# Late Carboniferous paleoichnology reveals the oldest full-body impression of a flying insect

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Insects were the first animals to evolve powered flight and did so perhaps 90 million years before the first flight among vertebrates. However, the earliest fossil record of flying insect lineages (Pterygota) is poor, with scant indirect evidence from the Devonian and a nearly complete dearth of material from the Early Carboniferous. By the Late Carboniferous a diversity of flying lineages is known, mostly from isolated wings but without true insights into the paleoethology of these taxa. Here, we report evidence of a full-body impression of a flying insect from the Late Carboniferous Wamsutta Formation of Massachusetts, representing the oldest trace fossil of Pterygota. Through ethological and morphological analysis, the trace fossil provides evidence that its maker was a flying insect and probably was representative of a stem-group lineage of mayflies. The nature of this current full-body impression somewhat blurs distinctions between the systematics of traces and trace makers, thus adding to the debate surrounding ichnotaxonomy for traces with well-associated trace makers.

Ephemeroptera | ethology | ichnology | Pennsylvanian

**F**ull-body impressions (FBIs) of insects are rare in the fossil record, and most record the body plan and ventral morphology of ground-dwelling, primitively wingless insects, such as the ichnogenus *Tonganoxichnus* (1, 2). Even rarer are the FBIs of flying insects, the Volichnia (3). FBIs are distinct from compression fossils or natural casts of insect bodies, in that the former are trace fossils and preserve evidence that the animal was alive before and after it made the impression. The same distinction can be made between mortichnia (4) and FBIs, because the former give clear indication that the maker died while or soon after making the trace. FBIs are unique among trace fossils because they preserve detailed evidence of the maker's ventral anatomy and provide reliable evidence of its identity in addition to ethological data. Special sedimentologic and taphonomic conditions are required to preserve FBIs; these requirements may be why they are so rare. Nonetheless, such traces represent the only direct observation of otherwise rarely preserved organisms in the fossil record.

An FBI from the Wamsutta Formation (Late Carboniferous) of southeastern Massachusetts preserves details of the ventral anatomy and behavior of a stem-group mayfly (superorder Ephemeropterida) that landed in soft mud in a marginal freshwater habitat. This FBI is the earliest occurrence in the fossil record of an FBI of a flying insect, and it provides enough morphological detail to allow possible identification of the maker. Believed to be among the first pterygote lineages, excepting *Rhyniognatha* (5, 6), the earliest body fossil records of basal crown-group Ephemeroptera are from the Permian, particularly Protereismatidae (6), and even more primitive stem-group taxa (e.g., Syntonopterodea) are from the Late Carboniferous (6, 7). Older evidence of winged insects exists in the form of body and wing compressions (5, 6, 8), as well as some indirect trace evidence of putative orthopteroid feeding (9), all of lineages other than Ephemeroptera. The majority of the Ephemeroptera body fossil record is comprised of wings; therefore, the trace fossil provides information about the body plan of the

earliest mayflies and their relatives that wing fossils do not. More significantly, the FBI somewhat blurs the usual distinctions between trace and body fossils and the traditional dichotomy between paleoichnological and paleontological systematics and taxonomy.

## Geological Context

The geological context of the fossil locality is described in *SI Geological Context*.

## Systematic Paleoichnology

The following discussion is a systematic description of the trace fossil morphology and its relation to the morphology of the insect that created it. Rather than a purely descriptive approach, as advised with most trace fossils (10), this paper takes a mixed descriptive–interpretive tack, treating the specimen as if it were a body fossil. The material is housed in the Fossil Insect Collection, Division of Entomology, University of Kansas Natural History Museum, as SEMC-F97 (ATL-SM-2–31/32-SEMC-97) (Fig. 1).

### SEMC-F97

**Description.** The specimen is on two opposing slabs, ~10 × 6 × 1 cm thick, of red, fine sandstone with thin mudstone drapes (Fig. 1 *A* and *B*). The surfaces of the slabs exhibit portions of two slightly asymmetric ripple marks and a number of small, shallow burrows that are oriented parallel to bedding planes [*Cochlichnus* ichinospecies (isp.) and *Helminthoidichnites* isp.]. The trace is preserved as a negative epirelief with corresponding positive hyporelief representing a natural cast of the primary surface (Fig. 1*A* and *B*) and is nearly bilaterally symmetrical overall and 36 mm in total length. It is divided into three main sections longitudinally that are equivalent to the tagmata of the insect body plan, i.e., head, thorax, and abdomen (Fig. 1*C*). Most anteriorly, there is a bedding plane disturbance that does not seem to be related morphologically to the trace maker. Close to this disturbance, a shallow, oval depression 3.5 mm wide represents an impression of a portion of the head of the insect and may represent an impression of the labium (Fig. 1*C*, "Lab?"). This anterior depression is separated from the thorax by a shallow, elongate, 1.5-mm impression made by the prothorax (Fig. 1*C*, "Pt").

The thoracic impression is 3.8 mm at its widest between the front and middle pair of legs. Within the depression are smaller features that divide it and give the appearance of separate plates. The first of these partitions is a small, transverse semicircular ridge that protrudes above the base of the main depression by about 0.5 mm, representing sediment that squeezed between two

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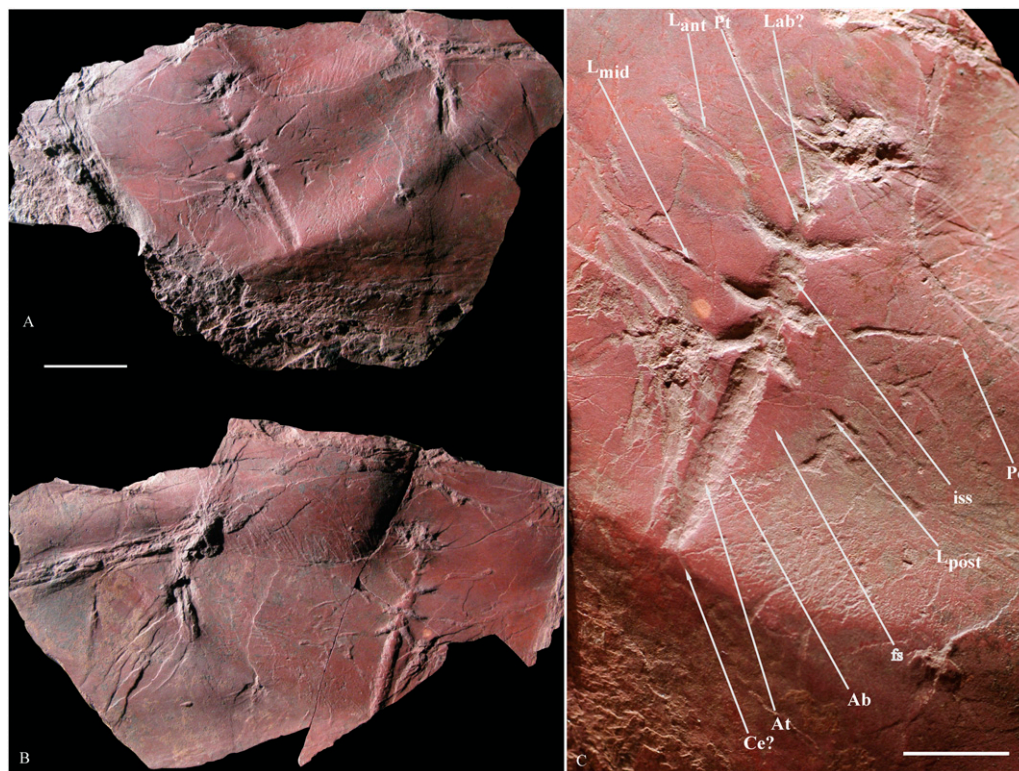
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**Fig. 1.** Views of specimen SEMC-F97. (*A*) Lower-facing side preserving trace fossil in concave epirelief. Two ripple mark crests are evident in this view running from left to right across the bedding plane. (*B*) Upper-facing side (in convex hyporelief). Possible incipient mud cracks are visible to the left of the trace fossil. (*C*) Macrophotograph of the trace fossil with key features labeled. Illumination is from due north to highlight small transverse features. See text for more information. Ab, abdomen; At, articulation; Ce, cerci; Fs, femoral striae; iss, intersegmental suture; Lab, labium; $L_{ant}$, anteriorly directed legs; $L_{mid}$, antero-laterally directed legs; $L_{pos}$, posteriorly directed legs; Pc, pretarsal claw impressions; Pt: prothorax. (Scale bars: *A* and *B*, 20 mm; *C*, 10 mm.)

adjacent sclerites (Fig. 1*C*, "iss"). Along the length of this tagma, six long, narrow impressions diverge and taper distally, representing impressions of the legs. The first set is directed anteriorly (Fig. 1*C*, "$L_{ant}$"), the second set is directed antero-laterally (Fig. 1*C*, "$L_{mid}$"), and the third set is directed posteriorly (Fig. 1*C*, "$L_{post}$"). Multiple small impressions exist beyond the distal portions of the leg impressions that are comparable to pretarsal claw impressions nearer to the body (Figs. 1*C*, "Pc," and 2*B*).

The third and most posterior section of the trace is a segmented, elongate ovoid impression, 3.8 mm wide × 20.6 mm long, which does not taper significantly until its most distal portion and which represents the abdomen (Fig. 1*C*, "Ab"). At least 10 segments can be observed within the abdominal impression. Differential curvature of tergite boundaries, convex–anterior on segments 1–8 vs. convex–posterior on segments 8–10, indicate a possible upward bend of the distal portion of the abdomen midway between the eighth segment (Figs. 1*C*, "At," and 2*A*). Two narrow impressions lie in curved projection from the terminus of the final tapered segment, representing the drag marks of some of the terminal structures, either both cerci or one cercus and the median caudal filament (Figs. 1*C*, "Ce?," and 2*C*).

Posterior of the left meso- and metafemoral impressions and right metafemoral impression are a series of three thin, semi-parallel striae that lead from the femora to the posterior of the body impression for variable distances (Figs. 1*C*, "fs," and 2*A*). The longest of these striae leads in a posterior direction from the right metafemur ~10 mm parallel to the abdomen (Fig. 2*A*). These striae indicate the presence of some flexible projections on the ventral posterior portion of the femur, possibly flexible spines or stiff setae. Furthermore, these striae indicate the direction of movement of the animal as it came to rest in the body impression.

Outside the reach of the limb impressions that correlate to the deepest impression of the body are a series of shallower impressions of all three right legs (Figs. 1 *A* and *B* and 3. Each leg impression is in close contact with its predecessor, and the overlapping series of leg impressions form a pattern of emplacement that begins distal to the body and becomes more proximal to the deepest impression. In the case of the foreleg impressions, the pattern shows a translation to the left, then rotation about an axis near the tibia–tarsus joint (Figs. 1*C* and 3). Relative overlap is not as clear in the hindleg impressions, but these impressions indicate a pivot about an axis that may have been represented by the coxa–trochanter joint or the femur–tibia joint and then a shift to the left to the position of deepest impression. The middle leg did not make as many impressions, but several tarsal impressions indicate multiple contacts with the substrate while translating to the left and rotating about the tibia–tarsus joint.

The absence of distinct head or wing impressions indicates those portions of the body were held above the substrate. Although a series of narrow imprints perpendicular and parallel to the body axis (Figs. 1 *A* and *B* and illustrated in blue in Fig. 3) may have been produced by wing movements, they perhaps are the result of multiple impressions of the legs as the animal moved laterally as well as in place. Spine drag marks emanating from the posterior edge of femora suggest forward movement of at least 8.8 mm before making the deepest impression. Multiple, isolated claw impressions exist distal from the body axis and were the result of the animal's touching down before landing.
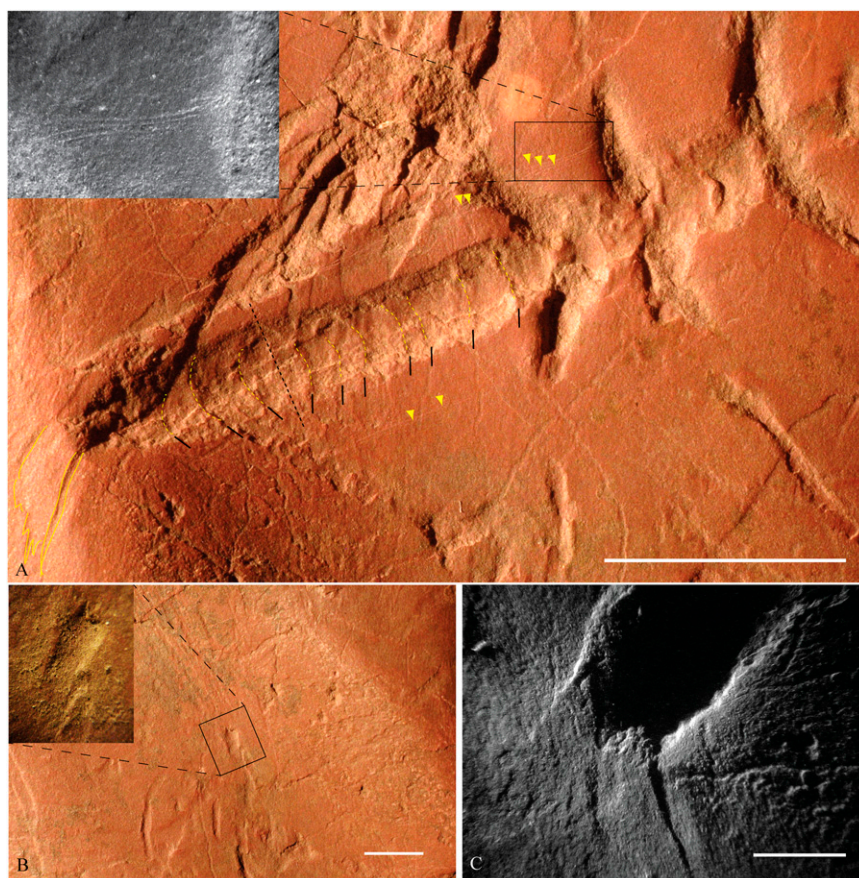
**Fig. 2.** Close-up views of small areas of the trace fossil described in text. (*A*) Thoracic and abdominal region view showing striae left behind femora (indicated by small arrowheads and enlarged in *Inset*); variable curvature of abdominal terga (highlighted by curved dashed lines, with a straight line indicating possible plane of inflection); and outline of cercal drag marks. (Scale bar: 10 mm.) (*B*) Close-up of one pretarsal claw impression on the middle leg, enlarged in *Inset*. (Scale bar: 5 mm.) (*C*) Close-up of abdominal terminus showing cercal and medial filament drag marks (basal articulations of the three structures are discernible along the margin of the last segment). (Scale bar: 2 mm.)

**Trace Maker Identity.** The general body form of the trace can rule out the apterous lineages of Archaeognatha or Zygentoma (bristletails and silverfish), which would have crouched low to the substrate and typically have noticeable head appendages, particularly if an individual were as deeply impressed into the mud as is this fossil. Additionally, the organization of the thoracic sclerites and head are not correct for either of these orders (6), and putative trackways of primitively wingless insects are otherwise well characterized (1, 2) and in no way resemble that of SEMC-F97. The superorder Paleodictyopterida may be excluded also, most notably because of the absence of an impression of the rostrum. Paleodictyopterida were "beaked" insects, with mouthparts that were modified for piercing and sucking and that were folded beneath the body (6). No impression of these structures exists along the specimen; had these structures been present, they would have conclusively left a mark, given the depth of the impression, particularly along the thorax. The superorder Odonatoptera, comprising the griffenflies, dragonflies, and damselflies, can be eliminated because in this lineage the abdomen is articulated much higher on the thorax and would have made a significantly lighter impression into the substrate along its entire length, and there would not have been elongate caudal appendages (cerci, terminal filaments, and so forth). By contrast, in Ephemeropterida the abdomen is positioned much lower and typically is in contact with the substrate, particularly basally, and the most apical portion frequently is upturned, as in the trace. There is no evidence of an external ovipositor or

enlarged male terminalia; the absence of the former similarly excludes stem-group Odonatoptera. Conversely, there is evidence of the basal articulations of the two cerci and a medial, caudal filament (Fig. 2*C*), present only in Ephemeropterida among winged insects. The presence of this medial filament also excludes other metapterygotan lineages such as the stem-group neopteran family Paoliidae. Although crown-group Ephemeroptera have reduced hind wings, those taxa in the Paleozoic had fore- and hind wings of similar construction (6), and the leg positions and orientation also match that of Ephemeroptera.

Although crown-group stoneflies (Plecoptera) are not known or predicted to extend deep into the Carboniferous, the trace's morphology permits exclusion of these insects as the trace maker. Such attributes include the typically widely spaced coxal articulations in Plecoptera, resulting in a squat stance caused by distinct separation between the coxae (as also is true for mayfly naiads, but not for the winged subimagos or adults). By contrast, in the trace the coxae are clearly contiguous. The prothoracic segment in immature and adult stoneflies typically is broad, even broader than the head (particularly so in basal lineages), whereas in the trace the contact of the prothoracic segment is narrower than the head, as seen in stem-group (e.g., Protereismatidae) and basal crown-group Ephemeroptera. The forelegs of primitive Plecoptera are relatively short; in Ephemeroptera and in the trace fossil these legs are more elongate (note how far forward the forelegs are in all instances of contact during movement: Fig. 3). Basal Plecoptera tend to have a broad and flattened body

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**Fig. 3.** Sketch of trace fossil indicating directions of movement of the insect's appendages as it moved onto the substrate. See text for discussion. (Scale bar: 20 mm.)

rather than the more slender and elongate bodies of Ephemeroptera and the trace. Plecoptera have elongate filiform antennae; although these antennae would not necessarily have made contact with the substrate, they probably would have done so at some point, given the low stance of these animals, the depth of the impression, and the likelihood that the insect would have antennated the surface around it. No impressions indicative of antennae are evident. Conversely, Ephemeroptera have arista-like antennae, which are short and do not extend beneath the head (6) and therefore would not have contacted the substrate unless the insect had been forced headfirst into the mud. Although it has been argued that stem-group Ephemeroptera had elongate antennae (11), this assertion has not been supported by further critical analyses (12). Finally, stoneflies are neopterous insects and, when landing, fold the wings back over the abdomen. Accordingly, there should have been additional marks, particularly from the large anal fan of the hind wing, caused by the movement of wings either being extended outward from this position or being moved into repose; the absence of such marks in the trace, is consistent with wings being raised tent-like over the body.

Overall, the impression is not consistent with what we know of stem-group (the "Protoperlaria" of earlier authors) and basal crown-group Plecoptera or the other aforementioned lineages and instead agrees with an attribution to Ephemeropterida. Given that Ephemeroptera and the primitive apterous orders have a subimaginal stage, it is not possible to state conclusively that the trace maker was an adult individual. In Ephemeroptera the subimago, which lacks operational genitalia for mating and therefore is not a true adult, does have functional wings like the adult. Thus, the trace maker was either a subimago or an adult. It is tantalizing to attempt a more refined familial attribution for the trace, but unfortunately the classification of Paleozoic Ephemeropterida is based largely on details of wing venation, which are unknown for SEMC-F97, and the overall impression of the thorax and abdomen could fit several Late Paleozoic ephemeropteroid lineages. Biogeographically, however, Syntonopteridae and Protereismatidae are among the most likely candidates.

## Discussion

**Taphonomy.** SEMC-F97 was preserved adjacent to two asymmetric ripples, although the detail and depth of the trace indicate a nearly emergent substrate at the time the trace was made. The size and weight of the proposed trace maker suggest the substrate must have been heavily saturated to record such detailed characters but not oversaturated to the point of infilling upon the departure. The superposition of fine-grained mudstone over fine sandstone provided a supportive and yielding casting medium for the insect's body. Saturation, current indicators, and the fine-grained nature of the entire rock unit indicate an ephemeral setting that experienced repeated flooding and draining. After the insect departed, the mold created on the primary surface (the negative epirelief) was filled by fallout from suspension after water levels rose again, as indicated by the preservation of extremely fine detail in the resultant trace. Such situations might be found in areas adjacent to small pools and ponds in a larger floodplain that was able to drain rapidly after flooding but was wet enough not to cause destructive desiccation.

**Ethology.** The importance of the current specimen lies in its morphological detail and the potential of identifying the trace maker. Moreover, a few behaviors can be interpreted from this fossil that support its identification as a flying insect and, more specifically, as belonging to the mayfly lineage. Overall, the deep body impression without a clear trace of the head reflects the tendency of the trace maker to squat low when on the ground, with its abdomen in contact with the substrate. The distal portion of the abdomen seems to have been flexed upward based on the variable convexity of the tergal impressions. There are no clear trackways leading to or from the main body impression, consistent with an insect that flew into position rather than having moved there from adjacent locations. The leg and tarsal impressions that are present do not form an organized arrangement or trackway, unlike the typical behavior of nonflying terrestrial arthropods, which produce well-organized series of tracks as they move (13). The trace maker clearly was not adapted for moving over the particular substrate with its legs.

There are several possible explanations for movement and variable preservation of the body and leg impressions. Using both the taphonomy and toponomy of the trace, we can reconstruct some elements of the animal's movement and from there are able to offer two hypotheses. Because of the variation in topography of the substrate, portions of it could have been slightly submerged in water while other portions were emergent. The area in which the deepest body impression was made is slightly elevated above the ripple troughs, and the ripple heights (trough to crest) decrease into that area, indicating shoaling of the ripples. This topography would indicate the entire insect was not in full contact with the substrate at all times while making the trace fossil. The shallow leg impressions are made preferentially near the crests and lee sides of ripples. These impressions and the terminal filament drag marks indicate movement of the body to the left. Two possible interpretations are that (*i*) a shallow pool of water in the low-lying areas would have allowed the insect to skim above the substrate with intermittent contact before "docking" at the margin of a shallow pool and resting its full weight in the muddy substrate and making the deepest impression, or (*ii*) instead of skimming in contact with the water surface before coming to rest, the insect may have glided or flown from above, with appendages that extended down to the emergent portions of the substrate making initial contact before final landing, resulting in the distal tarsal impressions and with the force of landing making a deeper impression on the sediment that was fully saturated because of its proximity to the puddle margin. Under the latter scenario, the insect may have landed to take up water or solutes from puddles or because of incidental

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interaction with wind or standing vegetation. Adults of crown-group mayflies have vestigial mouthparts, but Paleozoic members of the lineage apparently did not (6).

Although both hypotheses seem plausible, it is not clear that skimming behavior is represented in stem-group Ephemeroptera or any of the earliest Pterygota. Although skimming is documented in naiads of derived stoneflies (Plecoptera) and some modern Ephemeroptera (14, 15), it is not known in any basal members of these unrelated orders or even in basal Plecoptera (16). More significantly, the morphology of early ephemeropteran immatures [e.g., the absence of gill or other breathing structures in immature Protereismatidae (6)] indicates that they probably were terrestrial. Indeed, terrestrial immatures appear in all of the modern lineages of primitive fliers, including stem-group and other Paleozoic Ephemeroptera, stem-group Odonatoptera, and Paleodictyopterida. Aquatic immatures appear to be a feature only in crown-group Ephemeroptera and, independently, in crown-group Odonatoptera and crown-group Plecoptera, the latter of which belongs to the wholly unrelated clade Polyneoptera (6). Accordingly, there is no evidence that early flying insects were aquatic in any life stage or that they had the associated behavior of skimming on the water's surface. Therefore support for the skimming hypothesis is entirely ad hoc, and, pending the discovery of obviously aquatic immatures from the Paleozoic for any of these lineages, skimming behavior is entirely speculative. All phylogenetic and paleontological evidence indicates that skimming is a derived novelty, acquired independently by multiple lineages subsequent in their evolution (16). Accordingly, current evidence favors the interpretation provided in the second hypothesis that the insect flew or glided down from above.

**Taxonomic Considerations.** Although the FBI has enough distinct characters to identify the trace maker reliably, as a trace fossil it inherently cannot meet the requirements of a biotaxon by the International Code of Zoological Nomenclature (ICZN), so giving the FBI a biological binomen must be ruled out immediately. Synonymizing trace and body fossil taxa cannot be considered either, because in Article 23.7.3 the ICZN explicitly states that ichnotaxa and biotaxa do not compete for priority (17).

The trace fossil described here is distinctive enough to warrant the erection of a new ichnogenus under standard ichnotaxonomic procedures. However, the true utility of an ichnotaxon is to facilitate communication among scientists regarding a common morphology and interpretation of ethology across multiple specimens. Ichnotaxa, to be useful, must be recurrent through time and/or space (18). It is not constructive to assign an ichnotaxon at this time, because the conditions required to produce an FBI of a large flying insect with significant morphological detail would be exceedingly rare in the geologic record. Such an assignment would be counterproductive, because only a single specimen has been recovered, and erecting a new ichnotaxon on such a foundation would contribute to ichnotaxonomic clutter. If one or more trace fossils very similar to the specimen discussed in this paper were discovered, then an ichnotaxon would be appropriate to promote scientific discussion about possible common behaviors.

The lone FBI of interest in this paper probably represents atypical and/or rare behavior but provides a significant amount of morphological data about the trace maker. Giving the trace maker an ichnological name adds unnecessary confusion for those studying comparable body fossils. In the case of this fossil, it is clearer and more accessible to the researcher to refer to specimen SEMC-F79 as an FBI of Ephemeroptera.

A case might be made for changing the ICZN to allow FBIs of live animals with significant detail to be treated as a type of body fossil (as natural fossil casts are treated now). Indeed, greater biological meaning is conveyed when FBIs are treated as body fossils. Future consideration of this taxonomic question is warranted, particularly if and when a well-preserved FBI is treated as a type specimen.

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