The track record of Mesozoic birds: evidence and implications

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SUMMARY

The occurrence, systematics, palaeobiological and evolutionary significance of Mesozoic bird and bird-like tracks are reviewed in the light of recent new discoveries in East Asia, Africa and North America. The most abundant footprint evidence currently comes from Lower Cretaceous deposits of East Asia and North America, where there is now a substantial track record for shorebirds. However, there is also a significant record of pre-Cretaceous bird-like tracks.

The Cretaceous Jindong Formation of South Korea has recently yielded over 30 localities and stratigraphic levels, tripling the previous record worldwide and providing evidence of hitherto unknown large waders: *Jindongornipes kimi* ichnogen. et ichnosp. nov. Like other previously named ichnotaxa, this bird track type probably represents a charadriiform species. It is included with *Ignotornis* and *Koreanaornis* in the new ichnofamily Ignotornidae. Lower Cretaceous bird tracks are abundant, typically show high densities (100–300 tracks m^2) and often occur in association with invertebrate traces, inferred to have been made by the organisms on which the birds were feeding. Such track evidence suggests that waterbird communities were well-established by the end of the Early Cretaceous. This is about 30 Ma before the purported waterbird radiation inferred from Upper Cretaceous avian skeletal remains, but is consistent with hypotheses that suggest an ancestral shorebird stock.

Bird and bird-like tracks from the Jurassic and Late Cretaceous are variable in morphology, still poorly understood, and sometimes attributed to small coelurosaurian dinosaurs. However, current evidence suggests that the Jurassic aviform ichnogenus *Trisauropodiscus* may be of avian origin. It is sufficiently distinct from typical grallatorid (coelurosaurian) tracks to warrant recognition of a new ichnofamily (Trisauropodiscidae), which includes the newly described ichnospecies *Trisauropodiscus moabensis* from North America.

Bird and bird-like tracks from both the Jurassic and Cretaceous are shown to be much more abundant and distinctive than previously supposed. Moreover, they add significantly to our understanding of early avian evolution and palaeoecology, and provide insights into the timing of events in avian evolution.

1. INTRODUCTION

The fossil footprint record suggests that the 'Age of Dinosaurs' is an appropriate name for the Mesozoic. To date, over 99% of all Mesozoic tracksites exhibit exclusively dinosaurian or reptilian tracks. The total number of sites from which mammal, amphibian and bird tracks are unequivocally known is small. In recent years, however, there has been an increasing number of reports of bird tracks, particularly from Cretaceous strata. The footprint record for this class in the Mesozoic is now significantly improved and currently more extensive than for either mammals or amphibians.

Based on current knowledge there appears to be some persuasive evidence for pre-Cretaceous bird tracks. The criteria used to identify avian tracks compel us to consider at least three Jurassic sites that warrant serious attention. Regardless of how the Jurassic track record is interpreted, unequivocal bird tracks occur in significant numbers towards the end of the early Cretaceous, in Aptian and Albian times, particularly in North America and East Asia. These tracks were formed almost exclusively by small wading birds and suggest an avian radiation much earlier than previously supposed. Most footprints can be readily accommodated in the few ichnogenera that have been proposed to date. In contrast, late Cretaceous bird tracks are not so abundantly known and, as yet, remain poorly documented.

The aim of this paper is to report on known occurrences and new finds, and to assess their significance from an evolutionary and palaeoecological viewpoint. In addition, attempts are made to emend the existing taxonomy and update the status of collections. Criteria for defining bird tracks are also reviewed and discussed.

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2. HISTORY OF DISCOVERY AND RESEARCH

In the early part of the 19th Century, large numbers of 'bird tracks' were reported from the Mesozoic, particularly from the Lower Jurassic of New England (Hitchcock 1858). The supposed avian origin of these tracks was disproved when the majority were later determined to be dinosaur tracks. Given the now well-established close relationship between coelurosaurian dinosaurs and birds (Gauthier 1986), this dismissal of purported bird track evidence could prove premature. Birds arose directly from some of the theropod ancestors responsible for making these tracks. Bird origins undoubtedly occur before the late Jurassic (Olsen 1985; Chatterjee 1991). Given the existence of true birds such as *Archaeopteryx* by the late Jurassic, there is every reason to expect to find true avian tracks in the fossil record at least as early as the Jurassic. We suggest herein that at least one Jurassic ichnogenus, *Trisauropodiscus*, must be considered as very avian in appearance.

The first widely accepted report of Mesozoic bird tracks was published by Mehl (1931), who named the ichnospecies *Ignotornis mcconnelli* from the Dakota Group (late Albian–early Cenomanian) of Colorado. The holotype (UCM-17614; figure 1) is housed at the University of Colorado Museum at Boulder, although little topotype material is available. Much of it was removed from the outcrop by amateur collectors (R. Young, personal communication), leaving no *in situ* evidence of the stratigraphic position from which the type material originated. Fortunately a significant amount of new material was discovered by M.G.L. from a known stratigraphic horizon (about 20 m below the top of the Dakota Group) at a locality very near the type locality (Lockley *et al.* 1989). A large slab with tracks, and a replica, (MWC 203.1; figure 2) are now on display at the Nakasato Dinosaur Center, Gunma Prefecture, Japan (Lockley *et al.* 1989; Obata & Matsukawa 1990).

Bird tracks were next reported from the late Cretaceous (Maastrichtian) of Morocco (Ambroggi & Lapparent 1954). However, these tracks were not named or described in detail, and, so far as we know,

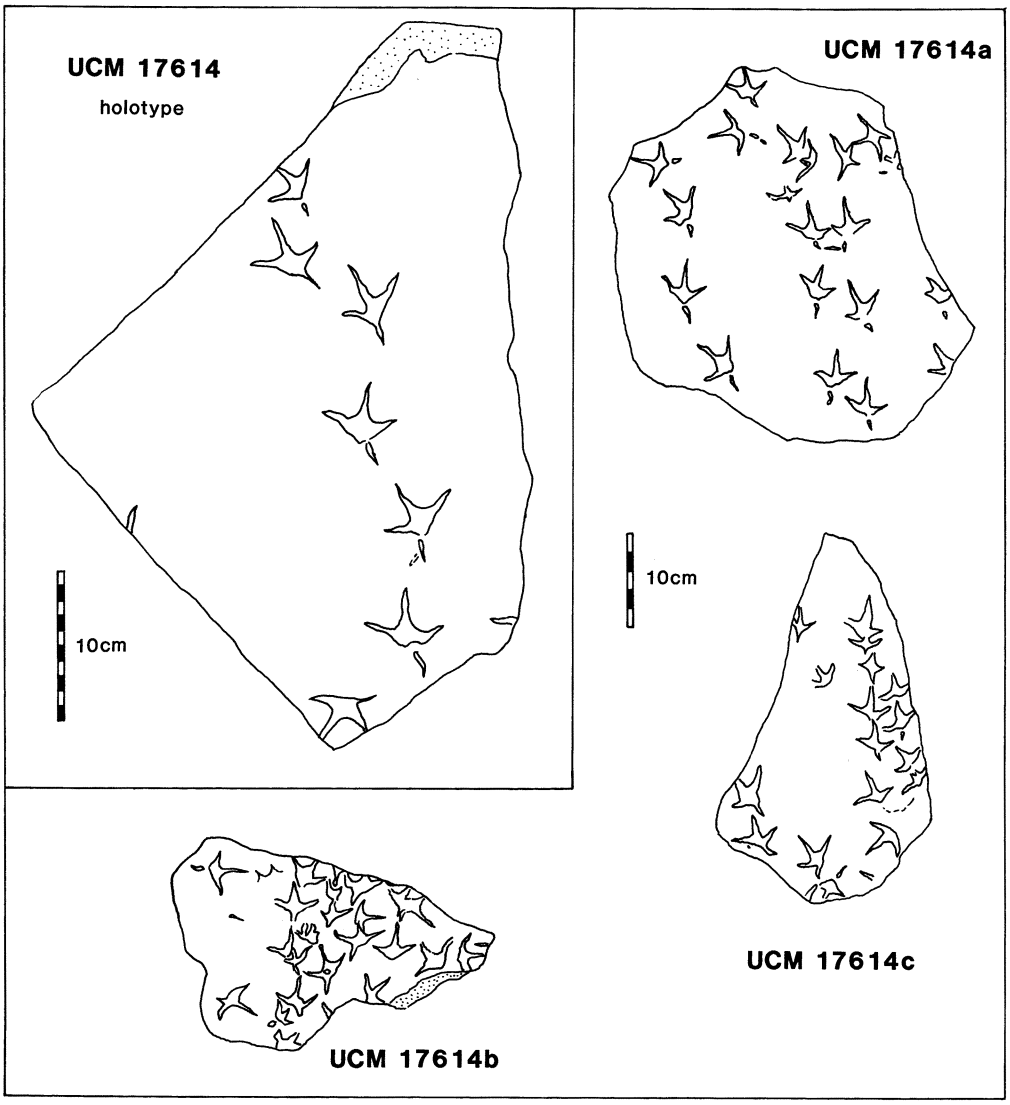

Figure 1. The holotype of *Ignotornis mcconnelli* Mehl 1931, with detail of a single trackway (Dakota Group, Colorado; UCM 17614).

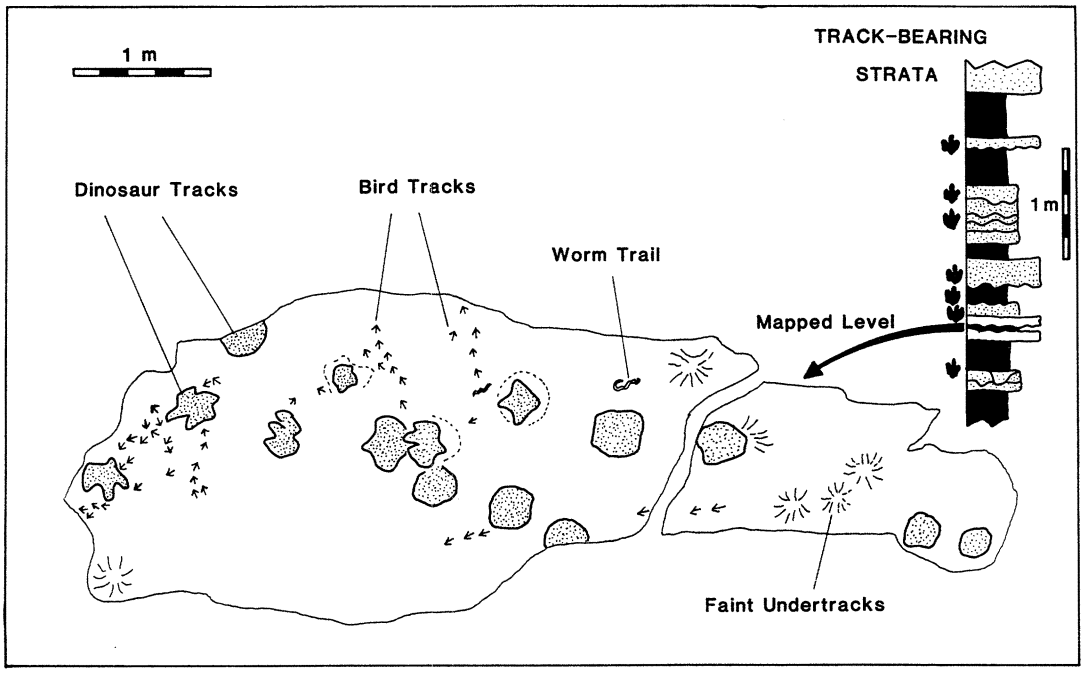

Figure 2. A large slab (MWC 203.1) from the Dakota Group of Colorado, exhibiting bird and dinosaur tracks. The bird footprints are assigned to *Ignotornis mcconnelli*. The slab was recovered from an exposure near the type locality.

specimens or replicas are not available in any recognized repository.

In 1969, Kim reported bird tracks from about 40 m below the top of the Haman Formation (Lower Cretaceous) of South Korea. Although Kim suggested that the Haman Formation is late Cretaceous in age, Choi (1985) has more recently suggested that these deposits are probably Aptian to early Albian in age. Kim (1969) proposed the new ichnotaxon *Koreanaornis hamanensis*, but did not compare the tracks with the material described by Mehl (1931). The type specimen was cataloged as DGSU 00158 (DGSU = Department of Geology, Seoul University) but, according to Kim (personal communication, 1990), the holotype was misplaced when the Geology Department moved to a new location. Fortunately a useful slab with topotype specimens is preserved as part of an outdoor exhibit (DGSU unnumbered specimen), and another is lodged in the Kyungpook National University collections (KPE 50001) (figure 3 herein).

In the early 1970s, Ellenberger (1970, 1972) described a series of diminutive Lower Jurassic bird-like tracks as the new ichnogenus *Trisauropodiscus*. Some tracks are so bird-like that Ellenberger assigned names such as *T. aviforma* and *T. superaviforma*. Despite the striking bird-like morphology of these tracks they have received little attention. We herein suggest that at least two other trackways, from North Africa (Ishigaki 1985) and North America (Lockley 1991), closely resemble *Trisauropodiscus* and deserve serious attention as possible avian tracks (see Systematics section below).

In 1981, Currie reported on an assemblage of tridactyl bird tracks from the Lower Cretaceous (Aptian–Albian) Gething Formation of western Canada. He named the specimens *Aquatilavipes swiboldae* (Currie 1981) (figure 4 herein) and compared them with the *Ignotornis* material from Colorado, but not with the *Koreanaornis* material from Korea. He illustrated over 220 tracks in an area of about 1.5 m^2

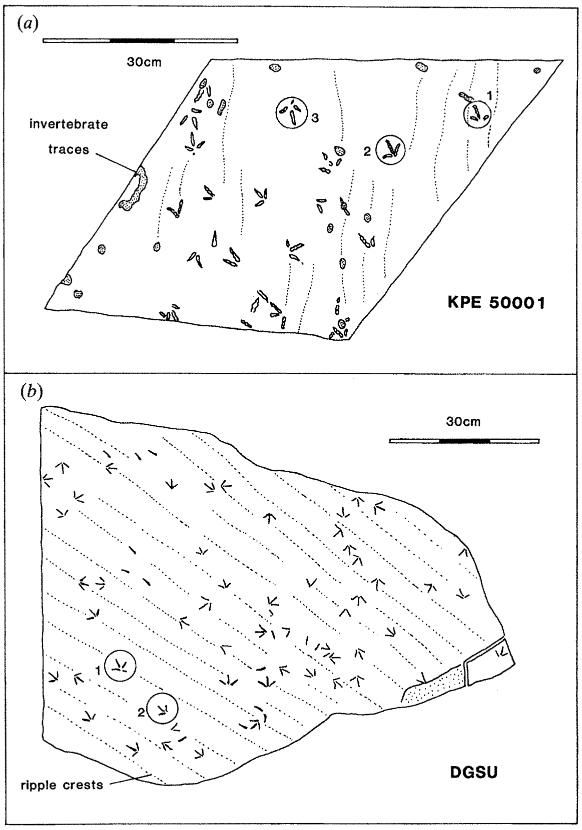

Figure 3. Topotype material of *Koreanaornis hamanensis* from the Lower Cretaceous of South Korea. (*a*) KPE 50001, lectotype; (*b*) DGSU unnumbered specimen.

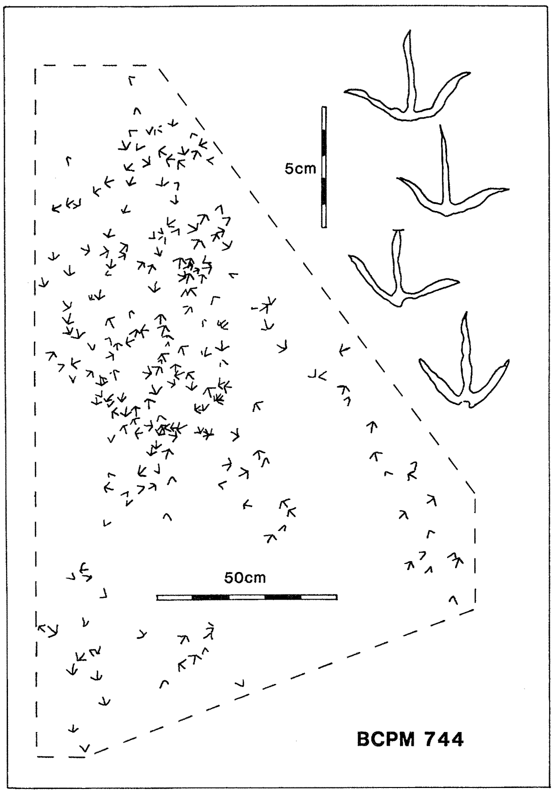

Figure 4. *Aquatilavipes swiboldae* Currie 1981, based on holotype and topotype material in the Tyrrell Museum (BCPM 744, and associated tracks); Lower Cretaceous (Aptain), western Canada.

(Royal British Columbia Museum (RBCM) 744) (figure 4 herein). Additional tracks occur on Royal Tyrrell Museum of Paleontology (RTMP) specimen 79.23.27.

In 1986, Alonso & Marquillas reported late Cretaceous (Maastrichtian) bird tracks from Argentina and named them *Yacoraitichnus avis*. Unlike all previously discovered Mesozoic bird tracks, *Y. avis* was distinctive because it displayed clear digital pad impressions (figure 5). However, Alonso & Marquillas (1986) did not compare *Y. avis* with any of the aforementioned ichnospecies. The holotype is preserved in the palaeontological section, National University of Salta.

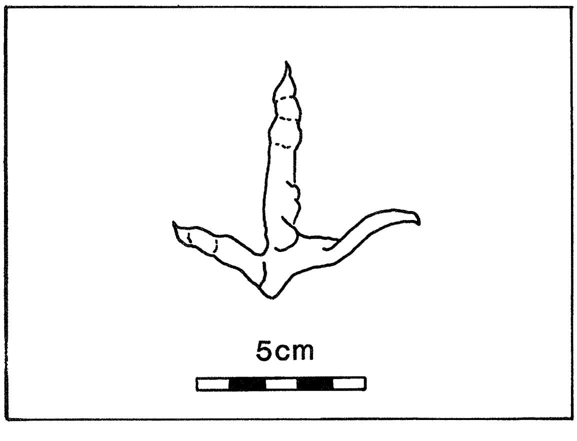

Figure 5. *Yacoraitichnus avis* after Alonso & Marquillas (1986); Upper Cretaceous (Maastrichtian), Argentina.

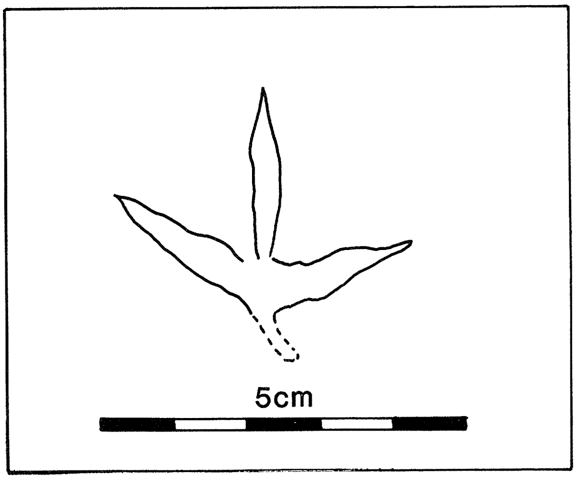

Figure 6. '*Aquatilavipes sinensis*' Zhen *et al.* 1987 from Lower Cretaceous of China; drawn from photograph provided courtesy of Zhen *et al.* (see text for details).

Zhen *et al.* (1987) reported tracks from the Lower Cretaceous of Sichuan Province, China, and named them *Aquatilavipes sinensis*. However, the tracks were not illustrated or discussed in any detail, so the name is invalid. Herein we include an outline traced from a photograph given to M.G.L. by Zhen (figure 6). Note the four digit impressions, a feature that is not characteristic of *Aquatilavipes*, which Currie (1981) defined as a tridactyl track. We think the track resembles *Koreanaornis hamanensis*.

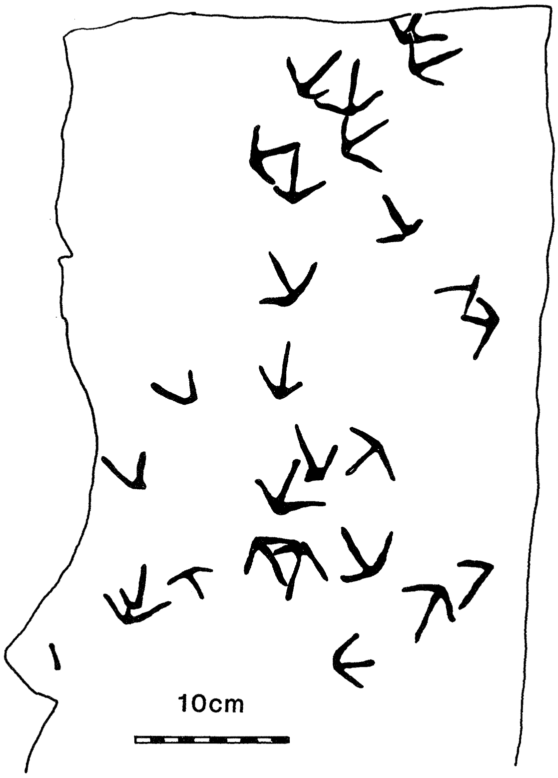

Figure 7. Unnamed bird tracks from the Lower Cretaceous Tetori Group of Japan (after Anon. 1987*a*).

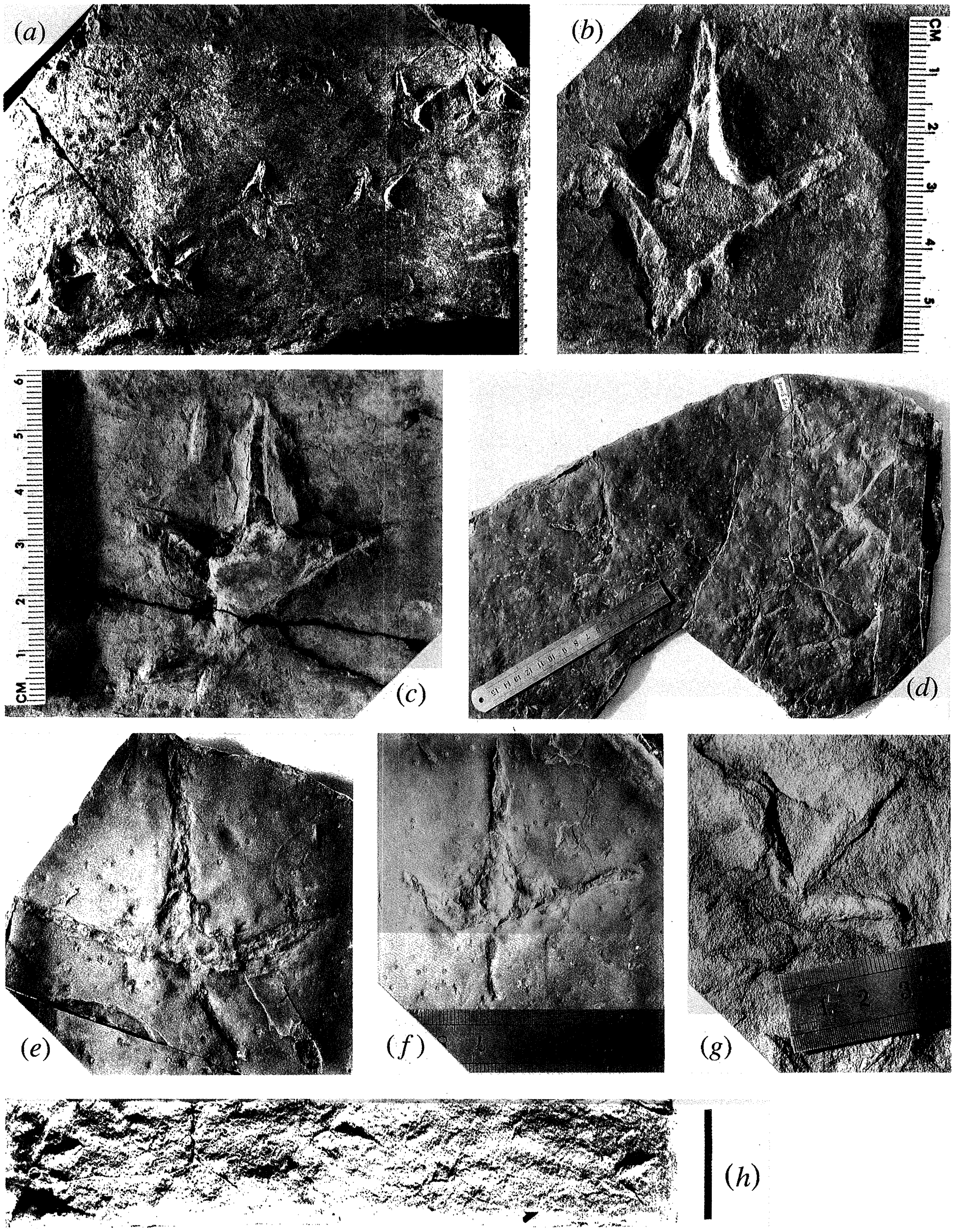

Figure 8. (*a*) *Ignotornis mcconnelli*: holotype; Cretaceous Dakota Group, Colorado; slab showing six tracks, including those shown in (*b*) and (*c*) (UCM 17614; cm scale in lower right). (*b*) *Ignotornis mcconnelli*: detail of one of the tracks shown in (*a*) (cm scale on right). (*c*) *Ignotornis mcconnelli*: detail of one of the tracks shown in (*a*) (cm scale on left). (*d*) *Jindongornipes kimi* sp. nov.: Cretaceous Jindong Formation, South Korea; slab showing five tracks, including those shown in (*e*) and (*f*) (KPE 50006; cm scale in lower left). (*e*) *Jindongornipes kimi* sp. nov.: paratype; Cretaceous Jindong Formation, South Korea (KPE 50006; track is 7.5 cm wide). (*f*) *Jindongornipes kimi* sp. nov.: holotype; Cretaceous Jindong Formation, South Korea (KPE 50006; cm scale along bottom). (*g*) *Aquatilavipes swiboldae*: Lower Cretaceous Gates Formation, Alberta (RTMP 90.30.1; cm scale in lower right). (*h*) *Trisauropodiscus moabensis* sp. nov.: holotype; latex mould of trackway from Jurassic Navajo Formation, Utah (CU-MWC 181.3; scale bar to the right of the trackway is 10 cm long).

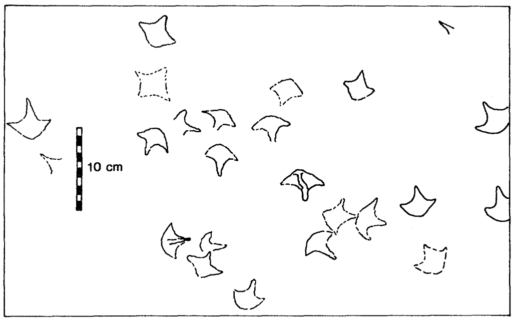

Figure 9. Tracks of a bird with webbed feet from the Uhangri Formation of South Korea. Redrawn from Chun (1990, p. 10a). Track density estimated at about 100 per square metre.

Leonardi (1987, plate XVIIIc) illustrated a slab with Maastrichtian bird tracks from Rio Negro Province, Argentina. The slab is housed in the Museo Civico, Venice, Italy, and measures about 35 cm by 35 cm, although the exact scale is not given. Based on the calipers in the illustration, the tracks are about 4–5 cm long and 6–7 cm wide. The slab reveals a high density of complete and incomplete tracks preserved as casts. The tracks have not been named.

Bird tracks were also reported from the Valanginian age, Izuki Formation (Tetori Group) of Japan in 1987 (Matsukawa 1991). These were illustrated in a newspaper article and a museum exhibit brochure (Anonymous, 1987*a*, *b*), but have not been named or described formally (figure 7). However, Azuma (personal communication, 1991) suggests that they may be assigned to *Aquatilavipes*. We have observed the specimens and agree with this identification.

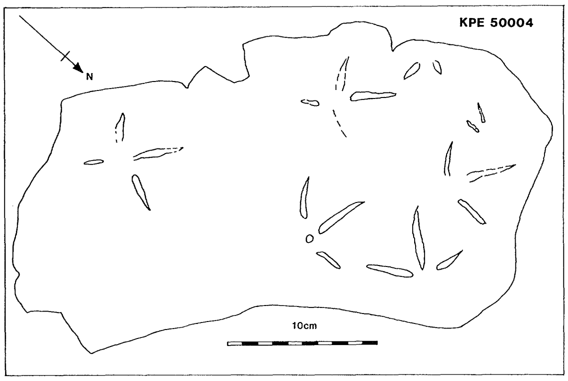

Figure 10. Bird tracks from the Jindong Formation. Large tracks are *Jindongornipes kimi*; small tracks are indeterminate (Silbawi Section; lower bird track horizon: KPE 50004).

Parker & Balsley (1989) reported an assemblage of unusual bird-like footprints from a late Cretaceous (Campanian) coal mine in Utah. These footprints were not named or described in any detail, although it was suggested that the tracks reveal a hesperornithiform morphology. Recently, however, Robison (1991, p. 325) reported ‘three different types of bird tracks from the Late Cretaceous (Campanian) Blackhawk Formation’. These tracks are different from those reported by Parker & Balsley (1989), and thus suggest a variety of avian trackmakers at this time.

Currie (1989) reported that small tridactyl footprints from the Dunvegan Formation, Alberta, may be attributable to hesperornithiform birds. One slab with eight tracks is preserved in the University of Alberta Paleontology Museum (UALVP 25271). Currie (personal communication) also reports that two well-preserved tridactyl tracks assigned to *Aquati-*

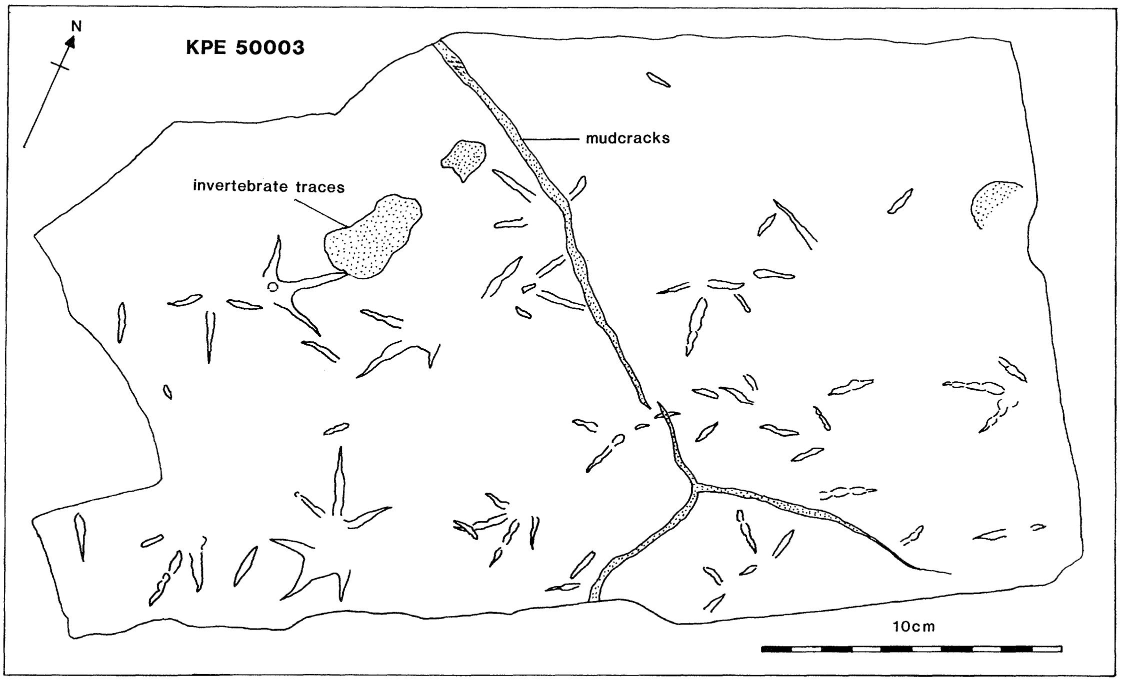

Figure 11. Bird tracks of *Koreanaornis hamanensis* from the Jindong Formation (Silbawi Section; middle bird track horizon: KPE 50003).

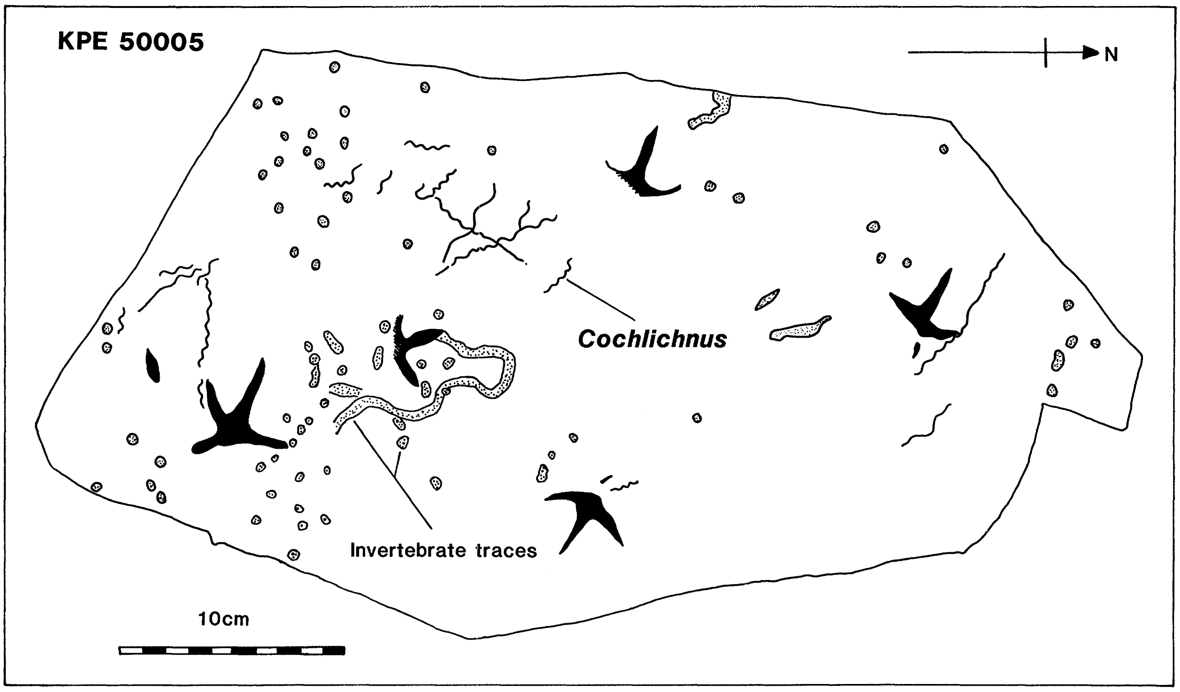

Figure 12. Bird tracks of *Koreanaornis hamanensis* from the Jindong Formation (Silbawi section; upper bird track horizon: KPE 50005).

lavipes swiboldae have been recovered from the Lower Cretaceous Gates Formation of Alberta (RTMP 90.30.1) (figure 8 herein).

In 1990, Chun reported and illustrated abundant bird tracks from a single locality in the Uhangri Formation of South Korea (figure 9). The tracks occur in lacustrine shoreline deposits and have been dated as late Cretaceous (i.e. younger than the 85–92 Ma Hwangsan Tuff, but older than the 63–67 Ma old Haenam basin intrusives). The Uhangri tracks are particularly interesting because they reveal traces of webbing, and thus appear to be the oldest known tracks of birds with webbed feet. Chun (1990, p. 37) compared them with tracks from the Eocene Green River Formation of North America which, according to Fedducia (1978, 1980), were made by the flamingo-like bird *Presbyornis*.

The most recent bird footprint discoveries were made in 1990 and 1991 by M.G.L., S.Y.Y., R.F.F. and S.K.L. at 31 localities in the Jindong Formation of South Korea (Yang *et al.* 1990; Lockley *et al.* 1991). This formation overlies the Haman Formation, and is probably Aptian–Albian in age (Choi 1985). There appear to be at least two quite distinct footprint types in the Jindong Formation, including one that closely resembles *Koreanaornis* (see figures 10–12). The formation is also the first to have yielded multiple bird-track horizons that are stratigraphically well located. The large amount of material including Kyungpook National University, Earth Science Department (KPE) specimens KPE 50002-15 is summarized herein, and will be described in detail elsewhere.

In addition to reviewing and illustrating the above-mentioned Cretaceous bird tracks, we show that some Jurassic tridactyl and tetradactyl tracks are extremely bird-like and must be considered in any comprehensive discussion of the Mesozoic track record of birds.

3. CRITERIA FOR BIRD TRACK RECOGNITION

At the outset it is worth stressing that, except in rare cases where invertebrate trackmakers have been found fossilized at the end of their trails, it is ultimately impossible to match most fossil tracks with prehistoric trackmakers with absolute certainty. Conversely, however, we can make intelligent deductions about trackmaker affinity based on morphology, age, habitat, etc. Moreover, trackmaker identification is one of the cardinal objectives of vertebrate ichnology, and much progress has been made in recent years (Lockley 1991). Some authors have referred Mesozoic bird-like tracks to coelurosaurs. For example, Haubold (1984) attributed *Trisauropodiscus* to a coelurosaur (but noted its aviform characteristics), and Thulborn (1990) referred *Ignotornis* to the Coelurosauria. In both instances, these authors also refer very different *Grallator*-like tracks (see figure 15) to the Coelurosauria without a discussion of the differences.

In an attempt to address this problem, we stress that most *Grallator*-like tracks show narrow digit divarication angles, relatively robust (wide) digit impressions compared with bird tracks, and distinctive pad impressions in well-preserved examples. These features are not typical of most bird tracks. This suggests that coelurosaur tracks include dinosaurian-like and bird-like tracks, a conclusion that forces us to view tracks as instructive in shedding some light on bird origins. We have strictly defined the criteria used in characterizing tracks as bird-like, and attempted to apply these criteria uniformly regardless of age.

Because there have been few studies of Mesozoic bird tracks, there are few guidelines for the recognition of fossil avian footprints. Criteria that have guided most authors to varying degrees are: (i) similarity of fossil tracks to those of modern birds; (ii) small size; (iii) slender digit impressions, with indistinct differentiation of pad impressions; (iv) wide divarication angle (about 110°–120° or more) between digits II and IV; (v) a posteriorly directed hallux (digit I); (vi) slender claws; (vii) distal curvature of lateral (II and IV) claws away from central axis of foot.

In this paper we have considered all these criteria for each purported bird-track ichnotaxon. Other criteria which are important, although less relevant to track morphology, are: (viii) track density; (ix) associated fossils and feeding behaviour; (x) sedimentological evidence regarding track-bearing deposits.

These latter criteria are important for the following reasons. It is known from modern observations that waterbirds make abundant tracks in shoreline sediments while feeding (Frey & Pemberton 1987). Such prolonged activity in environments suitable for track formation creates high track density and may result in the formation of feeding traces (bill or dabble marks). High track density results not only from prolonged activity, but also from high activity levels among many species of small waterbird (Cohen *et al.* 1990, 1991). Tertiary fossil evidence, especially from shoreline sediments of the Eocene Green River Formation, reveals localized high track densities and evidence of feeding traces (dabble marks) made by bird beaks (Erickson 1967). This particular example is of a bird with webbed feet, possibly *Presbyornis* (Fedducia 1980). Webbing is typical of some waterbirds (e.g. ducks, flamingos, etc.) but is absent on the feet of many waders. In this report we have only discovered one Mesozoic example (see Chun 1990), but one in which there is a local high density of webbed foot tracks. Other Tertiary examples of bird tracks worth noting include Weidmann & Reichel (1979), Alonso (1985, 1987), Plaziat (1964), Mangin (1962) and Raaf *et al.* (1965).

Whenever possible, we have attempted to estimate track density and describe any evidence of possible feeding traces, or the traces made by invertebrates upon which the trackmakers may have been feeding.

4. OTHER MISCELLANEOUS BIRD-LIKE TRACKS

Based on the above criteria, there are a number of other Mesozoic tracks that are very bird-like in appearance, even though their possible avian affinity has not been considered or previously discussed in any detail.

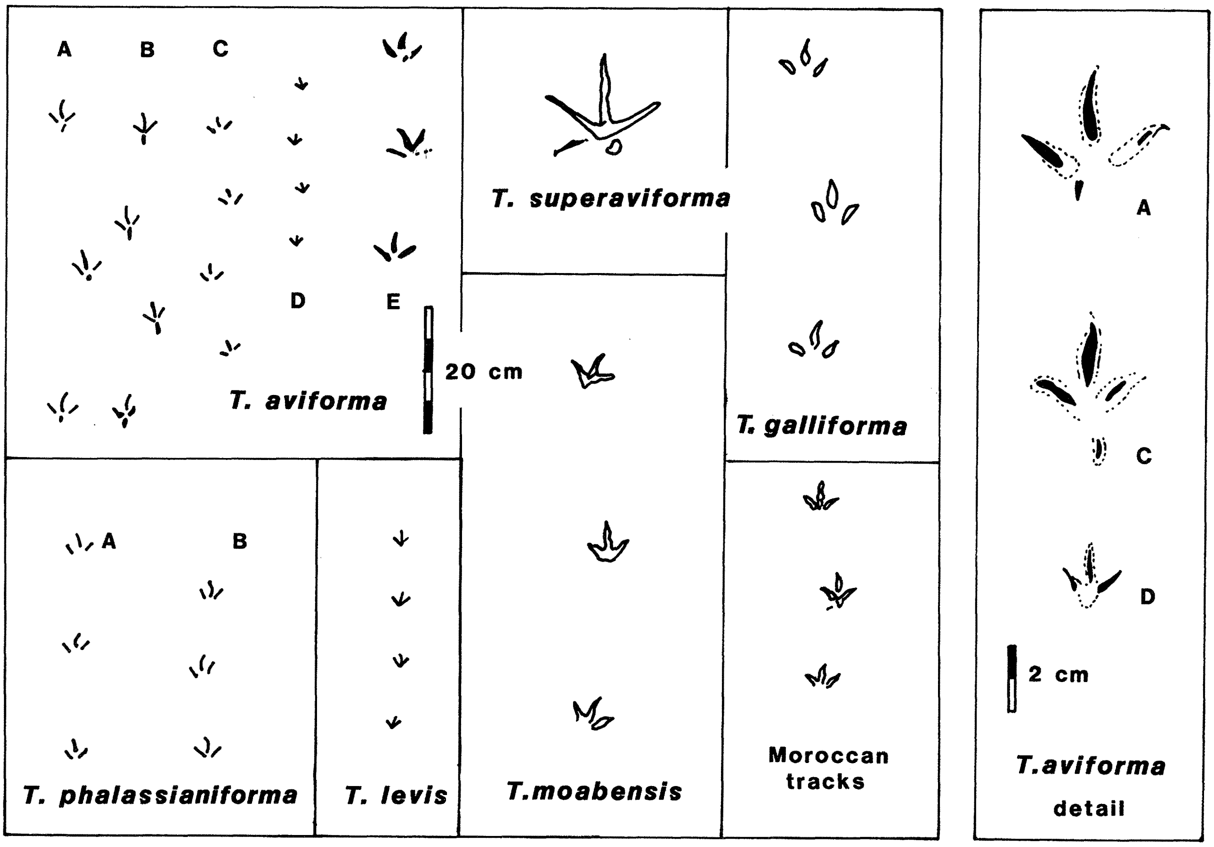

Figure 13. Aviform *Trisauropodiscus* tracks from Africa and North America. All except *T. moabensis* sp. nov. and the Moroccan tracks based on Ellenberger (1972). (Note that *T. superaviforma* is far larger than all other ichnospecies; see text for details.)

The first and oldest examples come from Upper Triassic to Lower Jurassic rocks in northern and southern Africa, as well as in Lower Jurassic rocks of western North America. The tracks resemble those of modern birds with respect to most of the first seven criteria listed above. They fall within the size range encountered in modern avian trackmakers and in the Cretaceous assemblages discussed herein. Digit divarication angles average about 110° (see figures 13 & 14), a phenomenon rarely, if ever, encountered in dinosaur footprints. Some of these distinctive tracks have been named *Trisauropodiscus* (Ellenberger 1972), based on material from the Stormberg beds in southern Africa. We provisionally refer the North African and North American specimens to the same ichnogenus (see Systematic section).

It is worth noting that, in addition to the small tracks reported from these areas, large slender-toed tracks have been reported from the early Mesozoic of southern Africa (*Trisaurodactylus superavipes*; Ellenberger 1974), Morocco (Ishigaki 1985, 1986*a*, *b*) and North America (figure 15 herein). The large footprints are quite distinctive, but most remain unnamed and unstudied. For convenience, we illustrate the three examples together and suggest that their occurrence in beds containing small bird-like tracks may be significant with respect to debates about their possible avian affinity.

There are several other early Mesozoic tracks that may be considered bird-like to varying degrees; for example, *Sillimanius tetradactylus* Hitchcock (1845), *Argoides macrodactylus*, *A. minimus*, *Triaenopus lulli* and *T. emmonsii*, Lull (1953). Although we encourage ichnologists to re-examine these bird-like ichnites, we follow Haubold (1984, p. 49) in focusing on *Trisauropodiscus* and other similar forms that have already been referred to as 'aviform'.

Another example of bird-like tracks comes from late Jurassic deposits in Spain, and was illustrated by Valenzuella *et al.* (1988) (figure 16). These tracks show high divarication angles and an unusual asymmetry to the foot. They resemble the late Cretaceous tracks described by Parker & Balsley (1989) (Figure 17 herein). However, with respect to digit width and evidence for a hallux and slender claws, they do not conform very closely with the criteria established for avian affinity. They remain problematic until more material is studied thoroughly.

A third example is taken from the Cretaceous of Israel (Avnimelech 1966, plate VI) (figure 18 herein). This track is very bird-like, despite Avnimelech's interpretation of it as a theropod manus print. Thulborn (1990, figure 6.9 m) re-illustrated what is either the same track or a very similar one from the same locality (figure 18). Given the fact that theropod manus prints are vitually unknown, particularly in the late Mesozoic, we tentatively suggest that this particular footprint may be a bird track that was previously misinterpreted as dinosaurian in origin.

5. SYSTEMATICS

Class Aves

Ignotornidae ichnofam. nov.

Type genus: *Ignotornis* Mehl 1931.

Diagnosis

Tetradactyl, slightly asymmetric bird tracks with variably preserved, posteriorly directed hallux impressions typically showing significant medial rotation towards trackway midline. Digit impressions slender, with variably preserved pad impressions and distal claw traces. Base of digit I elevated above plantar

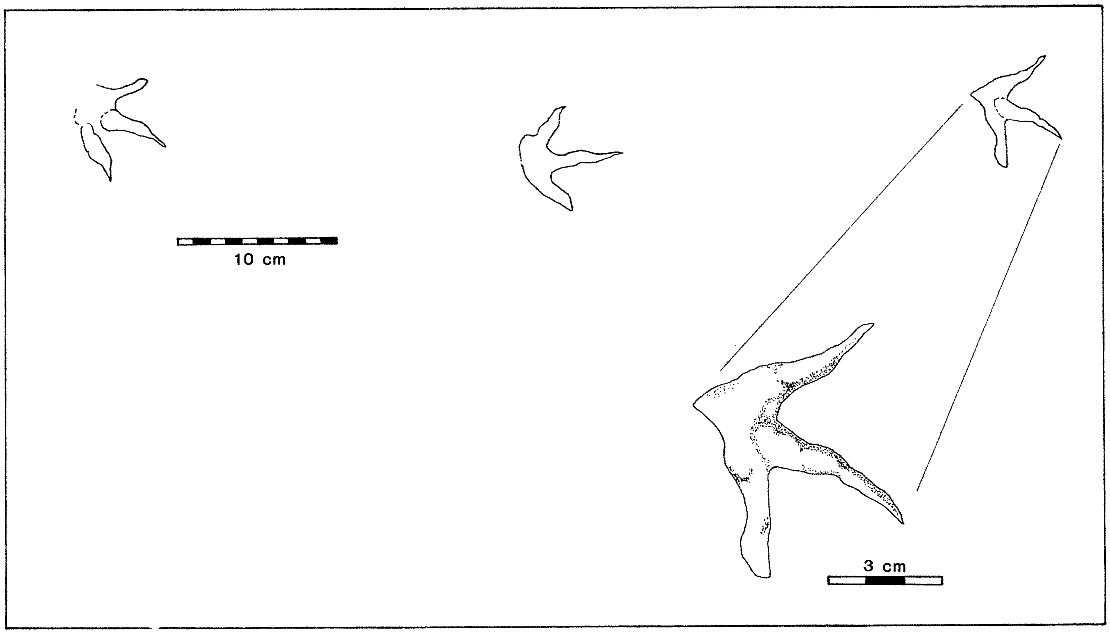

Figure 14. Detail of *Trisauropodiscus moabensis* ichnosp. nov.

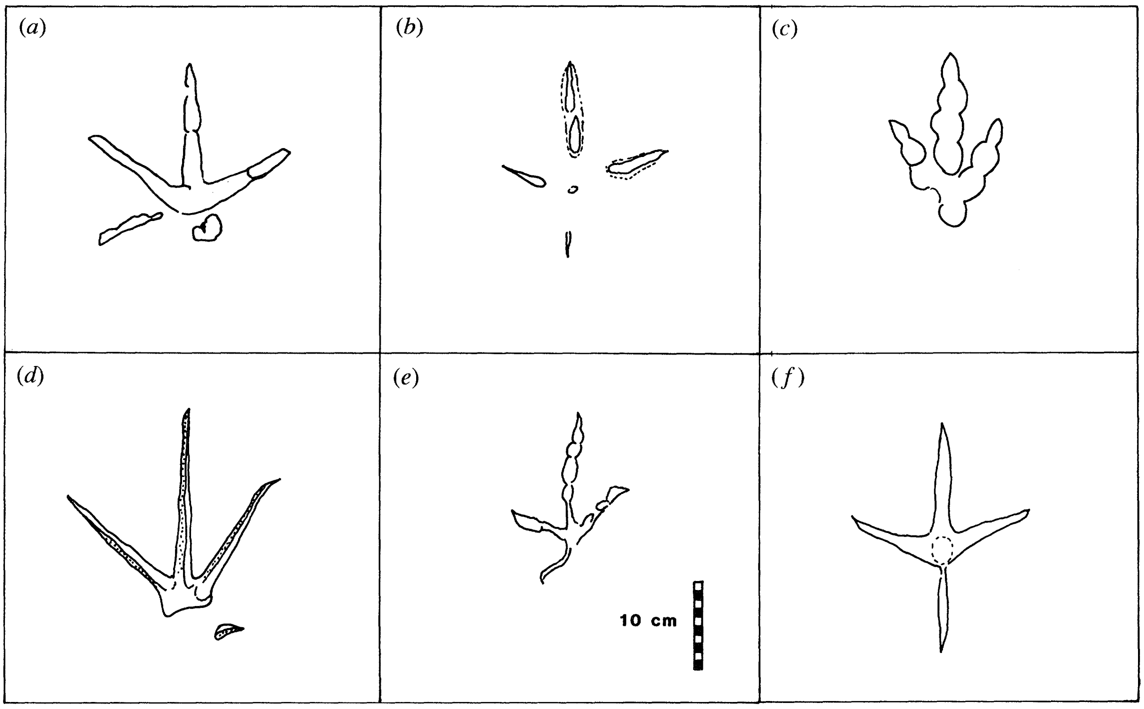

Figure 15. (*a*) *Trisauropodiscus superaviforma* from southern Africa (after Ellenberger 1972). (*b*) *Trisaurodactylus superavipes* from southern Africa (after Ellenberger 1972). (*c*) Typical *Grallator* track from Utah. (*d*) Unnamed Lower Jurassic track from Morocco (after Ishigaki 1985). (*e*) Unnamed Lower Jurassic track from Utah (M. G. Lockley, unpublished data). (*f*) Goliath heron track (after Cohen *et al.* 1990). (All to same scale.)

surface of foot. Pad impressions numbering up to 4 in digit III and up to 5 in digit IV. Divarication between digits II and IV high, averaging between 110°–120° (range 90°–150°). Trackways variable, but often showing slight to pronounced inward (positive) rotation of foot. Track width (distance from impression of digit II toe-tip to impression of digit IV toe-tip) ranges from about 2.5 cm to 7.5 cm.

Discussion

This ichnofamily is based on *Ignotornis mcconnelli*, the first bird-track ichnogenus and ichnospecies described from the Mesozoic. We agree with Mehl (1931) that *Ignotornis* represents a plover-like bird (Family Charadriidae) or a similar wader. The Cretaceous tracks are virtually indistinguishable from those of modern representatives of this family. Current evidence suggests that *Ignotornis* tracks and trackways are similar to *Koreanaornis* and *Jindongornipes* in general morphology,

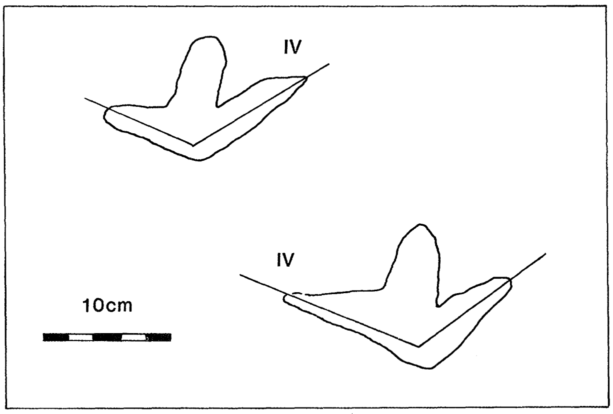

Figure 16. Bird-like late Jurassic tracks from northern Spain (after Valenzuela *et al.* 1988).

Figure 17. Bird-like tracks from late Cretaceous (Campanian) deposits of eastern Utah (after Parker & Balsley 1989). With permission from Cambridge University Press.

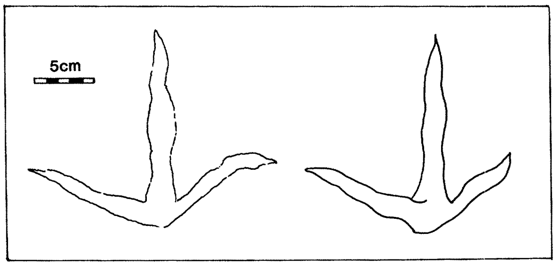

Figure 18. Bird-like middle Cretaceous (early Cenomanian) track from the Cretaceous of Israel (left, redrawn after Avnimelech (1966); right, after Thulborn (1990)).

differing mainly in size and the variability of preservation of details such as hallux and digital pad impressions. It should be noted that all three of the above-mentioned ichnogenera are sometimes represented by tridactyl footprints where the hallux impression is not preserved (figures 19, 20, 22). Similarly many examples do not preserve digital pad impressions. The degree to which individual digit impressions are interconnected proximally is also in part a function of preservation.

Ichnogenus: *Ignotornis* Mehl 1931

Ignotornis Mehl, 1931, p. 443.

Type species: *Ignotornis mcconnelli* Mehl 1931.

Ignotornis mcconnelli Mehl 1931 emend. Figures 1, 2 and 8*a–c*.

Ignotornis mcconnelli Mehl, 1931, p. 444, figure 1.

Material

Holotype – UCM-17614, housed in Hunter Museum at the University of Colorado at Boulder.

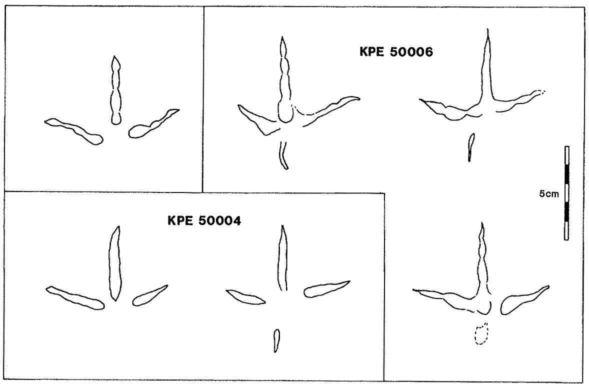

Figure 20. *Jindongornipes kimi* from the Jindong Formation.

Horizon and Locality

Track-bearing horizons occur in the upper part of the Dakota Group; in clay pits 5 km north of Golden, Colorado.

Emended description

Tetradactyl bird tracks with posteriorly directed hallux impression and fine acuminate claw traces on all four digits. Footprints averaging 5 cm wide (range 4.7–5.2 cm) and 5.7 cm long including hallux (range 5.5–5.8 cm) in trackway with holotype. Tracks about 4 cm long, excluding hallux. Second and fourth digits markedly divaricate (from 90°–115°). Base of first digit elevated above plantar surface of foot. All toes clawed, claw impressions extending about 4–5 mm beyond terminal phalangeal pad impressions; phalangeal pad impressions obscure. Hallux impressions often bent indicating two distal phalanges in contact with substrate.

Discussion

At present, *Ignotornis mcconnelli* is known only from footprints preserved as natural casts in sandstone. In

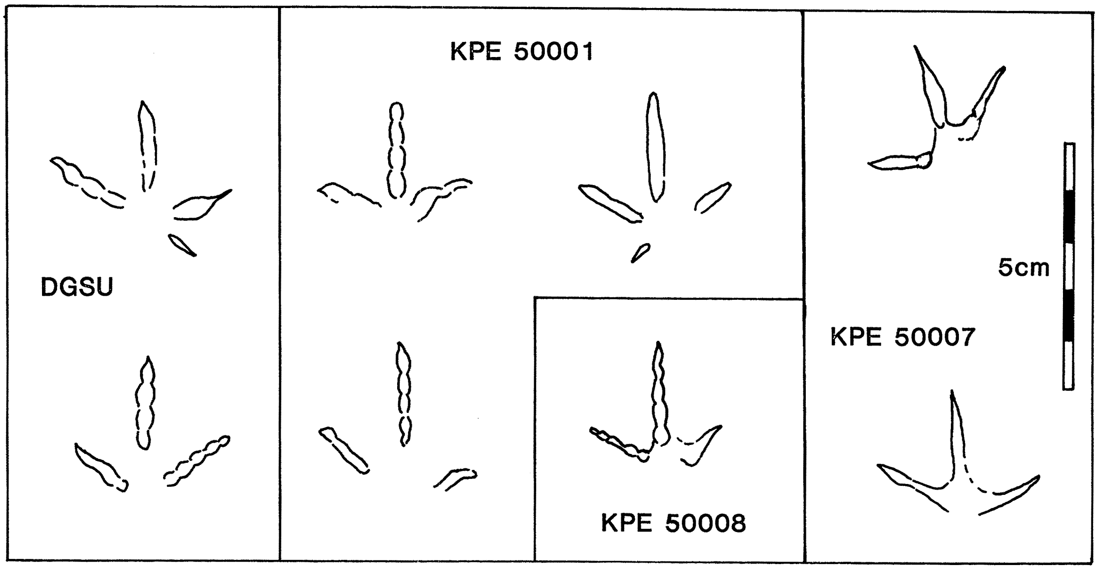

Figure 19. *Koreanaornis hamanensis* tracks from the Haman and Jindong Formations (note presence of hallux and digital pad impressions in some footprints).

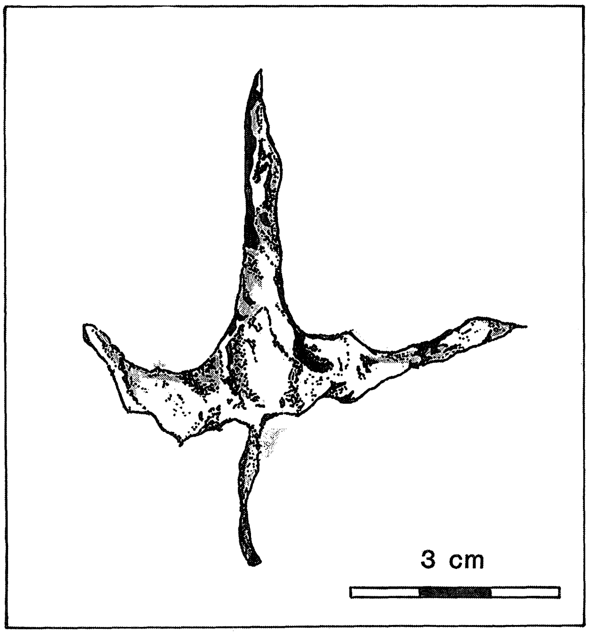

Figure 21. Detail of *Jindongornipes kimi* from holotype specimen KPE 50006; see also figures 8*d*, 1 and 20.

most cases (UCM-17614 specimens) the tracks are quite deep, suggesting progression over a soft substrate, and all four digit impressions are clear. However, in MWC-203 the casts indicate shallower tracks and hallux impressions are indistinct or absent.

Ichnogenus: *Koreanaornis* Kim 1969

Koreanaornis Kim, 1969, p. 248.

Type species: *Koreanaornis hamanensis* Kim 1969.

Koreanaornis hamanensis Kim 1969 emend. Figures 3, 11–12, 19 and 22.

Koreanaornis hamanensis Kim, 1969, p. 248–249, plate 5, figures 17–18.

Material

Topotypes – KPE 50001 and DGSU (Department of Geology, Seoul University) unnumbered specimen (Figure 3). Plesiotypes – KPE 50003 (figure 11), KPE 50005 (figure 12), KPE 50007 (figure 22).

Horizon and Locality

Holotype and paratypes: from upper part of the Haman Formation, about 12 km north of Masan city, southern Gyeongsang Province, Korea. Plesiotypes: from coastal exposures of the Jindong Formation, near Dukmyeongri, Koseong-gun, Kyeongsangnam Province, Korea.

Emended description

Small tetradactyl bird tracks with faint hallux impressions preserved in some specimens, but often appearing tridactyl. Digit impressions slender but often showing up to four digital pad traces in digit III impressions and five pad traces in digit IV impressions; digital pad traces only 2–3 mm in length. Digit traces often separate (i.e. not connected proximally). Claw traces variable, slender and obscure. Trackway poorly known but showing evidence of inward (positive) rotation. Track width ranges from about 2.5 cm to 4.4 cm (toe-tip II impression to toe-tip IV impression); wider than long except when hallux is preserved. Divarication between digits II and IV averaging about 120° (range 105°–125°).

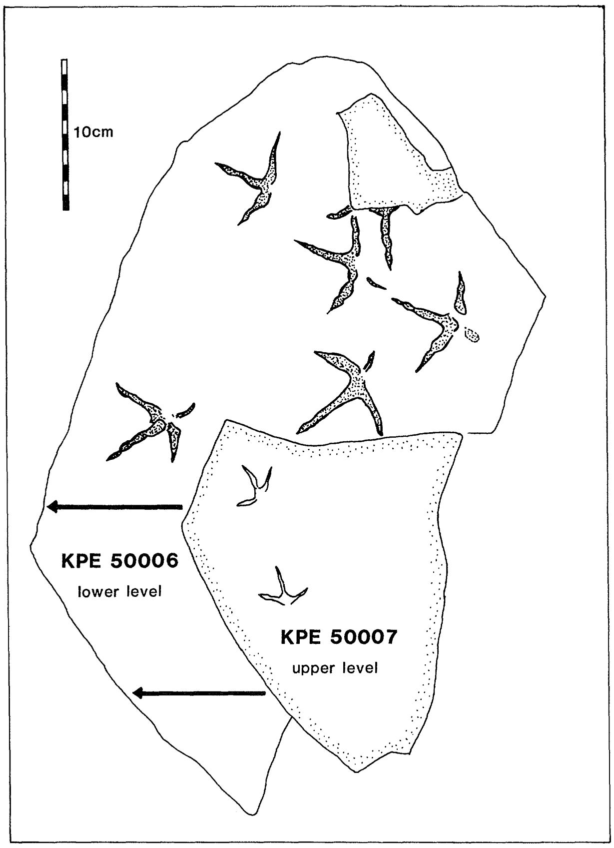

Figure 22. KPE 50006: well-preserved *Jindongornipes kimi* tracks. KPE 50007: well-preserved *Koreanaornis hamanensis* tracks.

Discussion

Kim (1969) originally described *K. hamanensis* as a tridactyl track. Although the holotype has been misplaced, slabs with topotype material display well-preserved tracks, including some with hallux impressions. We agree with Kim (1969) that the tracks resemble those of various modern species of plover (genus *Charadrius*).

Many of the recently discovered small tracks from the Jindong Formation are indistinguishable from *K. hamanensis* (see figure 19). For this reason, we believe that the small tracks from the Haman and Jindong Formations should be assigned to the same ichnotaxon.

Jindongornipes ichnogen. nov.

Type species: *Jindongornipes kimi* (described below).

Jindongornipes kimi ichnosp. nov. figures 8*d–f*, 10, 20–22.

Material

Holotype – KPE 50006 (figures 20–22). Paratypes – KPE 50004 (figure 10).

Horizon and Locality

Jindong Formation; coastal exposures near Dukmyeon village, Koseong-gun, Kyeongsangnam Province, Korea.

Description

Moderately large tetradactyl bird tracks with well-developed hallux impression. Up to four phalangeal pad impressions in digit III trace. Number of pad impressions in digits II and IV unknown, but at least three. Hallux impression often bent suggesting two distal phalanges in contact with substrate. Divarication between digits II and IV very pronounced, ranging from 125°–150°. Digit IV impression often wide proximally with a posteriorly directed heel that gives track a pronounced asymmetry. Track width ranging between 65–75 mm (measured between distal ends of digits II and IV). Track length, with hallux, up to 80 mm. Trackway variable but with only slight positive rotation and pace angulation about 140°.

Discussion

Jindongornipes kimi is the largest bird track hitherto reported from the Lower Cretaceous. Examples are typically twice the size of *Koreanaornis hamanensis* from the same formation. *Jindongornipes* is also consistently larger than *Ignotornis mcconnelli* from Colorado and *Aquatilavipes* from Canada and East Asia.

Etymology

Generic epithet means bird track from the Jindong Formation; specific epithet refers to Professor Emeritus B. K. Kim (Seoul National University), who discovered and described the first fossil bird tracks from the Korean Penninsula.

Ichnofamily uncertain

Ichnogenus: *Aquatilavipes* Currie 1981.

Aquatilavipes Currie, 1981, p. 259.

Emended diagnosis

Made by a bipedal animal with three slender functional pedal digits. Width greater than length; average divarication of digits II and IV greater than 100°. Digit IV longer than digit II and shorter than digit III. Sharp claw impression on each digit. No hallux impression. Faint digital pad impressions numbering at least 3–4 in digit III.

Discussion

Currie (1981) based *Aquatilavipes* on the ichnospecies *A. swiboldae* (figure 8*g*) and stated that it is a tridactyl track. He also noted that the tracks average 4–5 cm wide and 3–4 cm long. We have emended his generic diagnosis only to add the final sentence identifying pad impressions that number at least 3–4 in digit III but are often obscure in other digits. Currie also notes that the foot is slightly asymmetrical, digit II being shorter than digit IV and digit III.

We consider that the Valanginian age bird tracks from Japan are best assigned to *Aquatilavipes* because they are identical in size and always show only three-digit impressions. Although the lack of hallux impressions may be in part a function of preservation, or behaviour, on present evidence *Aquatilavipes* appears distinct from *Ignotornis*, *Jindongornipes* and *Koreanaornis*. If a hallux impression were associated with *Aquatilavipes* – as is apparently the case in *A. sinensis* from China (figure 6) – it would be difficult to distinguish from *Koreanaornis* except on the basis of modest size differences. However, the Chinese specimen is inadequately described, so we consider it inadvisable to draw further conclusions. Moreover, Currie (personal communication) advises us that *Aquatilavipes* is distinct from *Ignotornis*. We therefore suggest that there is probably a spectrum of Lower Cretaceous waterbirds, ranging from those with a well-developed hallux (*Ignotornis* and *Jindongornipes*) through those with a small hallux (*Koreanaornis*) to those with a smaller or vestigial hallux (*Aquatilavipes*) that did not make contact with the substrate.

Trisauropodiscidae ichnofam. nov.

Type genus: *Trisauropodiscus* Ellenberger 1972.

Diagnosis

Tetradactyl or tridactyl slender-toed aviform tracks with wide digit divarication angles. Size range from about 2–7 cm (width divarication between digits II and IV in the range of 90°–120°. Trackways with relatively long steps (about four times foot length) and positive (inward) rotation of axis of digit III. Hallux length and orientation variable; impressions faint or absent in some examples.

Discussion

Ellenberger (1972) described *T. aviforma* as comprising several varieties (A–E) representative of a group of mainly small tracks with obvious avian characteristics (figure 13 herein). We consider some ichnospecies (e.g. *T. galliforma*) to be very similar in general size and shape to the North American example (*T. moabensis* sp. nov). Others, however, in particular *T. superaviforma*, are much bigger than *T. aviforma* and its allies, and resemble tracks made by very large modern birds such as the Goliath Heron (Cohen *et al.*, 1990; see figure 15 herein). We therefore consider that such tracks are inappropriately placed in the ichnogenus *Trisauropodiscus*, and should be considered separately (figure 15).

Ellenberger (1972) also described other bird-like tracks, including *Masitisauropus*, with purported feather impressions where the manus (wing) had apparently come in contact with the substrate. Because we are unable to examine the original outcrop or replicas of the specimens on which this intriguing interpretation was based we cannot comment further on this particular report.

Trisauropodiscus Ellenberger 1972

Trisauropodiscus Ellenberger 1972, p. 81.

Trisauropodiscus moabensis ichnosp. nov. figures 8*h*, 13 and 14

Table 1. *Data on Trisauropodiscus moabensis*

(Divarication is for angle between digit II and IV impressions.)

specimen number	length/cm	width/cm	step[a]/cm	divarication
trackway 181.3				
181.3a	6.0	7.0	28	117°
181.3b	6.6	7.0	29	106°
181.3c	6.4	7.4		102°
track 181.2				
181.2	6.0	6.6		110°

[a] Values in the step column are for the distance between adjacent footprints in a trackway (i.e. between footprints 181.3a and 181.3b, and between 181.3b and 181.3c).

Material

Holotype – MWC trackway replica 181.3.

Horizon and Locality

Lower part of the Navajo Formation; Potash Road Dinosaur Track-site, 7 km southwest of Moab, Utah.

Etymology

Specific epithet refers to an ichnite from near Moab, Utah.

Description

Small tridactyl tracks with wide divarication angles and a relatively long step. Footprint length ranging from 6.0–6.6 cm; footprint width ranging from 6.6–7.4 cm ($n=4$). Divarication between impressions of digits II and IV averaging about 110° (range 100°–117°). Step 28–29 cm; pace angulation 167°; trackway width 9 cm. Mean inward (positive) rotation of axis of toe III is 21° (range 10°–28°). Pad impressions indistinct. Slender claw impressions on digit III, but indistinct distal digital impressions on digits II and IV. (Table 1 summarizes data on size, step, and digit divarication of *Trisauropodiscus moabensis*.)

Discussion

Only four well-preserved tracks are known from a site along the Potash Road near Moab, Utah. Three of these (MWC 181.3) compose a clear bird-like trackway with a long step (figure 14). The fourth (MWC 181.2) is an isolated footprint. All tracks are tridactyl and extremely bird-like.

Until now there has been little reliable documentation of pre-Cretaceous bird-like tracks. The vast majority of small tridactyl early Jurassic footprints are *Grallator*-like. Tracks with obvious avian characteristics have been reported mainly from Cretaceous and younger sediments. The occurrence of truly bird-like tracks in Lower Jurassic sediments is therefore of considerable significance, implying the presence of avian ancestors as much as 40 Ma before *Archaeopteryx*. To date the most abundant Jurassic age bird-like tracks are the several *Trisauropodiscus* ichnospecies described by Ellenberger (1970, 1972). The occurrence of similar tracks in Lower Jurassic sediments of North Africa (Ishigaki 1985) and North America lends support to the idea that early Mesozoic bird or bird-like tracks are more widespread then previously supposed. We currently know of another early Jurassic locality in Utah where bird-like tracks are preserved. These will be described in detail elsewhere.

Evidence of pre-*Archaeopteryx* fossil remains are currently limited to Chatterjee's (1987) report of *Protoavis* from the late Triassic, a form that has recently been described in detail (Chatterjee 1991). Assuming that Chatterjee's interpretation of *Protoavis* is correct, then it is logical to assume that bird or bird-like tracks will be found in Jurassic rocks. Such inferences are also consistent with the suggestion of Olsen (1985) that a pre-*Archaeopteryx* Jurassic fossil record of birds might fruitfully be sought.

The occurrence of *Trisauropodiscus moabensis* sp. nov. allows for comparison with the small bird-like tracks in Lower Mesozoic deposits of Africa (Ellenberger 1972; Ishigaki 1985, figure 7*a*). Like *T. moabensis*, most of these small tracks (figure 13 herein) are vitually indistinguishable from the tracks of post-Jurassic waterbirds. The main differences are that *T. moabensis* displays wider digit divarication angles (average 110° compared with 90° for the Moroccan ichnites), and that it lacks the hallux impression seen in some of the African trackways. Thus it should be distinguished from most of the African trackways only at the specific level. In size and general appearance, it is probably closest to *T. galliforma*. As discussed above, the presence of a hallux impression is not necessarily a critical diagnostic feature in higher level ichnotaxonomy (Baird 1957). Many bird trackways reveal tridactyl and tetradactyl footprints in consecutive sequences, with the variation resulting from substrate consistency, step length, behaviour, etc. The trackmaker of *T. moabensis* probably had a hallux that would have left a trace on soft substrates. The holotype trackway was impressed on relatively firm ground.

6. ASSOCIATED ICHNOFAUNA

In almost all cases, the bird and bird-like tracks reported herein occur in association with dinosaur tracks. At many of the localities there is also evidence for the activity of invertebrates. In few cases, however, is there evidence for tracks of any other tetrapods.

We infer that, in many cases, bird-like tracks were found as the result of reports of larger, more obvious dinosaur tracks, because authors did not specify whether bird tracks occur on the same bedding planes as the dinosaurian ichnites. Similarly, invertebrate traces have often not been discussed in any detail or at all. This makes it unclear as to whether they occur at the same horizons or not. In this section, we have reported on the invertebrate ichnites wherever possible.

(*a*) *Navajo Formation (Lower Jurassic), Utah*

The bird-like tracks of *Trisauropodiscus moabensis* sp. nov. occur on a bedding plane with dinosaur tracks attributed to *Grallator sensu stricto* and *Eubrontes*. There are also a few invertebrate traces, consisting of plug-shaped vertical burrows, on the same bedding plane.

(*b*) *Stormberg beds (Upper Triassic-Lower Jurassic), southern Africa*

According to Ellenberger (1970, p. 354), most of the small species of *Trisauropodiscus* occur in zone A/6 of the Lower Stormberg, in conjunction with various named tridactyl tracks that are presumably attributable to dinosaurs. According to Ellenberger (1970), this is stratigraphically above zones with abundant large synapsid tracks (e.g. *Pentasauropus*) and below the upper Stormberg zone B/1, which contains dinosaur tracks (*Moyenisauropus*) and small mammaloid tracks.

(*c*) *Atlas Mountains (Lower Jurassic), Morocco*

The bird-like tracks from this region have been found in association with tracks of sauropod and theropod dinosaurs. Invertebrate traces were not reported (Ishigaki 1985, 1986*a*, *b*). Tracks occur at a number of different localities.

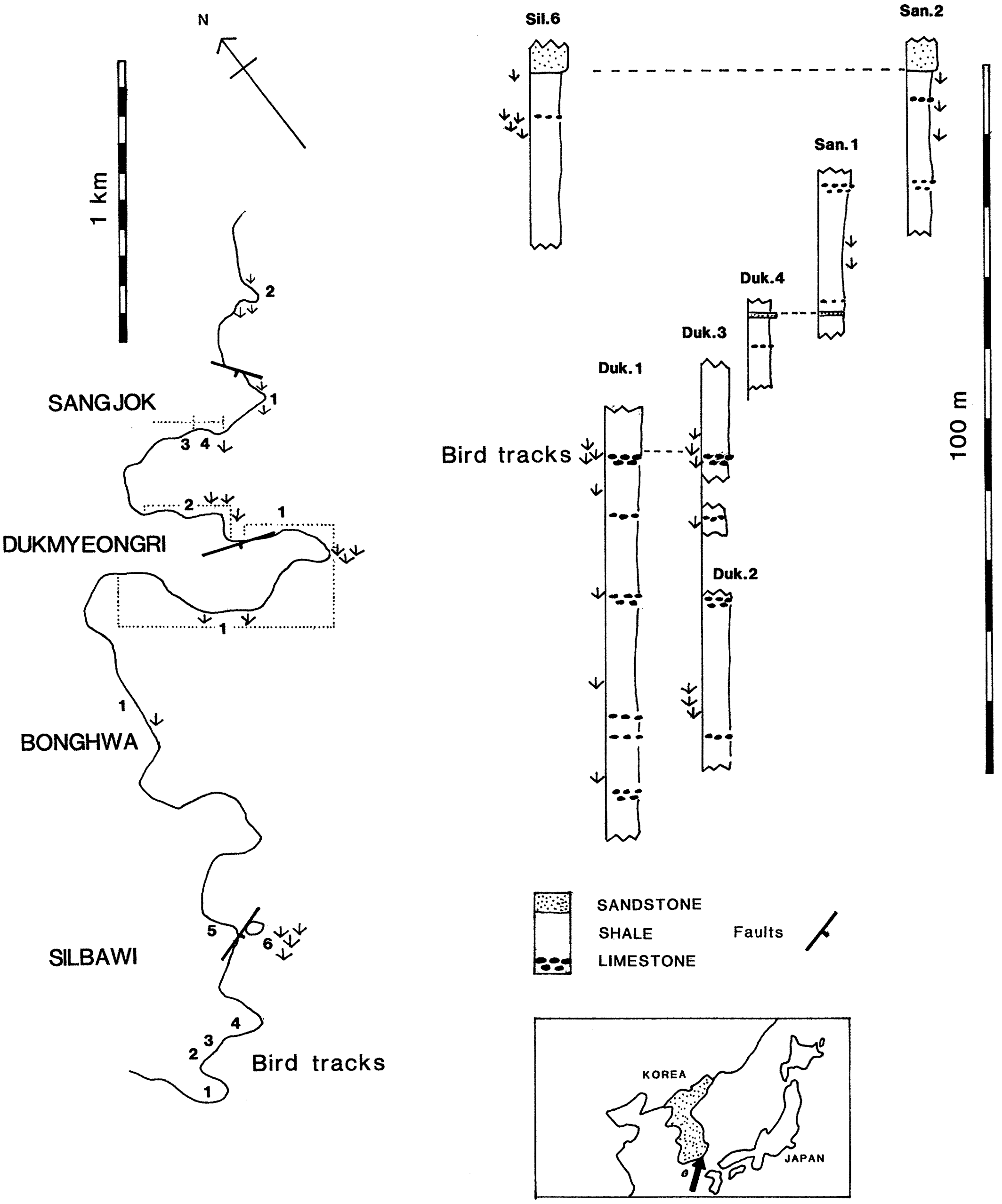

Figure 23. Geographical and stratigraphic location of important bird track localities along a 3 km section of coastline near Dukmeongri village, South Korea. (Lower part of section not shown because of structural complications that hamper precise stratigraphic correlation.)

(*d*) ***Ribadessella (Upper Jurassic), Spain***

Problematic bird-like tracks are found in association with tracks of tridactyl bipedal dinosaurs (theropods and ornithopods) and quadrupedal forms (probably sauropods). Many of these tracks occur at different localities (i.e. not on the same bedding planes as the bird-like ichnites).

(*e*) ***Dakota Group (Lower Cretaceous), Colorado***

When Mehl (1931) originally reported the discovery of *Ignotornis mcconnelli*, he also described a number of peculiar tracks attributed to other vertebrates, i.e. *Walteria jeffersonensis*, a purported aigialosaur trackway, and a possible *Anomoepus* (dinosaurian) track. However, the material on which these latter ichnotaxa were based (A635 and B635, University of Missouri) is problematic because only sketchy line drawings were presented by Mehl. Moreover, attempts to relocate the material for further study have been unsuccessful. We regard the assignments as dubious.

At that time dinosaur tracks were virtually unknown from the Dakota Group; they are now known in considerable abundance, often occurring in association with diverse invertebrate trace fossil assemblages (Chamberlain 1976, 1985; Lockley 1985, 1987, 1991). The recent discovery of more *Ignotornis* tracks associated with dinosaur footprints (Lockley *et al.* 1989) was, at that time, the first detailed report of dinosaur and bird tracks on the same bedding plane (MWC 203.1). *Planolites*-like traces were also recorded, and one of the dinosaur trackways was tentatively assigned to cf. *Amblydactylus*, attributable to an ornithoped trackmaker.

The larger picture of the Dakota ichnofauna is much broader. Along the Colorado Front Range the Dakota Group is replete with track-bearing horizons, particularly in the upper part. *Caririchnium* is the most abundant ichnogenus, attributed to a quadrupedal ornithopod. There is also a relatively common slender-toed coelurosaur track found at several localities (Lockley 1989, 1990), as well as some evidence for other theropod dinosaurs (Lockley 1985, 1987). Moreover, Chamberlain (1976, 1985) has described a diverse invertebrate ichnofauna including such well-known forms as *Ophiomorpha*, *Diplocraterion*, *Rhizocorallium*, *Arenicolites*, *Skolithos*, *Thalassanoides* and others. Taken together, the trace fossil evidence suggests a mosaic of coastal plain depositional environments inhabited by dinosaurs, birds and abundant invertebrates as part of a diverse biota.

(*f*) ***Haman Formation (Cretaceous), South Korea***

In his report of bird tracks from the Haman Formation, Kim (1969) also described various invertebrate trails and burrows, and suggested that they might be attributable to worms, gastropods and crabs. At least two of the sinuous horizontal trails he described can be attributed to the invertebrate ichnogenus *Cochlichnus*.

(*g*) ***Jindong Formation (Cretaceous), South Korea***

Recently discovered bird tracks from the Jindong Formation are associated with abundant dinosaur tracks and invertebrate traces. The dinosaur tracks include several types attributable to theropods, sauropods and ornithopods (Yang 1982; Lim *et al.* 1989). To date, none of these dinosaur tracks have been named; however, they are known to include small and large brontosaur trackways resembling *Brontopodus sensu lato* (Farlow *et al.* 1989), ornithopod pes tracks that resemble *Caririchnium* (but show no manus impressions) and a few small theropod tracks.

Invertebrate traces include *Cochlichnus* and a number of vertical, inclined and horizontal cylindrical filled burrows that range from 1 mm to 2 cm in diameter.

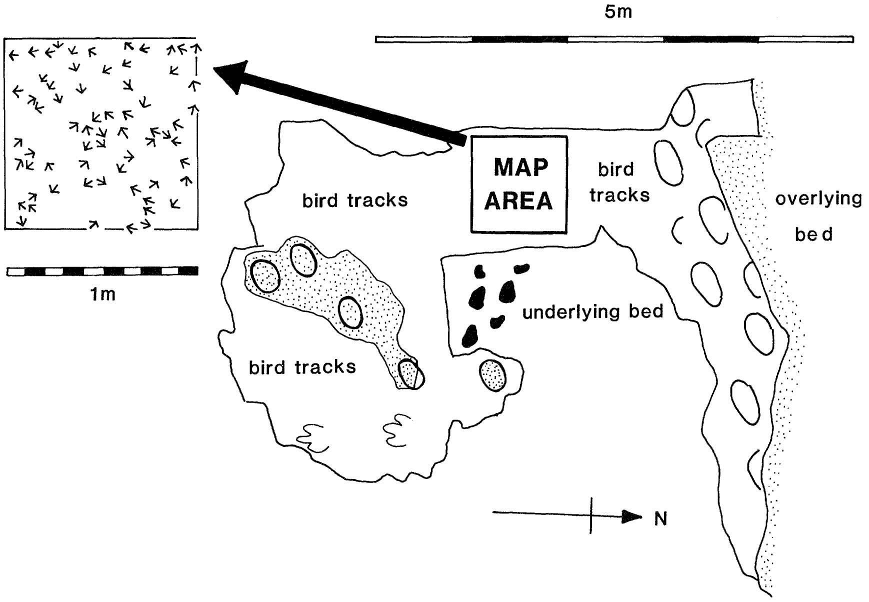

Figure 24. Large bird track site, Dukmyeongri section.

In most cases, bird tracks occur on bedding planes from which dinosaur tracks have not been recorded but on which invertebrate traces occur. This may reflect local microhabitat variation (cf. Cohen *et al.* 1990) or the limited extent of individual bedding plane exposures. Out of a total of about 300 dinosaur track-bearing bedding planes, and an additional 30 or more with bird tracks (figure 23), the two track types only co-occur on one well-exposed bedding plane (figure 24). This is only the second such example of bird and dinosaur ichnites on the same bedding plane after the aforementioned Dakota specimen (figure 2).

(*h*) *Gething Formation (Aptain), Western Canada*

Aquatilavipes footprints from the Gething Formation originate from successions rich in dinosaur tracks. The track-bearing slab (figure 4) exhibits ripple marks, 'invertebrate trails and the entrances to burrows' (Currie, personal communication). These exposures were flooded by the Peace River Dam Construction Project, and large numbers of fossil footprint specimens were collected during a rescue excavation. Among these were dinosaur tracks referred to the ornithopod ichnogenus *Amblydactylus* and the theropod ichnogenus *Irenesauripus* (Currie 1983; Currie & Sarjeant 1979).

(*i*) *Yacoraite Formation (Maastrichtian), Argentina*

Yacoraitichnus avis is associated with various dinosaur tracks, including possible hadrosaur footprints (*Hadrosaurichnus*) and various theropod tracks. The aforementioned Maastrichtian tracks from Rio Negro Province (Leonardi 1987) have not been reported in association with other tracks (p. 118 herein).

(*j*) *Sichuan Province (early Cretaceous), China*

According to Zhen *et al.* (1987), bird tracks assigned to *Aquatilavipes* occur in association with various unusual small dinosaur footprints, including a two-toed (didactyl) track (*Deinonychosaurichnus*) attributed to a deinonychosaurid.

(*k*) *Tetori Group (Lower Cretaceous), Japan*

There are few Mesozoic fossil tracks from Japan, although an increasing number have been discovered in recent years. Scarce, identifiable dinosaur tracks are known from the Kuwajima Formation of the Tetori Group (Manabe *et al.* 1989; Azuma 1990). Some are small ornithopod tracks, others small theropod footprints. The stratigraphic position of the bird track specimen (figure 7) is within the upper part of the Izuki Formation, in beds that correlate approximately with the dinosaur-track-bearing beds.

(*l*) *Mesa Verde Group (Upper Cretaceous), Utah*

Probable bird tracks from the Mesa Verde Group of Utah are associated with abundant dinosaur tracks. The most common footprints are large ornithopod tracks attributed to hadrosaurs. Various theropod tracks are also known, and there is some evidence for ceratopsian dinosaur tracks.

7. PALAEOECOLOGY AND PALAEOENVIRONMENTS

Based on the information given above and available documentation of the sedimentology of several of the track-bearing deposits, it is possible to reconstruct some of the palaeoenvironments in which Mesozoic avian trackmakers were active, and understand their behaviour to some degree. Given the uncertainty regarding possible Jurassic bird tracks, and the lack of documentation from some of the Cretaceous sites, we have confined our discussion to the Jindong, Haman and Uhangri Formations of Korea, and the Lower Cretaceous Dakota and Gething Formations of western North America.

(*a*) *The Haman and Jindong Formations*

Although there is limited information available on the Haman Formation, Kim (1969) made a number of valuable observations. He inferred (Kim 1969, p. 250) that the track-bearing sediments represent part of a 'fluvio-lacustrine' sequence deposited under 'savanna-type' climatic conditions. Among the common inorganic sedimentary structures observed are 'symmetrical rounded ripple marks' (*sensu* Kim, 1969), which are observed on both topotype slabs (figure 3), 'sun cracks' and raindrop impressions. We infer that this evidence is indicative of a lake shoreline environment. Bird tracks and invertebrate traces, including small *Cochlichnus* and various larger unnamed burrows, suggest an environment conducive to significant biotic activity. As suggested by Kim (1969, p. 248–249), the evidence indicates the presence of small waders feeding on invertebrates, presumably along the lake shore.

Recent discoveries of bird tracks at over 30 different stratigraphic horizons in the Jindong Formation have done much to substantiate the interpretations of Kim (1969) for the upper part of the Haman Formation. The Jindong Formation is replete with mud-cracked and ripple-marked horizons, and also exhibits raindrop impressions at some localities. Although we have not yet recorded or collected bird tracks from a clearly rippled surface, they often occur on undulatory or mud-cracked surfaces, and in association with invertebrate traces. Moreover, the track-bearing beds are found in close stratigraphic proximity to beds with symmetrical, straight-crested wave ripples. Having measured about 200 m of section in detail, we infer a lacustrine environment subject to alternations of sand–silt deposition with mud and carbonate. The presence of mud-cracks, small-scale wave ripples and dinosaur tracks throughout this sequence is strong evidence for a shallow lake that persisted for a significant period of time. In the upper 110 m of section, where stratigraphic continuity is well established, we have recorded 204 track-bearing horizons (figure 23). This averages out at about one horizon every 54 cm for all levels. Although bird track levels are not known with such frequency throughout the succession, in some areas there are as many as five recorded in 1 m of section. This clearly suggests a very complete and continuous record of animal activity in the Jindong lake succession.

Invertebrate trails include *Cochlichnus* (figure 12) and two types of filled burrows: small vertical tubes about 1–2 mm in diameter and up to about 1 cm deep, and larger 1–2 cm diameter plug-like burrows. Both burrow types are very common in association with the bird track levels, as well as at other horizons. They also sometimes occur in horizontal or oblique orientations. Burrows with intermediate diameters (about 0.5 cm) also occur locally (see figure 12) as do some with indistinct internal meniscate structures (cf. *Scoyenia*). The density of small (1–2 mm diameter) burrows has been measured at 13 000 per m^2 (based on specimens KPE 50006–50007).

It is important to note that the two types of bird track (*Koreanaornis* and *Jindongornipes*) usually occur separately. Particular stratigraphic levels are either heavily dominated, or exclusively tracked, by one of the two footprint types. The reasons for this pattern of mutual exclusion are not known with certainty. However, the distribution could be related to the combined effects of size, water depth and feeding habits. Larger birds may wade in shallow water several centimetres deep, whereas the smaller varieties feed on emergent strandlines. Such localized differences in distribution are commonly observed in modern lakes (Cohen *et al.* 1990) and have even been observed in Tertiary lacustrine deposits (Alonso 1985, 1987). In the latter study, tracks were used as palaeobathymetric indicators, suggesting that different track types could help define shoreline to shallow lake trends in the stratigraphic record. If Jindong birds were also influenced by water depth, then we might infer that the *Koreanaornis* track-maker frequented the shoreline whereas the *Jindongornipes* track-maker waded in the shallows. This is the first report of a Mesozoic deposit with two avian track-makers. It is worth noting that the evidence that different bird tracks are mutually exclusive in many cases is mirrored by a similar relation of mutual exclusion between sauropod and ornithopod dinosaur tracks (Lockley *et al.* 1991*b*). Thus there are indications that both bird and dinosaur tracks record differences in ecology and microhabitat preference among the track-makers.

Studies of some of the larger specimens and better-exposed Jindong and Haman track-bearing levels allow calculation of bird track density over known areas. For example, Haman Formation specimen DGSU (figure 3) reveals a minimum of 65 partial and complete tracks of *K. hamanensis*, in an area of about 0.5 m^2, thus a density of 130 tracks m^{-2} can be estimated. The extrapolated density for *K. hamanensis* from Haman Formation specimen KPE 50001 is very similar, with about 110–120 tracks m^{-2}.

The density of *K. hamanensis* tracks from the Jindong Formation is more variable, possibly because of the larger number of available specimens. KPE 50003 reveals a minimum density of 300–400 tracks m^{-2} (figure 11). High densities are also recorded for KPE 50008.

It is also worth noting that the extrapolated track density for the Japanese specimen (figure 7) is about

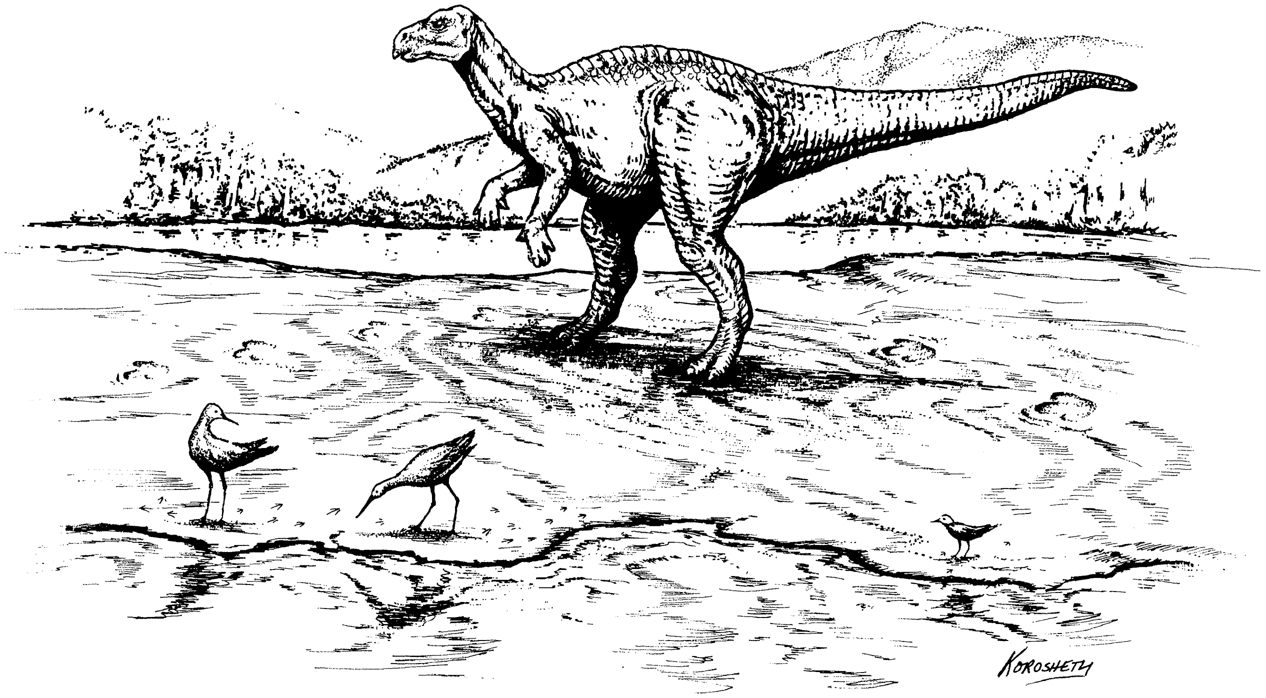

Figure 25. Reconstruction of bird and ornithopod track-makers in a Cretaceous lakeshore paleoenvironment. Based on trackway evidence from the Jindong Formation of South Korea. Artwork by Paul Koroshetz, modified after Lockley (1991, p. 105).

200 tracks m^{-2} even though the tracks are not very similar to *K. hamanensis* and have been provisionally referred to *Aquatilavipes*.

The density of *Jindongornipes* tracks was estimated from KPE 50004 (about 80 tracks m^{-2}) and KPE 50006 (about 60 tracks m^{-2}). Direct mapping of 1 m^2 at the largest track site (Bed number DUK-1-27:206) revealed a density of recognizable tracks of 65 tracks m^{-2} (see figure 24).

These results are interesting for several reasons. Firstly, high track density is fairly typical of shoreline environments inhabited by modern waders. Such patterns attest to the concentrated activity of birds in a relatively localized area. They may also reflect high activity levels, particularly among the smaller, more energetic, species (see Cohen *et al.* 1980). Generally the limitations of outcrop prevent precise estimation of the lateral extent of densely tracked areas. In one case, however, we were able to trace a track-bearing unit (Duk-1-27:206) to another location 700 m away (fig. 23).

In addition to the bird and invertebrate traces discussed above, the Jindong Formation is replete with dinosaur footprints, attributable to abundant sauropods and ornithopods and a few theropods. In one case (site Duk-1-27:206), dinosaur tracks are present at the same horizon as bird tracks (figures 24 and 25). Here the dinosaur tracks have prominent mud rims, suggesting a relatively soft, easily deformed substrate at the time of trackmaking activity.

(*b*) *The Dakota Group*

The sedimentology and stratigraphy of the Dakota Group has been intensively studied, not least because of the importance of certain units as oil and gas reservoirs (see, for example, Weimer (1983) and references therein). The results of these studies suggest that the track-bearing facies, including parts of the Van Bibber Shale and the J Sandstone, represent a mosaic of coastal plain facies ranging from tidal flats (McKenzie 1972) to coal-bearing swamp and levee deposits (Lindstrom 1976) associated with river systems.

In the Dakota Group, *Ignotornis* bird tracks are associated with purported levee deposits (Lindstrom 1976) that also contain relatively deep ornithoped and theropod tracks, as well as horizontal *Planolites*-like invertebrate trails, Unlike the aforementioned Jindong Formation, there is as yet no evidence for multiple bird-track horizons, even though multiple dinosaur track-bearing beds are known (Lockley *et al.* 1989). This suggests that the Dakota palaeoenvironment may not have been widely suitable as a habitat for birds or as a site for preservation of small tracks. However, this conclusion may be premature because many outcrops have not yet been examined in detail. Based on specimens UCM 17614 and MWC 203, there were several *Ignotornis* track-makers active in a small area. The density of preserved tracks is about 250 tracks m^{-2} based on figure 1. The density of *Ignotornis* tracks for MWC 203 is much less (about 4–5 tracks m^{-2}) but is over 25 tracks m^{-2} towards the left side of the block (figure 2).

(*c*) *The Gething Formation*

Like the Dakota Group track-bearing beds, the Gething Formation footprints are associated with coal-bearing facies variously described as fluvio-deltaic. Because bird tracks are only reported from a single locality, it is tempting to conclude that the habitat was not suitable for large populations of birds. However, in the one large known specimen (RBCM 744; figure 4) a high track density of about 140–150 tracks m^{-2} is evident. This suggests that, at least locally, bird populations and activity patterns may have been comparable to the situation inferred for the Jindong palaeoenvironment.

8. EVOLUTIONARY IMPLICATIONS OF MESOZOIC BIRD TRACK ASSEMBLAGES

In recent years there has been an exponential increase in the rate of discovery of new Mesozoic bird track localities (figure 26). This suggests that the paucity of reports reflects lack of research in the field rather than any real scarcity of fossil bird tracks. Given this situation, the prospect that new discoveries will enhance our knowledge is good.

Even so, Mesozoic bird tracks are still relatively poorly known. However, recent discoveries, particularly those from the Jurassic Navajo Formation and the Cretaceous Jindong Formation, add substantially to perspectives on evolution and show the potential for discovering extensive evidence in Mesozoic deposits.

We suggest that tracks may shed light on bird evolution during at least two Mesozoic epochs, first during the early Jurassic when *Trisauropodiscus* and its allies appeared in Africa and North America, and later in the early Cretaceous when there was a radiation of shorebirds recorded in East Asia and North America. Conventional wisdom holds that there is as yet no unequivocal evidence for pre-*Archaeopteryx* birds, and that the shorebird radiation

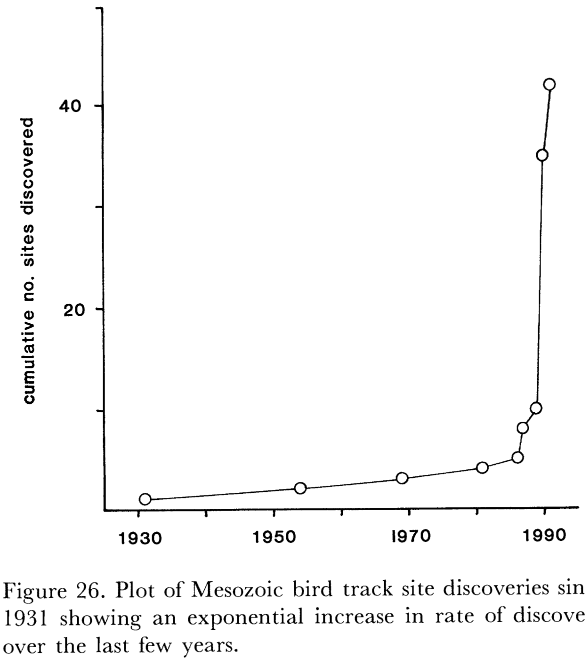

Figure 26. Plot of Mesozoic bird track site discoveries since 1931 showing an exponential increase in rate of discovery over the last few years.

occurred in the late Cretaceous (Fedducia 1980). The track record suggests that both assumptions need reevaluation.

With respect to the late Triassic – early Jurassic appearance of *Trisauropodiscus* assemblages, we note the following. In his original descriptions, Ellenberger (1972) stressed the remarkable bird-like appearance of the tracks, calling them 'aviform'.

> 'Ces animaux forment un genre très spécifique . . . étonnamment semblables pour l'apparence des pistes, aux empreintes des oiseaux du Crétace et de l'Eocène.' (Ellenberger 1972, p. 81)
>
> 'These animals [track-makers] form a very specific genre . . . remarkably similar in the appearance of their trackways to the footprints of Cretaceous and Eocene birds.' (Our translation.)

Ellenberger was an experienced ichnologist who was familiar with classic *Grallator* track assemblages (often attributed to coelurosaurian dinosaurs), and knew that the aviform morphology of these tracks was significant and different.

It is surprising that ichnologists have not looked more closely at *Trisauropodiscus* because of its aviform characteristics. The discovery of similar tracks in North Africa and North America (Ishigaki 1985; Lockley 1991) supports the contention that small, aviform tracks are widespread and worthy of recognition as a significant component of early Jurassic ichnological assemblages. The fact that they are bird-like, as distinct from dinosaur-like (for example, like *Grallator* or other accepted dinosaur ichnites), raises an important point of principle. Can we dismiss their aviform characteristics simply because they are older than known bird skeletal remains, yet attribute similar Cretaceous and Tertiary tracks to birds? We suggest that such a dismissal is inconsistent and unacceptable, especially in the light of new evidence for early Mesozoic bird-like taxa such as *Protoavis* (Chatterjee 1991), and other evidence of pre-Cretaceous birds, such as feathers (Rautian 1978).

As pointed out by Currie (1981) and Olsen (1985), until recently there has not been much good fossil evidence of early Cretaceous birds. Moreover, those that are known – *Ambiortus* and *Enaliornus* (see Olsen 1985), *Mesoiberornis* (Sanz *et al.* 1988), and others (Rao & Sereno 1990) – are different from the Charadriiformes-like birds that we infer as the track-makers for most of the footprints discussed herein. Thus, the track record includes a greater diversity of waterbirds in the early Cretaceous than could be inferred from the skeletal record. To have become as widespread, abundant, and diverse as the Lower Cretaceous track record indicates, they must have undergone significant radiation between Valanginian and Aptian times. As Olsen (1985) suggests, it remains to be seen to what extent new fossil evidence will shed further light on the evolution of birds, but certainly the early Cretaceous track record is very significant with respect to waders and their allies.

The evidence for an early Cretaceous shorebird radiation is extensive and compelling. It is manifest in the Jindong Formation in two ways: first as multiple track-bearing horizons, and second in the presence of at least two distinct track-makers. Neither phenomenon had previously been reported from any Mesozoic formation.

We also note that the late Cretaceous webbed foot tracks are by far the oldest yet reported. They evidently predate the Eocene flamingo-like *Presbyornis* tracks by about 30 Ma. The discovery of these tracks is consistent with the existence of 'flamingos or flamingo-like birds' in the Cretaceous fossil record (Feduccia 1978; Brodkorb 1963), and Feduccia's inferences that these birds derived from an older 'ancient shorebird stock'.

9. PALAEOECOLOGICAL DISCUSSION

The presence of bird tracks in association with invertebrate traces is of interest from a palaeoecological and palaeoenvironmental viewpoint, allowing for assessment of the biotic diversity in lacustrine and other shoreline environments. Detailed study of the affinity of invertebrate traces found with bird tracks should elucidate these palaeoecological relations further.

In most of the Cretaceous examples cited above, bird tracks occur in association with abundant large ornithopod tracks and common theropod footprints. They also occur with sauropod tracks in the Jindong palaeoenvironment. The significance of these co-occurrences is uncertain. It could simply be a function of small sample size, or relate to the fact that ornithopod and theropod tracks are very common in the Cretaceous, whereas tracks of sauropods and most other vertebrates are much less common. However, it could be that bird–dinosaur track co-occurrences have some significance in terms of ichnofacies composition. Lockley & Conrad (1989) and Lockley (1991) have suggested that there is a large-ornithopod ichnofacies associated with clastic, coastal plain, coal-bearing facies and a sauropod–theropod ichnofacies associated with carbonate platform environments and calcareous lacustrine deposits. Most Mesozoic bird tracks are associated with the former ichnofacies, although the Jindong Formation provides a notable exception to this generalization. However, we can conclude that birds and dinosaurs frequented a variety of shoreline environments, particularly in the early Cretaceous. Their tracks are now known to occur on the same bedding planes in both the Dakota and Jindong Formations (figures 2, 24 and 25).

10. CONCLUSIONS

The recent rapid increase in discovery of Mesozoic bird track sites is symptomatic of the present renaissance in vertebrate ichnology. At least some early Jurassic tracks (*Trisauropodiscus*) are very bird-like and distinct from the well-known coelurosaurian ichnites known as *Grallator*. If they were found in post-Jurassic strata, they would readily be accepted as avian in origin. Cretaceous bird tracks are far more abundant than previously reported and suggest a radiation of shorebirds by or before Aptian–Albian time, some 30 Ma earlier than usually postulated.

We conclude that tracks warrant further study because of their potential to provide palaeontologists with an improved understanding of the origin, evolutionary history and palaeoecology of birds.

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Note added in proof (2 April 1992): J. Moratella, Univ. Autonoma, Madrid (written communication 1992) reports that small bird-like tracks have been discovered at a Cretaceous dinosaur tracksite in northern Spain.

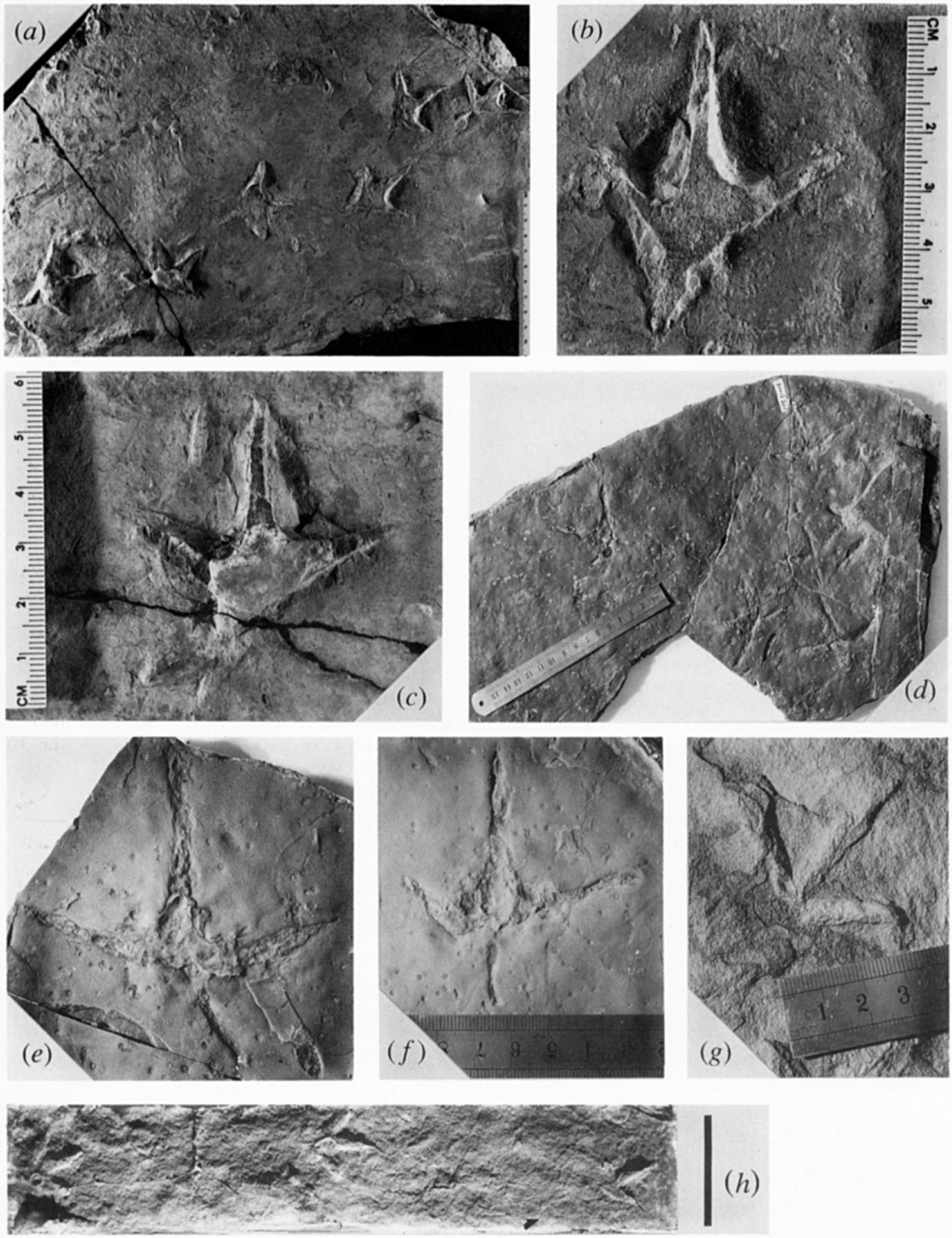

Figure 8. (*a*) *Ignotornis mcconnelli*: holotype; Cretaceous Dakota Group, Colorado; slab showing six tracks, including those shown in (*b*) and (*c*) (UCM 17614; cm scale in lower right). (*b*) *Ignotornis mcconnelli*: detail of one of the tracks shown in (*a*) (cm scale on right). (*c*) *Ignotornis mcconnelli*: detail of one of the tracks shown in (*a*) (cm scale on left). (*d*) *Jindongornipes kimi* sp. nov.: Cretaceous Jindong Formation, South Korea; slab showing five tracks, including those shown in (*e*) and (*f*) (KPE 50006; cm scale in lower left). (*e*) *Jindongornipes kimi* sp. nov.: paratype; Cretaceous Jindong Formation, South Korea (KPE 50006; track is 7.5 cm wide). (*f*) *Jindongornipes kimi* sp. nov.: holotype; Cretaceous Jindong Formation, South Korea (KPE 50006; cm scale along bottom). (*g*) *Aquatilavipes swiboldae*: Lower Cretaceous Gates Formation, Alberta (RTMP 90.30.1; cm scale in lower right). (*h*) *Trisauropodiscus moabensis* sp. nov.: holotype; latex mould of trackway from Jurassic Navajo Formation, Utah (CU-MWC 181.3; scale bar to the right of the trackway is 10 cm long).