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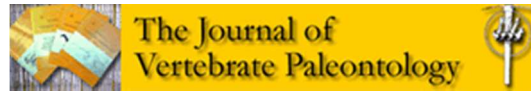
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**Neither bones nor feet: track morphological variation and
"preservation quality"**

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15 Neither bones nor feet: track morphological variation and “preservation quality”
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19 STEPHEN M. GATESY^{*,1} and PETER L. FALKINGHAM²
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24 ¹Department of Ecology and Evolutionary Biology, Brown University, Providence,
25
26

27 Rhode Island 02912 U.S.A., stephen_gatesy@brown.edu;
28

29 ²School of Natural Sciences and Psychology, Liverpool John Moores University,
30
31

32 Liverpool L3 3AF U.K., pfaltingham@live.co.uk
33
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41 RH: GATESY AND FALKINGHAM—TRACK VARIATION AND QUALITY
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6 ABSTRACT—As purely sedimentary structures, fossil footprints are all about shape. Correctly
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8 interpreting the significance of **their** surface topography requires understanding the sources of
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10 morphological variation. Differences among specimens are most frequently attributed to either
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12 taxonomy (trackmaker) or to preservation quality. “Well-preserved” tracks are judged more
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14 similar to pedal anatomy than “poorly preserved” ones, but such broad-brush characterizations
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16 confound two separate episodes in a track’s history. Current evaluations of track quality fail to
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18 distinguish among behavioral, formational, intravolumetric, and post-formational sources of
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20 variation. Based on analogy with body fossils, we recommend restricting assessments of track
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22 preservation quality to modifications that take place only after a track is created. Ichnologists
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24 need to try to parse the relative influence of factors affecting disparity, but we currently lack an
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26 adequate vocabulary to describe the overall shapes and specific features of formational variants.
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INTRODUCTION

Fossil footprints offer unique insights into the behavior of extinct species, as well as their presence in a particular time, place, and environment (Sarjeant, 1975; Thulborn, 1990; Lockley, 1991). Vertebrate animals moving across deformable ground leave behind valuable clues about pedal anatomy and *in vivo* limb function (gait, speed, posture, movement, loading). The field of dinosaur locomotion, in particular, has advanced tremendously based on information from tracks and trackways (Alexander, 1976; Farlow, 1981; Gatesy et al., 1999; Milàn et al., 2006; Bernardi and Avanzini, 2011; Avanzini et al., 2012). When combined with data from skeletal and soft-tissue remains, such trace evidence can be integrated into a more vibrant picture of ancient life.

Over our years studying dinosaur footprints and reading the ichnological literature, we **have** encountered several terms that have persistently caused confusion. Although clarification of unclear language may always be worthwhile, the impact of particular expressions differs widely. In our opinion, among the most problematic are the extremely common **variants** of the word “preserve,” which are directly relevant to track formation, fossilization, collection, and analysis. Herein, we maintain that “preservation” and “preserved,” as currently used to assess footprint specimen quality, are doing more harm than good. More importantly, terminological ambiguities regarding “preserve” are not just semantic trivialities, but also symptoms of more fundamental conceptual difficulties.

At the heart of our concerns is a central pillar of ichnology—morphological variation among tracks. Accurate interpretation depends on being able to correctly attribute the overall shape, specific features, and sometimes even minute details of specimens to their underlying causes.

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3 **Building on the work of Diaz-Martinez et al. (2009)**, we introduce an organization of anatomical,
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5 organismal and environmental factors responsible for generating diversity in footprint
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7 morphology. This variation scheme serves as the basis for a discussion of “preservation quality”
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9 and highlights an inherent weakness in the current, overly-broad use of the “well-preserved” to
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11 “poorly preserved” spectrum.
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18 RESULTS AND DISCUSSION

21 **Saints Preserve Us**

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24 “Preservation” and “preserved” are ubiquitous in publications on vertebrate footprints, as
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26 well as in conversations with colleagues. Both words span a range of definitions. At one end of
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28 the spectrum (meaning 1), “preservation” is used synonymously with conservation, as in the
29
30 safeguarding or perpetuation of an object. In a curatorial sense, one might regard the classic
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32 specimens acquired by Hitchcock in the mid 1800’s and still housed at Amherst College as being
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34 “preserved” for ongoing study. More commonly, this meaning of the term is used for a track’s
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36 entire history. Mesozoic footprints that we examine today have clearly survived for millions of
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38 years, and were thus “preserved” as part of the fossil record. Whatever the timescale, this first
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40 meaning is so general as to be relatively innocuous; we are only able to encounter the subset of
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42 ancient tracks that are still available. Researchers may differ in their interpretation of footprint
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44 evidence, but disagreements would not be possible in the absence of preserved specimens.
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51 A second usage focuses on the proximate factors necessary for **long-term survival**. Many
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53 workers are interested in the conditions conducive to track formation and burial (Tucker and
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55 Burchette, 1977; Laporte and Behrensmeyer, 1980; Milàn et al., 2005; Carmona et al., 2011;
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3 Huerta et al., 2012; de Souza Carvalho et al., 2013). Only a subset of steps taken by an animal
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5 throughout its lifetime will fall on receptive substrates and leave a noticeable deformation. In
6
7 turn, only a fraction of tracks will persist to be interred and fossilized. The emphasis of meaning
8
9 2 is on the “preservation potential” of particular environments and the sedimentological factors
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11 governing “preservation bias” (Genise et al., 2009; Falkingham et al., 2011; Castanera et al.,
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13 2013; Thomson and Droser, 2015). Survival of a footprint to the present day (meaning 1) is only
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15 relevant after these initial preservational hurdles (meaning 2) have been successfully negotiated.
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20 Our dissatisfaction has arisen largely from the widespread use of “preserve” terms to denote
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22 assessments of track quality (meaning 3). This third usage is readily identifiable by a spectrum of
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24 qualifiers: “exquisitely preserved,” “exceptionally preserved,” “beautifully preserved,” “very
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26 well preserved,” “well preserved,” “best preserved,” “better preserved,” “less than perfectly
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28 preserved,” “badly preserved,” “poorly preserved,” and others (e.g., Meyer et al., 1994; Farlow
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30 et al., 2012a). The problem is not necessarily that readers are prone to confusion among the three
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32 definitions; a writer’s intention is usually obvious from context. We trust that most will
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34 understand the phrase “clearly preserved tridactyl tracks” (Gatesy et al., 1999:141) to be a
35
36 statement of relative quality (meaning 3) rather than a declaration of obvious existence
37
38 (meanings 1 and 2). Nevertheless, we hereafter specify “preservation quality” for this third
39
40 connotation rather than writing just “preservation” to avoid ambiguity.
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46 Our own prior usage notwithstanding, we take issue with the third definition. Although an
47
48 informal, or even formal (Alcalá et al., 2016; Belvedere and Farlow, 2016), subjective grading of
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50 specimen preservation quality may seem innocent enough, we have serious doubts about current
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52 practice. The assumptions inherent in this endeavor, as well as their ramifications, call for closer
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3 examination. We begin by considering the many factors responsible for generating disparity—
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5 why do tracks differ in shape and size?
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10 **Morphological Variation among Tracks**

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12 Fossil tracks left by the fauna inhabiting a geographical area at a given time will exhibit
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14 disparate morphologies. One obvious potential source of track variation is anatomical difference
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16 among appendages contacting the substrate. Dissimilar indenters are likely to leave dissimilar
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18 tracks. For example, major morphotypes among Paluxy River tracks (Fig. 1A; Bird 1939; Farlow
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20 et al. 2012b) are best explained by overall foot structure, which differs between sauropods and
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22 theropods. Within a species, tracks often reflect variation related to differences in age, sex,
23
24 health, and other traits among individuals. The range of track sizes at Davenport Ranch has been
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26 attributed to a mixed herd of adults and juveniles (Fig. 1B; Bird 1985; Lockley 1994). Each
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28 individual's limbs typically vary anatomically as well, either between a tetrapod's pes and manus
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30 (Fig. 1C) or among a polyped's many extremities.
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37 Track variation can also arise from an animal's behavioral repertoire, such as particular
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39 locomotor gaits, swimming, resting, feeding, display, or other activities (Milner et al., 2009;
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41 Wilson et al., 2009; Lockley et al., 2016; Milner and Lockley, 2016). When performing different
42
43 actions, coordination within and among limbs often alters the extent and relative placement of
44
45 ground contact. Behavioral transitions can change **imprints** dramatically even within a single
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47 trackway, as when a digitigrade walker adopts a plantigrade foot posture to sit (Fig. 1D).
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51 Despite repeatedly contacting the ground with the same limbs during the same behavior (for
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53 example, a walking biped's hind feet), tracks from a single individual are known to vary
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55 considerably. Here we introduce the term “formational variation” to describe differences
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3 produced during the act of track creation. As discussed by Padian and Olsen (1984) and many
4
5 others, footprint morphology arises from the dynamic interaction of anatomy and substrate.
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7 Therefore, even small differences in substrate consistency (grain size, hydration, homogeneity),
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9 slope (degree and direction of incline), and behavior (walking speed, acceleration, turning radius,
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11 motivation), can alter footfall dynamics. Such differences manifest as step-to-step changes in
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13 foot motion and, more permanently, as inconsistent displacement of sediment—disparate tracks.
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17 Figure 2 shows sets of tracks made by a **single individual bird** (Helmeted Guineafowl,
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19 *Numida meleagris*) striding slowly across **a plastic trough (125 cm long, 30 cm wide, 20 cm**
20
21 **deep) filled with** substrates of different consistency. Of the many variables affecting formational
22
23 variation, substrate properties are known to play a key role (Bennett and Morse, 2014; Razzolini
24
25 et al., 2014) and are relatively easy to manipulate under experimental conditions (Brand, 1979;
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27 Gatesy et al., 1999; Manning, 2004; Milàn and Bromley, 2008; Jackson et al., 2010). After the
28
29 bird walked across a dry, granular substrate (**dry poppy seeds; Falkingham and Gatesy, 2014**)
30
31 and cohesive muds of varying hydration (**~60 μm glass bubbles, ball clay, and water**), the
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33 topography of the air-sediment interface was reconstructed by photogrammetry (Falkingham,
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35 2012). Three-dimensional models were scaled, aligned, and rendered in grayscale based on
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37 height to form the composite figure for comparison.
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44 Tracks made in our dry sand analogue (Fig. 2B) are vaguely cruciform depressions bordered
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46 anteriorly by raised rims (Falkingham and Gatesy, 2014). Distinct digit impressions are absent,
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48 as steep features are impossible due to the relatively low angle of repose. Tracks left in mud
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50 show sharper contours and crisper boundaries, but exhibit extreme morphological diversity (Fig.
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52 2C-H). Shallow tracks left in firm mud (Fig. 2C) most closely resemble static anatomy (Fig. 2A),
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54 whereas others could be erroneously interpreted as webbed (Fig. 2D, E). As mud hydration
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3 increased, the bird sank deeper (Fig. 2F-H), thereby capturing more of its foot movement
4 through the three-dimensional volume of sediment (Gatesy et al., 1999; Avanzini et al., 2012;
5 Falkingham and Gatesy, 2014).
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10 Formational variation can be readily observed at the originally visible surface, which
11 represents the upper boundary of a volumetric phenomenon (Hitchcock, 1841; Allen, 1989,
12 1997). In laminated rocks, exposure of deeper bedding planes within a single volume is another
13 important source of variation (Manning, 2004; Haubold et al., 2005; Milàn and Bromley, 2008).
14 Differences among uppermost (true) and deeper (undertrack) surfaces are expected as forces are
15 transmitted and dissipated through the surrounding substrate (Fig. 3A). Hitchcock (1848; 1858)
16 cleaved many deeply impressed specimens into several slabs, revealing dramatic changes in
17 track morphology with depth caused by foot penetration (Fig. 3B).
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29 Finally, each “fresh” track volume (and thus each “fresh” track surface nested within)
30 undergoes different types and degrees of modification after being formed (e.g., Scott et al.,
31 2010). Impact of additional limbs (e.g. a pes overprinting a manus), settling/collapse of the
32 sediment, burrowing, compression, distortion, erosion, and cracking (Fig. 3C) can occur prior to
33 lithification. Once fossilized, some of these same processes may alter track surface morphology
34 both before and after exposure. Variable amounts of damage from human discovery, collection,
35 preparation, and handling can also accrue (Fig. 3C).
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46 In Figure 4 we outline factors responsible for morphological variation among fossil tracks.
47 On the left, we use a branching diagram to depict variation at seven categorical levels. Thus, a
48 fauna is composed of multiple species, each made of multiple individuals, each of which has
49 multiple appendages. During each of multiple behaviors, a foot forms multiple track volumes,
50 each comprised of multiple surfaces, each undergoing multiple modifications to yield multiple
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3 potential specimens. A complete representation of our scheme would require an expanding tree
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5 that splits into manifold paths, of which we show just one.
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8 On the right, we've clustered our seven sources of variation into three groups: anatomical,
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10 organismal, and environmental. Our groupings differ from the intrinsic/extrinsic breakdown of
11
12 Diaz-Martinez et al. (2009), but some sources are common. Interspecific, intraspecific, and
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14 appendage variation (Fig. 4A-C) is responsible for the anatomy of the indenter (foot) making the
15
16 track. We treat behavioral variation as a non-anatomical organismal factor affecting intralimb
17
18 and interlimb movement patterns (Fig. 4D). Variation during track creation (Fig. 4E, F) arises
19
20 through an interaction between organismal and environmental factors. For example, sub-surface
21
22 toe trajectories and sinking depth are dynamically coupled to substrate properties and
23
24 heterogeneity. We regard post-formational variation (Fig. 4G) as an exclusively environmental
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26 factor (following Diaz-Martinez et al., 2009). Modifications from climatic conditions (cracking,
27
28 erosion) and geological milieu (compression and other distortions) are obviously environmental.
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30 Other organisms (and other parts of the same organism) can also modify a "fresh" track, but may
31
32 be considered external to the single appendage most responsible.
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38 Armed with this framework, we can now return to the issue of preservation quality. Before
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40 discussing tracks, we first consider the quality of fossilized skeletal material, for which similar
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42 "preserve" terms are routinely applied.
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48 **Skeletal Preservation Quality**

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50 As a biological structure, a bone has a specific morphology at the moment of an animal's
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52 demise (Fig. 5A). Although we focus on overall shape here, morphology can apply to tissue level
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54 features or at cellular and molecular scales as well (e.g., Schweitzer et al., 2007). Following
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3 death, the accumulating effects of taphonomic processes (weathering, scavenging, trampling,
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5 microbial breakdown, diagenesis, distortion, erosion) and human collection/preparation alter the
6
7 bone's original morphology to various degrees. Well-preserved specimens are deemed more like
8
9 the initial state than poorly preserved ones, which have suffered greater postmortem
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11 modification.
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15 For the skeleton, a direct comparison of preservation quality among homologous elements is
16
17 often possible because their starting condition is assumed to have been essentially identical. Thus
18
19 one can assess relative preservation quality of metatarsal III between feet of an individual or
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21 among different individuals. Even if morphologies differ among elements, preservation quality
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23 among a sample of bones (cervicals best within the vertebral series) or skeletons (specimen A
24
25 best, specimen C worst) can be evaluated based on evidence of damage and loss of symmetry.
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27 Although the complete absence of skeletal modification is unlikely over long durations, at the
28
29 level of gross morphology such a pristine state can often serve as a suitable preservational ideal.
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35 Paleontologists are acutely aware of the need to attribute variation among specimens to either
36
37 antemortem (biological) or postmortem factors (Fig. 5A). Mistaking biological variation as
38
39 posthumous modification, or vice versa, can easily undermine research (e.g., Cunningham et al.,
40
41 2012). For example, do the shapes of femoral mid-shaft cross sections vary because of genetics
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43 and disparate limb loading in life or from differential postmortem distortion? Are differences in
44
45 bone porosity and surface texture products of ontogeny or taphonomy? What damage is
46
47 attributable to injury, disease, and healing rather than scavenging or trampling? Although both
48
49 sets of variation processes are always at play, the distinction between antemortem and
50
51 postmortem processes is crucial for shrewd hypothesis formulation and judicious testing.
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Track Preservation Quality

“Well-preserved” tracks are typically described as having topographies with crisp boundaries that clearly distinguish the print from the surrounding surface. Within this silhouette, internal contours such as digital pad impressions, claw impressions, and integumentary impressions may be present (e.g., Thulborn, 1990; Lockley, 1991; Belvedere and Farlow, 2016). “Poorly preserved” tracks vary widely, but are recognized by some combination of undesirable attributes. Low quality specimens are said to possess ill-defined boundaries, lack morphological details, suffer from erosion or collapse, display various distortions, or exhibit an abundance of so-called “extramorphologic characters” (Peabody, 1948:296), which do not “portray the anatomy of the animal.” Are such generalizations reasonable? We believe that skeletal fossils provide much-needed context for revisiting footprint preservation quality.

Like bones, tracks can also be viewed as having a two-part history. Previously (Falkingham and Gatesy, 2014), we likened the development of a footprint throughout a step (track ontogeny) to changes in a growing individual (organismal ontogeny). Although footprints obviously lack the death event of body fossils, we consider the end of track formation to be the closest equivalent demarcation between phases (Fig. 5B, C). During formation, the trackmaker’s foot is actively involved in reorganizing a volume of sedimentary particles into a new configuration. Formation ends when the relevant limb is no longer in contact with the local substrate and any energy imparted by the foot has dissipated. Beyond this point, abiotic and biotic factors (many identical to those affecting bones) become responsible for any subsequent modification of the “fresh” track.

Despite body and trace fossils having analogous phases in their histories, correspondence is lost when quality is evaluated. Whereas bone preservation quality connotes the degree of

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3 postmortem modification, track preservation quality combines behavioral, formational,
4 intravolumetric, and post-formational variation into a single assessment (Fig. 5B). Like
5 paleontologists working with body fossils, ichnologists need to be able to deconstruct the many
6 sources of morphological variation in tracks (Lockley, 1986; Milàn, 2006; Diaz-Martinez et al.,
7 2009; Dalman and Weems, 2013; Razzolini et al., 2014). Yet using “preservation” as an
8 umbrella term for quality confounds two separate episodes in a track’s history.
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17 We would be less concerned about this issue if post-formational processes (Fig. 4G) were
18 responsible for the majority of disparity among tracks made by a single animal’s foot, but such is
19 seldom the case. Rather, dynamic foot-substrate interactions during formation (Fig. 4E, F)
20 generate the preponderance of morphological variation within the same behavior (Gatesy et al.,
21 1999; Kubo, 2010). Ichnologists routinely acknowledge intravolumetric variation (true tracks
22 *versus* undertracks) as an important factor in morphological variation (Fig. 3A), and rightly so.
23 Yet despite post-formational processes sometimes affecting depths differentially, gross surface to
24 surface distinctions largely arise during the creation of a track (Allen, 1989; Falkingham and
25 Gatesy, 2014).
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41 **Footprints are neither Bones nor Feet**

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44 Either explicitly or implicitly, preservation quality is a ranking of *fidelity*—a specimen’s
45 accuracy of reproduction. How far does a specimen depart from some ideal state? A fossil bone’s
46 preservation quality connotes *fidelity to its condition at death*. To be consistent, a fossil track’s
47 preservation quality should signify reproduction accuracy relative to an analogous point in its
48 history. Yet such is not the case. Instead, the ichnological tradition is for preservation quality to
49 denote a specimen’s *fidelity to pedal anatomy*.
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3 The prevailing view embodies what we deem a “mold-based” perspective. In such a
4 conceptual framework, tracks are regarded as variably flawed copies of the feet. With each
5 ground contact, an animal has the opportunity to replicate pedal shape, but factors such as
6 behavior, substrate consistency, limb movement, and later degradation introduce reproduction
7 errors. “Poorly preserved,” low quality tracks suffer from more egregious inaccuracies than
8 “well-preserved,” high quality tracks, which more closely resemble the indenter’s morphology.
9 We take issue with this tradition, both in theory and in practice.

10
11 A fundamental weakness of using fidelity to pedal anatomy to assess preservation quality is
12 the complete absence of the object itself. Whereas each bone in a foot has a fixed morphology
13 upon death, there is no fixed “original” when it comes to that same foot’s prints. Body parts
14 grow and develop over a lifetime before reaching their ideal preservation state at death. By
15 contrast, tracks simply do not exist prior to their brief, comparatively instantaneous, formation.
16 Only after sedimentary particles are redistributed *de novo* with each footfall is there anything
17 physical to be preserved. This episodic, “one-off” nature of track formation should dictate the
18 way we address variation and preservation quality among track morphologies.

19
20 Returning to formational variants (Fig. 2), our sampling from **one bird on** different substrates
21 would likely be regarded as ranging from well to poorly preserved. Other than the shallowest
22 tracks (Fig. 2C), **which come closest to being “elite” (Lockley and Meyer, 2000; Gatesy, 2003;**
23 **Belvedere and Farlow, 2016)**, most **impressions** strongly differ from pedal anatomy (Fig. 2A).
24 For some examples (Figs. 2F-H), measured lengths, widths, and angles would deviate
25 substantially from the toe geometry of the standing bird. **The question is not which of these**
26 **specimens are “well enough preserved” to warrant naming new ichnotaxa or even assignment to**
27 **existing ichnotaxa. At issue is the pervasive prejudice that low anatomical fidelity can be largely**

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3 attributed to some combination of weathering and undertrack depth. Yet all in Figure 2 are
4 unweathered prints left in the “tracking surface” (Forñós et al., 2002) and would be considered
5 “true” tracks under most definitions (e.g., Lockley, 1997). Likewise, we object to dismissing
6 such tracks as distorted and dominated by extramorphologic characters. Distortion implies
7 alteration of an initially more accurate state, but such forms were never foot-like (Lockley,
8 1986). Each track’s morphology is uniquely generated through its inception. In truth, the entire
9 track volume is extramorphologic—always *outside* the indenting biological appendage itself.
10 Dinosaur tracks are not “mummified” soft tissues; pretending otherwise is courting trouble.

11
12 Thus, we advocate for a different standard of comparison. Footprints are not feet, and so their
13 quality should not be judged based on an anatomical ideal. Rather, a track’s preservation quality
14 is best assessed by its *fidelity to its condition at the end of formation* (Fig. 5C). This more
15 restrictive definition more closely parallels that used for body fossils (Fig. 5A), in which post-
16 mortem modifications dictate preservation quality. Moreover, limiting track preservation quality
17 to assessment of post-formational variation speaks to formational variation more equitably.
18 Morphological differences arising during track creation are best ascribed to the mechanical
19 processes that formed them, not to unspecified “vagaries of preservation” (Manning, 2004:100).
20 Therefore, and perhaps counter-intuitively, every track in Figure 2 is actually “well-preserved”
21 using our more restricted definition of preservation quality.

22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 CONCLUSIONS

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53 The broad ichnological connotation of “preserve” can be divided into three basic meanings.
54 We have no qualms with the most generic use of “preservation” for describing the perpetuation
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3 of footprints as physical objects through time (meaning 1). Fossil tracks that exist today have
4 been preserved as part of the fossil record and can be preserved in the field and in collections.
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6 However, when addressing the proximate causes of ultimate preservation (meaning 2), preserve
7 terms could be amended. Given the two-phase history of tracks (Fig. 5C), maintaining
8 “preservation potential” to describe the probability of a track’s survival in different environments
9 seems justified. But to describe the likelihood of tracks being created in different substrates, we
10 suggest replacing “preservation bias” with “formation bias.” Switching terms more clearly
11 separates the formation event, during which a track is created, from all subsequent events leading
12 to its modification or demise. For example, the odds of foot contact forming a track in soft mud
13 are always quite high (formational bias) irrespective of the mud’s environmental setting, which
14 dictates any individual track’s chance of persistence (preservational bias).
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29 Our greatest concern regards meaning 3. The current criterion for track preservation
30 quality—*fidelity to pedal anatomy*—is flawed. We do not believe that fossil footprints formed in
31 dry sand or semi-liquid mud should be likened to a crushed and distorted fossil femur covered in
32 hematite. Yet current language misleadingly equates the initial, formation-based disparity among
33 tracks with the later, degradation-based variability among dead bones. An individual appendage
34 has a one-to-many relationship to track morphology (Figs. 1D, 2, 4). Variation arising from
35 behavior, formation dynamics, and sampling depth is the expected outcome of tracking events,
36 not noise or error befouling an otherwise pristine mold of the foot. Incorporating all non-
37 anatomical factors into assessments of preservation quality muddles too many processes to be
38 constructive (Fig. 5B).
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53 Ultimately, ichnologists comparing fossil tracks must try to parse the relative influence of
54 multiple sources of morphological variation (Fig. 4; Diaz-Martinez et al., 2009). Is indenter
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3 anatomy (Fig. 4A-C), behavior (Fig. 4D), track creation (Fig. 4E, F), or post-formation
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5 modification (Fig. 4G) most responsible for differences among specimens? Given that several
6
7 sources are always involved, how does each contribute to the aggregate? To make strong
8
9 inferences, we suggest splitting a track's history into two phases (Fig. 5C). The morphology of
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11 "fresh" tracks at the end of formation must be accurately interpreted, preferably at multiple
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13 depths. Only then can the separate impacts of overprinting, cracking, erosion, preparation
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15 damage, and other post-formational modifications be distinguished.
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20 However, if preservation quality *sensu stricto* no longer includes the effects of behavioral,
21
22 formational, and intravolumetric variation, we're left with a dearth of terms to describe these
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24 key sources of track disparity. **Instead of** a simple rank of qualifiers along a single axis, a much
25
26 more comprehensive, multi-dimensional, and detailed vocabulary is sorely needed. **Most tracks**
27
28 **in Figure 2 are not easily assigned to Belvedere's and Farlow's 0-3 preservation scale, which is**
29
30 **defined as "completely independent of substrate characteristics" (2016: 96). How does one**
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32 **address variation arising almost entirely from substrate differences on a scale that excludes this**
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34 **source? Rather than try to dismiss foot-sediment interactions, establishing** terms that integrate
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36 elements of both substrate consistency and foot motion will allow complex morphologies (Figs.
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38 2, 3B) to be more accurately described. We believe that this area is particularly rich for
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40 exploration, but progress requires acknowledging the weakness of the currently pervasive, mold-
41
42 based system. **Any benefits of a simple scale of preservation quality (e.g., Belvedere and Farlow,**
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44 **2016) may be outweighed by the risks of viewing the diversity of track morphology through an**
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46 **overly limited lens.**
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53 **Formational variation, which arises through** the complex interplay among pedal anatomy,
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55 kinematics, and substrates consistency during **creation** of a track, is not well documented for any
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3 taxon, even humans. Rather than trying to avoid features that don't fit an anatomically biased
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5 search image, we can begin to describe track morphology much better by elucidating how it
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7 emerges from the summation of each organism-environment interaction (e.g., [Falkingham and](#)
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9 [Gatesy, 2014](#)) and subsequent modifications (e.g., Marty et al., 2009). Terminology that distorts
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11 or obscures this intimate association between formation and form has significant implications for
12
13 the day-to-day practice of footprint-based paleontology—how we search for, measure, describe,
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15 understand, and ultimately “see” tracks.
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FIGURE CAPTIONS

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FIGURE 1. Organismal sources of variation among track morphologies. **A**, interspecific differences in hind foot structure are strongly expressed in theropod and sauropod track shape (modified from Falkingham et al., 2014); **B**, intraspecific variation in ontogenetic stage (1-3) is responsible for size differences among tracks of herding sauropods (modified from Bird, 1985); **C**, anatomical distinction between appendages leads to manus-pes track disparity in *Chirotherium* (modified from Baird, 1957); **D**, behavioral variation explains shape differences in walking and sitting *Anomoepus* (modified from Olsen and Rainforth, 2003). [column width]

FIGURE 2. Formational variants from an individual Helmeted Guineafowl walking on substrates of different consistency. **A**, plantar view of the right foot and right lateral view of walking on a solid substrate; **B**, tracks left in dry poppy seeds; **C-H**, tracks in muds of increasing hydration. Scale bar equals 2 cm for foot and 5 cm for tracks. [full page width]

FIGURE 3. Intravolumetric and post-formatinal variation. **A**, changes in topography with depth in a sectioned emu track (modified from Milàn and Bromley, 2008); **B**, four surfaces from shallowest (left) to deepest (right) of a deep Connecticut Valley track (modified from Hitchcock, 1848); **C**, highly detailed tracks within a Beneski Museum of Natural History at Amherst College specimen (ACM-ICH 9/14) exhibit cracks arising prior to lithification (white arrows) combined with damage to the block (diagonal fracture) and specific track features (asterisks) during excavation. [column width]

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FIGURE 4. Morphological differences among track specimens can be attributed to variation at multiple levels on a branching diagram. **A-C**, anatomical sources of variation; **A-F**, organismal sources of variation; **E-G**, environmental sources of variation; **E-F**, variation arises during track creation from an interaction among organismal and environmental factors. [2/3 page width]

FIGURE 5. Morphological variation in bones and tracks arises from distinct processes in two sequential phases, which are represented differently in evaluation of preservation quality (gray boxes). **A**, preservation quality is restricted to post-mortem modification for fossil bones; **B**, currently, track preservation quality encompasses disparity arising both during and after track formation; **C**, we propose restricting track preservation quality only to variation from post-formational modification. [2/3 page width]

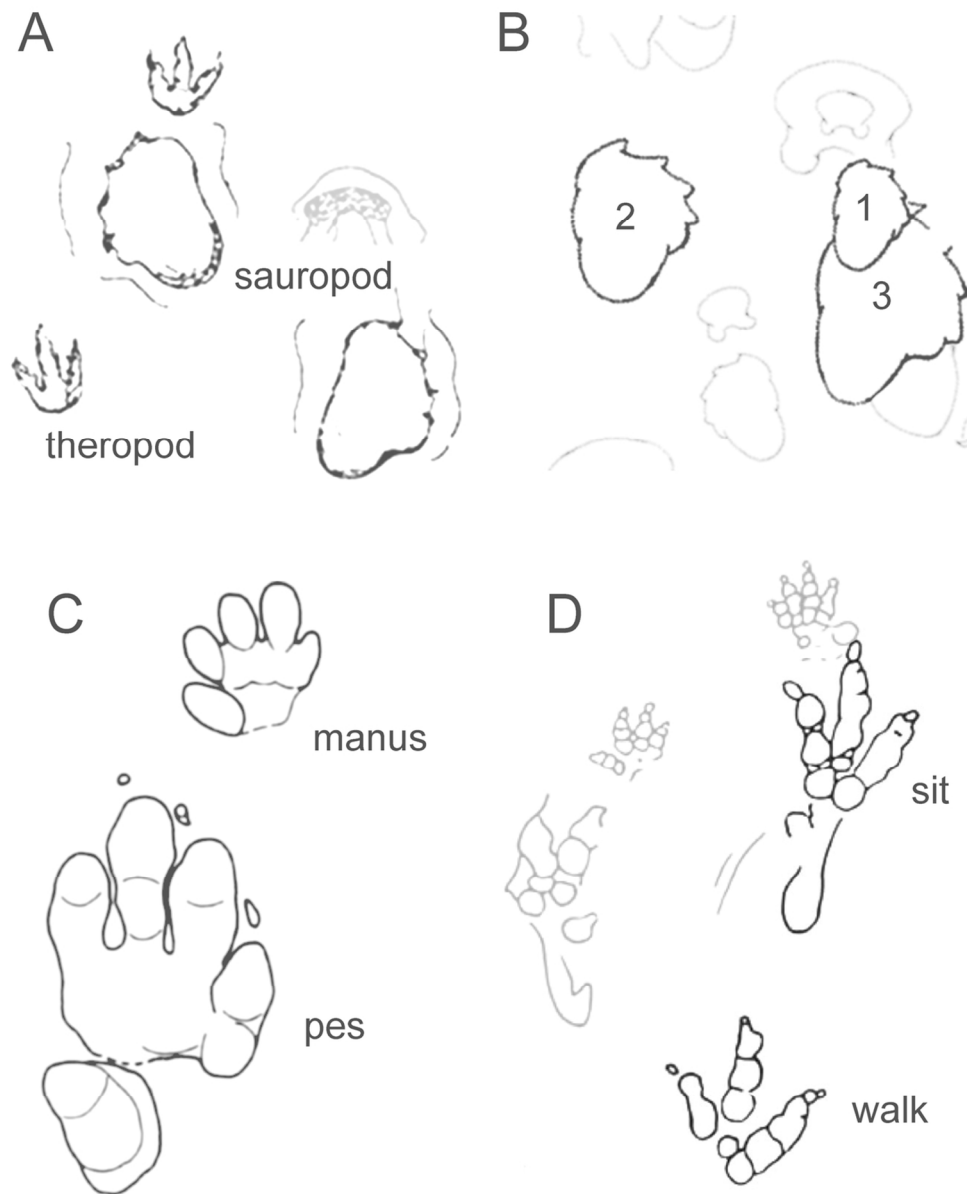


FIGURE 1. Organismal sources of variation among track morphologies. A, interspecific differences in hind foot structure are strongly expressed in theropod and sauropod track shape (modified from Falkingham et al., 2014); B, intraspecific variation in ontogenetic stage (1-3) is responsible for size differences among tracks of herding sauropods (modified from Bird, 1985); C, anatomical distinction between appendages leads to manus-pes track disparity in *Chirotherium* (modified from Baird, 1957); D, behavioral variation explains shape differences in walking and sitting *Anomoepus* (modified from Olsen and Rainforth, 2003).
[column width]

110x135mm (300 x 300 DPI)

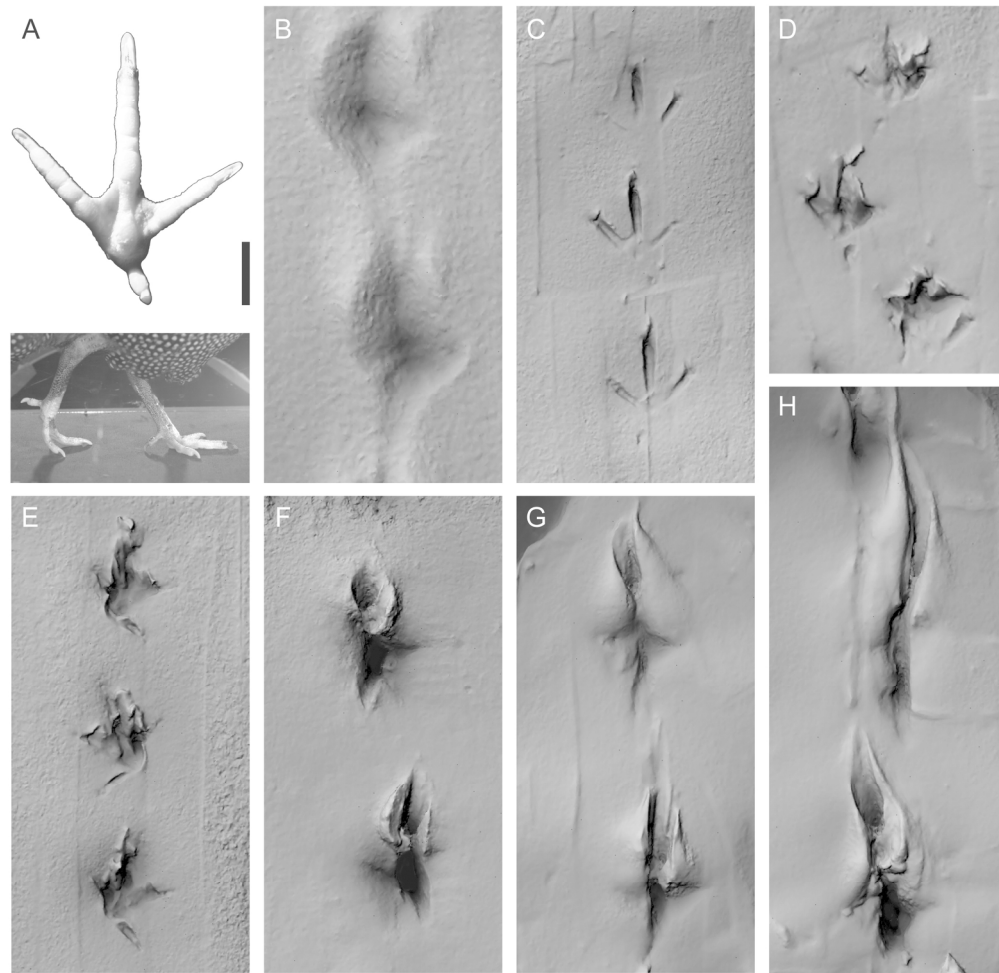


FIGURE 2. Formational variants from an individual Helmeted Guinea fowl walking on substrates of different consistency. A, plantar view of the right foot and right lateral view of walking on a solid substrate; B, tracks left in dry poppy seeds; C-H, tracks in muds of increasing hydration. Scale bar equals 2 cm for foot and 5 cm for tracks. [full page width]

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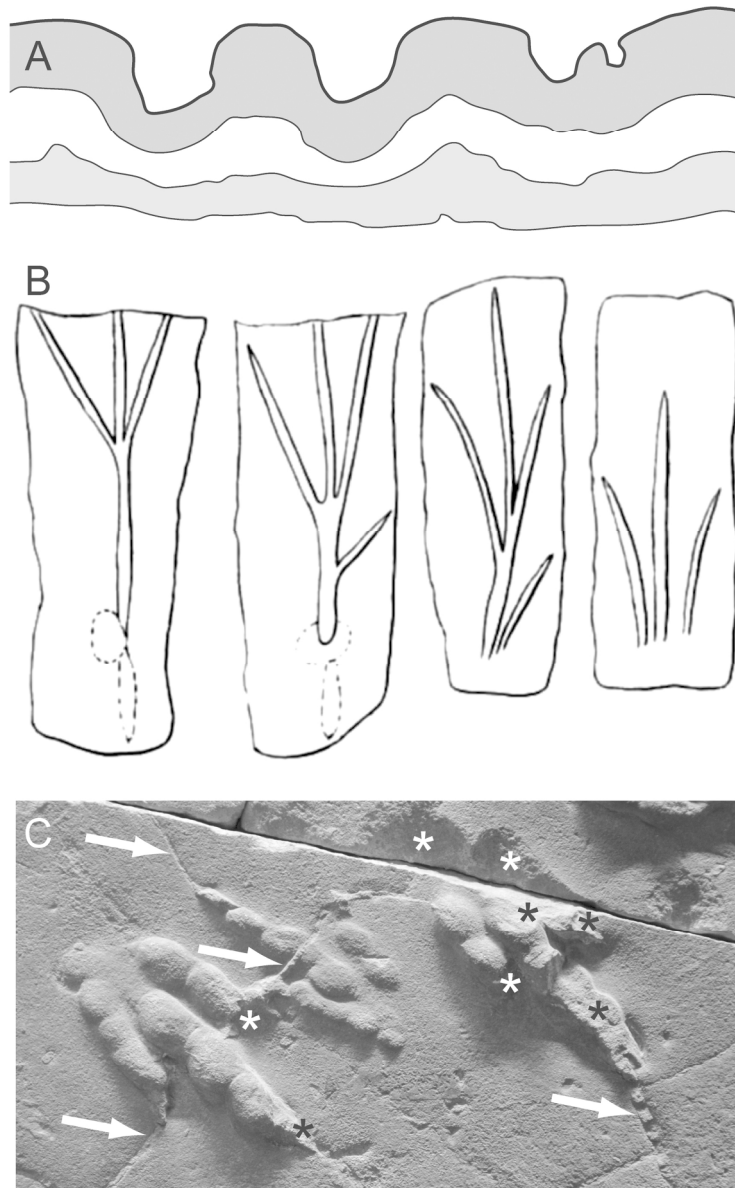
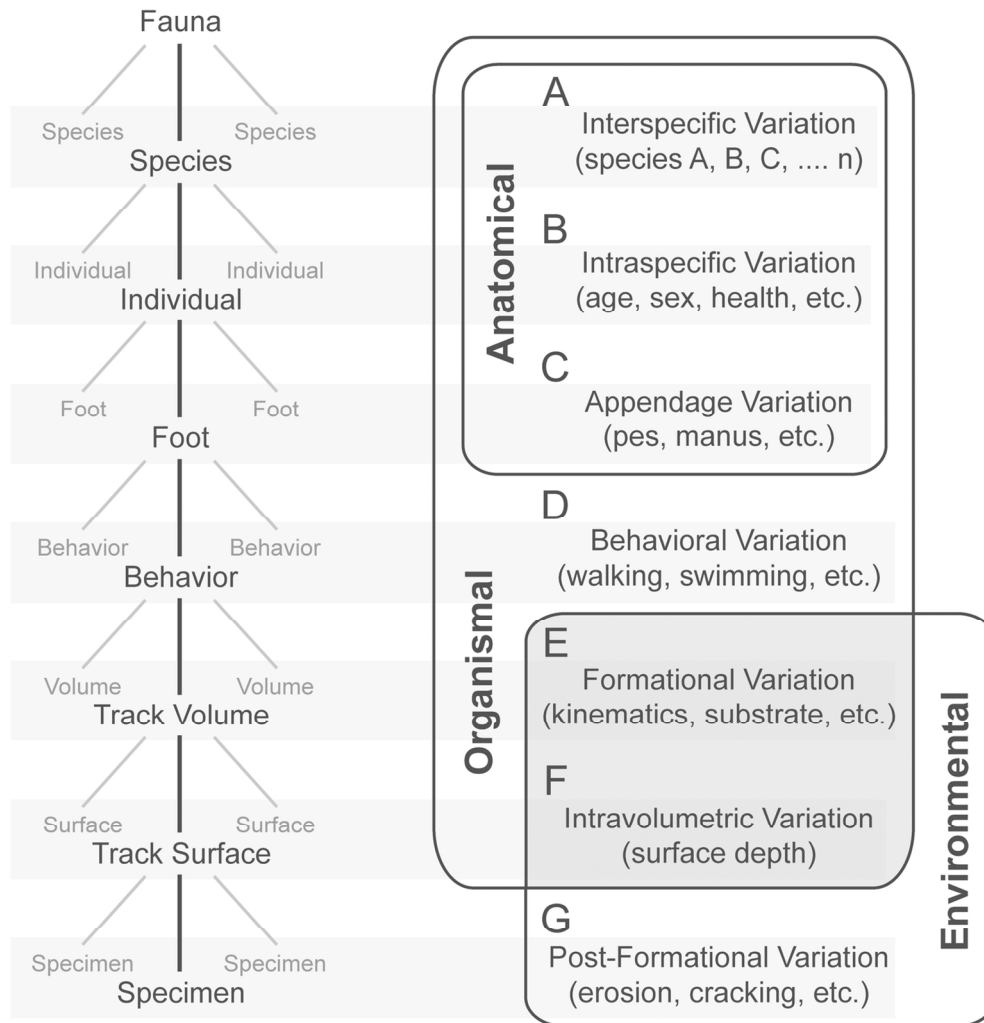


FIGURE 3. Intravolumetric and post-formational variation. A, changes in topography with depth in a sectioned emu track (modified from Milàn and Bromley, 2008); B, four surfaces from shallowest (left) to deepest (right) of a deep Connecticut Valley track (modified from Hitchcock, 1848); C, highly detailed tracks within a Beneski Museum of Natural History at Amherst College specimen (ACM-ICH 9/14) exhibit cracks arising prior to lithification (white arrows) combined with damage to the block (diagonal fracture) and specific track features (asterisks) during excavation. [column width]

146x238mm (300 x 300 DPI)



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FIGURE 4. Morphological differences among track specimens can be attributed to variation at multiple levels on a branching diagram. A-C, anatomical sources of variation; A-F, organismal sources of variation; E-G, environmental sources of variation; E-F, variation arises during track creation from an interaction among organismal and environmental factors. [2/3 page width]

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125x128mm (300 x 300 DPI)

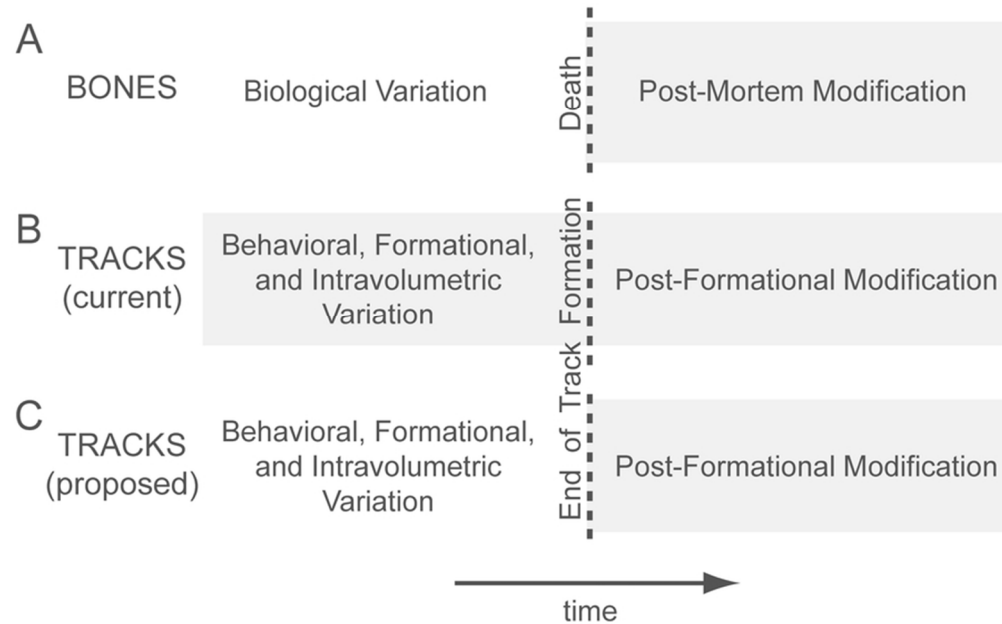


FIGURE 5. Morphological variation in bones and tracks arises from distinct processes in two sequential phases, which are represented differently in evaluation of preservation quality (gray boxes). A, preservation quality is restricted to post-mortem modification for fossil bones; B, currently, track preservation quality encompasses disparity arising both during and after track formation; C, we propose restricting track preservation quality only to variation from post-formational modification. [2/3 page width]

76x47mm (300 x 300 DPI)