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ARTICLE

DESCRIPTION OF BIRD TRACKS FROM THE KITADANI FORMATION (APTIAN), KATSUYAMA, FUKUI, JAPAN WITH THREE-DIMENSIONAL IMAGING TECHNIQUES

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ABSTRACT

The Early Cretaceous ichnofossils of birds numerously occur in South Korea and China. Together with rich skeletal record from northeastern China, they facilitate our understanding about distribution and diversity of birds during the time. In contrast, in Japan, the fossil record of the Early Cretaceous birds is poorly known. Here, we report two ichnotaxa of the Early Cretaceous birds from the Aptian Kitadani Formation. We employ three-dimensional imaging techniques to objectively document and describe the specimens. Specimens include FPDM-F-74 and FPDM-F-75 recovered from an alternating sequence of fine sandstone and mudstone of the Kitadani Formation cropping out in the Kitadani Dinosaur Quarry, Katsuyama, Fukui, Japan. FPDM-F-74 is large in size, bears slender digits with pointy ends (claw impressions), and lacks hallux and webbing traces. These characters allow assignment of FPDM-F-74 to cf. *Aquatilavipes* ichnosp. FPDM-F-74 is particularly large compared to other *Aquatilavipes* ichnospecies. FPDM-F-75 is smaller than FPDM-F-74, lacks hallux trace, and has webbing traces between digits II and III, and III and IV. It is assignable to cf. *Gyeongsangornipes* ichnosp. FPDM-F-75 is larger than most avian ichnotaxa with webbing traces. Its webbing traces between digits II and III, and III and IV are characterized by their extension only up to the proximal half of the digits. FPDM-F-75 differs from *Gyeongsangornipes lockleyi* from the Albian Jindong Formation, Gyeongsang, South Korea in having larger size and smaller divarication between digits II and IV, and the extension of webbing traces. These specimens indicate the presence of possibly two medium-sized avian taxa in the Kitadani Formation and increase our knowledge of the Early Cretaceous avifauna in Japan. Additionally, webbing traces in FPDM-F-75 and other late Early Cretaceous avian tracks from Asia may suggest that such morphological feature was common among the fossil birds during the time.

Key words : bird track, ichnology, Tetori Group, Early Cretaceous, three dimensional imaging

今井拓哉・築地祐太・東　洋一（2018）3次元計測手法による，北谷層（Aptian，福井県勝山市）から産出した鳥類足印化石の記録及び記載．福井県立恐竜博物館紀要 17：1–8.

前期白亜紀の鳥類足印化石は，韓国や中国から多数報告されている．これらの化石は，中国東北部で多産する鳥類骨格化石と合わせて，当時の鳥類の分布や多様性を理解する上で重要な資料となっている．一方で，日本における前期白亜紀の鳥類化石記録は非常に乏しい．本研究では，北谷層（Aptian）から産出した2種の前期白亜紀鳥類生痕タクサを報告する．研究には，より客観的な足印の記録，記載を行うために，3次元計測手法を用いた．標本はFPDM-F-74 及びFPDM-F-75 で，それぞれ福井県勝山市の北谷恐竜発掘現場に露出する北谷層の，細粒砂岩と泥岩の互層から産出した．FPDM-F-74 は足印長，足印幅が大きく，細長い趾と尖った趾遠位端（鉤爪跡）が見られる一方，第一趾跡や水かき跡がない．これらの特徴から，FPDM-F-74 はcf. *Aquatilavipes* ichnosp.と同定される．FPDM-F-74 は他の*Aquatilavipes*の種と比較しても大きなことが特筆される．FPDM-F-75 はFPDM-F-74 より小さい．また，第一趾跡が無いのは同じだが，第二趾と第三趾，及び第三趾と第四趾の間に水かき跡が見られる点で異なる．FPDM-F-75 はcf. *Gyeongsangornipes* ichnosp.と同定される．他の半蹼の鳥類足跡化石と比べて大きく，第二趾と第三趾，及び第三趾と第四趾間の水かき跡が趾全長の半分未満しか張り出さないことが特徴である．FPDM-F-75 は，韓国慶尚道のJindong層（Albian）から産出する*Gyeongsangornipes lockleyi*よりも大きく，総指間角が狭い上，水かき跡の張り出し加減が異なる．これらの標本は，北谷層に2種の中型鳥類が存在することを示唆し，日本における前期白亜紀鳥類相に関する新たな知見となる．また，FPDM-F-75 や他の複数のアジア産鳥類足跡化石に水かき跡が見られることから，この形態学的特徴は珍しいものではなかったと考えられる．

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INTRODUCTION

Recently, our understanding about distribution and diversity of the Early Cretaceous bird tracks from East Asia was dramatically advanced. A ubiquitous number of the Early Cretaceous bird tracks is described from the Albian Haman and Jindong Formations of in the Gyeongsang, South Korea (Lockley et al., 2012). The bird tracks from South Korea represent a great variety of size and forms and include at least five avian ichnofamilies. In addition, the Lower Cretaceous of various regions across China has yielded numerous bird tracks (Lockley et al., 2013). Together with the rich skeletal remains of birds from northeastern China and north China, the fossil record indicates that birds were a major component of the ecosystem in the continental Asia during the Early Cretaceous.

In contrast to these continental regions, fossil record of the Early Cretaceous birds is quite limited in Japan and restricted to the Berriassian to Aptian non-marine deposits cropping out in central Honshu (main island). In this regard, the fossil record of birds in the Tetori Group was first documented by Azuma (1993, Ph.D. dissertation) where seven separate bird tracks from the Aptian Kitadani Formation, uppermost Tetori Group, Katsuyama, Fukui are documented through photographs. Unwin and Matsuoka (2000) reports fragmentary bird skeletons from the Hauterivian Kuwajima Fromation, middle Tetori Group, Hakusan, Ishikawa, and suggests they may belong to Enantiornithes. Azuma et al. (2002) describes an assemblage of 37 avian tracks from the Hauterivian Itsuki Formation, middle Tetori Group, Ono, Fukui, and assigns them to a new ichnospecies *Aquatiravipes izumiensis*. In addition, Imai and Azuma (2015) describes a fossil eggshell fragment, *Plagioolithus fukuiensis*, from the Aptian Kitadani Formation and attributes it to an avian theropod.

The latter formation has been known to produce abundant vertebrate tracks (Azuma, 2003; Lee at al., 2010; Tsukiji et al., 2018), and putative avian tracks were occasionally recognized among them. Here, employing 3D imaging techniques as recommended by Arakawa et al. (2002), we describe two different morphotypes of bird tracks from the Kitadani Formation, FPDM-F-74 and FPDM-F-75. Examination of the specimens adds to our database of the Early Cretaceous avian fossil record and aids our understanding of avifauna during the Early Cretaceous of Japan.

GEOLOGICAL SETTINGS

The Tetori Group, distributed in central Japan, consists of marine and non-marine deposits of the Middle Jurassic to the Early Cretaceous in age. This group is subdivided into the Kuzuryu, Itoshiro, and Akaiwa Subgroups in ascending order (Maeda, 1961). A variety of terrestrial vertebrates is yielded in the Itoshiro and Akaiwa Subgroups (Fujita, 2003; Sano, 2015; Sano and Yabe, 2016). The Kitadani Formation occurs as the uppermost part of the Akaiwa Subgroup (Maeda, 1961), and was formed in a meandering fluvial system (Yabe and Shibata, 2011; Suzuki et al., 2015). The depositional age of the Kitadani Formation has recently been suggested as the Aptian (Sano, 2015; Sano and Yabe, 2016).

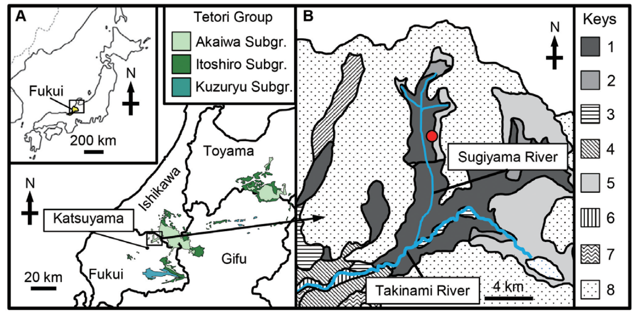

FIGURE 1. (**A**) Location map of Fukui, Japan, with distribution of the Tetori Group within the region. (**B**) Geological map around the Kitadani Dinosaur Quarry (red circle), modified from Shibata and Goto (2008). Keys: 1, Kitadani Formation and underlying Akaiwa Formation, Akaiwa Subgroup, Tetori Group; 2, Omichidani Formation; 3, Hida metamorphic rock; 4, Terrace deposit; 5, Nohi rhyolite; 6, Quaternary alluvial deposit; 7, Quaternary fan delta deposit; 8, Andesitic rock.

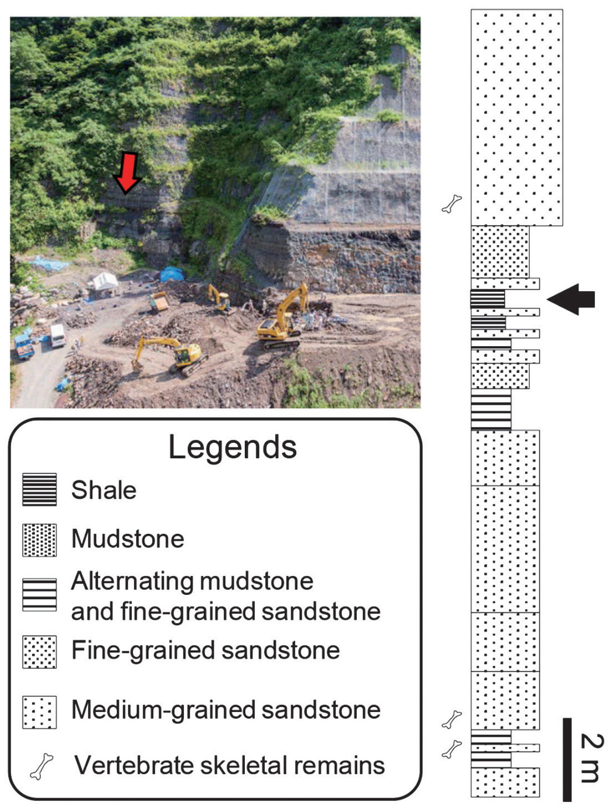

FIGURE 2. Photograph of the Kitadani Formation in the Kitadani Dinosaur Quarry, and a stratigraphic section of the formation taken at the red arrow in the photograph (modified from Tsukiji et al., 2018). The horizon from which the studied specimens were recovered is shown by the black arrow in the stratigraphic section.

The bird tracks described here come from the Kitadani Dinosaur Quarry. The quarry, where the Kitadani Formation crops out, is located along the left bank of Sugiyama River in the

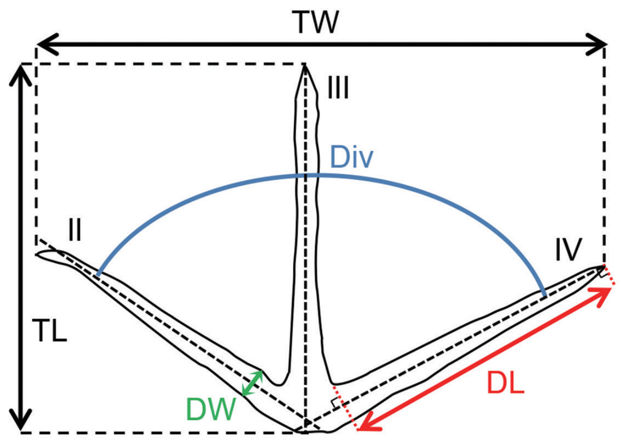

FIGURE 3. Measurement of tracks. See Leonardi (1987) for details. Abbreviations: Div, divarication angle; DL, digit length; DW, digit width; TL, track length; TW, track width.

northern part of Katsuyama, Fukui (Fig.1). Abundant vertebrate fossils including dinosaurs were collected from the quarry since 1989 (e.g., Azuma and Currie, 2000; Kobayashi and Azuma, 2003; Azuma et al., 2016). Furthermore, numerous vertebrate tracks, including those of amphibians (?), pterosaurs, and non-avian dinosaurs, were recovered (Azuma, 2003; Lee at al., 2010; Tsukiji et al., 2018). The specimens in this study occur in an alternating sequence of mudstone and fine sandstone within the Kitadani Formation along with amphibian (?), pterosaur, and non-avian theropod tracks (Fig. 2). Suzuki et al. (2015) interprets this sequence as a channel-fill deposit.

MATERIALS AND METHODS

In total of seven putative bird tracks were collected in 1991 from the Kitadani Formation in the Kitadani Dinosaur Quarry. Among them, two tracks, FPDM-F-74 (first documented by Azuma, 1993) and FPDM-F-75 (new specimen) exhibited clear topographic differences that could be captured with portable 3D imaging devices (Artec Spider and Artec Eva, Artec 3D), and further examined in this study. Upon acquiring the 3D data, they were processed to topographic images by image analysis software (VIVID2Rugle and 3D-Rugle, Medic Engineering Corporation). For measurements of tracks, we followed Leonardi (1987) (Fig. 3). Because digital pads are ambiguous in the studied specimens for measurements of true digit lengths, we measured free length (*sensu* Leonardi, 1987) instead.

SYSTEMATIC PALEONTOLOGY

Ichnofamily AVIPEDIDAE Sarjeant and Langston, 1994

Diagnosis.—Avian track showing three digits all directed forward; digits united or separate proximally; webbing lacking or limited to the most proximal part of the interdigital hypex.

Ichnogenus *Aquatilavipes* Currie, 1981

Diagnosis.—Three slender functional pedal digits; average total divarication angle > 100°, sharp claws; hallux impression lacking; and digit IV longer than digit II.

cf. *Aquatilavipes* ichnosp. (Fig. 4A–C)

Materials.—FPDM-F-74, single natural cast of left pes.

Horizon and Locality.—Kitadani Formation, Akaiwa Subgroup, Tetori Group, Kitadani Dinosaur Quarry, Katsuyama, Fukui, Japan.

Description.—FPDM-F-74 is 60 mm long and 94 mm wide, and TL/TW ratio is 0.63. Lengths of digits II, III, and IV are 40 mm, 50 mm, and 48 mm, respectively. Digit widths of digits II, III, and IV are 4 mm, 5 mm, and 7 mm, respectively. Divarication angles are 56° between digits II and III, and 61° between digits III and IV, resulting in the total divarication angle of 117° between digits II and IV (Table 1). Pointy distal ends, claw traces, are observed on digits II, III, and IV; those on digits II and IV curve slightly distally. Sediment fracture obscures portion of digit II, III, and IV proximally. In total of three digital pads are observable on the digit IV. Web traces are not observable. Heel impression is, while partially obscured, shallow-U shaped. Hallux trace is absent. Three-dimensional scan data is available in STL format as supplementary data (https://www.dinosaur.pref.fukui.jp/archive/memoir/17_Imai_supplemental_materials.zip).

Ichnofamily incertae sedis
Ichnogenus *GYEONGSANGORNIPES* Kim, Kim, Oh, and Lee, 2013

Diagnosis.—Asymmetrical semipalmate, strong mesaxonic bird track with three widely splayed thin digits impressions (II–IV) with sharp end, asymmetrical web traces proximal to mesial between digits II–III–IV

cf. *Gyeongsangornipes* ichnosp. (Fig. 4D–F)

Material.—FPDM-F-75, single natural cast of left pes.

Horizon and Locality.—Kitadani Formation, Akaiwa Subgroup, Tetori Group, Kitadani Dinosaur Quarry, Katsuyama, Fukui, Japan.

Description.—FPDM F-75 is 50 mm long and 71 mm wide, and FL/FW ratio is 0.71. Lengths of digits II, III, and IV are 29 mm, 35 mm, and 27 mm, respectively. Digit widths of digits II, III, and IV are 6 mm, 5 mm, and 7 mm, respectively. Divarication angles are 55° between digits II and III, and 46° between digits III and IV, resulting in the total divarication angle of 101° between digits II and IV (Table 1). Possible claw traces are present on digit III and IV. Likely webbing traces between digits II and III, and digits III and IV characterizes the specimen. Webbing traces extend less than half the lengths of digits. Heel impression is, while obscured, shallow-U shaped. Hallux trace is not observable.

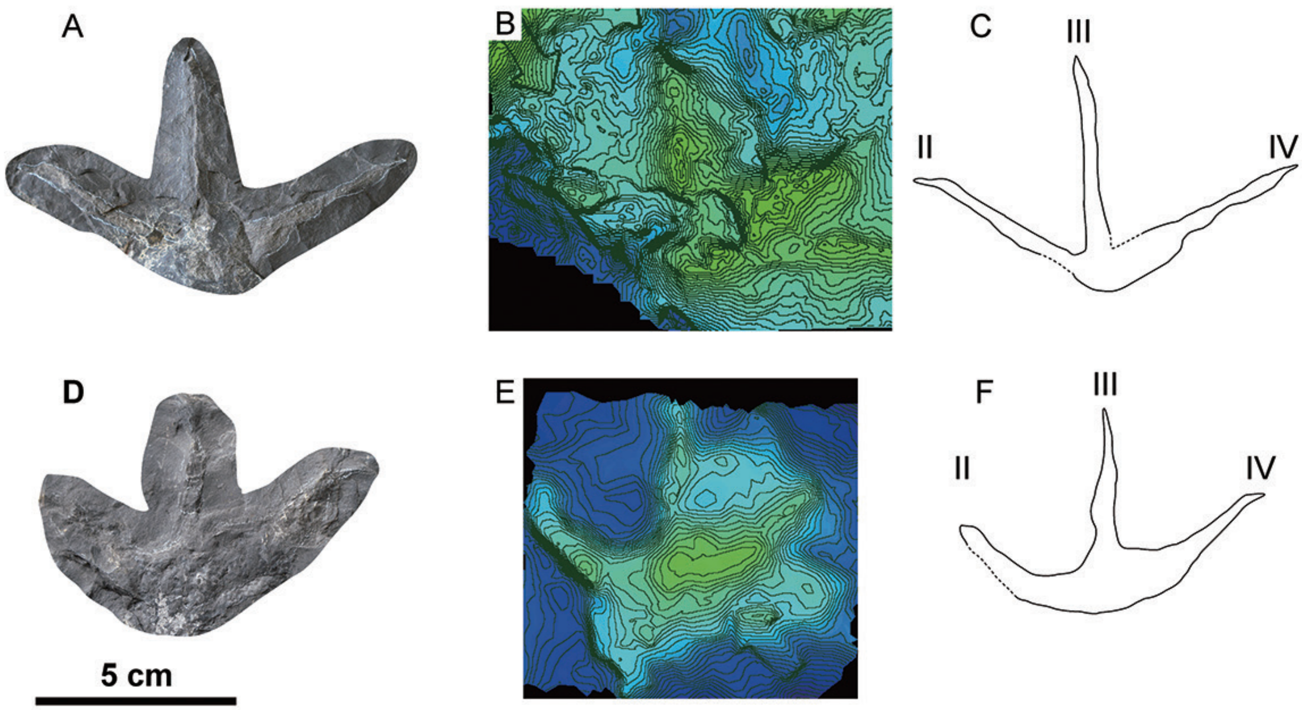

FIGURE 4. Photographs (left), topographic images (center), and line drawings (right) of the studied specimens. (**A–C**) FPDM-F-74. (**E–F**) FPDM-F-75. All are in the same scale. Dotted lines denote ambiguous track outlines. A contour interval is 0.3 mm. Note that the specimens are natural casts and appear convex.

Three-dimensional scan data is available in STL format as supplementary data.

DISCUSSION

Conventionally, Mesozoic tridactyl tracks with total divarication angles between digits II and IV > 100° have been assigned to birds (e.g., Currie, 1981). Lockley et al. (1992) provides a list of criteria to distinguish fossil avian tracks. These criteria include: 1, similarity to those of extant birds; 2, small size; 3, slender digit impressions, with indistinct differentiation of digital pad impressions; 4, wide divarication angle (approximately 110°–120°) between digits II and IV; 5, a posteriorly directed hallux; 6, slender claws; 7, distal curvature of lateral (II and IV) claws away from the central axis of the foot; 8, track density; 9, associated fossils and feeding behavior; and 10, sedimentological evidence regarding track-bearing deposits. This interpretation was recently challenged by Xing et al. (2015), which argues that extant-large-bird tracks may exhibit divarication angles < 100° and small-non-avian-theropod tracks have been reported to exceed total divarication angles of 100°. Xing et al. (2015) recommends using the footprint length to pace length ratio to confidently differentiate large-bird tracks and small-non-avian-theropod tracks. While the approach suggested by Xing et al. (2015) is acceptable, FPDM-F-74 and FPDM-F-75 are isolated tracks and do not permit measurements of the pace lengths. Therefore, we assign FPDM-F-74 and FPDM-F-75 to birds based on the following criteria after Lockley et al. (1992): 1, relatively small size compared to majority of non-avian theropod tracks; 2, slender digit impressions with indistinct digital pad impressions; 3, total divarication angles between digits II and IV > 100°; 4, slender claws; and 5, distal curvature of lateral claws away from the central axis of the foot. In FPDM-F-75, this interpretation is supported by the presence of webbing traces, which are not known from non-avian-theropod tracks to date. We also plotted total divarication against TL for selected small non-avian theropod

TABLE 1. Measurements of the studied specimens. Abbreviations: TL, track length; TW, track width.

Specimens	TL (mm)	TW (mm)	TL/TW	Digit lengths (mm)			Divarication			Digit widths (mm)		
				II	III	IV	II-III	III-IV	II-IV	II	III	IV
FPDM-F-74	60	94	0.63	45	50	48	56	61	117	4	5	7
FPDM-F-75	50	71	0.71	29	35	27	55	46	101	6	5	7

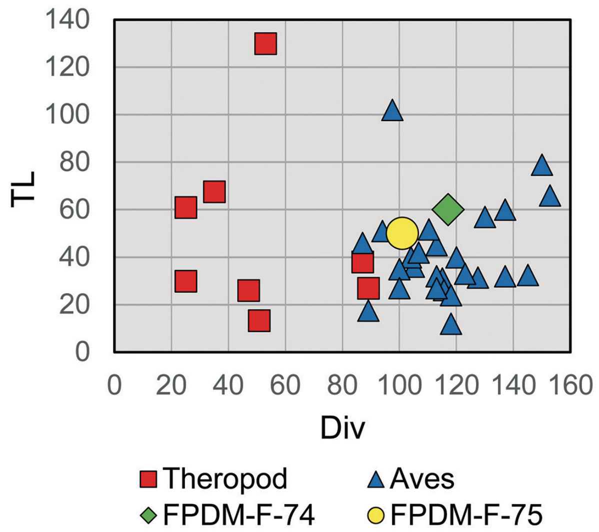

FIGURE 5. Scatter plot of TL (track length) against Div (divarication) for selected non-avian theropod ichnotaxa, the Early Cretaceous avian ichnotaxa, and FPDM-F-74 and FPDM-F-75 listed in Table 2.

tracks and the Early Cretaceous avian tracks that were previously described (Table 2), and added FPDM-F-74 and FPDM-F-75 to the scatterplot. These specimens are plotted with the cluster of avian tracks (Fig. 5), which is concordant with our interpretation.

Both FPDM-F-74 and FPDM-F-75 are characterized by relatively-large size and shallow-U-shaped heel impressions. On the other hand, major differences between the specimens include divarication angles between digits II and IV and presence of webbing traces only in FPDM-F-75. Nonetheless, these differences do not necessarily indicate that different species left the traces. For example, total divarication angles between digits II and IV is known to vary over ± 10° in a large wading bird, *Ardea herodias* (Xing et al., 2015) from the average. Thus, it is possible the difference of divarication angles between FPDM-F-74 and FPDM-F-75 merely represents this variation. While FPDM-F-75 does not exhibit webbing traces, it is possible that the lack of the webbing traces in FPDM-F-74 results from poor preservation. Thus, while we assign them to different ichnotaxa, their ichnomorphological differences possibly reflect preservational artefact.

FPDM-F-74 is characterized by its large size, which exceeds

TABLE 2. List of selected small non-avian theropod ichnotaxa, the Early Cretaceous avian ichnotaxa, and FPDM-F-74 and FPDM-F-75, with Div (divarication), TL (track length), and TW (track width).

	Ichnotaxon	TL (mm)	TW (mm)	Div (°)	Age	Country	Reference
Theropoda	*Grallator emensis*	27	16	89	Early Cretaceous	China	Zhen et al., 1994
	Grallator isp.	130	80	53	Barremian	China	Xing et al., 2009
	Minisauripus chuanzhuensis	30	18	25	Early Cretaceous	China	Zhen et al., 1994
	Minisauripus zhenshuonani	26	18	47	Berriassian-Barremian	China	Xing et al., 2016
	Minisauripus zhenshuonani	61	38	25	Aptian	South Korea	Lockley et al., 2008
	Ornithomimipodidae indet.	13	11	51	Late Cretaceous	USA	Lockley 2011
	Theropoda indet.	68	44	35	Toarcia–Plienbachian	USA	Lockley, 2011
	Theropoda indet.	38	31	87	Toarcia–Plienbachian	USA	Rainforth and Lockley, 1996
Aves	*Aquatilavipes* isp.	36	43	105	Aptian-Albian	South Korea	Kim et al., 2012; Huh et al., 2012
	Aquatilavipes isp.	40	44	104	Early Cretaceous	China	Xing et al., 2011
	Aquatilavipes swiboldae	45	57	113	Aptian	Canada	Currie, 1981
	Aquatiravipes sinensis	31	38	115	Early Cretaceous	China	Zhen et al., 1994
	Archaeornithipus meijidei	12	12	118	Berriassian	Spain	Vidarte, 1996
	Avipedidae indet.	32	43	113	Early Cretaceous	China	Li et al., 2002
	Donyangornipes sinensis	35	40	100	Albian-Cenomanian	China	Azuma et al., 2013
	Goseongornipes isp.	40	55	120	Early Cretaceous	China	Xing et al., 2011
	Goseongornipes markjonesi	33	44	145	Albian	South Korea	Lockley et al., 2006
	Gyeongsangornipes lockleyi	32	41	128	Early Cretaceous	South Korea	Kim et al., 2013
	Ignotornis gajinensis	57	55	130	Aptian-Albian	South Korea	Kim et al., 2012
	Ignotornis mcconnelli	42	47	107	Albian-Cenomanian	U.S.A.	Mehl, 1931; Lockley et al., 2009
	Ignotornis isp.	26	34	116	Aptian-Albian	South Korea	Lim et al., 2000
	Ignotornis yangi	33	45	123	Aptian-Albian	South Korea	Kim et al., 2006
	Jindongornipes kimi	60	75	137	Albian	South Korea	Lockley et al., 1992
	Koreanaornis anhuiensis	33	36	123	Early Cretaceous	China	Jin and Yan, 1994; Lockely et al., 2013; Xing et al., 2018
	Koreanaornis cf. *hamanensis*	24	34	118	Albian-Cenomanian	China	Azuma et al., 2013
	Koreanaornis dodsoni	46	51	87	Early Cretaceous	China	Xing et al., 2011
	Koreanaornis hamanensis	27	34	113	Albian	South Korea	Kim, 1969; Lockley et al., 1992; Kim et al., 2013
	Koreanaornis lii	32	46	137	Aptian-Albian	China	Xing et al., 2016
	Limiavipes curriei	79	63	150	Albian	Canada	McCrea et al., 2001; McCrea et al., 2014
	Magnoavipes asiaticus	18	18	89	Early Cretaceous	China	Matsukawa et al., 2014
	Moguiornipes robusta	51	56	94	Early Cretaceous	China	Xing et al., 2011
	Paxavipes babcockensis	27	30	100	middle-?upper Albian	Canada	McCrea et al., 2015
	Shandongornipes muxiai	66	53	153	Aptian-Albian	China	Li et al., 2005; Lockley et al., 2007; Lockley et al., 2013
	Tatarornipes chabuensis	52	60	110	Barremian	China	Lockley et al., 2012
	Wupus agilis	102	70	98	Berriasian-Santonian	China	Xing et. al., 2007; Xing et al., 2015
	FPDM-F-74	60	94	117	Aptian	Japan	This Study
	FPDM-F-75	50	71	101	Aptian	Japan	This Study

other Mesozoic *Aquatiravipes* ichnospecies. Nonetheless, even larger Early Cretaceous avian ichnotaxa, such as *Shandongornipes muxiai* Li, Lockley, and Liu, 2005, and *Limiavipes curriei* McCrea and Sarjeant, 2001, are known (Table 2). Thus, FPDM-F-74 is not exceptionally large among the avian tracks from the Early Cretaceous. FPDM-F-74 exhibits the diagnostic characters for *Aquatilavipes* erected by Currie (1981) (i.e., three slender functional pedal digits, average divarication angles > 100°, sharp claws, and no hallux impression, digit IV is longer than digit II). However, with only a single track, it is difficult to determine whether FPDM-F-74 is confidently assignable to *Aquatilavipes*.

Among known Mesozoic bird tracks with webbing traces, FPDM-F-75 is distinguished from all ignotornids by the lack of hallux impression (Kim et al., 2006). In addition, the size of specimens clearly exceeds those of other ignotorid ichnotaxa. The specimens are comparable in size to *Sarjeantopodus semipalmatus* Lockley, Nadon, and Currie, 2004, medium-sized webbed bird tracks from the Maastrichtian Lance Formation, Wyoming, U.S.A. However, in *S. semipalmatus*, the webbing traces between digits III and IV extends more than half the digit lengths, while not in FPDM-F-75. *Dongyangornipes sinensis* Azuma, Lu, Jin, Noda, Shibata Chen, and Zheng, 2003, is another bird ichnotaxon of middle-sized semi-palmate tracks whose webbing traces extend from the distal end of digits II and IV. FPDM-F-75 is larger in size and has both webbing traces from less than half the length of each digit. FPDM-F-75 differs from *Gyeongsangornipes lockleyi* Kim, Kim, Oh, and Lee, 2013 from the Albian Jindong Formation, Gyeongsang, South Korea in having larger size and smaller divarication. In addition, unlike *G. lockleyi*, FPDM-F-75 has both webbing traces extending less than half the length of digits.

The webbing trace in FPDM-F-75 is small in comparison to those of other fossil and extant birds, and its function for propulsion on or in the water is questionable. Indeed, according to Leonardi (1987, p. 47), (interdigital) web is regarded as "... characteristic of partially or wholly aquatic animals." However, in extant birds, interdigital web is present even in non-aquatic taxa such as grouse and some domesticated Galliformes (Kochan, 1994). The web of these birds is smaller than those in aquatic and semi-aquatic birds and comparable to the one inferred for FPDM-F-75. Thus, interdigital web does not necessarily imply water-related habitat and "incipient web" can be present in fossil birds for other (yet unknown) functional purposes.

Discovery of FPDM-F-74 and FPDM-F-75 in the Kitadani Formation indicates the presence of possibly two medium-sized avian taxa and increases our knowledge of the Early Cretaceous avifauna in Japan. Additionally, web traces in FPDM-F-75 and other aforementioned late Early Cretaceous avian tracks from Asia may suggest such morphological feature was not uncommon among the fossil birds during the time. The lack of trackways does limit our understanding about the ichnotaxonomy and ichnomorphology of the avian tracks in the Kitadani Formation, which should be elucidated with further excavation efforts in the formation in the future.

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