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Discovery of dinosaur footprints from the Lower Jurassic Lufeng Formation of Yunnan Province, China and new observations on *Changpeipus*

云南下侏罗统禄丰组恐龙足迹的发现和张北足迹属新观察

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Abstract:Herein described are two footprints that belong to the new ichnospecies *Changpeipus pareschequier* ichnosp. nov. from the Lower Jurassic Lufeng Formation near Yaozhan Village, Lufeng County, Yunnan Province, China. This is the first discovery of dinosaur footprints in the Lufeng Formation. The ichnogenus *Changpeipus* is revised after the re-study of its type specimens. Specimen IVPP V2472 2a, a supposed manus print that is part of the ichnogenoholotype of *Changpeipus carbonicus*, is re-studied herein and assessed as a pes print of a juvenile individual of the *Changpeipus carbonicus* track maker. *Changpeipus luanpingeris* is a junior synonym of *Changpeipus carbonicus*. *Changpeipus pareschequier* ichnosp. nov. resembles the ichnotaxon *Kayentapus*. Based on its characteristics, the footprints are presumably made by a member of the Coelophysoidea from the Lufeng Formation.

Key words: Lufeng County, Yunnan Province; Lower Jurassic Lufeng Formation; *Changpeipus; Kayentapus*

摘要:记述了云南省禄丰县腰站乡下侏罗统禄丰组2个恐龙足迹,命名了棋盘张北足迹(*Changpeipus pareschequier* ichnosp. nov.)一新种。这是在禄丰组中首次发现恐龙足迹化石,重新观察并修订了张北足迹一属的属征。滦平张北足迹(*Changpeipus luanpingeris*)应为石炭张北足迹(*Changpeipus carbonicus*)的亚成年个体,为同物异名。此前被认为是石炭张北足迹(*Changpeipus carbonicus*)前足迹的 IVPP V2472 2a,应为其未成年体的后足迹。张北足迹与卡岩塔足迹(*Kayentapus*)类似。综合种种特征,棋盘张北足迹(新种)的造迹恐龙很可能为禄丰组的腔骨龙类(Coelophysoidea)。

关键词:云南禄丰地区;下侏罗统禄丰组;张北足迹;卡岩塔足迹

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1 Introduction

Vertebrate fossils in the Lower Jurassic Lufeng Formation of the Lufeng Basin of Yunnan Province, which have been reported since the late 1930′s, placed an important role in the early career of the first Chinese dinosaur paleontologist, C. C. Young (Yang Zhongjian). In 1951, the vertebrate fauna from this unit was named the Lufeng Saurischian Fauna[1], and its fossils have been found in numerous places across Yunnan, including Lufeng, Yimen and Yuanmou. The dinosaur component of the Lufeng Saurischian Fauna comprises the prosauropods [2]*Lufengosaurus huenei*[3], *Lufengosaurus magnus*[4], *Yunnanosaurus huangi*[5] and "*Gyposaurus*" (*Anchisaurus*) *sinensis* [6-8], the basal sauropods *Chinshakiangosaurus chunghoensis*[7,9], *Jingshanosaurus xinwaensis*[10], *Kunmingosaurus wudingensis* [11] (nomen nudum), possibly "*Yunnanosaurus*" *robustus* [1], and an unnamed taxon[12], the theropods, *Megapnosaurus* sp.[13], "*Dilophosaurus*" *sinensis*[14] and possibly *Eshanosaurus deguchiianus*[15] (*Sinosaurus triassicus*[16] is a nomen dubium and *Lukousaurus yini*[16] is likely a crocodylomorph[13]), and the basal thyreophorans[17] *Tatisaurus oehleri* [18] and *Bienosaurus lufengensis* [19]. "*Dianchungosaurus lufengensis*[20]," a supposed ornithopod from the unit, is a chimera, with the holotype representing a crocodylomorph and the paratype an indeterminate prosauropod dinosaur[21]. Outside of Yunnan Province, the *Lufengosaurus* Fauna also occurs in the Red Bed of Gongxian, Weiyuan of the Sichuan Basin, also in Xizang and Guizhou province.

In early 2008, Wang Tao and the staff of The World Dinosaur Valley of Lufeng County reported two nonconsecutive dinosaur footprints in Yaozhan Village. This was the first discovery of dinosaur footprints in the Lower Lufeng Formation. Other tracks have been reported in the surrounding area, including *Lufengopus dongi*[22] in the Chuanjie Formation (formerly the Upper Lufeng Formation) and Xiyang dinosaur footprints[23-24] in the Fengjiahe Formation (Lower Jurassic).

2 Institutional abbreviations

BPV-FP=Beijing Natural History Museum, Beijing, China; GH = Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) field number; HGM=Henan Geological Museum, Zhengzhou, China; LDRC =Lufeng Dinosaur Research Center; IVPP= Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; ZLJ -ZQK =The World Dinosaur Valley Park, Lufeng County, Yunnan Province, China.

3 Geological setting

Bien named the exposed Red Bed in Lufeng Basin the Lufeng Series, and further divided it into Upper and Lower units[25]. Young determined the age of Red Bed to be Late Triassic based on the evolutionary "grades" of its vertebrate fossils [1]. In 1962, Sheng proposed an Early Jurassic age for the Lower Lufeng Formation and a Middle Jurassic age for the Upper Lufeng Formation[26]. In 1997, Zhang and Li mapped the position of Lao Changjing, Chuanjie, reporting the positions of dinosaur fossils in the lower part of Upper Lufeng Formation[27]. From 1999 to 2003, Fang and colleagues studied the stratigraphic section at Lao Changqing -Da Jianfeng in the Chuanjie Basin and restricted the name "Lufeng Formation" to what previously was the Lower Lufeng Formation and further divided it into Shawan and Zhangjia′ao members, and this opinion is followed here. Strata that had at various times been encompassed in the Upper Lufeng Formation were broken into the Chuanjie, Laoluocun, Madishan, and Anning formations[28].

The footprint fossils reported herein were discovered in a sage green siltstone opposite the Yu Tiaolou Restaurant at Zhuqingkou Reservoir, 2.2 kilometers southeast of Yaozhan Village (Fig.1). The sage green siltstone belongs to the Lufeng Formation (J_1lf). Chen et al.′s notes from 2004[29] provide the basis for the stratigraphic column in Figure 2.

4 Systematic ichnology

Changpeipus **Young, 1960**

Type ichnospecies

Changpeipus carbonicus Young, 1960 (Fig. 3)

Referred ichnospecies

Changpeipus bartholomaii Haubold, 1971
(nomen nudum)

Changpeipus luanpingeris Young, 1979

Changpeipus xuiana Lü et al., 2007

Holotype: IVPP V2472.2, IVPP V2472.2a, IVPP V2472.3, IVPP V2470, three natural molds on a slab from the Lower or Middle Jurassic of Liaoning, China.

Diagnosis: Medium-sized, tridactyl theropod tracks that lack manus and tail traces. Divarication angles between both digits II–III and III–IV greater than 25°. A metatarsophalangeal pad located more or less directly caudal to digit III. Digital pad areas increase toward the distal end of digit III. Digit IV projects farther cranially than digit II and exceeds digit II in length.

Description: The following features are characteristic of the type ichnospecies of *Changpeipus*, *C. carbonicus* (IVPP V2472.2, IVPP V2472.2a, IVPP V2472.3, IVPP V2470): claw impressions faint on middle digit; outline of track deltoid (= triangular); heel area triangular; heel pad clearly visible; digital pad formula x–2–3–3–x; and digit II impression distinctly shorter than digit IV impression. For IVPP V2472.2, the divarication between digits II–III is 25°, and between III–IV is 20°. For IVPP V2472.3, the same divarication angles are 25° and 40°, respectively. For IVPP V2470, they are 29° and 48°, respectively [30]. Thus, the known ranges for *C. carbonicus* are II–III 25–29° and III–IV 20–48°.

The vagary of the claw on digit III is almost certainly the result of a combination of the nature of the substrate and the style of locomotion that the track maker employed at the time the tracks were registered (as opposed to meaning that the track maker lacked a claw on digit III). The triangular shape and digital pad formula are typical of most theropod tracks and thus constitute poor diagnostic characters for the ichnotaxon. The triangular heel impression occurs only in IVPP V2472.2 and thus does not appear to characterize the ichnogenus. However, most tracks in the ichnogenoholotype possess a metatarsophalangeal pad, so this appears to be a genuine feature of the track maker. Metatarsophalangeal pads also occur in many *Grallator*-type and *Kayentapus*-type tracks. The greater degree of cranial projection of digit IV than digit II is maintained here as viable, but this requires more comparison with other ichnotaxa. Moreover, the digital pads of *C. carbonicus* increase in width towards distal ends of each digit (except for the claw impressions, which narrow again), especially in Digit III (Table 1).

For comparison to the new Lufeng specimens, the length and width of *C. carbonicus* were re-measured. The ratio of length/width for IVPP V2472.2 is 41 cm/20.2 cm = 2.03; for IVPP V2472.3, the ratio is 39.5 cm/25 cm = 1.58, and for IVPP V2470 (which has an incomplete heel area compared to the other two), the ratio is 29 cm/21 cm = 1.39. Thus, the known ratios for this ichnotaxon range from 1.58–2.03.

As the ichnogenoholotype, *Changpeipus carbonicus* exhibits all the aforementioned traits. Based on our reanalysis, *C. carbonicus* is further characterized (as an ichnospecies) by the following feature: digit II is wider than digit IV.

Changpeipus bartholomaii was erected for tracks from the Middle Jurassic Wallon Coal Measures of Australia, but has never received a formal description or diagnosis, and is therefore a nomen nudum[31].

Though smaller overall, the characteristics of *Changpeipus luanpingeris* (field number GH047, two footprints) are, according to Young's original description (p. 116), "basically the same as those of *C. carbonicus* with the exception of the angle between the three digits and heel area, which is 30°"[32]. We are uncertain exactly what Young meant by "the angle between the three digits and heel area" and thus cannot adequately comment on the validity or nature of

Fig. 1 Geographic map of the Zhuqingkou Reservoir dinosaur footprint locality (indicated by the footprint icon)(A) and the outcrop including the fossil locality (arrow)(B)

uncertain exactly what Young meant by "the angle between the three digits and heel area" and thus cannot adequately comment on the validity or nature of this character here. Digit II is the shortest, with a length of 80 mm, while digit III is the longest, with a length of 105 mm. Digit IV is 100 mm long. The tracks have incomplete heel areas, but have estimated lengths of 200 mm. Our remeasurements demonstrate their digit divarication angles as II–III 30° and III–IV 40°. Based on these differences, Young also took the difference in their age compared to *C. carbonicus* into consideration when erecting the new ichnospecies (*C. carbonicus* is Early to Middle Jurassic while *C. luanpingeris* is Late Jurassic [32]). But this is not necessary: generally speaking, the characteristics of *Changpeipus luanpingeris* are in accordance with those of *Chang-*

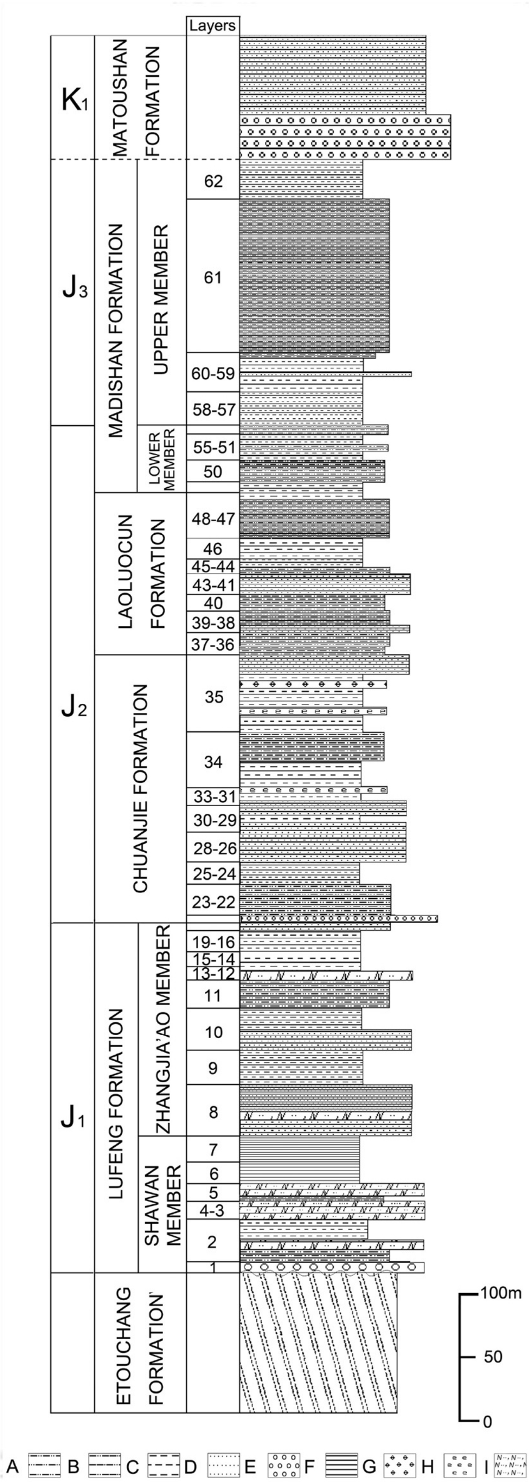


Fig. 2 Stratigraphic columns of the Jurassic strata of the Lufeng section (emended from Chen et al, 2004)

A—pelitic siltstone;B—sandy mudstone;C—mudstone; D—sandstone;E—conglomerate;F—shale;G—orthomicrite; H—orehomicrite containing fossils;I—arkose

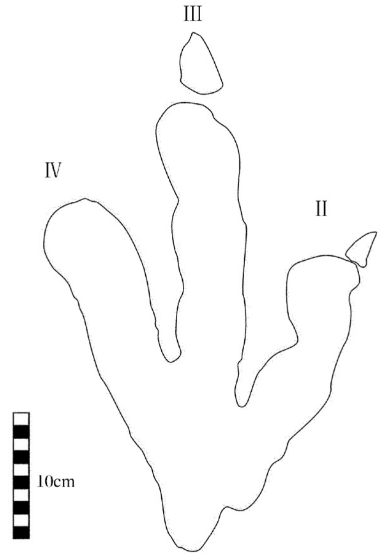


Fig. 3 Outline drawing of *Changpeipus carbonicus* (IVPP V2472.2)

Table 1 Measurements of digital pads of *Changpeipus carbonicus* (IVPP V2472.2)

Measurement*		length /mm	width /mm
Digit II	Pad 1	62.46	53.58
	Pad 2	67.16	64.17
Digit III	Pad 1	68.34	52.82
	Pad 2	62.33	56.84
	Pad 3	77.76	58.29
Digit IV	Pad 1	66.89	58.91
	Pad 2	79.97	54.51

note: *order of pads follows order of phalanges, from proximal to distal

peipus xuiana (HGM 41HIII−0098), is somewhat larger than either of the previous. Their length:width ratios are 1.9, within the range established by *C. carbonicus*. The divarications between digits are II−III 25° and III−IV 32°, again within the range of *C. carbonicus*. However, digit II is only slightly shorter than digit IV in *C. xuiana*, unlike the greater difference in *C. carbonicus*. Uniquely among *Changpeipus ichnospecies*, the distal part of the footprint possesses the imprint of a metatarsus[33], and for this reason a distinct ichnospecies is warranted. In other features, most characteristics of *Changpeipus xuiana* are in accordance with those of *Changpeipus carbonicus*.

Changpeipus pareschequier ichnosp. nov.

(Figs. 4,5 and Plate I)

Etymology: The ichnospecies name "*pareschequier*" from the French *par* "by" and *eschequier*, "chessboard" indicates that the discoverer found this fossil while collecting stone to make a Chinese chessboard.

Holotype: Two complete natural casts on a single slab housed at The World Dinosaur Valley Park. The tracks on the slab are cataloged individually as ZLJ-ZQK1 and ZLJ-ZQK2. A cast of the specimen is stored in the Lufeng Dinosaur Research Center, where it is cataloged as LDRC-v. x.1.

Type locality and horizon: Sage green siltstone of the Lufeng Formation (Lower Jurassic) opposite the Yu Tiaolou Restaurant at Zhuqingkou Reservoir, 2.2 kilometers southeast of Yaozhan Village.

Description: Both specimens (ZLJ-ZQK1 and ZLJ-ZQK2; Fig. 5) are natural casts. The footprints are tridactyl. In tridactyl or tetradactyl dinosaur tracks, the claws of digits II and IV point away from the axis of the foot while the claw of digit III is invariably bent inward toward the middle of the trackway [34]. Taking into account both Lull's claw angulation description and that natural track casts are the inverse of their natural mold counterparts, ZLJ-ZQK1 pertains to a right foot while ZLJ-ZQK2 is a left foot. ZLJ-ZQK2 is better preserved and provides the measurements in Table 2 and the basis for the following description.

The ratio of length/width of the footprint is 1.29. The imprints of a large, round metatarsophalangeal pad and phalangeal pads are clear. The metatarsophalangeal pad is an unusual feature for a theropod track; typically, non-avian theropod tracks lack any indication of such a feature (but exceptions exist, for example, tracks of *Dromaeopodus* [35]). The track and the track maker's mode of locomotion when the track was registered cannot be considered

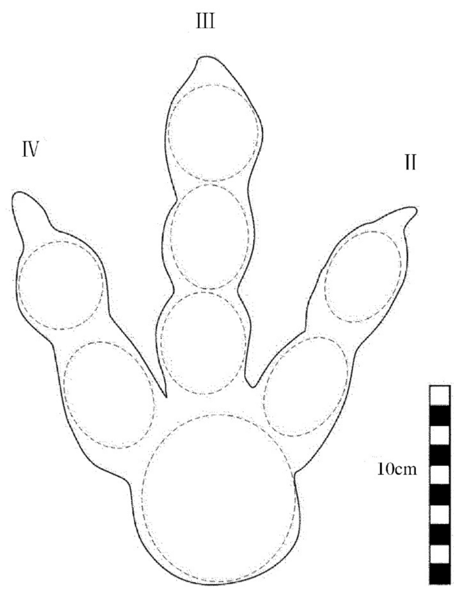


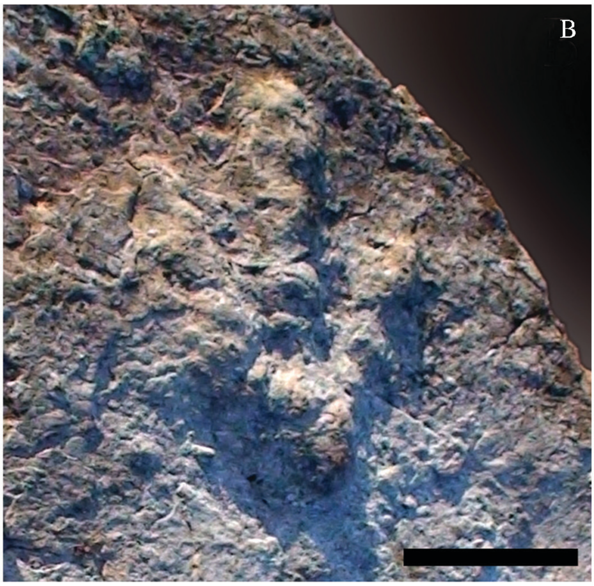
Fig. 4 Outline drawing of *Changpeipus pareschequier* ichnosp. nov. (ZLJ-ZQK2)

Fig. 5 Distribution of the footprints of *Changpeipus pareschequier* ichnosp. nov.

semi-plantigrade, however, because no portion of the metatarsus itself is visible [36]. Digit II is the shortest and possesses two roughly equally long phalangeal pads. The gaps between pads are indistinct. Digit III is the longest, with three phalangeal pads. The areas en-

Plate I

Changpeipus pareschequier ichnosp. nov. ZLJ–ZQK2. scale bar = 10 cm



Low–angle light photograph of *Changpeipus pareschequier* ichnosp. nov. ZLJ–ZQK2. scale bar = 10 cm

Footprints of *Changpeipus pareschequier* ichnosp. nov. scale bar = 20 cm

Table 2 Measurements of *Changpeipus pareschequier* ichnosp. nov. ZLJ–ZQK2

Measurement	ZLJ-ZQK2
Maximum length	26.5 cm
Maximum width(distance between the tips of digits II and IV)	20.5 cm
Length of digit II*	14.9 cm
Length of digit III*	17.4 cm
Length of digit IV*	15.6 cm
Angle between digits II and III	28°
Angle between digits III and IV	28°
Angle between the digits II and IV	56°

note: *digital length measured to the rear margin of the caudalmost digital node

compassed by each pad increase toward the distal end of the digit. Its claw impression angles inward. Digit IV is quite short and possesses only two phalangeal pads, giving the track a pad formula of x–2–3–2–x. The angle between digits II and III is 28°, which equals the angle between digits III and IV.

ZLJ–ZQK1 is complete with the exception of the abraded distal end of digit II. There is a prominence at caudolateral end of the track that is absent in ZLJ–ZQK2. It may be an oddly shaped or oddly distorted metatarsophalangeal pad. It could also represent a pathology on the foot of the track maker, constituting osteogenic tissue and bone marrow that were replaced by a hyperplasic mass of fibrous tissue.

5 Discussion

Changpeipus pareschequier ichnosp. nov. tracks are tridactly, lacking a hallux impression, and are longer than wideth, with track lengths greater than 25 cm. Digit IV projects farther cranially than digit II. Divarication between digits II–III and III–IV are subequal, and between II and IV ranges from 50–60°. The toes terminate in short, sharp claw impressions. All these characteristics are typical features of big theropods[37].

Several other Jurassic theropod ichnotaxa have been recognized, both in China and elsewhere. At least some synonymy is probably present, and some have pronounced *Changpeipus* as possibly synonymous with *Grallator*[38–39], but there has not yet been a systematic attempt at revision, and such is beyond the scope of the current paper. Smaller and more gracile tracks (sometimes grouped together into the Anchisauripodidae or Grallatoridae[34]) from China include: *Grallator limnosus*[23] (Early Jurassic, Jinning, Yunnan Province), *Jeholosauripus ssatoi*[40] (Early Jurassic, Chaoyang, Liaoning Province and Chengde, Hebei Province = *Grallator ssatoi*[41]), *Schizograllator xiaohebaensis*[23] (Early Jurassic, Jinning, Yunnan Province = *Grallator* isp.[38–39]), *Paracoelurosaurichnus monax*[23] (Early Jurassic, Jinning, Yunnan Province = *Grallator* isp.[38–39]), *Zizhongpus wumaensis*[42] (Middle Jurassic, Zizhong, Sichuan Province = cf. *Kayentapus* isp.[39]), *Megaichnites jizhaishiensis*[42] (Middle Jurassic, Zizhong, Sichuan Province = cf. *Kayentapus* isp.[39]), *Chongqingpus nananensis*, *Chongqingpus yemiaoxiensis*, and *Chongqingpus microiscus*[42] (Middle Jurassic, Chongqing, Sichuan Province = *Grallator* isp.[39]), *Chuanchengpus wuhuangensis*[42] (Middle Jurassic, Zizhong, Sichuan Province = *Grallator* isp.[39]), *Laiyangpus liui*[30] (Late Jurassic, Laiyang, Shandong Province), and *Shensipus tungchuanensis*[43] (Early–Middle Jurassic, Tongchuan, Shanxi Province). Larger and more robust theropod tracks (sometimes placed in the ichnofamilies Eubrontidae or Gigandipodidae[34]) include: *Eubrontes platypus*[34] (Early Jurassic, Jinning, Yunnan Province), *Youngichnus xiyangensis*[23] (Early Jurassic, Jinning, Yunnan Province), *Jinlijingpus nianpanshanensis*[42] (Middle Jurassic, Zizhong, Sichuan Province), *Lufengopus dongi*[22] (Middle Jurassic, Lufeng, Yunnan Province), *Weiyuanpus zigongensis*[44] (Early Jurassic, Weiyuan, Sichuan Province), *Tuojiangpus shuinanensis*[42] (Middle Jurassic, Zizhong, Sichuan Province = cf. *Eubrontes* isp.[39]), *Chonglongpus hei*[42] (Middle Jurassic, Zizhong, Sichuan Province = *Gigandipus hei*[39]), *Changpeipus carbonicus*[30] (Early–Middle Jurassic, Fuxin, Liaoning Province and Huinan, Jilin Province), *Changpeipus luanpingeris*[32] (Late Jurassic, Luanping, Hebei Province), *Changpeipus xuiana*[33] (Middle Jurassic, Yima, Henan Province), and Shanshan theropod morphotypes A and B[45] (Middle Jurassic, Shanshan, Xinjiang).

Of all these tridactyl track reported in China, the maximum length is over 20 cm in *Kayentapus* (*Megaichnites*), *Lufengopus*, *Eubrontes* (*Tuojiangpus*), *Weiyuanpus*, *Changpeipus*, and Shanshan theropod morphotypes A and B. Differences between *Changpeipus pareschequier* and *Lufengopus* are: the divarications between digits of *C. pareschequier* (28°) are less than those of *Lufengopus* (II–III 29°, III–IV 35°) and in *Lufengopus*, the length of digit III is equal to the length of digit IV. Differences between *Changpeipus pareschequier* and *Megaichnites* are: the three digit impressions of *C. pareschequier* are connected each other whereas in *Megaichnites* they are not; the phalangeal pad formula of *C. pareschequier* is x–2–3–2–x but x–2–3–4–x in *Megaichnites*. *Changpeipus pareschequier* differs from *Weiyuanpus* because digit III in the latter is substantially longer than in the former: digit III projects only about 2.5 cm beyond digits II and IV in *C. eschequier* but in *Weiyuanpus*, digit III projects 7–9 cm[44]. *Tuojiangpus*, like *Megaichnites*, has a phalangeal pad formula of x–2–3–4–x. The interdigital divarications of *C. pareschequier* are larger than in *Eubrontes* (BPV–FP5: II–III 17°; III–IV 20°; *E. platypus* II–III 12°; III–IV 22°). Also, the ratio of length/width of *C. pareschequier* is 1.29, much less than that of *Eubrontes* (BPV–FP5: 1.78). Similarly, the divarication angles of *C. pareschequier* are greater than those of *Youngichnus* (II–III 10°; III–IV 11°). Additionally, in digit III of *C. pareschequier* is wider than digits II and IV while in *Youngichnus*, is narrower than digits II and IV. Shanshan theropod morphotypes A and B have not been classified in any ichnogenus or ichnospecies; they exhibit similarities to both *Changpeipus* and *Megaichnites*. However, they have generally wider angles of divarication than *C. pareschequier*.

C. pareschequier differs from *C. carbonicus* by having subequal angles of divarication between digits II–III and III–IV; in *C. carbonicus*, the angles are quite different. The metatarsophalangeal pad of *C. pareschequier* seems very large compared to that of *C. carbonicus*. In both *C. carbonicus* and *C. pareschequier*, the metatarsophalangeal pad impressions are round, which contrasts with the long, narrow, tapering metatarsal impression in *C. xuiana*. *C. pareschequier* differs from *C. xuiana* in lacking a discreet metatarsal impression, and the ratio of length/width of *C. pareschequier* is much less than that of *C. xuiana* (1.89). We conclude that the new track specimens represent a footprint morphology that is distinct from the others mentioned above and diagnosed by these unique features: subequal angles of divarication between digits II–III and III–IV, digital pad formula x–2–3–2–x, and big and round metatarsophalangeal pad.

We plotted and examined the distributions of the ratios of length/width (Fig. 6A) and digit divarication angles (Fig. 6B) of *Anchisauripus*[46–47], *Anomoepus*[34, 46–48], *Apatichnus*[34, 46, 49], *Changpeipus carbonicus*[30], *Changpeipus xuiana*[33], *Changpeipus pareschequier* ichnosp. nov., *Eubrontes*[34,46,50–51], *Gigandipus*[52], *Grallator*[40,49,53–54], *Chongqingpus*[42], *Tuojiangpus*[39, 42], *Chonglongpus*[39, 42], *Megaichnites*[39, 42], the Anhui[55] and Luanping[56] theropod tracks, *Lufengopus*[22], *Weiyuanpus*[44], Shanshan theropod morphotypes A and B[45], and *Kayentapus*[57]. In both graphs, all the ichnospecies of *Changpeipus* plot closely together and within relatively narrow ranges. However, they are not isolated: *Eubrontes platypus*, *Grallator limnosus*, and *Kayentapus hopii* plot not far away. This may indicate that there is less ichnotaxonomic variation than is presently recognized.

Comparison with well–known, more widely–distributed, contemporaneous theropod ichnotaxa, such as *Anchisauripus*, *Eubrontes*, *Grallator*, and *Kayentapus* is hindered by a lack of consensus on diagnostic features of each and how much synonymy is currently encompassed across ichnospecies and ichnogenera. Recent reviews of the subject[58–62] present evidence that all may be valid, but widely agreed–upon

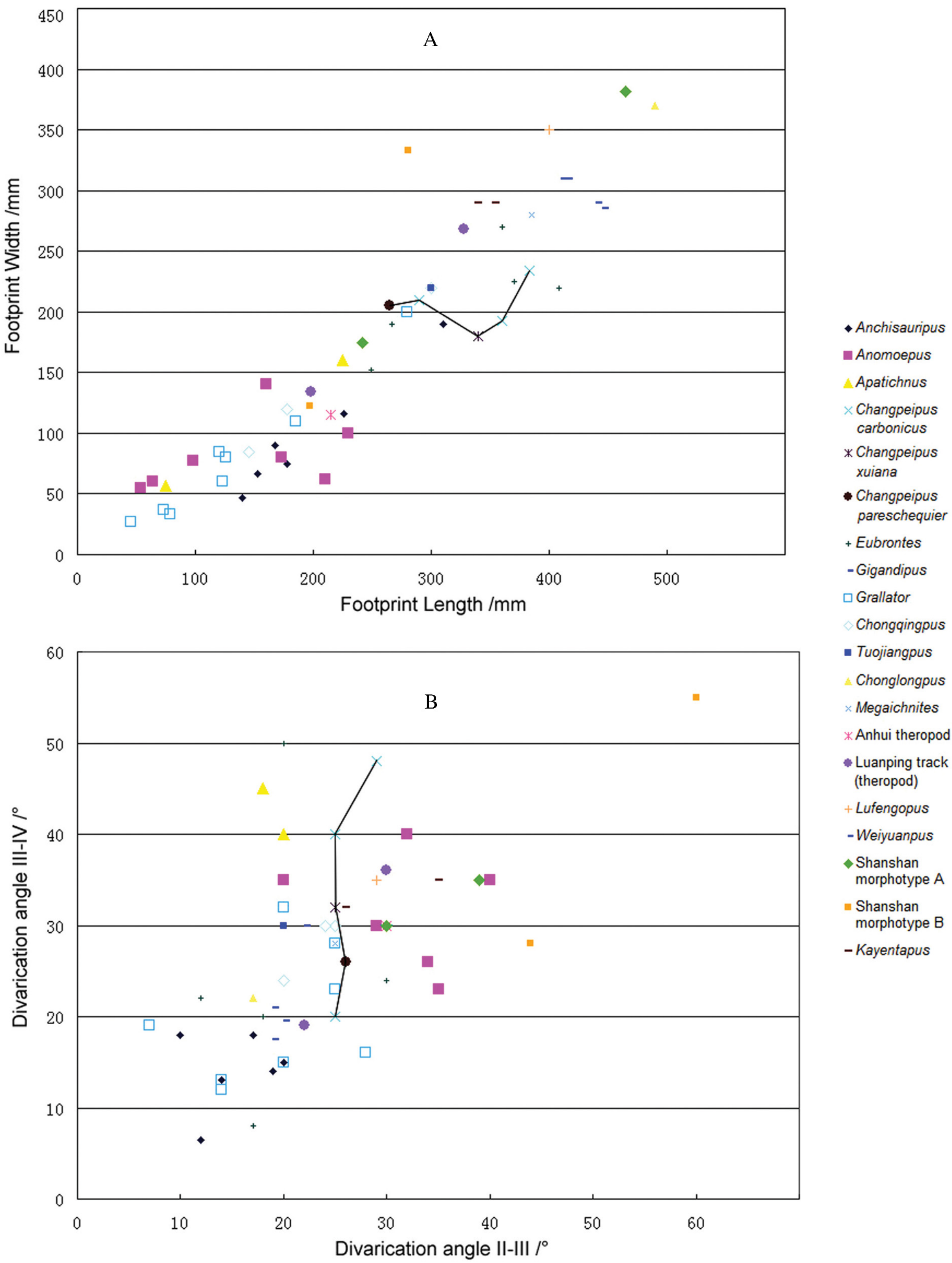


Fig. 6　Scatter diagram of width vs. length of theropod dinosaur footprints(A) and scatter diagram of divarications between digits II and III vs. divarications between digits III and IV of theropod dinosaur footprints(B) (lines connect ichnospecies of *Changpeipus*)

and consistently employed diagnoses for each are still wanting. *Eubrontes* tracks are >30 cm in length, have length/width ratios of 1.4–1.5, and have digits II and IV projecting cranially roughly equal distances [60] and generally have very robust digits, unlike any of the *Changpeipus* prints, so *Changpeipus* is appears to be distinct from *Eubrontes*. *Grallator* tracks are <15 cm long, have length/width ratios ≥2, and narrow divarication angles (10–30°)[60]. *Changpeipus* shares the latter two features, but with the exception of the small supposed manus print of *C. carbonicus*, are all larger. *Anchisauripus*, which has been considered a senior synonym of *Kayentapus* [63] and synonymous with *Grallator*[58], has a similar size range (~20 cm) and length/width ratio (~2.0), and average digital divarication angles (27°) as *Changpeipus*, but in *Anchisauripus*, digit II projects farther cranially than digit IV[60]. *Kayentapus* was differentiated from *Anchisauripus*, *Eubrontes*, and *Grallator* based in part on how it plotted against other ichnotaxa using some comparatively complex statistics[58]. Nevertheless, it has been characterized as having lengths of 11.5–40 cm, "high" divarication angles (with angle III–IV greater than II–III), and a well–defined metatarsophalangeal pad on digit IV[61]. Digit impressions are thinner and less robust than those of *Eubrontes*[59] and have digit IV with a strong divarication from digit III [64], supposedly a ceratosaurian (coelophysoid or other basal non–neotheropod in the current usage [64]) trait. *Changpeipus* differs in lacking the strongly divaricate digit IV and having a more centrally–placed metatarsophalangeal pad impression; it also has less pronounced claw impressions than most *Kayentapus* tracks do. Thus, *Changpeipus* can be maintained as a distinct ichnogenus pending further study of all ichnotaxa concerned. In addition, *Changpeipus* tracks exhibit a general increase in digital pad size from proximal to distal, a feature not noted in most specimens of these other ichnotaxa.

Lines connect ichnospecies of Changpeipus.

Young (1960: fig. 1 and plate IV) considered *Changpeipus carbonicus* IVPP V2472 2a (Fig. 7), a small trace adjacent to one of the larger pes prints, to be a manus print, the only such report in any of the *Changpeipus* ichnospecies. The maximum length of this trace is 130 mm and its maximum width is 70 mm. Digit II is 27 mm long, digit III is 75 mm, and digit IV is 34 mm. The ratio of length/width of the track is around 1.86 (the ratio of associated pes print IVPP V2472 2 is 2.03 and IVPP V2472.3 is 1.58). Its interdigital divarication angles are 32° for II–III and 13° for III–IV. Both digits III and IV project farther cranially than digit II.

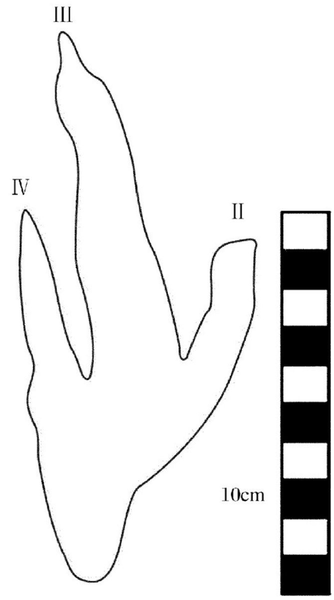


Fig. 7 Outline drawing of ostensible *Changpeipus carbonicus* manus impression IVPP V2472 2a

The interpretation of this track as a manus impression has been doubted: Zhen et al. thought the manus and pes footprints of *Changpeipus* needed further study[41], and Thulborn[37] thought that the ostensible manus print was made by a different animal than the pes prints. Using the same criteria outlined above for *C. pareschequier* tracks[34], IVPP V2472 2a pertains to a left foot. Morphologically, it does not resemble other ostensible theropod manus prints, which possess sharp claw traces, narrow divarication angles between the digits[37], and lack metacarpo–/metatarsophalangeal pad impressions. Likewise, the position of the ostensible *C. carbonicus* manus print is peculiar, situated lateral and at a marked angle to the pes print compared to other supposed theropod manus prints (e.g., *Delatorrichnus goyenechei*[65]). Overall, the isolation of tiny IVPP V2472 2a, combined with its divarication angles and presence of a caudal pad indicates that it is a small pes print made either by a different animal or, more likely, a juvenile individual of the *Changpeipus carbonicus* track maker. All morphological features and measurements are in accordance with those of *Changpeipus carbonicus* pes prints, such as digit IV exceeding digit II in length. These incongruities may be the result of the different ontogenetic stages of the track makers. More specimens of *C. carbonicus* are required to test these hypotheses.

Haubold[66] interpreted the *Changpeipus* track maker as a "carnosaur" (basically a large, robust theropod, not member of the Carnosauria *sensu stricto* as it is understood today [67]). Known theropod taxa in the *Lufengosaurus* Fauna that match this general description are "*Dilophosaurus*" *sinensis* and *Eshanosaurus deguchiianus*. The tracks are too large to have been made by known specimens of the small, gracile *Megapnosaurus,* which is also present in the fauna [9]. Like most footprints, it is impossible to ascribe the tracks to any particular taxon without a direct association. The pes of "*Dilophosaurus*" *sinensis* has received only perfunctory description, so it is impossible to say how well its pedal morphology fits *Changpeipus* tracks. *Eshanosaurus deguchiianus* was interpreted as pertaining to a relatively derived member of the Therizinosauroidea; if correct, derived therizinosauroid pedes are functionally tetradactyl and do not match *Changpeipus* morphology.

Early Jurassic tracks that are 20−40 cm long from the United States, Sweden, France, Poland, and China are very similar to *Kayentapus* and *Eubrontes* [68]. *Kayentapus,* and the similar *Dilophosauripus* [57] were thought to have been made by a theropod similar or identical to the sizeable theropods *Dilophosaurus wetherilli*[69] and *Lophostropheus airelensis*[70] based on their geographic, stratigraphic, and chronologic proximities to the only known skeletal remains of these theropods. Weems [58, 62, 71] instead advocated a prosauropod, such as *Plateosaurus engelhardti*, as *Kayentapus hopii* and *Eubrontes giganteus* track makers. Most paleontologists, however, maintain a theropodan track maker for tracks of this general morphology.

Changpeipus pareschequier not only constitutes the oldest dinosaur footprints in the Lufeng units, Yunnan Province thus far discovered, but also expands its geographic distribution from Liaoning, Jilin and Hebei, in northeastern China, and central Henan to Yunnan in southwestern China. This indicates that theropods with pedal morphologies capable of registering *Changpeipus* tracks were widely distributed across the Yangtze Platform in the Early Jurassic.

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