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AVIAN FORAGING ON AN INTERTIDAL MUDFLAT SUCCESSION IN THE EOCENE TANJUNG FORMATION, ASEM ASEM BASIN, SOUTH KALIMANTAN, INDONESIAN BORNEO

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ABSTRACT: **Moderately diverse trace fossil assemblages occur in the Eocene Tambak Member of the Tanjung Formation, in the Asem Asem Basin on the southern coast of South Kalimantan. These assemblages are fundamental for establishing depositional models and paleoecological reconstructions for southern Kalimantan during the Eocene and contribute substantially to the otherwise poorly documented fossil record of birds in Island Southeast Asia. Extensive forest cover has precluded previous ichnological analyses in the study area. The traces discussed herein were discovered in newly exposed outcrops in the basal part of the Wahana Baratama coal mine, on the Kalimantan coast of the Java Sea.**

The Tambak assemblage includes both vertebrate and invertebrate trace fossils. Invertebrate traces observed in this study include *Arenicolites*, *Cylindrichnus*, *Diplocraterion*, *Palaeophycus*, *Planolites*, *Psilonichnus*, *Siphonichnus*, *Skolithos*, *Thalassinoides*, *Taenidium*, and *Trichichnus*. Vertebrate-derived trace fossils include nine avian footprint ichnogenera (*Aquatilavipes*, *Archaeornithipus*, *Ardeipeda*, *Aviadactyla*, cf. *Avipeda*, cf. *Fuscinapeda*, cf. *Ludicharadripodiscus*, and two unnamed forms). A variety of shallow, circular to cylindrical pits and horizontal, singular to paired horizontal grooves preserved in concave epirelief are interpreted as avian feeding and foraging traces. These traces likely represent the activities of small to medium-sized shorebirds and waterbirds like those of living sandpipers, plovers, cranes, egrets, and herons. The pits and grooves are interpreted as foraging traces and occur interspersed with both avian trackways and invertebrate traces.

The trace fossils occur preferentially in heterolithic successions with lenticular to flaser bedding, herringbone ripple stratification, and common reactivation surfaces, indicating that the study interval was deposited in a tidally influenced setting. Avian trackways, desiccation cracks, and common rooting indicate that the succession was prone to both subaqueous inundation and periodic subaerial exposure. We infer that the Tambak mixed vertebrate-invertebrate trace fossil association occurred on channel-margin intertidal flats in a tide-influenced estuarine setting. The occurrence of a moderately diverse avian footprint and foraging trace assemblage in the Tambak Member of the Tanjung Formation illustrates that shorebirds and waterbirds have been using wetlands in what is now Kalimantan for their food resources since at least the late Eocene.

INTRODUCTION

Extant avian faunas of Island Southeast Asia have long been recognized as extraordinarily rich and diverse, with high levels of endemism and unique biogeographic patterns (Wallace 1863, 1869a, 1869b; Stattersfield et al. 1998; Jones et al. 2001, 2003; Ding et al. 2006; Cartensen and Olesen 2009; Meijer 2014). These faunas formed the basis for Wallace's original theories linking faunal distribution with the geological history of Indonesia (Wallace 1859, 1863). Although Wallace's later work bolstered these theories with data from other taxonomic groups, birds remained integral to his theories that the distribution of modern animals in Island Southeast Asia reflects the underlying geological history of the region (Wallace 1876, 1877, 1881; Satyana 1995b; Clode and O'Brien 2001). Although modern bird faunas are well known in Island Southeast Asia (e.g., Smythies 1960; Myers 2009; Phillipps 2012), the paleontology of avian faunas in this area remains poorly known (Meijer 2014). Avian body fossils are known from only seven sites and trace fossils from a single site (Lambrecht 1931; Weesie 1982; Wetmore 1940; Reis and Garong 2001; Stimpson 2009, 2012; Zaim et al. 2011; Zonneveld et al. 2011, 2012; Meijer 2014). Most of these fossils are Pleistocene to Holocene (Meijer 2014) with a single record of avian footprints from the Eocene Sawahlunto Formation in West Sumatra (Zaim et al. 2011; Zonneveld et al. 2011, 2012; Meijer 2014) and a single pelecaniform skeleton from the Eocene of Sumatra (Rich et al. 1986; Meijer 2014).

Recent fieldwork in the Eocene Tambak Member of the Tanjung Formation in the Asem Asem Basin in southern Kalimantan (Fig. 1) resulted in the discovery of a diverse and abundant avian ichnofauna. Bird tracks from the Tambak Member include a variety of anisodactyl tracks that occur in association with a diverse assemblage of invertebrate traces as well as numerous markings interpreted as foraging and feeding traces.

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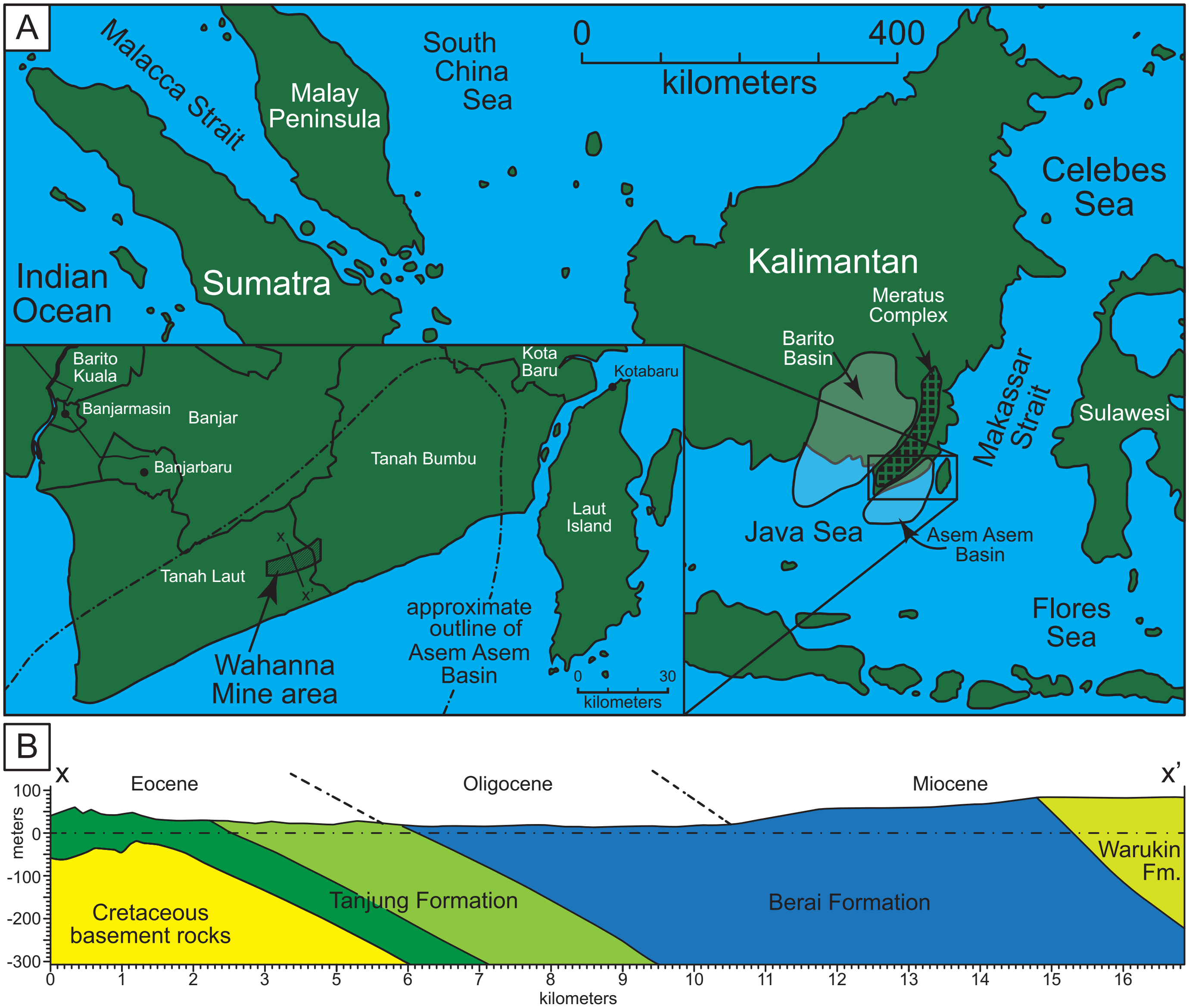


FIG. 1.—Location of the study area. **A**) Map showing the location of the study area on the coast of South Kalimantan and the locations of the Barito Basin, Asem Asem Basin and the Meratus accretionary complex. Inset map shows the location of the Wahana Mine area on the boundary between the Tanah Laut and Tanah Bumbu districts. **B**) Cross-section through the Wahana Mine area showing the regional dip to the southeast and the stratigraphic relationships between Mesozoic and Cenozoic formations in the study area.

This contribution describes and interprets these traces and discusses their importance. These traces provide insight into bird evolution in Island Southeast Asia and illustrate that shorebirds and waterbirds have been utilizing food resources in Kalimantan wetlands since at least the Eocene.

STUDY AREA

The study area is near the town of Satui, South Kalimantan, Indonesia, near the north shore of the Java Sea and west of the Makassar Strait (Fig. 1A). We focus on trace fossil assemblages that occur within Eocene strata of the Tanjung Formation. As with much of Kalimantan, tropical vegetation and weathering limits exposure of significant natural outcrop, and thus quarries, road cuts, and coal mines provide the best exposure to most sedimentary units. Outcrops observed in this study occur within the "super pit" of the Wahana Baratama Mine, a large open-cast coal mine approximately 85 kilometers east-southeast of the regional capital of Banjarmasin in Satui Regency.

GEOLOGICAL SETTING

The study area is located on the northern margin of the Asem Asem Basin, a narrow, northeast-trending Cenozoic basin on the southern coast of the province of South Kalimantan (Fig. 1A). The Asem Asem Basin is bounded to the northwest by the Meratus Mountains and to the east and southeast by the Paternoster Platform (van de Weerd and Armin 1992). The Meratus complex was initially formed during the Cretaceous as a result of a collision between two small continental blocks, although the nature of this collision remains poorly understood (Satyana 1995; Pubellier et al. 1999; Satyana and Armandita 2008). Similarities in Eocene and Oligocene stratigraphy between the Barito and Asem Asem basins suggest

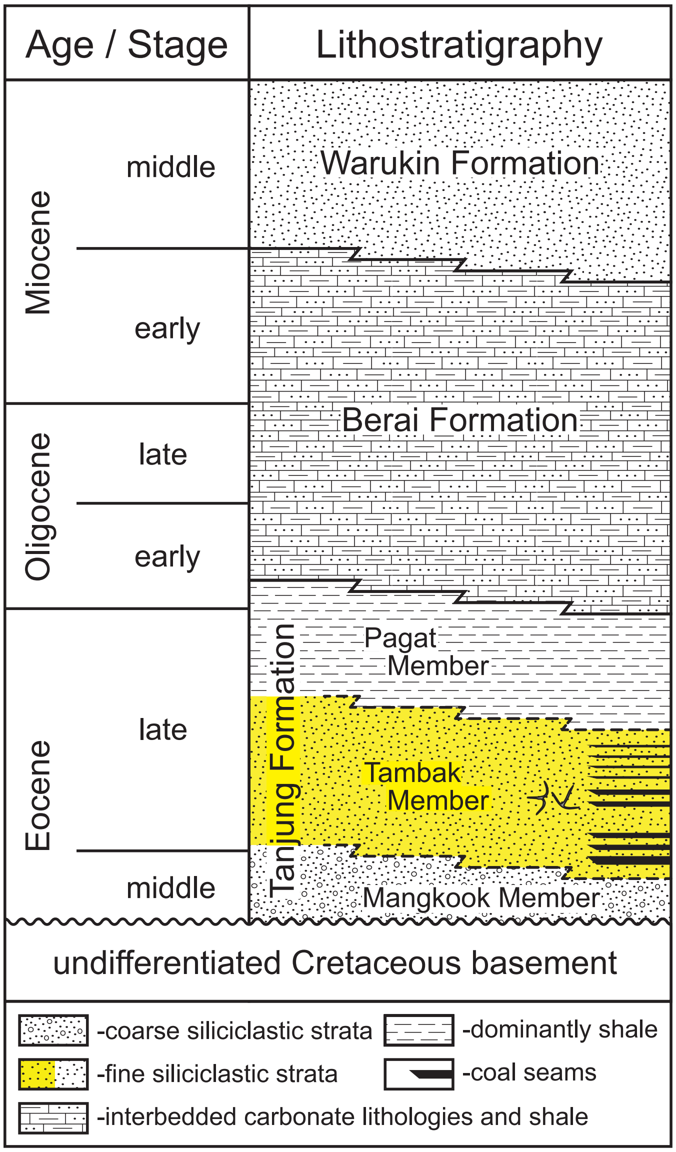


FIG. 2.—Paleogene and Neogene stratigraphy, southern Kalimantan, Indonesia. Only the Tambak and Pagat Members outcrop in the study area (after Witts et al. 2012b).

that the two basins formed from one larger basin that was separated in the Miocene by the final stage of uplift of the Meratus Mountains (Heryanto and Panggabean 2004; Mason et al. 1993; Hall 2012; Witts et al. 2012a, 2012b). The larger, older basin has been termed the 'proto-Barito' Basin (Witts et al. 2012a, 2012b). Pre 'proto-Barito' lithologies consist of Cretaceous sedimentary strata (Bon et al. 1996). Uplift and separation of the Barito and Asem Asem Basin resulted in a pronounced depositional dip to the south (Fig. 1B).

The middle Eocene to early Oligocene Tanjung Formation, recently subdivided into three lithostratigraphic members (Fig. 2), dominates the 'proto-Barito' basin fill (Witts et al. 2012b). Sediments of the basal Mangkook Member rest unconformably upon a pre-Eocene erosional surface (Satyana 1995b; Heryanto and Panggabean 2011; Witts et al. 2012b; Kristyarin et al. 2016). However, this interval is not exposed in the Wahana Mine, likely due to its dominantly coarse clastic composition and low proportion of coal.

The Mangkook Member is overlain by the Tambak Member (Fig. 2). The Tambak Member is overall finer grained than the Mangkook Member, has thicker, more abundant coals, and consists of intercalated coal beds, mudstone successions, and siltstone to very fine-grained sandstone beds with rare coarser units. The Pagat Member conformably overlies the Tambak Member (Zonneveld et al. in press A; Fig. 2). Within the study area, the Tambak Member comprises a mixed fluvial-marginal marine succession, whereas the Pagat Member is dominated by shallow marine and proximal offshore successions (Zonneveld et al. in press A). In the Barito Basin (sensu stricto) biostratigraphic data (based on palynomorphs and foraminifera) illustrates that the Mangkook Member correlates to the middle to upper Eocene, the Tambak Member to the late Eocene and the Pagat Member to the late Eocene to Early Oligocene (Witts et al. 2012b; Kristyarin et al. 2016). In the Asem Asem Basin study area the Mangkook Member is not exposed and the Tambak Member has not yet been dated. The Pagat Member has been dated using Larger Benthic Foraminifera as late Eocene, with the uppermost beds presumed to be Early Oligocene (Zonneveld et al. in press A).

Within the study area, Paleogene and Neogene strata dip gently to the southeast (Fig. 1B). The lowest sediments exposed at the Wahana Mine are included within the Tambak Member (sensu Witts et al. 2012b). The study interval occurs within this unit (Fig. 2). The Hanaman super pit in the Wahana Baratama coal mine is $\sim$ 4.5 km in length, 1.5 km in width, and $\sim$ 150 m in depth. A total of 21 coal seams and sub-seams have been identified. The study interval occurs between seams S6 and SM-1 (Fig. 3), which occurs midway through the section exposed in the mine. The bird tracks occur on heterolithic beds just below the S7 coal, which is one of the primary mining targets at Wahana.

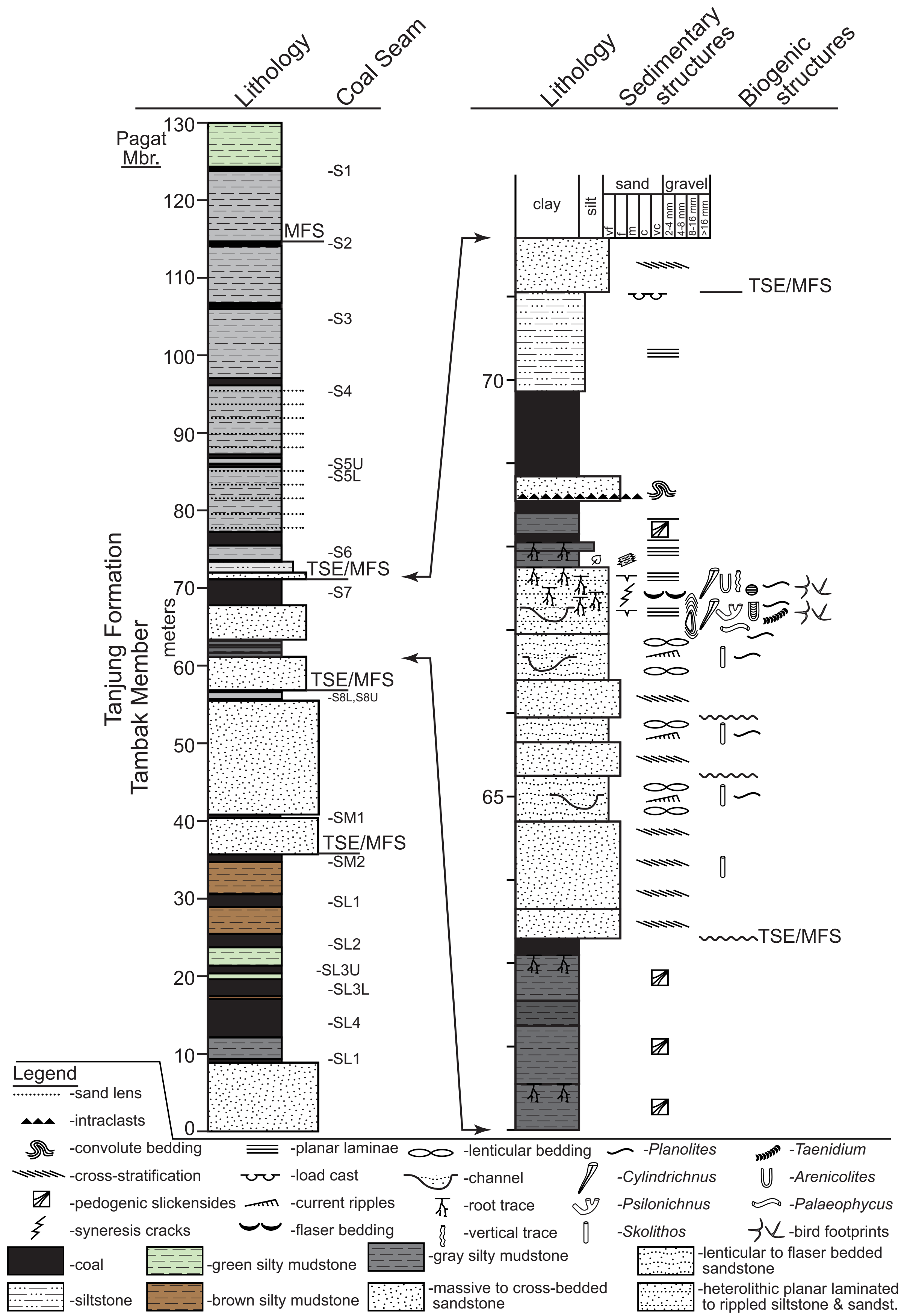
TERMINOLOGY

Most birds are digitigrade, with two or three toes pointing forward and one or two toes pointing backward (Fig. 4A). Bird legs are derived in that the proximals are fused with the tibia to form the tibiotarsus, and the distal and proximal metatarsals are fused to form the tarsometatarsus (Fig. 4A), which forms a third component to the leg (Proctor and Lynch 1993; Fig. 4A). Individual footprints may preserve only the distal portions of the pedal phalanges, or they may include the metatarsal pad where the phalanges meet (Fig. 4A). All avian footprints identified in the study area are anisodactyl. 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 (Fig. 4B–4D). Anisodactyl footprints may have all four digits on the same plane (sometimes called tetradactyl; Fig. 4B) or have a raised hallux that did not touch the substrate (referred to as incumbent anisodactyl or tridactyl; Fig. 4C). Incumbent anisodactyl tracks may preserve a distinct central metatarsal pad or may preserve only the distal portions of digits II through IV. A few footprints identified in the study area comprised semi-palmate anisodactyl footprints, with partial webbing between the three front toes (Fig. 4D).

Avian "tracks" refer to individual footprints, whereas "trackways" or "series" refer to two or more associated, typically sequential footprints. We use the words "mark" and "trace" in the broader, non-genetic sense (*sensu* Zonneveld et al. 2022). These terms become constrained when modifying phrases are added to them (e.g., claw mark, scratch mark, trace fossil, etc.). We most commonly use "trace" to denote a complete biogenic feature, whereas "mark" or "marking" denotes a component of a biogenic feature, such as a claw mark at the end of an avian footprint or a beak mark emplaced adjacent to a trackway.

METHODS

The stratigraphic succession in the study area has been measured by PT Wahana Baratama Mining personnel through analyses of core and sections


Lithology
Coal Seam
Lithology
Sedimentary structures
Biogenic structures
Pagat Mbr.
Tanjung Formation
Tambak Member
meters
130
120
110
100
90
80
70
60
50
40
30
20
10
0
-S1
MFS
-S2
-S3
-S4
-S5U
-S5L
-S6
TSE/MFS
-S7
TSE/MFS
-S8L,S8U
-SM1
TSE/MFS
-SM2
-SL1
-SL2
-SL3U
-SL3L
-SL4
-SL1
clay
silt
sand
gravel
vf
f
m
c
vc
2-4 mm
4-8 mm
8-16 mm
>16 mm
TSE/MFS
70
65
TSE/MFS
Legend
-sand lens
-intraclasts
-convolute bedding
-cross-stratification
-pedogenic slickensides
-syneresis cracks
-planar laminae
-load cast
-current ripples
-flaser bedding
-lenticular bedding
-channel
-root trace
-vertical trace
-Planolites
-Cylindrichnus
-Psilonichnus
-Skolithos
-Taenidium
-Arenicolites
-Palaeophycus
-bird footprints
-coal
-siltstone
-green silty mudstone
-brown silty mudstone
-gray silty mudstone
-massive to cross-bedded sandstone
-lenticular to flaser bedded sandstone
-heterolithic planar laminated to rippled siltstone & sandst.

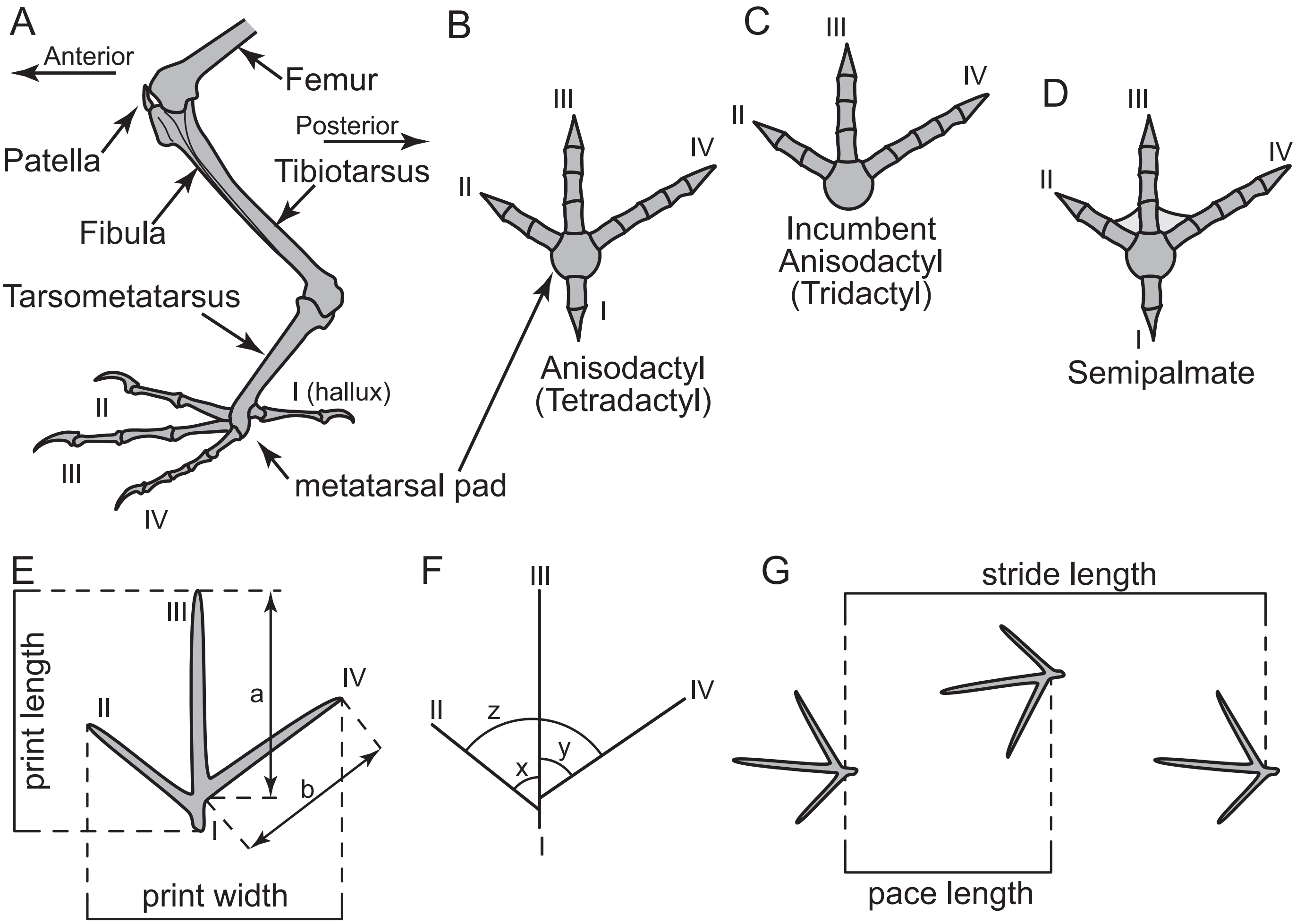


FIG. 4.—Terminology used in this manuscript. **A**) An avian leg and foot showing important bone elements. Anterior is towards the left; posterior to the right. Note that the foot illustrated exhibits a simple anisodactyl morphology. **B**) The toe arrangement in a simple anisodactyl foot. **C**) The toe arrangement in an incumbent anisodactyl foot. **D**) Sketch of a semipalmate anisodactyl foot. **E**) Footprint width and length in a recumbent anisodactyl footprint. Note that digit lengths (a, b) are measured from the center of the metatarsal pad to the tip of the digit. **F**) Divarication angles in an anisodactyl Footprint. Key: x = digit II–III divarication angle; y = digit III–IV divarication angle; z = digit II–IV divarication angle. **G**) Measurements of pace length and stride length in an anisodactyl footprint series.

exposed during mining operations. In addition, the entire Eocene succession exposed in the Wahana mine was assessed on the outcrop and a new composite section is presented here (Fig. 3). The interval with the bird footprints was measured at bed-scale detail and assessed for lateral lithofacies variability. The grain type, grain size, sorting, and the nature of physical and biogenic sedimentary structures were described, and samples obtained for further description and analyses. The thicknesses and contact types of all beds and laminae were assessed and traced over the full extent possible within the area of outcrop exposure. In all bioturbated beds, trace fossil assemblages were assessed for likely taxonomic identity, diversity, density, trace fossil completeness, and tiering relationships (Table 1). The identity of complex, three-dimensional invertebrate traces was ascertained by observing their exposed surfaces, followed by excavation with rock and chisel to assess their configuration within the outcrop. Although this resulted in destruction of the traces, we deemed this an acceptable method as the blocks were uncollectable and the study site was destined for destruction shortly after our work was completed.

Individual footprints are identified by the slab on which they occur (WAH01 through WAH06), the numbered trackway in which they occur (e.g., WAH01-01), the limb side with which the bird left the print (e.g., WAH01-01-L or R) and finally by the absolute placement of the footprint in the trackway (e.g., WAH01-01-L01; WAH01-01-R02). We chose not to number the sides in their own sequences since in several cases 'stutter steps' were observed, wherein the bird emplaced the same side twice in sequence. In other cases, a footprint in a series was absent due to overprinting by another trackway or damaged due to invertebrate bioturbation.

The maximum dimensions of each avian footprint, individual digit lengths, angles of divarication between preserved digits and, where measurable, pace length are provided (Tables 2, 3). Maximum footprint width and length (Fig. 4E, 4F) are provided for all complete footprints. Digit length was measured from the center of the metatarsal pad to the distal tip of the digit (Fig. 4E). Divarication angles are provided for the digits II–III, III–IV, and II–IV (Fig. 4F).

←

FIG. 3.—Vertical section through the Tambak member of the Tanjung Formation at Wahana Mine. Inset shows detail between coal seams 7 and 8, the horizon that produced the trace fossils discussed herein. Key: TSE = transgressive surface of erosion; MFS = marine flooding surface.

TABLE 1.—*Defining characteristics of invertebrate traces, avian footprint taxa and purported foraging traces identified in this study.*

Invertebrate Ichnotaxon	Description of Tambak traces	Interpretation
Arenicolites	Simple U-shaped tube without spreiten, tubes 1–4 mm in diameter, 9–22 mm deep.	Dwelling trace of a suspension-feeding polychaete or process-feeding amphipod.
Cylindrichnus	Elongate cone-shaped trace with concentric fill around a central core, 2–8 mm in diameter, 16–48 mm deep.	Dwelling trace of a suspension-feeding polychaete.
Diplocraterion	U-shaped tube with spreiten, tubes 2–8 mm in diameter, 8 to 43 mm deep	Dwelling trace of a suspension-feeding polychaete.
Palaeophycus	Unbranched, lined, cylindrical tubes, 3–12 mm in diameter.	Dwelling trace of a carnivorous polychaete.
Planolites	Unlined, unbranched, cylindrical tubes, 2–6 mm in diameter.	Trace of an infaunal deposit feeding worm
Psilonichnus	Cylindrical, commonly branching burrows with 1–3 openings, J and Y-shaped forms common, 25–50 mm in diameter, traces penetrate 15–42 mm deep.	Dwelling trace of brachyuran crustacean.
Siphonichnus	Vertical, unlined burrow, meniscate laminae, commonly in both concave and convex-downward orientations, laminae may be penetrated by a tube, 15 to 30 mm wide,140 to 280 mm long	Dwelling trace of an infaunal bivalve
Skolithos	Unlined to thinly lined, straight, vertical tubes, 2–6 mm in diameter, 10–40 mm deep	Dwelling trace of a wide range of invertebrates
Taenidium	Sinuous, unlined, horizontal, non-branching burrows with mildly arcuate meniscate backfill, 1.5 to 3 mm wide, <20–>60 mm long.	Deposit feeding trace of polychaetes or arthropod larvae
Thalassinoides	Complex three-dimensional branching network of cylindrical horizontal tubes connected to vertical shafts, 10–20 mm wide, 200–800 mm deep.	Dwelling trace of decapod crustaceans
Trichichnus	Thread-like cylindrical trace, primarily vertical, slightly sinuous, <0.5 mm in diameter, up to 20 mm long.	Combined feeding/dwelling trace of deposit feeding invertebrate/bacterial filaments
Footprint Ichnotaxon	**Description of Tambak traces**	**Key references**
Aquatilavipes group A	Incumbent anisodactyl, digit II–IV divarication > 100°, digit III longer than IV which is longer than II, digits II and III straight, angular 'heel'	Azuma et al. (2002); Currie (1981); Fiorillo et al. (2011); Lockley et al. (2015)
Aquatilavipes group B	Incumbent anisodactyl, digit II–IV divarication > 100°, digit III longer than IV which is longer than II, digits II and III arcuate, curved 'heel'	Zonneveld et al. (2011)
Archaeornithipus	Simple anisodactyl, (tetradactyl), slender toes, digit II–IV divarication < 150°, digit III longer than digits II and IV, digit I present but very short	Fuentes Vidarte (1996)
Ardeipeda	Simple anisodactyl, (tetradactyl), digit II–IV divarication < 140°, digit II–III and III–IV divarication similar, digit I shortest	Panin and Avram (1962) Sarjeant and Langston (1994) Kessler (1995); Lockley et al. (2007)
Aviadactyla	Incumbent anisodactyl, digit II–IV divarication > 95°, digits converge but do not connect, metatarsal pad impression not preserved	Sarjeant and Langston (1994); Sarjeant and Reynolds, 2001
cf. *Avipeda,*	Incumbent anisodactyl, digit II–IV divarication < 100°, digit III <25% longer than digits II and IV	Sarjeant and Langston (1994); McCrea and Sarjeant (2001); Abbassi et al. (2015)
cf. *Fuscinapeda*	Incumbent anisodactyl, pronounced metatarsal pad, digit II–IV divarication < 120°, digit III longest, digits II and IV ~ equal	Sarjeant and Langston (1994); McCrea and Sarjeant (2001); Krapovickas et al. (2009)
cf. *Ludicharadripodiscus*	Simple anisodactyl-semipalmate, digit II–IV divarication < 110–135°, short hallux, partial webbing between digits II and III and between III and IV.	Ellenberger (1980); McCrea and Sarjeant (2001)
Unnamed form A	Simple anisodactyl, digit II–IV divarication ~40°, digits converge but do not connect, metatarsal pad impression not preserved, digit III longest, digit I shortest	-
Unnamed form B	Incumbent anisodactyl semipalmate, divarication ~120°, hallux absent, pronounced metatarsal pad, partial webbing between digits II and III and between III and IV.	-
Inferred foraging traces	**Description of Tambak traces**	**Interpretation**
Type I	Circular to ovoid pits and divots, 2–10 mm in diameter and 1–8 mm deep, some circular forms are similar to the ichnotaxon *Conichnus* but have pointier terminae	Peck marks or probe marks
Type II	V-shaped gouges, usually with a deeper end and a shallower end, symmetrical and V-shaped in cross-sectional profile	Peck marks or appendage scratch marks
Type IIIA	Single groove, 1–2 mm deep, 1–7 mm wide	Sweep mark
Type IIIB	Paired grooves, 1–2 mm deep, 1–2 mm wide	Sweep mark
Type IV	Strongly dimpled bedding plane	Peck marks

Pace length was estimated by measuring the distance between the metatarsal pad centers in adjacent footprints and is reported for the foremost footprint of the pair (Fig. 4G, Tables 2, 3). Other landmarks (such as the front or back of the metatarsal pad or the tip of digit III) were deemed unreliable because these points were often ambiguous or obscured due to drag marks or slippage on a wet substrate. Where the center of the metatarsal pad could not be assessed, an equivalent point was selected from adjacent footprints to use as a landmark (e.g., toe tip to toe tip). Stride length was estimated by measuring two identical landmarks (preferentially the metatarsal pad) on two sequential footprints on the same side (Fig. 4G).

Purported foraging marks were measured, sketched and photographed in the field. Where possible, samples were observed, both in bedding plane aspect as well as in cross-sectional view on the edge of slabs. In several cases these traces occurred on fissile shale or siltstone beds and the traces

Table 2.—*Measurements of footprints on slab WAH01.*

Print ID	Print width (mm)	Print length (mm)	Digit I length (mm)	Digit II length (mm)	Digit III length (mm)	Digit IV length (mm)	Stride length (cm)	Divarication II–III	Divarication III–IV	Total divarication
1-1-R1	56	41	-	27	30	271	138	53°	85°	138°
1-1-L1	50	34	-	24	28	23	126	63°	78°	151°
1-1-R2	55	41	-	29	31	23	140	50°	81°	131°
1-1-L2	-	-	-	18	28	-	112	-	70°	-
1-1-R3	55	40	-	20	31	20	134	49°	84°	133°
1-1-L3	55	39	-	23	29	25	130	72°	65°	137°
1-1-R4	-	-	-	-	-	-	115	-	-	-
1-1-L4	53	35	-	16	28	24	112	73°	57°	130°
1-1-R5	52	44	-	26	40	22	115	74°	46°	130°
1-1-L5	46	41	-	24	35	18	120	55°	52°	107°
1-1-R6	52	-	-	-	-	-	130	-	-	-
1-1-L6	59	-	-	-	-	-	125	-	-	-
1-1-R7	-	-	-	16	25	-	-	-	-	-
1-2-L-1	29	25	9	12	9	9	50	102°	55°	157°
1-2-R-2	29	30	8	12	13	9	52	52°	73°	125°
1-2-L-3	35	28	7	10	11	10	43	92°	66°	158°
1-2-R-4	31	31	6	13	15	11	50	68°	106°	174°
1-2-L-5	32	36	7	15	19	13		70°	76°	146°
1-2-R-6	22	-	9	10	-	8		-	-	
1-2-L-6	36	35	10	16	15	13	55	62°	72°	134°
1-2-R-7	36	34	9	12	19	15	59	83°	53°	136°
1-2-L-8	29	31	5	10	19	13	40	76°	53°	129°
1-2-R-9	32	33	9	13	20	14	59	64°	58°	122°
1-2-L-10	36	32	4	15	18	15	71	51°	72°	123°
1-2-R-11	34	32	8	17	17	9	120	67°	61°	128°
1-2-R-12	31	31	4	14	17	11	77	75°	57°	132°
1-2-L13	29	22	8	11	11	14	50	80°	74°	154°
1-2-R14	34	34	9	17	17	17	63	52°	83°	135°
1-2-L15	35	24	4	14	13	13	-	80°	67°	147°
1-3-R1	32	34	-	18	34	23	75	61°	50°	111°
1-3-L1	31	36	-	19	36	21	84	81°	46°	127°
1-3-R2	29	35	-	17	35	19	87	55°	65°	120°
1-3-L2	36	-	-	20	-	20	145	73°	57°	130°
1-3-R3	36	31	-	20	-	17	64	54°	90°	144°
1-3-L3	28	-	-	20	-	20	18	60°	39°	99°
1-3-R4	35	-	-	18	-	20	77	66°	61°	127°
1-3-L4	-	28	-	-	20	19	54	76°	66°	142°
1-3-R5	-	28	-	-	18	21	78	44°	54°	98°
1-3-L5	35	-	-	19	-	22	80	81°	44°	125°
	-	23	-	-	18	21	91	38°	62°	100°
1-3-L6	32	-	-	19	-	23	11	86°	38°	124°
1-3-R7	-	-	-	21	-	-	-	48°	-	-
1-4-L-1	25	17	-	14	8	8	78	59°	67°	126°
1-4-R-2	24	20	-	10	17	8	60	70°	56°	126°
1-4-L3	26	25	-	14	20	9	85	69°	56°	125°
1-4-R4	23	-	-	10	5	9	64	59°	63°	122°
1-4-L5	26	17	-	12	13	10	70	62°	62°	124°
1-4-R6	24	13	-	9	10	12	62	74°	54°	128°
1-4-L7	21	21	-	10	15	10	56	55°	59°	114°
1-4-L8	-	-	-	-	6	11	88	61°	-	-
1-4-R9	19	29	-	12	13	15	66	68°	54°	122°
1-4-L10	-	-	-	11	-	-	65	-	-	-
1-4-L11	-	25	-	-	19	10	71	-	56°	-
1-4-R-12	28	11	-	11	5	13	68	77°	58°	135°
1-4-L-13	27	14	-	13	13	9	85	83°	61°	144°
1-4-R-14	29	12	-	9	9	14	80	76°	47°	123°
1-4-L-15	31	18	-	13	14	16	70	82°	67°	149°
1-4-R-16	-	-	-	15	16	11	68	78°	47°	125°
1-4-L-17	28	-	-	16	-	13	-	-	-	135°
1-5-R1	22	17	-	-	14	12	56	66°	60°	126°
1-5-L1	24	14	-	-	13	11	42	65°	71°	136°
1-5-R2	19	12	-	-	12	14	52	60°	64°	124°
1-5-L2	23	19	-	-	19	16	39	57°	53°	110°

TABLE 2. *Continued.*

Print ID	Print width (mm)	Print length (mm)	Digit I length (mm)	Digit II length (mm)	Digit III length (mm)	Digit IV length (mm)	Stride length (cm)	Divarication II–III	Divarication III–IV	Total divarication
1-5-R3	30	18	-	-	18	15	53	72°	55°	127°
1-5-L3	31	17	-	-	15	15	-	73°	58°	131°
1-6-R1	2.7	-	-	18	18	11	96	84°	73°	157°
1-6-L1	2.3	2.9	9	12	20	11	79	72°	72°	144°
1-6-R2	2.8	3.0	13	16	19	12	50	91°	68°	159°
1-6-L2	2.8	2.6	9	14	17	14	-	62°	77°	139°
1-7-R2	20	21	-	23	18	21	48	24°	25°	49°
1-7-L2	29	15	-	16	16	18	47	-	-	-
1-7-L3	18	25	-	26	19	21	67	19°	19°	38°
1-7-R3	15	19	-	18	-	18	59	-	-	47°
1-7-L4	20	19	-	14	17	12	42	-	-	-
1-7-R4	28	26	-	25	23	25	-	29°	29°	58°
1-x-i	18	15	-	11	13	13	-	46°	40°	86°
1-x-ii	27	22	-	12	17	15	-	67°	34°	101°
1-x-iii	28	13	-	11	7	10	-	60°	64°	124°
1-x-iv	31	22	-	14	19	13	-	63°	57°	120°
1-x-v	32	20	-	13	16	16	-	69°	65°	134°
1-x-vi	33	23	-	17	20	17	-	58°	55°	113°
1-x-vii	30	22	-	16	21	17	-	61°	59°	120°
1-x-viii	28	20	-	11	17	15	-	56°	64°	120°
1-x-ix	30	24	-	15	20	14	-	55°	81°	136°
1-x-x	34	33	14	20	18	14	-	108°	81°	190°
1-x-xi	15	48	11	21	38	21	-	21°	18°	39°

were examined by carefully separating laminae and measuring the observable dimensions on each piece. In this way the dimensions of these traces and their absolute depth into the substrate could be ascertained.

Figures and tables in this manuscript refer to tracks associated with each of these slabs. Although avian track horizons were observed to be laterally extensive at Wahana Baratama Mine, the tracks studied herein are associated with six main slabs (WAH01-06) that were selected due to preservation and safe accessibility (e.g., several trackways observed in actively worked parts of the mine could not be safely accessed). Isolated footprints (i.e., those not clearly associated with a series or trackway) are identified by the slab they are on and the identifier X (e.g., WAH01-X).

Tracks, trackways, and associated foraging trace fossils and invertebrate trace fossils were photographed and sketched in the field. All original, unaltered digital images obtained in this study (both figured and not figured) have been incorporated into the University of Alberta Ichnology collections. Lithology samples, some of which preserve tracks and partial trackways were collected and incorporated into the University of Alberta Ichnology collections. The larger trackways could not be collected due to logistical constraints in a remote field site. Several slabs that could be moved were placed in front of the PT Wahana Baratama Mining field office, where they currently remain. Trace fossils attributed to fossil birds and their foraging and feeding behavior were compared with material that has been observed, cast, and photographed on intertidal flats and lake margins: Craig Bay, Vancouver Island, Canada; Frasier River Delta, Canada; Wahana Beach, Kalimantan, Indonesia; Lake Manyara, Tanzania; Antelope Island, Great Salt Lake, Utah and Hartney Bay, Alaska (Zonneveld et al. in press B).

TABLE 3.—*Measurements of footprints on slab WAH02.*

Print ID	Print width (mm)	Track length (mm)	Digit II length (mm)	Digit III length (mm)	Digit IV length (mm)	Stride length (cm)	Divarication II–III	Divarication III–IV	Total divarication (II–IV)
2-x-i	-	22	-	21	19	-	66°	59°	125°
2-1-L1	31	22	13	21	14	6.4	71°	61°	133°
2-1-R1	31	21	16	19	15	6.1	59°	72°	132°
2-1-L2	33	21	13	18	21	2.8	82°	53°	136°
2-1-R2	32	22	17	21	16	6.2	64°	72°	136°
2-1-L3	32	24	17	19	16	6.1	73°	72°	146°
2-1-R3	33	26	17	19	14	6.8	51°	81°	132°
2-1-L4	35	27	18	22	15	6.6	75°	60°	136°
2-1-R4	29	31	13	25	14	7.6	58°	70°	128°
2-1-L5	36	33	18	27	15	-	75°	54°	129°
2-2-L1	67	46	26	37	26	13.2	62°	65°	127°
2-2-R1	62	46	31	39	21	13.5	58°	84°	142°
2-2-L2	65	40	26	38	32	13.0	70°	64°	134°
2-2-R2	58	46	26	36	28	14.1	51°	78°	129°
2-2-L3	55	44	32	32	33	-	65°	69°	134°

RESULTS

Numerous invertebrate traces occur in association with the avian footprints and trackways. The invertebrate traces were described and identified to ichnogenus level (Table 1). These include *Arenicolites*, *Cylindrichnus*, *Diplocraterion*, *Palaeophycus*, *Planolites*, *Psilonichnus*, *Siphonichnus*, *Skolithos*, *Taenidium*, *Thalassinoides*, and *Trichichnus*. Root traces, commonly with carbonized cores, are also common on most rock slabs analyzed in this study, and poorly preserved leaf compressions, under separate study, are common in some associated fine-grained strata.

Avian ichnotaxa includes seven named ichnotaxa and two undescribed forms. These include *Aquatilavipes*, *Archaeornithipus*, *Ardeipeda*, *Aviadactyla*, cf. *Avipeda*, cf. *Fuscinapeda*, cf. *Ludicharadipodiscus*, a narrow heron-like print, and an anisodactyl, semipalmate print. Descriptions of these traces are provided (Table 1) and their diagnostic parameters (size, divarication, etc.) are also provided (Tables 2–6). A number of other biogenic features occur on trackway slabs and are closely associated with the tracks themselves. These are discussed below.

The avian trace fossils discussed herein were observed in an approximately meter-thick bed that occurs 65 meters above the base of the section. The bird track interval occurs in a siltstone to very fine-grained sandstone-dominated unit (63.3 to 67.7 m; Fig. 3) bound by intercalated coal and carbonaceous mudstone. This unit consists of fine-grained sandstone at its base and is intercalated with very fine-grained sandstone and siltstone in its upper half (Figs. 3, 5).

A sharp, erosional contact at 63.3 meters heralds an abrupt shift from low-grade coal and carbonaceous mudstone with numerous pedogenic slickensides to well-sorted, massive to cross-stratified fine-grained sandstone (Figs. 3, 5). This grades into a thin (55 cm) interval of heterolithic, intercalated, lenticular to wavy-bedded siltstone/silty mudstone and very fine-grained sandstone (Fig. 6A). Bidirectional ripples (herringbone cross lamination) and reactivation surfaces are common in fine-grained and very fine-grained sandstone beds. Load-casting is at the contact between silty mudstone/siltstone and overlying current-rippled sandstone units in the lenticular to wavy bedded facies (Fig. 6A). Additional sharp erosional surfaces occur at 65.3 m and at 66.0 meters, both characterized by cross-stratified, fine-grained sandstone grading up into heterolithic, intercalated, lenticular-bedded siltstone and very fine-grained sandstone (Fig. 3).

The lower heterolithic horizons are characterized by low-diversity trace fossil assemblages consisting of *Skolithos* and *Planolites* (Fig. 3). The upper heterolithic succession has a moderately diversity trace fossil assemblage consisting of *Arenicolites*, *Cylindrichnus Diplocraterion*, *Palaeophycus*, *Planolites*, *Psilonichnus*, *Siphonichnus*, *Skolithos*, *Taenidium*, *Thalassinoides* and *Trichichnus* (Figs. 3, 6B–6F). Five of these ichnogenera are vertical forms and appeared as concentric circles (*Cylindrichnus*), solitary dots (*Skolithos*), paired dots (*Arenicolites*) or large, circular to ovoid traces (*Psilonichnus* and *Thalassinoides*) on the bedding planes. These trace fossils were observed in vertical view on slab edges, and in three-dimensional aspect on broken blocks confirming their ichnogeneric identification. Many of the larger traces, particularly *Psilonichnus* and *Thalassinoides*, have a passive fill, characterized by alternating mud and sand laminae.

Root traces are common, particularly in the upper half of the heterolithic succession (Figs. 3, 6D, 6E). Wrinkle marks occur on many bedding planes in the heterolithic facies. Avian trace fossils, including avian tracks, trackways and foraging traces are common in the upper meter of the heterolithic succession (Fig. 3). The heterolithic succession is characterized by a broad suite of physical sedimentary structures, including planar laminae, lenticular bedding, wavy bedding and flaser bedding, small-scale load casting, current ripples, small channel-like features/scour features, desiccation cracks (which commonly, but not always, emanate from individual avian footprints), and syneresis cracks.

A total of 12 trackways, ranging in length from three to 17 tracks each, and 45 individual tracks were studied in detail (over a total of 148 individual tracks). Pertinent measurements of avian trace fossils discussed herein are provided (Tables 2–6). The Tambak avian ichnofauna consists of approximately eight ichnospecies in seven named ichnogenera (*Aquatilavipes*, *Archaeornithipus*, *Ardeipeda*, *Aviadactyla*, cf. *Avipeda*, cf. *Fuscinapeda*, cf. *Ludicharadripodiscus*) and two unnamed forms (Fig. 7, Table 1). It is uncertain how many biological species these traces represent, however within-ichnotaxa size distributions and morphological variance suggest that these traces represent more diversity than a simple count of ichnotaxa would indicate.

Avian traces occur on five rock slabs (WAH 01-05; discussed below). Only two footprints of unnamed ichnotaxon 1 and one footprint of unnamed ichnotaxon 2 were identified and, although photographed and sketched, the specimens were not collectable. Thus, these traces are not formally named at this time. Table 1 provides a synopsis of the ichnotaxa and their defining characteristics, as identified in this study. All slabs studied preserved numerous invertebrate trace fossils as well as abundant traces interpreted to represent avian foraging and feeding (Figs. 6, 8–15). Solitary and paired grooves, V-shaped scratch marks, and circular to subcircular/oval, commonly conical solitary, paired and clustered pits were observed proximal to many trackways and occurred on every slab examined in this project.

Distribution of Traces on Sample WAH01

Sample WAH01 contains seven distinct trackways (trackways WAH01-1 to WAH01-7) and 11 isolated tracks, for a total of 86 individual footprints preserved in concave epirelief on a bedding plane surface (Fig. 8, Table 2). The trackways are primarily preserved in concave epirelief. They cross over each other in several areas and include both surface tracks and near-surface undertracks (Fig. 8). Trackways on this slab include *Aquatilavipes*, *Ardeipeda*, *Aviadactyla*, cf. *Fuscinapeda*, and an unnamed ichnotaxon (Figs. 8, 9, Table 2). Some trackways were emplaced in water-saturated sediment, whereas others were emplaced in damp, consolidated sediment, as is illustrated in detail preserved in individual footprints and trackways.

Trackway WAH01-1 comprises a series of 13 comparably large, incumbent anisodactyl footprints assigned to *Aquatilavipes* (Fig. 8). The first three footprints in the series exhibit a distinct digit III drag mark behind the foot pad, whereas the last three footprints in the series are less distinctly preserved, with an indistinct tarsal pad and poorly preserved proximal pedal phalange impressions. Overall divarication between digits II and IV in trackway WAH01-1 ranges from 130° to 151° and the stride length ranges from 112 to 140 mm (Table 2).

Trackway WAH01-2 comprises 16 footprints of a small incumbent anisodactyl bird that walked in a semicircle across the top of the slab (Fig. 8). These footprints are assigned to *Ardeipeda*. There is a missing left footprint between footprints 11 and 12, which was overprinted by footprint 3 of trackway WAH01-1 (Fig. 8). This trackway is characterized by several toe drags. Evidence of lateral shifting of digit 3 occurs on footprints 2-1, 2-8, and 2-13. Overall divarication between digits II and IV in trackway WAH01-2 ranges from 122° to 151°, and the stride length ranges from 40 to 94 mm (not including the 120 mm gap between footprints 2-R11 and 2-R12 where a left footprint is not preserved; Table 2).

Trackways WAH01-3 through WAH01-5 consist of trackways made by small to moderate-sized elevated anisodactyl birds. These trackways are all consistent with *Aquatilavipes.* Trackway WAH01-3 exhibits high variability in stride length (11–145 mm) as well as digit III toe drag marks preserved with nearly every footprint (Figs. 8, 9, Table 2). The first few footprints in this series are preserved in excellent detail (3 on the preservation scale proposed by Marchetti et al. 2019), whereas the last few are more poorly defined (1–2 on the Marchetti scale). Lateral shifting of the


A
coal S7
TSE/MFS
coal S8l
B
bird track interval
coal S7
TSE/MFS

digit III impression occurs in the third footprint in the succession. Pace length is highly variable, ranging from 11 mm to 145 mm, with a stutter-step occurring with the last two footprints in the series (Fig. 9). Most of the individual footprints are connected by digit III toe drag marks (Figs. 8, 9). Long, linear groove marks, both solitary and paired, occur adjacent to this trackway (Fig. 9). Digit II–IV divarication angles are highly variable, ranging from 99° to 144° (Table 2).

Trackway WAH01-4 (Fig. 8) consists of 17 individual footprints, the last few of which preserve a pronounced digit III drag mark. WAH01-4 is tentatively assigned to cf. *Aquatilavipes* based on its divarication angle. The WAH01-4 stride length is variable, albeit more consistent than that of WAH01-3, ranging from 56 to 88 mm (Fig. 8, Table 2). Preservation and morphology of these footprints is quite variable, with several only partially preserved, and thus not usable for size assessment. Digit II–IV divarication angles are relatively consistent, with all but two ranging in between 124° and 128°. Trackway WAH01-5 consists of six moderately preserved footprints with stride length ranging from 39 to 56 mm (Table 2). In several of the footprints, the central toe pad is absent. WAH01-5 exhibits digit II to digit IV divarication angles of approximately 126° (110° to 136°).

Trackway WAH01-6 (Fig. 8) consists of four moderate-sized anisodactyl footprints with a distinct hallux, a stride length ranging from 50 to 96 mm, and digit II to IV divarication angles ranging between 139° and 157°. These footprints are consistent with a small species of *Archaeornithipus*. The footprint margins are crisp and well-defined, with no preserved toe drag-marks between individual footprints.

Trackway WAH01-7 (Fig. 8) consists of nine, small elevated anisodactyl, semipalmate footprints with digit II to IV divarication angles between 42° and 95° (average of 64°) and a stride length of 42 to 67 mm. Trace widths and length-to-width ratios are unusually variable, and trace margins are typically poorly defined. This trackway may be associated with some of the footprints included within the isolated footprint category.

Eleven isolated footprints were also noted on WAH01. Most of the isolated footprints were small to mid-sized tridactyl footprints. Nine of these footprints are tridactyl (elevated anisodactyl) footprints consistent with cf. *Avipeda*, *Aquatilavipes*, *Aviadactyla*, and *Fuscinipeda* (Fig. 8). One footprint (1-x-x) (Fig. 8) consists of a moderate-sized incumbent anisodactyl footprint, and the final footprint (1-x-xi) (Fig. 8) consists of a moderate sized anisodactyl footprint with a very narrow digit II–IV divarication angle and an unusually elongated hallux.

Sample WAH01 is characterized by abundant invertebrate trace fossils (Figs. 8, 9). *Cylindrichnus*, *Skolithos*, and *Trichichnus* are exceptionally abundant, with 30 to 60 burrow openings per decimeter^2. *Diplocraterion* and *Psilonichnus* openings occur on the bedding plane in abundances of approximately 2–3 each per meter^2. Abundant *Palaeophycus* and *Planolites* are apparent in cross-sectional profile on the edges of WAH01. Horizontal and vertical root traces, most with carbon cores, are abundant. Wrinkle structures, attributed to sediment binding by cyanobacteria, also occur on slab WAH01.

Numerous, elongate (8 to 70 mm), slender (0.5 to 2 mm), solitary and paired grooves (Fig. 9) were found near several trackways, such as WAH01-03 (an *Ardeipeda* trackway). Small (2–5 mm wide, up to 5 mm deep), cone-shaped divots and short (2–8 mm), arrow-shaped/V-shaped grooves or gouges were found adjacent to many of the smaller *Aquatilavipes* traces.

Distribution of Traces on Sample WAH02

Sample WAH02 preserves two distinct trackways. Trackway WAH02-01 includes 10 footprints, and WAH02-02 includes five footprints (Table 3, Fig. 10). The traces are preserved in convex hyporelief on the sole surface of a siltstone slab. Trackway WAH02-1 consists of small (averaging 32 mm × 25 mm) elevated anisodactyl footprints that are wider than they are long and are characterized by moderate digit II–IV divarication angles (averaging ∼ 134°). A distinct heel is preserved in most footprints, and thus, they are assigned to cf. *Fuscinapeda*. Several individual footprints record a lateral shift in the digit III impression (Fig. 10C, 10D), and the trackway records a somewhat meandering path (based on the shifts in digit III orientation between footprints on each side).

Trackway WAH02-02 consists of moderately large (averaging 61 mm × 44 mm) anisodactyl footprints that are wider than they are long and characterized by moderate digit II–IV divarication angles (averaging ∼ 136°) (Fig. 10, Table 3). These traces have been assigned to *Aquatilavipes* (species group A) (Figs. 7, 10). The tracks are approximately evenly spaced and curve slightly across the slab (Fig. 10A, 10B). Detailed preservation of foot morphology of both WAH01-02 (Fig. 10D) and WAH02-02 (Fig. 10E) show that the surface of the slab is near the horizon of emplacement.

Long (20 to 185 mm), slender (< 2 mm), linear to gently curved groove marks, both solitary and paired, occur adjacent to both trackways on WAH02 (Figs. 10B, 11A, 11B). These groove marks occur both oblique to and parallel with the trackways with which they are associated. Solitary and clustered of small (2–8 mm wide), cone-shaped holes also occur. As with all the studied slabs with bird footprints, WAH02 is characterized by numerous, small invertebrate trace fossils including *Cylindrichnus*, *Arenicolites*, and *Skolithos* (Table 3).

Distribution of Traces on Sample WAH03

Sample WAH03 (Fig. 12) preserves one distinct trackway and two isolated footprints. The traces are preserved in convex hyporelief on the sole surface of a siltstone slab and comprise undertrack preservation. The trackway includes five, approximately sub-equally spaced incumbent anisodactyl footprints assigned to *Ardeipeda* sp. Despite full preservation of all four toes, the footprints are wider than they are long. The digit II–IV divarication is moderate (∼ 127°–135°) (Table 4). One of the two isolated footprints is identical in shape, size, and morphology to the footprints in WAH03-01 whereas the other (WAH03-x-x1) is a wide, elevated anisodactyl underprint with a moderately high digit II–IV divarication angle.

In addition to numerous invertebrate trace fossils, such as *Arenicolites*, *Cylindrichnus*, *Diplocraterion*, *Skolithos*, and *Taenidium*, numerous cone-shaped holes and groove marks are preserved on the bedding plane (Fig. 12).

Distribution of Traces on Sample WAH04

Sample WAH04 comprises a series of fragments from a large slab (100 cm × 100 cm). The slab is an underprint bedding plane, with most footprints infilled with sediment. The traces Avian traces cross back and forth over it, with numerous footprints cross-cutting and overprinting each other (Figs. 13, 14). The fragment, illustrated in Figure 13 and summarized in Table 5, consists of three moderate-sized anisodactyl underprints with a reduced, albeit distinct, hallux (Fig. 13). This bedding plane is characterized by numerous conical pits interpreted as probe marks, several V-shaped grooves interpreted as peck marks, and elongate grooves (Fig. 13). The surface is characterized by extensive dimpling. Horizontal trace fossils consistent with *Taenidium*, concentric tubes assigned to *Cylindrichnus*, vertical shafts assigned *Skolithos*, branching vertical shafts assigned to *Thalassinoides*, and numerous root traces with carbonaceous cores are common on this surface (Fig. 13).

←
FIG. 5.—Outcrop photographs of the Wahana mines section between coals S8 and S7. **A**) Complete section, from coal S8 and coal 7 to higher in the section. The 63.3 meter coplanar transgressive surface of erosion/marine flooding surface is identified. **B**) Detail of the upper part of the bird track section. The 63.3 meter coplanar transgressive surface of erosion/marine flooding surface and the main bird track interval are identified.

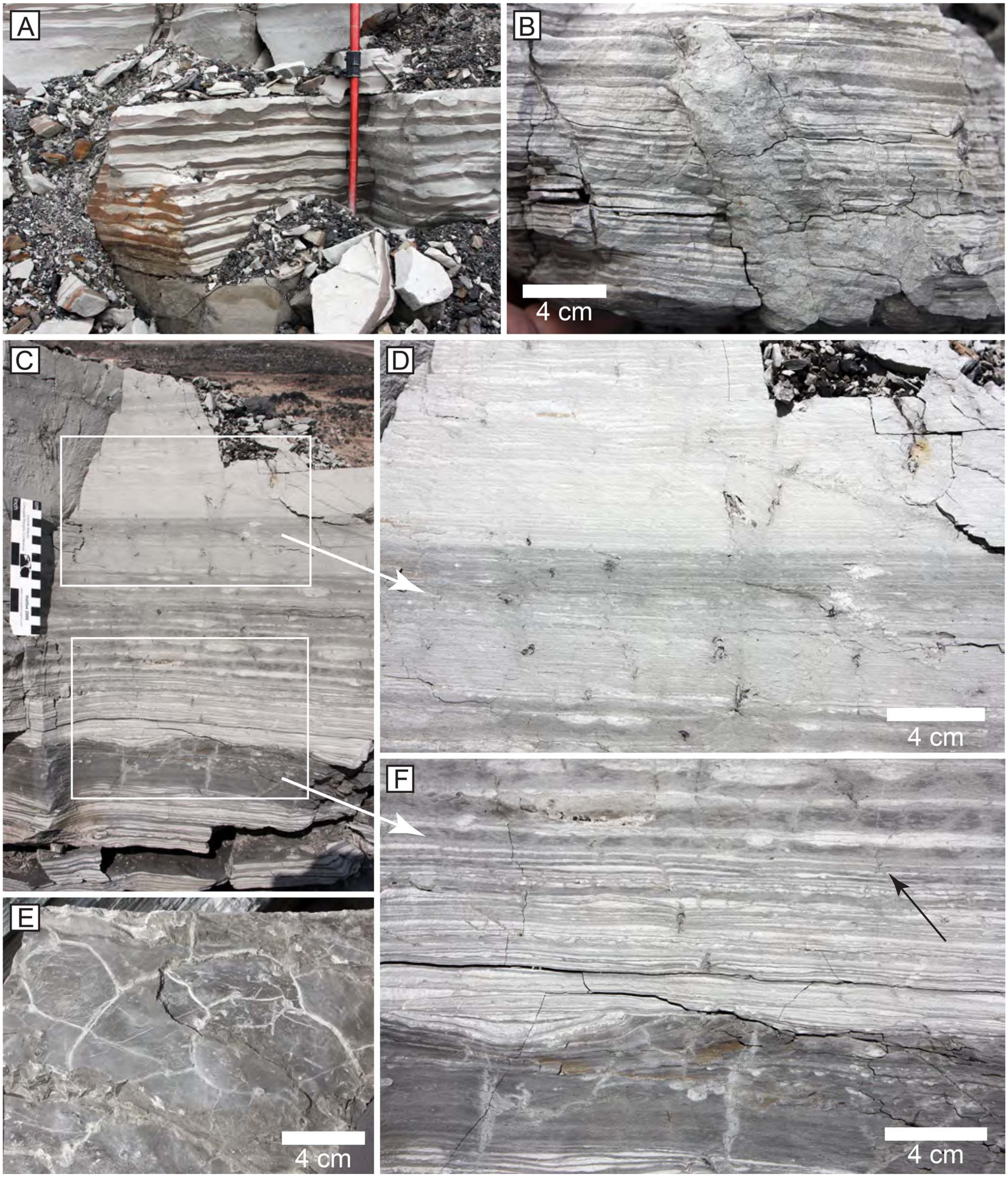


FIG. 6.—Lithology photographs through the study interval. **A**) Lenticular to wavy bedded sandstone, siltstone and silty shale deposited in an intertidal flat setting. **B**) Large *Psilonichnus* penetrating through a finely interlaminated siltstone and sandstone succession. Although the photograph illustrates only a simple, unlined, vertical shaft, excavation of this trace revealed a horizontal component attached to an adjacent shaft. **C**) Detailed shot through the bird track horizon. The base of the bedset occurs at a load cast horizon at a shale-sandstone contact. **D**) Interlaminated siltstone and very fine-grained sandstone with low-diversity trace fossil assemblage dominated by small horizontal traces (*Planolites*) and diminutive vertical traces (*Cylindrichnus*, *Arenicolites*, and *Trichichnus*). **E**) Bedding plane photograph of synaeresis cracks from the lower part of D. **F**) Photograph of the basal part of D showing synaeresis cracks and low-diversity trace fossil assemblage.

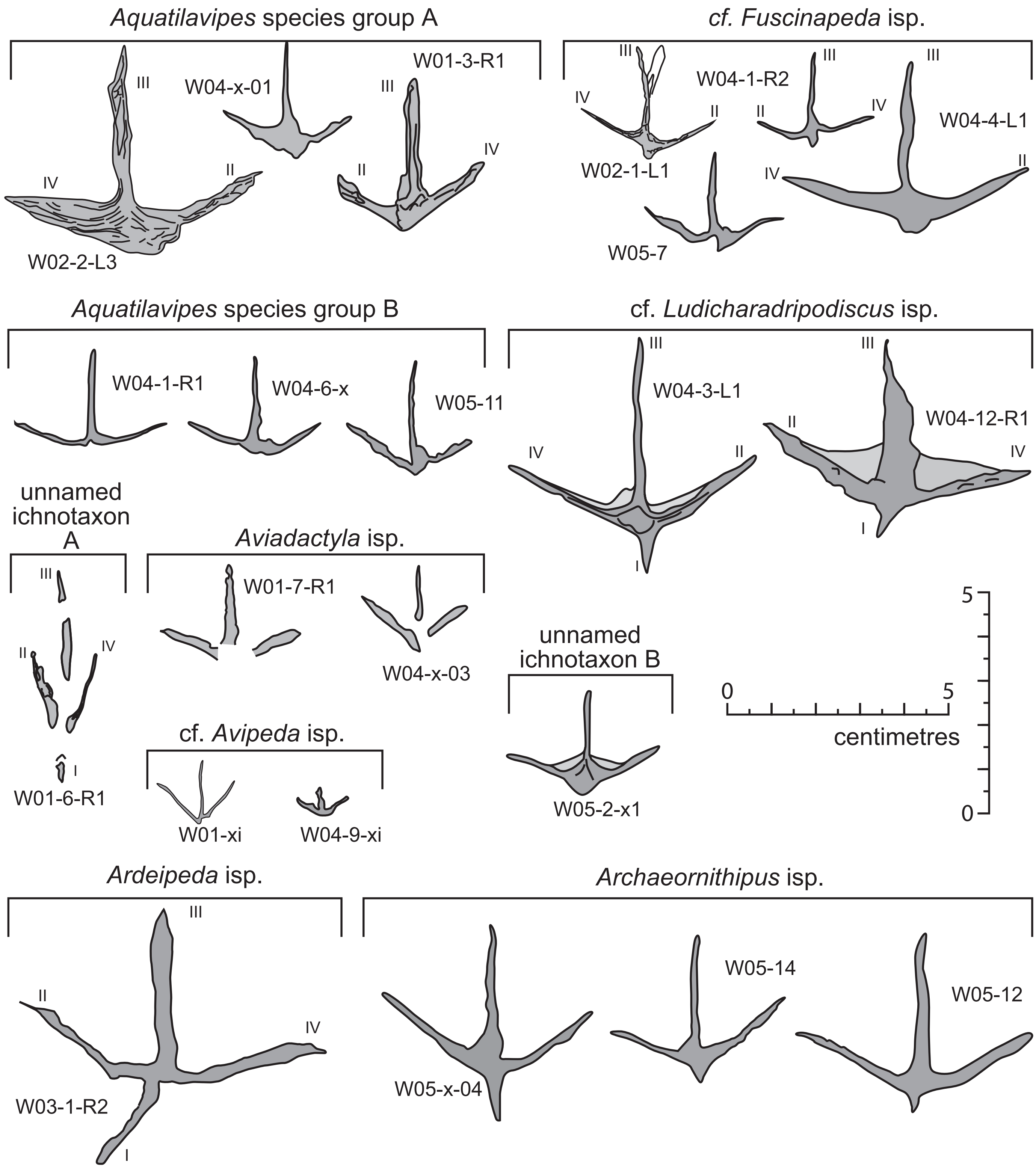


FIG. 7.—Representative Bird footprint taxa identified in the Tambak Member of the Tanjung Formation, Asem Asem Basin, Kalimantan. These taxa include *Aquatilavipes* isp. *Avipeda* isp., *Ardeipeda* isp., *Aviadactyla* isp., *Ludicharadripodiscus* isp. and an unnamed ichnotaxon charactered by an elongate digit III and a very narrow digit II–IV divarication angle. *Aquatilavipes* are broken into two groupings, one with thick and robust digits II and IV that form an acute angle at the heel and the second with slender digits II and IV and a more rounded 'heel'.

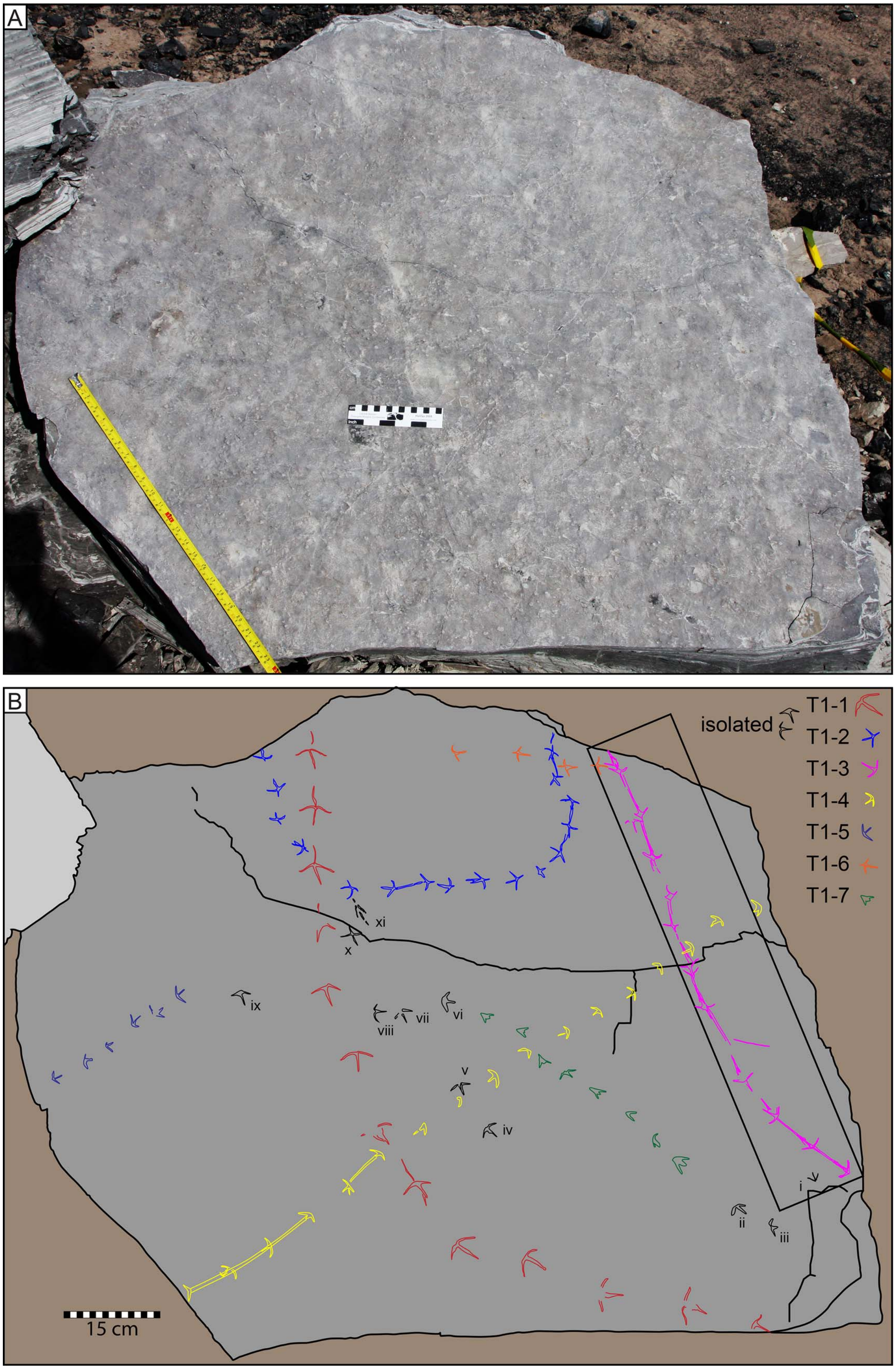
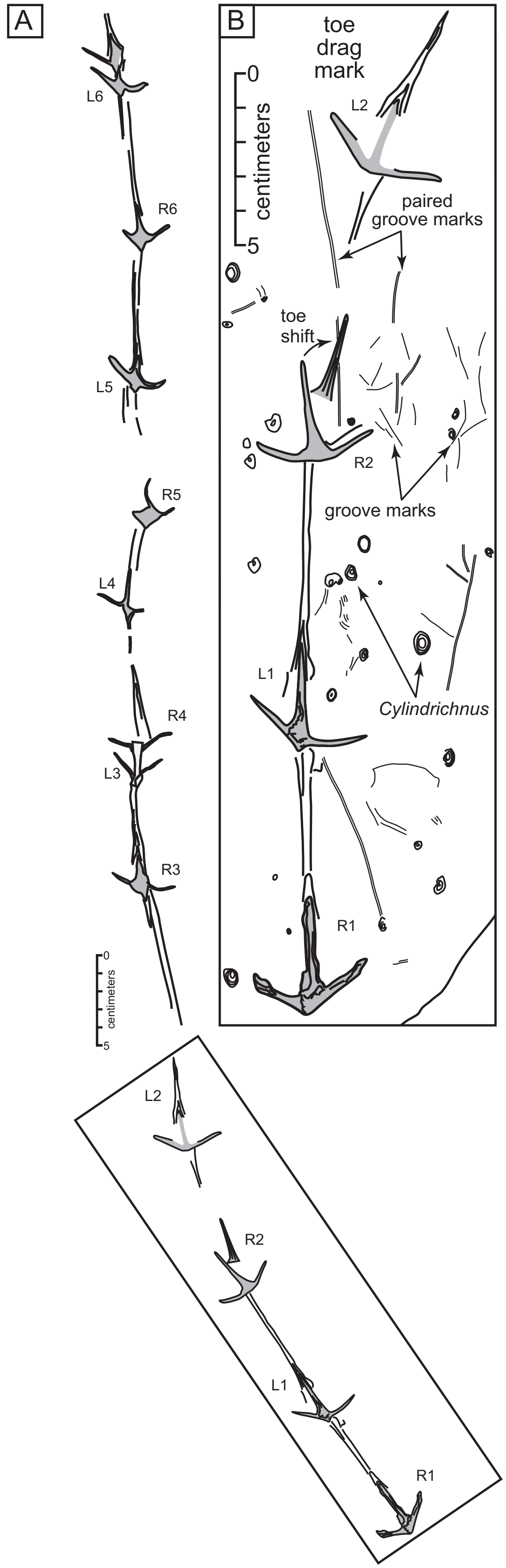


FIG. 8.—Photograph and sketch of slab WAH01. This slab includes seven distinct trackways as well as several isolated footprints. **A**) Photograph of the slab W1 surface. **B**) Sketch showing the seven trackways and eleven isolated footprints on slab W1. Box shows the area illustrated in figure 9.



Trackway WAH04-1, with its reduced but distinct hallux, is assigned to cf. *Archaeornithipus* (Fig. 13). Trackways 4-2 and 4-10 are assigned to a small species of cf. *Aquatilavipes* with a narrow digit III drag mark associated with each footprint (Figs. 13, 14). Trackways 4-3 and 4-4 exhibit an elongate hallux and are assigned to cf. *Ardeipeda* (Fig. 13). Isolated footprint 4-6 is assigned to cf. *Aquatilavipes* and 4-9 is assigned to cf. *Avipeda*. (Fig. 13). Isolated footprints 4-5, 4-7, 4-8, and 4-11 are not preserved sufficiently well for ichnogeneric identification. The photographed slab is the under-surface of a bedding plane, and all avian trackways on this slab are undertracks; thus, all footprint ichnotaxonomic identifications herein are tentative (Figs. 13, 14).

Trackway WAH04 includes multiple fragments containing numerous elevated anisodactyl footprints (*Aquatilavipes* and *Fuscinapeda*), incumbent anisodactyl footprints (*Ardeipeda*), and rare semipalmate anisodactyl footprints (cf. *Ludicharadripodiscus* sp. and unnamed ichnotaxon B) (Fig. 7). Similarly, to all other specimens analyzed in this study, the fragments that comprise WAH04 exhibit numerous invertebrate traces (Figs. 13, 14). The WAH04 fragments are characterized by extensive dimpling as well as conical pit traces (Fig. 11C, 11D). V-shaped gouges and arcuate linear grooves were also observed. In addition, desiccation cracks bifurcate many of the traces on this slab and seem to preferentially penetrate through the bird footprints (Fig. 13).

Distribution of Traces on Sample WAH05

Slab WAH05 consists of 14 scattered tracks, including both elevated anisodactyl footprints consistent with *Fuscinapeda* and *Aquatilavipes* and incumbent anisodactyl footprints consistent with *Archaeornithipus* (Fig. 15, Table 6). The traces on slab WAH05 are preserved in convex hyporelief on an undertrack surface, just below the horizon of emplacement. Numerous shallow, circular to ovoid, conical pits, U-shaped grooves, V-shaped marks, and invertebrate traces also occur on this specimen. Horizontal and vertical root traces with carbon cores are abundant on the bedding plane. The bedding plane that comprises the surface of WAH05 appears to have been an undersurface a millimeter or two below the surface of occupation; however, similar preservation and appearance suggests that the bulk of traces were emplaced on the same surface.

Attributes of Purported Foraging Traces

As mentioned above, a number of other structures occur in association with the avian trackways summarized above. These include small, shallow, circular to ovoid divots and pits (Type I traces), V-shaped gouges (Type II traces), as well as straight to gently arcuate paired and singular grooves (Type IIIA and IIIB traces) and dimpled surfaces (Type IV traces) (Figs. 8–15, Table 1).

The circular and ovoid divots (Type I traces) are similar in shape to tiny *Conichnus*, which is what they were initially attributed to. They are 2–10 mm in diameter and 1–8 mm in depth. Most are oval in outline (Fig. 11C), which is inconsistent with *Conichnus*. The conical nature of the traces was made evident by separating individual

←

FIG. 9.—Sketch of trackway WAH01-3 from the slab illustrated in Figure 8. **A**) Trackway WAH01-3. Note the irregular gait (particularly the closely spaced steps at L3-R4 and at L6) and the gently meandering nature of the trackway. **B**) Detail of the area around footprints R1 through L2. As well as distinct toe drag marks, this area of slab 1 includes abundant groove marks, likely probe marks and numerous invertebrate traces assigned to *Cylindrichnus* isp. Note that after footprint R2 the bird changed direction slightly, evidenced by a toe shift and a change in overall track orientation.

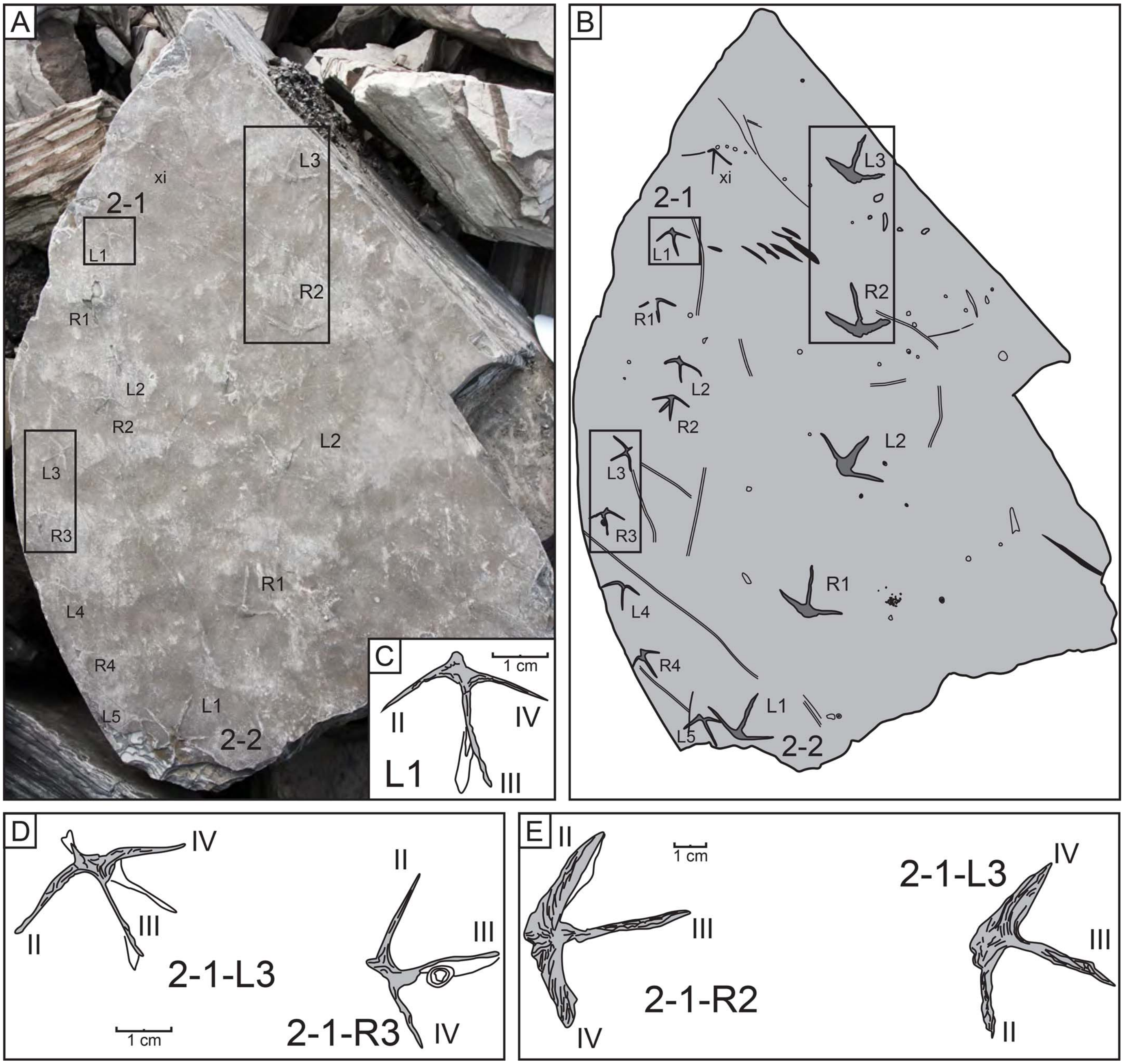


FIG. 10.—Photograph and sketch of slab WAH02. This slab includes two distinct trackways as well as abundant peck marks, probe marks, and sweep traces. **A**) Photograph of the slab W2 surface. **B**) Sketch of the slab surface, showing numerous peck marks and groove marks. Note that the partial footprint labeled as 'xi' may be associated with trackway WAH02-1 but it is not included due to uncertainty and its incompleteness. **C**) Detail of footprint WAH02-1-L1. **D**) Detail of footprints WAH02-1-L3 and WAH02-1-R3. **E**) Detail of footprints WAH02-2-R2 and WAH02-2-L3.

laminae of fissile slabs and by observing divots on the edge of some slabs. The V-shaped gouges (Type II traces) are 6 to 20 mm in length, with a deeper end and a shallower end, and typically exhibit a V-shaped profile.

The simple, singular grooves (Type IIIA traces) are shallow ($\sim$ 1 mm), moderate in width (0.5–5 mm), 2 to 6 cm in length and commonly occur in clusters. Both singular and paired grooves are internally smooth and devoid of internal structures or ornamentation. The paired grooves (Type IIIB traces) are shallow (0.5 to 2 mm depth), narrow (1–2 mm in width), range from $\sim$ 2 to 20 cm in length, and have sharp to moderately diffuse margins (Fig. 11A, 11B). Several bird-track horizons were characterized by a densely dimpled surface to the sediment, consisting of abundant, small, shallow divots, giving the laminae a smoothed-crenulated appearance in vertical aspect (Fig. 11D).

The circular to ovoid pits, paired and singular grooves, V-shaped gouges, and dimpled surfaces invariably occur in close association with avian footprints. The discrete traces occur most commonly with organized trackways, whereas the dimple marks commonly occur with abundant, randomly oriented footprints. Most traces occur within one footprint width of a trackway. None of the features interpreted

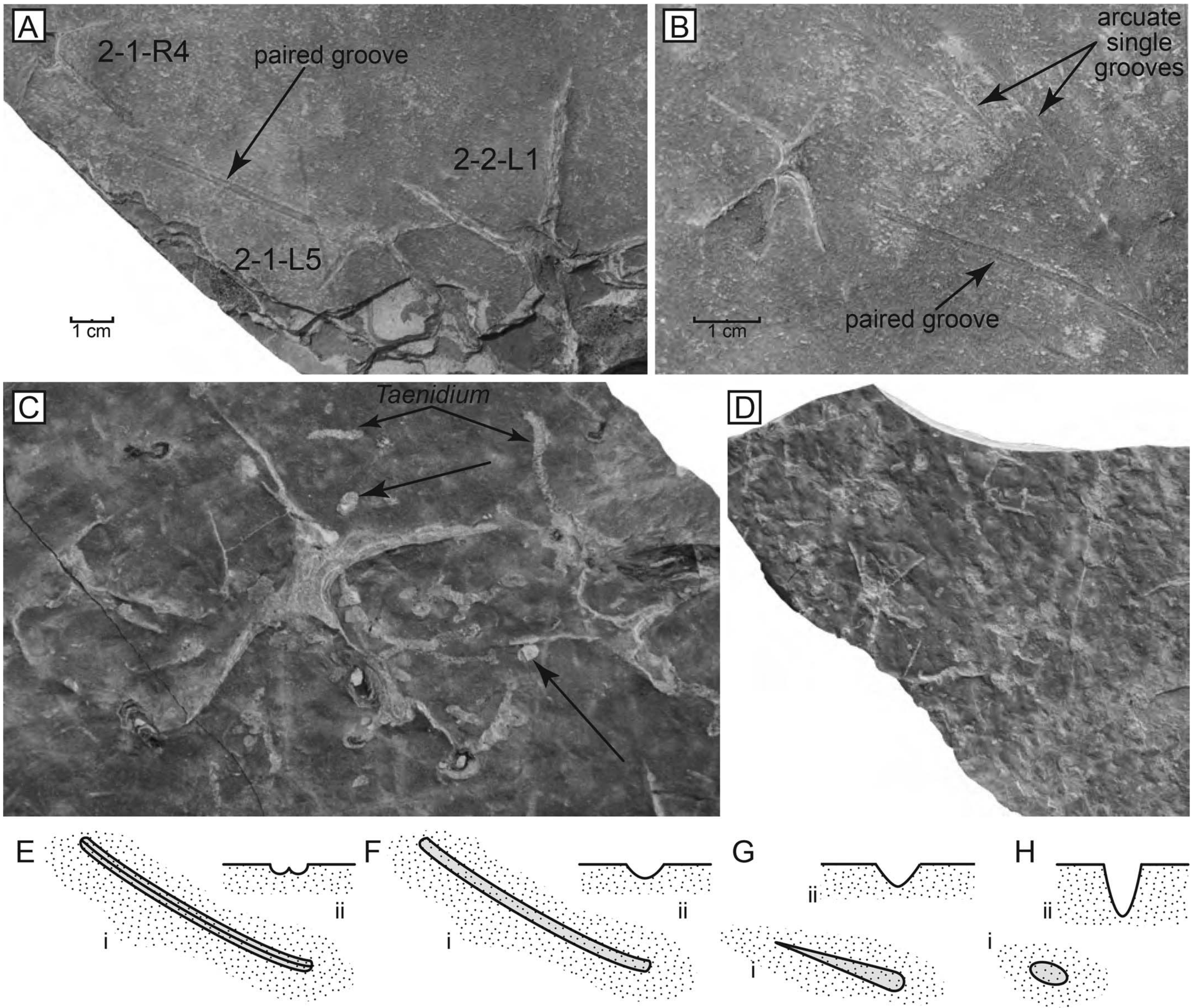


FIG. 11.—Photographs of avian foraging traces. **A**) Paired groove (arrow) between footsteps WAH02-1-L5 and WAH02-1-L1. **B**) Paired and arcuate single grooves beside footstep WAH02-1-L3. **C**) Oval peck marks (arrows) on slab WAH04 in association with an indeterminate footprint. Peeling back individual laminae revealed that these traces were cone-shaped in the third dimension. **D**) Pervasive dimple marks on bedding plane WAH04.

herein as traces occurred more than 2.5 footprint widths away from a trackway.

DISCUSSION

The Tanjung Formation in the Asem Asem Basin study area forms part of an overall fining-upwards, retrogradational succession. The Mangkook Member (not exposed at Wahana) represents deposition in braided and meandering fluvial channels and adjacent floodplains. The Tambak Member (discussed herein) preserves sluggish fluvial to estuarine or deltaic channels adjacent to channel-margin mudflats, poorly drained alluvial plains, swamps (the sources of the coals), and marshes. The Pagat Member records deposition in a mud-dominated, open coastal setting (Witts et al. 2012a, 2012b; Zonneveld et al. in press A) (Fig. 16A).

Sedimentological and ichnological evidence indicate that the Tambak Member in the study area was deposited in a coastal plain setting in meandering fluvial, low-relief floodplain and tide-influenced deltaic or estuarine depositional subenvironments (Fig. 16A, 16B). The succession of gray carbonaceous mudstone with common rooting and abundant pedogenic slickensides interbedded with coal beds immediately above and below the sandstone-dominated succession in which the bird trackways occur (Fig. 3), record deposition in low lying mires and poorly drained alluvial lowlands (e.g., Breyer and McCabe 1986; Witts et al. 2012B; Gingras et al. 2012). We interpret the sharp contact of cross-stratified sandstone overlying the coal and carbonaceous mudstone facies (Fig. 3) to record migration (or avulsion) of a fluvial channel into the area (e.g., Kraus 1996; Kraus and Wells 1999; Jones and Hajek 2007).

The Tambak coals in the Barito Basin were deposited in rheotrophic mires with palm- or fern-dominated vegetation and overall low sulfur content indicating minimal marine influences (Fikri et al. 2022). Coals at Wahana in the study area are much closer to the paleocoastline and probably had more significant marine influences.

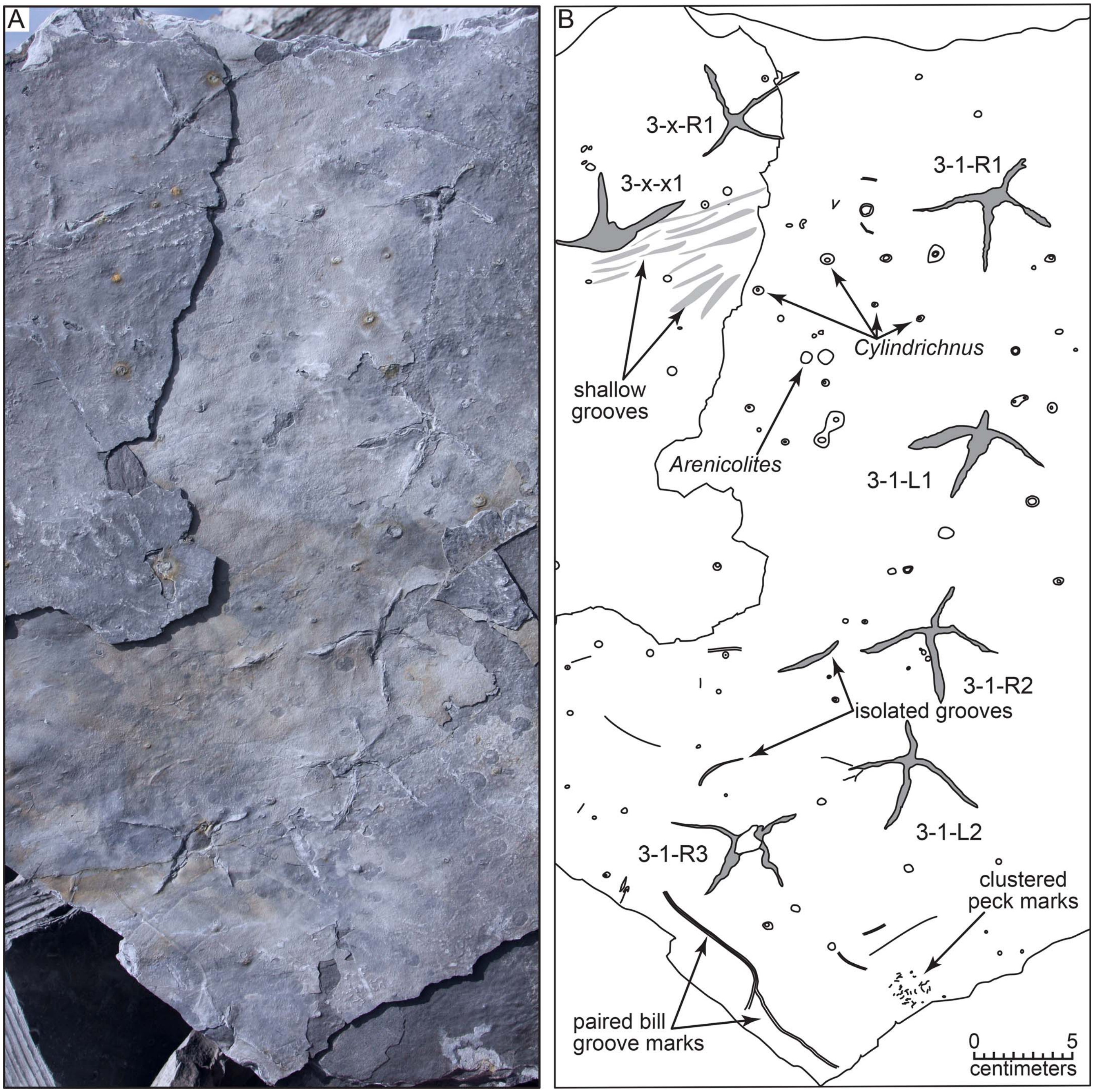


FIG. 12.—Photograph and sketch of slab WAH03. **A**) Photographs of WAH03. **B**) Sketch of avian trackway, foraging traces and invertebrate traces on slab WAH03. Concentric circles are clearly trace fossils, most commonly *Cylindrichnus*, but some of the other ovoid and circular traces are likely peck marks and probe marks. The main trackway on this slab is that of a bird with an anisodactyl foot (*Ardeipeda* sp.). An isolated *Aquatilavipes* occurs at top left.

The interbedded, heterolithic, very fine-grained sandstone with siltstone and silty mudstone successions (Figs. 3, 5, 6) are characterized by lenticular, wavy, and flaser bedding. This indicates conditions of alternating current bedload transport with suspension settling during slack water intervals and thus, these are common characteristics of successions deposited in intertidal settings (Reineck and Wunderlich 1968; Klein 1971; Terwindt and Breusers 1972; Clifton 1983; Flemming 2011). Interbedded intervals of cross-bedded sandstone with heterolithic, flaser and wavy-bedded sandstone/mudstone are common in the lower parts of inner estuary and upper parts of middle estuary settings (e.g., Dalrymple and Choi 2007; Shchepetkina et al. 2016.) but are also like sedimentary successions in mixed tide and fluvially controlled deltaic complexes such as the modern Mahakam River delta (e.g., Gastaldo et al. 1995).

The trace fossil assemblage comprises a moderately diverse *Psilonichnus* ichnofacies association (Frey and Pemberton 1987; Pemberton and Wightman 1992; Gingras et al. 1999, 2000a, 2012; Buatois et al. 2005; MacEachern et al. 2012; Baucon and Felletti 2013), characteristic of deposition in a marginal marine, tidally influenced setting. The alternating mud

TABLE 4.—*Measurements of footprints on slab WAH03.*

Print	Print width (mm)	Print length (mm)	Digit I length (mm)	Digit II length (mm)	Digit III length (mm)	Digit IV length (mm)	Stride length (mm)	Divarication II–III	Divarication III–IV	Total Divarication (II–IV)
3-1-R1	64	54	17	24	29	29	109	60°	73°	133°
3-1-L1	62	48	13	32	34	27	90	48°	82°	129°
3-1-R2	61	52	18	27	33	31	58	60°	75°	135°
3-1-L2	60	50	16	26	30	33	78	61°	69°	130°
3-1-R3	57	54	18	23	27	28	-	67°	60°	127°
3-2-R-1	55	61	21	28	36	26	-	75°	52°	128°
3-3-x-1	65	37	-	24	27	38	-	81°	62°	142°

and sand laminae within many of the larger trace fossils indicate that they are 'tubular tidalites' (*sensu* Gingras and Zonneveld 2015), underscoring the significance of tidal influence in the heterolithic facies. The mix of ethologies represented by the invertebrate trace fossil assemblage includes dwelling traces of predators and scavengers, equilibrichnia and domichnia of infaunal suspension feeders, and fodinichnia of infaunal deposit feeders, all consistent with modern intertidal settings (e.g., Frey and Pemberton 1987; Gingras et al. 1999, 2000a, 2000b; Pearson and Gingras 2006; Baucon and Felletti 2013; Zonneveld and Gingras 2013; Zonneveld et al. 2014). The diminutive sizes of many of the traces implies environmental stress and is consistent with emplacement in a brackish depositional setting (Gingras et al. 1999, 2012; Pearson and Gingras 2006).

The co-occurrence of root traces, desiccation cracks, syneresis cracks, avian footprints with current ripples, wavy bedding, and localized channel-like features indicate deposition under widely varying current and exposure conditions, which is consistent with intertidal deposition (e.g., Clifton 1983; Frey and Pemberton 1987; Gingras et al. 1999, 2000a; Flemming 2003, 2005, 2011) (Fig. 16B). Evidence in trackway WAH01 of birds walking on closely adjacent patches of soft and soupy substrates (Figs. 8, 9) is consistent with emplacement in an intertidal flat or bar setting (Figs. 16B, 17). Bird footprints commonly act as nucleation sites for desiccation cracks, particularly in areas where there is organic binding of the sediment (Master 1991; Genise et al. 2009).

The avian footprints in this study represent at least nine avian ichnogenera: *Archaeornithipus*, *Ardeipeda*, *Aquatilavipes*, *Aviadactyla*, cf. *Avipeda*, *Fuscinapeda*, cf. *Ludicharadripodiscus*, and two unnamed ichnotaxa. *Archaeornithipus* and *Ardeipeda* represent the movements of egret- or heron-like birds (e.g., Fuentes Vidarte 1996; Baucon and Felletti 2013). At least three size groupings of *Archaeornithipus*, indicating that several different heron-like birds (Ardeidae) occurred in the Tambak fauna.

Aquatilavipes are similar in shape to those emplaced by modern plovers (Charadriidae) and stilts (Recurvirostridae) (Elbroch and Marks 2001; McCrea and Sarjeant 2001; Lockley et al. 2015). The Tambak traces include small forms in the size range of modern plovers as well as large forms in the size range of modern stilts. It is assumed that this ichnotaxon represents at least two avian taxa in the study area. *Aviadactyla* are small, elevated anisodactyl footprints, wherein the bird walked weight-forward leaving impressions of the anterior portion of toes II through IV and no impression of the metatarsal pad (Serjeant and Reynolds 2001). These tracks are similar to those emplaced by modern oystercatchers (Haematopodidae) and some species of plover (Elbroch and Marks 2001).

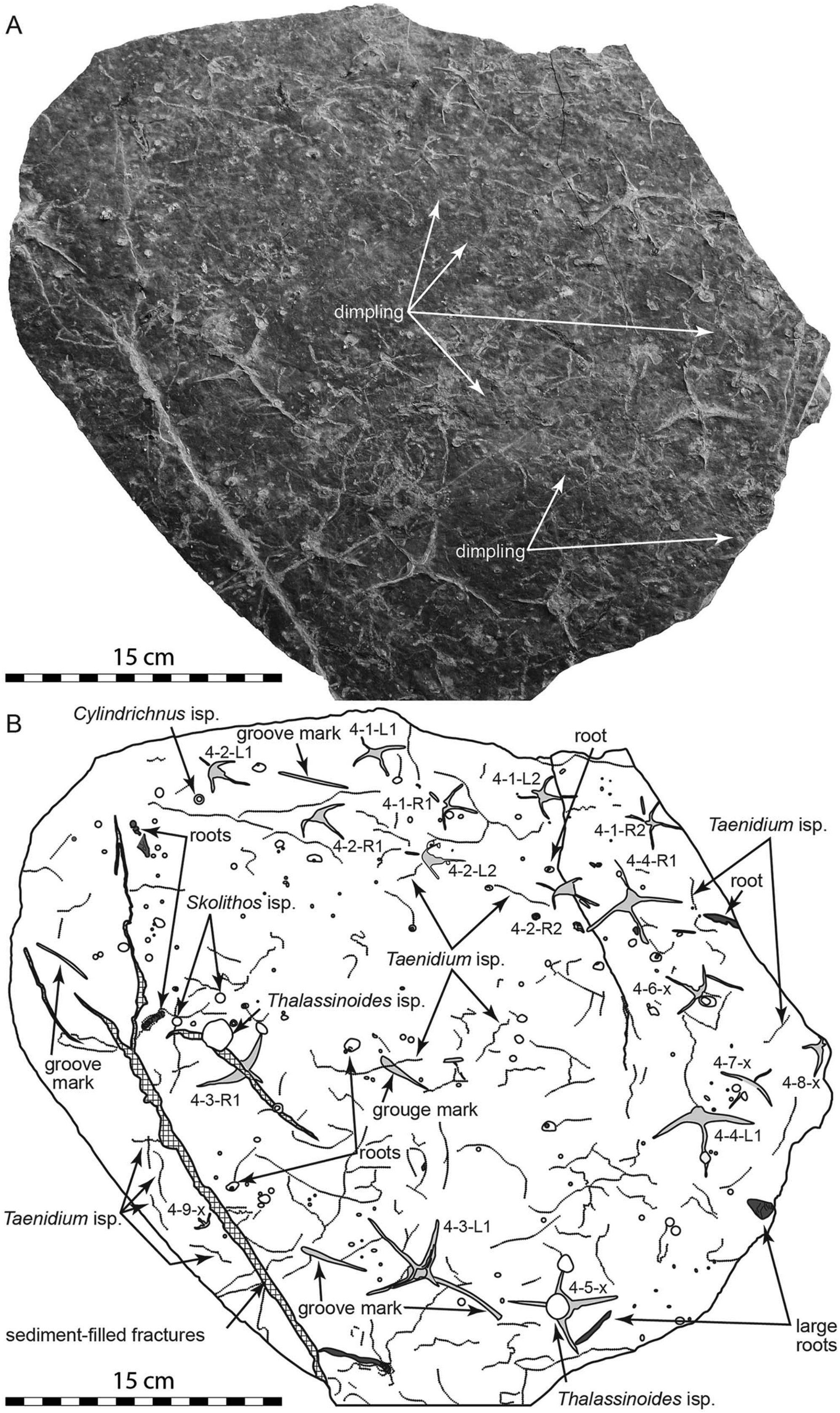
Aviadactyla and cf. *Avipeda* are consistent with charadriiform shorebirds that forage in a weight-forward fashion. Footprints assigned to cf. *Avipeda* in the study area include a bird with very slender toes and the smallest bird in the study interval. *Fuscinapeda* in the study interval is represented by several small to moderate-sized forms consistent with charadriiform shorebirds. The trackways included in cf. *Ludicharadripodiscus* and unnamed ichnotaxon B were likely made by a moderate-sized charadriiform shorebird (Ellenberger 1980) although it also bears similarities to tracks of birds in the ciconiiform and gruiform lineages. *Ludicharadripodiscus* was first described from Eocene fossils from Garrigues-Sainte-Eulalie in southern France (Ellenberger 1980) but has also been observed in Cretaceous successions (McCrea and Serjeant 2001) from western Alberta, Canada.

The tracks and trackways identified in this study are commonly accompanied by small, sediment-filled, *Conichnus*-like, circular to ovoid divots (Type I traces), V-shaped marks (Type II traces), and elongated singular and paired grooves (Type III traces) (Fig. 11A–11C, Table 1). In several cases, the traces occur on bedding planes characterized by extensive 'dimpling' (Type IV traces) (Fig. 11D, Table 1). These traces are all interpreted to record avian foraging activities in the Tambak intertidal (Figs. 16, 17).

Shorebirds employ a wide variety of feeding styles including pecking, probing, stabbing, and sweeping (e.g., Sutherland et al. 2000; Nebel et al. 2005; Jing et al. 2007; Zonneveld et al. in press B). Shorebirds forage in and on substrates using visual cues, tactile cues, or both (Baker 1979; Quammen 1982; Grant 1984; Backwell et al. 1998; Sutherland et al. 2000; Nebel et al. 2005; Jing et al. 2007; Van Dusen et al. 2012). Tactile searching is particularly important when the visibility of prey is hampered, such as in shallow muddy water, in areas with moderately thick sea grass, and in areas where the prey is hidden within the sediment (Wilson 1991, 1994; Piersma et al. 1996; Santos et al. 2009). Many of the Tambak trackway slabs are characterized by numerous root traces, indicating that the Tambak avifauna foraged on partially vegetated intertidal flats.

Type I traces are consistent with either probe marks or peck marks reported from modern shorebirds (Frey and Pemberton 1987; Elbroch and Marks 2001; Falk et al. 2010; Zonneveld et al. 2011, in press B). Although simple peck marks and probe marks may be similar in appearance, pecking is a visual foraging tactic and peck marks are usually quite shallow whereas probing is a tactile foraging tactic and the probe marks may be deeper (Frey and Pemberton 1987; Elbroch and Marks 2001; Falk et al. 2010, 2014; Zonneveld et al. 2011, in press B). Peck marks emplaced by modern birds are typically randomly distributed whereas probe marks may be random or organized in distinct patterns or clusters (Frey and Pemberton 1987; Elbroch and Marks 2001; Falk et al. 2010; Zonneveld et al. 2011, in press B). Individual birds may use a combination of both tactics during a single foraging period (Sutherland et al. 2000; Nebel and Thompson 2005; Nebel et al. 2005; Jing et al. 2007).

Probe marks emplaced by living shorebirds are circular, oval, or lunate in profile; conical in shape; and partially to fully surrounded by a raised rim of sediment (Elbroch and Marks 2001; Falk et al. 2010; Abbassi et al. 2015; Zonneveld et al. in press B). Probing occurs when a beak is pressed directly into the sediment and withdrawn in the same direction. Some shorebirds exhibit a modified probing behavior referred to as gaping, in


A
dimpling
dimpling
15 cm
B
Cylindrichnus isp.
groove mark
4-1-L1
4-2-L1
root
4-1-L2
4-1-R1
4-1-R2
Taenidium isp.
roots
4-2-R1
4-2-L2
4-4-R1
root
Skolithos isp.
4-2-R2
Taenidium isp.
Thalassinoides isp.
4-6-x
groove mark
4-7-x
4-8-x
4-3-R1
grouge mark
4-4-L1
roots
Taenidium isp.
4-9-x
4-3-L1
4-5-x
groove mark
sediment-filled fractures
large roots
15 cm
Thalassinoides isp.

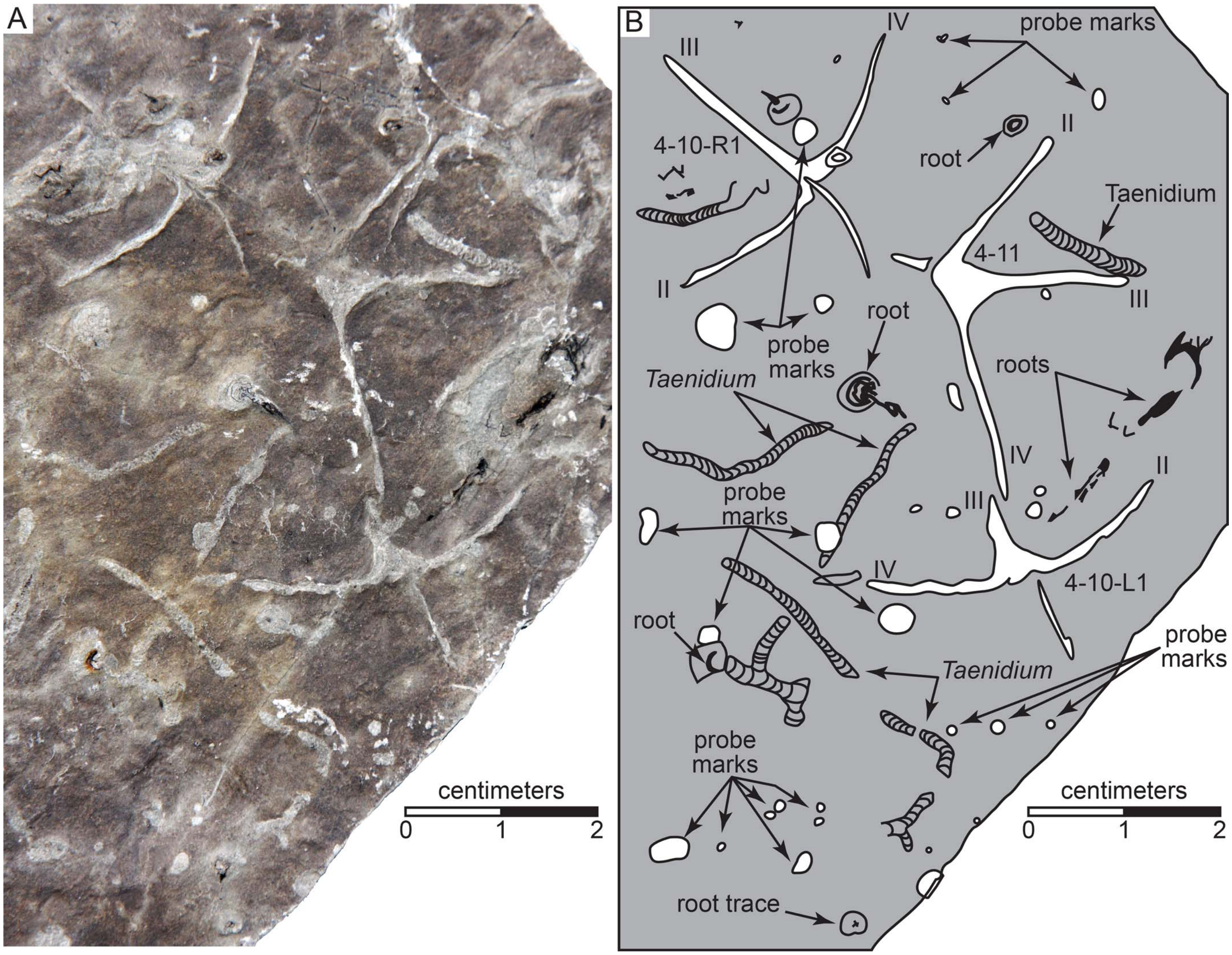


FIG. 14.—Photograph and sketch of a small fragment of slab WAH04. **A**) Close-up photograph of the fragment. **B**) Sketch showing the vertebrate and invertebrate traces on the surface of WAH04.

which the mouth is opened while withdrawing the beak (Elbroch and Marks 2001) resulting in an oval/subcircular hole. Probing occurs when the food resource the bird is seeking occurs buried within the sediment (shallow infauna), may involve shallow probing or deep probing, and may occur when the bird is walking, standing or a combination (Hancock et al. 1992). Probe marks emplaced by modern charadriiform birds, such as Dunlins and Sandpipers, commonly occur in linear trends or systematic clusters (e.g., Burton 1974; Mouritsen and Jensen 1992; Weber and Haig 1997; Rylander 2002), reflecting efficient, systematic tactile foraging for unseen prey. Other probers walk forward with periodic, random solitary probes in order to identify prey-rich foraging grounds (Zonneveld et al. in press B).

Traces interpreted as peck marks/probe marks in the study interval occur in association with all avian footprint taxa in the study interval. They are particularly common in association with *Aquatilavipes*, *Archaeornithipus*, and *Fuscinapeda*. It is worth noting that none of the Type I traces were observed to occur in linear trends or systematic clusters suggesting that these trace record either random probes, peck marks at surficial prey, or a combination of both.

Type II traces are consistent with two types of visual foraging behaviors: pecking and scratching. Peck marks emplaced while a bird was walking forwards may result in a glancing impact of a bird's bill with the sediment surface and V-shaped groove, deeper at one end than the other (Elbroch and Marks 2001; Falk et al. 2010; Zonneveld et al. 2011, in press B). These traces most commonly occur in damp sediment near the shoreline and, in modern examples, commonly have a ridge or plug of sediment kicked up by insertion and extraction of the beak in the sediment (Falk et al. 2010). Peck marks are emplaced when the food resources sought occur at, or near, the sediment surface (Hancock et al. 1992). Alternatively, similar marks may be emplaced by a bird's claw as it scratches at objects on the sediment surface (Zonneveld et al. in press B).

←
FIG. 13.—Photograph and sketch of a large fragment from slab WAH04. **A**) Photograph of the fragment. Note the dimpled appearance to the surface of WAH04. **B**) Sketch of avian trackway, foraging traces and invertebrate traces on a large fragment of slab WAH04. This slab preserved numerous invertebrate traces as well as avian trackways, isolated footprints and foraging traces.

TABLE 5.—*Measurements of footprints on slab WAH04. Key: inc. = incomplete.*

Print ID	Print width (mm)	Print length (mm)	Digit I length (mm)	Digit II length (mm)	Digit III length (mm)	Digit IV length (mm)	Stride length (cm)	Divarication II–III	Divarication III–IV	Total divarication (II–IV)
4-1-L1	32	22	3	15	16	14	59	89°	75°	164°
4-1-R1	30	22	2	15	18	14	62	71°	59°	130°
4-1-L2	30	23	3	15	18	13	69	70°	65°	135°
4-1-R2	31	23	3	14	19	12	-	76°	71°	147°
4-2-L1	25	25	-	13	21	14	72	60°	44°	104°
4-2-R1	26	24	-	13	21	13	74	61°	54°	115°
4-2-L2	23	26	-	14	21	12	78	47°	46°	93°
4-2-R2	24	24	-	13	21	13	-	55°	53°	108°
4-3-L1	51	52	9	26	39	35	156	62°	65°	127°
4-3-R1	51	-	-	33	-	24	-	-	-	129°
4-4-R1	57	41	-	38	27	23	138	75°	62°	137°
4-4-L1	61	39	-	31	28	27	-	73°	69°	142°
4-5-x	42	-	-	-	27	23	-	74°	69°	143°
4-6-x	33	27	-	17	19	15	-	67°	65°	132°
4-7-x	32	23	-	12	18	14	-	80°	71°	151°
4-8-x	-	-	-	14	-	-	-	63°	-	-
4-9-x	13	8	-	6	5	6	-	64°	57°	121°
4-10-L1	32	-	-	18	22	16	-	74°	72°	146°
4-10-R1	34	22	-	17	21	17	-	73°	72°	145°
4-11-x	39	25	6	19	20	24	-	48°	74°	122°
4-12-R1	62	47	7	33	35	31	-	55°	78°	133°
4-13-x	32	11 (inc.)	-	15	8 (inc.)	16	-	81°	66°	147°
4-14-x	35	20	-	17	16	14	-	73°	72°	145°
4-15-x	33	23	-	18	18	16	-	70°	73°	143°
4-16-x	41	18 (inc.)	-	19	15	22	-	48°	74°	122°
4-17-x	-	24	-	24	22	-	-	55°	-	-
4-18-x	27	25	-	16	23	17	-	64°	57°	121°
4-19-x	60	40 (inc.)	-	26	33 (inc.)	28	-	55°	94°	149°

Type III traces are similar to sweep marks emplaced by waterbirds foraging in shallow water (Swennen and Yu 2005; Kim et al. 2012; Zonneveld et al. in press B). Spoonbills, ibises, and avocets walk in shallow waters, making broad sweeping motions with their bills to locate prey (Swennen and Yu 2004, 2005; Zonneveld et al. in press B). Sweeping most commonly occurs in shallow water while these long-billed shorebirds forage for fish, aquatic invertebrates, or plants (Hancock et al. 1992; Swennen and Yu 2005, 2008; Zonneveld et al. in press B). Sweep marks are emplaced when the bill tip makes contact with the sediment-water interface. Spoonbill sweeping results in paired, arcuate grooves that are approximately perpendicular to the direction of travel and commonly exhibit a back-and-forth pattern overprinted in part by avian footprints (Swennen and Yu 2004, 2005, 2008). Avocet sweeping commonly results in solitary and paired, U-shaped, gently arcuate grooves on the sediment surface (Zonneveld et al. in press B). These traces may exhibit a back-and-forth pattern similar to avocet sweep marks, or may occur as solitary markings oriented parallel, oblique, or perpendicular to the direction of travel.

Other birds, such as some heron, feed by stirring their bill back and forth in the sediment, typically right beside the trackway (Zonneveld et al. in press B). In the Tambak Member, groove marks were observed in close association with bird footprints (Figs. 8, 9) but were not observed on bedding planes devoid of footprints. Clustered groove marks (Fig. 8) are interpreted to result from a bill-stirring behavior. Long, straight to arcuate, solitary and paired grooves (Figs. 9, 10) are interpreted to record sweeping behavior. Short, wide isolated grooves (Fig. 8) may record short weep marks, but alternatively may record a location where a bird clawed at a surface object with its foot. We note that solitary groove marks bear some similarity to the ichnotaxon *Haplotichnus*. However, their close association with avian trackways, and similarity in dimensions and appearance to the paired/bilobed groove marks prevent us from using that taxonomic term. They are most likely a preservational variant of the bilobed forms.

Type IV traces (Table 1) consist of densely dimpled bedding planes that occur in association with randomly oriented avian footprints (Fig. 11D). Dimpled surfaces can result from microbial binding of a sediment surface, commonly forming when gas bubbles form beneath a microbial layer (Noffke et al. 2001; Rose and Chavetz 2011). Dimpled surfaces can also occur due to intensive avian activity. Avian-affiliated dimpling (Fig. 11D) occurs when food resources are present and pervasive at the sediment surface and intensive pecking has ensued (Zonneveld et al. in press B). We have observed similar dimpling in modern environments where small shorebirds such as sandpipers and plovers feed on surficial biofilms (Zonneveld et al. in press B). In these cases, the behavior produced a densely dimpled surface with occasional deeper pitting and short, narrow, solitary and paired grooves on the sediment surface. Biofilm feeding has been observed in a variety of short-billed shorebirds, including sandpipers and dunlins (Elner et al. 2005; Kuwae et al. 2008, 2012; Mathot et al. 2010; Jiménez et al. 2015; Beninger and Elner 2020), although the sediment structures produced were not illustrated. Biofilm grazing behavior has been observed on subaerially exposed damp surfaces recently exposed by dropping tides and on sand and mudflats adjacent to lakes (Elner et al. 2005; Kuwae et al. 2008, 2012; Mathot et al. 2010; Jiménez et al. 2015; Beninger and Elner 2020). Recent studies have shown that biofilms comprise an important food resource for migrating shorebirds, particularly smaller shorebirds such as dunlins and sandpipers (Elner et al. 2005; Kuwae et al. 2008; Mathot et al. 2010; Kuwae et al. 2012; Hall et al. 2021).

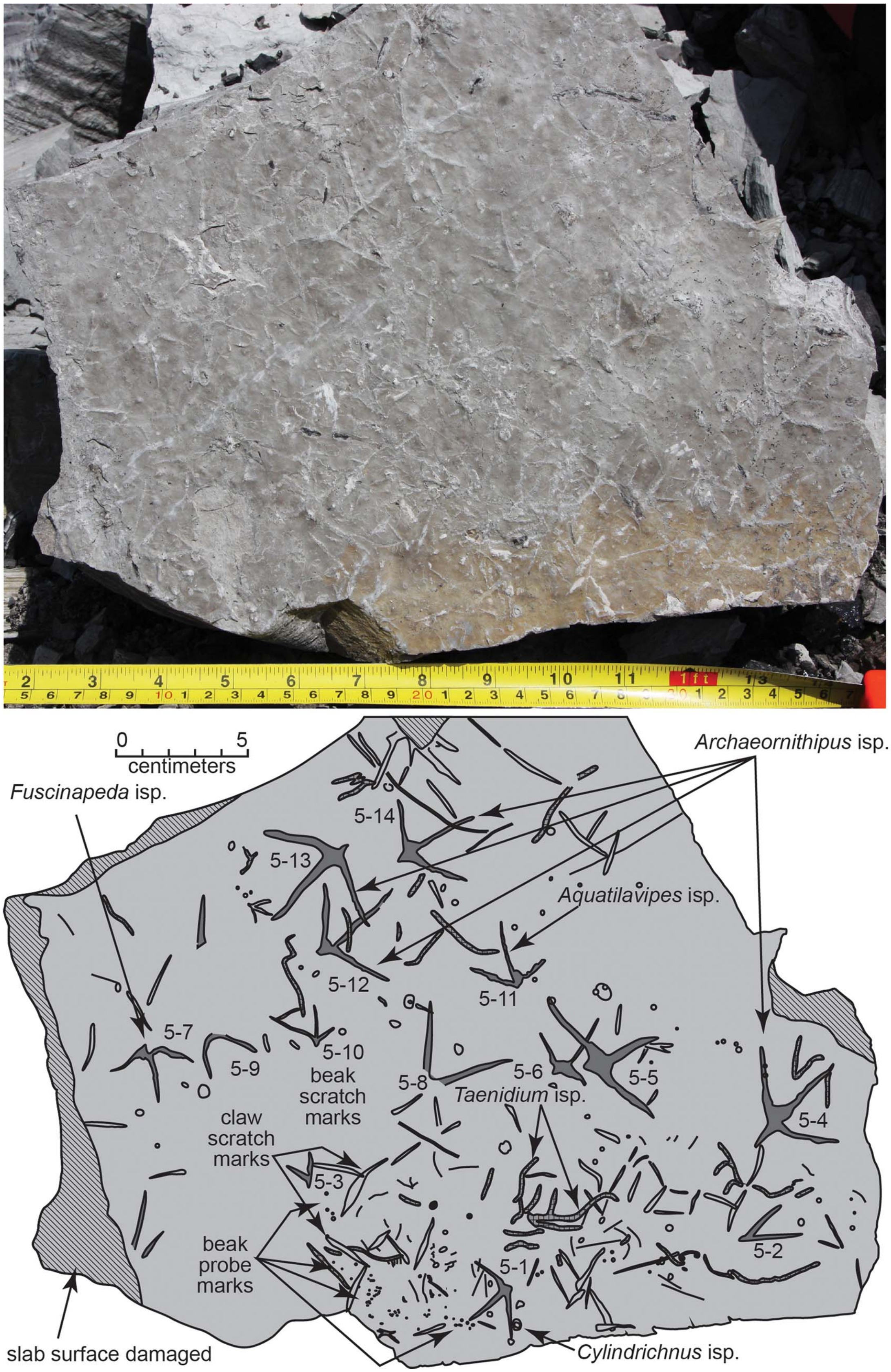


FIG. 15.—Photograph and sketch of a fragment of slab WAH05. A) Close-up photograph of the fragment. B) Sketch showing the vertebrate and invertebrate traces on the surface of WAH05.

TABLE 6.—*Measurements of footprints on slab WAH05.*

Print ID	Print width (mm)	Print length (mm)	Digit I length (mm)	Digit II length (mm)	Digit III length (mm)	Digit IV length (mm)	Stride length (cm)	Divarication II–III	Divarication III–IV	Total divarication (II–IV)
5-1	33	21	-	17	20	19	-	54°	77°	131°
5-2	-	26	-	19	24	-	-	42°	-	-
5-3	-	14	-	11	12	-	-	61°	-	-
5-4	47	44	13	29	31	26	-	53°	58°	111°
5-5	61	32	3	31	27	31	-	63°	105°	168°
5-6	26	27	-	17	23	10	-	61°	79°	140°
5-7	32	23	-	16	20	17	-	59°	64°	123°
5-8	-	29	-	28	29	-	-	67°	-	-
5-9	-	20	-	16	18	-	-	77°	-	-
5-10	26i	16i	3	21	13i	8i	-	70°	51°	121°
5-11	29	24	-	18	24	15	-	50°	64°	114°
5-12	45	38	4	24	33	26	-	48°	72°	120°
5-13	54	41	5	30	34	29	-	65°	66°	131°
5-14	41	34	5	20	28	24	-	63°	57°	120°

Many biofilm grazers have specialized bristles on their tongues that facilitate gathering biofilms (Elner et al. 2005; Kuwae et al. 2008) and have been shown to consume large quantities of biofilm on their migration towards their breeding grounds (Kuwae et al. 2008). All dimpled surfaces observed in the study material were associated with abundant bird footprints and thus are interpreted to record intensive surface grazing through pecking.

Variability in trace preservation on slab WAH01 and between the different slabs indicate that the Tambak trackways were emplaced on substrates with varying firmness and water saturation (Table 7). Substrate consistency and sediment moisture content play a central role in the occurrence and nature of trace preservation (e.g., Ekdale 1985; O'Brien 1987; Gingras et al. 1999, 2000b; Minter et al. 2007; Hamer and Sheldon 2010). Some tracks have sharp, well-defined margins (Table 7, Figs. 8, 10, 11) implying emplacement on a damp, consolidated 'soft' substrate (a 'softground' sensu Ekdale 1985; Gingras et al. 2000b). Other trackways show evidence of emplacement on water-saturated sediment (a 'soupground' sensu Ekdale 1985), such as elongate digit III toe drag marks behind individual footprints and raised ridges of sediment on the lateral margins of the traces (Figs 8, 9). Trackway WAH01-04 exhibits emplacement on a damp, consolidated 'soft' substrate in the first eleven footprints and emplacement on a soupy substrate in the last six footprints implying variable substrate consistency in closely spaced areas, all consistent with emplacement on exposed intertidal mudflats.

Many of the Tambak trackways are circuitous (Fig. 8) or characterized by abrupt changes in direction and irregular stride length (Figs. 8–11). Other specimens form 'trample grounds' where numerous shorebirds walked in multiple directions (Figs. 12, 13). All these behaviors are indicative of shorebird foraging (Elbroch and Marks 2001; Falk et al. 2010; Zonneveld et al. in press B). Trample grounds occur where flocks of shorebirds aggregate, typically taking advantage of subaerially exposed, resource-rich areas (Zonneveld et al. in press B). Irregular changes in direction and gait are common indicators of foraging shorebirds that use visual cues to locate prey (Zonneveld et al. in press B).

Coastal beaches, mudflats, swamps, and marshes are crucial habitats for migrating shorebirds, albeit typically in the short term (e.g., Burger et al. 1977; Mercier and McNeil 1994; Colwell 2010; Murray and Fuller 2015). During annual migrations, shorebird densities in these areas can be exceptionally high, with otherwise solitary species concentrating in dense multi-species aggregates competing for rich food resources (Recher 1966; Recher and Recher 1969; Burger et al. 1977; Quammen 1982, 1984; Mercier and McNeil 1994). Although many species of wading birds use intertidal areas to forage during seasonal migrations, access to food resources is temporally limited to low tide intervals when invertebrate-rich substrates are accessible (Burger et al. 1977; Tiedemann and Nehls 1997; Lourenço et al. 2008). However, infaunal prey may retreat deeper within their burrows at low tide, decreasing their accessibility to foraging birds. Thus, shorebirds that forage in intertidal settings commonly follow the tide, foraging as the tide retreats and resting during rising tide and high tide intervals (Burger et al. 1977; Tiedemann and Nehls 1997; Dias et al. 2006).

Kalimantan occurs, at present, in the heart of the East-Asian-Australasian Flyway, playing a major role as a stopover in shorebird and waterbird migration, from locations in Australia and maritime Southeast Asia to breeding locations in the northern extremes of the northern hemisphere (e.g., Dingle 2004; Nebel 2007; Bamford et al. 2008; Amano et al. 2010; Minton et al. 2011). Migratory shorebirds and waterbirds depend on 'staging sites' where they pause to rest and refuel on migrations that may span several thousand kilometers (Murray and Fuller 2015).

Intertidal areas, particularly tidal flats, comprise important staging areas due to plentiful and accessible food resources (Colwell 2010; Murray and Fuller 2015). Prey includes a wide variety of taxa, such as shrimp, crabs, amphipods, bivalves, gastropods, polychaetes, fish, and biomats (e.g., Cadée 1990; Mercier and McNeil 1994; Thrush et al. 1994; Hamilton et al. 2003; Elner et al. 2005; Mendonça et al. 2007; Kuwae et al. 2012; Murray and Fuller 2015; Schnurr et al. 2019; Hall et al. 2021). The occurrence of a moderately diverse avian footprint and foraging trace assemblage in the Tambak Member of the Tanjung Formation illustrates that shorebirds and waterbirds have been using wetlands in what is now Kalimantan for their food resources since at least the late Eocene.

CONCLUSIONS

The Tambak Member of the Tanjung Formation in the Asem Asem Basin, exposed in the Wahana Mine area near Satui, South Kalimantan records deposition on a low-relief tropical coastal plain. Analysis of interbedded silty mudstone, siltstone, coal, and very fine to fine-grained sandstone succession in the middle Tambak Member revealed a unit

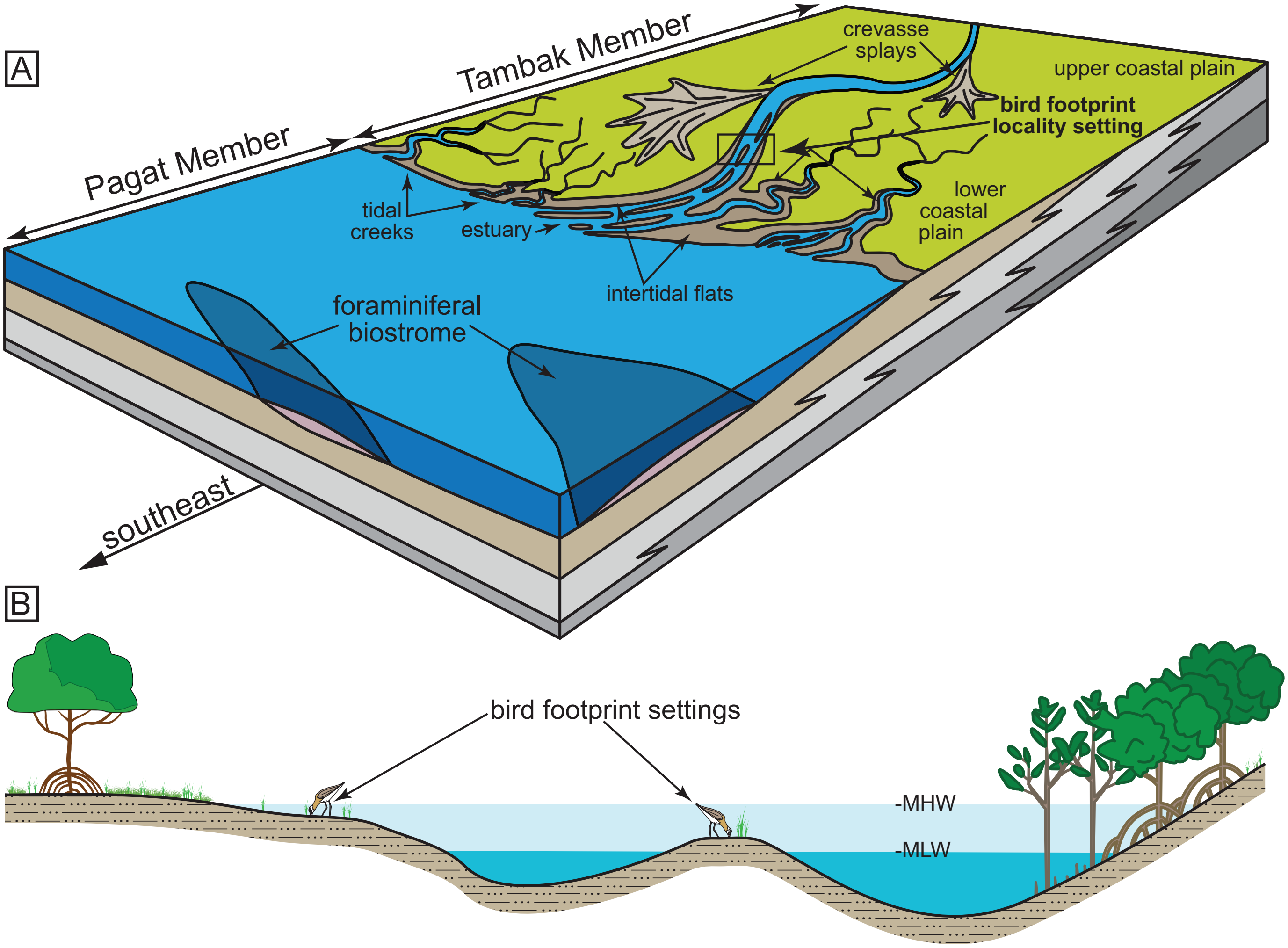


FIG. 16.—Interpreted depositional model of the upper Tambak and Pagat Members in the Satui area, Kalimantan. **A**) Schematic showing the distribution of depositional subenvironments (based in part on Witts et al. 2012; Zonneveld et al. in press A). **B**) Cross-section through a Tambak estuarine channel showing the interpreted setting of the avian trackways discussed herein.

characterized by numerous invertebrate and vertebrate trace fossils. The co-occurrence of sharp-based cross-stratified sandstone, lenticular to wavy-bedded siltstone/silty mudstone, and very fine-grained sandstone with bi-directional ripples and common reactivation surfaces indicates that this interval was deposited in a tidally modulated, likely estuarine, depositional setting.

The trace fossil association in the study interval comprises a moderately diverse assemblage consisting of *Arenicolites*, *Cylindrichnus*, *Diplocraterion*, *Palaeophycus*, *Planolites*, *Psilonichnus*, *Siphonichnus*, *Skolithos*, *Taenidium*, *Thalassinoides*, and *Trichichnus*. This association includes traces made by infaunal deposit feeders and infaunal suspension feeders as well as the dwelling traces of polychaetes, amphipods, decapods, and bivalves. The mix of ethologies is consistent with the *Psilonichnus* ichnofacies, consistent with the interpretation of a coastal, marginal marine depositional setting.

Vertebrate-derived trace fossils include avian footprints/trackways and traces interpreted to represent avian foraging. Avian footprint ichnogenera include *Aquatilavipes*, *Archaeornithipus*, *Ardeipeda*, *Aviadactyla*, cf. *Avipeda*, *Fuscinapeda*, cf. *Ludicharadripodiscus*, and two unnamed forms. Many of these ichnogenera are represented by multiple forms and thus, it is likely that the Tambak avian ichnofossil assemblage represents the activity of a moderately diverse shorebird and waterbird community.

Many trackways are associated with a variety of solitary and paired groove marks, V-shaped gouges, and conical divots. These features are identical to sweep marks, peck marks, and probe marks made by foraging shorebirds and waterbirds. Several of the bedding planes studied exhibited a dimpled fabric, identical to dimple-grounds in modern settings wherein shorebirds forage for biofilm to augment their diet of invertebrates and organic detritus. The diversity and co-occurrence of invertebrate and avian trace fossils, as well as the abundance of traces attributed to foraging behavior suggest that Tambak intertidal successions were important sources of food for Eocene birds.

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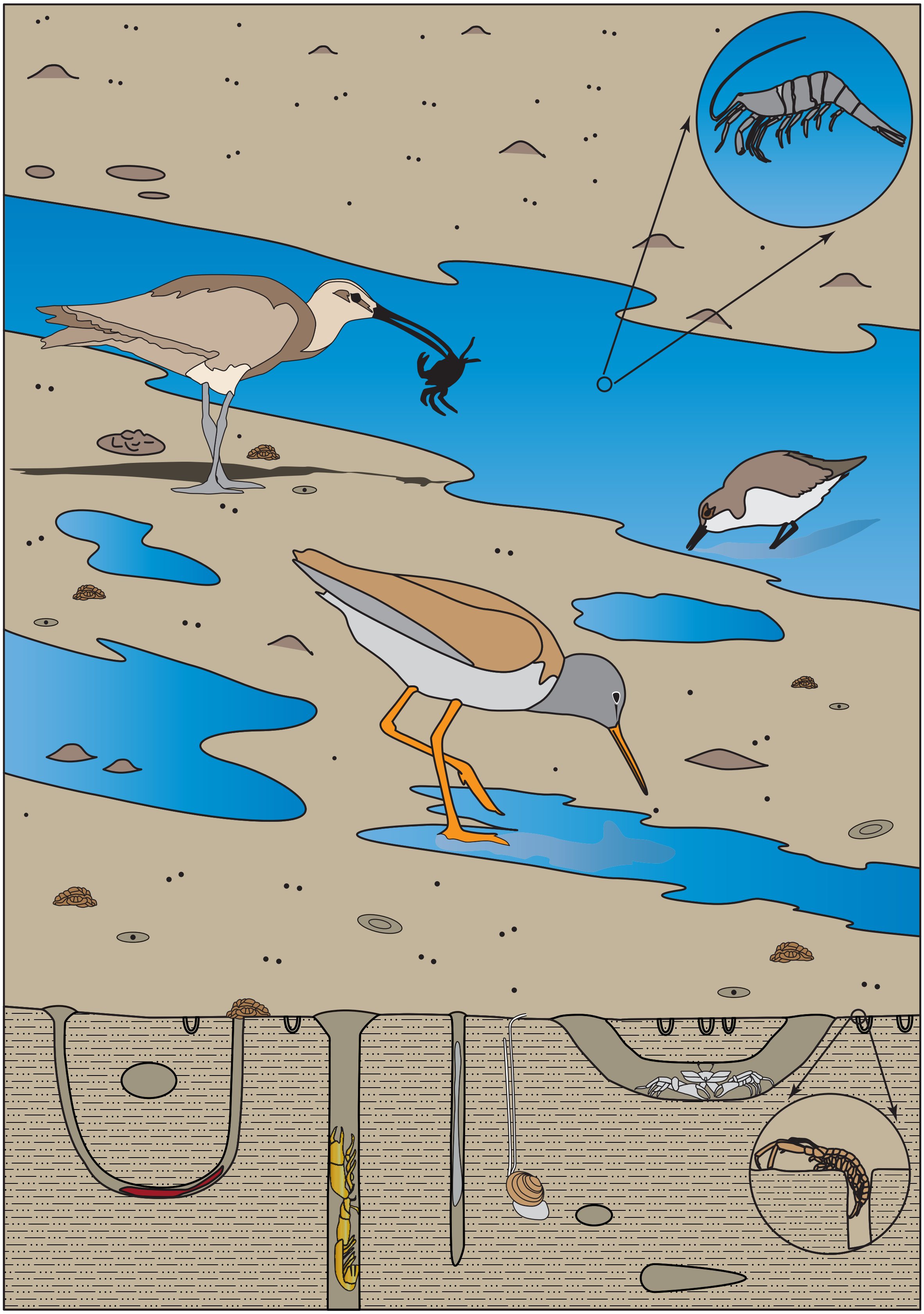

FIG. 17.—Reconstruction of the Wahanna intertidal flat succession showing a variety of shorebirds feeding and browsing for intertidal invertebrates.

TABLE 7.—*Substrate consistency and footprint preservation. Substrate categories from Ekdale (1985), Gingras et al. (2000b), Lettley et al. (2007).*

Substrate	Characteristics	Trace preservation	Wahanna examples
Soupground	Water-saturated, incompetent substrate, closer to a viscous fluid than to a true solid.	Common deformation of footprints, common dragmarks, common splash marks.	WAH01-03; WAH01-2; WAH01-3; WAH01-04 (part)
Softground	Competent, unconsolidated sediment, may be damp.	Footprints well-defined with crisp, clear margins, drag marks rare.	WAH01-04 (part), WAH01-5; WAH02-1; WAH02-2; WAH03-1; WAH04-06
Stiffground	Stable substrate, compacted but friable.	Traces limited to light scuff marks and claw marks.	NA
Firmground	Firm, compacted sediment.	Traces typically absent, claw marks possible.	NA
Hardground	Lithified/cemented sediment.	No traces left by bird feet.	NA

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