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Asianopodus-type footprints from the Hekou Group of Honggu District, Lanzhou City, Gansu, China and the "heel" of large theropod tracks

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Abstract

An increasing number of dinosaur tracksites have been reported from the Cretaceous Hekou Group deposits of the Lanzhou-Minhe Basin in the Gansu Province region. These include small sites such as the Huazhuang tracksite, from the Honggu District reported here, the Zhongpu tracksite with multiple track levels but few well-preserved tracks, other small tracksites currently under investigation, and the large and diverse Liujixia National Dinosaur Geopark site at Yanguoxia, where intensive study is ongoing. Collectively these sites reveal that ichnofaunas in the Hekou Group are widespread and diverse. The Huazhuang tracksite yields a small assemblage of moderately well-preserved theropod tracks assigned to *Asianopodus*. This is the first report of *Asianopodus* from the Hekou Group. Huazhuang *Asianopodus* belongs to the *Eubrontes* morphotype. The large theropod tracks from Lanzhou-Minhe Basin were left by large theropod trackmakers with the same general foot morphology. The specimens are described in detail and compared with other theropod track morphotypes from the Lower Cretaceous of China and elsewhere. In general, although the metatarsophalangeal pads of some Jurassic *Eubrontes*-type tracks are aligned with the axis of digit III, this feature appears most common in the Early Cretaceous theropod (*Eubrontes*-type) tracks.

Keywords: Theropod tracks; *Asianopodus*; *Eubrontes*; Hekou Group; Lower Cretaceous; Honggu District

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1. Introduction

There are a growing number of dinosaur tracksites known from the Hekou Group in the Lanzhou-Minhe Basin in Gansu Province. The best known is the Liujixia National Dinosaur Geopark located at Yanguoxia. As the largest site in the region, it is very important and it is already established that the geopark's dinosaur–pterosaur track assemblages are high in diversity, yielding several type specimens (Du et al., 2002; Peng et al., 2004; Zhang et al., 2006; Xing et al., 2013a). The park is already a focal point for Mesozoic tracks research in western China and all of Asia. Since 2012, a team led by the first author of this paper has been working to prepare and study these tracks, as well as those found at other smaller sites in the Lanzhou-Minhe Basin, for example at the Zhongpu locality (Xing et al., in press). These and other newly discovered tracksites are also being described and will be published elsewhere.

The first record of dinosaur tracks in the Lanzhou-Minhe Basin came in July, 1998, when researchers from China University of Geosciences (Wuhan), the Regional Investigation Team of Gansu Province discovered tracks in the Early Cretaceous Huazhuang area of Lanzhou City (Cai et al., 1999a) (Fig. 1). This discovery paved the way for the later discoveries of abundant dinosaur tracks at Yanguoxia (Du et al., 2002). The tracks at

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Fig. 1. Geographic position of the Huazhuang dinosaur footprint locality (footprint icon). There are at least four tracksite areas in the Lanzhou-Minhe Basin: 1, Huazhuang tracksite (this study); 2, Yanguoxia tracksites area, including at least 11 exposed tracksites, and six tracksites that are covered; 3, Guanshan tracksites area, including at least three exposed tracksites. 4, Zhongpu tracksites area, including at least five exposed tracksites.

the Huazhuang area were later collected by China University of Geosciences (Wuhan), and stored at the Yifu Museum. Cai et al. (1999a) made a brief description on the Huangzhuang tracks, but without detailed morphological analysis. Herein we offer a more detailed account of these specimens.

2. Geological setting

The Lanzhou-Minhe Basin is situated on the boundary of Gansu Province and Qinghai Province, and encompasses an area of 11 300 km^2. The basin is a fault basin that developed on the Middle Qilian Mountains uplift zone. The red siliciclastic rocks of this basin with single lithology and considerable thickness are classified as the Hekou Group (Gansu Provincial Bureau of Geology and Mineral Resources, 1997), which is Early Cretaceous in age (Tang et al., 2008). The Hekou Group is divided into the Zhujiatai, Yanguoxia, Honggucheng, and Huazhuang Formations (Cai et al., 1999b, 2000, 2002), and into eight informal formation-level units (Zhang et al., 2003). The dinosaur tracks are known from the gray or gray-green fine sandstone of the No. 6 informal formation-level unit (Zhang et al., 2003) (Fig. 2). These fine sandstones have planar cross bedding, which may indicate a lakeshore environment (Cai et al., 2001; Chen, 2013).

The age of the Tianjialou Hekou Group is controversial. Sporopollen assemblages from the Hekou Group were interpreted as being of Barremian–Aptian (Yu et al., 1982). Based on regional ostracod successions of the Early Cretaceous East Asia the age of the Hekou Group was considered to be Barremian (Hayashi, 2006). Tang et al. (2008) considered the age of the Hekou Group to be 143–109 Ma, on the basis of the sedimentary facies and susceptibility of rocks in the Lanzhou-Minhe Basin.

3. Systematic ichnology

Saurischia Seeley, 1888
Theropoda Marsh, 1881
Asianopodus Matsukawa, Shibata, Koarai and Lockley, 2005

Asianopodus isp.
(Figs. 3, 4)

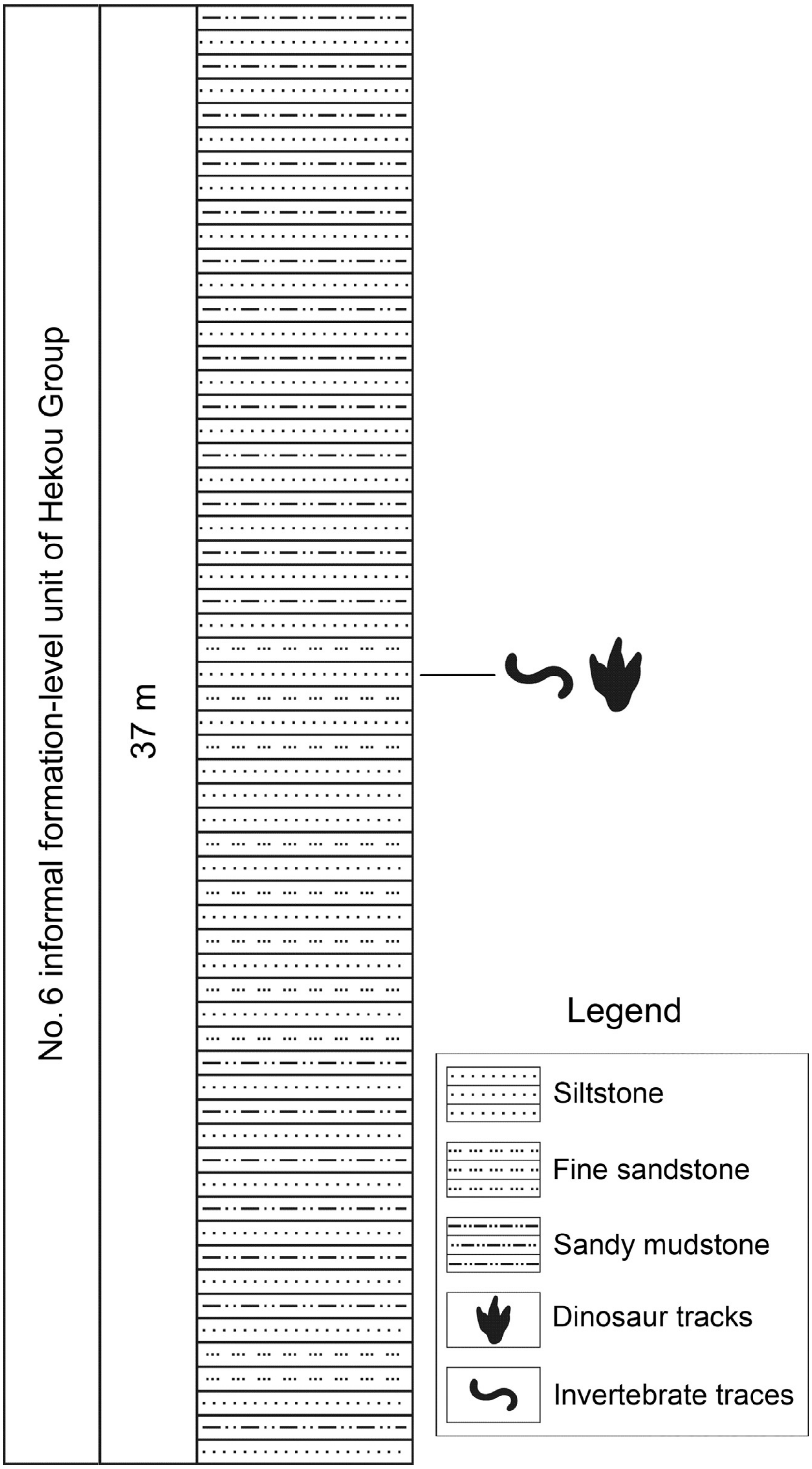

Fig. 2. Stratigraphic section of the No. 6 informal formation-level unit of Hekou Group at the Huazhuang track locality (emended from Cai et al., 2001).

Material. Three complete and one incomplete natural molds found on a single slab from the Huazhuang tracksite are cataloged as HZ.1a–d (Figs. 3, 4; Table 1). The original tracks are housed and displayed in the Yifu Museum at China University of Geosciences (Wuhan).

Locality and horizon. No. 6 informal formation-level unit, Hekou Group, Lower Cretaceous. Huazhuang tracksite, Lanzhou City, Gansu Province, China.

Description. The tracks are well preserved as natural molds (concave epireliefs) showing typical tridactyl, theropod pad

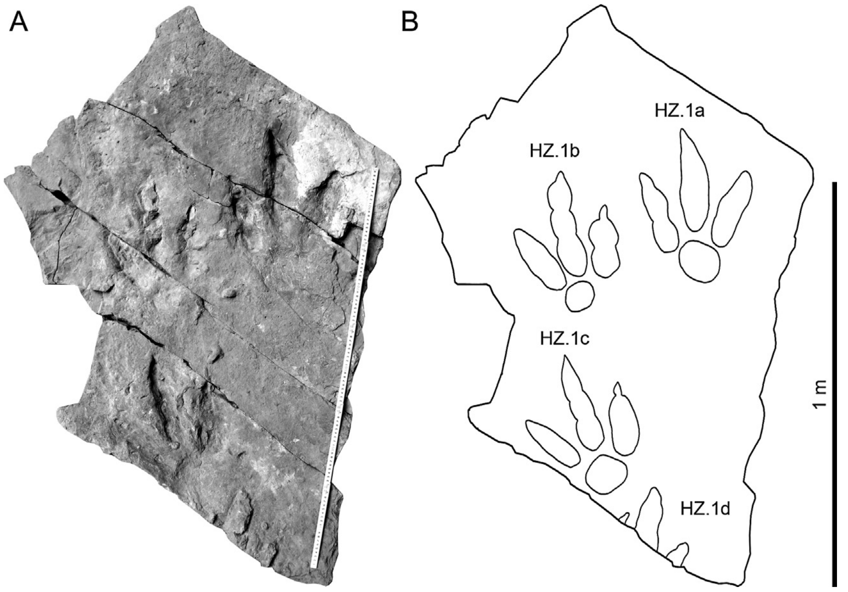

Fig. 3. Theropod tracks from the Huazhuang tracksite. (A) and (B) overview with photograph and interpretative outline drawing.

Table 1
Measurements (in cm) of the theropod tracks from the Huazhuang tracksite.

Number	L/R	ML	MW	D	LD II	LD III	LD IV	II–III	III–IV	II–IV	L/W	M
HZ.1a	R	39.0	26.5	4.0	20.5	26.5	31.0	22°	28°	50°	1.5	0.43
HZ.1b	L	35.5	24.5	3.0	19.0	25.5	28.0	21°	32°	53°	1.4	0.52
HZ.1c	L	36.5	27.0	2.6	19.0	24.5	29.0	22°	31°	53°	1.4	0.49
Mean	–	37.0	26.0	3.2	19.5	25.5	29.3	22°	30°	52°	1.4	0.48

Abbreviations: L/R: left/right; ML: maximum length; MW: maximum width; D: maximum depth; LD II: length of digit II; LD III: length of digit III; LD IV: length of digit IV; II–III: angle between digits II and III; III–IV: angle between digits III and IV; II–IV: angle between digits II and IV; L/W: Maximum length/Maximum width; M: mesaxony (length/width ratio for the anterior triangle).

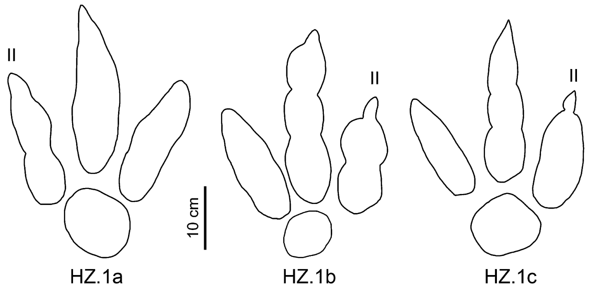

Fig. 4. Interpretative outline drawing of Huazhuang theropod tracks.

configurations, with 2 and 3 digital pads corresponding to digits II and III respectively, and a typical trace of digit IV with less clearly defined digital pads. Distal claw traces are also clearly visible. The average length of the Huazhuang tracks is 37 cm, the average length/width ratio is 1.4, and the average divarication angle is 52° between digits II and IV.

HZ.1a is the best preserved, with digit III being the longest and directed anteriorly, with medially rotated distal claw trace. The claw marks of digit II and digit III are sharp, whereas the claw mark of digit IV appears blunt. The metatarsophalangeal pad is located axially posterior to the axis of digit III and is well-developed and sub-round. The heel area, comprising the proximal area of these digitigrade tridactyl footprints, represents the metatarsophalangeal pad area for all three digits, and constitutes 27–32% of the footprint length. Digit II has two digit pads. Digit III appears to have coalesced pads. The phalangeal pads of digit IV are also coalesced and less distinct. The divarication angle between digit II and digit IV is 50° and the divarication angle between digit II and digit III (22°) is less than between digit III and digit IV (28°).

HZ.1b–d are generally consistent with HZ.1a in morphology. HZ.1b is the smallest but the morphology is quite diagnostic. Digit II is well impressed with two phalangeal pads. The distal part of digit III of HZ.1b is partly filled with sediment, but clearly shows three digital pad traces. Digit IV is shallow and also partly infilled, and shows a gap between the anterior part and the metatarsophalangeal pad area. HZ.1c also shows two slightly differentiated digital pad traces on digit II. Digit III clearly shows three digital pads traced on with no obscuring infill. The traces of digits II and IV appear coalesced, probably due to imperfect preservation. HZ.1d consists only of the second phalangeal pad of digit II, part of digit III, and the claw mark of digit IV, all still filled with sediment from the overlying layer. Based on their relative positions, HZ.1d (left) and HZ.1a (right) might constitute a single step, 90 cm long.

Discussion. HZ.1a is slightly deeper than the other tracks (see Table 1), and the rounded claw mark of digit IV suggests that the ungual penetrated deeper into the substrate and left a blunt impression at the surface (Wilson et al., 2009).

HZ.1a–c have developed metatarsophalangeal pads that align with the axis of digit III, a diagnostically useful trait. In general, the Huazhuang theropod tracks and the Zhongpu theropod tracks (Xing et al., in press) resemble the Yanguoxia large theropod tracks (Zhang et al., 2006, morphotype 1). The former are tridactyl tracks, with an average length of 41.9 cm and an average divarication angle of 52°, and the latter are tridactyl tracks, with an average length of 32 cm and an average divarication angle of 61°. Both the Zhongpu and the Yanguoxia theropod tracks have developed metatarsophalangeal pads that are close to the axis of digit III and lean slightly toward digit IV.

The average length:width (L/W) ratio of the anterior triangle of HZ tracks is 0.48 ($N = 3$), which suggests they are weakly mesaxonic tracks and belong to the *Eubrontes* morphotype (Lockley, 2009). This value is close to that of Zhongpu theropod tracks (0.47, $N = 3$) and to the value of the Yanguoxia large theropod tracks (0.52, $N = 2$). The large theropod tracks at all three of these sites were left by large theropod trackmakers with the same general foot morphology that is evidently typical of the Lower Cretaceous Lanzhou-Minhe Basin.

The Huazhuang theropod tracks (Fig. 5A) resemble *Asianopodus pulvinicalx* (Matsukawa et al., 2005) (Fig. 5B), both having distinct bulbous heel impression (Matsukawa et al., 2005). Another possible shared characteristic is the heel impression being separated from the three digits, but this characteristic may depend to some degree on the hardness of the substrate, or they are shallow undertracks (Piñuela, 2012). However, *Asianopodus pulvinicalx* is relatively small, about 78% of the length of the Huazhuang specimens. Li et al. (2011) described *Asianopodus robustus* from Inner Mongolia (Fig. 5C). *A. robustus* is larger than *A. pulvinicalx*, but shows few other significant differences from *Chapus lockleyi* (Li et al., 2006) (Fig. 5D, E), except for a less well defined heel pad and overall size (the type of *C. lockleyi* is larger than *A. robustus*). *Chapus lockleyi* has a more or less distinct bulbous heel impression like *Asianopdus*, except that it is slightly more strongly connected to the proximal end of the trace of digit IV. *A. pulvinicalx* and *A. robustus* have a distinct and short digit III, which differs substantially from the longer digit III of the Huazhuang specimens. However, given the insufficiency of the specimens, the Huazhuang theropod tracks are temporarily assigned to *Asianopodus* isp., which are the large *Asianopodus* type tracks.

4. The "heel" of large theropod tracks

Tridactyl theropod tracks have long been controversial in ichnotaxonomy. Some tracks with similar morphology are assigned to different ichnogenera. When Lockley et al. (2013) reviewed Chinese tetrapod tracks, almost all named morphotypes ("types") were re-assigned to better-known tracks with historical priority. Simple observation of modern tracks as well as recent published studies indicates that, at the same tracksite, wet and slippery sediments may lead to apparent significant morphological differences among tracks made by the same trackmaker, or those assigned to the same ichnogenus (ichnotaxon) at paleosites (Marty et al., 2009; Xing et al., 2014a). The morphology of the "heel" (metatarsophalangeal pad of digit IV) is an important characteristic in theropod tracks. "Heel" refers mainly to the metatarsophalangeal pad of digit IV. In general larger animals appear to have better developed heel pads (Lockley, 2007). Thus a well-developed heel pad is diagnostic of *Asianopodus*, but not smaller theropod tracks like *Grallator* (Olsen et al., 1998). Likewise a large heel pad is diagnostic of 28 cm long *Dromaeopodus* (Li et al., 2007) but not 10–11 cm long *Velociraptorichus* (Lockley et al., in press).

The Lower Cretaceous large theropod tracks yielded from the Huazhuang area, even those from the Lanzhou-Minhe Basin (Zhang et al., 2006, morphotype 1), cannot be considered similar, in morphology, to *Eubrontes*: compare Fig. 5A with 5F and 5G, which as noted above more closely resemble *Asianopodus*, based on the comparatively wide divarication angle and the metatarsophalangeal pad being located at the axis of the track.

The typical Jurassic *Eubrontes*-type tracks, exemplified by the type specimen of *Eubrontes giganteus* from the Lower Jurassic of Connecticut, USA (Fig. 5F) (Weems, 1992; Lockley, 2009), are variable as shown by comparing them with other Lower Jurassic examples from Connecticut (Fig. 5G) (Ishigaki and Fujisakai, 1989).

Eubrontes-type tracks are reported from the Cretaceous, such as *Eubrontes* (?) *glenrosensis* (Fig. 5H) from Lower Cretaceous of Texas (Shuler, 1935; Adams et al., 2010; Farlow et al., 2012), but they have not been described in detail, and the type has no well-defined digital pad traces (Fig. 5C). Chinese large theropod tracks that could be considered *Eubrontes*-like, such as *Chapus lockleyi* (Li et al., 2006) and *Asianopodus robustus* (Li et al., 2011) from the Lower Cretaceous of Inner Mongolia, and possibly cf. *Therangospodus* from the Lower Cretaceous of Shandong (Fig. 5I) (Xing et al., 2013a), show more or less well-developed metatarsophalangeal pads aligned with the axis of digit III. Some specimens from Japan and Thailand also show this feature (Matsukawa et al., 2005). In general, although the metatarsophalangeal pads of some Jurassic *Eubrontes*-type tracks are aligned with the axis of digit III, this feature appears most common in the Early Cretaceous theropod (*Eubrontes*-type) tracks. The trend toward larger axial heel impressions is also exhibited in the Jurassic and the Cretaceous *Jialingpus* (*Grallator*-type) (Xing et al., 2014b).

Numerous large theropod tracks were discovered in the Lower Jurassic of Poland (see Gierliński et al., 2001, 2004; Niedźwiedzki, 2006, 2011; Niedźwiedzki and Remin, 2008) in the deposits dated as lower Hettangian, upper Hettangian, and Pliensbachian. The largest specimens are about 55–60 cm long and show rather unusual morphology as compared with the typical Early Jurassic theropod ichnotaxa (e.g., *Anchisauripus*, *Eubrontes*) hitherto established. Tracks are about 10–20 cm longer than the largest specimens of the theropod track of *Eubrontes giganteus* Hitchcock, 1845 from the Early Jurassic ichnofauna of the Newark Supergroup, USA (Olsen et al., 1998) and *Kayentapus soltykovensis* (Gierliński, 1991) from the Early Jurassic of the Holy Cross Mountains, Poland (Gierliński, 1991;

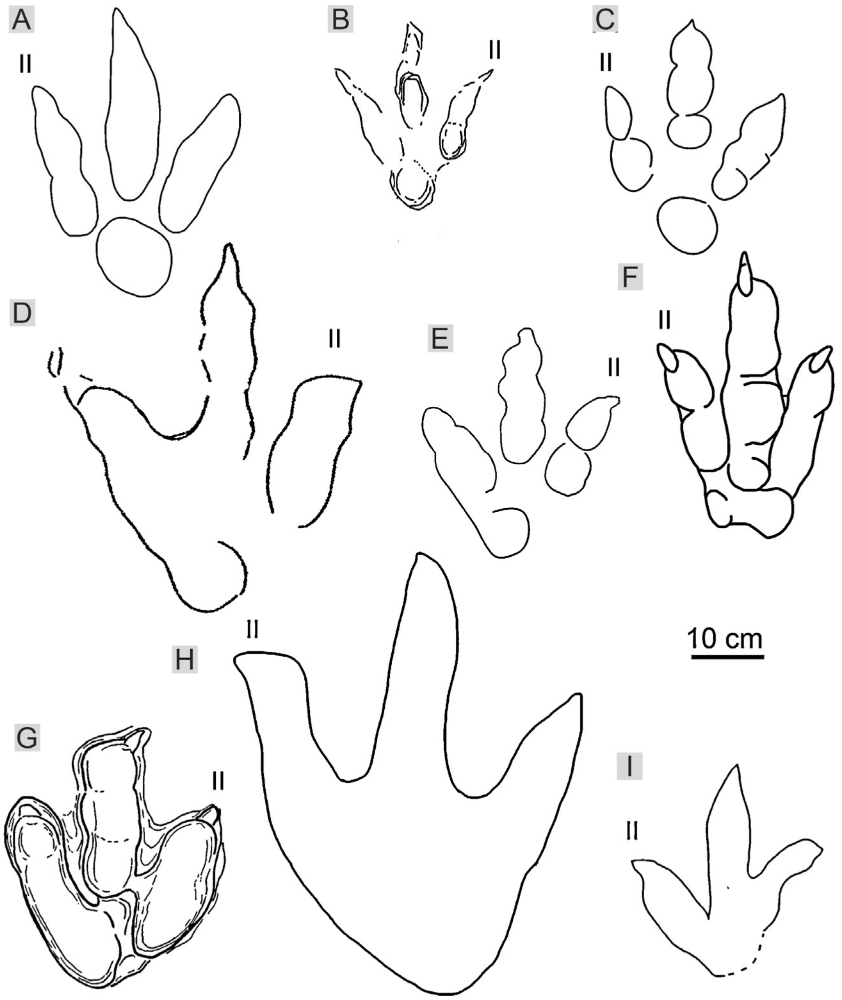

Fig. 5. *Eubrontes*-type tracks from Jurassic and Cretaceous. (A) Huazhuang specimen HZ.1a (this study); (B) *Asianopodus pulvinicalx*, Lower Cretaceous, Japan (Matsukawa et al., 2005); (C) *Asianopodus robustus*, Lower Cretaceous, Inner Mongolia, China (Li et al., 2011); (D) the type specimen of *Chapus lockleyi*, Lower Cretaceous, Inner Mongolia, China (based on Li et al., 2006, pl. I-2, by Lockley MG); (E) referred specimen of *Chapus lockleyi*, Lower Cretaceous, Inner Mongolia, China (Li et al., 2011); (F) *Eubrontes giganteus* type specimen, Lower Jurassic, Connecticut, USA (Weems, 1992); (G) *Eubrontes*, Lower Jurassic, Connecticut, USA (Ishigaki and Fujisakai, 1989); (H) *Eubrontes* (?) *glenrosensis*, Lower Cretaceous, Texas, USA (Adams et al., 2010); (I) cf. *Therangospodus*, Lower Cretaceous, Shandong, China (Xing et al., 2013a).

Gierliński et al., 2004; Lockley et al., 2011). All gigantic Polish theropod tracks have a relatively large heel area, larger than in *Eubrontes*, and are more similar in this feature to large theropod tracks from the Late Jurassic and Cretaceous.

The heel area constitutes 32–35% of the footprint length in the Lower Jurassic specimens from Poland. In *Eubrontes giganteus*, the heel area makes up only 27–29% (e.g., Lockley and Mickelson, 1997; Olsen et al., 1998; Gierliński et al., 2001, 2004). Interestingly, tracks with such large and spread metatarsophalangeal pads resemble that of the Middle Jurassic (Bathonian) Ardley tracks from the Oxfordshire, UK (Day et al., 2004), the Late Jurassic tracks known as ichnogenus *Megalosauripus* Lessertisseur, 1955 (Lockley et al., 1996, 1998a), *Eubrontes glenrosensis* Shuler, 1935 from the Lower Cretaceous of Texas (Shuler, 1935; Adams et al., 2010), the giant theropod track from the Upper Cretaceous coal mine in Utah, USA (Peterson, 1924; track named as *Tyrannosauropus petersoni* Haubold, 1971), track from the Raton Formation, near Cimarron, New Mexico, USA and named as *Tyrannosauripus pillmorei* (see Lockley and Hunt, 1994) (Fig. 6) and the footprints described in this paper (Figs. 3 and 4).

Among the more advanced theropods, the tetanurans, metatarsals II, III, and IV are generally more packed together than in the earlier coelophysoids and Jurassic-Cretaceous ceratosaurians (Tykoski and Rowe, 2004; Holtz et al., 2004). On the other hand, the proximal phalanx of digit III (phalanx III1) often became relatively longer. Thus, a triangular space between the distal ends of metatarsals II, III, and IV was compressed laterally, and then the pad beneath the metatarsophalangeal joint of digit IV might be located relatively farther posteriorly, whereas the elongation of phalanx III1 has replaced a pad beneath joint of phalanx III1 and III2 (usually the most proximal pad of digit III) anteriorly (Wright, 2004). This is probably reflected by a very large metatarsophalangeal area (heel area), which is observed in many post-Early Jurassic theropod footprints (Gierliński et al., 2001).

Given such discoveries as the Early Jurassic *Cryolophosaurus* Hammer and Hickerson, 1994 from Antarctica

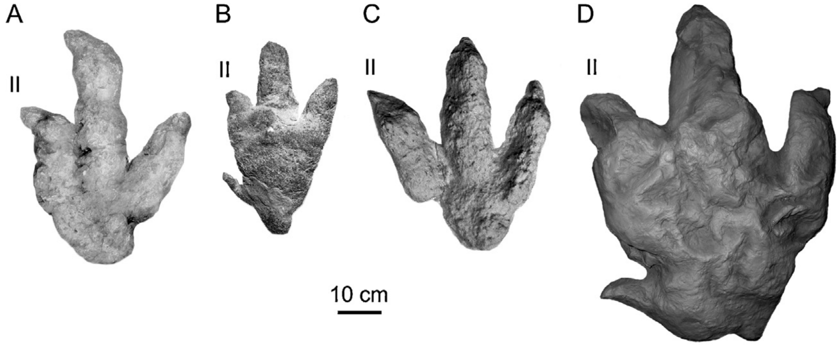

Fig. 6. Jurassic and Cretaceous theropod tracks with a large heel area. (A) cf. *Megalosauripus* isp. from the Early Jurassic of Poland (adapted from Gierliński et al., 2001); (B) *Megalosauripus* isp. from the Late Jurassic site of Cabo Mondego in Portugal (adapted from Lockley et al., 1998a); (C) *Eubrontes* (?) *glenrosensis* Shuler, 1935, from the Lower Cretaceous of the West Verde Creek, Texas. (D) *Tyrannosauripus pillmorei* Lockley and Hunt, 1994 from the Raton Formation, near Cimarron, New Mexico, USA.

and the Middle Jurassic *Monolophosaurus* Zhao and Currie, 1993 from China, the occurrence of large or gigantic theropod tracks (probably tracks of early tetanurans) before the Middle–Late Jurassic is not a surprise. However, it is worth noting that large tracks (more than 40 cm long) are relatively rare in rocks older than the Upper Jurassic, and there were only five sites with the pre-Oxfordian theropod tracks, which exceed half meter in length (Morales and Bulkley, 1996; Gierliński et al., 2001, 2004; Day et al., 2004; Niedźwiedzki, 2006; Niedźwiedzki and Remin, 2008).

Determined by the relation between the evolution of the theropod foot skeleton (metatarsus, phalanges) and coeval large-theropod tracks, the trackmaker of the Late Triassic–Early Jurassic *Kayentapus* is undoubtedly a middle to large-sized theropod. The type ichnospecies *K. hopii* from the Lower Jurassic Kayenta Formation was left probably by a dilophosaur trackmaker (Welles, 1971; Lockley et al., 2011). For *Kayentapus*, the considerably large divarication angle, three separated digits, and small-sized metatarsophalangeal pad correspond to the relatively loose metatarsus of a dilophosaur (see Welles, 1984, fig. 36). Similar tracks have been discovered in China, such as *Kayentapus wumaensis* and *Kayentapus jizhaishiensis* (Lockley et al., 2013).

Eubrontes type tracks are more robust than *Kayentapus*, and have been statistically differentiated by Weems (1992). However, due to the comparably smaller quantity of large-sized theropods from the Early Jurassic, these *Eubrontes* are difficult to correlate with specific trackmakers. Abundant *Eubrontes* tracks in the East Berlin Formation and Dinosaur State Park in Connecticut are exhibited with a large *Dilophosaurus* type (Farlow and Galton, 2003). *Eubrontes* has been yielded from the Early Jurassic in China as well (such as Li et al., 2010; Lockley et al., 2013). Meanwhile, abundant *Changpeipus* has been discovered in China (Xing et al., 2009). *Changpeipus* has been regarded as the sister ichnotaxon of *Eubrontes* (Lockley et al., 2013; Xing et al., 2014a). For these tracks, most metatarsophalangeal pads are not developed (see Lockley et al., 2013, fig. 2). *Changpeipus pareschequier* (Xing et al., 2009, 2014a) is probably an exception; however, the available sample size is seriously limited ($N = 2$).

The large Middle–Late Jurassic theropod tracks have abundant potential trackmakers, primarily allosauroids (such as *Allosaurus*, *Sinraptor*, *Yangchuanosaurus*) and torvosaurids (such as *Megalosaurus*). Usually these theropods have more developed and more robust metatarsus and phalanges, such as *Allosaurus fragilis* (Madsen, 1976) and *Torvosaurus tanneri* (Britt, 1991). North American *Eubrontes* and *Therangospodus–Megalosauripus* assemblages have developed metatarsophalangeal pads; however, the location is not at the axis of the track (Lockley et al., 1998a, 1998b). The metatarsophalangeal pads are not developed in the Middle Jurassic large theropod tracks of China, such as *Chongqingpus–Kayentapus* from Chongqing (Xing et al., 2013b); Late Jurassic *Therangospodus–Megalosauripus* assemblage has been discovered in China (Xing et al., 2011).

In Laurasia, some branches of the Carnosauria survived well beyond the Early Cretaceous, including allosauroids, carcharodontosaurids, and (though less common) spinosaurids. However, the skeletal remains of large Chinese theropods from this period are rare. The known material is incomplete; for example, the remains of *Kelmayisaurus petrolicus* (a basal carcharodontosaurid) include only the maxilla and the alveolus (Brusatte et al., 2012). The foot characteristics of theropods are largely conservative, and no significant changes in the morphology of metatarsals or phalanges occurred during this period in any of the major carnosaur linages (Currie and Carpenter, 2000). However, during this period, the metatarsophalangeal pads of large theropod tracks in North America and China are generally more robust (Fig. 5C–F). During the Late Jurassic–Cretaceous, the arctometatarsus (the proportionately slender metatarsals with metatarsal III “pinched out” proximally between II and IV, that makes the metatarsals further compact) (Holtz, 1994, 1995) appeared in coelurosaur theropods. Coelurosaur trackmakers are known to have left large metatarsophalangeal pads at the middle axis of digit III, such as *Tyrannosauripus* from Colorado, USA (Lockley and Hunt, 1994) and *Dromaeopodus* tracks from Junan, Shandong Province, China (Li et al., 2007). The arctometatarsus is reflected in the tracks of coelurosaurs because they have comparatively wide divarication angle and the metatarsophalangeal pad is located at the axis of the track (Wright, 2004).

The first tracks with a large heel area appear in the fossil record in the beginning of Jurassic (Hettangian) and are associated with relatively large or even gigantic theropod tracks. Probably the origin of large metatarsophalangeal pad is strictly connected with the emergence of large sized tetanuran theropods (Gierliński et al., 2001).

5. Conclusion

The material of *Asianopodus* presented in this paper indicates that footprints of large theropods from the Lower Cretaceous strata of the Hekou Group (Lanzhou-Minhe Basin) are comparable to well-known Early Jurassic ichnogenus *Eubrontes*. The stratigraphic and geographic distribution of the Jurassic and Cretaceous *Eubrontes*-like footprints offers promise of an improved understanding of large theropod evolution. The *Asianopodus* footprints from the Hekou Group show a relatively large metatarsophalangeal area. Such a large metatarsophalangeal area is usually observed in the large theropod footprints from the post-Lower Jurassic strata. The metatarsophalangeal pads of some Jurassic *Eubrontes*-type tracks are aligned with the axis of digit III and this feature appears most common in the Lower Cretaceous theropod (*Eubrontes*-type) tracks.

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