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Evidence that the fossil insect trackway *Bifurculapes laqueatus* Hitchcock, 1858 was made underwater

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ABSTRACT:

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Three trackways attributable to the ichnospecies *Bifurculapes laqueatus* Hitchcock, 1858 found in Lower Jurassic rocks of the Newark Supergroup in northeastern North America are preserved in association with current lineations. Each trackway takes turns so that parts of the trackway parallel the current lineations. This parallelism is interpreted as evidence that the trackmakers were entrained in flowing water and had to change course due to the current. If this interpretation is correct, then morphological differences between *B. laqueatus* and terrestrial insect trackways could be explained by the trackmaker moving subaqueously. Further, *B. laqueatus* would constitute only the second insect trackway from this region to be recognized as being made subaqueously. From an ecological standpoint, the aquatic insects that made *B. laqueatus* were probably near the base of the local food chain, the apex predators of which were piscivorous theropod dinosaurs.

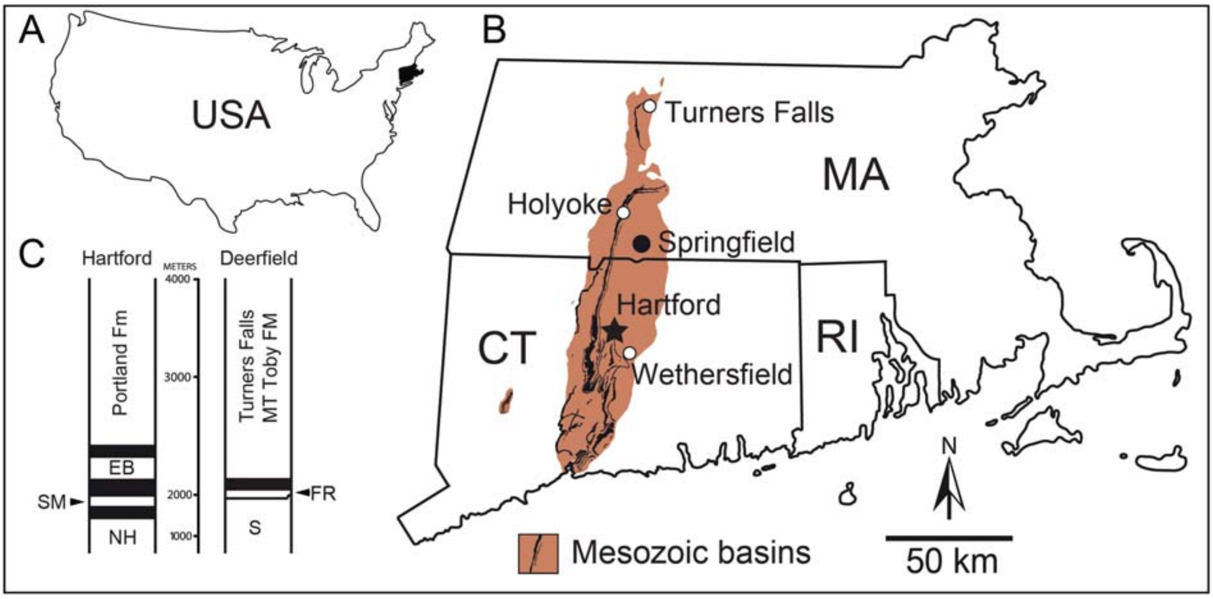
Key words: Aquatic; Ichnology; Arthropods; Mesozoic; Jurassic.

INTRODUCTION

Aquatic insects are a crucial component for the proper functioning of modern freshwater ecosystems, where they provide food for other organisms, as well as serve as water filterers, sediment aerators, and detritus processors (Hershey and Lamberti 2001). The colonization of aquatic environments by insects consisted of a protracted series of adaptations by numerous insect groups at various intervals throughout Earth history. In an adaptive radiation during the Late Triassic and Early Jurassic, standing bodies of water such as ponds and lakes were colonized by insects to form the first lacustrine entomofaunas (Wootoon 1988; Ponomarenko 1996; Merritt and Wallace 2003; Sinitshenkova 2003).

Body fossils constitute the primary evidence for these lacustrine entomofaunas (e.g., Olsen *et al.* 1978; Fraser *et al.* 1996), but trace fossils, such as trackways, trails, and burrows, can fill important gaps where body fossils are scarce or absent (e.g., Uchman *et al.* 2007, 2009, 2011, 2018; Buatois *et al.* 2016). One region where Late Triassic and Early Jurassic body fossils are rare is southern New England, USA, where lacustrine rocks of the Newark Supergroup preserve only sparse – and usually poorly preserved – insects (McDonald 1992). Despite their depauperate body fossil record, these rocks, found in the Hartford and Deerfield basins, contain abundant insect trace fossils that were described in the 19th century (e.g., Hitchcock 1858, 1865).

It seems reasonable that some of the trackways from the Hartford and Deerfield basins were produced by aquatic insects, and indeed, Getty and Loeb (2018) showed that *Lunulipes obscurus* (Hitchcock, 1865) (see Getty 2017 for genus name modification) was most likely produced by a water boatman (Corixidae). *Lunulipes obscurus,* however, is just one of the many ichnogenera that Hitchcock (1858, 1865) attributed to insect activity, and other than noting



Text-fig. 1. Geological context of the *Bifurculapes* specimens illustrated in Text-fig. 2. A – Map of the contiguous 48 United States, showing southern New England shaded in black. B – Map of southern New England with lower Mesozoic rocks shaded. Sedimentary rocks are brown and igneous rocks are black. Turners Falls, Holyoke, and Wethersfield are locations from which *Bifurculapes laqueatus* Hitchcock, 1858 has been recovered regionally. Abbreviations: CT, Connecticut; MA, Massachusetts; RI, Rhode Island. C – Simplified stratigraphic columns of the Hartford and Deerfield basins. Abbreviations: EB, East Berlin Formation; FR, Fall River beds; NH, New Haven Formation; S, Sugarloaf Formation; SM, Shuttle Meadow Formation

their occurrence in lacustrine rocks (e.g., Huber *et al.* 2003), none of the ichnogenera have been evaluated to determine if they were produced underwater. (The trackways' association with lacustrine rocks is not sufficient to demonstrate that they were produced underwater because lake levels can fluctuate, and terrestrial insects can thus make trackways on lakebeds during lowstands; Minter *et al.* 2012).

Among the ways that a fossil trackway might be shown to have been produced underwater is to match its morphology with that of modern aquatic insects, as Getty and Loeb (2018) did. Yet another is to find trackways that show evidence of their maker interacting with the water in which they lived. One trackway that might have been made underwater is *Bifurculapes laqueatus*, which was described by Hitchcock (1858), and later revised by Getty (2016, 2018a) and Getty and Burnett (2019). In this paper, evidence is presented that the maker of *B. laqueatus*, which is from Lower Jurassic rocks of the Hartford and Deerfield basins, changed direction in the presence of a current (as recorded by current lineations), thus indicating that the trace was made underwater. This means that *B. laqueatus* is the trace of an insect that was part of the adaptive radiation in the Early Jurassic that formed the lacustrine entomofauna.

GEOLOGICAL CONTEXT

The *B. laqueatus* specimens evaluated in this paper were found in the Hartford and Deerfield basins of southern New England, northeastern USA (Text-fig. 1). The basins are a part of the Newark Supergroup, which was formed as Pangea rifted prior to the opening of the Atlantic Ocean (Olsen 1978, 1997). Rifting that produced the Newark Supergroup began by the Late Triassic, continued into the Early Jurassic, and ended by the Middle Jurassic (Manspeizer and Cousminer 1988; Olsen *et al.* 1992). During rifting, the basins filled with sediments that are primarily of fluvial and lacustrine origin, as well as basaltic lavas and some volcanic ash. Throughout the time during which rifting occurred, monsoonal paleoclimate conditions predominated (Parrish 1993) and there was a long dry season (Hubert 1978).

Basin subsidence was slow during the Triassic and sedimentation was primarily fluvial, forming the arkosic conglomerates of the New Haven Formation of the Hartford Basin and the Sugarloaf Formation of the Deerfield Basin (but see Weems *et al.* 2016 for an extensive synonymy of lithostratigraphic names across the Newark Supergroup basins). In the Early Jurassic, however, crustal extension rates increased, causing normal faults on the eastern edge of the basins to coalesce to form asymmetrical, east-dipping half-grabens (Schlische and Olsen 1990). Due to the asymmetry of the basin, the beds tilt and thicken eastward. Sedimentation shifted from fluvial to lacustrine as lakes occupied the basins during the time of rapid crustal extension. The lake deposits are represented by the Fall River beds and the Turners Falls Formation in the Deerfield Basin, and by the Shuttle Meadow, East Berlin, and lower Portland formations in the Hartford Basin. The Lower Jurassic lake deposits exhibit regularly repeating patterns of gray and black shale formed in deeper, permanent lakes separated by red mudstone and sandstone formed in shallower, ephemeral lakes. Olsen (1986) proposed that Milankovich cycle-influenced climate changes account for the cyclicity of the lacustrine strata, although this has been called into question by Tanner and Lucas (2015). Along with rapid subsidence in the Early Jurassic, there was a 600-ka interval of volcanism called the Central Atlantic Magmatic Province that produced basaltic lava flows (Olsen *et al.* 1996), the earliest of which have been implicated in the end-Triassic extinction event (Blackburn *et al.* 2013).

Two of the three specimens that will be discussed below (i.e., those in Text-fig. 2A, B and 2E, F) were collected from lacustrine beds of the Lily Pond locality (Hitchcock 1858, 1865), which is of Early Jurassic age and exposes rocks of the Turners Falls Formation of the Deerfield Basin. Beds at the Lily Pond locality include both ephemeral and perennial lake deposits (Olsen *et al.* 1992). The third specimen (Text-fig. 2C, D) was collected by the author from debris at a site in the Hartford Basin known locally as the Gary Gaulin dinosaur tracksite (42º11’51.74” N, 72º38’41.16” W), which exposes rocks of the East Berlin Formation. The rocks at the Gaulin site compare favorably with those that were interpreted by Gierlowski-Kordesch and Rust (1994) and Drzewiecki and Zuidema (2007) as having been formed under playa conditions, and Getty (2016, 2018b) therefore has interpreted them as playa lake deposits.

Institutions and abbreviations

The specimens examined in this study are housed at the Beneski Museum of Natural History at Amherst College (Amherst, Massachusetts) and the Yale Peabody Museum of Natural History at Yale University (New Haven, Connecticut). The abbreviations for these institutions are, respectively, ACM ICH (the latter three letters indicating that the specimen is part of the ichnology collection) and YPM IP (the latter two letters indicating that the specimen is part of the invertebrate paleontology collection).

METHODS

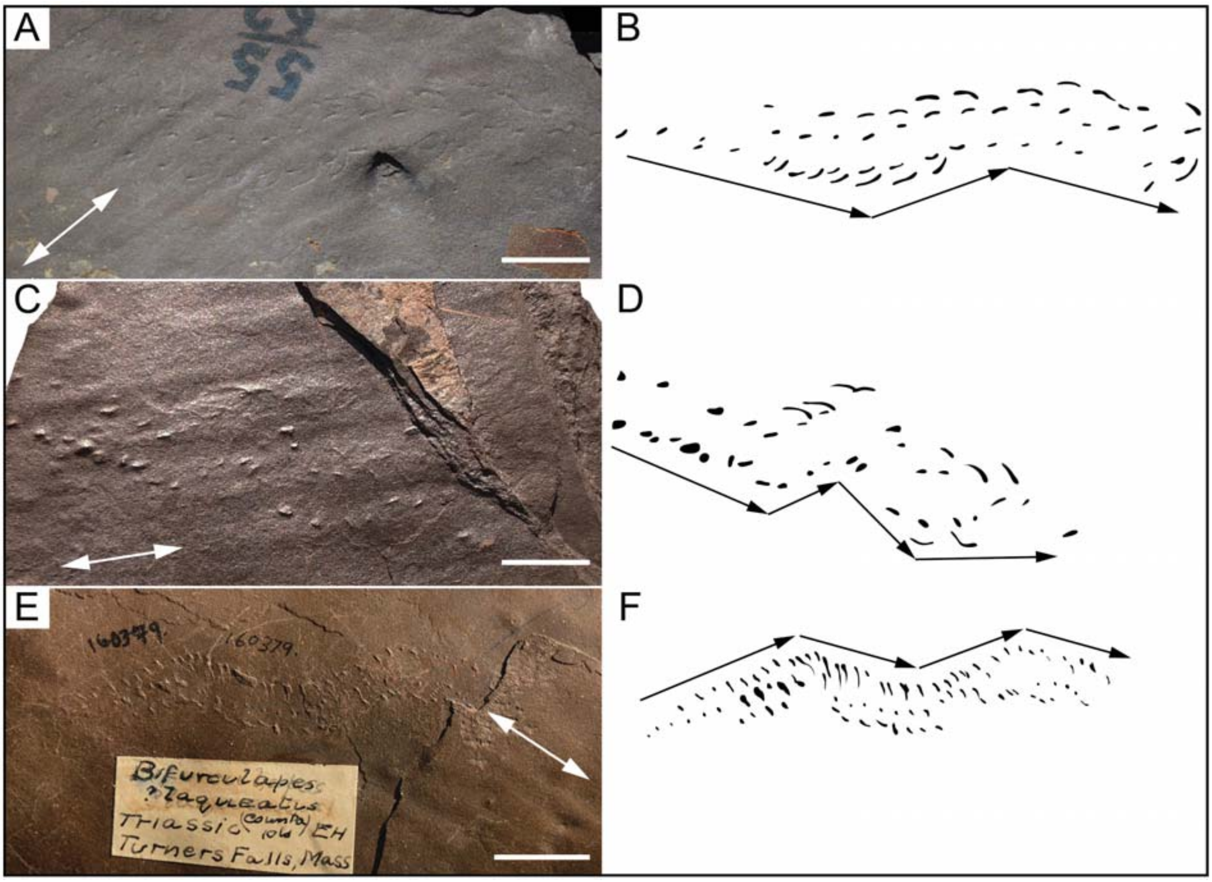
The slabs, as well as the trace fossils and sedimentary structures on them, were examined and photographed under low-angle light. All measurements were then taken from the photographs, which were imported into the public-domain image processing and analysis program ImageJ (Rasband 1997–2004). Trackway sinuosity was calculated by measuring the curved path of the trackway relative to its straight length.

Experimental trackways were produced both subaqueously and subaerially for comparison with the fossils. The aquatic insects, collected from ponds in Connecticut, included the giant water bug (Belostomatidae) *Belastoma flumineum* Say, 1832 and the whirligig beetle (Gyrinidae) *Dineutus discolor* Aubé, 1838. The subaqueous experiments were conducted using saturated clay under a shallow (0.5 to 1.0 cm) layer of water. The methodology for setting up the container in which the animals swam is described by Getty and Loeb (2018). The subaerial trackway experiments were conducted with crickets (*Acheta domestica* Linnæus, 1758) that were purchased from a local pet food store and allowed to walk across a flat bed of clean, fine-grained quartz sand.

OBSERVATIONS OF THE FOSSILS

Specimen ACM ICH 55/62 (Text-fig. 2A, B)

This specimen consists of a small medium gray slab of laminated, micaceous, silty fine-grained sandstone. As seen in plan view, the slab has five sides and has maximum dimensions of 8.5 by 5.3 cm. Traces on this slab, which include a *Bifurculapes laqueatus* [this is the type of *B. curvatus* Hitchcock, 1865, which Getty (2016) synonymized with *B. laqueatus*], as well as a fish trail called *Undichna* Anderson, 1976 and an indeterminate dinosaur claw imprint, are preserved as natural casts (the counterpart specimen, ACM ICH 55/52, preserves the traces



Text-fig. 2. *Bifurculapes laqueatus* Hitchcock, 1858 exhibiting evidence of trackmaker interaction with flowing water. A, B – Photograph and interpretive drawing of trackway on ACM ICH 55/62. C, D – Photograph and interpretive drawing of trackway on ACM ICH 305. E, F – Photograph and interpretive drawing of trackway on YPM IP 160379. The lines with double arrowheads in the photographs indicate the orientation of the long axes of the current lineations; the arrows in the interpretive drawings indicate the direction of travel for the trackmaker. Scale bars are 10 mm

as molds). Beside the laminations, sedimentary structures preserved on the slab include faint, parallel and undulatory marks that are broadly U-shaped in cross section. These U-shaped structures are up to 3 mm wide and up to 51 mm long. They vary in width (all widen in the same direction), and fade out at their ends. In places, troughs give way to ridges, and vice versa. The *B. laqueatus*, which is 8.6 cm long around its curves, has a straight length of 8.1 cm, and thus a sinuosity of 1.06. It makes two turns, which divides the trackway into three segments. The central part of the trackway is at a 19º oblique angle to the U-shaped sedimentary structures, whereas the beginning and end segments of the trackway are more strongly oblique, at 49º and 53º respectively, relative to the U-shaped structures. The trackway becomes asymmetric in the vicinity of the first turn in that the tracks within the series become more widely spaced from each other on the left side of the trackway than on the right; some of the inner tracks on the right side of the trackway are nearly on the trackway midline. Tracks on the outside of the trackway, especially near the turns, are markedly longer than others.

Specimen ACM ICH 305 (Text-fig. 2C, D)

This specimen consists of a small brownish gray slab of laminated, micaceous, silty fine-grained sandstone. The slab is triangularly shaped and has maximum dimensions of 16.5 by 13.5 cm. A single *Bifurculapes* is preserved as a natural cast on the slab. The trackway is rather irregular, but series of two tracks can be discerned, so it can be attributed to *B. laqueatus*. Additional sedimentary structures include desiccation cracks preserved on the bed top, as well as faint, parallel, and undulatory structures that occur on three laminae on the bottom of the slab. These are, like the structures on ACM ICH 55/62, broadly U-shaped in cross section and fade out at their ends. They are up to 5 mm wide and have lengths of up to 40 mm, although they were longer because their ends are not preserved on the slab. The *B. laqueatus* is 6.0 cm long and has a straight length of 5.6 cm, which gives a sinuosity of 1.07. It takes three abrupt turns, thus dividing it into four segments. These segments are oriented 31º, 0º, 39º, and 11º, respectively, relative to the U-shaped sedimentary structures. The trackway is markedly asymmetric and the tracks on the outside of the turns are strongly curved.

Specimen YPM IP 160379 (Text-fig. 2E, F)

This specimen is a small, brown, rectangular slab measuring 12.1 by 13.5 cm, and is composed of laminated, micaceous, silty fine-grained sandstone. There are faint, parallel, and undulatory U-shaped structures on the slab. These structures are more pronounced on the bottommost lamina, but also occur on an overlying lamina on which a single trackway, which was previously attributed to *B.*? *laqueatus*, is preserved. The U-shaped structures are up to 6 mm wide. They fade out at their preserved ends, but due to their occurrence on the edge of the slab their total lengths cannot be measured. The trackway is 8.4 cm long and is preserved as a natural cast. It exhibits three directional changes, which divides it into four segments. The straight length distance of the trackway is 8.0 cm, and therefore it has a sinuosity index of 1.05. The segments are oriented at 48º, 0º, 39º, and 15º with respect to the U-shaped sedimentary structures. The trackway exhibits asymmetry in that the inner tracks from the track series often overlap the trackway midline.

INTERPRETATIONS

The faint, U-shaped sedimentary structures on ACM ICH 55/62, ACM ICH 305, and YPM IP 160379 are similar in size and overall morphology to current lineations (Allen 1964; Stow 2005), and are consequently interpreted as such herein. Further support for this interpretation comes from the observation that in continental systems, such structures are often associated with strongly seasonal climates in which precipitation peaks at certain times of year (Fielding 2006), and, as was noted previously, these conditions prevailed during the time that the sediments of the Hartford and Deerfield basins were laid down (e.g., Hubert 1978; Parrish 1993). Experimental data show that current lineations form in plane-bedded silt and sand in the upper flow regime (Allen 1964; Nichols 1999), and therefore the beds on which the trackways were impressed were deposited by fast-flowing currents.

The question then becomes when the trackways were made relative to the deposition of the sediments by the current. It is possible that the trackways were made after the flow had died down, or even subaerially after the water had evaporated. For example, terrestrial insects could have paralleled the current lineations to feed on detritus that settled in troughs, but this possibility seems unlikely because no such detritus is actually preserved in the troughs. Further, as Uchman *et al.* (2018) argued for trackways produced in Pleistocene glacial lakes, the asymmetry of the trackways is suggestive of the animals interacting with flowing water. It seems more plausible, then, that the animals were underwater and moving oblique to the flow, which caused them to drift slightly and have to change directions in order to stay on course.

SIGNIFICANCE

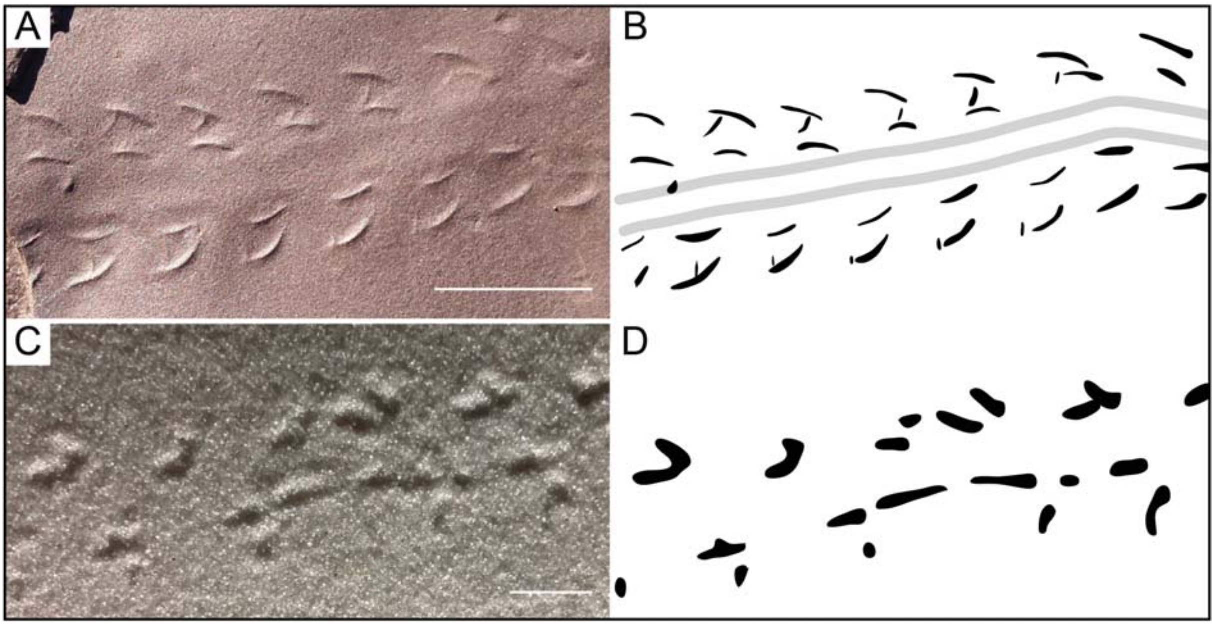
The recognition that the trackways preserved on ACM ICH 55/62, ACM ICH 305, and YPM IP 160379 were produced underwater is significant for two reasons. First, it provides a possible explanation as to why two insect trackways common in the Hartford and Deerfield basins that were made by insects – *B. laqueatus* and *Lithographus hieroglyphicus* Hitchcock, 1858 – look so much different from each other. The latter ichnospecies is commonly regarded as having been made subaerially (e.g., Davis *et al.* 2007), but the former might have been produced subaqueously. To argue that *B. laqueatus* was made underwater requires the extrapolation of subaqueous locomotion to other *B. laqueatus* that are not associated with current lineations. Whereas this might seem like a stretch at first, there is evidence to support this extrapolation. For example, much larger, but morphologically similar trackways from the Cretaceous of Spain that were originally attributed to *Hamipes didactylus* Hitchcock, 1858 by de Gilbert *et al.* (2000) and later reassigned to *Bifurculapes* isp. (Getty 2018a), were formed in subaqueous settings that lack evidence of subaerial exposure. Similarly, Uchman *et al.* (2009, fig. 5b–c) illustrated trackways that were made in glacial lake sediments that, although attributed to *Warvichnium ulbrichi* Walter, 1985 strongly resemble *B. laqueatus*.

Second, the recognition that *B. laqueatus* was made underwater provides invaluable context for understanding the ecosystem of the Early Jurassic Hartford and Deerfield basins. Numerous researchers (e.g., Wright 1997; Farlow and Galton 2003; Getty 2005; Getty *et al*. 2012, 2015) have suggested, based on ichnological data, that terrestrial carnivorous dinosaurs were more numerous than herbivores in these basins. In order to address this issue, some researchers (e.g., Olsen 2010) have proposed that the carnivores ate fish. Considering that fish body fossils are incredibly numerous in black shales (McDonald 1992), and that their trails are found at localities with dinosaur tracks (Getty 2018b), this explanation is reasonable. Nonetheless, this raises the question of what the fishes were eating. Coprolites indicate that large fishes, such as the coelacanth *Diplurus* Newberry, 1878 ate smaller ones, and the small fishes must have consumed invertebrates such as insects (McDonald 1992). *Bifurculapes laqueatus* is, along with *L. obscurus,* the work of insects that could have served as a food source for the smaller fish. Given that *B. laqueatus* is significantly more common than *L. obscurus* (only 11 trackways of the latter are known; Getty and Loeb 2018), the *B. laqueatus* trackmaker probably would have been a more important part of the Early Jurassic lacustrine food chain in these basins.

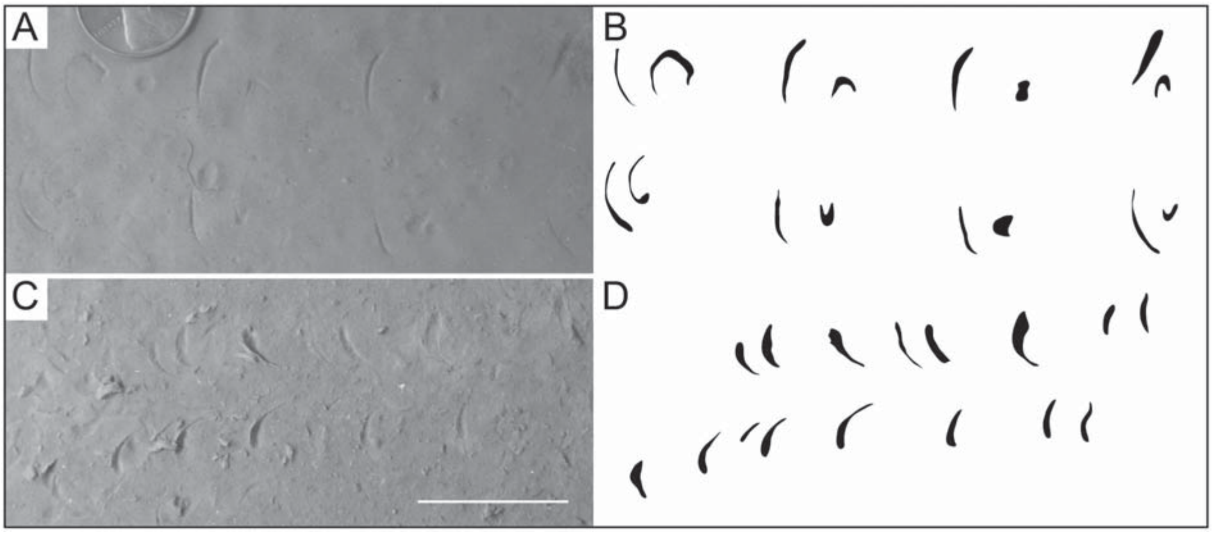
IDENTIFYING POSSIBLE TRACKMAKERS

Getty (2016) summarized previous researchers' hypotheses regarding the makers of *Bifurculapes*, which include crustaceans and insects, and evaluated different hypotheses. In particular, he favored an insect maker for *B. laqueatus* because of general similarities the fossils had with darkling beetle trackways illustrated by Eiseman and Charney (2010). These were produced subaerially and therefore it was implied that *B. laqueatus* had been made subaerially as well. Differences between the modern and fossil trackways, such as the longest track being on the inside of the track series in the modern trackways, and on the outside of the trackway in the fossils, were not explained. These differences were confirmed by observing additional modern trackways in the literature (e.g., Gutteridge 2017, p. 45), and by producing trackways with crickets (*Acheta domestica*) in fine, subaerial sand (Text-fig. 3). The recognition that *B. laqueatus* was made underwater provides a potential explanation for why the fossil trackways differ from the modern ones.

The *B. laqueatus* maker remains unidentified, although some groups of aquatic insects can be ruled out based on experimental results. For example,



Text-fig. 3. Fossil and modern trackways for comparison. A, B – Photograph and interpretive drawing of *Bifurculapes laqueatus* Hitchcock, 1858 on ACM ICH 300. C, D – Photograph and interpretive drawing of an experimentally produced trackway made by a cricket (*Acheta domestica* Linnæus, 1758) subaerially in fine-grained sand. Scale bars are 10 mm



Text-fig 4. Experimentally produced aquatic insect trackways for comparison to *Bifurculapes laqueatus* Hitchcock, 1858. A, B – Photograph and interpretive drawing of a trackway produced by the giant water bug (Belostomatidae) *Belastoma flumineum* Say, 1832. C, D – Photograph and interpretive drawing of a trackway made by the whirligig beetle (Gyrinidae) *Dineutus discolor* Aubé, 1838. Coin in A is 19.05 mm; scale bar in C is 10 mm

trackways of predaceous diving beetles (Dytiscidae), water boatmen (Corixidae), and backswimmers (Notonectidae) were figured by Getty and Loeb (2018) and do not resemble *B. laqueatus.* Neither do the trackways of giant water bugs (Belostomatidae) or whirligig beetles (Gyrinidae), which are shown in Text-fig. 4. Given the major radiation of aquatic insects in the Late Triassic and Early Jurassic, significant work would need to be done to identify the maker, and it would require the study of body fossils because some of the groups are extinct and therefore cannot be used in experiments.

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