

First report of lacertiform (lizard) tracks from the Cretaceous of Asia



Kyung Soo Kim ^a, Martin G. Lockley ^{b, *}, Jong Deock Lim ^c, Laura Pinuela ^d, Lida Xing ^e, Hae Won Moon ^a

^a Department of Science Education, Chinju National University of Education, Shinan-dong, Jinju, Kyungnam 660-756, South Korea

^b Dinosaur Trackers Research Group, University of Colorado Denver, P.O. Box 173364, Denver, CO 80217-3364, USA

^c Natural Heritage Center, National Research Institute of Cultural Heritage, 927 Yudeng-ro, Seo-gu, Daejeon, 302-834, South Korea

^d Museum of the Jurassic, Asturias, Spain

^e School of the Earth Sciences and Resources, China University of Geosciences, Beijing, China

ARTICLE INFO

Article history:

Received 23 June 2016

Received in revised form

19 August 2016

Accepted in revised form 25 August 2016

Available online 26 August 2016

Keywords:

Cretaceous

Korea

Lizard

Footprints

ABSTRACT

The well-preserved trackway of a lacertiform, lizard-like trackmaker from the Haman Formation (Cretaceous) of Korea is described as *Neosauroides koreaensis* ichnogen. et ichnosp. nov. This is the only example of a Cretaceous lacertiform or lizard-like trackway currently known in the global track record. Although lacertiform trackways, mostly assigned to the ichnogenus *Rhynchosauroides*, are common in the global Triassic, they are almost entirely absent in the Jurassic and Cretaceous. Moreover, ichnological classification criteria allow that *Neosauroides* is morphologically distinct from *Rhynchosauroides* at the genus level, and more like the tracks of the extant lizard *Sceloporus*. The reasons for the conspicuous lack of post-Triassic occurrences are not certain, but not due to a post-Triassic lack of potential lizard trackmakers. Thus, the preservation biases are likely due to paleobiological factors such as trackmaker ecology and paleoenvironmental preference.

© 2016 Elsevier Ltd. All rights reserved.

1. Introduction

Tracks of lizard-like (lacertiform) species are abundant in the Upper Triassic in many regions, especially in Europe, North America, Africa and South America, where the classic lacertiform morphotypes are represented by the well-known and well-studied ichnogenus *Rhynchosauroides*. They are also reported from the Upper Permian of Italy (Valentini et al., 2007). However, tracks of this type are mysteriously absent in most of the track record of these and other regions in the Jurassic and Cretaceous, even though skeletal remains of Cretaceous lizards are known from Asia (Gao and Cheng, 1999; Evans and Wang, 2010; Xu et al., 2014) and other regions (Nydham and Voci, 2007). Most of these reports deal only or primarily with cranial elements (teeth and jaws), providing no information on foot morphology. However, the report by Evans and Wang (2010) describing the new species *Liushusaurus acanthocaudata* is particularly instructive because it deals with exquisite preservation of the whole skeleton, including both manus and pes. The aforementioned sudden disappearance of a previously-

common track type is not easily explained by any obvious paleobiological interpretation and, as discussed below, remains an open question. However, it cannot be attributed to the disappearance of lizard like trackmakers.

Thus, the discovery of a well-preserved lacertiform trackway in the Cretaceous Haman Formation fills a large gap in the global track record of lizard-like tracks. Not only is this the first report of this general track morphotype from the Cretaceous of Korea, it is also the first report of this type from the Cretaceous of Asia and indeed from the Mesozoic of Asia. We herein describe this trackway in detail and compare it with similar morphotypes from the track record.

2. Geological setting and associated ichnofaunas

The tracks described here are preserved as natural casts on a small slab of fine-grained sandstone found at the Gain-ri tracksite, Changseon Island, Gyeongnam District, designated as Korea Natural Monument No. 499 (Fig. 1). The Haman Formation belongs to the Hayang Group of the Gyeongsang Supergroup comprised conformably of the Chilgog Formation, Silla Conglomerate, and Haman and Jindong formations in ascending order (Fig. 2). The Kusandong Tuff (1–5 m thick) occurs in the uppermost part of the

* Corresponding author.

E-mail address: Martin.Lockley@UCDenver.edu (M.G. Lockley).

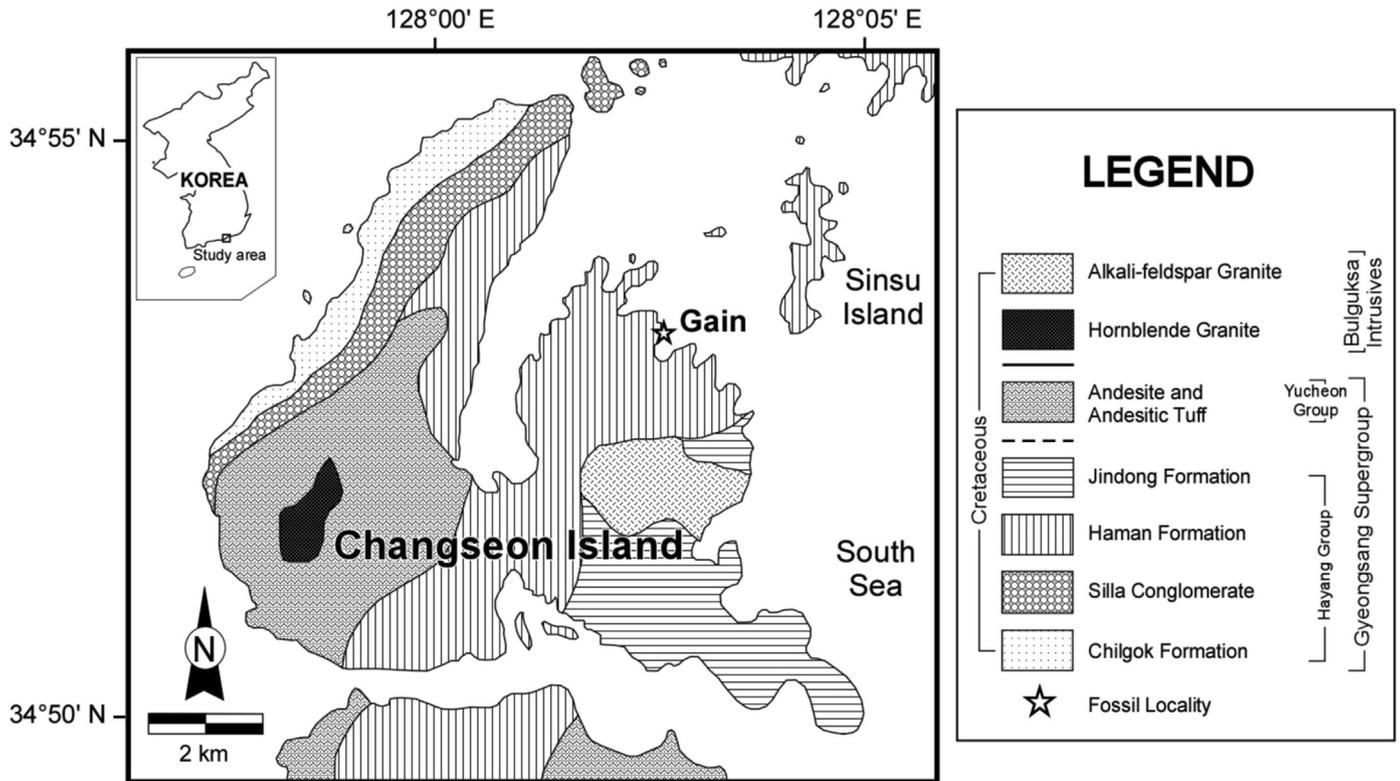


Fig. 1. Geologic map of the fossil locality (Choi et al., 2002).

Haman Formation and has been regarded as a key bed for the subdivision and basinwide correlation of the Upper Cretaceous strata in the Gyeongsang Basin (Chang, 1975; Chang et al., 1997, 1998). The results of radiometric analyses in the Kusandong Tuff were 97.1 ± 2.0 Ma and 97.3 ± 1.8 Ma (zircon U–Pb age using LA-ICP-MS; Jwa et al., 2009) and 103 ± 1.2 Ma and 103.0 ± 2.3 Ma (zircon SHRIMP U–Pb age; Kim et al., 2011). The Haman Formation is inferred to be of “mid” Cretaceous, Albion – Cenomanian age (105–97 Ma) by Kang and Paik (2013). The dominant Haman Formation lithologies are reddish shale, sandy shale, and white to greenish and gray sandstone with minor intercalating tuffaceous and pebbly sandstone (Chang, 1975). In the study area, the non-biogenic sedimentary structures such as ripple marks, desiccation cracks, raindrop imprints, and cross stratifications indicate marginal lacustrine environments.

In addition these facies are well known for yielding abundant vertebrate footprints and invertebrate traces. Many dinosaur and bird tracks including *Koreanaornis hamanensis* (Kim, 1969; Baek and Yang, 1997; Lim et al., 2000, 2002) have been reported from the Haman Formation. Recently described vertebrate tracks include the smallest known dinosaur tracks (ichnogenus *Minisauripus*; Lockley et al., 2008; Kim et al., 2012a), didactyl dromaeosaurid tracks *Dromaeosauripus hamanensis* and *Dromaeosauripus* ichnosp. (Kim et al., 2008), sauropod tracks *Brontopodus pentadactylus* (Kim and Lockley, 2012), bird tracks *Ignotornis yangi* and *I. gajinensis* (Kim et al., 2006, 2012b), and pterosaur tracks *Pteraichnus* ichnosp., and *Haenamichnus gainensis* (Kim et al., 2006, 2012c). In addition to these reports, the formation has yielded various new dinosaur track assemblages containing didactyl dromaeosaurid, bird and pterosaur tracks in abundance (Lim et al., 2010; Moon and Kim, 2013; Son et al., 2014; Kim et al., 2015). In short the Haman Formation is proving to be a rich source of hitherto unrecognized tetrapod tracks which add significantly not just to the Cretaceous track

record of Korea, but more widely to the Asian and global track records.

3. Description of trackway

3.1. General features

The lacertiform trackway described here has the specimen number CUE 130304L (CUE = Chinju National University of Education). It consists of the natural casts of four consecutive manus pes sets (Figs. 3 and 4). The pes tracks, situated behind, and slightly lateral to the manus tracks are incomplete showing only three clear digits traces, inferred to represent digits II, III and IV, of a pentadactyl pes. However, pes trace morphology is consistent in all three tracks with the outer digit trace IV being the longest, with a pronounced outward rotation of the digit long axis, and terminating in a hook-like terminal toe (claw) trace directed anteriorly. Incomplete pes tracks are common in trackways attributed to lizard-like (lacertiform) trackways as shown in the illustrated summary of 21 ichnospecies of the Triassic ichnogenus *Rhynchosaurooides* (Baird, 1957, fig. 9; Haubold, 1984, fig. 98). In fact it could be argued that the incompleteness of many pes tracks is “typical” and reflects the postural behavior of the lizard during foot registration. This is easily confirmed by reference to the small number of modern field guides and other studies that illustrate the variability and incompleteness of the trackways of extant lizards (Murie, 1974; Stuart and Stuart, 2000; Farlow and Pianka, 2000). Given these constraints the Korean trackway is remarkably consistent and complete in the registration of consecutive manus pes sets, and superior in terms of completeness to many lacertiform trackways assigned ichnotaxonomic labels. The manus impressions, for example, are complete and quite symmetrical about the axis of the longest digit (III). They

Age (Ma)	System/Series	Stage	The formations in the Gyeong Basin			
70	Cretaceous	Upper	Maastrichtian	Goseong Formation	Bulguksa granites	
			Campanian			
			Santonian			
			Coniacian			
			Turonian			Jindong Formation
			Cenomanian			
		Lower	Albian	Haman Formation		
				Silla Conglomerate		
				Chilgok Formation		
				Jinju Formation		
			Aptian	Hasandong Formation		
					Barremian	Nakdong Formation
Hauterivian						

Fig. 2. Stratigraphy of Gyeongsang Supergroup, modified after Kang and Paik (2013).

consistently show all five digit traces I–V preserved, and are aligned parallel to the midline of the trackway.

3.2. Justification for erecting a new ichnotaxon

The naming of ichnotaxa has been much discussed and is sometimes challenged as unnecessary on the grounds that some track material is poorly preserved, incomplete or synonymous with an existing ichnotaxon (see below, including acknowledgements). For this reason we discuss and justify the need for erecting a new ichnotaxon in the case of the lizard-like trackway reported here and named as *Neosauroides koreaensis*. Not only is the naming of ichnotaxa sanctioned by the ICZN (1999), but a number of standard conventions have been established to ensure sound practice. The most straightforward of these include the guidelines provided by Peabody (1955, p. 915) which recommend a minimum “of three consecutive sets of footprints, thus establishing gait and body proportions as well as anatomical detail of the feet.” [His italics]. He also recommends selecting the “clearest” footprints. The trackway segment here designated as *Neosauroides koreaensis* meets these requirements fully with four “consecutive sets.” It also conforms to all the “Ten Paleoeichnological Commandments” of Sarjeant (1989), which includes the minimum trackway segment proposed by Peabody (1955), and the common sense recommendation that the footprints should be “markedly different from all described types.”

These standard conventions are potentially compromised in cases where ichnologists incorrectly interpret “differences” in

preservation of footprints as evidence for meaningful differences in the anatomy of the feet of trackmakers. It is for this reason that Hunt and Lucas (2005, 2007a) made a distinction between biotaxonomic ichnotaxa which reflect trackmaker foot morphology and extramorphological ichnotaxa which reflect foot-substrate interactions rather than trackmaker foot morphology. We do not deny that there are cases where track names have been erected without adequate attention to these guidelines: i.e., with undue attention to extramorphological factors (Lucas, 2007). In some cases such questionable names have proliferated in literature dealing with intensely studied stratigraphic units containing many tracks of common and abundant ichnotaxa. For example, Hunt and Lucas (2007b) listed 32 ichnospecies of *Rhynchosauroides* named between 1842 and 1979, all of which are Triassic in age, and few of which are defined on the basis of a single sequence of three or more consecutive well-preserved footprints, on a substrate without other overlapping or overlapped footprints (cf. Haubold, 1984). This list does not include additional *Rhynchosauroides* ichnospecies names introduced subsequently (e.g., Silva et al., 2008).

Given the current status of ichnogenus *Rhynchosauroides* there can be little justification for assigning the Korean ichnite *Neosauroides* to an existing ichnospecies within ichnogenus *Rhynchosauroides* unless it can be shown that the morphology is clearly and unambiguously coincident with one of the many species reported by these authors. This is not the case. Even in theory making such a correlation would be difficult given that some ichnospecies were poorly defined (potential *nomina dubia*) and/or based on poor extramorphological material that does not permit reliable comparison: see for example Haubold (1984, figs. 87 and 98) who illustrated 21 ichnospecies of *Rhynchosauroides* based only on ectaxonic manus and pes sets, not trackways.

Thus, as shown here, the Korean trackway (*Neosauroides koreaensis*) is quite distinct in having a mesaxonic manus which distinguishes it from *Rhynchosauroides*. Peabody (1955, p. 916–917) made the little-noted observation that “a trackway, of a tetrapod is as a rule generically distinctive relative to zoological classifications.” This inference is consistent with our conclusion that the Korean trackway is more similar (at the “genus level”) to the trackway of the extant sagebrush lizard *Sceloporus graciosus* than it is to any of the *Rhynchosauroides* ichnospecies named from the Mesozoic. Thus, this modern trackway, which by convention is not formally named, could not be accommodated in *Rhynchosauroides* on morphological grounds, and should be considered distinct at the genus level. Finally it is important to note that, the complex and confusing situation surrounding some ichnotaxa, including *Rhynchosauroides* does not mean that equally complex issues surround the naming of all ichnotaxa. There are many distinctive ichnogenera that include only a few or a single ichnospecies: e.g., *Brontopodus* (Farlow et al., 1989) and *Dromaeopodus* (Li et al., 2008). As introduced here, *Neosauroides koreaensis* fits this latter, monospecific category. It is the only lizard-like trackway currently known from the Cretaceous, and is not assignable to any of the multiple, known lizard-like ichnospecies, primarily *Rhynchosauroides*, reported from the lower Mesozoic (Triassic). As a footnote to this argument it is pertinent to point out that many osteological taxa are based on very incomplete material, such as isolated teeth and jaw elements.

3.3. Systematic description

Neosauroides ichnogen. nov.

Figs. 3 and 4

Diagnosis. Small lizard-like trackway with ectaxonic lacertiform pes and pes trackway width being wider than the manus trackway



Fig. 3. Photograph of cast of holotype of *Neosauroides koreaensis* ichnogen. et ichnosp. nov. Compare with Fig. 3 for track designations.

width. Manus pentadactyl, distinctly mesaxonic and symmetric to subsymmetric, smaller than the pes and less outwardly rotated.

Type material. CUE (Chinju National University of Education) 130304L, a trackway composed of the natural casts of 4 consecutive pes and 4 consecutive manus tracks.

Derivation of ichnogenus name. Referring to track of a “new reptile.”

***Neosauroides koreaensis* ichnosp. nov.**

Type material. as for ichnogenus.

Derivation of ichnospecies name. Referring to the Republic of Korea.

Description. Pes traces incomplete appearing tridactyl and consisting only of the distal traces of digits II, III and IV, which are increasing in length; digit IV is longest, indicating an ectaxonic foot. Registered portion of pes track length (excluding proximal heel) is about 1.90 cm, measured parallel to the long axis of digit IV, and the pes track width is about 1.0 cm. Pes traces are rotated outward at

about 60° as measured along axis of digit IV relative to the trackway midline, or about 20° as measured along axis of digit III (cf. Leonardi, 1987), but with distal digit III and IV claw traces curved back inward towards trackway axis. Divarication between pes digits II – III and III – IV average 8.3° and 41.3°, respectively (N = 3).

Manus traces semi-plantigrade pentadactyl, mesaxonic and subsymmetrical with digit III being longest and digits I and V being shortest (III > IV > II > V = I). Manus situated anteromedial to pes in trackway. Digit traces with fine distal claw traces, but heel traces faint. Axis of digit III subparallel to trackway axis. Overall manus length averaging about 1.9 cm (range 1.5–2.4 cm depending on visibility of heel trace), with width averaging about 1.59 cm and less variable (1.50–1.65 cm). Digit divarication (I–V) averaging about 83° (range 76–86°); N = 4 for all preceding measurements. Manus digit traces I–V are more or less equally spaced with the following

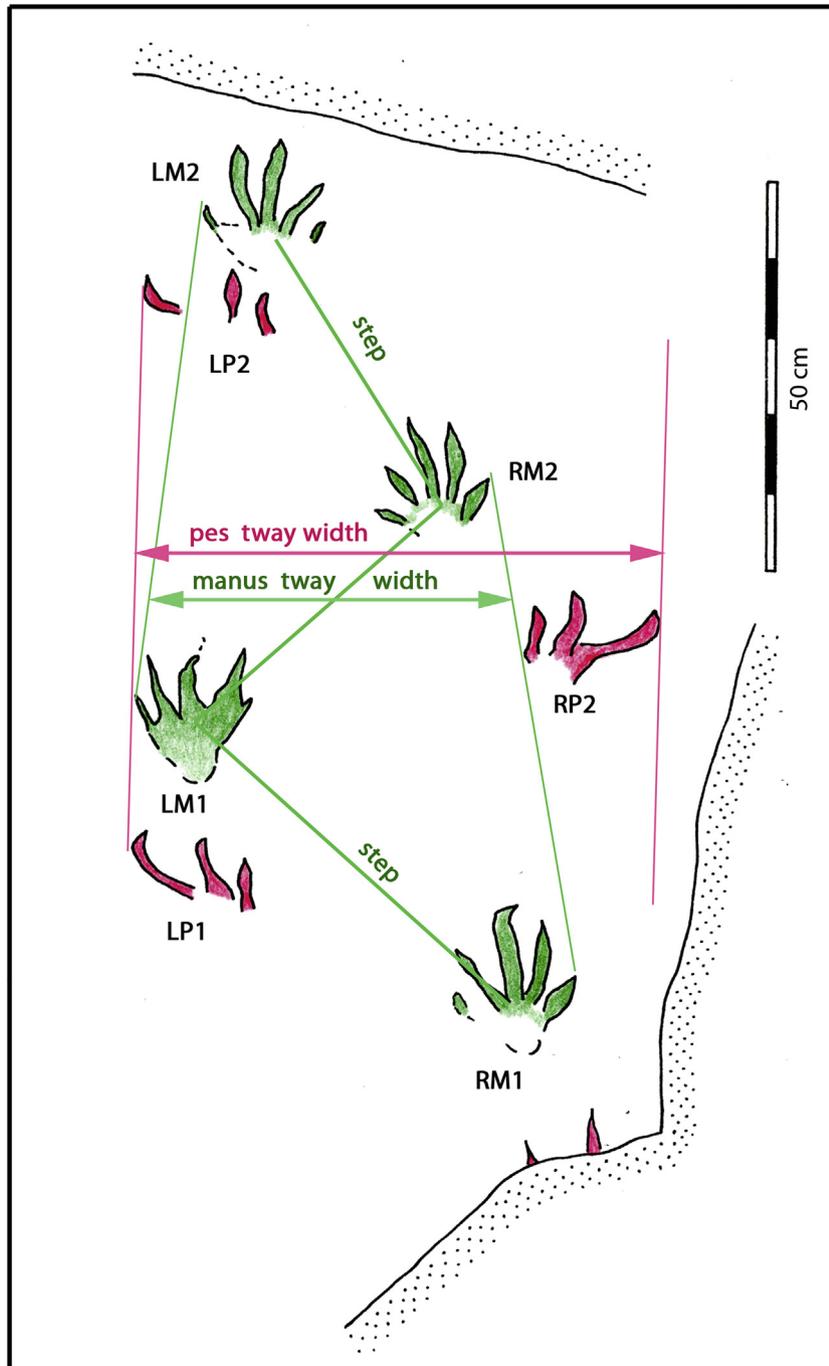


Fig. 4. Line drawing of *Neosauroides koreaensis* ichnogen. et ichnosp. nov., reversed to show original orientation of positive impression. Compare with negative cast view in Fig. 3.

mean divarication angles: I–II 19.5° ($N = 2$), II–III 26° ($N = 4$), III–IV 19.5° ($N = 4$) and IV–V 20.3° ($N = 4$).

Trackway parameters are based on designating consecutive pes–manus sets in the sequence RP1–RM1, LP1–LM1, RP2–RM2 and LP2–LM2 (Fig. 4) with the RP1 trace being only partially visible on the edge of the block, and thus providing no useful morphometric data. Outer pes trackway width (6.7 cm) is greater than the outer manus trackway width (4.8 cm). Pes step 6.1 and 5.5 cm for LP1–RP2 and RP2–LP2, respectively (stride 7.3 cm) corresponding with a pace angulation of 80° . Manus step sequence 5.6, 4.2 and 4.2 cm for RM1–LM1–RM2–LM2 sequence, with corresponding strides of 6.5 and 6.4 cm and pace angulations of 85° and 101° . Tail trace not observed.

3.4. Interpretation of trackway

The trackway width parameters for the pes and manus tracks indicate a wider straddle for the pes and a stronger outward rotation based on the longest digit (IV), or following Leonardi (1987) as measured for the orientation of the medial digit (III). In comparison with the manus straddle and manus tracks orientation it appears the pes registration pattern may indicate longer, more sprawling limbs, with longer, outwardly rotated feet. By contrast the manus registration pattern indicates smaller feet and shorter less sprawling limbs. These differences may account for the manus tracks being more completely impressed, as the front feet were in a position that was more under the body, where body weight was

transmitted more vertically, rather than more laterally as in the case of the pes. It can be argued that the incomplete preservation of the pes, not just in *Neosauroides* (showing only digit traces II, III and IV) but in other lacertiform trackways of both extant and extinct lizards, is in fact “characteristic” or typical of lacertiform track-makers, and representative of posture during gait or progression. It is possible for formal ichnotaxonomy to recognize that full registration of all foot digits may not be typical, and that postural factors lead to distinctive, even incomplete patterns of foot registration (e.g., Avanzini, 1998; Avanzini et al., 2011).

4. Comparative ichnology

As noted above, lacertiform tracks and trackways are rare if not unknown in most of the upper Mesozoic: i.e., in most of the Jurassic and Cretaceous. A very few isolated tracks, as distinct from trackways, have been reported from the Jurassic of North America (Foster, 2003; Foster and Lockley, 2006) and Spain (García-Ramos et al., 2002; Avanzini et al., 2010). In the latter case, a single track was assigned to the well-known Triassic ichnogenus *Rhynchosauroides*, and reported as the first known occurrence from the Upper Jurassic (Avanzini et al., 2010). In this case the track, interpreted as a manus, is clearly ectaxonic and not mesaxonic like *Neosauroides*. Thus, it is fundamentally distinct from the Korean specimen at least at the genus level. Abundant lacertiform tracks, some with recognizable trackway segments and well-defined and easily-differentiated manus–pes sets, appear to be known only from the Upper Permian and Triassic where the ichnogenus *Rhynchosauroides* is ubiquitous. This ichnotaxon, originally described by Maidwell (1911) from the Triassic of England, has been reported from many sites in Europe (Avanzini and Renesto, 2002), North America (Baird, 1957; Lockley and Hunt, 1995; Hunt and Lucas, 2007b) and South America (Melchor and de Valais, 2006; Silva et al., 2008) where they occur at numerous locations, and have been used in some cases for biochronology (Avanzini and Mietto, 2008).

Comparison between *Rhynchosauroides* and the Haman ichnotaxon described here as *Neosauroides* clearly shows that while the pes in both ichnogenes has a typical asymmetric, ectaxonic and typically lacertiform morphology, with digit IV the longest, the morphology of the manus is significantly different, being symmetrical to subsymmetrical and mesaxonic in *Neosauroides* with digit III the longest. This is in contrast to the manus of most *Rhynchosauroides* ichnospecies which like the pes is strongly ectaxonic as shown by Demathieu and Oosterlink (1983) and Avanzini and Renesto (2002, fig. 3). It is also of interest that the mesaxonic manus of *Neosauroides* (short digit IV) is similar to *Prorotodactylus* from the Lower Triassic of Poland (Brusatte et al., 2011) and *Apatopus* from the Upper Triassic of North America (Padian et al., 2010).

Rhynchosauroides trackways mostly show lateral overstep of the manus by the pes, which is in contrast to the Korean specimens shown here (Hendrik Klein written communication). However, the unusual ichnospecies *Rhynchosauroides retroversipes* described by Silva et al. (2008) from Brazil appears not to have an ectaxonic manus, which would make it the only ichnospecies with a non-ectaxonic manus assigned to *Rhynchosauroides*. However, the reversed orientation of the pes in this Brazilian ichnotaxon is unusual, and the manus in the Brazilian ichnospecies is different from that seen in the Korean trackway in having short digit traces that are very widely splayed and in some cases reveal that only three or four digits registered traces. It is also debatable as to whether the difference in the manus allows inclusion of the Brazilian ichnospecies in the ichnogenus *Rhynchosauroides*, when the ichnogenus diagnosis clearly refers to an ectaxonic manus.

There are relatively few studies of modern lizard tracks (Padian and Olsen, 1984; Farlow and Pianka, 2000; Kubo, 2010) and relatively few field guides that show clearly defined trackways with manus and pes morphology (Halfpenny, 1998: Fig. 5 here). However, enough is known of manus and pes morphology to distinguish between species with ectaxonic manus such as the those of the Komodo Dragon (Padian and Olsen, 1984) and other varanid lizards (Kubo, 2010) and other lizard groups with mesaxonic manus such as the gecko *Eublepharis macularius* (Kubo, 2010). In this latter case while the manus is mesaxonic (not ectaxonic) the divarication between digits I and V is very wide ($>200^\circ$) and so very different from the Korean example. In this regard the *Neosauroides* manus is very similar to the tracks of some modern lizards, as illustrated in various field guides: e.g. the sagebrush lizard *Sceloporus graciosus* (Halfpenny, 1998; Fig. 5).

5. Discussion

Broadly speaking the age difference between Early to Late Triassic *Rhynchosauroides* (between ~250 and ~200 Ma) and Cretaceous *Neosauroides* (~100 Ma) is of the same order of magnitude as the difference between the Cretaceous tracks and modern lizard tracks. However, Kubo (2010) has shown that modern lizard tracks are morphologically quite variable, as was probably the case among Cretaceous lizards. It is possible to show greater similarities between the manus morphology of Cretaceous *Neosauroides* and the tracks of extant lizard species such as *Sceloporus graciosus* than between *Neosauroides* and most ichnospecies of the Triassic ichnogenus *Rhynchosauroides*. The body fossil species *Liushusaurus acanthocaudata* from the Lower Cretaceous of Inner Mongolia (Evans and Wang, 2010) is about the same age as the Korean trackway (*Neosauroides koreaensis*) described here. The size of the feet is also a relatively close match for the trackway. However, the difference in morphology between the foot of the body fossils and the tracks prevents us from inferring a perfect or near-perfect “Cinderella” match (cf. “Cinderella Syndrome” of Lockley, 1998). The *Liushusaurus* manus is slightly ectaxonic with digits III and IV almost the same length, rather than clearly mesaxonic as in the trackway. Digits II and V are much longer than in the trackway. Thus the relative digit lengths are $III = IV > II = V > I$ in *Liushusaurus* as compared with $III > II = IV > I = V$ in the *Neosauroides* trackway.

In recent years the Cretaceous of Korea has become well known for the abundance and diversity of tetrapod tracks, including tracks attributed to non-avian tridactyl and didactyl theropods, birds, sauropods and ornithopods. The Jindong and Haman Formations, the upper two units of the Hayang Group (Fig. 2), are particularly well-known for the abundance of track bearing levels (Lockley et al., 2006, 2012 and references herein). Furthermore, recent discoveries and reports by the senior authors and their colleagues have shown that the abundance and diversity of tracks in the Jinju, Haman, and Jindong formations are all equally impressive (Kim et al., 2015). In addition to the avian and non-avian dinosaur groups, including the lizard (lacertiform) tracks described here, known from the Jindong and Haman Formations, the Jinju Formation has been a source for recent discoveries of turtle tracks (Kim and Lockley, 2016) and small crocodylian tracks (Park et al., 2016). All three of these represent major tetrapod track groups newly reported from the Sindong and Hayang groups. This suggests the already well demonstrated ichnological potential of these two groups is far from exhausted, despite the increased publication rate, reviewed by Yang (2015) which records the publication of more than 120 papers of which more than 80 have been published since 2000.

It is surprising that lacertiform or lizard tracks are so rare in the Jurassic and Cretaceous in comparison with their abundance in the

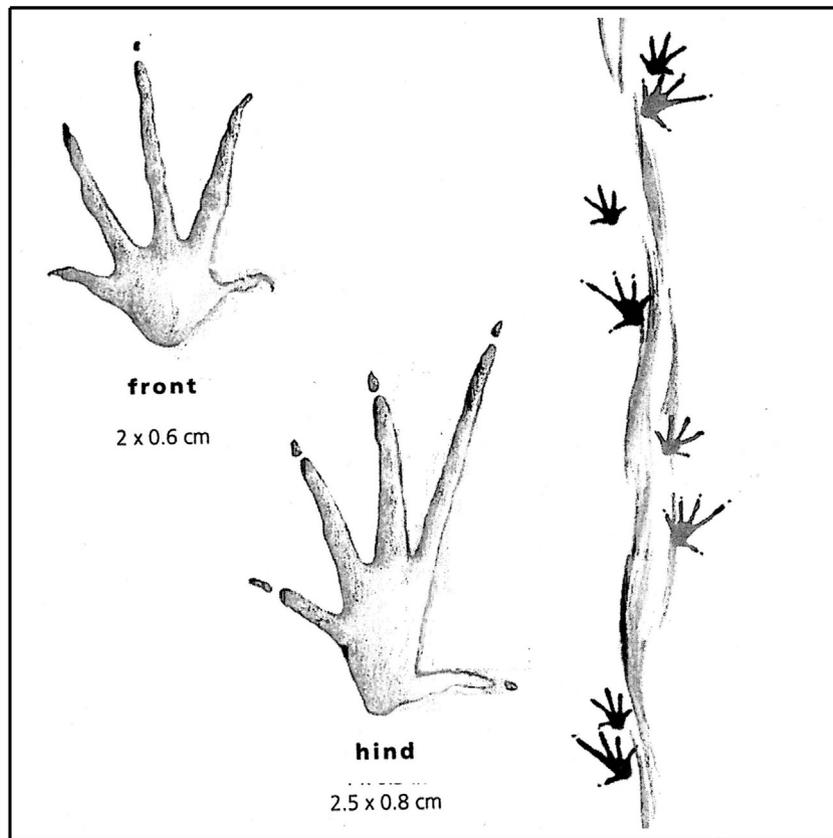


Fig. 5. Trackway of the sagebrush lizard *Sceloporus graciosus* from the western USA. Modified after Halfpenny (1998).

Triassic. Various explanations are possible that would broadly fall into two categories: paleobiological, having to do with paleoecology and paleogeographical distribution of trackmakers or geological, pertaining to facies distributions and preservation biases related to such factors as size and substrate conditions. In the case of the rare reports of isolated lacertiform tracks from the Upper Jurassic of North America and Spain (Foster and Lockley, 2006; Avanzini et al., 2010) it is possible to infer a preservational bias, because the majority of associated tracks are large and the track-bearing facies are not suitable for preservation of small tracks: i.e., not dominated by fine grained substrates conducive to registration of small tracks. However, in the case of the Korean lizard trackway, the only one currently known from anywhere in the Cretaceous, it is associated with a large number of small tracks of birds, pterosaurs and diminutive tetrapods, from lacustrine basin facies. This weakens the argument that the lack of such tracks is due to any size-related or substrate-related preservational biases. Thus, we conclude that paleoecological factors, were the more likely influence. For example, predation pressures on small lizards, possibly from birds and pterosaurs, may have been greater in Cretaceous lakeshore habitats than they were in the Triassic. Such paleoecological factors may help explain rarity of such trackmaking species in certain habitats: i.e., implying preference of the trackmakers for habitats other than those lacustrine basin facies where registration of small tracks was common. Some Cretaceous lizard body fossils are associated with special preservation conditions in lake deposits (Evans and Wang, 2010) whereas others are associated with non-lacustrine deposits (Gao and Cheng, 1999). The most diverse assemblages of Mesozoic lizard body fossils are known from the Upper Cretaceous of Mongolia (Gao and Norell, 2000; Norrel et al., 2007) and are associated with a sample of at least 30 species recovered from predominantly eolian and alluvial fan deposits in

arid to semiarid environments, which also created special preservation conditions. Lizard tracks have not been reported from these deposits, which are unsuitable for registration and preservation of small tracks. Thus, we infer that deposits such as the Haman Formation currently still offer the best potential for further discoveries of this type of track, regardless of whether they originally represented optimal lizard habitats during the Cretaceous. It is tempting to infer that lizards may have shown a greater preference for arid desert habitats in the late Mesozoic (Late Cretaceous), than they did in the early Mesozoic (Triassic), when their tracks are abundant in fluvio-lacustrine shoreline settings. However this is a speculative inference that may simply reflect the high diversity of the aforementioned body fossil sample from the Mongolia.

6. Conclusions

Neosauroides koreaensis ichnogen. et ichnosp. nov. is the first lizard-like (lacertiform) trackway reported from the Mesozoic of Asia, and globally represents the only known example from the Cretaceous track record. *N. koreaensis* is characterized by an incompletely registered ectaxonic, pentadactyl pes, typifying the gait of many lacertiform trackmakers, and a slightly smaller but well-defined mesaxonic pentadactyl manus. The trackway pattern is regular with pes straddle wider than manus straddle and with pace angulations between ~80 and 100°. The pes tracks of *N. koreaensis* are similar to *Rhynchosauroides*, which is only abundant in the Triassic, but the manus tracks are quite different and more like those of extant lizards (genus *Sceloporus*). This difference in large part justifies erecting the new ichnogenus *Neosauroides*. Moreover, *Rhynchosauroides* is represented by a very large number of ichnospecies of uncertain validity and is clearly in need of comprehensive revision.

Neosauroides koreaensis ichnogen. et ichnosp. nov. occurs in lacustrine basin facies with many other small and large tracks. Thus the scarcity of lizard-like lacertiform tracks in the Cretaceous of Korea is evidently not related to substrate conditions or bias against the preservation of small tracks but rather to other paleoecological factors. For example, many Cretaceous lizard body fossil remains occur in quite different facies. *N. koreaensis* adds significantly to the diversity of major trackmaker groups already known from the Haman Formation. The size and age of the Early Cretaceous genus *Liushusaurus acanthocaudata* from China are both broadly similar to the size and age of *N. koreaensis* tracks. However, the manus morphology of this taxon is inconsistent with the manus track morphology, and so a close morphological match between the species and ichnospecies cannot be demonstrated. Making potential matches between these Cretaceous tracks and body fossils of the same or similar age are hampered on the one hand by the rarity of trackways and on the other by the lack of foot skeletons in most body fossil taxa.

Acknowledgments

The National Research Institute of Cultural Heritage (NRICH-1605-A25F-1) supported this research. MGL, LP and LX thank the organizers of the Spring Meeting of the Korean Earth Science Society and Gyeongnam Goseong International Symposium, for support of travel to Korea in April 2016 and for access to the specimen described in the collaborative study undertaken here. We also thank Hendrik Klein, Neumarkt, Germany for reading the manuscript and his evaluation of the new ichnotaxon proposed here in relation to the well-known ichnogenus *Rhynchosauroides*. Spencer Lucas, New Mexico Museum of Natural History and Science offered further useful comments on *Rhynchosauroides* ichnotaxonomy which, like us, he considers over-split and in need of revision. We also thank Eduardo Koutsoukos (Editor, Cretaceous Research) and an anonymous reviewer for advice on this same topic, and for suggesting more discussion of the body fossil record of Cretaceous lizards and how that record may relate to the track record.

References

- Avanzini, M., 1998. Anatomy of a footprint: bioturbation as a key to understanding dinosaur walk dynamics. *Ichnos* 6, 129–139.
- Avanzini, M., Mietto, P., 2008. Lower and Middle Triassic footprint based biochronology in the southern Alps. *Oryctos* 8, 3–13.
- Avanzini, M., Renesto, S., 2002. A review of *Rhynchosauroides tirolicus* Abel, 1926 ichnospecies (Middle Triassic: Anisian–Ladinian) and some inferences on *Rhynchosauroides* trackmaker. *Rivista Italiana di Paleontologia e Stratigrafia* 108, 51–66.
- Avanzini, M., Pinuela, L., García-Ramos, J.C., 2010. First report of a lizard-like footprint from the Late Jurassic (Asturias, Spain). *Journal of Iberian Geology* 36, 175–180.
- Avanzini, M., Pinuela, L., García-Ramos, J.C., 2011. Late Jurassic footprints reveal walking kinematics of theropod dinosaurs. *Lethaia*. <http://dx.doi.org/10.1111/j.1502-3931.2011.00276.x>.
- Baek, K.S., Yang, S.Y., 1997. Preliminary report on the Cretaceous bird tracks of the Lower Haman Formation, Korea. *Journal of the Geological Society of Korea* 34, 94–104 (in Korean with English abstract).
- Baird, D., 1957. Triassic reptile footprint faunules from Milford, New Jersey. Harvard College, Museum of Comparative Zoology, Bulletin 117, 449–520.
- Brusatte, S.L., Niedzwiedzki, G., Butler, R.J., 2011. Footprints pull origin and diversification of dinosaur stem lineage deep into Early Triassic. *Proceedings of Royal Society B: Biological Sciences* 278, 1107–1113.
- Chang, K.H., 1975. Cretaceous stratigraphy of Southeast Korea. *Journal of the Geological Society of Korea* 11, 1–23.
- Chang, K.H., Park, S.O., Kim, H.S., 1997. Cretaceous stratigraphy and geologic history of medial Kyongsang Basin: tectonics and volcanism. *Geosciences Journal* 1, 2–13.
- Chang, K.H., Lee, Y.J., Suzuki, K., Park, S.O., 1998. Zircon morphology, CHIME age and geological significance of Kusandong Tuff. *Journal of Geological Society of Korea* 34, 333–343.
- Choi, P.Y., Choi, H.I., Hwang, J.H., Kee, W.S., Choi, Y.S., Koh, H.J., Song, K.Y., Kim, J.C., 2002. 1:2500 Explanatory note of the Mokpo and Yeosu sheets. Korea Institute of Geoscience and Mineral Resources, 45 pp. (in Korean).
- Demathieu, G., Oosterlink, H.W., 1983. Die Wirbeltier-Ichnofauna aus dem Unteren Muschelkalk von Winterswijk (Die Reptilfährten aus der Mitteltrias der Niederlande). *Staringia* 7, 1–51.
- Evans, S.E., Wang, Y., 2010. A new lizard (Reptilia: Squamata) with exquisite preservation of soft tissue from the Lower Cretaceous of Inner Mongolia, China. *Journal of Systematic Palaeontology* 8 (1), 81–95.
- Farlow, J.O., Pianka, E.R., 2000. Body form and trackway pattern in Australian desert monitors (Squamata: Varanidae); comparing zoological and ichnological diversity. *Palaios* 15, 235–247.
- Farlow, J.O., Pittman, G., Hawthorne, M., 1989. *Brontopodus birdi*, Lower Cretaceous sauropod footprints from the U. S. Gulf Coastal Plain. In: Gillette, D.D., Lockley, M.G. (Eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, pp. 371–394.
- Foster, J.R., 2003. Paleoeological analysis of the vertebrate fauna of the Morrison Formation (Upper Jurassic), Rocky Mountain region, USA. *New Mexico Museum of Natural History and Science Bulletin* 23, 1–95.
- Foster, J., Lockley, M.G., 2006. Preservation and abundance patterns in the ichnological record of the Morrison Formation (Upper Jurassic, North America). In: Foster, J.R., Lucas, S.G. (Eds.), *Paleontology and Geology of the Upper Jurassic Morrison Formation*, New Mexico Museum of Natural History and Science Bulletin, 36, pp. 203–316.
- Gao, J., Cheng, Z., 1999. A new lizard from the Lower Cretaceous of Shandong, China. *Journal of Vertebrate Paleontology* 19 (3), 456–465.
- Gao, K., Norrel, M.A., 2000. Taxonomic composition and systematics of Late Cretaceous lizard assemblages from Ukhaa Tolgod and adjacent localities, Mongolian Gobi Desert. *Bulletin American Museum Natural History* 249, 1–118.
- García-Ramos, J.C., Lires, J., Pinuela, L., 2002. Dinosaurios: Rutas por el Jurásico de Asturias. *La Voz de Asturias*, Grupo Zeta, Lugones (Siero), 204 pp.
- Halfpenny, J.C., 1998. *Scats and Tracks of the Rocky Mountains*. Falcon, Publishing Inc, Helena, Montana, 145 pp.
- Haubold, H., 1984. *Saurierfährten*, second ed. A. Ziemsen Verlag, Wittenberg Lutherstadt, 231 pp.
- Hunt, A.P., Lucas, S.G., 2005. Tetrapod Ichnofacies and their utility in the Paleozoic. *Alabama Paleontological Society Monograph* 1, 113–119.
- Hunt, A.P., Lucas, S.G., 2007a. Tetrapod Ichnofacies: a new paradigm. *Ichnos* 59–68.
- Hunt, A.P., Lucas, S.G., 2007b. A new tetrapod ichnogenus from the Upper Triassic of New Mexico with notes on the ichnotaxonomy of *Rhynchosauroides*. *New Mexico Museum of Natural History and Science, Bulletin* 41, 71–76.
- ICZN, 1999. *International Code of Zoological Nomenclature*, fourth ed. International Trust for Zoological Nomenclature, London, 306 pp.
- Jwa, Y.-J., Lee, Y.I., Orihashi, Y., 2009. Eruption age of the Kusandong Tuff in the Cretaceous Gyeongsang Basin, Korea. *Geosciences Journal* 13, 265–273.
- Kang, H.C., Paik, I.S., 2013. Review on the geological ages of the formations in the Gyeongsang Basin, Korea. *Journal of the Geological Society of Korea* 49, 17–29 (in Korean with English abstract).
- Kim, B.K., 1969. A study of several sole marks in the Haman Formation. *Journal of the Geological Society of Korea* 5, 243–258.
- Kim, J.Y., Lockley, M.G., 2012. New sauropod tracks (*Brontopodus pentadactylus* ichnosp. nov.) from the Early Cretaceous Haman Formation of Jinju area, Korea: implications for sauropods manus morphology. *Ichnos* 19, 84–92.
- Kim, J.Y., Lockley, M.G., 2016. First report of turtle tracks from the Lower Cretaceous of Korea. *Cretaceous Research* 64, 1–6.
- Kim, J.Y., Kim, S.H., Kim, K.S., Lockley, M.G., 2006. The oldest record of webbed bird and pterosaur tracks from South Korea (Cretaceous Haman Formation, Changseon and Sinsu Islands): more evidence of high avian diversity in East Asia. *Cretaceous Research* 27, 56–69.
- Kim, J.-Y., Kim, K.S., Lockley, M.G., Yang, S.Y., Seo, S.J., Choi, H.I., Lim, J.D., 2008. New Didactyl Dinosaur footprints (*Dromaeosauripus hamanensis* ichnogen. et ichnosp. nov.) from the Early Cretaceous Haman Formation, south coast of Korea. *Palaeogeography, Palaeoclimatology, Palaeoecology* 262, 72–78.
- Kim, J.-S., Cho, H., Son, M., Sohn, Y.K., 2011. Geological age of the Gyeongsang Supergroup. In: 2011 Fall Joint Annual Conference of The Geological Societies in Korea (Abstract), Jeju, October 26–29, 20 pp. (in Korean).
- Kim, K.S., Lockley, M.G., Kim, J.Y., Seo, S.J., 2012a. The smallest dinosaur tracks in the world: occurrence and significance of *Minisauripus* from East Asia. *Ichnos* 19, 66–74.
- Kim, J.Y., Lockley, M.G., Seo, S.J., Kim, K.S., Kim, S.H., Baek, K.S., 2012b. A paradise of Mesozoic birds: the world's richest and most diverse Cretaceous bird track assemblage from the Early Cretaceous Haman Formation of the Gajin Tracksite, Jinju, Korea. *Ichnos* 19, 28–42.
- Kim, J.Y., Lockley, M.G., Kim, K.S., Seo, S.J., Lim, J.D., 2012c. Enigmatic giant pterosaur tracks and associated ichnofauna from the Cretaceous of Korea: implication for the bipedal locomotion of pterosaurs. *Ichnos* 19, 50–65.
- Kim, K.S., Seo, S.J., Kang, S.H., Choi, Y.K., Choi, J.W., Shin, D.H., Kim, J.H., Yoo, J.S., Bae, S.-I., Kim, N.J., 2015. A report on attendance audit of fossil heritage in the neighborhood facilities site construction of Sangchon-ri, Jinseong-myeon, Jinju, Gyeongnam, Korea. *Korea Geoheritage Research Center*, 94 pp. (in Korean).
- Kubo, T., 2010. Extant lizard tracks: variation and implications for paleoichnology. *Ichnos* 17, 187–196.
- Leonardi, G., 1987. *Glossary and Manual of tetrapod Footprint Paleichnology*. Dipartimento nazionale de Producao Mineral, Brasilia, 75 pp.

- Li, R., Lockley, M.G., Makovicky, P., Matsukawa, M., Norell, M., Harris, J., 2008. Behavioral and faunal implications of deinonychosaurian trackways from the Lower Cretaceous of China. *Naturwissenschaften* 95, 185–191.
- Lim, J.D., Zhou, Z., Martin, L.D., Baek, K.S., Yang, S.Y., 2000. The oldest known tracks of web-footed birds from the Lower Cretaceous of South Korea. *Naturwissenschaften* 87, 256–259.
- Lim, J.D., Martin, L.D., Zhou, Z., Baek, K.S., Yang, S.Y., 2002. The significance of Early Cretaceous bird tracks. In: Zhou, Z., Zhang, F. (Eds.), *Proceedings of the Fifth Symposium of the Society of Avian Paleontology and Evolution*, p. 157.
- Lim, J.D., Kong, D.Y., Kim, K.S., Kim, T.H., 2010. New dinosaur tracksite and unusual theropod footprints from the Cretaceous of Korea. In: *Program and Abstracts of 70th Anniversary Meeting Journal of Vertebrate Paleontology*, 122A.
- Lockley, M.G., 1998. The vertebrate track record. *Nature* 396, 429–432.
- Lockley, M.G., Hunt, A.P., 1995. *Dinosaur Tracks and Other Fossil Footprints of the Western United States*. Columbia University Press, 338 pp.
- Lockley, M.G., Houck, K., Yang, S.-Y., Matsukawa, M., Lim, S.-K., 2006. Dinosaur dominated footprint assemblages from the Cretaceous Jindong Formation, Hallayo Haesang National Park, Goseong County, South Korea: evidence and implications. *Cretaceous Research* 27, 70–101.
- Lockley, M.G., Kim, S.H., Kim, J.Y., Kim, K.S., Matsukawa, M., Li, R., Li, J., Yang, S.Y., 2008. *Minisauripus*—the track of a diminutive dinosaur from the Cretaceous of China and Korea: Implications for stratigraphic correlation and theropod foot morphodynamics. *Cretaceous Research* 29, 115–130.
- Lockley, M.G., Huh, M., Kim, J.-Y., Lim, J.-D., Kim, K.-S., 2012. Recent advances in Korean vertebrate ichnology: the KCDC comes of age. *Ichnos* 19, 1–5.
- Lucas, S.G., 2007. Tetrapod footprint biostratigraphy and biochronology. *Ichnos* 14, 5–38.
- Maidwell, F.T., 1911. Notes on footprints from the Keuper of Runcorn Hill. *Proceedings of the Liverpool Geological Society* 11, 140–152.
- Melchor, R.N., de Valais, S., 2006. A review of Triassic tetrapod track assemblages from South America. *Palaeontology* 49, 355–379.
- Moon, H.W., Kim, K.S., 2013. Paleoeological diversity of vertebrate trace fossils from the Gain-ri tracksite, Namhae County, Gyeongnam, Korea. In: *Proceedings of Fall Meeting of the Korean Earth Science Society*, pp. 174–175 (in Korean).
- Murie, O., 1974. *A Field Guide to Animal Tracks*, second ed. Houghton Mifflin Co., Boston. 375 pp.
- Norrel, M.A., Gao, J., Conrad, J., 2007. A new Platynotan Lizard (Diapsida: Squamata) from the late Cretaceous Gobi Desert (Omnogov), Mongolia. *American Museum Novitates* 3605, 1–22.
- Nydam, R.L., Voci, G.E., 2007. Teiid-Like Scincomorphan Lizards from the Late Cretaceous (Campanian) of Southern Utah. *Journal of Herpetology* 41, 211–219.
- Padian, K., Olsen, P.E., 1984. Footprints of the Komodo dragon and the trackways of fossil reptiles. *Copeia* 1984, 662–671.
- Padian, K., Li, C., Pchelnikova, J., 2010. The trackmaker of *Apatopus* (Late Triassic North America) implications for the evolution of archosaur stance and gait. *Paleontology* 53, 175–189.
- Park, H.D., Kim, K.S., Lim, J.D., Kim, H.D., 2016. A preliminary study on crocodyle tracks from the Cretaceous Jinju Formation of Jinju City, Gyeongnam. In: Kim, K.S., Kim, D.H., Lim, J.D. (Eds.), *Spring Meeting of the Korean Earth Science Society and Gyeongnam Goseong International Symposium*, Gyeongnam Educational Welfare Center April 7-8th 2016, p. 143 (in Korean).
- Peabody, F.E., 1955. Taxonomy and the footprints of Tetrapods. *Journal Paleontology* 29, 915–918.
- Sarjeant, W.A.S., 1989. 'Ten Paleochronological Commandments': a standardized procedure for the description of fossil vertebrate footprints. In: Gillette, D.D., Lockley, M.G. (Eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, pp. 369–370.
- Silva, R.C., Ferigolo, J., Carvalho, I.S., Fernandes, A.C.S., 2008. Lacertoid footprints from the Upper Triassic (Santa Maria Formation) of Southern Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology* 262, 140–156.
- Son, M.J., Kim, K.S., Lim, J.D., Kim, J.M., Ha, S.W., Choi, J.W., 2014. Pterosaur tracks from Jinseong-myeon, Jinju, Gyeongsangnamdo, Korea. In: *Proceedings of Fall Meeting of the Korean Earth Science Society*, p. 94 (in Korean).
- Stuart, C., Stuart, T., 2000. *A Field Guide to the Tracks and Signs of Southern and East African Wildlife*, third ed. Struik Publishers, Cape Town. 310 pp.
- Valentini, M., Conti, M.A., Mariotti, N., 2007. Lacertoid footprints of the Upper Permian Arenaria di Val Gardena Formation (Northern Italy). *Ichnos* 14, 193–218.
- Xu, L., Wu, X., Junchang, L., Jia, S., Zhang, J., Pu, H., Zhang, X., 2014. A New Lizard (Lepidosauria: Squamata) from the Upper Cretaceous of Henan, China. *Acta Geologica Sinica (English Edition)* 88 (4), 1041–1050.
- Yang, S.Y., 2015. Study history and research ethics of the dinosaur, pterosaur and bird tracks from Korea. *Journal of the Geological Society of Korea* 51, 127–140.