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ARTICLE

ICHNOTAXONOMIC REVISION OF DINOSAUR TRACKS FROM THE LOWER CRETACEOUS TETORI GROUP, JAPAN

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ABSTRACT

Recently, ichnotaxonomic description and comparison of dinosaur tracks were developed by objective and quantitative analyses using three-dimensional digital data. However, many dinosaur tracks from the Tetori Group discovered in the 1990's were described on the basis of classical methods. We developed ichnotaxonomic descriptions for 14 dinosaur tracks from the Tetori Group in the Kuzuryu and Shiramine areas from objective and quantitative analyses. Our assessments of the 14 tracks identified five theropods and seven iguanodontids as trackmakers. Ichnotaxonomic comparisons show that the theropod tracks include the ichnofamilies Grallatoridae and Eubrontidae, and the iguanodontid tracks include the ichnogenera *Caririchnium* and *Amblydactylus*. The Tetori Group has yielded dinosaur tracks from at least three different horizons, and we subdivided this ichnoassemblage into the Itsuki, Akaiwa, and Kitadani dinosaur ichnofauna on the basis of the depositional age. These dinosaur ichnofaunas are dominated by theropods and iguanodontids; however, the ichnofaunal diversity of the Itsuki dinosaur ichnofauna is lower than those of the Akaiwa and Kitadani dinosaur ichnofaunas. This difference is probably related to depositional environments.

Key words: dinosaur track, Tetori Group, Lower Cretaceous, ichnotaxonomy, Kuzuryu area, Shiramine area

築地祐太・酒井佑輔・東洋一（2019）下部白亜系手取層群から産出した恐竜足跡化石の生痕化石分類学的な再検討．福井県立恐竜博物館紀要 18：1–20.

近年，恐竜足跡化石の生痕化石分類学的な記載や比較は，3 次元デジタルデータを用いた客観的・定量的な手法によって発展してきた．しかし，1990 年代に手取層群から発見された恐竜足跡化石の多くは，古典的な手法のみに基づいて記載されている．本研究では，近年の手法を用いて九頭竜および白峰地域の手取層群から産出した 14 点の恐竜足印化石の生痕化石分類学的な再検討を行った．再検討の結果，5 点の獣脚類と 7 点のイグアノドン類の足印化石が再同定された．また，獣脚類の足跡化石には生痕化石科 Grallatoridae と Eubrontidae が含まれ，イグアノドン類の足跡化石には生痕化石属 *Caririchnium* と *Amblydactylus* が含まれることが分かった．手取層群から産出する恐竜足跡化石は，少なくとも 3 つの層準から産出しており，本研究ではそれらを堆積年代に基づいて，伊月・赤岩・北谷恐竜生痕化石動物群に細分した．これらの生痕化石動物群は，獣脚類とイグアノドン類が優勢なことで特徴づけられるが，伊月恐竜生痕化石動物群は赤岩・北谷恐竜生痕化石動物群に比べ多様性が低い．これは，堆積環境の違いによるものと考えられる．

INTRODUCTION

Detailed morphological examination of dinosaur tracks is the most basic and important in ichnotaxonomic classification (e.g., Thulborn, 1990; Arakawa et al., 2002; Falkingham et al., 2018; Marchetti et al., 2019). In most cases until the 2000s, the depiction of dinosaur tracks was done by photos or illustrations drawn by researchers or professional artists, but there could be differences on the illustrations of the same specimens (Arakawa et al., 2002).

Many dinosaur tracks were reported from several localities of the Lower Cretaceous Tetori Group in the 1990s (Manabe et al., 1989; Kunimitsu et al., 1990; Azuma and Takeyama, 1991; Azuma et al., 1992; Kojima et al., 1992). Among them were several dinosaur tracks from the Kuzuryu and Shiramine areas described and illustrated by different researchers (Azuma and Takeyama, 1991; Lockley and Matsukawa, 1998). Azuma and

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Takeyama (1991) first described seven dinosaur tracks from these areas. Using moiré pictures to illustrate the specimens, they described them as multiple ichnotaxa, whereas Lockley and Matsukawa (1998) showed different illustrations of the specimens and argued that these ichnotaxa are *nomina dubia*. Because their interpretation lacked objective and quantitative assessments, ichnotaxonomic classifications of these specimens are indefinite.

Recent developments in three-dimensional (3D) laser-scanning technology have permitted more objective and quantifiable interpretations of dinosaur tracks (e.g., Arakawa et al., 2002; Lockley, 2009; Xing et al., 2018; Falkingham et al., 2018). We therefore reexamined ten dinosaur tracks from the Tetori Group in the Kuzuryu and Shiramine areas that were originally described or reported in the 1990s (Azuma and Takeyama, 1991; Azuma et al., 1992; Kojima et al., 1992) (Table 1). We additionally carried out ichnotaxonomic description of unpublished four dinosaur tracks from same areas.

GEOLOGICAL SETTING

The Tetori Group is a Lower Cretaceous sequence distributed in the Inner Zone of southwestern Japan, on the eastern margin of Asia (Oishi, 1933; Maeda, 1961; Kusuhashi et al., 2002; Matsukawa et al., 2006a; Sano, 2015; Yamada and Sano, 2018) (Fig. 1A). Abundant terrestrial vertebrate fossils, including dinosaurs, have been recovered from this group (Fujita, 2003; Sano, 2015).

The Tetori Group in the Kuzuryu area is composed of the Yambara, Ashidani, Obuchi, Itsuki, and Nochino Formations in ascending order (Sakai et al., in press) (Fig. 1B). The Itsuki Formation is composed mainly of alternating beds of sandstone and mudstone. Plant, mollusk, and vertebrate fossils commonly occur in the Itsuki Formation (e.g., Oishi, 1933; Maeda, 1952, 1957; Matsukawa and Ido, 1993; Manabe, 1999; Fujita, 2002; Sakai et al., 2016, in press). Some vertebrate tracks, including those of dinosaurs and birds, have been recovered from the Itsuki Formation (Azuma and Takeyama, 1991; Azuma et al., 2002). The Nochino Formation is composed of coarse-grained sandstone, conglomerate, and alternating beds of sandstone and mudstone. Dinosaur tracks as well as fossil plants have been recovered from this formation (Azuma et al., 1992; Matsukawa et al., 2005; Sakai et al., in press).

The Tetori Group in the Shiramine area is composed of the Gomijima, Kuwajima, Akaiwa, and Kitadani Formations in ascending order (Sakai et al., 2018) (Fig. 1B). The Kuwajima Formation is composed mainly of alternating beds of sandstone and mudstone, and plant, mollusk, vertebrate remains, and dinosaur tracks commonly occur in this formation (e. g. Oishi, 1933; Maeda, 1958, Kimura et al., 1978; Manabe and Barrett, 2000; Isaji et al., 2005; Sakai et al., 2018). The Akaiwa Formation is composed of coarse-grained sandstone, conglomerate, and alternating beds of sandstone and mudstone, and fossil plants, turtles, and vertebrate tracks have been recovered from this formation (Azuma and Takeyama, 1991; Matsuoka et al., 2001; Matsukawa et al., 2005; Hirayama et al., 2012; Sakai et al., 2018).

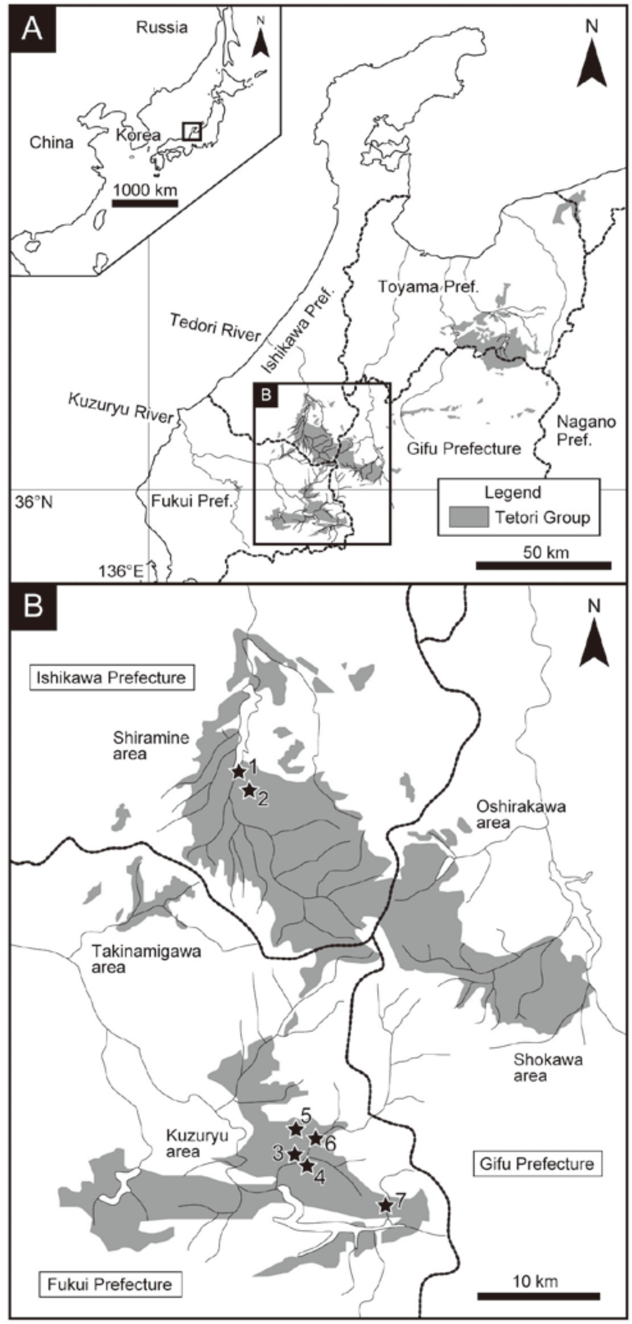

FIGURE 1. **A**, Distribution of the Tetori Group (Maeda, 1961). **B**, Map showing the dinosaur track localities in the Kuzuryu and Shiramine areas. 1, Kaseki-Kabe in the Shiramine area. 2, Byakodan in the Shiramine area. 3, Nochino in the Kuzuryu area. 4, Itsuki in the Kuzuryu area. 5, Nagakuradani in the Kuzuryu area. 6, Maesaka in the Kuzuryu area. 7, Hayashidani in the Kuzuryu area.

MATERIALS AND METHODS

The studied 14 specimens were recovered from the Kuzuryu

TABLE 1. List of materials.

No.	Original article or report	Trackmaker / Ichnotaxa (orginal article or report)	Trackmaker / Ichnotaxa (this study)	Locality	Horizon	Mold/Cast
ISBEV003	Azuma and Takeyama (1991)	Theropod / *Baykudansauropus*	Thgeropod / Grallatoridae	Byakodan, Shiramine area	Akaiwa Formation	Mold
ISBEV001	Azuma and Takeyama (1991)	Theropod / *Kuwajimasauropus*	Theropod / Eubrontidae	Kaseki-kabe, Shiramine area	Kuwajima Formation	Cast
FPDM-F-170	Azuma and Takeyama (1991)	Theropod / *Itsukisauropus*	Theropod / indet.	Nochino, Kuzuryu area	Itsuki Formation	Mold
OMFJ F-1	unpublished		Theropod / indet.	Nochino, Kuzuryu area	Itsuki Formation	Cast
ISBEV004	unpublished		Theropod / indet.	Kaseki-kabe, Shiramine area	Kuwajima Formation	Cast
FPDM-F-164	Azuma and Takeyama (1991)	Iguanodontid / *Shiraminesauropus*	Iguanodontid / *Caririchnium* isp.	Kaseki-kabe, Shiramine area	Kuwajima Formation	Cast
ISBEV002	Azuma and Takeyama (1991)	Iguanodontid / *Gigantoshiraminesauropus*	Iguanodontid / *Caririchnium* isp.	Kaseki-kabe, Shiramine area	Kuwajima Formation	Cast
FPDM-F-173	Azuma and Takeyama (1991)	Iguanodontid / *Shiraminesauropus*	Iguanodontid / *Caririchnium* isp.	Hayashidani, Kuzuryu area	Itsuki Formation	Cast
OMFJ F-2	Kojima et al. (1992)	Iguanodontid / indet.	Iguanodontid / *Amblydactylus* isp.	Hayashidani, Kuzuryu area	Itsuki Formation	Cast
OMFJ F-3-T1	unpublished		Iguanodontid / *Amblydactylus* isp.	Itsuki, Kuzuryu area	Itsuki Formation	Cast
OMFJ F-3-T2	unpublished		Iguanodontid / Iguanodontipodidae	Itsuki, Kuzuryu area	Itsuki Formation	Cast
OMFJ F-4	Azuma et al. (1992)	Iguanodontid / indet.	Iguanodontid / Iguanodontipodidae	Nagakuradani, Kuzuryu area	Nochino Formation	Cast
OMFJ F-5	Azuma and Takeyama (1991)	Iguanodontid / indet.	uncertain	Nochino, Kuzuryu area	Itsuki Formation	Cast
OMFJ F-6	Azuma et al. (1992)	Theropod / indet.	uncertain	Maesaka, Kuzuryu area	Nochino Formation	Cast

and Shiramine areas (Table 1). Among eight tracks, including FPDM-F-170 and 173, and OMFJ F-1 to 6, were found in the Kuzuryu area. Azuma and Takeyama (1991) described FPDM-F-170, 173, and OMFJ F-5 from the Itsuki Formation, Kojima et al. (1992) reported OMFJ F-2, 4, and 6 from the Itsuki and Nochino Formations, among which OMFJ F-4 and 6 were described by Azuma et al. (1992). Recently, three new tracks, including OMFJ F-3 and 4 (including two tracks), were recovered from the Itsuki Formation. Another five tracks, including FPDM-F-164 and ISBEV001 to 004, have been recovered from the Kuwajima and Akaiwa Formations in the Shiramine area, and FPDM-F-164 and ISBEV001 to 003 have been described by Azuma and Takeyama (1991).

Using a portable 3D-imaging device (Artec Eva, Artec 3D), we captured 3D digital data of these specimens. However, ISBEV003 could not be captured because the impression of this specimen is filled by sediments. We processed the digital data of these materials into topographic images by image-analysis software (VIVID2Rugle and 3D-Rugle, Medic Engineering Corporation) and then, using a digital program (Adobe Illustrator CC, Adobe Systems Incorporated), traced outlines of the materials based on macroscopy and the topographic images.

For measurements, we measured the following parameters: footprint length (FL) and footprint width (FW); total divarication (TD), divarication between digits II and III (D II-III), and divarication between digits III-IV (D III-IV); anterior triangle length (ATL) and anterior triangle width (ATW) (Fig. 2). We used standard methods of Leonardi (1987) to measure FL, FW, TD, D II-III, D III-IV, and PL and modified methods of Weems (1992) and Lockley (2009) for ATL and ATW. We also performed bivariate analysis, setting FL/FW against ATL/ATW ratios for comparison with other dinosaur tracks.

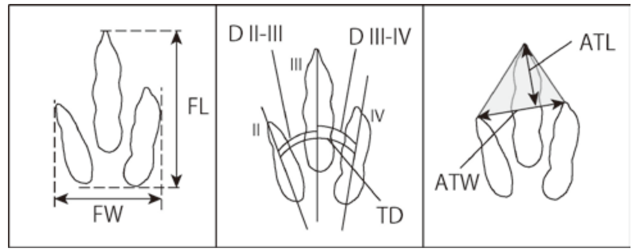

FIGURE 2. Measurement of dinosaur tracks modified from Leonardi (1987) and Lockley (2009). FL, footprint length. FW, footprint width. D II-III, divarication between digits II and III. D III-IV, divarication between digits III and IV. TD, total divarication. ATL, anterior triangle length. ATW, anterior triangle width.

SYSTEMATIC ICHNOLOGY

THEROPOD TRACKS

Ichnofamily GRALLATORIDAE Lull, 1904

Diagnosis.—Small bipedal forms; footprint tridactyl, limbs very long; no manus nor caudal impression.

GRALLATORIDAE indet. (Fig. 3A; Table 2)

Material.—ISBEV003, Byakodan specimen of Azuma and Takeyama (1991), a natural mold from the Shiramine area.

Horizon and locality.—Byakodan in the Shiramine area, Hakusan City, Ishikawa Prefecture, Lower Cretaceous Akaiwa Formation of Tetori Group, Japan.

Description.—ISBEV003 is an isolated left pes track of natural mold. Although the depression of the footprint is closely packed by sediments, the footprint outline is visually recognizable (Fig. 3A). This specimen exhibits small size, comparatively slender digit impressions with sharp distal ends, and a (narrow) metatarsophalangeal impression. FL is longer than FW, and its mesaxony is strong. Digit III is longer than the digit IV, which is longer than the digit II. The proximal part of digit IV connects to the metatarsophalangeal impression, which is approximately situated on the longitudinal axis of the footprint.

Remarks.—The specimen ISBEV003 was first described as the ichnospecies *Byakudansauropus shiraminensis* (Azuma and Takeyama, 1991). Matsukawa et al. (1995) noted that the description is undiagnostic and lacking ichnotaxonomic comparison. Lockley and Matsukawa (1998) considered that this ichnotaxon is a *nomen dubium*.

On the other hand, our ichnotaxonomic revision indicates that ISBEV003 is comparable to the ichnofamily Grallatoridae. Generally, the ichnofamily Grallatoridae is characterized by FL < 25 cm, by a pes track longer than its width (FL > FW), and by strong mesaxony (Lull, 1904; Olsen et al., 1998). These features are also seen in ISBEV003.

The ichnofamily Grallatoridae or *Grallator*-like tracks have been discovered and described from around the world. In East Asia, most of them were considered to be the ichnogenera *Grallator* and *Jialingpus* (Lockely and Matsukawa, 2009; Lockley et al., 2013). *Grallator* is characterized by FL/FW > 2 and by TD in the range of 10 °–30 ° (Olsen et al., 1998). The TD of ISBEV003 is much wider than that of *Grallator*, and its FL/FW = 1.35, far lower than is characteristic of *Grallator*. *Jialingpus* has distinctively well-preserved phalangeal pad, hallux, and metatarsal impressions (Zhen et al., 1983; Lockley et al., 2013; Xing et al., 2014). Although the specimen ISBEV003 has metatarsophalangeal impression, it lacks well-preserved phalangeal pad and hallux impressions. From the above, the specimen ISBEV003 lacks distinct features from other ichnogenera, and we concluded that this specimen is not assigned to any ichnogenera.

Ichnofamily EUBRONTIDAE Lull, 1904

Diagnosis.—Large bipedal forms, more or less rounded claws, digits broad with distinct phalangeal pads. Foot functionally, possibly structurally tridactyl as the hallux claw never impresses. No caudal trace.

TABLE 2. Metrics of dinosaur footprints from the Kuzuryu and Shiramine areas (in centimeters and degrees).

Ichnotaxa	No.	FL	FW	TD	D II-III	D III-IV	FL/FW	ATL/ATW
Grallatoridae								
	ISBEV003	8.4	6.5	66	38	28	1.29	0.53
Eubrontidae								
	ISBEV001	32.1	21.1	58	37	21	1.52	0.55
Theropoda indet.								
	FPDM-F-170	39.2			32			
	OMFJ F-1			72	31	41		
	ISBEV004	11.5	9.0+	66	45	21	1.28-	0.43-
***Caririchnium* isp.**								
	FPDM-F-164	14.1	13.4	35	3	32	1.05	0.39
	ISBEV002	38	37.6	87	42	45	1.01	0.39
	FPDM-F-173	20.6	16.9	61	35	26	1.22	0.5
***Amblydactylus* isp.**								
	OMFJ F-2	35.8	38.8	70	38	32	0.92	0.34
	OMFJ F-3-T1	37.1	38.8	62	26	36	0.96	0.36
	OMFJ F-3-T2				36			
Iguanodontipodidae								
	OMFJ F-4	24.1+	29.6	60	6	54	0.81+	0.33
uncertain								
	OMFJ F-5	27.4	23.7	67	10	57	1.16	0.56
	OMFJ F-6	45.5+	36.6	36	12	24	1.24+	

EUBRONTIDAE indet. (Fig. 3B; Table 2)

Material.—ISBEV001, Shiramine specimen C of Azuma and Takeyama (1991), a natural cast from the Shiramine area.

Horizon and locality.—The Kaseki-Kabe in the Shiramine area, Hakusan City, Ishikawa Prefecture, Lower Cretaceous Kuwajima Formation of Tetori Group, Japan.

Description.—ISBEV001 is an isolated right pes track natural cast. This footprint is characterized by large size, and a well-developed metatarsophalangeal impression. FL is notably longer than FW, and its mesaxony is strong. The digits II and III

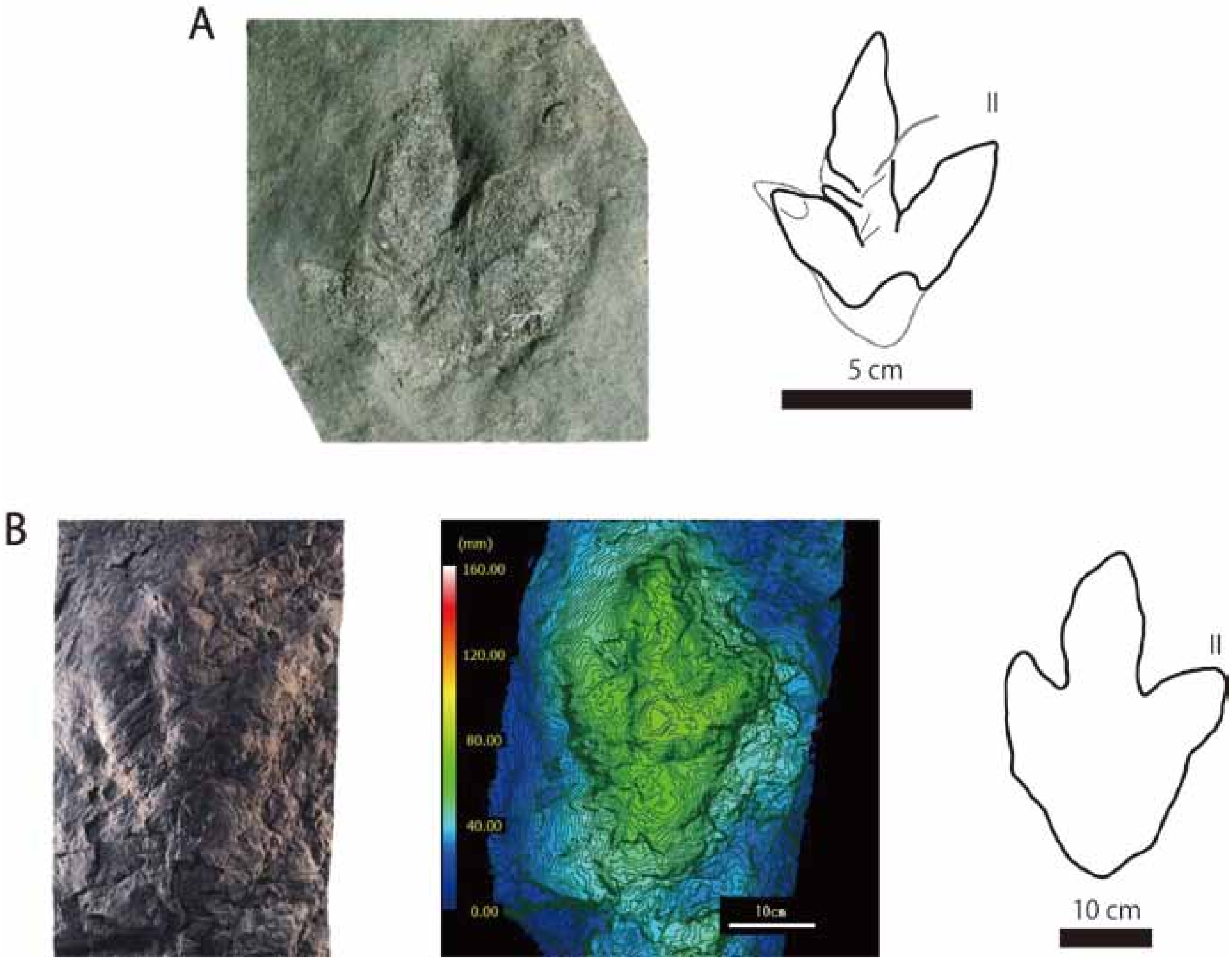

FIGURE 3. Theropod tracks from the Shiramine area. **A,** ISBEV003. **B,** ISBEV001. Figure parts include photo, topographic image, and sketch from left to right. Color bar of each topographic image shows a depth of the footprint. II of each sketch means digit II impression.

impressions are well depressed and are deeper than the digit IV impression. A weak notch is visible between proximal parts of the digits II and III impressions. The distal part of digit III is curved slightly inward.

Remarks.—The specimen ISBEV001 was first described as the ichnospecies *Kuwajimasauropus shiraminensis* (Azuma and Takeyama, 1991). However, this ichnospecies is considered as a *nomen dubium* because the description lacks adequate diagnosis and comparison with other tracks (Lockley and Matsukawa, 1998).

Our revision suggests that ISBEV001 is comparable to the ichnofamilies Eubrontidae, Tyrannosauripodidae, and Ornithomimipodidae, which are formed by large theropods and larger than 25 cm in FL (Lull, 1904; Thulborn, 1990; Olsen et al., 1998; Lockley et al., 2011; McCrea et al., 2014). The type specimens of ichnogenus *Asianopodus* is also larger than 25 cm in FL (Matsukawa et al., 2005; Li et al., 2011).

Eubrontidae is the most typical ichnofamily of among large-sized theropod footprint, and its diagnostic features are recognized in ISBEV001 except for distinct phalangeal pad impressions. On the other hand, the specimen ISBEV001 is different from Tyrannosauripodidae on the basis of tapered distally digit impressions with claw marks (McCrea et al., 2014). Ornithomimipodidae is characterized by wider TD than 60° and separated proximal part of digit II from other parts of track, which are absent in ISBEV001 (Lockley et al., 2011). *Asianopodus* is characterized by a well-developed metatarsophalangeal pad impression on the longitudinal axis (Matsukawa et al., 2005). Although a well-developed metatarsophalangeal impression is seen in ISBEV001, it does not form pad impression. Thus, we concluded that ISBEV001 is assigned to the ichnofamily Eubrontidae.

The ichnofamily Eubrontidae includes the ichnogenera *Eubrontes*, *Megalosauripus*, and *Chapus* (Hitchcock, 1845; Li et al., 2006; Razzolini et al., 2017). *Eubrontes* and *Chapus* have no well-developed metatarsophalangeal impression, unlike

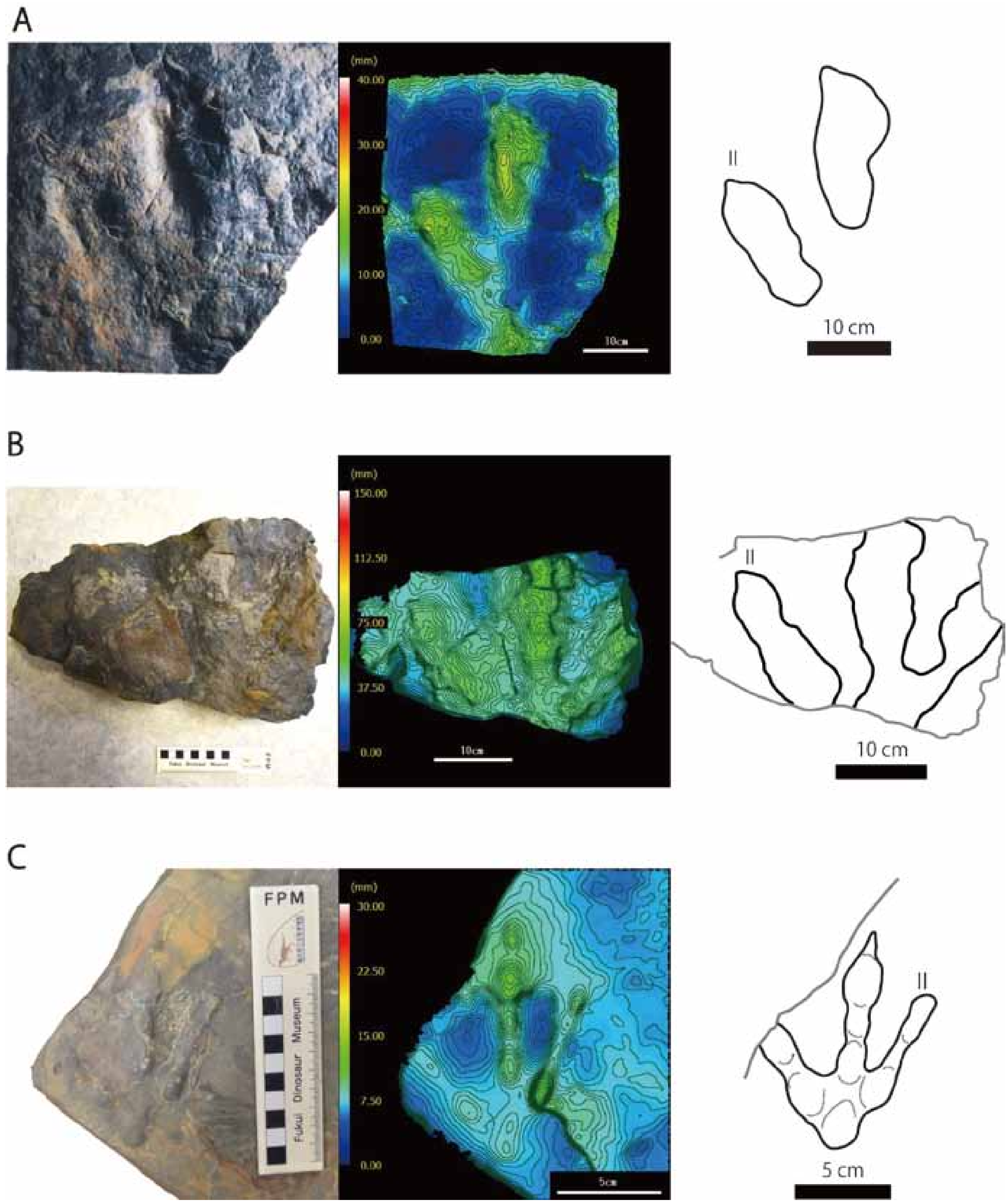

FIGURE 4. Theropod tracks from the Kuzuryu and Shiramine areas. **A,** FPDM-F-170. **B,** OMFJ F-1. **C,** ISBEV004. Figure parts include photo, topographic image, and sketch from left to right.

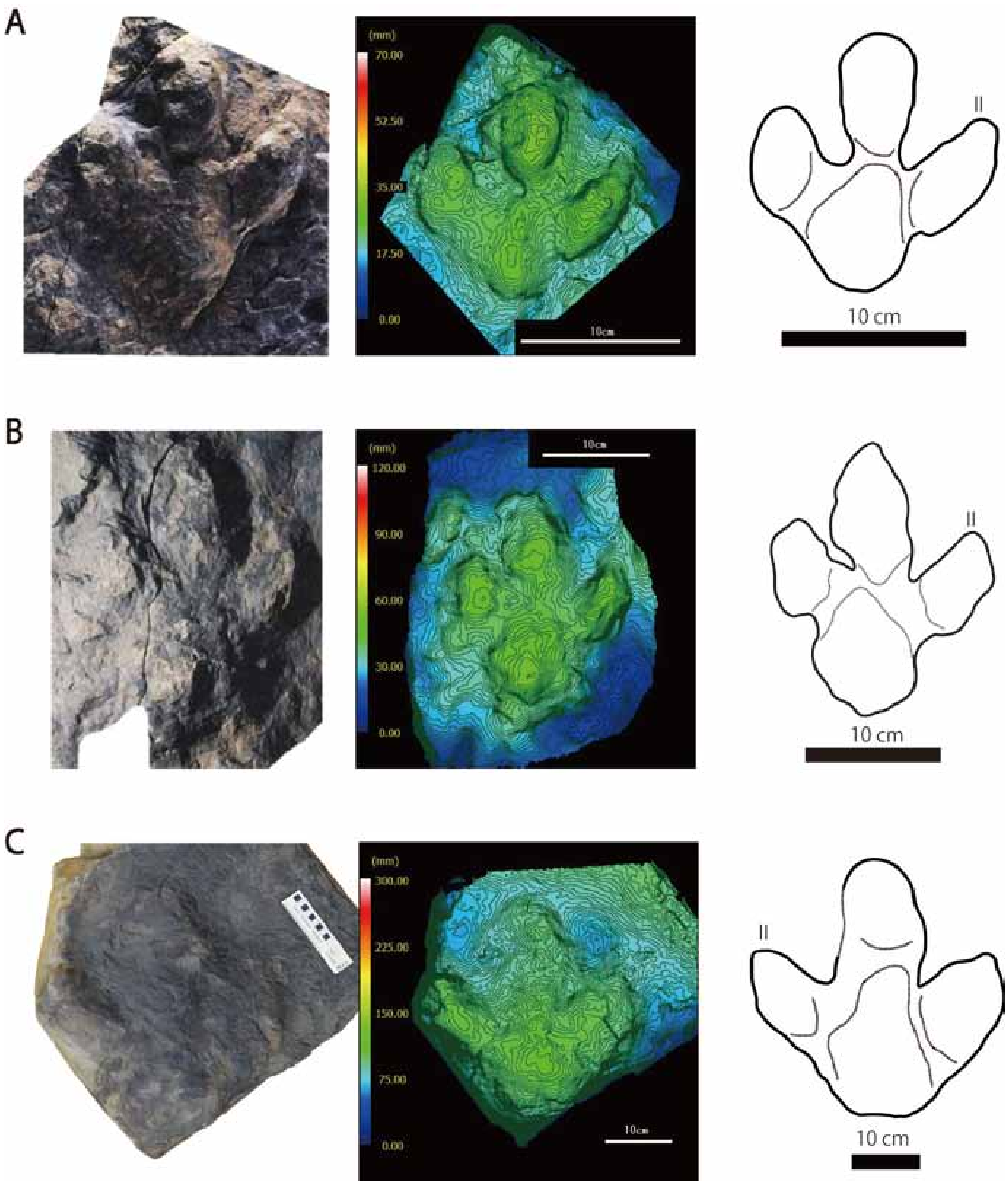

FIGURE 5. *Caririchnium* isp. from the Kuzuryu and Shiramine areas. **A,** FPDM-F-164. **B,** FPDM-F-173. **C,** ISBEV002. Figure parts include photo, topographic image, and sketch from left to right. Color bar of each topographic image shows a depth of the footprint. II of each sketch means digit II impression.

Megalosauripus and ISBEV001. *Megalosauripus* is diagnosed by "Elongate heel (metatarsophalangeal impression), relative to length of digit impression III" (Lockley et al., 1998). The specimen ISBEV001 also has an elongate metatarsophalangeal impression. However, the specimen ISBEV001 is a single footprint, and the border between digit III and metatarsophalangeal pad is inadequate. Therefore, we concluded to assign this footprint to the ichnofamily Eubrontidae.

OTHER THEROPOD TRACKS (Fig. 4A–C)

Materials.—Three isolated pes tracks. FPDM-F-170, Itsuki specimen A of Azuma and Takeyama (1991), a natural mold from the Kuzuryu area. OMFJ F-1, a natural cast from the Kuzuryu area. ISBEV004, a natural cast from the Shiramine area.

Horizons and localities.—FPDM-F-170 and OMFJ F-1 from Nochino in the Kuzuryu area, Ono City, Fukui Prefecture, Lower Cretaceous Itsuki Formation of Tetori Group, Japan. ISBEV004 from the Kaseki-Kabe in the Shiramine area, Hakusan City, Ishikawa Prefecture, Lower Cretaceous Kuwajima Formation of Tetori Group, Japan.

Descriptions.—Three isolated pes tracks from the Itsuki and Kuwajima Formations are incomplete tracks but represent typical morphology of theropod tracks such as sharp-ended, slender digit impressions.

The specimen FPDM-F-170 is probably a right pes track of natural mold (Fig. 4A). This footprint is a large size and preserves digits II and III impressions, whereas the digit IV impression is lacking. The distal part of the digit III impression is turned slightly toward the left side. The phalangeal pad and metatarsophalangeal impressions are not preserved.

The specimen OMFJ F-1 is probably a left pes track of natural cast (Fig. 4B). This specimen is a large size and shows a mesaxonic morphology. The distal parts of the digits III and IV impressions and proximal part of the metatarsophalangeal impression are lacking. The proximal part of the digit II impression is separated from those of digits III and IV impressions. TD is relatively wide, and the phalangeal pad impressions of each digit are not preserved.

The specimen ISBEV004 is a right pes track of natural cast (Fig. 4C). This footprint is a small size and shows a mesaxonic morphology. The digit impressions are slender and preserve the phalangeal pad impressions. The phalangeal formulae are two, three, and three in digits II, III, and IV, respectively. However, the distal part of the digit IV impression is not present, which we interpret to mean that the digit IV mark probably consisted of four phalangeal pad impressions. The proximal phalangeal pad of digit IV forms a metatarsophalangeal impression, which is slightly outside the longitudinal axis of the footprint. The digit II impression is deeper than the digit IV impression, and D II-III is notably narrower than D III-IV.

Remarks.—The specimen FPDM-F-170 was originally described as the ichnospecies *Itsukisauropus izumiensis* (Azuma and Takeyama, 1991). This ichnotaxon is now considered as a *nomen dubium* because of inadequate preservation and lacking ichnotaxonomic comparison (Lockley and Matsukawa, 1998). OMFJ F-1 and ISBEV004 have not been reported so far.

The specimens FPDM-F-170 and OMFJ F-1 are large tracks (FL > 25 cm), but these tracks are not comparable with other large theropod ichnotaxa because the tracks are incomplete. The specimen ISBEV004 is similar to small theropod ichnotaxa such as the ichnofamily Grallatoridae and ichnogenus *Asianopodus*. The ichnofamily Grallatoridae is characterized by narrow TD and strong mesaxony, unlike ISBEV004. The ichnogenus *Asianopodus* is mesaxonic and sub-symmetrical track. *Asianopodus* also has a bulbous metatarsophalangeal pad impression on the longitudinal axis (Matsukawa et al., 2005). On the other hand, the specimen ISBEV004 has a slightly vertically long metatarsophalangeal pad which is slightly outside the longitudinal axis, and its D III-IV is wider than II-III.

IGUANODONTID TRACKS

Ichnofamily IGUANODONTIPODIDAE Vialov, 1988 sensu Lockley, Xing, Lockwood and Pond, 2014, emend. Díaz-Martínez, Pereda-Suberbiola, Pérez-Lorente and Canudo, 2015

Diagnosis.—Mesaxonic, tridactyl, sub-symmetrical pes tracks that are as wide as or wider than long; one pad impression in each digit and one in the heel; digit pads longer than wide; well-developed notches in the proximal part of the digit II and IV impressions; manus tracks occasionally present and much smaller than the pes tracks.

Ichnogenus *CARIRICHNIUM* Leonardi, 1984, emend. Díaz-Martínez, Pereda-Suberbiola, Pérez-Lorente and Canudo, 2015

Diagnosis.—Pes tracks belonging to Iguanodontipodidae, with a large heel impression that is rounded, centered and wide (wider than the width of the proximal part of the digit III impression); short, wide digit impressions.

CARIRICHNIUM isp. (Fig. 5)

Materials.—Three isolated tracks. FPDM-F-164 and ISBEV002, Shiramine specimens A and B of Azuma and Takeyama (1991), natural casts from the Shiramine area. FPDM-F-173, Hayashidani specimen of Azuma and Takeyama (1991), a natural cast from the Kuzuryu area.

Horizons and localities.—FPDM-F-164 and ISBEV002 from the Kaseki-Kabe in the Shiramine area, Hakusan City, Ishikawa Prefecture, Lower Cretaceous Kuwajima Formation of Tetori Group, Japan. FPDM-F-173 from Hayashidani in the Kuzuryu area, Ono City, Fukui Prefecture, Lower Cretaceous Itsuki Formation of Tetori Group, Japan.

Descriptions.—The specimen FPDM-F-164 is a relatively small iguanodontid track that shows mesaxonic and short, wide

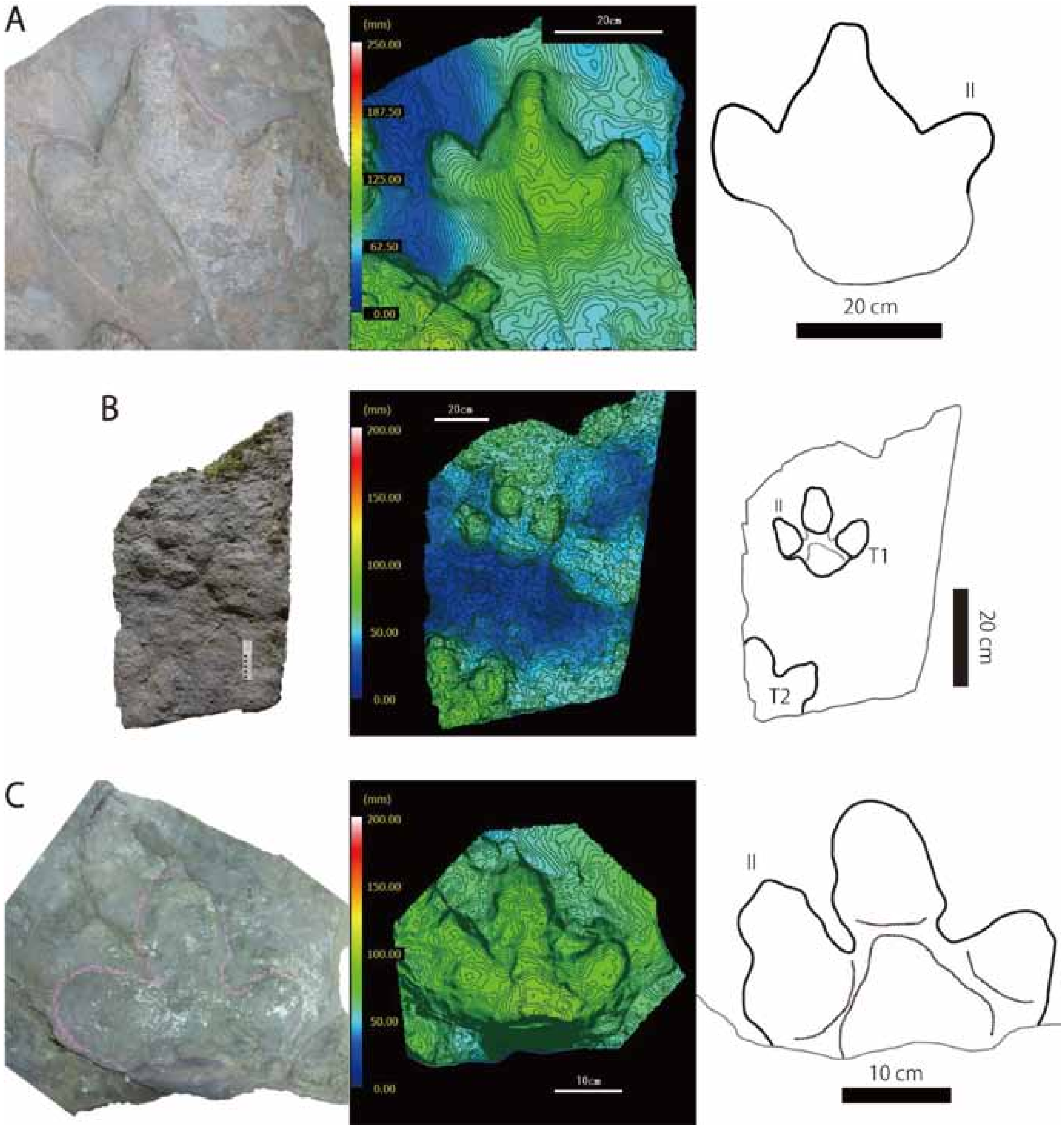

FIGURE 6. *Amblydactylus* isp. and iguanodontid track from the Kuzuryu area. **A,** OMFJ F-2. **B,** OMFJ F-3. **C,** OMFJ F-4. Figure parts include photo, topographic image, and sketch from left to right. Color bar of each topographic image shows a depth of the footprint. II of each sketch means digit II impression.

digit impressions with blunt distal ends. The digital pad and metatarsophalangeal pad impressions are well-preserved. The digits II and III impressions are slightly deeper than the digit IV impression. The metatarsophalangeal pad impression, which is larger than the digital pad impressions, is triangular and is longer than it is wide. The specimen FPDM-F-173 is similar but slightly larger, and its mesaxony is stronger than FPDM-F-164 (Table 2).

The specimen ISBEV002 is much larger than FPDM-F-164, but similar to FPDM-F-164 in morphology. The digits II and IV impressions are well-preserved, but the digit III impression is eroded. The digit II and metatarsophalangeal impressions are deeper than other parts of the track. The widths of digits II and III are almost the same, while that of digit IV is wider than those of other digit impressions.

Remarks.—The specimens FPDM-F-164 and 173 were originally described as the ichnospecies *Shiraminesauropus reini* and *S. hayashidaniensis* respectively, and ISBEV002 was described as the ichnospecies *Gigantoshiraminesauropus matsuoi* (Azuma and Takeyama, 1991). Matsukawa et al. (1995) pointed out that these specimens are inadequate and undiagnostic, and ichnotaxonomic comparison was not taken into the description. Lockley and Matsukawa (1998) considered that these ichnotaxa are *nomina dubia*. On the other hand, Díaz-Martínez et al. (2015) noted that these tracks are classified within the ichnofamily Iguanodontipodidae.

The ichnofamily Iguanodontipodidae includes several valid ichnogenera such as *Iguanodontipus*, *Caririchnium*, *Amblydactylus*, and *Hadrosauropodus* (Lockley et al., 2014; Díaz-Martínez et al., 2015). Among them, *Caririchnium* is characterized by pes tracks for which FL > FW, large metatarsophalangeal impressions, relatively strong mesaxony, three well-separated digital pads, and one metatarsophalangeal pad impression (Lockley et al., 2014; Díaz-Martínez et al., 2015; Xing et al., 2015; Tsukiji et al., 2018). FPDM-F-164, ISBEV002, and FPDM-F-173 show these morphologies. Thus, we concluded that these tracks are attributed to the ichnogenus *Caririchnium*.

Ichnogenus *AMBLYDACTYLUS* Sternberg, 1932, emend. Currie and Sarjeant, 1979

Diagnosis.—Bipedal, with three functional pedal digits. The outer contours of digits II and IV diverge at low angle from the longitudinal axis of the ichnite. A distinct posterior impression is produced by a metatarsal-phalangeal pad. Interdigital webs link the proximal portions of the fleshy digital pads; the digits end in blunt claws or pointed hooves. The ichnite is almost as wide as, or wider than, it is long.

AMBLYDACTYLUS isp. (Fig. 6A, B)

Materials.—Two tracks from the Kuzuryu area. OMFJ F-2, Hayashidani specimen 2 of Kojima et al. (1992), a natural cast. OMFJ F-3-T1, a natural cast.

Horizons and localities.—OMFJ F-2 from Hayashidani and OMFJ F-3-T1 from Itsuki tracksites in the Kuzuryu area, Ono City, Fukui Prefecture, Lower Cretaceous Itsuki Formation of Tetori Group, Japan.

Descriptions.—The specimen OMFJ F-2 is a large pes track with short, wide digit impressions that have blunt distal ends (Fig. 6A). The proximal width of digit III impression is greater than those of other digit impressions. Digits II and III impressions are deeper than other parts of the footprint. The proximal margin of the footprint is shallow, and its outline is somewhat indistinct. The outer margins of digits II and IV impressions are nearly parallel to the longitudinal axis. The digital pad and metatarsophalangeal pad impressions are not preserved.

The specimen OMFJ F-3 is composed of two pes footprint natural casts, numbered T1 and T2 (Fig. 6B). T1 is shallower than T2, and the directions of each track are almost in the same. Thus, these footprints do not compose a trackway. Because T2 is incomplete, it is described in a separate section below. T1 is a well-preserved footprint that shows tridactyl, mesaxony, and quadripartite morphology. The digit impressions are deeper than the metatarsophalangeal pad impression. The proximal parts of each digit impression are well detached from the metatarsophalangeal pad impression. The metatarsophalangeal pad is wider than long, and its proximal margin is rounded.

Remarks.—The specimen OMFJ F-2 was first reported by Kojima et al. (1992). However, ichnotaxonomic description and detailed illustration have not been published. The specimen OMFJ F-3 have not been reported so far.

The specimens OMFJ F-2 and OMFJ F-3-T1 are characterized by wider pes track than its length and by relatively weak mesaxony. These morphologies are seen in the ichnogenera *Amblydactylus* and *Hadrosauropodus* (Currie and Sarjeant, 1979; Díaz-Martínez et al., 2015; Tsukiji et al., 2018). Díaz-Martínez et al. (2015) proposed that the type ichnogenus *A. gethingi* is a *nomen dubium* but *A. kortmeyeri* is valid and removed to the ichnogenus *Caririchnium*. Tsukiji et al. (2018) mentioned that *A. gethingi* is a *nomen dubium*; however, *A. kortmeyeri* differs from *Caririchnium* on the basis of following features: 1) wider pes track than its length with weak mesaxony; 2) wider metatarsophalangeal impression than its length. We therefore concluded that *Amblydactylus* should be divided from *Caririchnium*, and *A. kortmeyeri* is a new type ichnospecies.

Currie and Sarjeant (1979) diagnosed that *Amblydactylus* has interdigital webs, which is absent in OMFJ F-2 and OMFJ F-3-T1. Because interdigital webs of iguanodontid tracks were reinterpreted as mud structures (Lockley and Hunt, 1995; Lockley et al., 2003), we rejected this feature as diagnosis. OMFJ F-2, OMFJ F-3-T1, and the ichnogenus *Amblydactylus* show rounded posterior margin of the track. However, the ichnogenus *Hadrosauropodus* is characterized by a bilobed posterior margin of the track (Lockley et al., 2003). Thus, the specimens OMFJ F-2 and OMFJ F-3-T1 are attributed to the ichnogenus *Amblydactylus*.

OTHER IGUANODONTID TRACKS

IGUANODONTIPODIDAE indet. (Fig. 6B, C)

Material.—Two tracks from the Kuzuryu area. OMFJ F-3-T2, a natural cast. OMFJ F-4, Nagakuradani specimen of Azuma et al. (1992), a natural cast.

Horizon and locality.—OMFJ F-3-T2 from the Itsuki in the Kuzuryu area, Ono city, Fukui Prefecture, Lower Cretaceous Itsuki Formation of Tetori Group, Japan. OMFJ F-4 from Nagakuradani in the Kuzuryu area, Ono City, Fukui Prefecture, Lower Cretaceous Nochino Formation of Tetori Group, Japan.

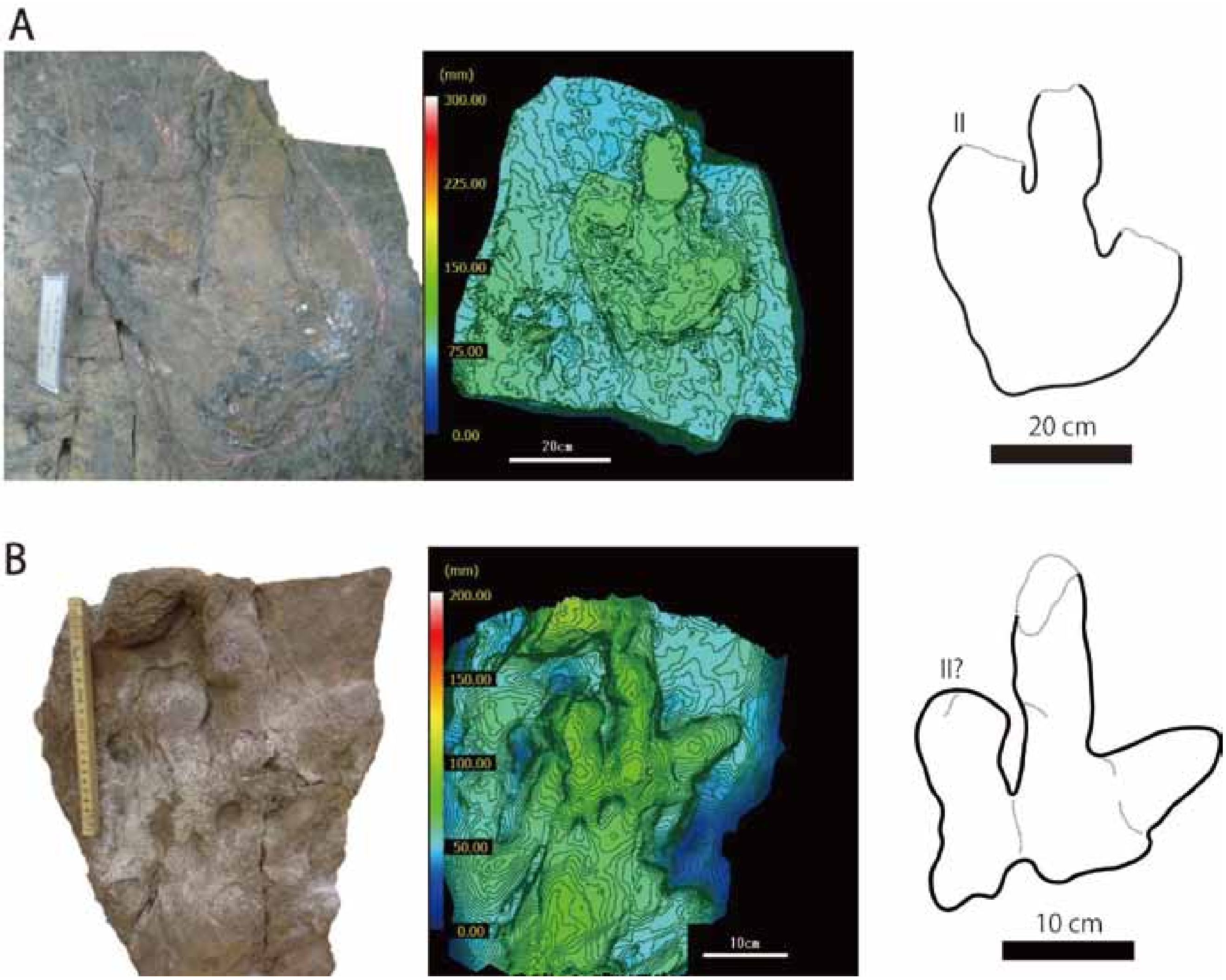

FIGURE 7. Possible dinosaur tracks from the Kuzuryu area. **A,** OMFJ F-5. **B,** OMFJ F-6. Figure parts include photo, topographic image, and sketch from left to right. Color bar of each topographic image shows a depth of the footprint. II of each sketch means digit II impression.

Description.—Although OMFJ F-3-T2 is well-impressed and deeper than OMFJ F-3-T1, it lacks the digit IV impression and proximal part of the footprint. The digital pad and metatarsophalangeal pad impressions are not detached, and the distal ends of digits are rounded.

The specimen OMFJ F-4 shows mesaxony and quadripartite morphology (Fig. 6C). This footprint lacks a proximal track margin. The digit II impression is deeper than that of digit III, which is deeper than that of digit IV. The digit IV impression is shorter than other digit impressions. The width of the metatarsophalangeal pad impression is wider than that of the digit III impression. D II-III is much narrower than D III-IV.

Remarks.—The specimen OMFJ F-3-T2 is preserved in the same block of OMFJ F-3-T1. Although this footprint is incomplete, it can be seen that digit impressions are short and wide with rounded distal end. Thus, we attributed that this footprint is the ichnofamily Iguanodontipodidae. The specimen OMFJ F-4 was first reported by Kojima et al. (1992) and described by Azuma et al. (1992) subsequently. They considered that this footprint was formed by iguanodontids. We agree with their interpretation and classified this footprint as the ichnofamily Iguanodontipodidae. The specimen OMFJ F-4 shows weak mesaxony, and such morphology is typically seen in the ichnogenera *Amblydactylus* and *Hadrosauropodus*. However, the posterior margin of this track, which is important for ichnotaxonomic classification of iguanodontid tracks, was not preserved (Díaz-Martínez et al., 2015). Thus, we could not assign this footprint to any iguanodontid ichnogenus.

INDETERMINATE DINOSAUR TRACKS (Fig. 7A, B)

Materials.—Two isolated tracks from the Kuzuryu area. OMFJ F-5, Itsuki specimen B of Azuma and Takeyama (1991), a natural cast. OMFJ F-6, Meoto-sugi specimen of Azuma et al.

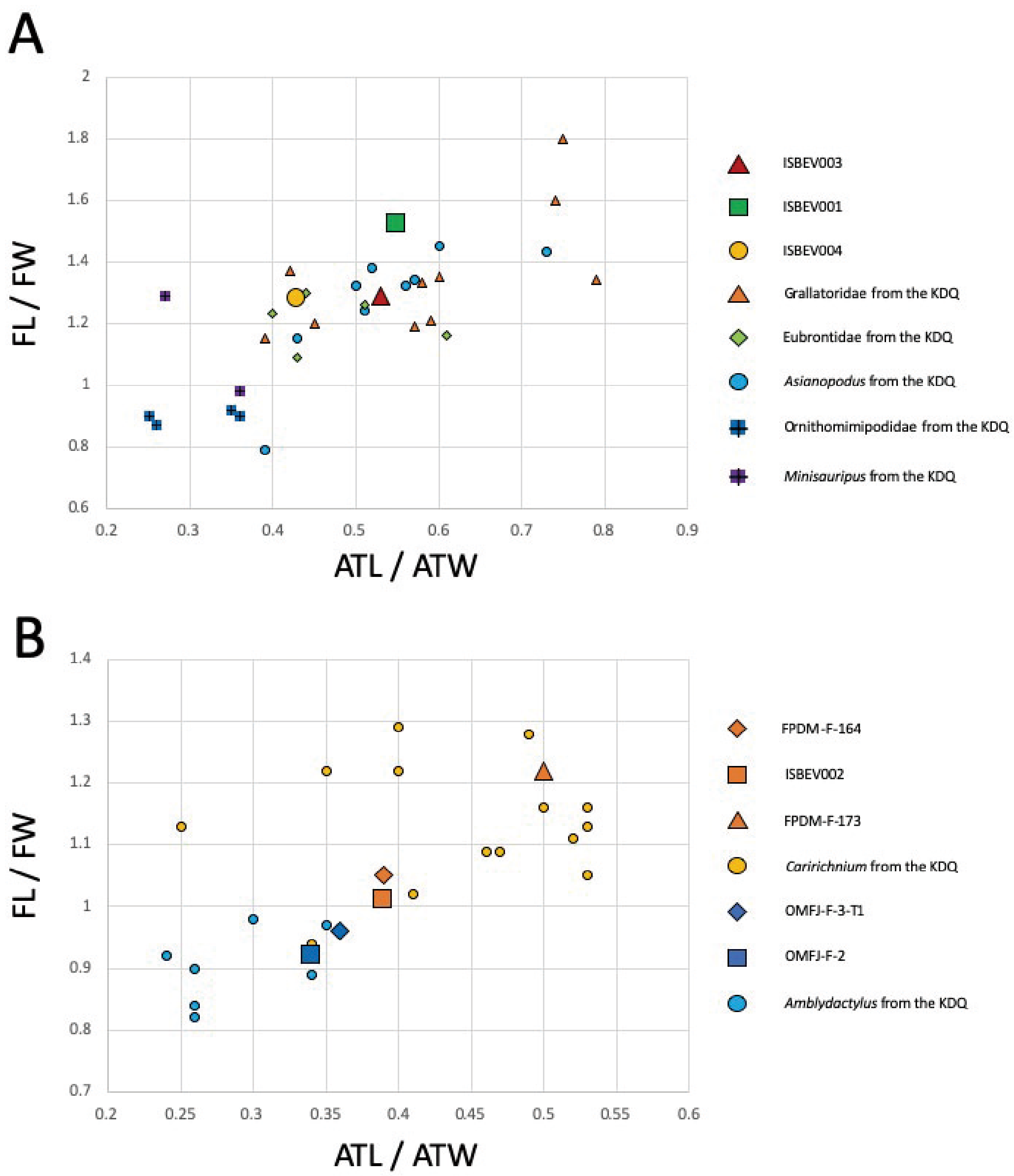

FIGURE 8. Bivariate analysis (FL/FW ratio plotted against ATL/ATW ratio) of tridactyl tracks from Tetori Group. **A,** Theropods. **B,** Iguanodontids. Plots of Kitadani dinosaur quarry (KDQ) specimens are modified from Tsukiji et al. (2018, 2019).

(1992), a natural cast.

Horizons and localities.—OMFJ F-5 from Nochino in the Kuzuryu area, Ono City, Fukui Prefecture, Lower Cretaceous Itsuki Formation of Tetori Group, Japan. OMFJ F-6 from Maesaka in the Kuzuryu area, Ono City, Fukui Prefecture, Lower Cretaceous Nochino Formation of Tetori Group, Japan.

Descriptions.—The specimen OMFJ F-5 is a large pes track natural cast, which shows a flattened preservation (Fig. 7A). The digit impressions exhibit mesaxonic morphology and are relatively wide. The distal ends of each digit are lacking, and the phalangeal pad impressions are not preserved. The posterior part of the track is somewhat narrow and rounded.

The specimen OMFJ F-6 is a large pes track natural cast that shows a tridactyl and strongly mesaxonic morphology (Fig. 7B). The digit impressions are relatively slender with rounded distal ends. The posterior part of the track is shallow and ill-formed. D II-III is much narrower than D III-IV (Table 2). The phalangeal pad and metatarsophalangeal pad impressions lack definition.

Remarks.—The specimen OMFJ F-5 was first reported by Azuma and Takeyama (1991) and identified as an iguanodontid footprint. However, this footprint lacks distal ends of digit impressions, which are important parts to classify a trackmaker between theropod or iguanodontid (e.g., Thulborn, 1990). Therefore, we could not determine the trackmaker of this footprint.

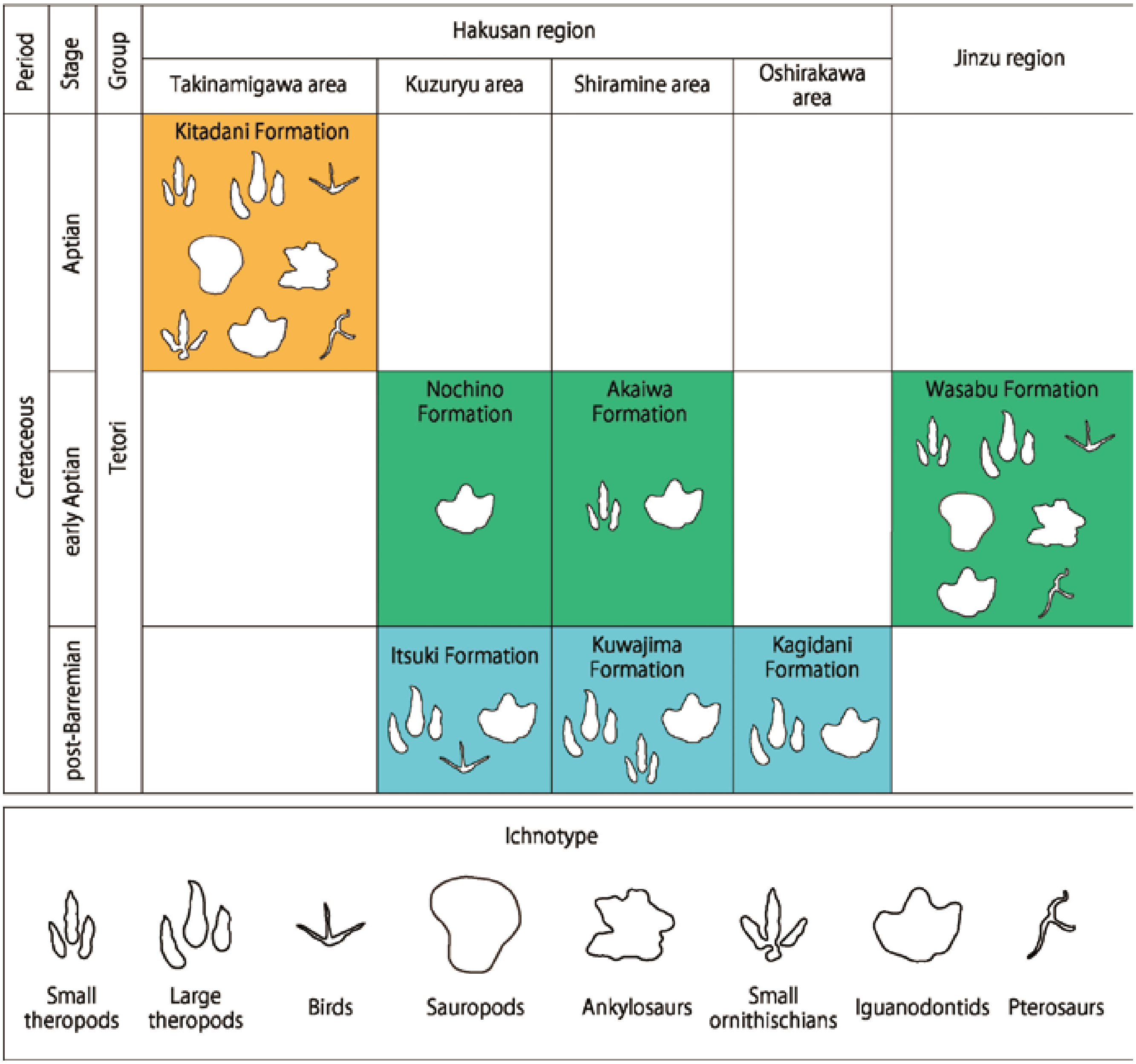

FIGURE 9. Dinosaur ichnofauna from the Tetori Group. Orang, Kitadani dinosaur ichnofauna. Green, Akaiwa dinosaur ichnofauna. Blue, Itsuki dinosaur ichnofauna.

The specimen OMFJ F-6 was first reported by Kojima et al. (1992) and assigned to theropod footprint by Azuma et al. (1992). This footprint has rounded distal ends of digit impressions, which is typical morphology of iguanodontid tracks. However, iguanodontid tracks are characterized by a large well-defined metatarsophalangeal impression, which is not seen in this track (e.g., Díaz-Martínez et al., 2015). Thus, we could not identify the trackmaker of this footprint.

DISCUSSION

Ichnotaxonomic revision

Azuma and Takeyama (1991) first described following ichnotaxa: *Byakudansauropus shiraminensis* (ISBEV003), *Kuwajimasauropus shiraminensis* (ISBEV001), *Itsukisauropus izumiensis* (FPDM-F-170), *Shiraminesauropus reini* (FPDM-F-164), *S. hayashidaniensis* (FPDM-F-173), and *Gigantoshiraminesauropus matsuoi* (ISBEV002). Among them, *B. shiraminensis*, *K. shiraminensis*, and *I. izumiensis* were considered as theropod tracks, and *S. reini*, *S. hayashidaniensis*, and *G. matsuoi* were iguanodontid tracks. In addition, they assigned OMFJ F-5 to an iguanodontid track. Matsukawa et al. (1995) referred that the trackmakers of these tracks are theropods and iguanodontids. On the other hand, they noted that these ichnotaxa are inadequate preservation, undiagnostic, and lacking ichnotaxonomic comparison with other tracks. Lockley and Matsukawa (1998) followed their suggestion and considered that these ichnotaxa are *nomina dubia*. However, objective and quantitative analyses have not been taken into consideration.

Our revision of dinosaur tracks using 3D digital data shows more adequate morphological observation. For example, phalangeal and metatarsophalangeal pad impressions of FPDM-F-164 were well-defined and illustrated in our figures, whereas not in previous studies. In addition, this study carried out the bivariate analysis plotting the FL/FW and ATL/ATW ratios, which was not taken into consideration of previous studies. Three theropod tracks, including ISBEV001, 003, and 004, show similar pattern to the ichnofamilies Grallatoridae, Eubrontidae, and the ichnogenus *Asianopodus* from the Kitadani Formation (Fig. 8A). Among the specimen ISBEV003 has diagnostic features of the ichnofamily Grallatoridae, and ISBEV001 has those of the ichnofamily Eubrontidae. Three iguanodontid tracks, including FPDM-F-164, 173, and ISBEV002, plot in same patterns of the ichnogenus *Caririchnium* from the Kitadani Formation, whereas OMFJ F-2 plots in the lower left part of the graph, concordant with the ichnogenus *Amblydactylus* from the Kitadani Formation (Fig. 8B). Although OMFJ F-3-T1 shows the medium value between the *Caririchnium* and *Amblydactylus*, its metatarsophalangeal pad impression is wider than long, which is same with *Amblydactylus*. These results strongly support ichnotaxonomic division of theropod and iguanodontid tracks from the Kuzuryu and Shiramine areas.

Dinosaur ichnofauna in the Tetori Group

Our ichnotaxonomic division of dinosaur tracks from the Kuzuryu and Shiramine areas revealed that their trackmakers are theropods and iguanodontids. Among the ichnofamilies, Grallatoridae and Eubrontidae of theropod and the ichnogenera *Caririchnium* and *Amblydactylus* of iguanodontid ichnotaxa have also been recovered from the Kitadani Formation in the Takinamigawa area (Tsukiji et al., 2018, 2019). Recently, the ichnofamilies Eubrontidae and Iguanodontipodidae (*Amblydactylus*-type) have been recognized in the Kagidani Formation in the Oshirakawa area (Tsukiji et al., in press). Previous studies suggested that the assemblage of dinosaur ichnofauna from the Tetori Group in the Hakusan region is characterized by theropod- and iguanodontid-dominated community (Matsukawa et al., 2005, 2006b; Tsukiji et al., in press). The result of this study supports these suggestions.

On the other hand, Matsukawa et al. (2005, 2006b) interpreted that the dinosaur tracks from the Tetori Group are yielded in the same horizon stratigraphically and are grouped into the same assemblage. However, on the basis of recent stratigraphic and geochronological studies suggests that there are three horizons of dinosaur track bearing in the Tetori Group (Sano, 2015; Sano and Yabe, 2016; Sakai et al., 2018; Nagata et al., 2018). Therefore, we propose a new interpretation of the dinosaur track assemblage from the Tetori Group. We subdivided this assemblage into following three ichnofaunas: 1, Itsuki dinosaur ichnofauna from the Itsuki, Kuwajima, and Kagidani Formations (Barremian); 2, Akaiwa dinosaur ichnofauna from the Akaiwa, Nochino, and Wasabu Formations (early Aptian); and 3, Kitadani dinosaur ichnofauna from the Kitadani Formation (Aptian).

The ichnofaunal composition shows that the Itsuki dinosaur ichnofauna only yields theropod, bird, and iguanodontid tracks; however, the Akaiwa and Kitadani dinosaur ichnofaunas consist of diverse vertebrate ichnotaxa (Fig. 9). Although the Akaiwa and Nochino formations are composed of theropod and iguanodontid tracks, the Wasabu Formation in the Jinzu Region yields theropod, bird, sauropod, iguanodontid, ankylosaur, and pterosaur tracks (Matsukawa et al., 1997, 2002; Toyama Dinosaur Research Group, 2002; Fujita et al., 2003; Shigeno, 2003; Shigeno et al., 2004; Fujita, 2008). The Kitadani dinosaur ichnofauna is the most diverse in the Tetori Group and includes five ichnotypes of theropod, two ichnotypes of bird, sauropod, small ornithischian, two ichnotypes of iguanodontid, ankylosaur, and pterosaur tracks (Lee et al., 2010; Imai et al., 2018; Tsukiji et al., 2018, 2019).

Difference between the Itsuki and Akaiwa dinosaur ichnofaunas is indicated that the ichnofaunal change has occurred in the Tetori Group during the Barremian–Aptian age. It is concordant with the suggestion that the climatic change (warmer and dryer) has occurred in the Barremian–Aptian boundary on the basis of floral and faunal change (Sano and Yabe, 2016; Shibata et al., 2017; Sakai et al., 2018). However, sauropod, small ornithischian, and pterosaur remains have been reported from the Kuwajima Formation (Manabe and Barrett, 2000; Unwin and Matsuoka, 2000; Barrett et al., 2002; Ohashi and Barrett, 2009). The general facies analyses suggested that the Itsuki and Kuwajima Formations were deposited in estuarine delta environments (Azuma et al., 1992; Okazaki and Isaji, 2008), whereas the Wasabu and Kitadani formations were deposited in a meandering river system of inland zone (Shigeno, 2003; Shigeno et al., 2004; Yabe and Shibata, 2011; Suzuki et al., 2015). Therefore, the ichnofaunal diversity may have been influenced by the depositional environments.

There is a large number of discoveries of dinosaur footprints and tracksites from the Lower Cretaceous of East and Southeast Asia (e.g., Zhen et al., 1989; Chen et al., 2006; Matsukawa et al., 2006b; Lockley et al., 2013). Matsukawa et al. (2005) suggested that dinosaur ichno-assemblage from the Tetori Group is dominated by theropods and gracile-toed ornithopods (iguanodontids) and compared with dinosaur tracksites from the northeastern part of China. This study shows that the Itsuki dinosaur ichnofauna is also composed of theropod and iguanodontid footprints. This pattern is similar to dinosaur ichno-assemblage of the Xiguayuan Formation in Hebei

Province (Xing et al., 2019). In contrast, it is clearly different from those of the Jingchuan Formation in Nei Mongol and Tianjialou Formation in Shandong Province, which are dominated by theropod and sauropod footprints (Lockley et al., 2002, 2018; Xing et al., 2018).

However, the Itsuki dinosaur ichnofauna is composed of a few numbers, and most of them lack trackways and co-occurrences with other footprints. Further discoveries of dinosaur footprints from the Itsuki, Kuwajima, and Kagidani Formations are needed for our understanding about dinosaur ichnofaunas from the Tetori Group and comparisons with the other dinosaur ichnofaunas.

Recently, it was revealed that wide-toed iguanodontid footprints, such as *Amblydactylus* from the Kitadani and Itsuki Formations, have been recovered (Tsukiji et al., 2018). In addition, sauropod, ankylosaur, and pterosaur footprints were reported from the Akaiwa and Kitadani dinosaur ichnofaunas (Fujita, 2008; Tsukiji et al., 2016). Similar assemblage is reported from the Sichuan Basin, southwestern part of China, where yields various theropod, sauropod, iguanodontid (including wide-toed morphotype), ankylosaur, and pterosaur footprints (Xing and Lockley, 2016; Xing et al., 2016). Because a few of dinosaur body fossils were recovered from the Lower Cretaceous of the Sichuan Basin, this similarity may add new insights for our understanding of Asian dinosaurs during the Early Cretaceous age.

CONCLUSION

Morphological identification along with objective and quantitative analyses using 3D digital data revealed that dinosaur tracks from the Kuzuryu and Shiramine areas belonged to theropods (including the ichnofamilies Grallatoridae and Eubrontidae) and iguanodontids (including the ichnogenera *Caririchnium* and *Amblydactylus*).

Revision of dinosaur tracks in this study supports the previous suggestion that the dinosaur track assemblage in the Tetori Group is dominated by theropods and iguanodontids. In addition, this assemblage can be subdivided into the Itsuki, Akaiwa, and Kitadani dinosaur ichnofaunas based on the depositional age. The Itsuki dinosaur ichnofauna includes few varieties of dinosaur tracks, whereas the Akaiwa and Kitadani dinosaur ichnofaunas show diverse assemblage of dinosaur ichnotaxa. This difference may have been influenced by depositional environments; however, discoveries of additional specimens of the Itsuki dinosaur ichnofauna are needed for more rigorous discussion.

The 3D digital data, coupled with quantitative analysis of the data, were essential to identify the trackmakers. We strongly recommend that other dinosaur tracks from the Tetori Group should be described or reanalyzed using 3D digital data to further compare the ichnotaxonomy and ichnofauna in this region and to provide additional insights into the ecosystems of the Lower Cretaceous Tetori Group.

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SUPPORTING INFORMATIONS

Data DOI of materials are available from the following repositories:
FPDM-F-164, https://doi.org/10.6084/m9.figshare.8868767.v2
FPDM-F-170, https://doi.org/10.6084/m9.figshare.8868779.v2
FPDM-F-173, https://doi.org/10.6084/m9.figshare.8868788.v1
ISBEV001, https://doi.org/10.6084/m9.figshare.8868791.v1
ISBEV002, https://doi.org/10.6084/m9.figshare.8868797.v1
ISBEV004, https://doi.org/10.6084/m9.figshare.8868800.v1
OMFJ F-1, https://doi.org/10.6084/m9.figshare.8868803.v3
OMFJ F-2, https://doi.org/10.6084/m9.figshare.8868806.v1
OMFJ F-3, https://doi.org/10.6084/m9.figshare.8868809.v1
OMFJ F-4, https://doi.org/10.6084/m9.figshare.8868815.v1
OMFJ F-5, https://doi.org/10.6084/m9.figshare.8868818.v1
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