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Waterbird foraging traces from the early Eocene Green River Formation, Utah

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Non-technical Summary.—Trace fossils attributed to waterbird foraging are identified from mudflat successions in the Eocene of Utah. These traces occur in close association with the footprint taxon *Presbyornithiformipes feduccii*, which purportedly was emplaced by the extinct waterbird *Presbyornis pervetus*. Four distinct morphologies of foraging traces are identified, which are assigned to four new trace fossil taxa: *Erevnoichnus blochi*, *E. strimmena*, *Ravdosichnus guntheri*, and *Aptosichnus diatarachi*. These trace fossils are interpreted to record tactile (non-visual) foraging strategies by lake-margin waterbirds searching for prey.

Abstract.—Foraging traces associated with the web-footed avian footprint ichnotaxon *Presbyornithiformipes feduccii* are described. Four new ichnospecies in three new ichnogenera are established to identify and describe the traces that resulted from foraging behaviors. All four ichnotaxa are, in places, overprinted by *P. feduccii* footprints and occur either laterally to, or sinuously woven between, *P. feduccii* trackways and therefore were clearly emplaced by the *P. feduccii* tracemaker.

Erevnoichnus blochi new ichnogenus new ichnospecies is established for a series of pits, joined by a marginal groove, that are associated with web-footed bird trackways. This ichnotaxon is interpreted to record regular probing/gaping as a waterbird swept its head from side to side searching for food. *Erevnoichnus strimmena* n. igen. new ichnospecies is established for en-echelon, gently arcuate grooves produced through forward probing by a waterbird searching for food. *Ravdosichnus guntheri* new ichnogenus new ichnospecies is established for simple grooves with u-shaped profiles produced when a waterbird dragged its bill backwards through the sediment. *Aptosichnus diatarachi* new ichnogenus new ichnospecies is established for a broad, shallow groove/trough characterized by sinuous margins and a complex, irregular fill. It is interpreted to record thorough bill stirring in an area with common prey.

All four ichnotaxa named herein are interpreted to record tactile feeding behavior by a marginal lacustrine waterbird searching for prey. Their association with *Presbyornithiformipes feduccii* suggests that the purported tracemaker, *Presbyornis pervetus*, did not forage solely through filter-feeding but was also capable of tactile foraging for larger prey.

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Introduction

Marginal lacustrine settings are crucial foraging grounds for a wide variety of waterbirds, particularly as staging grounds during migration (e.g., Colwell and Oring, 1988; Taylor and Trost, 1992; Skagen et al., 2008; Bertzeletos et al., 2012; Howell et al., 2019; Sorensen et al., 2020). Consequently, footprints and trackways attributed to waterbirds are commonly reported from ancient lake-margin settings (e.g., Scrivner and Bottjer, 1986; Yang et al., 1995; Lockley et al., 2006, 2009, 2021; Zonneveld et al., 2011, 2012, in press A, in press B; Melchor et al., 2012; Scott and Smith, 2015). Numerous examples have been reported

from lake-margin successions in the Green River Formation of Wyoming and Utah (Curry, 1957; Erickson, 1967; Moussa, 1968; Feduccia, 1978, 1980; Grande, 1984; Yang et al., 1995; Olson, 2014; Scott and Smith, 2015; Lockley et al., 2021). Despite the abundance of trackways described, examples of foraging traces in association with avian trackways are rarely reported. Exceptions include the exquisitely well-preserved traces interpreted as 'dabble marks' emplaced in close association with a waterbird trackway assigned to the ichnotaxon *Presbyornithiformipes feduccii* Yang et al., 1995 (Erickson, 1967; Yang et al., 1995; Lockley et al., 2021).

The purported 'dabble marks' occur on the holotype plate, BYU 50694 (originally B20), of *Presbyornithiformipes feduccii*, meandering across seven sequential footprints and were clearly emplaced by the tracemaker of the footprints. They
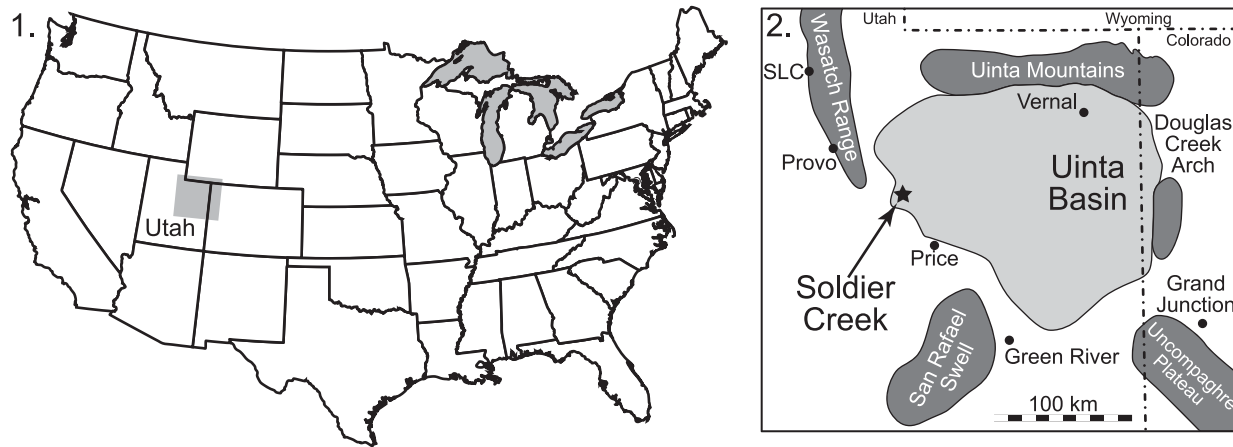
Figure 1. Location of the study material. (**1**) Map showing Utah, located in the central western U.S.A. (**2**) Map of northeastern Utah showing the location of Soldier Creek in the western Uinta Basin. The city labelled 'SLC' on the left side of the map is Salt Lake City.

were included in the description of *P. feduccii*, which is somewhat problematic. Although a lengthy description was provided, a distinct and succinct diagnosis was not included for *P. feduccii* (Yang et al., 1995). The description of the footprints is thorough and diagnostic, thus an emended diagnosis is not provided herein. In this contribution we separate the footprint taxonomy from the foraging trace taxonomy. The ichnotaxon *Presbyornithiformipes feduccii* is restricted to footprints and trackways regardless of the occurrence of foraging traces. The foraging traces are described, named, provided with distinct diagnoses, and the implications of these traces for waterbird behavior is discussed.

Study area

The trace fossils discussed herein were collected from the Green River Formation in the Soldier Creek area, in the southwestern corner of the Uinta Basin, ~50 km east of Spanish Fork, ~1 km north of highway 6, and ~4 km west of the abandoned townsite of Soldier Summit (Fig. 1). The Green River Formation is 1770 m thick in the Soldier Creek area (Moussa, 1969).

The Green River Formation occurs extensively in outcrop and subsurface in northeastern Utah, northwestern Colorado, and southwestern Wyoming (e.g., Surdam and Wolfbauer, 1975; Dickinson et al., 1988; Roehler, 1992, 1993; Smith et al., 2008; Töro and Pratt, 2015; Birgenheier et al., 2019; Walters et al., 2020). Sediments accumulated to the east of the Sevier thrust front, in lacustrine and lake-margin settings in a series of intermontane basins, including the Green River, Fossil, Uinta, Piceance, and Sand Wash basins, which developed during the later stages of the Laramide Orogeny (Bradley, 1925; Dickinson et al., 1988; Roehler. 1992, 1993; Rhodes et al., 2002; DeCelles, 2004; Smith et al., 2008; Murphey et al., 2011; Töro and Pratt, 2015; Birgenheier et al., 2019; Walters et al., 2020).

The material discussed herein was collected from a unit that was informally assigned to the lower delta facies of the Green River Formation (Bradley, 1931; Moussa, 1969) and is now included within the lower beds of the Sunnyside Delta interval of the lower beds of the Middle Member of the Green River Formation (Morton, 2003; Birgenheier et al., 2019; Wang and

Plink-Björklund, 2020; Fig. 2). The Sunnyside Delta preserves deposits of the California Paleoriver that drained highlands in the Mojave region to the south, flowed northwards and debouched into Lake Uinta (Remy, 1992; Morgan, 2003; Wang and Plink-Björklund, 2020).

Lake Uinta occurred during the interval that immediately succeeded the Paleocene–Eocene Thermal Maximum and continued through the early Eocene Climate Optimum (Birgenheier et al., 2019). The bird track interval occurs in the second of five climatically controlled lake phases that produced the deposits of Lake Uinta (Birgenheier et al., 2019). This phase was characterized by several severe hyperthermal events that were punctuated by more stable inter-hyperthermal conditions (Birgenheier et al., 2019). It should be noted that the Sunnyside Delta interval remains poorly dated because the youngest dated volcanic ash horizon occurs higher in the section and dating of the interval between the top of the Paleocene and the top of the Sunnyside Delta has been interpolated using presumed sedimentation rates (Remy, 1992; Birgenheier et al., 2019). Thus, the Soldier Creek bird track horizon can be constrained as early Eocene but may have been deposited at any point during the middle–late Wasatchian to earliest Bridgerian North American Land Mammal Ages (Smith et al., 2004, 2014; Gunnell et al., 2014), possibly co-eval with deposition of the Wilkins Peak Member in the Green River Basin (Smith et al., 2008; Smith and Carroll, 2015).

Vertebrate trackways occur in three limestone intervals that occur interbedded with marlstone and paper shale (Moussa, 1968, 1969) in the lower part of the Sunnyside Delta interval (Fig. 2). It is uncertain from which of these horizons the avian foraging traces discussed herein were sourced, however all three of these horizons occur within a 7-m interval that can be correlated for several km (Moussa, 1968, 1969) and thus it is presumed that there is minimal age difference between them.

Terminology

Avian anatomy.—This contribution is focused on waterbird foraging traces that occur adjacent to avian footprints and trackways. All footprints observed in the study material were

		Uinta Formation	
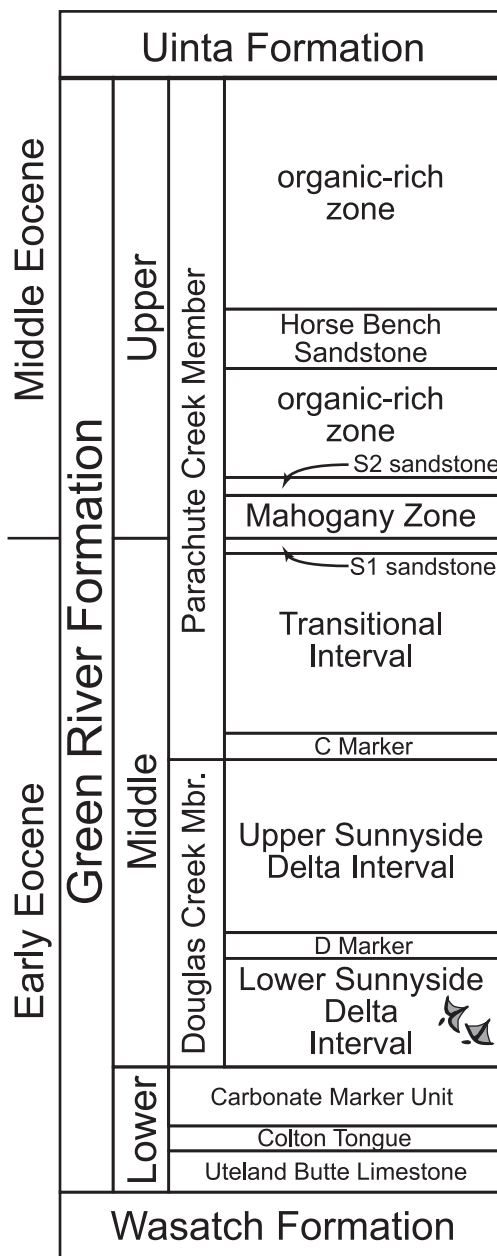
Figure 2. Stratigraphic column of the Eocene succession in the Soldier Creek, Utah region (adapted from Birgenheier et al., 2019). The horizon of the Soldier Creek bird foraging trace locality occurs in the lower Sunnyside Delta interval, denoted by a pair of waterbird footprints.

emplaced by anisodactyl birds. In the anisodactyl arrangement, digits II, III, and IV (digit III in the center) are oriented forwards and digit I (the hallux) is oriented backwards. Anisodactyl prints may be simple (all four digits on the same plane) or incumbent (the hallux raised). Both of these arrangements occur in footprints in the study material. Some bird feet have webbing to aid in swimming or walking on soft or soupy sediment. Palmate tracks occur in the study material. In the palmate arrangement the webbing is limited to the areas between toes II and III and toes III and IV. Avian tracks or prints refer to individual footprints whereas trackways or series refer to two or more associated, typically sequential footprints.

In addition to their feet, shorebirds and waterbirds commonly interact with the sediment surface with their keratinous bills, which consist of the maxillary rhamphotheca (= rhinotheca) comprising the upper bill and the mandibular rhamphotheca (= gnathotheca) comprising the lower bill. In all modern birds the rhamphothecae are composed of dense keratin and are devoid of teeth. Rhamphothecae exhibit significant diversity among bird taxa, functioning as forceps, sieves, nutcrackers, and teeth in different bird groups (Hieronymus and Witmer, 2010).

Ichnological terminology.—Some workers separate the terms 'trace' and 'mark' to separate structures produced by physical and biological means (e.g., Ekdale et al., 1984; Vallon et al., 2015). We avoid this restriction here, because this invokes assumptions about the origin of the features and is contrary to convention used in the greater ichnological, biological, zoological, anthropological, archaeological, medical, and forensic literature (Zonneveld et al., 2022). In particular, waterbird- and shorebird-foraging traces are commonly identified as marks (peck marks, probe marks, dabble marks, etc.; e.g., Barbosa and Moreno, 1999; Elbroch and Marks, 2001; Zonneveld et al., 2011, 2012, in press A). Thus, in the interest of consistency with cross-disciplinary practice, the term 'mark' is used here for any substrate modification feature regardless of assumptions of origin (Zonneveld et al., 2022).

The fossils described herein occur on fine-grained limestone slabs or plates. They occur as both epichnia and hypichnia. Epichnial plates represent original bioturbated bedding planes. Hypichnial plates illustrate the basal surfaces of the overlying beds. Thus, mounds and ridges on a hypichnial plate would have been pits and grooves, respectively, on the bedding plane on which the original traces were emplaced. Concomitantly, hypichnial grooves and pits originally would have been ridges and mounds, respectively. Sketches of the trace fossils described herein are presented as epichnia to facilitate discussion of the original tracemaker perspective. For each new ichnotaxon the descriptions and diagnoses are written in reference to the holotype, which is clearly identified as occurring on either a hypichnial or epichnial plate.

The purported foraging traces discussed herein invariably occur in close association with *Presbyornithiformipes feduccii* footprints and trackways. Thus, orientation terminology of the traces, such as anterior, posterior, ahead, and behind, are applied in reference to the orientation of the associated footprints. As mentioned previously, a formal diagnosis was not provided for either the ichnogenus *Presbyornithiformipes* or for the type and only ichnospecies, *P. feduccii* (Yang et al., 1995). Rather, a detailed description of the holotype and paratypes was provided. In this description reference is made to 'dabble marks', which are also described (Yang et al., 1995).

The *Presbyornithiformipes feduccii* footprints and the ichnotaxa discussed herein form compound trace fossils. In compound traces, the individual components are treated individually (Pickerill and Narbonne, 1995; Bertling et al., 2007, 2022; Petti et al., 2014). The latter authors argued for emplacement of a 'C' in the ichnotaxonomic names (e.g., *Presbyornithiformipes* C *Aptosichnus* n. igen.), however this practice has not come into common usage, and we do not use it here.

Regardless, the components that were emplaced during avian foraging and those emplaced by the overprinting *P. feduccii* footprint are clearly differentiable and clearly comprise distinct ichnotaxa. Following ichnological conventions for dealing with compound trace fossils (see discussions in Pickerill and Narbonne, 1995; Bertling et al., 2007, 2022) we restrict the ichnotaxon *Presbyornithiformipes feduccii* to the footprints and provide names for associated foraging traces herein.

Finally, it is also worth noting that vertebrate trackways and other associated traces are often preserved on multiple bedding planes beneath the original, occupied horizon. Undertracks (a track preserved on a bedding plane lower than the surface on which the animal walked) lack the detail of the occupied surface bedding plane. We also use the word "overtrack" for hypichnial samples that preserve bedding plane surface ~1 mm or more above the trackway. Undertracks and overtracks do not preserve the same level of detail as original impression surfaces. The exquisite detail of *Presbyornithiformipes feduccii* footprints associated with the foraging traces discussed herein indicates that many of the bedding planes illustrated in this manuscript represent original impression surfaces.

Material and methods

The trace fossils discussed in this paper occur on the bedding planes of fine-grained limestone beds. Ten of the studied specimens (BYU 50695, BYU 50696, BYU 50697, BYU 50698, BYU 50699, BYU 50812, BYU 50867, BYU 50946, BYU 50947, and BYU 50948) represent original material. Specimen BYU 50694 (originally B20) is a cast of the original because the original cannot be located at present. These specimens were donated to Brigham Young University by the Gunther family. Most were collected from float; however, the nature of the outcrop limits the zone from which the specimens could have originated to the lower Sunnyside Delta interval (as discussed previously). All specimens were photographed with low-angle light to highlight three-dimensional features on the traces. The fossils were photographed with and without whitening via clay sprayed on using the solvent-based aerosol Spotcheck™ SKD-S2 developer made by Magnaflux (to give specimens a uniform color, reducing visual "noise").

Repository and institutional abbreviation.—The trace fossils discussed herein are cataloged in the Brigham Young University (BYU) vertebrate paleontology collections.

Systematic paleontology

Ichnogenus *Erevnoichnus* new ichnogenus

Type ichnospecies.—*Erevnoichnus blochi* n. igen. n. isp.

Other ichnospecies.—*Erevnoichnus strimmena* n. igen. n. isp.

Diagnosis.—Sinuous to linear trends of ovoid or elongate attached hypichnial mounds, mounds may be discrete, distinct, spaced at a distance and attached at one end by a low ridge of sediment, or closely spaced and partially overlapping. In epichnial samples the trace consists of pits, connected in some examples by a shallow groove.

Known occurrence.—Early Eocene of Utah, U.S.A.

Etymology.—From the Greek Ερευνώ (= Erevnó), meaning 'to investigate' and 'and ίχνος (= ichnos) meaning 'trace'.

Remarks.—The holotype of the type species is preserved as a hypichnion. In epichnial aspect, specimens of *Erevnoichnus* n. igen. occur in two distinct forms, which are assigned to the two ichnospecies named herein: discrete pits attached by an elongate groove (Figs. 3, 4, 5.1–5.3, S1, S2, S4, S5), and elongate, overlapping, en-echelon pits (Figs. 5.4, 6.1–6.3, S3). All specimens of *Erevnoichnus* n. igen. from the study area occur in association with footprints and trackways assigned to *Presbyornithiformipes feduccii* (Figs. 3–7, Supplementary figs. S1–S5). *Erevnoichnus* n. igen. occurs either laterally to *P. feduccii* trackways or between individual footprints. The paratypes *Erevnoichnus* n. igen. are, in areas, overprinted by *P. feduccii* footprints.

Specimens of *Erevnoichnus* n. igen. from the study area are preserved in both convex hyporelief on the sole surfaces of bedding planes (Figs. 3, S2, S5) and as concave epirelief on the upper surfaces of bedding planes (Figs. 4, 7, S1, S3, S4). In epichnial specimens, *Erevnoichnus* n. igen. consists of either obliquely oriented pits attached at one end by a slender, elongate groove, or as a series of overlapping, en-echelon elongate pits/short grooves. All specimens of *Erevnoichnus* n. igen. observed in this study are preserved as three-dimensional features, with grooves or pits that penetrate into the sediment surface that commonly are accompanied by mounds and ridges of sediment pushed up and to the sides (Figs. 3–7, S1–S5).

The observed dimensions of *Erevnoichnus* n. igen. are variable both within a single occurrence as well as between occurrences. In epichnial examples, the front part of each individual pit is typically deeper, sloping upward to the back. Small ridges or mounds of sediment are commonly pushed up on the sides of the pits and the connecting groove. *Erevnoichnus* n. igen. observed in this study occur in a sinuous pattern, associated with *P. feduccii* footprints (Figs. 3–7, S1–S5).

Erevnoichnus n. igen. may bear a superficial resemblance to various ichnospecies of *Lockeia* James, 1897. Isolated pits may look superficially like shallow *L. siliquaria* James, 1879, or *L. amygdaloides* (Seilacher, 1953) (Seilacher and Seilacher, 1994). Linked specimens bear a similarity to *L. cunctator* Schlirf, Uchman, and Kümmel, 2001. However, *Erevnoichnus* n. igen. differs from *Lockeia* in several important aspects. *Erevnoichnus* n. igen. has a pronounced asymmetry, which is absent in *Lockeia*. This asymmetry includes both the groove emplaced on one side of the pits as well as the pits themselves, which may be tapered from a deeper end to a shallower end and exhibit a pronounced bilateral (left to right) asymmetry (Fig. 3.1). The individual pits tend to be much shallower than in *Lockeia*. Rather than the consistently obtuse terminus and almond-shaped outlined characteristic of *Lockeia*, *Erevnoichnus* n. igen. pits are

Figure 3. (**1–3**) Specimen BYU 50812 illustrating *Presbyornithiformipes feduccii*, *Avipeda* isp., and the holotype of *Erevnoichnus blochi* n. igen. n. isp. (**1**) Photograph of the entire plate illustrating a series of 12 mounds linked by a ridge on the basal surface of a plate of calcareous mudstone in association with two complete and one partial *P. feduccii* footprints and several unassociated *Avipeda* footprint undertracks. (**2**) Closeup of the hypichnial mounds and connecting ridge that comprises the holotype of *E. blochi* n. igen. n. isp. (**3**) Closeup of three of the hypichnial mounds that comprise a portion of the holotype of *E. blochi* n. igen. n. isp.

typically more olive-shaped in outline. *Treptichnus* Miller, 1889 (particularly *T. pedum* [Seilacher, 1955]) also bears a superficial similarity to *Erevnoichnus* n. igen. (e.g., Jensen, 1997; Vannier et al., 2010), but lacks the symmetrical to asymmetrical pits that are the hallmark of *Erevnoichnus*.

Erevnoichnus blochi new ichnospecies
Figures 3–5, 7, S1, S2, S4, S5

Holotype.—BYU 50812, a series of twelve mounds linked by a ridge preserved as a hypichnion on the basal surface of a plate of calcareous mudstone (Figs. 3.1–3.3; 5.1).

Paratypes.—BYU 50694 (originally B20), a series of seven epichnial pits linked by a shallow groove on the cast of the upper surface of a plate of calcareous mudstone (Figs 4.1, 4.2, 5.2) and BYU 50695, which is a sinuous series of epichnial pits
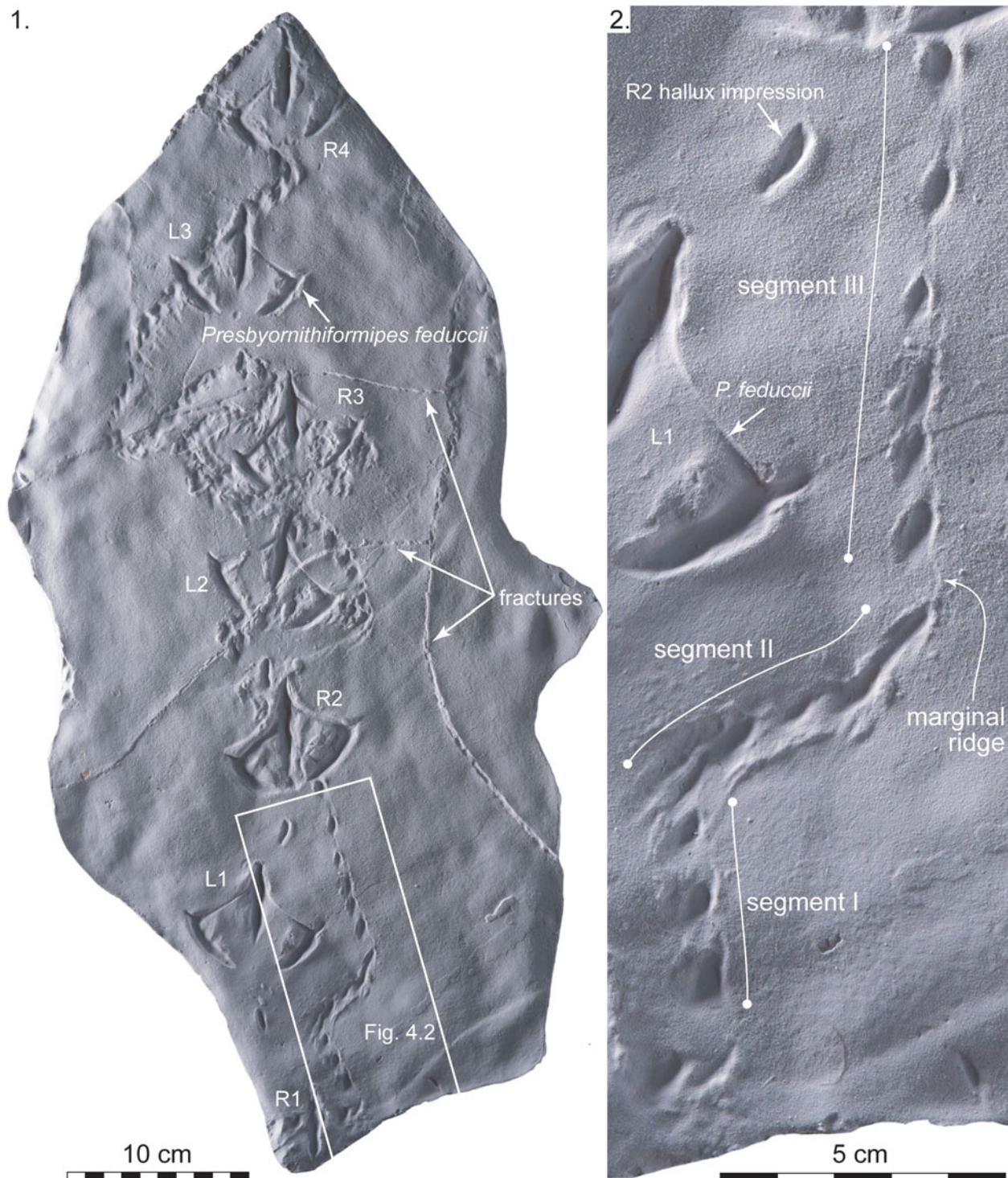
Figure 4. Specimen BYU 50694 (originally B20) illustrating *Presbyornithiformipes feduccii* and *Erevnoichnus blochi* n. igen. n. isp. (**1**) Photograph of a cast of the plate illustrating the paratype of the footprint ichnotaxon *P. feduccii* adjacent to several types of foraging traces. The trackway consists of seven footprints numbered sequentially according to their side (left = L; right = R). (**2**) A series of seven pits linked by a shallow groove on the cast of the upper surface of a plate of calcareous mudstone. The trace labeled Segment III comprises a paratype of *E. blochi* n. igen. n. isp. The original of this plate was numbered "B20" (see Erickson, 1967).

connected by a shallow groove and separated by low mounds of sediment (Figs 5.3, S1.1, S1.2).

Diagnosis.—Sinuous to linear trend of symmetrical ovoid to asymmetrical ovoid (with one blunt end and one tapered end),

or elongate mounds joined by a low ridge of sediment when preserved in hypichnial preservation; length of mounds 150–250% the width; axis of mounds oblique to trend of connecting ridge; mounds may be discrete, distinct and spaced at a distance, or may be closely spaced and partially
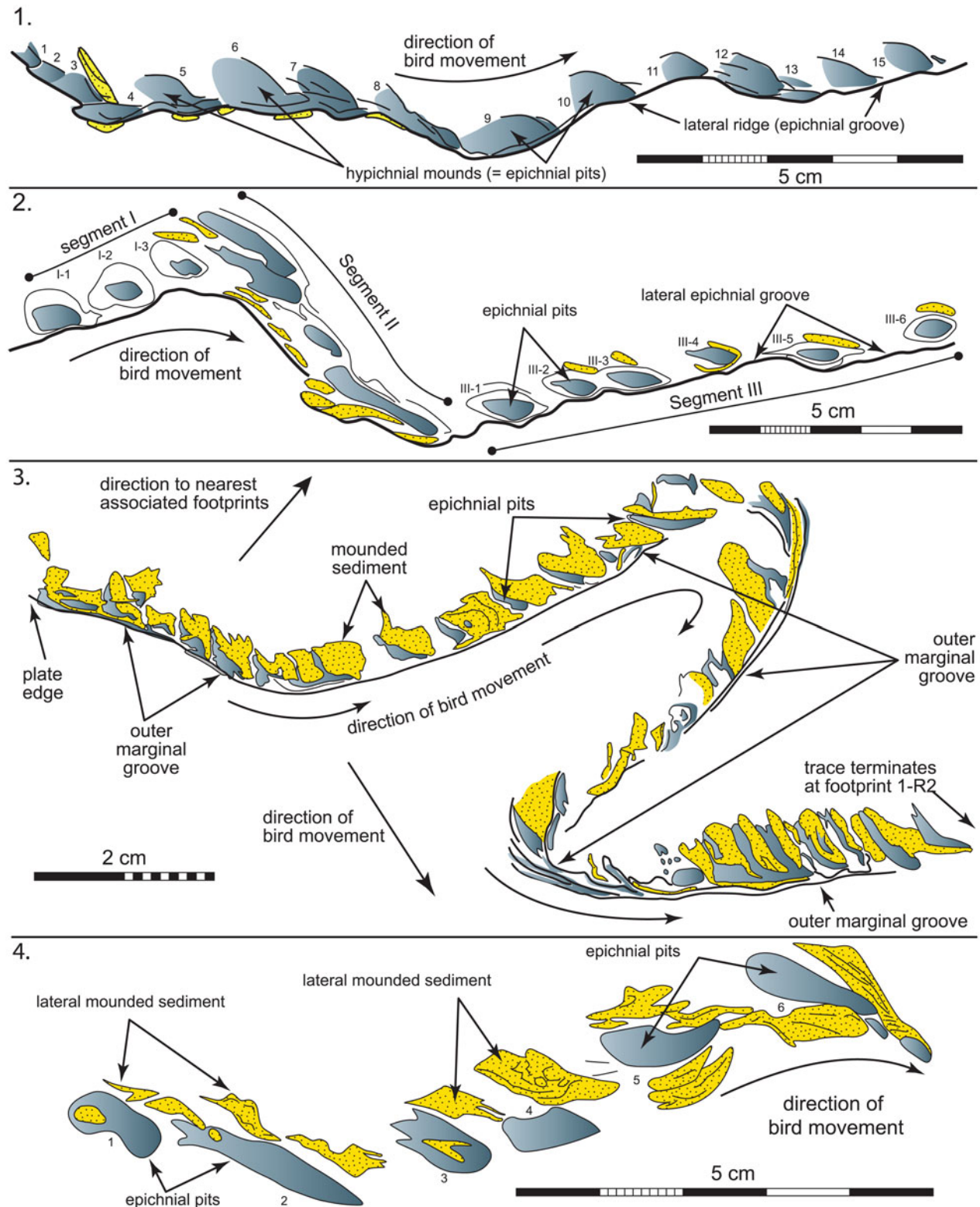
Figure 5. Sketches of the holotype and paratypes of *Erevnoichnus blochi* n. igen. n. isp. and *E. strimmena* n. igen. n. isp. The blue-gray color denotes pits and grooves, and the yellow stippled pattern denotes adjacent sediment mounds. (**1**) Sketch of the holotype of *E. blochi* n. igen. n. isp. on plate BYU 50812 (Fig. 3.2), presented in concave epirelief (the opposite of the preserved plate); note the connecting lateral ridge that runs along the outside edge of the trace. (**2**) Sketch of paratype slab 1 of *E. blochi* n. igen. n. isp. (Fig. 4.2) on plate BYU 50694 (originally B20), which is preserved in concave epirelief. (**3**) Sketch of paratype slab 2 of *E. blochi* n. igen. n. isp. on plate BYU 50695 (Fig. S1). (**4**) Sketch of the holotype of *E. strimmena* n. igen. n. isp. on plate BYU 50867 based on photographs in Figure 6.2 and 6.3.
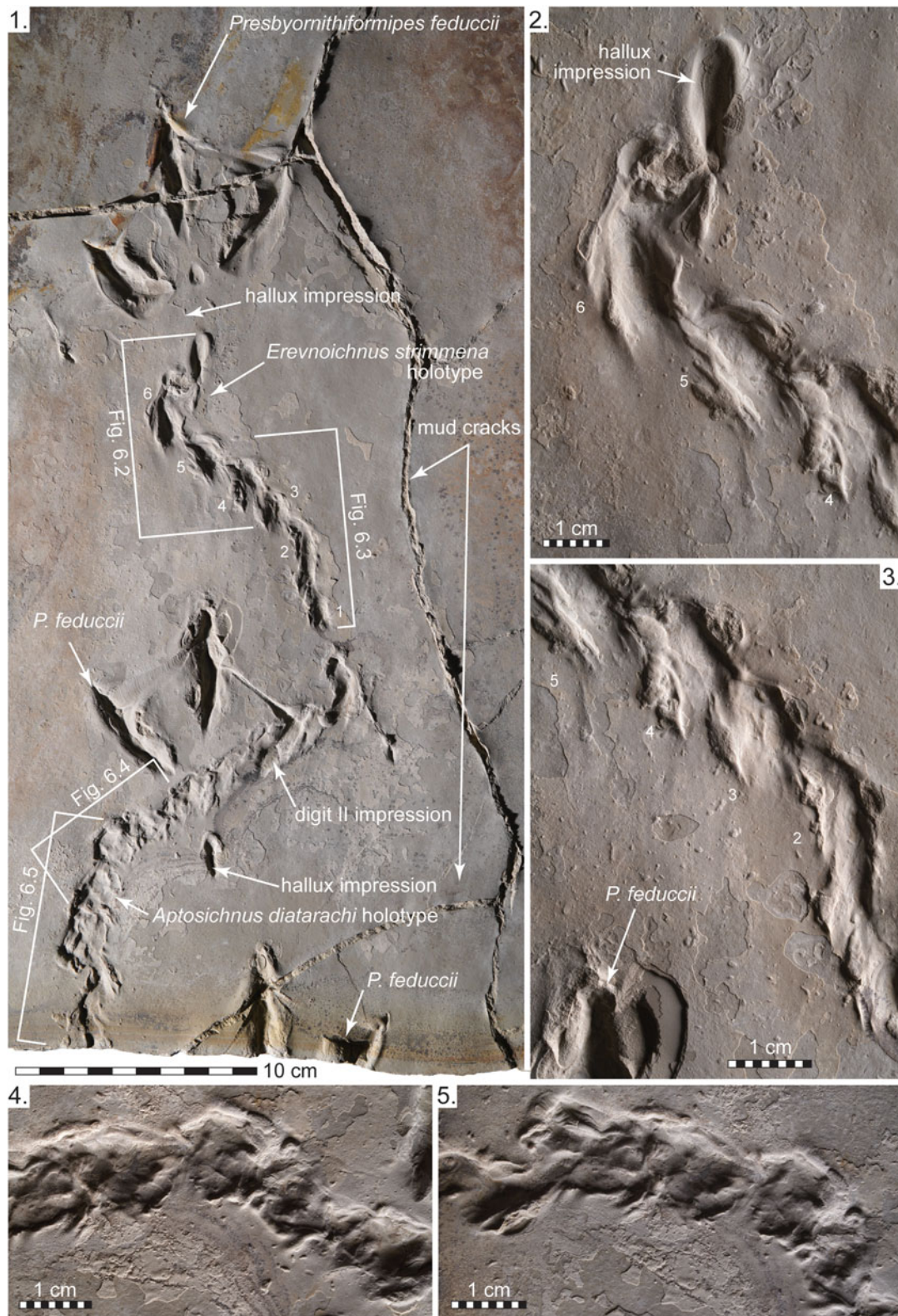
Figure 6. (**1–5**) Specimen BYU 50867 illustrating *Presbyornithiformipes feduccii*, *Erevnoichnus strimmena* n. igen. n. isp., and *Aptosichnus diatarachi* n. igen.-n. isp. (**1**) Photograph of the portion of the plate with avian footprints and associated foraging traces showing the holotypes of *E. strimmena* n. igen. n. isp. and *A. diatarachi* n. igen. n. isp. These holotypes are separated by an impression of digit II from a left footprint of *P. feduccii*. (**2**) Closeup of the distal end of *E. strimmena* n. igen. n. isp. that terminates at a hallux impression of *P. feduccii* showing pits 4 through 6. (**3**) Closeup of the proximal end of *E. strimmena* n. igen. n. isp. that terminates at a hallux impression of *P. feduccii* showing pits 2 through 5. (**4**) Closeup of the proximal segment of *A. diatarachi* n. igen. n. isp. (**5**) Closeup of the distal segment of *A. diatarachi* n. igen. n. isp.

Figure 7. Specimen BYU 50698 illustrating *Presbyornithiformipes feduccii*, *Erevnoichnus blochi* n. igen. n. isp., and *Ravdosichnus guntheri* n. igen. n. isp. (**1**) Photograph of the entire plate illustrating two distinct *P. feduccii* trackways crossing each other. Trackway 1, crossing the plate from top to bottom, consists of three complete footprints and two partial prints and is associated with an elongate, sinuous *E. blochi* n. igen. n. isp. Trackway 2, which crosses the plate from right to left, is not clearly associated with a foraging trace. (**2**) Closeup of the *E. blochi* n. igen. n. isp. foraging trace between footprints 1-L2 and 1-R3. (**3**) Closeup of the holotype of *R. guntheri* n. igen. n. isp. between footprints 1-R2 and 1-L2. (**4**) Closeup of the foraging trace between footprints 1-L1 and 1-R2.

overlapping. In epichnial preservation, the trace consists primarily of associated pits attached by a shallow groove.

Occurrence.—Early Eocene of Utah, U.S.A.

Description.—The holotype of *Erevnoichnus blochi* n. igen. n. isp. is preserved in convex hyporelief in association with three *Presbyornithiformipes feduccii* footprints (Figs. 3.1–3.3, 5.1). Paratype 1 (BYU 50694, originally B20) occurs on the holotype plate of *Presbyornithiformipes feduccii* in concave epirelief in association with six complete and one partial *P. feduccii* footprints (Figs 4.1, 4.2, 5.2). Paratype 2 (BYU 50695) is a highly sinuous trend associated with non-diagnostic palmate footprints (Fig. S1.1, S1.2). The pits and mounds are closely spaced and are associated with a connecting groove.

Individual mounds in the holotype are 4–9 mm wide, 8–15 mm long, and < 1–7 mm high. Individual pits on paratype 1 are 3–8 mm wide, 8–10 mm long, and < 1–5 mm deep. The connecting groove or ridge is variable in width, from a trace to < 4 mm to > 4 mm wide, with a depth of < 1 mm to as deep as 3 mm. In the holotype and paratype the groove/ridge is always present. The groove typically does not penetrate as deeply as the pits and thus, in an undertrace, the groove could be absent, and the trace would consist of a linked series of associated pits.

The paratype specimens on BYU 50694 (formerly B20) consist of a section of four linked pits (Figs. 4.2, 5.2, segment I), and a second section of six linked pits (Figs. 4.2, 5.2, segment III). These two segments are linked by a broad groove with three elongate pits in its center (Figs. 4.2, 5.2, segment II). The morphological difference of segment II from segments I and III reflects a lateral shift by the tracemaker. Although this shift is not inferred to record a substantial change in tracemaker behavior, it is morphologically variant and distinct from the holotype and paratypes of *Erevnoichnus blochi* n. igen. n. isp. Although segment II is not separated here as a distinct ichnotaxon, it is also not included in the *E. blochi* n. igen. n. isp. hypodigm.

The paratype specimen on BYU 50695 consists of a sinuous trend of > 25 pits with associated ridges and mounds and a long, thin groove on the outer margin of the trace. The pits and mounds overlap each other, rendering absolute measurements difficult. The preserved pits are 1–3 mm wide and 5–12 mm long. The mounded sediment forms ridges, which are 2–8 mm wide and 4–8 mm long between and overlapping the pits. The marginal groove occurs on the side of the trace farthest from associated footprints, flipping sides at meander bends to retain this 'outer' positioning (Figs. 5.3, S1).

Plates BYU 50696, 50697, 50698, 50947, and 50948 preserve additional specimens of *Erevnoichnus blochi* n. igen. n. isp., most in association with *Presbyornithiformipes feduccii* footprints (Figs. 7, S1, S2, S4, S5). Some *E. blochi* n. igen. n. isp. comprise roughly linear trends (Figs. 3, 4, S4), however most examples meander sinuously across the rock plates (Figs. 7, S1, S2, S4, S5). These latter traces are commonly overprinted by the footprints of the tracemaker, resulting in short (80–150 mm) segments separated by *P. feduccii* footprints.

In the holotype, the groove-connected pit trend meanders gently, within a fairway twice the width of the trace (Figs. 3.1–3.3, 5.1). In other cases, the bird's head swung the full width of the associated trackway (i.e., from the right side of right footprints to the left side of left footprints), or farther, before arching back in the reverse direction (e.g., Figs. 4, S2, S5). In most cases, *E. blochi* n. igen. n. isp. were emplaced directly within the track width (e.g., Figs. 4, S2), however in other cases, *E. blochi* were emplaced slightly to the left or right of the locomotion fairway (Fig. 3).

Etymology.—After Jonathan I. Bloch, in acknowledgement of his life-long contributions to Paleogene vertebrate paleontology.

Remarks.—The holotype and paratypes of *Erevnoichnus blochi* n. igen. n. isp. occur in thinly bedded carbonate strata deposited on the margin of Eocene Lake Uinta. The close association of this trace with *Presbyornithiformipes feduccii* footprints (Figs. 3, 4; 7, S1, S2, S4, S5) support a genetic association of the two trace types. The plate with paratype specimen 1 (Fig. 4) has been illustrated in several other manuscripts wherein the foraging traces have been referred to as 'dabble marks' or 'dabble traces' emplaced by the tracemaker of *P. feduccii* (Erickson, 1967; Yang et al., 1995; Lockley et al., 2021). Although we concur that *E. blochi* n. igen. n. isp. represents waterbird foraging behavior, we disagree that these are dabble marks. Dabbling is a behavior common in some waterbirds such as ducks, teals, and grebes. Dabbling (sensu stricto) involves swimming or wading birds removing food from the surface of the water, commonly aided by surface tension transport, without submersing the eyes (e.g., Rubega and Obst, 1993; Rubega, 1997; Johnson and Rohwer, 2000). This foraging behavior is not preserved in the sediment record because it does not involve bill–sediment interaction.

Less commonly, the term 'dabbling' has also been used to describe the activity of some anatid waterbirds (such as Shelduck) wherein they grasp mouthfuls of sediment while swimming and sieve it with their lamellae for prey (Olney, 1965; Bryant and Leng, 1975; Thompson, 1981, 1982; Walmsley and Moser, 1981; Viain et al., 2011). This behavior has been termed 'sediment-dabbling' (Zonneveld et al., in press A) to differentiate it from true dabbling. Sediment-dabbling is a type of probe-filtering conducted by broad-billed waterbirds while walking in shallow water or, more commonly, while tipping-up (also referred to as upending) from a floating position (e.g., Swennen and van der Baan, 1959; Olney, 1965; Thomas, 1982; Miller, 1983; Guillemain et al., 2000; Rodríguez-Pérez and Green, 2006; Olsen, 2017).

The traces that sediment-dabbling produces have been referred to as dabble marks, dabbling holes, and dabble craters (Swennen and van der Baan, 1959; Olney, 1965; Thompson, 1981, 1982), which are discrete, almond-shaped, traces that are similar, in most regards, to clusters of the ichnotaxon *Lockeia siliquaria*. Dabble marks tend to occur in loose clusters and typically do not occur in association with trackways (Swennen and van der Baan, 1959; Zonneveld et al., in press A). The trace fossils herein included in *Erevnoichnus blochi* n. igen. n. isp., and illustrated elsewhere as 'dabble marks' (Erickson, 1967; Yang et al., 1995; Lockley et al., 2021), are inconsistent with sediment-dabbling behavior. Regular spacing of pits implies a systematic searching behavior, which is most

similar to the diverse probing techniques used by various modern waterbird groups.

The marginal groove or ridge that connects the pits/mounds invariably occurs on the far side of the trace, away from where the bird was standing (Figs. 3, 4, S1). It is typically narrow, regular in shape, and continuous. Its occurrence on the far side of the trace, away from the body of the bird, implies that it was formed by the maxillary rhamphotheca. The smoothness and continuity of the marginal groove or ridge imply that the maxillary rhamphotheca did not leave the sediment, and the bird's head maintained a consistent level while the bird foraged. This is particularly apparent in *E. blochi* n. igen. n. isp., which has a high degree of sinuosity wherein the marginal groove maintains its outer position both when the bird moved its activities to the left and when it moved it to the right (e.g., Figs. 5.3, S1, S5). The pits extend towards the bird's body, away from the marginal groove, and would have to have been formed by opening the bill and pushing sediment backwards with the mandibular rhamphotheca, a behavior analogous to the gaping behavior exemplified by some modern birds (see Cruz, 1978; Bühler, 1981; Orians, 1983; Elbroch and Marks, 2001; see Estrella and Masero, 2007, for discussion of this behavior).

The pattern of regular, approximately evenly spaced pits connected by a thin marginal groove (or ridge) that characterizes *E. blochi* n. igen. n. isp. (Figs. 3, 4, 7, S1, S2; S4, S5) reflects an unusual foraging behavior that combines gaping and sweeping behaviors (summarized in Zonneveld et al., in press A). Gaping occurs when a bird opens its bill within the substrate in order to expose buried prey (Cruz, 1978; Bühler, 1981; Orians, 1983; Elbroch and Marks, 2001; Estrella and Masero, 2007; Zonneveld et al., in press A). It has not been attributed previously to a broad-billed waterbird. Sweeping involves lateral movement of a bird's bill through the water or across a sediment surface While foraging, the bird walked forward slowly and paused while swinging its head from side to side, with its bill immersed a few mm or more into the sediment. The consistent thickness of the thin marginal groove indicates that, as the bird moved its head laterally, the depth of immersion of the maxillary rhamphotheca in the substrate remained steady. At regular spacings, the bird 'gaped' by moving its mandibular rhamphotheca in a reverse bite motion (i.e., the mandible pushing backwards in the sediment). Each gape mark formed a pit that extended from the marginal groove back towards the bird's body. In the holotype, paratype 1, and some other specimens, the gape pits are separated by several mm and are thus discrete and distinct from each other pit (Figs. 3, 4, 5.1, 5.2), with only the marginal groove produced by the maxillary rhamphotheca connecting the pits. In paratype 2, the gape pits and their associated spill piles are much closer, although each pit is distinct from its neighbor (Figs. 5.3, S1).

It should be noted that the holotype and paratypes occur on plates with *Presbyornithiformipes feduccii* that preserve great detail of the digits and webbing and thus record the actual horizon the birds occupied. Other plates are characterized by less well-preserved *P. feduccii* and are likely 'undertraces' (i.e., traces preserved on layers a mm or more below the occupied horizon). On some of these latter plates, the connecting marginal groove may not be preserved in its entirety (e.g., Figs S2.1, S2.2, S5).

Erevnoichnus strimmena new ichnospecies
Figures 5.4, 6.1–6.3, S3

Holotype.—BYU 50867, six imbricated troughs on the upper surface of a plate of calcareous mudstone.

Diagnosis.—Discrete imbricated troughs of systematically disturbed sediment; margins of trough undulatory; ridges of sediment on margins of constituent troughs.

Occurrence.—Early Eocene of Utah, U.S.A.

Description.—The holotype *Erevnoichnus strimmena* n. igen. n. isp. occurs on the same calcareous mudstone plate as the holotype of *Aptosichnus diatarachi* n. igen. n. isp. (Fig. 6.1–6.3). It occurs between two *Presbyornithiformipes feduccii* footprints in a short trackway. It initiates just to the right side of toe III of a left footprint and terminates at the hallux of a right footprint (Fig. 6.1).

Erevnoichnus strimmena n. igen. n. isp. consists of a series of short, straight to mildly sinuous grooves with a u-shaped profile emplaced in the sediment surface (Figs. 5.4, 6.1–6.3). The grooves are 5–8 mm wide, 12–22 mm long, and variable (< 1–5 mm) in depth. The axes of the grooves are generally within ~30° of each other. Individual grooves are typically 2–4 times longer than they are wide.

The grooves are linear to gently arcuate, with the anterior end pointing towards the initiation point of the next groove. Each groove has a low ridge of sediment pushed up to the front and anterior end, more rarely to the posterior end. Individual grooves may be deepest near their front, or towards the middle of the groove. Internal grooves and ridges are common and follow the arc or trend of the groove. The imbricated and arcuate to twisted nature of the component grooves and ridges gives *Erevnoichnus strimmena* n. igen. n. isp. a woven, rope-like appearance (Figs. 5.4, 6.1–6.3).

Etymology.—From the Greek στριμμένα (= strimména), meaning 'twisted' and 'and ίχνος (= ichnos) meaning 'trace', in allusion to the rope-like appearance of this trace.

Remarks.—*Erevnoichnus strimmena* n. igen. n. isp. is associated with *Presbyornithiformipes feduccii* and is interpreted as a foraging trace. The tracemaker's bill left contact with the sediment–water/sediment–air interface for only brief periods during formation of this trace, consistent with tactile foraging behavior (Zonneveld et al., in press A). Birds use their bills in tactile foraging by probing, gaping, sweeping, ploughing, and stirring (Elbroch and Marks, 2001; Zonneveld et al., in press A). This trace was emplaced by a bird utilizing regular, systematic forward probing behavior. The bird walked on water-saturated sediment, bobbing its head up and down, and moving it laterally, with numerous consistent, short probes of its bill into the sediment ahead of itself. The movements were regular and predictable, with bill penetration occurring most deeply at the distal (anterior) end of the oval pit, with ridges of sediment most commonly pushed up to the distal end and anteriormost sides of the pit.

Ichnogenus *Ravdosichnus* new ichnogenus

Type ichnospecies.—*Ravdosichnus guntheri*.

Diagnosis.—As for the ichnospecies.

Known occurrence.—Early Eocene of Utah, U.S.A.

Etymology.—From the Greek ράβδωση (= rávdosi) meaning 'groove and ίχνος (= ichnos) meaning 'trace'.

Remarks.—The holotype of *Ravdosichnus guntheri* n. igen. n. isp., the sole ichnospecies within this ichnogenus, occurs between right and left *Presbyornithiformipes feduccii* footprints (the 3rd and 4th footprints in a five-print trackway). The paratypes occur between, and laterally adjacent to, two *P. feduccii* footprints, supporting the interpretation of a genetic relationship between the two ichnotaxa. Some specimens occur on a slab that also includes *Erevnoichnus blochi* n. igen. n. isp. traces, implying that the *P. feduccii* tracemaker emplaced both trace types.

Ravdosichnus guntheri new ichnospecies
Figures 7.1, 7.3. 7.4, 8, 9

Holotype.—BYU 50698, a distinct epichnial trough on the upper surface of a plate of calcareous mudstone between two *Presbyornithiformipes feduccii* footprints designated 1-L1 and 1-R2 (Fig. 7.3).

Paratypes.—BYU 50698, a distinct, gently meandering, epichnial trough on the upper surface of a plate of calcareous mudstone between two *Presbyornithiformipes feduccii* footprints designated 1-R2 and 1-L2 (Fig. 7.4);

BYU 50948, a distinct epichnial trough on the upper surface of a plate of calcareous mudstone between two *Presbyornithiformipes feduccii* footprints designated R1 and L1 (Fig. 8).

Diagnosis.—Simple, straight to gently sinuous groove in the sediment surface, approximately consistent in width, depth approximately consistent throughout its trend; u-shaped cross-sectional profile; low marginal ridges common; length greater than three times the width, typically greater than five times the width.

Known occurrence.—Early Eocene of Utah, U.S.A.

Description.—*Ravdosichnus guntheri* n. igen. n. isp. is named for a gently meandering groove between *Presbyornithiformipes feduccii* on specimen BYU 50698 (Figs. 7.1, 7.3, 9.1). The holotype is an ~40 mm long groove that is 3–4 mm wide and 2–3 mm deep (Figs. 7.3, 9.1). The edges are characterized by a low ridge of sediment pushed up from the groove. The trace extends from slightly ahead of footprint 1-R2 and is terminated when overprinted by the hallux and metatarsal pad of footprint 1-L2 (Fig. 7.1, 7.3). Most specimens of *R. guntheri* n. igen. n. isp. consist of simple, even troughs (Figs. 7.3, 9.1, 9.3), however some have wavy margins (Figs. 7.4, 9.2).

Etymology.—After the Gunther family, who have donated many of the specimens discussed in this manuscript.

Remarks.—*Ravdosichnus guntheri* n. igen. n. isp. is the simplest of the foraging traces. The holotype meanders slightly and, based on the pushed-up ridge or rim of sediment (Figs. 7.1, 7.3, 9.1), was emplaced when the substrate was quite soft but
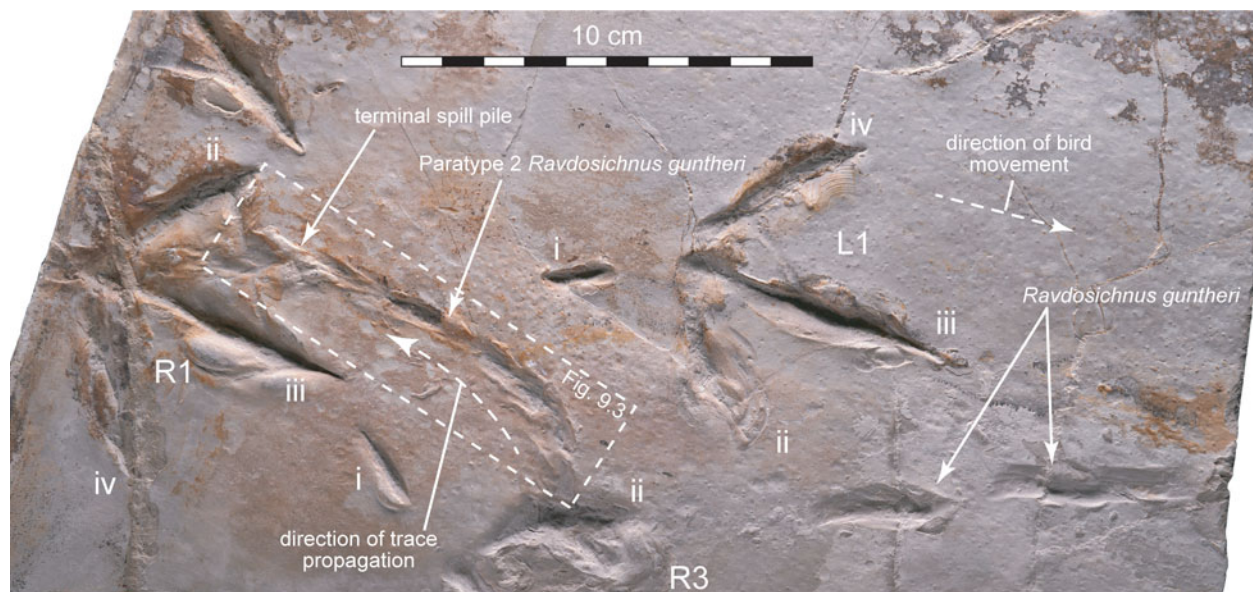
Figure 8. Specimen BYU 50948 with three specimens off *Ravdosichnus guntheri* n. igen. n. isp., including a specimen designated paratype 2, which is preserved in concave epirelief. Paratype 2 comprises an elongate groove with low ridges of pushed-up sediment on both sides. Two other specimens referred to *R. guntheri* n. igen. n. isp. also occur on this slab.
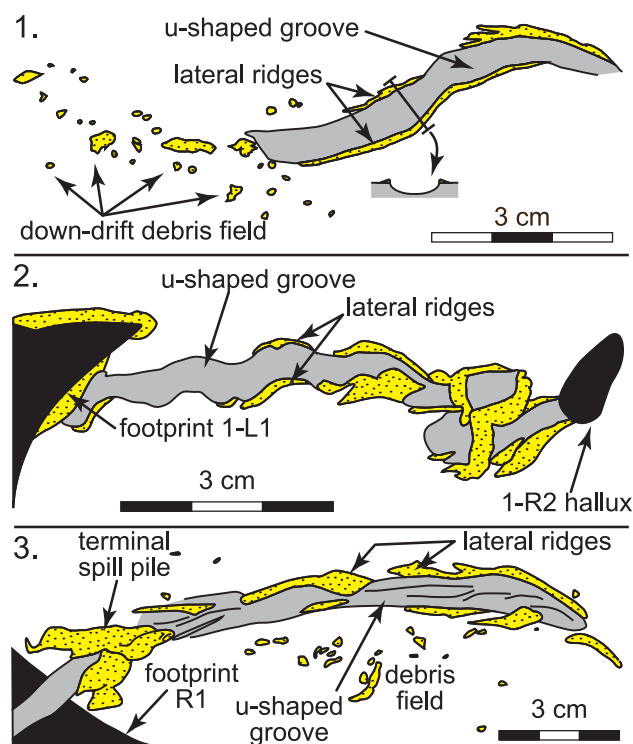
Figure 9. Sketches of the holotype and paratype 1 of *Ravdosichnus guntheri* n. igen. n. isp. based on BYU 50698. Partial *Presbyornithiformipes feduccii* tracks are illustrated in black, pits and grooves are illustrated in gray, and the yellow stippled pattern indicates mounds and ridges. (**1**) Sketch of the holotype of *R. guntheri* n. igen. n. isp. Source photograph is indicated in Figure 7.3. (**2**) Sketch of paratype 1 of *R. guntheri* n. igen. n. isp. Source photograph is indicated in Figure 7.4. (**3**) Sketch of paratype 2 of *R. guntheri* n. igen. n. isp. on slab BYU 50948. Source photograph is indicated in Figure 8.

not soupy. Paratype 1 of *R. guntheri* n. igen. n. isp., which occurs on the same limestone slab as the holotype (BYU 50968), consists of a gently meandering groove with marginal ridges of pushed-up sediment (Fig. 7.4). Paratype 2 of *R. guntheri* n. igen. n. isp. occurs on slab BYU 50948 and consists of a groove ~ 8 cm in length and 6–8 mm in width that has marginal ridges of pushed-up sediment and ends in an ~2-cm long terminal spill pile (Figs. 8, 9.3).

The nature of the pushed-up rim/sediment ridge and the occurrence of a spill of granular detritus behind the holotype of *Ravdosichnus guntheri* n. igen. n. isp. (Figs. 7.3, 9.1) indicate that the bird created this trace by pulling its bill backwards through the sediment. The lack of a posterior pile of sediment and the occurrence of granular detritus suggest that some winnowing of the mud-sized fraction occurred, suggesting that this trace was emplaced as the waterbird foraged in shallow water. In contrast, paratype 2 preserves a large (~2.5 cm × 1 cm) plug of sediment that was pushed backwards out of the groove (Figs. 8, 9.3). This indicates that the trace was emplaced with a pull of the rhamphotheca backwards from a more distal location proximally towards the front of the bird's right foot (i.e., the opposite direction of the bird's movement). *Ravdosichnus guntheri* n. igen. n. isp. involved long, isolated pulls of the bill through the sediment in a reverse-scraping or ploughing motion resulting in a simple, elongate trough.

Ichnogenus *Aptosichnus* new ichnogenus

Type ichnospecies.—*Aptosichnus diatarachi.*

Diagnosis.—Discrete trough or series of imbricated troughs of chaotically to systematically disturbed sediment; margins of trough undulatory; trace may occur in a linear or gently sinuous trend.

Known occurrence.—Early Eocene of Utah, U.S.A.

Etymology.—From the Greek απτός (= aptós) meaning 'tactile' and ίχνος (= ichnos) meaning 'trace', in allusion to the emplacement of these traces during tactile mud stirring by an aquatic bird bill.

Remarks.—*Aptosichnus* n. igen. differs from *Erevnoichnus* n. igen. in consisting of an elongate trough with a complex internal fill rather than a series of en-echelon pits/short grooves or obliquely oriented pits attached by a slender, shallow groove. *Aptosichnus* n. igen. differs from *Ravdosichnus* n. igen. in the occurrence of undulatory margins and variably complex fill, in contrast to the simple, u-shaped trough that characterizes *Ravdosichnus*.

The holotype of *Aptosichnus diatarachi* n. igen. n. isp. occurs on the same slab as the holotype of *Erevnoichnus strimmena* n. igen. n. isp. Both ichnotaxa occur in the same long sinuous trend and are overprinted by footprints in a trackway assigned to *Presbyornithiformipes feduccii* (Fig. 6). As discussed previously, these palmate incumbent anisodactyl footprints have been attributed to the Eocene waterbird *Presbyornis pervetus* Wetmore, 1926, in the Green River Formation in Utah. Although clearly emplaced by the same individual animal, the two traces are morphologically distinct and record different foraging behaviors, and thus are included in distinct ichnotaxa. This is consistent with accepted ichnotaxonomic practice. Trace fossils are named based on distinct morphologies, which in turn are interpreted to record distinct behaviors (Pickerill and Narbonne, 1995; Bertling et al., 2007, 2022). *Aptosichnus diatarachi* n. igen. N. isp. and *Erevnoichnus strimmena* n. igen. n. isp. fit this description. On the holotype slab of both ichnotaxa, the two individual holotypes are physically separated from each other by the digit II impression of the first *P. feduccii* footprint on the plate, are morphologically distinct, and record distinct foraging behaviors.

Aptosichnus diatarachi new ichnospecies
Figures 6.1, 6.4–6.5, 10

Holotype.—BYU 50867, an elongate trough of disturbed sediment running from 3 cm above the edge of the holotype plate until the digit II impression of the first complete footprint on the holotype plate.

Diagnosis.—Broad, shallow groove/trough, with irregularly undulate margins and irregular pattern of inner grooves and ridges; one side of groove deeper than the other; groove/

trough occurs in straight to curved segments with a change in orientation at segment boundaries.

Occurrence.—Early Eocene of Utah, U.S.A.

Description.—The holotype of *Aptosichnus diatarachi* n. igen. n. isp. is preserved in concave epirelief on the upper surface of a plate of calcareous mudstone (Fig. 6.1, 6.4, 6.5). It comprises an irregular broad, shallow trough or groove that is 10–16 mm wide and is partially infilled with disturbed sediment (Figs. 6.1, 6.4, 6.5, 10.). The holotype consists of two approximately straight segments oriented at ∼40° from each other. The first segment is 52 mm long and the second segment is 67 mm long. The depth is variable and generally shallow (< 3 mm).

The floor of the broad groove is complex, with numerous internal mounds and ridges. In the first segment of the trace, many of the internal mounds and ridges are oriented parallel to oblique to the burrow margins (Fig. 6.4). In the second segment of the trace, the internal mounds and ridges are oriented primarily oblique to perpendicular to the trace margins (Fig. 6.4). The margins of the trace are irregularly sinuous to scalloped. In the holotype, the floor of the broad groove is shallower on one side (left relative to the direction of trace emplacement) and deeper on the other. This latter feature is not considered diagnostic of this ichnospecies.

Etymology.—From the Greek διαταραχή (= diatarachí), meaning 'disorder' and 'and ίχνος (= ichnos) meaning 'trace', in allusion to the chaotic appearance of this trace

Remarks.—As with all purported foraging traces discussed herein, the holotype of *A. diatarachi* n. igen. n. isp. is associated with *Presbyornithiformipes feduccii* (Fig. 6.1). In *A. diatarachi* n. igen. n. isp., the tracemaker stirred the sediment more intensively, but much more randomly than in any of the other traces discussed in this contribution. The consistent width through most of the trace (Figs. 6.1, 6.4, 6.5, 10) implies that the bird stirred its bill back and forth in a consistent, narrow arch. Evidence that the tracemaker's bill left contact with the sediment surface during emplacement of

the trace is lacking. This is consistent with the tactile foraging behavior referred to as bill-stirring (Zonneveld et al., in press A). Although the resulting trace is rather irregular and chaotic in appearance, it is clear that the tracemaker's bill penetrated to approximately the same depth throughout the trace.

Discussion

The traces discussed herein all occur in association with avian footprints, specifically those assigned to *Presbyornithiformipes feduccii*. It is likely that the foraging traces described herein always occur in association with footprints and foraging trackways because these types of foraging behaviors are characteristic of walking foragers rather than swimming foragers. Regardless, the association of these traces with *P. feduccii* has not been included in the diagnosis for any of the new ichnotaxa established herein because we assume that other bird taxa may make similar foraging traces.

Ethological implications.—The four ichnotaxa are morphologically distinct from each other and record several, distinct behaviors. *Erevnoichnus blochi* n. igen. n. isp. records a combined sweeping/gaping behavior wherein the bird moved its head from left to right, opening its bill at approximately regular intervals to open troughs/pits in the sediment (Figs. 11.1, 12.1). The pits were produced by the mandibular rhamphotheca during periodic opening of the mouth and the connecting groove was produced by the mandibular rhamphotheca as it was pulled laterally across the sediment surface. Neither anterior–posterior movement of the neck, nor rotation of the head were necessary, and the head was maintained at a consistent elevation above the substrate while foraging.

Erevnoichnus strimmena n. igen. n. isp. represents a probing behavior wherein the bird pushed its bill forward into the sediment (Figs. 11.2, 12.2). The bird lifted its head and neck and moved them laterally before reinserting its bill into the sediment and probing again (Figs. 11.2, 12.2). The result is a series of en-echelon elongate pits/grooves emplaced in an elongate linear trend. These pits, although closely spaced, are distinct from each other. This morphology is consistent with systematic
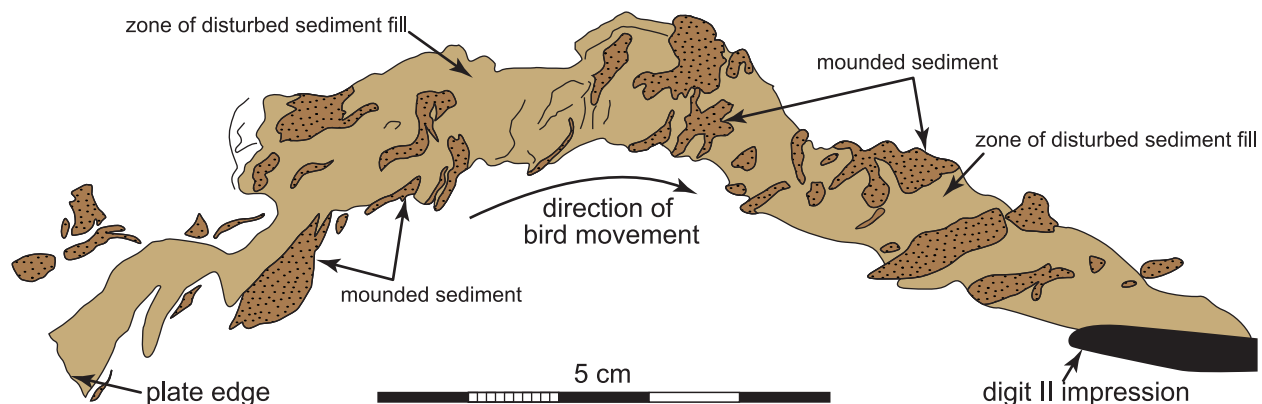
Figure 10. Sketch of the holotype of *Aptosichnus diatarachi* n. igen. n. isp. on plate BYU 50867 based on photographs in Figure 6.4 and 6.5. Partial *Presbyornithiformipes feduccii* tracks are illustrated in black, ridges are denoted in stippled dark brown, and the zone of disturbed fill is denoted in tan brown.
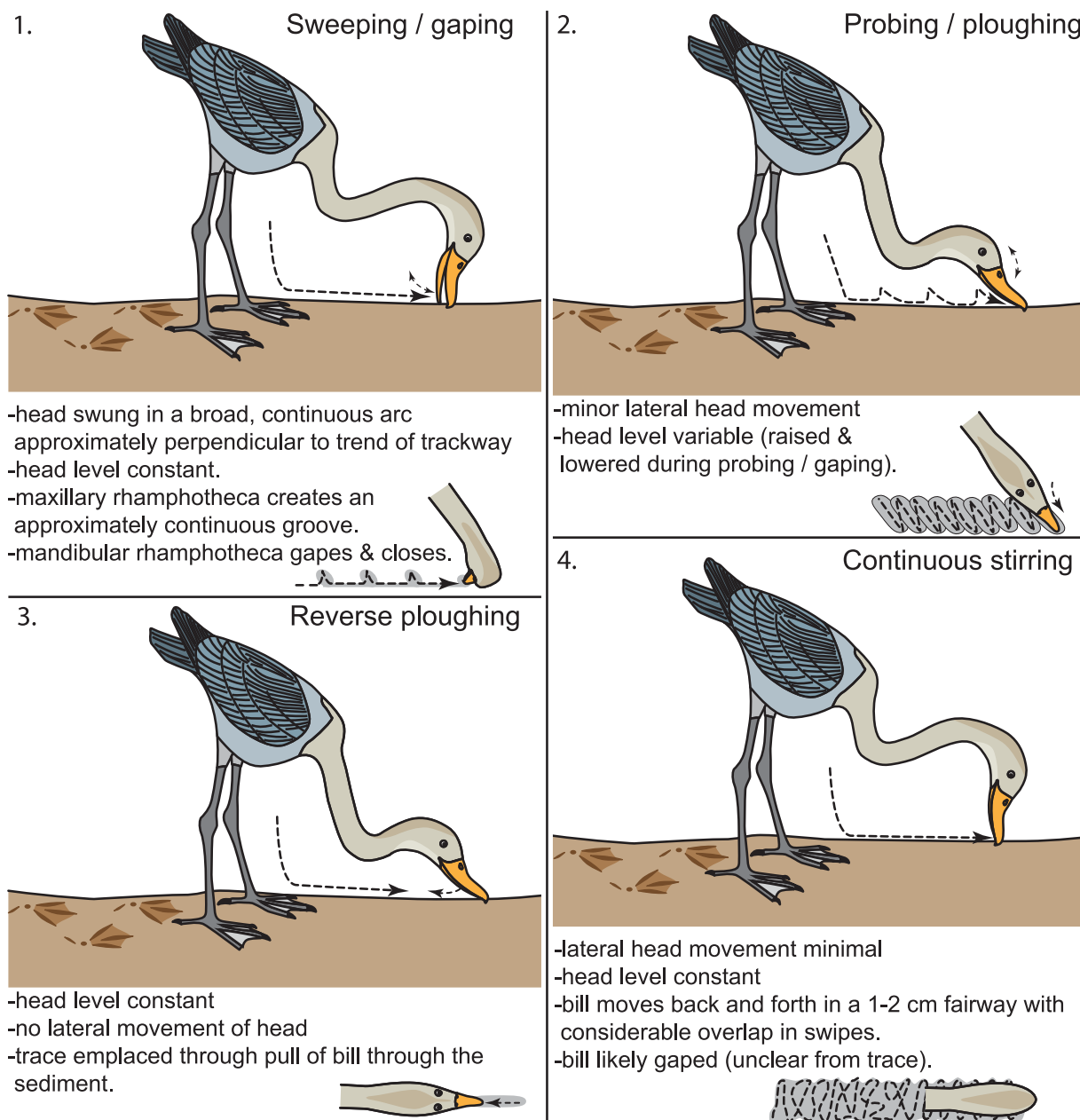
Figure 11. Interpretation of foraging behaviors discussed in this study. Reconstruction of *Presbyornis pervetus* (the inferred tracemaker) based on artwork by José Marcos Fraccaroli, Antonin Jury, and the skeleton presented in Olson and Feduccia (1980a). Each panel includes a side view of the bird (top) and looking down on the animal's head (bottom), illustrating both the vertical and lateral movement of the bill (dashed lines). (**1**) *Presbyornis pervetus* involved in sweep-gaping behavior. This behavior involved an arcing sweep of the head from left to right and right to left across the trend of the trackway, with the head held static with regards to distance from the sediment surface and the mandibular rhamphotheca gaping in a regular and systematic fashion. This behavior would have produced *Erevnoichnus blochi* n. igen. n. isp. (**2**) *Presbyornis pervetus* involved in modified stirring/ploughing behavior. This involved both vertical movement (up and down) and oblique-lateral movement of the head resulting in a series of obliquely oriented en-echelon grooves. It is likely that gaping was involved in emplacement of this trace. This behavior would have produced *E. strimmena* n. igen. n. isp. (**3**) *Presbyornis pervetus* involved in reverse ploughing/bill-pulling behavior resulting in simple linear to mildly sinuous grooves in the sediment. This behavior would have produced *Ravdosichnus guntheri* n. igen. n. isp. (**4**) *Presbyornis pervetus* involved in continuous stirring behavior. This involved lateral movement of the bill and/or head (bottom) with minimal vertical movement (top). The resultant trace is an elongate trough infilled with disturbed sediment and characterized by in-trough and lateral piles of sediment. This behavior would have produced *Aptosichnus diatarachi* n. igen. n. isp.

probing, which is a foraging behavior adapted to searching for a buried food resource. Although there are some morphological similarities between the traces, *E. strimmena* n. igen. n. isp. lacks the marginal groove that characterizes *E. blochi* n. igen. n. isp., which involved an up-and-down motion to the head and an anterior–posterior push of the bill forward, as well as lateral shift of the position of the head between probes.

Ravdosichnus guntheri n. igen. n. isp. represents a simple, elongate drag of the bill through the sediment in a reverse-scraping/ploughing motion (Figs. 11.3, 12.3). This behavior may be more common than the material identified in this study suggests since simple grooves are unremarkable and are likely commonly overlooked in the field. The movement required only a backwards drag of a broad bill through the
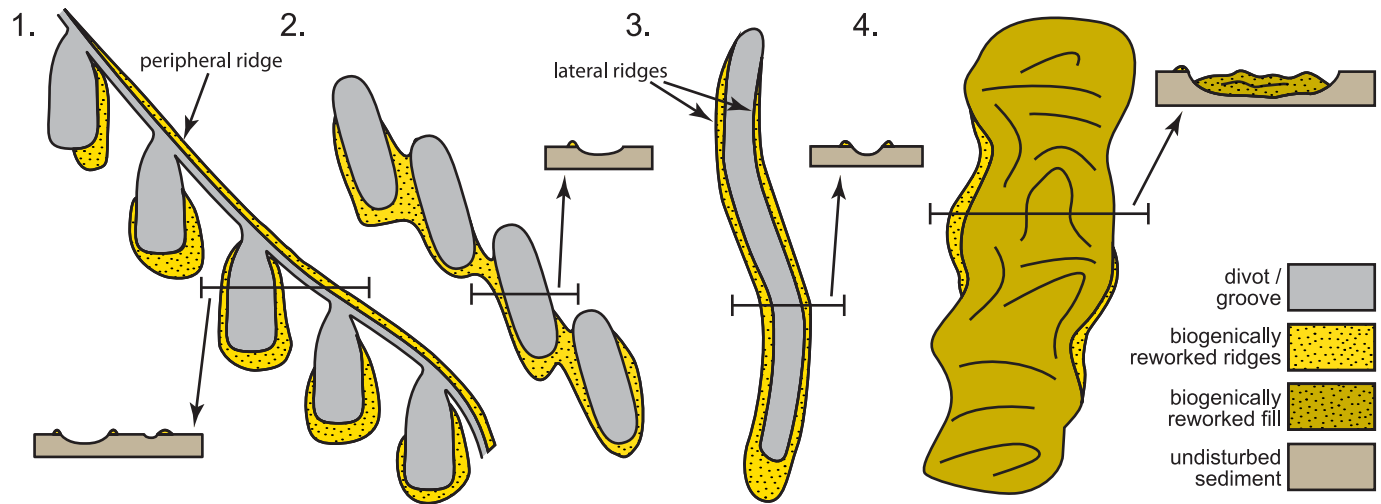
Figure 12. Cartoon schematics, in map and cross-sectional view, of the traces discussed herein. (**1**) *Erevnoichnus blochi* n. igen. n. isp., illustrating the peripheral groove and discrete, individual pits (divots). (**2**) *Erevnoichnus strimmena* n. igen. n. isp., illustrating the lack of a peripheral groove and the closely spaced, overlapping pits (divots) and ridges. (**3**) *Ravdosichnus guntheri* n. igen. n. isp., illustrating a simple, slightly sinuous groove with lateral ridges of sediment. (**4**) *Aptosichnus diatarachi* n. igen. n. isp., illustrating a wide trough with a complex fill of reworked sediment.

sediment, although in some examples the movement was slightly sinuous (Fig. 7.4).

Aptosichnus diatarachi n. igen. n. isp. records continuous stirring of the bill through the sediment (Figs. 11.4, 12.4). The foraging trace averages 12 mm wide and is approximately consistent throughout most of its length. This trace does not constitute true sweeping in the sense of the long, arcuate sweeping that is characteristic of waterbirds, such as avocets and spoonbills (e.g., Barbosa and Moreno, 1999; Elbroch and Marks, 2001; Swennen and Yu, 2008). *Aptosichnus diatarachi* n. igen. n. isp. (Fig. 6.4, 6.5) records a behavior that has been termed 'bill-stirring', which is a foraging method utilized by some modern herons (Zonneveld et al., in press A).

All trace fossils described herein were emplaced on an identical calcareous mud substrate. Similarities in the preservation and depth of associated *Presbyornithiformipes feduccii* footprints indicate that water saturation levels were similar as well. Thus, differences in the morphology of the traces are interpreted to record true changes in foraging behavior. Sediment type and water saturation being equal, the most likely variables are changes in prey occurrence, prey type, and prey abundance. Behaviors, such as the sweep-gaping exemplified by *Erevnoichnus blochi* n. igen. n. isp. and the probing represented by *E. strimmena* n. igen. n. isp., are systematic foraging techniques that are ideally suited for searching for an unknown food resource. Similarly, *Ravdosichnus guntheri* n. igen. n. isp. represents a bird bill dragged through the mud, tactilely feeling for a food resource of unknown location. In contrast to these traces, *Aptosichnus diatarachi* n. igen. n. isp. may represent a behavior ideally suited to access the maximum amount of the food resources known to occur in a small area.

The association of four distinct ichnotaxa, each representing a distinct foraging technique, in association with *Presbyornithiformipes feduccii* indicates behavioral plasticity in the tracemaker's foraging behavior. The bird was able to change its behavior in response to various stimuli. The ability to shift foraging behavior in response to different stimuli is particularly apparent in the holotype plate of *Erevnoichnus strimmena* n. igen. n. isp. and *Erevnoichnus blochi* n. igen. n. isp., which occur associated with a short *Ravdosichnus guntheri* n. igen. n. isp. and a *P. feduccii* trackway. This plate records an individual animal foraging in shallow water on the edge of Lake Uinta and trying different techniques to locate food resources.

Regular probing/gaping behavior, represented by *Erevnoichnus blochi* n. igen. n. isp., probing behavior, represented by *E. strimmena* n. igen. n. isp., and reverse ploughing/bill pulling, represented by *Ravdosichnus guntheri* n. igen. n. isp., may have been utilized while searching for appropriate prey. *Aptosichnus diatarachi* n. igen. n. isp. likely records behavior that was useful when the occurrence of prey in an area occurred in moderate abundance but the individual prey items needed to be located.

Implications for the inferred tracemaker.—The close association of *Erevnoichnus blochi* n. igen. n. isp., *E. strimmena* n. igen. n. isp., *Ravdosichnus guntheri*, and *Aptosichnus diatarachi* n. igen. n. isp. with *Presbyornithiformipes feduccii* provides a unique opportunity to contribute to knowledge about the evolution of behavior in an ancient avian lineage. *Presbyornithiformipes feduccii* were emplaced by a waterbird with palmate, incumbent anisodactyl feet and a broad bill. It has been attributed to the Eocene anseriform *Presbyornis pervetus* (Olson, 1977; Feduccia, 1978, 1980; Olson and Feduccia, 1980a; Grande, 1984; Yang et al., 1995; Lockley et al., 2021), an assessment with which we concur. Although formerly interpreted as a potential ancestral form to both lineages, recent work illustrates that these groups are not closely related and places *Presbyornis* within Anseriformes (Ericson, 1997, 2000; Livezy, 1997; Mayr, 2009; Zelenkov, 2021).

Another possible candidate is the middle Eocene waterbird *Juncitarsus gracillimus* Olson and Feduccia, 1980a, which was collected from the Twin Butte beds of the Bridger Formation (Olson and Feduccia, 1980a). *Juncitarsus* has been interpreted

as one of the oldest fossil forms in the flamingo lineage (Olson and Feduccia, 1980a, b; Torres et al., 2015), although recent work has suggested that it falls outside the true flamingo lineage (Mayr, 2014). Although *Juncitarsus* possessed anisodactyl feet in the approximate size range of *P. feduccii*, the Twin Butte Member has been reliably dated as Upper Bridgerian (Br3) (Gunnell et al., 2009) and significantly post-dates the study interval. It is worth noting that the traces described herein differ significantly from traces attributed to modern flamingo foraging (Zonneveld et al., in press A). Flamingos filter feed on algae and invertebrates using lamellae in their bills to separate food from silt and mud (Bildstein et al., 1991; Glassom and Branch, 1997; Beauchamp, 2017). They commonly use their feet to stir up the sediment and potential food resources and filter-feed on the stirred-up material (Bildstein et al., 1991; Glassom and Branch, 1997; Beauchamp, 2017). Modern flamingo foraging produces linear, sinuous, and ring-shaped troughs produced through a process called foot paddling (Gihwala et al., 2017; El-Hacen et al., 2019; Salvador et al., 2022). To date, biogenic sedimentary structures due to bill-substrate interaction have not been reported (Zonneveld et al., in press A).

Presbyornis pervetus is a more likely candidate because it is well known from early Eocene strata in Utah and southwestern Wyoming, as well as Paleocene and early Eocene strata elsewhere (Wetmore, 1926; Olson and Feduccia, 1980a, b; Dyke, 2001; Kurochkin et al., 2002). A survey of birds reported from the Green River Formation (Grande, 1984, 2013) indicates that *P. pervetus* is the only waterbird known from the Green River Formation that is consistent with *Presbyornithiformipes* in terms of foot shape and size and with *Erevnoichnus* n. igen., *Ravdosichnus* n. igen., and *Aptosichnus* n. igen. in terms of bill shape and size. Bones and eggshell of *Presbyornis pervetus* are common along the ancient shorelines of Lake Gosiute, Fossil Lake, and Lake Uinta (Wetmore, 1926; McGrew and Feduccia, 1973; Feduccia and McGrew, 1974; Feduccia, 1976, 1978; Leggitt et al., 1998, 2007; Loewen and Buchheim, 1998; Cavigelli, 2008). These fossils commonly occur in association with gastropods, turtle bone, and crocodile bone in accumulations have been interpreted as paleostrandline deposits (McGrew and Feduccia, 1973; Feduccia and McGrew, 1974; Leggitt et al., 1998, 2007). The co-occurrence of egg material and abundant, commonly monospecific (in terms of the avian fauna) accumulations of *P. pervetus* bone suggest that these animals were gregarious and lived in large colonies (Feduccia and McGrew, 1974; Feduccia, 1976; Leggitt et al., 1998, 2007).

Presbyornis has been interpreted as a filter-feeder by some workers, based on the similarity of the *Presbyornis* bill to the bills of modern ducks (Olson and Feduccia, 1980a, b; Feduccia, 1995, 1999), the presence of lamellae on the inner surface of its beak (Ericson, 2000; Stidham, 2001), and the proportions of the beak relative to total skull length (Stidham, 2001). Olsen (2017) reconstructed the *Presbyornis* diet as seeds and small invertebrates based on comparison of the shape of the *Presbyornis* bill with those of modern and fossil anseriforms. Based on morphometric analyses of the skull and mandible, Li and Clarke (2016) argued that *Presbyornis* is most similar to the modern mixed feeder *Cygnus olor* Gmelin, 1789, and the specialized feeders *Polysticta* Eyton, 1836, and *Stictonetta* Reichenbach, 1853. Zweers and Vanden Berge

(1996) suggested that the morphology of the paraglossum indicates the possibility of piston-like tongue movements similar to that in modern ducks, consistent with filter feeding. Others noted that the quadrate bone is dissimilar to any modern filter-feeder and is consistent with primitive, non-filter-feeding galliforms (Elzanowski and Stidham, 2010; Elzanowski, 2014). Zelenkov and Stidham (2018), in a reanalysis of all available studies, concluded that effective filtration of very small food items was likely impossible, although filtration of detritus, along with larger food items, likely occurred.

Evidence from avian foraging traces in the study interval supports the Zelenekov and Stidham (2018) interpretation. *Erevnoichnus* n. igen., *Ravdosichnus* n. igen., and *Aptosichnus* n. igen. all preserve evidence of tactile foraging behaviors (Fig. 11) wherein birds probed, swept, and stirred the sediment, likely searching for small invertebrate prey such as mollusks and arthropods. These traces are not consistent with filter feeding in water or soupy sediment for microscopic organics, but rather are consistent with markings emplaced by birds using different tactile behaviors to feel with their bills for larger prey in the sediment (Zonneveld et al., in press A).

All foraging traces that occur in association with *Presbyornithiformipes feduccii* represent tactile foraging techniques. We acknowledge that some aspects of the skeletal architecture of *Presbyornis pervetus,* such as the occurrence of lamellae on the inner surface of its beak, suggest some limited filtering feeding (Olson and Feduccia, 1980a, b; Feduccia, 1995, 1999; Ericson, 2000; Stidham, 2001). However, if *Presbyornis pervetus* was indeed the tracemaker of *P. feduccii, Erevnoichnus blochi* n. igen. n. isp., *E. strimmena* n. igen. n. isp., *Ravdosichnus guntheri*, and *A. diatarachi* n. igen. n. isp. then, consistent with the interpretation by Zelenkov and Stidham (2018), it was also a tactile forager eating larger prey items as well.

Conclusions

Presbyornithiformipes feduccii from the early to middle Eocene Green River Formation in the Uinta Basin at Soldier Creek, Utah, occurs in association with several distinct traces attributed to waterbird foraging. Four ichnotaxa are named for these foraging traces: *Erevnoichnus blochi* n. igen. n. isp., *E. strimmena* n. igen. n. isp., *Ravdosichnus guntheri* n. igen. n. isp., and *Aptosichnus diatarachi* n. igen. n. isp.

Erevnoichnus blochi n. igen. n. isp. consists of a series of olive-shaped pits that occur in a sinuous trend and are joined by a thin, shallow marginal groove. Although similar traces previously have been interpreted as dabble marks, *E. blochi* n. igen. n. isp. is morphologically distinct from true dabble marks and records a distinct, sweeping/gaping behavior. *Erevnoichnus strimmena* n. igen. n. isp. is established for a series of closely spaced oval to arcuate en-echelon grooves produced by a forward probing motion by a waterbird searching for prey.

Ravdosichnus guntheri n. igen. n. isp. is established for simple elongate grooves where a waterbird dragged its bill through the sediment. This behavior likely records a bird searching for appropriate prey in an area where prey is highly suspected. *Aptosichnus diatarachi* n. igen. n. isp. is established

for a broad, shallow groove/trough characterized by sinuous margins and a complex, irregular fill. It is interpreted to record foraging by reverse scraping/ploughing.

All four behaviors are related. *Erevnoichnus blochi* n. igen. n. isp. and *Aptosichnus diatarachi* n. igen. n. isp. record endmember behaviors (sweep-gaping and bill-stirring, respectively). *Erevnoichnus strimmena* n. igen. n. isp. preserves aspects of both probing and reverse ploughing and is an intermediate behavior between probing and ploughing. Similarly, *Ravdosichnus guntheri* n. igen. n. isp. records long, simple pulls of the bill through the sediment, which is a behavior distinct from, but clearly related to bill-stirring. All traces occur associated with footprints and trackways assigned to *Presbyornithiformipes feduccii*, which was likely emplaced by the ancient waterbird *Presbyornis pervetus*. These traces clearly indicate that the trace-maker was a tactile forager, searching for moderate-size to large prey items buried in the substrate. If their inferred emplacement by *Presbyornis pervetus* is correct, then *P. pervetus* did not forage solely through filter-feeding but was also capable of tactile foraging for larger, infaunal prey.

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Declaration of competing interests

The authors declare no competing interests.

Data availability statement

Supplementary figures available from the Zenodo digital repository: https://zenodo.org/records/8378371

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