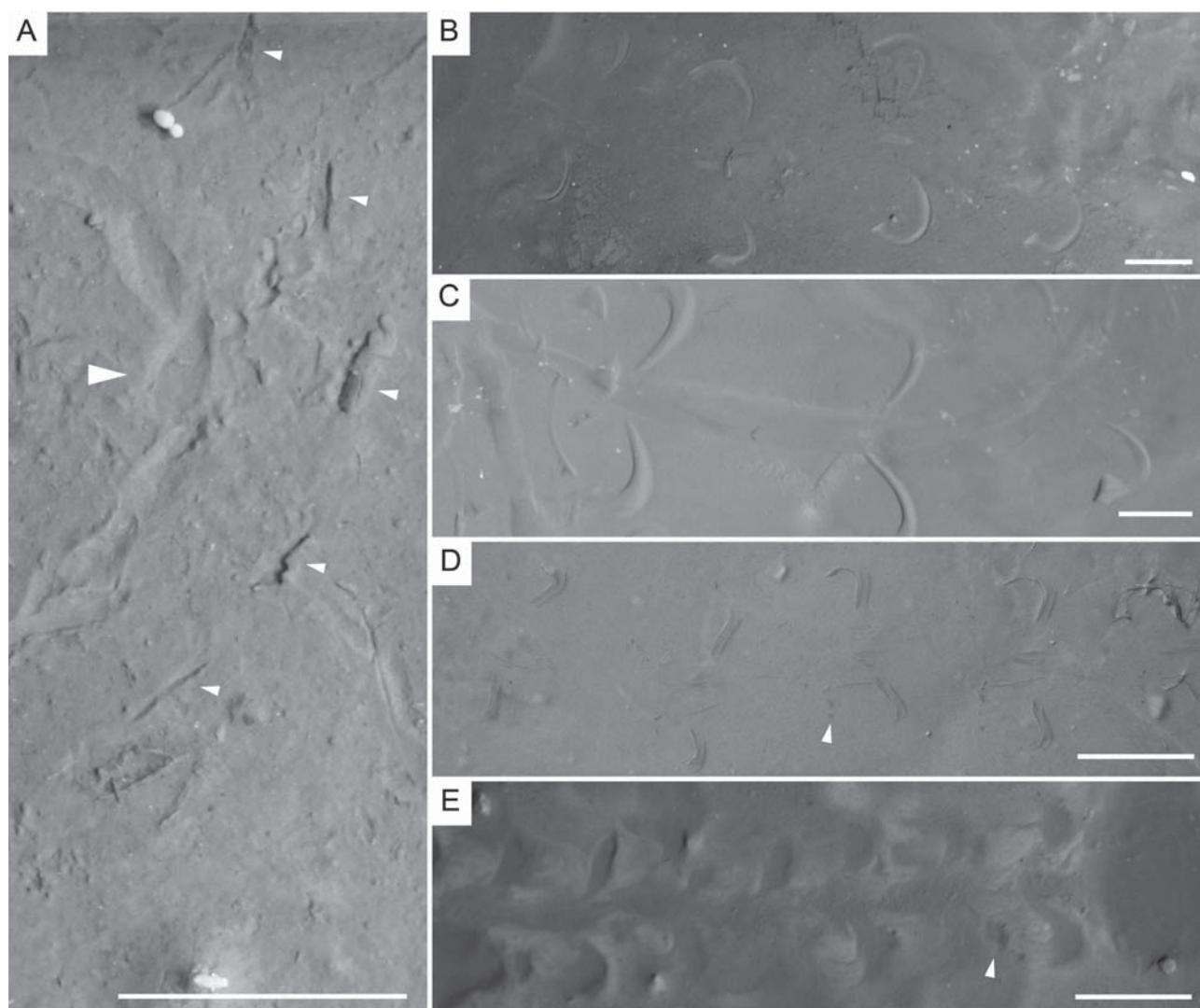


Fig. 6. Experimentally produced trackways; **A:** trackway produced by *Notonecta* sp. in soft mud. The segmented medial furrow is indicated with a large arrowhead whereas individual tracks are indicated with small arrowheads; **B:** trackway produced by *Hesperocorixa* sp. in soft mud under ~ 3.3 mm water; **C:** trackway produced by *Hesperocorixa* sp. in soft mud under ~ 3.5 mm water. **D:** trackway produced by *Graphoderus liberus* in firm mud under ~ 3.6 mm water; note the small imprints made by another set of appendages (one is arrowed) on both sides; **E:** trackway produced by *Graphoderus liberus* in soft mud under a film (ca. 1 mm) of water with small imprints again arrowed; Animal in A moved toward bottom of figure; all others moved from right to left. – Scale: 5 mm.

below the water surface than the metathoracic legs. Consequently, it would be expected that, if these animals produced trackways, they would consistently include medial furrows. The one trackway that was produced by a backswimmer included a prominent furrow mark made by the animal's dorsal surface (Fig. 6A). Considering that not all *Lunulipes obscurus* (e.g., Fig. 3C, E) exhibit medial furrows, then it seems unlikely that Early Jurassic backswimmers made the fossil traces. Furthermore, the imprints left by the leg in the experimentally produced trackway were straighter than the curved ones observed in the fossils,

and were oriented more closely to parallel to the trackway midline than in the fossil.

The repichnia made by the water boatmen and the predaceous diving beetles more closely resemble *Lunulipes obscurus* than the one produced by the backswimmer. For example, the trackways produced by each of these groups consists of crescentic tracks that are oriented approximately perpendicular to the trackway midline, and medial drags are intermittently present. The water boatman trackways produced in the present experiments differ from the fossils, however, in having tracks that are noticeably wider

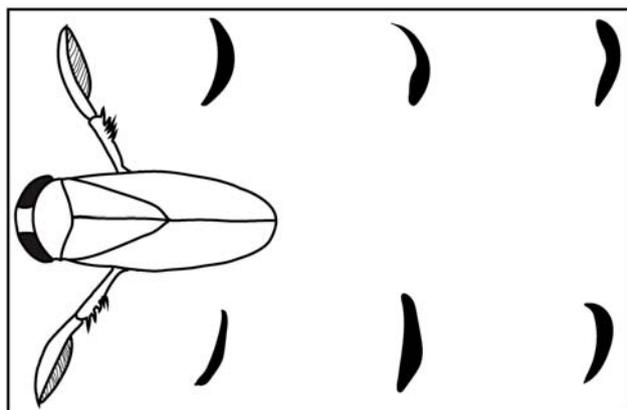


Fig. 7. Line drawing illustrating a water boatman (Corixidae) as a possible producer for *Lunulipes obscurus*. The animal is moving from right to left and has its metathoracic legs, which it uses for swimming, extended. The paddles incised the sediment during previous strokes of the legs, producing crescentic tracks.

laterally than medially; that is, the individual tracks are broad and wedge shaped on the outside of the trackway but taper to a point near the trackway midline. They are also more strongly curved and taper in the direction in which the animal traveled. That said, METZ (1987) illustrated a water boatman trackway in which some of the tracks more strongly resembled the fossils.

The predaceous diving beetle trackways differed from the fossils in exhibiting two types of tracks. The larger tracks were produced by the metathoracic legs and the smaller ones, which are arrowed in Fig. 3D–E, were produced by one of the more anterior pairs of legs. Considering that *Lunulipes obscurus* does not exhibit two different types of tracks, we deem it unlikely that the trace fossils were made by a predaceous diving beetle that swam in a manner similar to *Graphoderus liberus*. Given the evidence at hand, we propose that *Lunulipes obscurus* was produced by an aquatic insect similar to a water boatman and provide a reconstruction (Fig. 7) showing such an insect in the act of making a trackway.

7. Conclusions

The ichnospecies *Lunulipes obscurus*, which had remained enigmatic since it was first described in 1864, has been reevaluated and a new diagnosis provided. All samples that were said to include *Lunulipes* or *Lunulipes*-like traces were examined. It was shown that the ichnospecies is restricted to two slabs, and that other slabs have unrelated burrows/surface trails or fractures on them. The morphology of *Lunulipes obscurus* suggests that, with one exception, its arthropod maker beat a single pair of

legs synchronously during locomotion, which precludes myriapods and most crustaceans, the groups to which it had previously been attributed. Rather, this type of locomotion is used by aquatic insects such as backswimmers (Notonectidae), water boatmen (Corixidae), and predaceous diving beetles (Dytiscidae). Neoichnological experiments with species from each of these insect groups indicate that water boatmen produce trackways that are more similar to the fossil than the trackways of backswimmers and predaceous diving beetles. Consequently, we argue that *Lunulipes obscurus* is the work of an Early Jurassic member of the Corixidae, or an unknown insect that employed a similar swimming method. *Lunulipes* therefore provides the first evidence of aquatic insects like water boatmen in the Deerfield Basin. If this attribution is correct, *Lunulipes* is also the first trace fossil evidence of this group of insects anywhere. Finally, this trackway demonstrates the utility of using trace fossils to supplement the insect body fossil record in places where body fossils are scarce.

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Addresses of the authors:

PATRICK R. GETTY, Department of Geology, Collin College, 2800 E. Spring Creek Parkway, Plano, Texas, 75074, U.S.A.

SAMUEL B. LOEB, 33 West Branch Road, Weston, Connecticut, 06883, U.S.A.

E-mails: PGonsoulinGetty@collin.edu; loeb_samb@yahoo.com

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