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First trackway evidence of gregarious dinosaurs from the Lower Cretaceous Tetori Group of eastern Toyama prefecture, central Japan

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Early Cretaceous slender-toed bipedal dinosaur tracks are reported from the eastern part of the Tetori area, central Japan. They are small, bipedal and tridactyl impressions assigned to *Toyamasauripus masuiae* ichnogen. and ichnosp. nov. based on biometric analysis. Thirty-three individuals of *Toyamasauripus masuiae* show the highest density of footprints of any dinosaur track-sites in Japan. This is also the first trackway evidence of gregarious dinosaurs reported from Japan. *Toyamasauripus masuiae* appears to represent a small bipedal dinosaur track-maker that was relatively abundant. As no bones are known from the track-bearing beds, the footprints add much to our knowledge of dinosaur faunas at this time.

KEY WORDS: dinosaur tracks; slender-toed bipedal dinosaurs; gregarious behavior; Lower Cretaceous; Japan.

1. Introduction

Many tracks of slender-toed biped dinosaurs (probably ornithopods) have been found in the Lower Cretaceous Tetori Group of central Japan (Figure 1). This includes 13 trackways evidently representing gregarious individuals, and shows the highest density of dinosaur tracks of any Japanese track-site.

In eastern Asia, including China, Mongolia, Korea and Japan, dinosaur fossils are found in various sedimentary rocks, environmentally defined on the basis of palaeontological and sedimentological criteria as shallow marine, deltaic, fluvial, lacustrine, swamp, alluvial fan and eolian (e.g., Jerzykiewicz & Russell, 1991; Dong, 1992; Matsukawa & Obata, 1994; Matsukawa *et al.*, submitted). The psittacosaurid fauna defined on the basis of Late Jurassic to Early Cretaceous faunas of China is considered an ecological equivalent of fluvial and lacustrine deposits in eastern Asia (Matsukawa & Obata, 1994). The most eastern extension of this fauna is also recognizable in the Tetori Group, Japan (Azuma, 1991; Dong, 1992; Matsukawa & Obata, 1994). This means that the Japanese islands were located in the eastern part of the Asian continent during the Late Jurassic to Early Cretaceous. Therefore, similar dinosaur faunas existed in NE China and the Tetori areas in east Asia, as revealed by the occurrence of common dinosaur tracks together in the same or similar ichnofacies and palaeogeographical setting (Matsukawa & Obata, 1994; Matsukawa *et al.*, 1995). These specimens have been attributed to both theropod and iguanodontid dinosaurs. Although the specimens in the Tetori Group were assigned to a number of ichnogenera and ichnospecies by Azuma & Takeyama (1991), Matsukawa *et al.*

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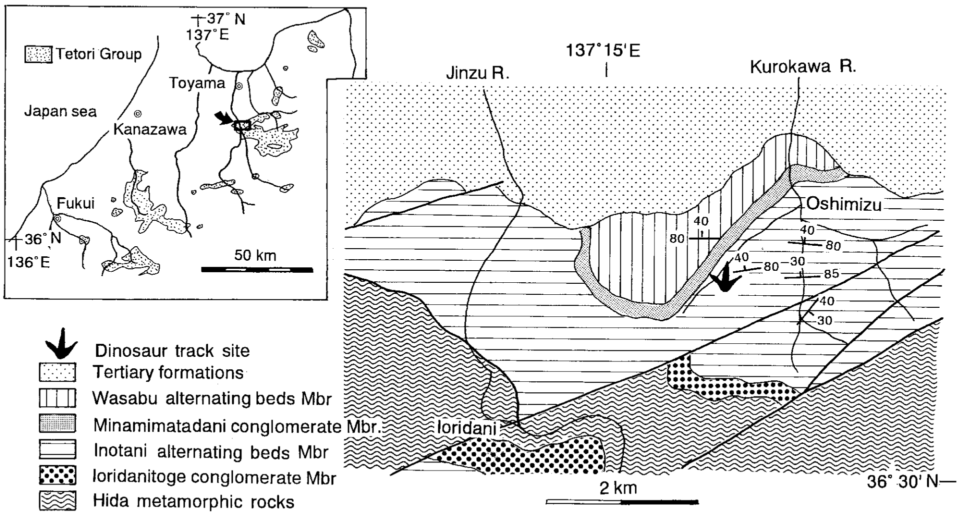

Figure 1. Locality map.

(1995) considered it premature to engage in detailed systematic discussion with such small samples based on isolated tracks that lacked well-preserved morphological detail.

In this paper, we describe the dinosaur tracks from the Tetori Group in east Toyama Prefecture, central Japan, and discuss the behaviour of the track-makers and characteristics of the sedimentary environments.

2. Geological setting

Many dinosaur tracks were found in the upper part of the alternating beds of sandstone and shale of the Inotani Member of the Nagatogawa Formation, Tetori Group (Yamada, 1986) (Figure 2). Although these beds were originally named the Kumanogawa and Joganjigawa formations (Takenami & Maeda, 1959) and the Shidakadani Alternation (Maeda, 1958), the stratigraphy has since been revised. Because Yamada's (1986) stratigraphy observes current regulations of stratigraphic nomenclature we use it herein.

The Tetori Group is distributed on the Japan Sea side of Honshu, and is composed mainly of nonmarine conglomerates, sandstones and mudstones. Remarkable lateral and vertical changes in lithofacies are observed between separate outcrop areas which, together with a scarcity of index fossils and key beds, has led to many formation names. Of these, three subgroups established by Maeda (1961), the Kuzuryu, Itoshiro and Akaiwa in ascending order, have been generally accepted (Figure 2).

The Inotani Member of the Nagatogawa Formation, containing dinosaur tracks, occupies the eastern part of the Tetori area. The Tetori Group in its eastern part is divided, in ascending order, into the Higashisakamori, Nagatogawa and Atotsugawa formations (Yamada, 1986). Shallow marine deposits of the upper part of the Higashisakamori Formation yield the ammonites *Perisphinctes* sp., *Kranaosphinctes* sp. and others, and marine bivalves including *Myophorella* sp. and *Inoceramus* sp.; these correlate with the Kuzuryu Subgroup. Therefore, a Callovian to Oxfordian age is assignable to the formation (Maeda, 1958).

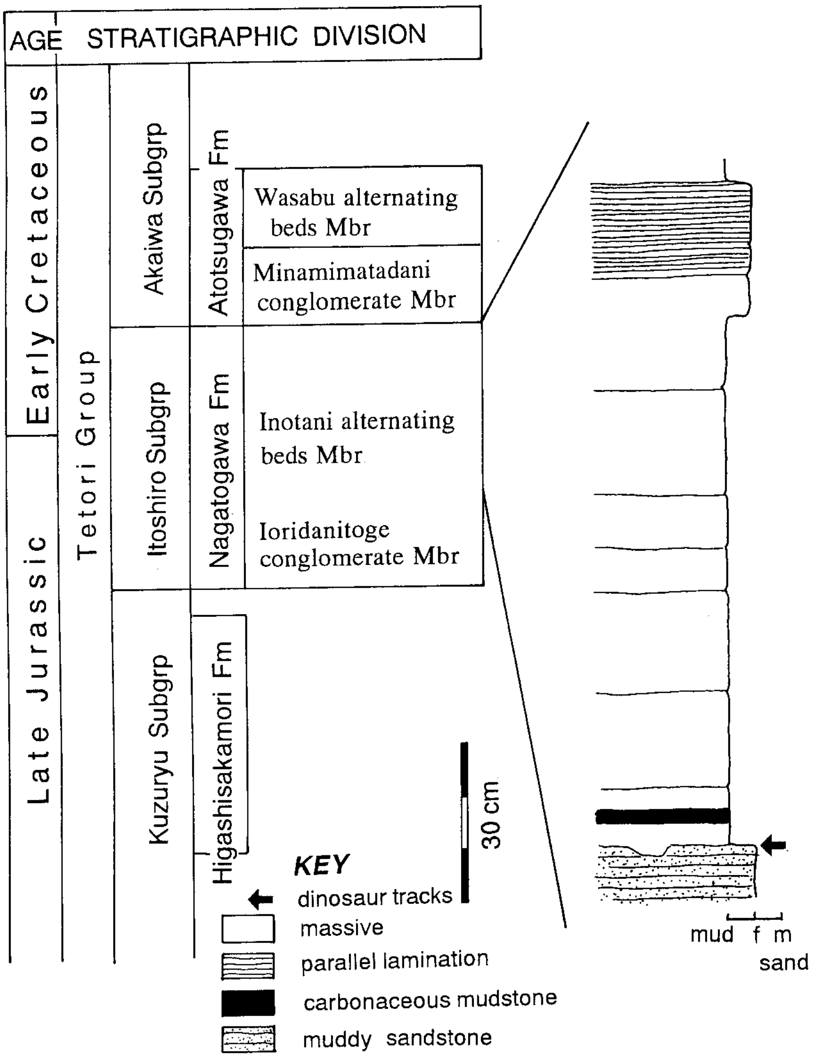

Figure 2. Upper Jurassic to Lower Cretaceous columnar section of the eastern part of the Tetori Group in Toyama, Japan. f: fine grained, m: medium grained.

Although there are two interpretations concerning the stratigraphic relationship between the Higashisakamori and the overlying Nagatogawa Formation, as an unconformity (Maeda, 1958) or a fault (Nozawa *et al.*, 1981), the latter formation correlates with the Itoshiro Subgroup. The upper part of the Inotani Member is probably Early Cretaceous in age; therefore, the member as a whole encompasses both Upper Jurassic to Lower Cretaceous deposits.

The Nagatogawa Formation consists of the lower Ioridanitoge conglomerate Member and the upper Inotani alternating beds Member. The conglomerate of the Ioridanitoge Member is distributed along the margin of the Tetori Group, and is made up predominantly of granitic and gneissic cobble to boulder gravels. The overlying Inotani Member has a wider distribution than the Ioridanitoge Member, and consists of alternating beds of thick sandstone and thin shale with terrestrial plant debris. The upper part of the Inotani Member, which contains the dinosaur tracks, consists of interbedded sandstones showing convex-up geometry and some trough cross-stratification. Mudstones in generally sandy and carbonaceous rock locally contain slump structures. Some sequences contain couplets of beds consisting of trough cross-stratified sandstone and thin mudstone beds with slump structures. These are interpreted as coarsening-upward cycles of prograding mouth bars on a lake margin. The dinosaur tracks were discovered as moulds on the surface of the very fine sandstone bed, which represents a proximal mouth bar palaeoenvironment.

3. Systematic ichnology

Toyamasauripus Matsukawa ichnogen. nov.

Diagnosis. Narrow trackway of a small biped, typically 3–10 cm in length, with high pace angulation. Tridactyl track consists of slender digits with variably preserved pad impressions and projecting small heel, and is slightly asymmetrical, mesaxonic, and about as long as wide. Divarication between digits II and IV averaging about 90° (range 60°–136°). End of digit III curves inward.
Etymology. Originating from Toyama Prefecture, Japan.
Type specimens. Holotype—TGUSE-DT 1001 (d in Figure 3; 2e in Figures 6, 7) and paratypes—TGUSE-DT 1002 (c in Figure 3; 1a in Figure 6) and TGUSE-DT 1003 (a in Figure 3; 16 in Figure 6), housed in Tokyu Gakugei University as rubber moulds of original specimen.
Type locality. Oshimizu, Ooyama-machi, Kaminiikawa-gun, Toyama Prefecture
Type horizon. Lower Cretaceous of the Inotani alternating beds Member, Nagatogawa Formation, Itoshiro Subgroup, Tetori Group.

Discussion. *Toyamasauripus* has characteristics of both theropod and/or ornithopod tracks (Thulborn, 1990; Lockley, 1991). It has a narrow trackway, tapering digits with a V-shaped outline and impressions of claws. Footprints are

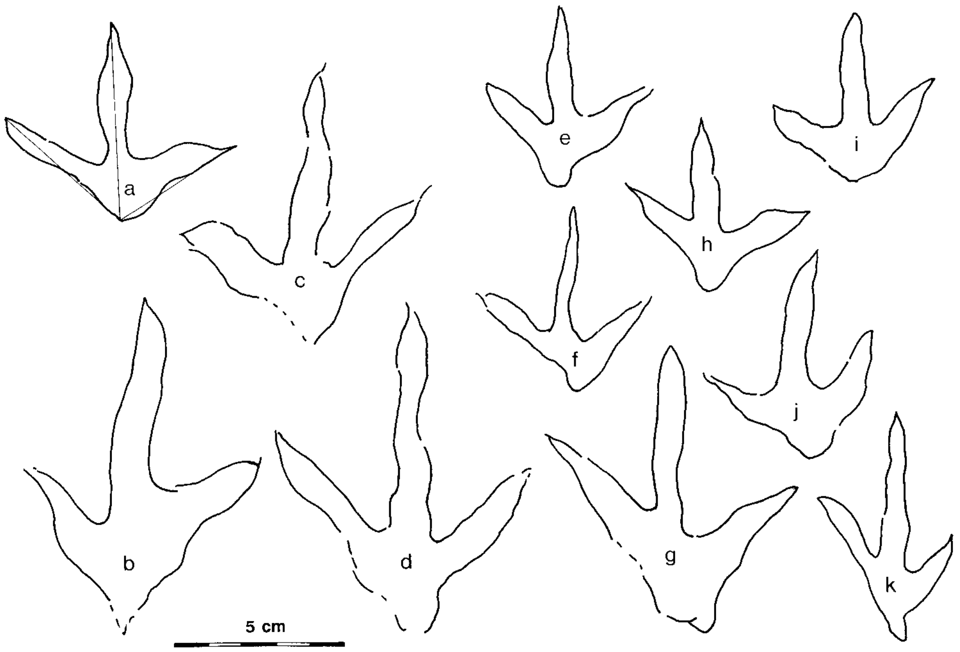

Figure 3. Slender-toed gracile tracks, *Toyamasauripus masuiae*. a: 16 in Figure 6, b: 1h, c: 1a, d: 2e, e: 24b, f: 24a, g: 2h, h: 6a, i: 17b, j: 17a, k: 2h.

Figure 4. Trackway 1 on the surface of the exposure. Arrows show tracks.

tridactyl with digit III being longer than the other two. The ratio of footprint length/width is, however, similar to that of purported ornithopod tracks, as is the short step and symmetry of the track.

Spanish Early Cretaceous trackways of a small track-maker, from a locality know as Valdevajes (or Valdebrajos) in La Rioja Province, have been the subject of much debate, and are attributed by some authors to coelurosaurs (Casanovas-Cladellas *et al.*, 1991) and by others to the ornithopod *Hypsilophodon* (Aguirrezabala *et al.*, 1985; Viera & Torres, 1992; Martin-Escorza, 1992). Regarding the debate, Lockley *et al.* (in press) agreed with the interpretation that the tracks are attributable to *Hypsilophodon* because they show ornithopod footprint characteristics (symmetrical, as wide or wider than long, without well-defined claw impressions, with slight inward rotation of digit III and lack of well-defined pad impression).

Lockley *et al.* (in press) proposed the new ichnogenus *Dinehichnus* based on trackways of a small track-maker from the Upper Jurassic Morrison Formation, Colorado Plateau, and noted the similarity with Spanish tracks that are attributed to *Hypsilophodon*. Furthermore, they showed that they are found as sets of parallel trackways, presumably representing a gregarious group of track-makers, both in the Colorado Plateau region and at an Upper Jurassic site in Portugal.

Toyamasauripus also shows ornithopod characteristics (symmetrical, as wide or wider than long, without well-defined claw impressions, with wide digit divarication angle, slight inward rotation of digit III and lack of well-defined pad impression). In addition the tracks occur in at least three sets of parallel trackways representing a gregarious group of track-makers (described below). Therefore, the new ichnogenus may also be attributable to a track-maker such as *Hypsilophodon*, or a related genus. It is similar to *Dinehichnus* and comparable ichnites from Portugal and Spain except that it reveals digit impressions that are more slender, and some discrete pad impressions.

It has been common practice to correlate slender-toed tridactyl tracks (Lockley, 1991; Matsukawa *et al.*, 1995) with coelurosaurs (Thulborn, 1990). However, the lower ratio of stride length/footprint length and wide divarication of digits II and IV discriminate the present ichnogenus from pes prints attributed to coelurosaurs as summarized by Thulborn (1990). An equally strong case can be made for comparing the tracks with similar Jurassic *Anomoepus* footprints (Lull, 1953). The ratio of stride length/footprint length in *Toyamasauripus* is 5.5/1 to 6.1/1, compared to 7/1 to 8/1 for coelurosaurs (Thulborn, 1990) and to 3.1/1 to 6.0/1 for *Anomoepus* (Lull, 1953). Similarly, divarication of digits II and IV in *Toyamasauripus* is 80° to 110°, but only 45° to 50° in coelurosaurs as defined by Thulborn (1990), and 42° to 72° in *Anomoepus* (Lull, 1953). These differences in track and track morphology are very significant.

Tracks of *Toyamasauripus* are distinguished from those attributed to ornithomimids and similar dinosaurs (Sternberg, 1926, 1932; Thulborn, 1990) because the former has a smaller pace angulation and positive rotation of digit III. Cretaceous bird tracks described by Lockley *et al.* (1992) somewhat resemble the tracks of the *Toyamasauripus*, their outline consisting of slender digits and a small heel, but are distinguished by their smaller size and wider divarication angle between II and IV. In many cases bird tracks also show a posteriorly directed hallux and are associated with very high density track assemblages.

Toyamasauripus masuiae Matsukawa ichnosp. nov.
Figures 3a–k, 4, 5A–D

Diagnosis. As for ichnogenus.
Etymology. After Mrs Masui Hamuro, wife of Toshikazu Hamuro, one of the authors.

Description. Fifty-two pes tracks consisting of three slender digits and small heel. They range from 3.3–9.4 cm in length and 3.2–7.8 cm in width (Table 1). Small specimens, less than 6.5 cm in length, have a tendency to be wider than long, but large specimens are longer than wide. Slender digits are broad proximally, but gently taper to a sharp point distally (Figure 3). Digit III is longer than the other two and its end curves inward. The specimens are slightly asymmetrical with a v-shaped outline and projecting small heel. A slight posterior indentation is present along the posterior margin of digit II. The inter-digital angle between digits II and IV ranges from 60°–127°.

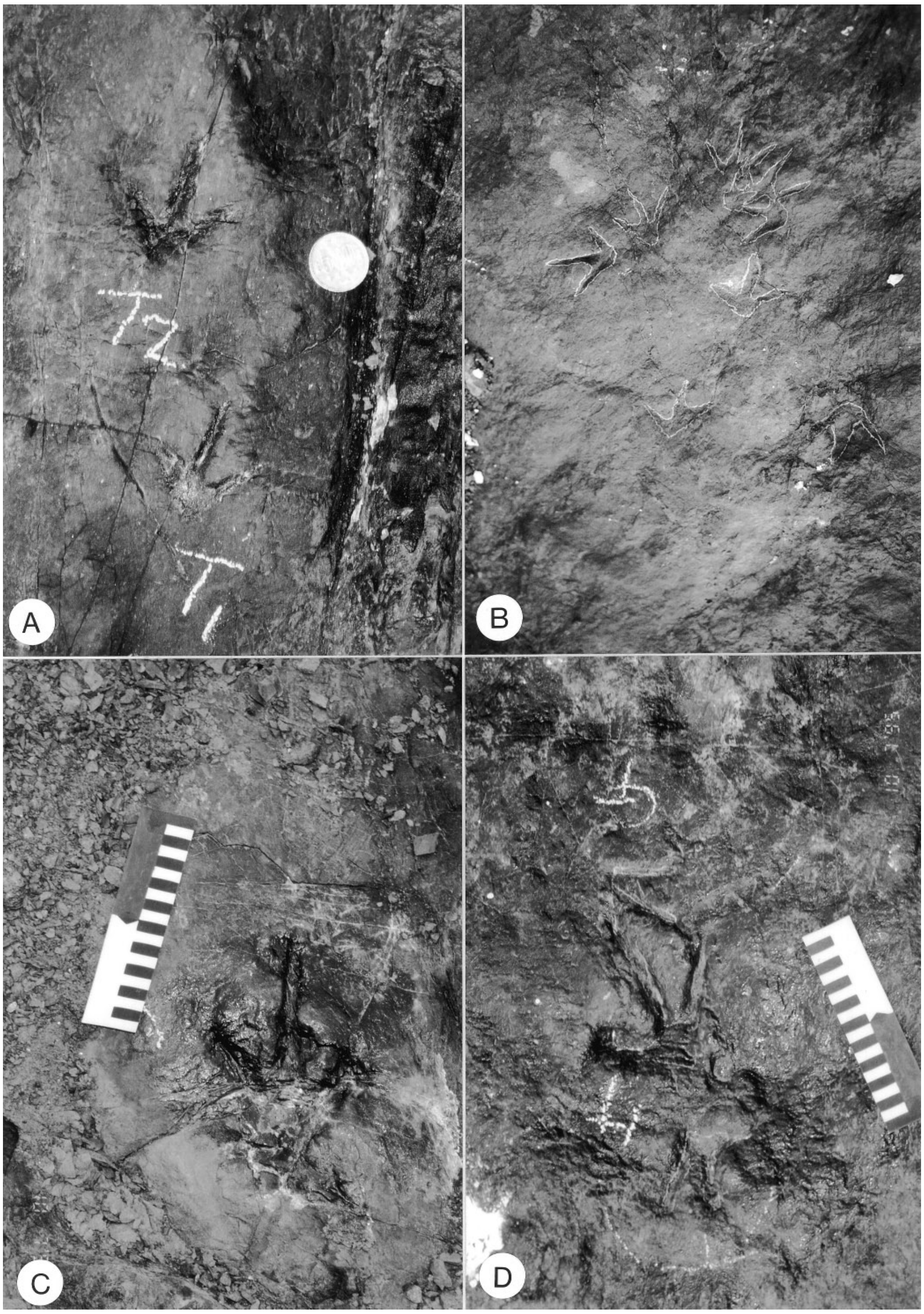

Figure 5. Some selected tracks. A, tracks 24a (T1) and 24b (T2); B, high density of tracks; C, track 2e; D, tracks 1a, 7 (G), 8 (H). Scales by coin and bars indicate 2.5 cm and 5 cm respectively.

Two trackway sequences consisting of more than four tracks can be recognized: Trackway 1 is made up of tracks 1a–f and 1h–j (Figures 6, 7); Trackway 2 of 2a, 2c–e, 2h and 2i. Both trackways reveal a biped, with steps of 21.5–26.0 cm and strides of 41.5–54.0 cm in Trackway 1, and steps of 22.0–26.4 cm and strides of 45.0–51.2 cm in Trackway 2 (Figures 6, 7, Table 2).

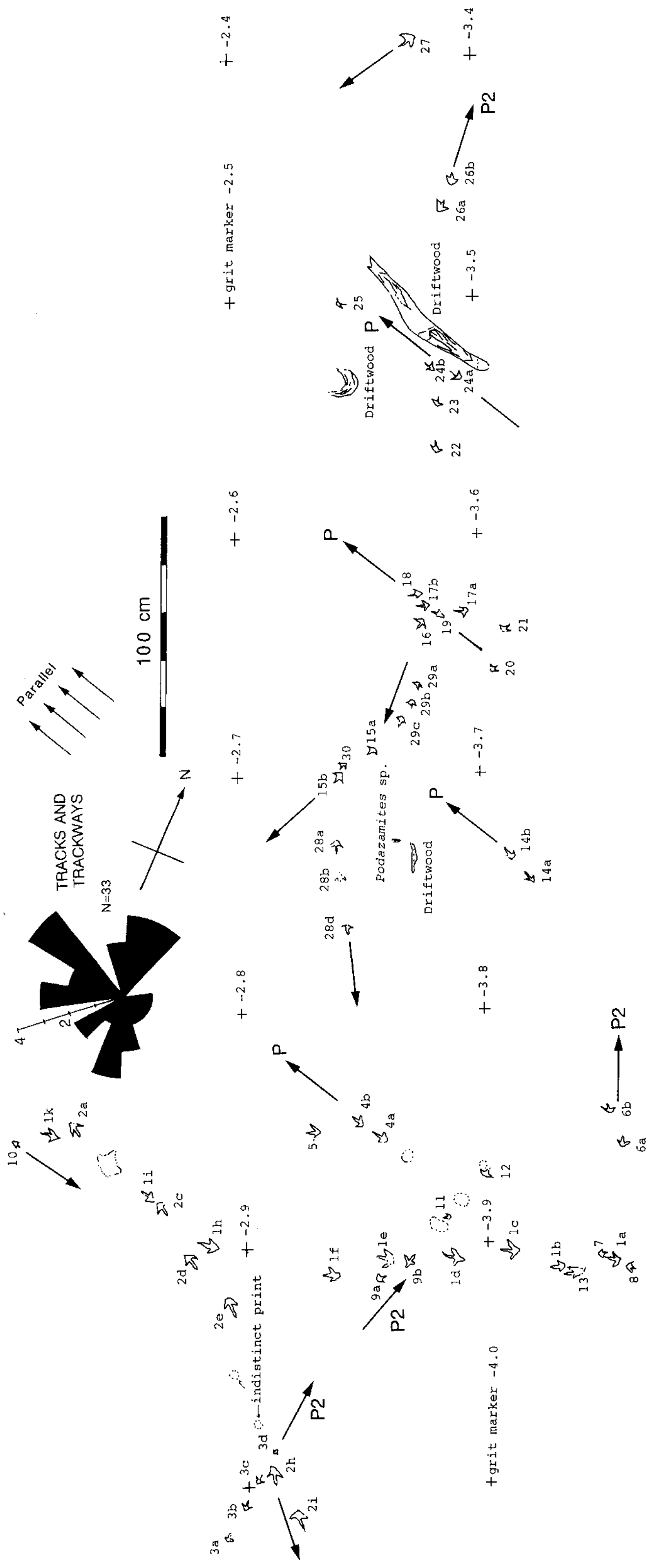

Figure 6. Distribution map of *Toyamasauripus masuiae* on the surface of the exposure showing concentration of track directions, with a rose diagram indicating trackway orientations.

Table 1. Measurements of *Toyamasauripus masuiae*. Linear dimension in mm. L/W; simple ratio of track length vs. width; A.II–IV, divaricate angle of digits II and IV; A.II–III, divaricate angle of digits II and III; A.III–IV, divaricate angle of digits III and IV

Track	Length	Width	L/W	FW/FL	A.II-IV	A.II-III	A.III-IV
1	8.21	7.83	1.05	0.95	79	39	40
2	8.3	6.5	1.28	0.78	81	40	41
3	5	5.17	0.97	1.03	98.5	48.5	50
4	6.75	5.5	1.23	0.81	70	30	40
5	5	5	1.00	1.00	75	35	40
6	5.85	5.75	1.02	0.98	94.5	47.5	47
7	4.5	5	0.90	1.11	94	41	53
8	4.3	5	0.86	1.16	108	40	68
9	4.65	5	0.93	1.08	103	40	63
10	4.4	3.2	1.38	0.73	60	25	35
11	3.3	3.6	0.92	1.09	95	45	50
12	4	7	0.57	1.75	136	63	73
13	9.4	6	1.57	0.64	47	22	25
14	6.3	4.4	1.43	0.70	69.5	35	34.5
15	5.25	6	0.88	1.14	118.5	55	63.5
16	5.5	7	0.79	1.27	110	50	60
17	5.35	5.5	0.97	1.03	88	40	48
18	5.2	4	1.30	0.77	66	30	36
19	6	4	1.50	0.67	61	26	35
20	4	4	1.00	1.00	90	40	50
21	4	5	0.80	1.25	100	40	60
22	4.5	5	0.90	1.11	105	30	75
23	5.5	4.5	1.22	0.82	127	60	67
24	5.1	4	1.28	0.78	85	44	41
25	4	3.5	1.14	0.88	113	36	77
26	5.05	6	0.84	1.19	93	53.5	39.5
27	6.5	7	0.93	1.08	85	45	40
28	5	4.5	1.11	0.90	92	42	50
29	4	3.67	1.09	0.92	108	48	60
30	4.4	5	0.88	1.14			
31	6.2	5.7	1.09	0.92			
32	4.5	4.5	1.00	1.00			
33	6.6	7.5	0.88	1.14			

Biometry. The measurements of the tracks are shown in Table 1. The frequency distribution of the characters examined (i.e., length, width, L/W and A.II–IV) are given in Figure 8. This clearly shows that the characters of width and divarication angle between II and IV have an approximately normal distribution. Characteristics of length and L/W are skewed to the left. Biometric characters of the tracks are shown in Table 3. The coefficient of variation values for all these parameters is similar. Chi-square values (χ^2) generally indicate no departure from normal distribution patterns (at the 5% confidence level) except for the length which is the most variable part of the track. The null hypothesis, therefore, would not be rejected in general and the specimens examined are judged to represent individuals from a single population. This statistical conclusion is consistent with the fact that many tracks are from the same trackways.

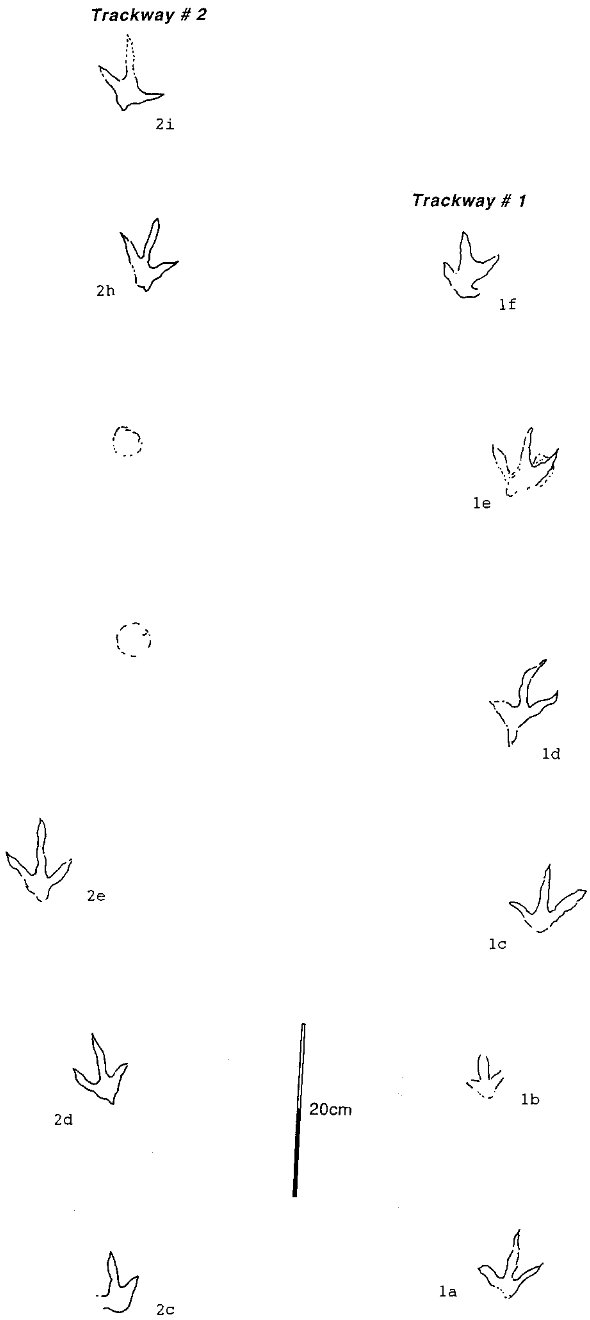

Figure 7. Two trackways of *Toyamasauripus masuiae*.

The average relative growth of track length vs. width is demonstrated in Table 4 and Figure 9. The correlation coefficient value (r) shows medium correlativity, and is significant at the 5% level. Furthermore, the t-value of the correlation coefficient is significant at the 5% level.

Comparison. Some dinosaur tracks from the Lower Cretaceous Tetori Group were illustrated by Azuma (1995). Four specimens among them (Azuma, 1995,

Table 2. Measurements of trackways of *Toyamasauripus masuiae*

Trackway 1

Pace			Stride	SL/FL	Pace Angulation			Length	Width	FW/FL	A.II-IV	A.II-III	A.III-IV
a,b	21.5	Ra,c	41.5	5.19	abc	150	a	8	7	0.88	91	53	38
b,c	22	Lb,d	43	6.14	bcd	157	b	7	?		78	34	42
c,d	22.5	Rc,e	50	6.25	cde	177	c	8	8.5	1.06	90	50	40
d,e	26	Ld,f	50	5.88	def	163	d	8.5	8	0.94	85	25	60
e,f	25	Re,?		?			e	9	8	0.89	67	37	30
		Lf,h	54	6.35			f	8.5	8	0.94	71	41	30
							g	?	?		?	?	?
							h	8.5	7.5	0.88	78	38	40

Trackway 2

Pace			Stride	SL/FL	Pace Angulation			Length	Width	FW/FL	A.II-IV	A.II-III	A.III-IV
a,b	22.4	La,c	48.8	6.97			a	7	6.5	0.93	69	25	44
b,c	26.4	Rb,d	51.2	5.69			b	?	?		?	?	?
c,d	25	Lc,e	50	7.14	cde	171	c	7	6.5	0.93	100	40	60
d,e	25	Rd,f	?				d	9	6.5	0.72	70	30	40
e,f	?	Le,g	46.5	4.89			e	9.5	6.5	0.68	76	44	32
f,g	?	Rf,h	?				f	?	?		?	?	?
g,h	25	Lg,i	45	6.00			g	?	?		?	?	?
h,i	22						h	8.5	6.5	0.76	73	32	41
							i	7.5	6.5	0.87	99	69	30

p.101, top right and middle left) are characterized by having a v-shaped outline, three tapering digits, a small heel, a 60–80° inter-digital angle between digits II and IV, and an inward curvature of the end of digit III. It is suggested that three specimens are possibly allied to the present species.

The theropod tracks illustrated by Matsukawa *et al.* (1995, pp. 6, 7, figs 3–5) from the Lower Cretaceous in Manchuria, Korea and Japan differ from the present specimens in having a larger pes size.

The present specimens are also distinguished from the illustrated specimens of *Columbosauripus ungulatus* (Sternberg, 1932, pp. 65–67, pl. 3, figs 3, 4) from the Aptian of British Columbia, Canada. The former has three slender digit impressions, a smaller heel with posterior projection, and a slight indentation in the posterior margin of digit II.

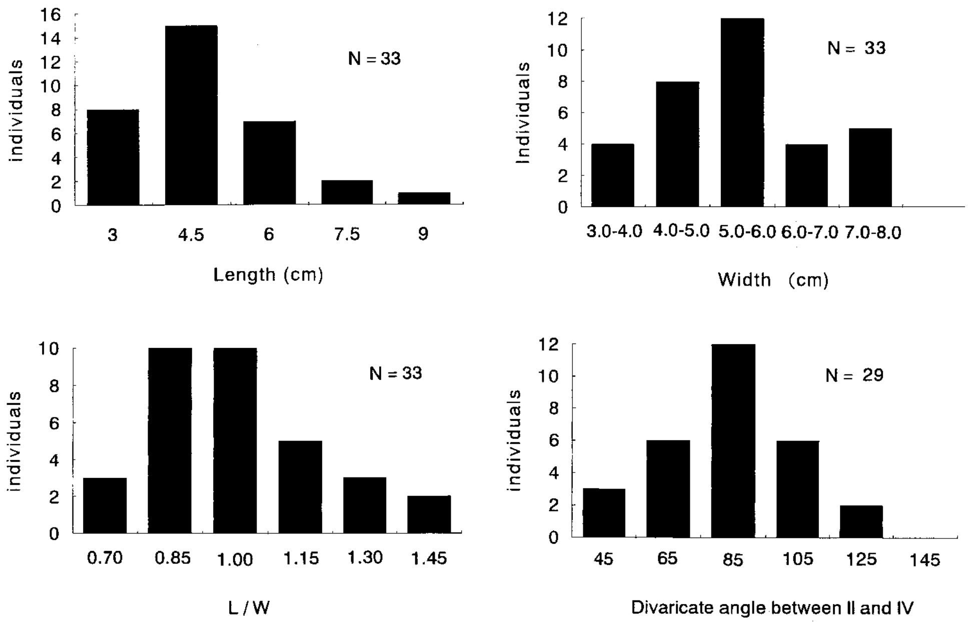

Figure 8. Histogram showing the frequency of selected characters.

Table 3. Biometric characters of *Toyamasauripus masuiae*. N, sample size; m, mean value; σ, population standard deviation; s, standard deviation; *V*, Pearson's coefficient of variation; $\chi^2_{0.05}$, chi-square value at 0.05 significant limit; ν, degree of freedom; value underlined is significant

	Length	Width	L/W	A.II-IV
N	33	33	33	29
m	5.35	5.19	1.05	91.45
σ	1.35	1.18	0.22	20.27
s	1.36	1.20	0.21	20.63
V	25.18	22.79	20.98	22.17
$\chi^2_{0.05}$	<u>21.24</u>	4.55	6.28	2.26
ν	3	3	3	3

4. Discussion

Thirty-three individuals of *Toyamasauripus masuiae* are recognized from separate trackways in an area of approximately 3 × 7 m on the surface of the outcrop (Figure 6). This is the highest density of tracks for any dinosaur track-site in Japan. Furthermore, the trackways are oriented in three preferred directions: northward, northwestward and southward. This suggests a gregarious animal. The Group P, consisting of parallel trackways 4, 14, 19 and 24 shows estimated speeds ranging from 1.21–1.50 km/hr, and Group P2, 3, 6, 26 and 9, suggests 1.59–2.08 km/hr (Figure 6, Table 5). This means that movement for both groups was at almost the same speed. Furthermore, in Group P there was a very regular spacing between individual animals.

Although many small theropod and ornithopod body fossils have been recorded from the Lower Cretaceous in eastern Asia (Dong, 1979, 1992; Weishampel, 1990; Azuma, 1991, 1995; Matsukawa & Obata, 1994), there has been no evidence of a gregarious habit. Based on track evidence elsewhere, some small Early Jurassic theropods had a gregarious habit; for example, *Grallator* in North America (Ostrom, 1972; Lockley, 1991), and mid-Cretaceous coelurosaurs in Queensland, Australia (Thulborn & Wade, 1979, 1984). But much more track evidence of gregarious small ornithopods is becoming known from Upper Jurassic to Lower Cretaceous successions in the Colorado Plateau, Spain and Portugal

Table 4. Data on the average relative growth of *Toyamasauripus masuiae*. N, sample size; α, growth index (slope of the reduced major axis); r, correlation coefficient; $r \pm s_r$, correlation coefficient ± standard error; df, degree of freedom; $t_{0.05}$, student t-test value at 0.05 significant limit

	L vs W
N	33
α	0.5702
r	0.5749
$r \pm s_r$	0.5749 ± 0.147
df	31
$t_{0.05}$	0.3913

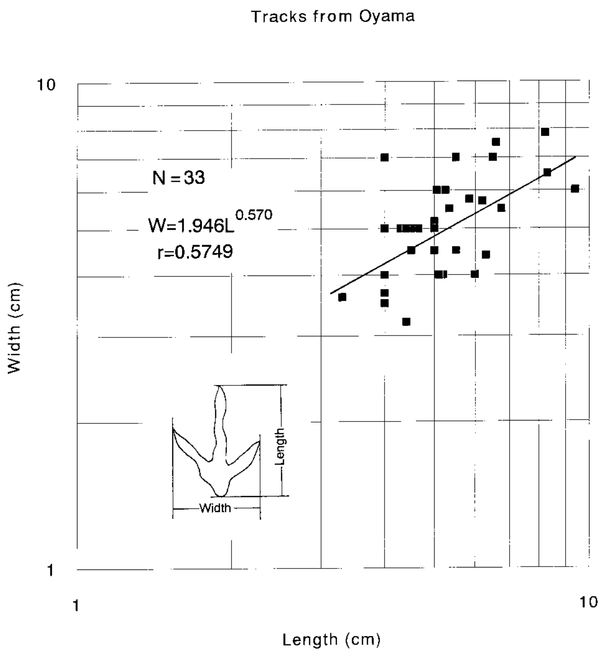

Figure 9. Diagram showing the average relative growth of *Toyamasauripus masuiae*.

(Aquirrezabala *et al.*, 1985; Viera & Torres, 1992; Lockley *et al.*, 1997), and is being further investigated (Lockley, 1995).

The Early Cretaceous dinosaur fauna in China and Japan is characterized by *Psittacosaurus*, associated with freshwater fossils including the fish *Lycoptera*, the conchostracan *Eoestheria*, the insect *Ephemeropsis*, the bivalves *Nakamuranaia* and *Nippononaia*, the ostracod *Cypridea*, and terrestrial plants of the *Acanthopteris-Ruffordia* flora (Hao *et al.*, 1986). The animal association was named the Jehol fauna by Grabau (1928). It occurs widely in northern China. *Psittacosaurus* occurs in the Lianmuqin (Xingjiang), Lisangou (Nei Mongol), Xinpongnaobao

Table 5. Measurements on tracks of *Toyamasauripus masuiae* and speed estimates. All measurements in cm. Speed estimated using the formula of Alexander (1976): $V = 0.25g^{0.5} \cdot SL^{1.67} \cdot h^{-1.17}$ where SL is stride length (twice step length for a parenthesis) and h = hip height estimated as for times foot-length

Trackway	Footprint			Step	Stride	SL/FL	Speed:m/s	Speed:km/hr
	Length	Width	w/l					
Group P								
1h to 1k	0.083	0.071	0.86		0.501	6.04	0.89	3.22
1a to 1f	0.082	0.078	0.95		0.477	5.82	0.83	3.01
4	0.063	0.054	0.86	0.115	0.23	3.65	0.34	1.21
14	0.063	0.044	0.70	0.13	0.26	4.13	0.41	1.49
19	0.040	0.040	1.00					
24	0.051	0.0425	0.83	0.113	0.226	4.43	0.42	1.50
Group P2								
3	0.049	0.054	1.10	0.138	0.266	5.43	0.58	2.08
6	0.058	0.057	0.98	0.15	0.3	5.17	0.58	2.08
26	0.051	0.056	1.10	0.117	0.234	4.59	0.44	1.59
9	0.055	0.056	1.02	0.145	0.29	5.27	0.58	2.08

(Nei Mongol), Guyang (Nei Mongol), Bingou (Liaoning) and Chingshan (Shandong) formations (Dong, 1979; Weishampel, 1990). Although the Jehol fauna, including *Psittacosaurus*, has been employed as a time indicator, it occurs in deposits of both Late Jurassic (e.g., Chang *et al.*, 1987; Wang *et al.*, 1985) and Early Cretaceous (e.g., Hao *et al.*, 1986; Chen, 1983) age and is, therefore, of limited biostratigraphic significance. It is characteristic of fluvial and lacustrine deposits and, pending further biochronological refinement, is better viewed as a palaeoecological index (Matsukawa & Obata, 1994). Although discrepancies between trace and body fossil records in dinosaur communities are recognized in the Jehol fauna, both are associated with fluvio-lacustrine deposits in eastern Asia.

The Japanese islands, including the Tetori area, were part of the eastern margin of the Asian continent during the Early Cretaceous (Matsukawa *et al.*, 1987, 1993; Matsukawa & Obata, 1993, 1994; Matsukawa & Tsuneoka, 1993). The similarity of footprints between NE China and Japan supports this interpretation and suggests that ichnofaunas in both areas belong to the same ichnofacies, and possibly the same palaeogeographic province (Matsukawa *et al.*, 1995).

There are few dinosaur body fossil records that might correlate with *Toyamasauripus masuiae*. The first possibility is with the hypsilophodontids, from the Tetori Group in Japan (Azuma, 1991; Hasegawa *et al.*, 1990; Matsukawa & Obata, 1994) and from the Barun Goyot Formation in Mongolia (Jerzykiewicz & Russell, 1991). The second possibility is with the theropods from both the Tetori Group in Japan and the Tugul Group in western China. Included in the possible list of theropods known from body fossils are dromaeosaurids (Azuma, 1991; Dong, 1992; Currie, 1994; Matsukawa & Obata, 1994), and ornithomimids from the Shihehudag Formation in Mongolia and the Sebayashi Formation in Japan (Barsbold & Perle, 1984; Matsukawa & Obata, 1994; Matsukawa *et al.*, submitted). Therefore the track record is a significant addition to our knowledge (Figure 10).

Conclusions

1. Many tracks of slender-toed gracile bipeds have been found in the Lower Cretaceous Tetori Group of central Japan. They are described as *Toyamasauripus masuiae* Matsukawa ichnogen. and ichnosp. nov. The new ichnogenus might be attributable to *Hypsilophodon* or a related ornithopod based on the track characteristics. The possibility of a theropod track-maker, however, cannot be ruled out.
2. The parallel trackways of *Toyamasauripus masuiae* suggest gregarious behavior.
3. Thirty-three individuals of the *Toyamasauripus masuiae* are recognized in approximately 3×7 m of outcrop. This is the highest density of tracks of any dinosaur track-site in Japan.

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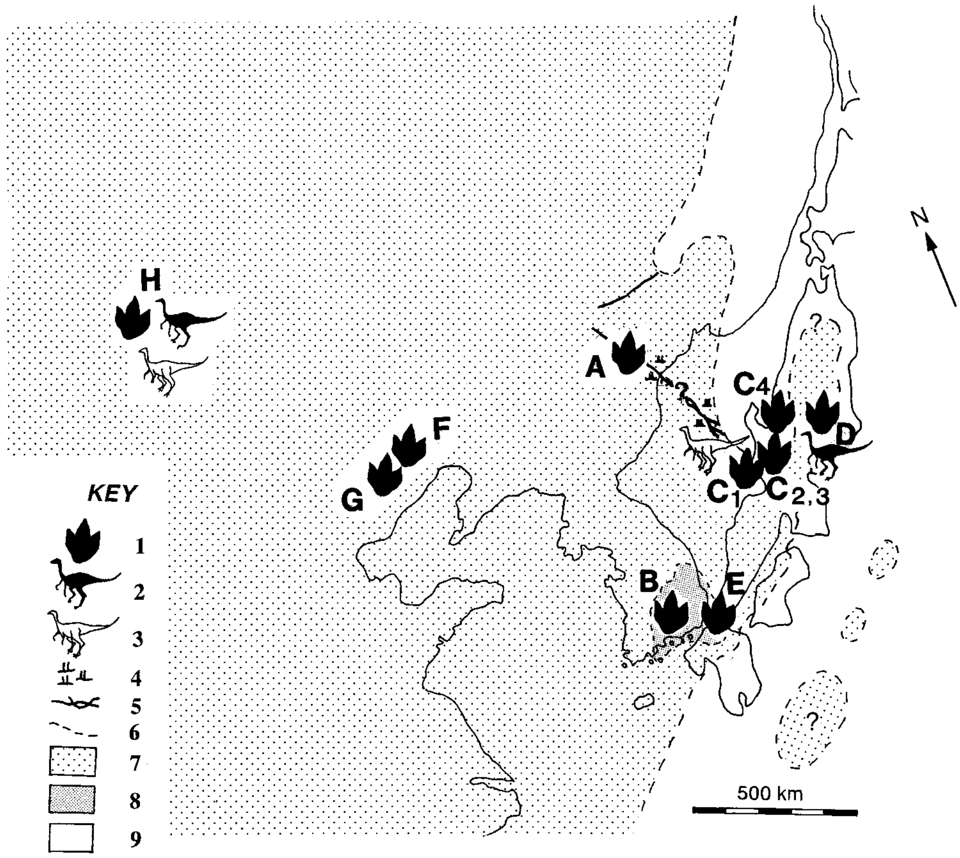

Figure 10. Distribution of dinosaur tracks and body fossil records of coelurosaurids and ornithomimids in relation to an inferred palaeogeographical map for the Early Cretaceous of eastern Asia. The map is based on Matsukawa & Obata (1993, 1994), Matsukawa & Tsuneoka (1993), Matsukawa *et al.* (1993). A, Yanji, eastern Jilin province; B, Dukmyeongri, South Korea; C1, Kuwajima and Kitadani, Tetori, Japan; C2, Izuki, Tetori, Japan; C3, Oshirakawa, Tetori, Japan; C4, Toyama, Tetori, Japan; D, Sanchu, Japan; E, Yoshimo, Japan; F, Chaoyang, Liaoning province; G, Luanping, Hebei province; H, Choir, Mongolia. 1, dinosaur tracks; 2, ornithomimid body record; 3, coelurosaurid body record; 4, flood plain; 5, fluvial system; 6, presumed coast line; 7, land; 8, lake; 9, sea.

track-site. We are also grateful to the referees and editor for their helpful comments. Thanks are extended to Masui Hamuro and members of Toyama Paleontological Research Club, Kazuto Koarai, Kazuhisa Kawashima, Takehiro Nakajima (Tokyo Gakugei University) and Satoru Hagimoto (Nihon Unversity) for their kind help in collecting fossils. The Kitanihonshimbunsha Newspaper Co. helped us in various ways. The study was financially supported in part by the Science Research Fund of the Japanese Ministry of Education, Science and Culture (Mombusho) (Matsukawa, no. 06640603, 1994–1996; Okada, no. 06304001 for Cooperative Research, 1994–1995).

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