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First record of bird tracks from Paleogene of China $(Guangdong Province)^{\diamondsuit}$



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ABSTRACT

The record of Paleogene bird traces is quite scarce, especially when compared with the Mesozoic. Avian tracks have been reported mainly from western North America and the Middle East, with some sites also present in Europe and Sumatra. Here the first record of Eocene bird tracks from East Asia is reported. The track bearing level is recorded at the upper part of the Huayong Formation (lower Eocene), one of the continental units of the Sanshui Basin.

More than 350 footprints were documented from three collected slabs. Many footprints were found in trackways, five morphotypes were identified and assigned to four ichnotaxon: *Gruipeda* sp., *Aviadactyla* sp., *Avipeda* sp., and *Fuscinapeda* sp. The ichnotaxonomical identifications are supported by canonical variate analysis (CVA) based on the better preserved traces. These surfaces show a varied ichnofaunal assemblage composed of small and medium shorebirds, large "game" birds, crane-like birds and heron-like birds, providing a more complete picture than was previously known of Early Eocene avian faunal assemblages in Asia.

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1. Introduction

Little attention has been paid to the tracks of Paleogene birds; known tracksites are few in number and often found alongside other types of vertebrate tracks, including mammals and amphibians (Mustoe, 2002). Paleogene bird tracks are most commonly found in western North America (U.S.A. and Canada: e.g. Moussa, 1968; Johnson, 1986; Sarjeant and Langston, 1994; Lockley and Hunt, 1995; McCrea and Sarjeant, 2001), and the Middle East (Abbassi and Lockley, 2004; Ataabadi and Khazaee, 2004; Yousefi Yeganeh et al., 2011), with trackways also discovered in Europe (Ellenberger, 1980) and Sumatra (Zonneveld et al., 2011). In comparison to their Mesozoic counterparts, Paleogene bird tracks are

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relatively few in number and are more restricted in their distribution. To date, no Cenozoic bird tracks had ever been reported from East Asia. The first discovery of Paleogene bird tracks from the early Eocene of Guangdong Province, southeast China is here described; ichnotaxonomical attribution was carried out using classical qualitative descriptions, and morphotypes were analyzed using multivariate statistical analyses to test whether morphologically similar ichnotaxa within the sample are distinct morphotypes. The majority of known Mesozoic and Cenozoic bird tracksites encompass traces attributable to waterbirds analogous to extant shoreand wading birds, and birds with webbed feet. One Mesozoic tracksite preserves zygodactyl birds (Li et al., 2005; Lockley et al., 2007). All known Paleogene bird tracks were produced either by water-margin dwelling birds, including such ichnogenera as Ardeipeda, Charadriipeda, Presbyornithiformipes, and Aquatilavipes (Sarjeant and Langston, 1994; Yang et al., 1995; Mustoe, 2002; Zonneveld et al., 2011), or large, flightless birds (Patterson and Lockley, 2004). Morphotypes range from very small shorebird tracks to medium-sized heron-like tracks, and also include large tracks that are attributed to Gastornis (Diatryma in Buffetaut, 2004; Patterson and

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Lockley, 2004). Tracks from perching or zygodactyl birds are not known from the Paleogene.

The Sanshui Basin, located in the northwest of Pearl River Delta with an area of 3300 km², is an important sedimentary basin in South China. Lower Cretaceous to Eocene sediments nearly 4000 m thick were deposited in the center of the basin (Zhang et al., 1993). During the Guangzhou-Sanshui Highway extension project in 2009, a strip of stratigraphic section 210 m long and 6 m high was excavated to the north of Shicheng High School, Shicheng Township, Nanhai District (Fig. 1A). On March 26th, 2010, abundant bird tracks were discovered by Chanhui Zhao in the section, which was the first discovery of bird tracks in Paleogene rocks in the south of China. In June 2011, the principal author of this paper inspected the track site and the track-bearing slabs were collected and documented.

2. Geological setting

The non-marine Paleocene-Eocene strata in the Sanshui Basin have a thickness of 3000 m. The strata are divided from bottom to top into the Paleocene Xinzhuang Formation, the Buxin Formation, the Baoyue Formation and the Lower Eocene Huayong Formation (Zhang et al., 1993). The Huayong Formation, distributed in the center of the basin, is currently the typical representative of Eocene sediment in South China. The lower part of the Huayong Formation is the Xiqiaoshan Layer, with a thickness of 600–700 m, is approximately 51 Ma (determined by K–Ar dating), whereas the upper part of the Huayong Formation is the 300 m thick Jinxinggang Layer. The Shishan track site consists of interbedded gray thin and moderately thick fine sandstone and charcoal gray argillaceous siltstone, and a layer of gray-green mudstone. The outcrop characteristics are similar to the Jinxinggang Layer of the Huayong Formation (Zhang, 1989). The bird tracks are preserved on the gray thin fine sandstone (Fig. 1B).

The Huayong Formation represents the uppermost deposits of the Sanshui Basin. The Sanshui Basin was a seasonal enclosed lake, which frequently underwent seawater intrusion in the Paleogene (Liu et al., 2004). Compared with the earlier deposits, the lake basin area decreased significantly. The north central basin contains shallow lacustrine deposits and a small-sized delta in the west basin, with extrusive volcanic rocks discovered in south central parts of the basin. The eastern area of the basin is composed of alluvial plain sediment (Fig. 1B; Hou et al., 2007). To date a variety of vertebrate fossils, such as fishes, frogs, turtles, crocodiles, and birds (*Sanshuiornis zhangi*, Wang et al., 2012) have been discovered from the Huayong Formation (Li et al., 2005; Hou et al., 2007).

There is some debate as to whether the Huayong Formation was deposited during the Early or Middle Eocene. Wang et al. (2012) consider the Huayong Formation as Middle Eocene (Zhang, 1999; Li et al., 2005). However, the result of an updated ostracod assay suggests that the Huayong Formation is Early Eocene in age (Zhang et al., 2008), which we adopt in this paper.

3. Methods and tracks

3.1. Methods

The slabs were photographed in detail by one of the authors (ARF) who also took the measurement of the best-preserved tracks directly in the museum. The images were used to create a scaled high-resolution photo-mosaic of the slabs which was used by MB to label the tracks, create the line drawings, and measure all prints using Photoshop. The comparison between the measurement of the physical specimens and those from the photo-based drawings shows an average difference of approximately 1 mm, providing a control on the accuracy of the measurements made from the digital media. Measurements and description are made according to Leonardi (1987) and Elbroch and Marks (2001). Data collected includes: footprint length (FL), footprint



Fig. 1. (A) Geographical location of the tracksites; (B) stratigraphic log of the Huayong Formation.

width (FW), interdigital angles (II^III; III^IV, II^IV, I^II), digit length (II-L, III-L, IV-L, I-L), and digit width (II-W, III-W, IV-W, I-W). All measurements are reported in Supplementary Data 4; those reported in the morphotypes descriptions represent average values.

3.1.1. Multivariate analysis

Canonical variate analyses (CVA) were conducted using Paleontological Statistics (PAST) version 2.17 (Hammer et al., 2001). Canonical variate analysis projects a multivariate data set down to one dimension in a way that maximizes separation between three or more a priori separated groups: in this case, the a priori groups are morphologically distinct tracks and trackways on the separate slabs. The p_{same} between two a priori groups was determined using Hotelling's t^2 test (the multivariate version of the *t*-test, Hammer and Harper, 2006) to determine significance at $p \ge 0.05$.

Several prints were not included in the multivariate analyses due to ambiguous preservation: many prints were preserved only as line-like



Fig. 2. IVPP V 18341-1 (Yizu slab) surface. (A) Outline drawings; (B) photograph of the slab. Scale bar in the photograph: 8 cm.

impressions of digits, without any digit morphology that could be used to make an unambiguous ichnotaxonomic assignment. Also, for the smaller prints the presence of digit I was not used in the assignment of the a priori groups, as the presence of digit I is inconsistent, and it could be selectively preserved as a result of the trackmaker behavior, the substrate consistency, or a mix of the two.

3.2. Material

Two slabs containing a minimum of 340 footprints from the Shishan tracksite were collected by Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China, where they are cataloged individually as IVPP V 18341-1 (Yizu slab;



Fig. 3. IVPP V 18341-2 (Erzu slab) surface. (A) Outline drawings; (B) photograph of the slab. Scale bar in the photograph: 8 cm.



Fig. 4. LUGP3-002 (Linyi slab) surface. (A) Outline drawings; (B) photograph of the slab. Scale bar in the photograph: 10 cm.

Fig. 2, Supplementary Data 1) and IVPP V 18341-2 (Erzu slab; Fig. 3, Supplementary Data 2). At least 21 footprints that are preserved in another single slab from the same site were collected by Institute of Geology and Palaeontology, Linyi University, Linyi City, Shandong, China, where they are cataloged as LUGP3-002 (Linyi slab; Fig. 4, Supplementary Data 3). Photogrammetric 3D models of the Yizu and Erzu slabs, generated following the procedures of Mallison and Wings (2014), can be download at https://copy.com/bn6DBm0f3U40.

3.3. Track description

Although the slabs have a limited surface, there are more than three hundred tracks preserved. The substrate at the time of footprint impression was soft, and several track details were obscured by sediment collapse (e.g. digital pad impressions). Most of the footprints occur as isolated tracks, although some trackways are present and are generally short. Partial asymmetric webbing has been noticed on some tracks, typically present in tracks of extant semi-palmate birds. Based on print morphology and size it was possible to discriminate five different groups:

- Morphotype 1: large (average FL = 4.7 cm, FW = 6.3 cm), anisodactyl tracks with incumbent foot structure; prints symmetrical (II^III \approx 59°; III^IV \approx 59°); digit III the longest; digit I inconsistently preserved and oriented medially to posteromedially, with a high digit I^II divarication (121° on average); metatarsal pad impression is often present, aligned with the long axis of digit III, and well separated from the digits (Fig. 5). Trackways are narrow, with digit III almost in-line with the trackway midline: pace length is equivalent to three times foot-print length (FL).
- Morphotype 2: small to medium (average FL = 2 cm; FW = 2.4 cm) anisodactyl tracks, slightly asymmetrical (II^III < III^IV) with a wide but variable interdigital II^IV angle (average 105°), slender tapering digits with claw marks (ungual impressions); digits II and III converge proximally



Fig. 5. Track e.43 from IVPP V 18341-2 (Erzu slab), example of Morphotype 1. (A) Outline drawings; (B) photograph. Scale in cm.

while digit IV is usually separate; digit I (when present) is short and close to the proximal part of the foot, and lack digital pad impressions (Fig. 6). Short trackways are common and show short paces (circa 2 times FL). In the Erzu slab, a trackway of a running bird occurs: it is narrow, with a slight inward rotation of the foot impressions and a pace length that is almost five times FL.

- Morphotype 3: large (average FL = 6.7 cm; FW = 9.5 cm) anisodactyl tracks, wider than long, with wide interdigital II^IV angle (129°), slightly asymmetrical (II^III < III^IV); digits slender and elongated with digit III the longest; digit I intermittently present, shorter than digits II-IV, and follows the long axis of digit III. Digits II to IV are proximally connected in some prints; digit I is never connected proximally; rare metatarsal pad impressions (Fig. 7). Trackways are narrow, and the pace length is two to three times FL.
- Morphotype 4: small (average FL = 1.9 cm; FW = 2.9 cm) anisodactyl tracks, interdigital II^IV angle variable from wide to very wide (average 121°), with II^III (60°) slightly narrower than III^IV (62°); relatively thick tapering digits with claw marks (ungual impressions); possible asymmetrical webbing rarely occurs in some footprints;

digits can be either proximally separated or convergent; in the latter case, they form a rounded, not very pointed, "hallux" digit I intermittently present, and is short and well separated from the heel, with a very wide (153°) I^II angle (Fig. 8).

Morphotype 5: medium to large (average FL = 5.7 cm; FW = 7.7 cm) anisodactyl tracks, wider than long, with generally wide interdigital angle (137°), slightly asymmetrical (II^III > III^IV); digits slender and tapering with digit III and IV longer than digit II; no digital pad impressions are preserved; no clear proximal convergence of digits; webbing impressions present, and are more strongly developed between digits III–IV than between digits II–III, showing the typical semi-palmate condition of modern shorebirds (Fig. 9).

4. Ichnotaxonomical assignation and trackmaker interpretation

4.1. Qualitative interpretation

Most of the characteristics of Morphotype 1 are common among many bird tracks. However, the well separated and short digit I, and the frequent metatarsal pad impressions restrict the number of possible





Fig. 7. Track y.180 from IVPP V 18341-1 (Yizu slab), example of Morphotype 3. (A) Outline drawings; (B) photograph. Scale in cm.

ichnotaxa. Pavoformipes (Lockley and Delgado, 2007; Lockley and Bishop, 2014) and Gruipeda (Panin and Avram, 1962, emended Sarjeant and Langston, 1994 and De Valais and Melchor, 2008) are tetradactyl genera, whereas Uvaichnites (Díaz-Martínez et al., 2012) matches the overall morphology of the prints. Compared with Pavoformipes, Morphotype 1 is smaller, with slender digits, a less pronounced metatarsal pad impression, and widely-separated digits. Uvaichnites is larger, always tridactyl, has a well-defined metatarsal pad impression aligned with digit III, and possesses digital pad impressions on digits II and III. Also, Uvaichnites is a robust print, with much wider digital pads than observed in Morphotype 1. The type specimen of Gruipeda dominguensis, as described in De Valais and Melchor (2008), has "four digits, three of which are directed forward and larger and the forth (I) directed backward, spur-like and short". Considering the lack of the systematic occurrence of digit I, the more robust digits and the shallower preservation, different from the Argentinian holotype, Morphotype 1 is assigned only to cf. Gruipeda isp. This morphotype also occurs in a smaller variant (Fig. 6, print e.82), and quite common in the Erzu slab, which is tentatively assigned to cf. Gruipeda calcarifera (Sarjeant and Langston, 1994) for its reduced size and the frequent occurrence of a conjunction between digits III and IV.

The prints of *Gruipeda* may represent several possible trackmakers, given the variation of the size of the tracks depending on the ichnospecies. However, the tracks analyzed here are closer to those included by Elbroch and Marks (2001) in the chapter "Game Bird Tracks"; among these, the prints of Morphotype 1 similar (although different in size) with those of wild turkey (*Meleagris gallopavo*, p. 137), ruffed grouse (*Bonasa umbellus*, p. 127), and willet (*Tringa semipalmata*, p. 126).

Tracks similar to Morphotypes 2 and 4 can be compared to three ichnogenera: *Avipeda* (Vialov, 1965; emended by Sarjeant and Langston, 1994; Sarjeant and Reynolds, 2001), *Aviadactyla* (Kordos, 1985; emended by Sarjeant and Reynolds, 2001), and *Ardeipeda* (Panin and Avram, 1962; emended by Sarjeant and Langston, 1994) on the basis of the width of the interdigital angles and of the number of digits preserved. These three ichnotaxa have convergent or proximally united digits and an absence of webbing, but *Avipeda* has "short and thick digits" (Sarjeant and Reynolds, 2001), whereas *Aviadactyla* has "slender and flexible digits... [t]he digits lack inter-pad spaces. Interdigital span variable according to pace and substrate, ranging from about 80° to over 155°." (Sarjeant and Reynolds, 2001). *Ardeipeda* shows similar characteristics but is generally larger in size and has a



Fig. 8. Track e.74 from IVPP V 18341-2 (Erzu slab), example of Morphotype 4. (A) Outline drawings; (B) photograph. Scale in cm.



Fig. 9. Track y.140 from IVPP V 18341-1 (Yizu slab), example of Morphotype 5. (A) Outline drawings; (B) photograph. Scale in cm.

clear digit I impression, whose axis "...corresponds, or almost corresponds, with that of digit III" (Sarjeant and Langston, 1994).

Compared to Morphotype 2, *Avipeda* has thicker digits and a narrower divarication angle, whereas the tracks of Morphotype 2 share the most affinities with *Avidactyla* and *Ardeipeda*. Morphotype 2 shows great variability in the interdigital angles which is not only well documented in *Ardeipeda* and *Aviadactyla*, but also has several features that do not occur in these taxa, such as the scattered occurrence of digit I and the rare presence of probable digital pad impressions. For these reasons, and considering the larger size of digit I of *Ardeipeda*, Morphotype 2 is assigned to cf. *Aviadactyla* isp. Morphotype 4 has thick digits and, when present, a more "flattened" and more rounded proximal border than *Avidactyla*-like footprints, therefore it has tentatively been assigned to *Avipeda*, as described by Sarjeant and Reynolds (2001). Therefore, Morphotype 4 is assigned to cf. *Avipeda* isp. Both *Aviadactyla* and *Avipeda* are interpreted to be left by small waders similar to extant sandpipers (Sarjeant and Reynolds, 2001).

Although comparable in size to Morphotype 1, Morphotype 3 shows a wider interdigital angle by almost 20°, and may be compared to Fuscinapeda isp. (Sarjeant and Langston, 1994; emended by McCrea and Sarjeant, 2001). Fuscinapeda is characterized by a "total interdigital span greater than 95° and often exceeds 120°. Lengths of digits II and III may be similar, but digit IV is frequently somewhat larger" (McCrea and Sarjeant, 2001, p. 467), and "digits united proximally, frequently showing a distinctive heel. Webbing absent or restricted to the most proximal part of the interdigital angles" (Sarjeant and Langston, 1994, p. 13). Morphotype 3 possesses most of the features seen in Fuscinapeda, specifically in the organization of digits and the divarication angles; although not described in the ichnotaxon definition, Fuscinapeda taxon may occasionally present digit I impressions. Morphotype 3 is tentatively assigned to cf. Fuscinapeda isp., an ichnotaxon attributed to large wading birds similar to herons and flamingos (Sarjeant and Langston, 1994).

Morphotype 5 shows distinct semi-palmate webbing structures occupying the proximal inner hypicies of digits II and III, and III and IV. While Falkingham et al. (2009) suggest that webbing can be an apparent feature generated by foot pressure on water-saturated finegrained sediment, the repetition of large numbers of semi-palmate webbing traces with sharply-defined anterior margins, occurring in short trackways, strongly suggests that morphologic webbing structures are preserved (Fig. 8B.) Given the overall shape of the footprints and their size, they are also are comparable with *Fuscinapeda* (see Quantitative analysis), but the ichnotaxonomical identification of Morphotype 5 is not unique and relies on too many subjective factors. However, the substrate of these particular specimens at the time of foot registration may have had the best rheological features to preserve webbing, which may not be preserved in other specimens of *Fuscinapeda*. However, there is not enough data at this time to confidently assign Morphotype 5 to *Fuscinapeda* (however, see Quantitative analysis).

4.2. Quantitative analysis

4.2.1. Yizu Slab

Canonical variate analysis (CVA) reveals four significantly different morphologic groupings based on the a priori groupings made of the individual prints. Despite visual differences, the two *Fuscinapeda* groups (morphotypes 3 and 5) are not significantly different ($p_{same} = 0.065$). This suggests that the two groups of *Fuscinapeda* isp. are preservational variants of the same ichnospecies. Both *Fuscinapeda* isp.-like groups contain prints that are similar both in size and in high total divarication (Fig. 10).

Any statistical results on the *Gruipeda* isp. group (morphotype 1) are tentative as there are only two prints in the sample. However, despite their overall morphologic similarity to the *Avipeda* isp. (morphotype 4) and *Aviadactyla* isp. (morphotype 2) groups, the *Gruipeda* isp. group is significantly different from both *Avipeda* isp. ($p_{same} = 9.65 \times 10^{-10}$) and *Aviadactyla* isp. ($p_{same} = 2.58 \times 10^{-23}$). The analysis shows that the *Avipeda* isp. and *Aviadactyla* isp. groups are significantly different from one another, although they show some overlap in morphospace ($p_{same} = 7.50 \times 10^{-05}$). The differences are due to digit splay: the prints in the cf. *Avipeda* isp. group have a lower FL/FW ratio (X = 0.82) than do prints of the cf. *Aviadctyla* isp. group (X = 0.88). In other words, prints of cf. *Avipeda* isp. have on average a wider digit splay than do those of cf. *Avidactyla* isp.

4.2.2. Erzu slab

Canonical variate analysis (CVA) on the Erzu slab shows that there are two distinct size classes of tracks: the group containing the large *Gruipeda* isp. and the group containing the small cf. *Avipeda* isp. tracks (Fig. 11). Due to the small sample sizes of both the smaller cf. *Gruipeda calcarifera* and the large cf. *Avipeda* isp. groups (two prints for each group), the p_{same} results should only be treated as a preliminary result. Prints assigned to cf. *G. calcarifera* are not significantly different from any of the other identified groups, whereas the large cf. *Avipeda* sp. is not significantly different from the large *Gruipeda* isp. tracks ($p_{same} = 0.764$), despite the morphologic differences of a lack of a distinct DI, and a smaller total divarication in the large cf. *Avipeda* isp. tracks (Fig. 11).



Fig. 10. Canonical variate analysis graphical results of identified prints on the Yizu slab. There is no significant difference from those large tracks that appear to show proximal webbing (green) and those that do not (red). Both print types are similar to *Fuscinapeda texana*, and the slender digits and lack of webbing in the large slender prints (red) likely represent the *Fuscinapeda –* trackmaker walking on a firmer substrate than the trackmaker that produced the similarly-sized and shaped prints with thicker digits and proximal webbing.

Given the overall similarity in size (between 1.5 cm–2.5 cm) and the ephemeral preservation of DI, it is not surprising to see no significant difference between the small and medium cf. *Avipeda* isp. and cf. *Avidactyla* isp. groups ($p_{same} = 0.089$). The small cf. *Avipeda* isp. tracks have higher divarications II–III and III–IV and wider digits, although in the CVA only divarication acts as a significant separating vector between the cf. *Avidactyla* isp. and cf. *Avipeda* isp. groups. Discriminant analysis confirms the overall similarity of these two groups: prints assigned to cf. Avidactyla isp. and cf. Avipeda isp. groups show only a 72.3% correct identification ($p_{same} = 0.059$). The analysis on the Erzu slab highlights one of the drawbacks of relying exclusively on multivariate analyses for discerning discrete groups: two morphotypes that are visually similar may possess similar measured data. In the case of the Erzu slab, the multivariate analyses identify the Avipeda isp. and Avidactyla isp. groups as belonging to the same group.



Fig. 11. Canonical variate graphical results of the different track morphologies preserved on the Erzu slab. In morphospace there are two distinct size categories, although size is not the vector that contributes the largest amount of variation to the analyses. There is a close association with the cf. *Avipeda* isp. and cf. *Avidactyla* isp. groups in morphospace: this is not surprising given the difficulty in confidently separating the two morphotypes on the slab due to a high degree of variability in the preservation of the small tridactyl prints.

5. Discussion

Due to the problematic nature of Cenozoic avian ichnotaxonomy, these tracks were not identified down to the ichnospecific level, but provisionally only to the ichnogenus level. For the same reasons, no new ichnotaxa were amended and the morphotypes were referred only to existing ichnotaxa. Vertebrate ichnotaxonomy, because of its dependence on morphology and gait of the trackmaker combined with the sedimentological and rheological features of the substrates, is not without its challenges, and Cenozoic avian ichnotaxonomy is no exception. Cenozoic avian ichnotaxonomy has a history of inconsistent and ambiguous application. Many of the Cenozoic avian ichnotaxa erected in the 1960s were named after the proposed trackmaker based on vague similarities to extant analogs (e.g. Gruipeda after Grus, Ardeipeda after Ardea, etc.). Many revisions followed (e.g. Sarjeant and Langston, 1994; Sarjeant and Reynolds, 2001; Lockley and Harris, 2010) and quantitative methods are starting to be applied to lessen this confusion (Falk et al., 2011; Buckley et al., 2012; Buckley et al., in press), although the solution is still a work in progress. In the present analysis, the ichnotaxonomy of Paleogene avian tracks (discussed above) was not compared with the ichnotaxonomy of Mesozoic bird tracks, although several previous studies noted that these comparisons are, ultimately, necessary (Sarjeant and Langston, 1994; Sarjeant and Reynolds, 2001; Lockley and Harris, 2010).

Although multivariate statistical analyses have great potential to assist in clarifying the issue of the significance of ichnotaxonomic groups, multivariate statistics cannot be a primary tool in avian ichnotaxonomy as they are limited in their input data: linear and angular measurements will not capture the whole morphology of a footprint, and many visually different footprints will have similar linear measurements (Buckley et al., in press).

The difficulty in the identification avian traces increases with the reduction of the track size, resulting in the increase of lack of visible details. As shown in Figs. 10 and 11, small "Avipeda-like" or anisodactyl prints, although belonging to formal groups with broadly distinct different features, have a large amount of morphologic overlap. The ambiguity increases when considering those traces with possible webbing impressions. Although Falkingham et al. (2009) demonstrate that similar structures can be generated by mechanical reaction of substrates to the load produced by track registration (in the example used in their study of the semi-palmate Cretaceous track *Sargeantopodus*), the interdigital web trace is clearly not an extramorphological artifact, as the same surface also preserves other delicate features such as raindrop impressions. Conversely, tracks made by palmate trackmakers may not be preserved with webbing due to the substrate (Buckley, pers. obs. of *Branta canadensis* tracks in varying substrates).

It is worth noting that:

- The overlap of small tracks (morphotypes 2 and 4) in the canonical variate analyses (Figs. 10, 11) was also reflected in the qualitative analysis, whereas the differences between morphotypes 2 and 4 are restricted to size and few other variable parameters, such as the interdigital angle or the occurrence of digit I. Both methods were not able to distinguish the tracks at the ichnospecific level. Morphotypes 2 and 4 are more confidently distinguished based on qualitative features, specifically the thickness of the digits and the shape of the proximal margin of the prints.
- The presence of webbing is a variable that is not included in the quantitative analysis: as it is not a metric that is consistently, quantitatively documented in avian ichnotaxonomy. As such, webbing data were not to be used (and could not be considered) in the multivariate analyses. To date, the importance of webbing as a diagnostic feature is in qualitative comparisons, serving to highlight the amount of visual data that (at this time) is "missing" from quantitative analyses.
- Large tetradactyl tracks (morphotypes 1,3,5) were less difficult to

identify and were those with the highest number of details preserved. This is due to the relatively heavier weight of these trackmakers, whose pedes impress deeper in to the substrate; the preserved details may also be the result of earlier time of the impression when the sediment was softer, but this is difficult to confirm.

The tracks from the Sanshui region are among the first reported from the Cenozoic of East Asia (Xing et al., 2013) and the first from the Paleogene of China. The slabs, although small in surface area, preserve a large number of tracks belonging to different morphologies: from very small (<3 cm) to large (>6 cm) size, tridactyl or tetradactyl prints with (in some cases) partial webbing traces. These slabs show a varied faunal assemblage; however, due to the implicit limits of current trackmaker definition, it is possible to have but a general view of the avian faunal assemblage, which is likely composed of small and medium shorebirds, large "game" birds, and both crane- and heron-like wading birds. This characterizes the Shicheng site as the richest and most abundant in the Cenozoic of East Asia, and introduces new insights on the Paleogene avian fauna. The data presented here are also compatible with the body fossil record (Vickers-Rich et al., 1986, Wang et al., 2012), although a strict correlation is not possible due to the different paleoenvironments, the problems in the identification of the trackmaker, and the fragmentary record of both the trace and osteological material.

Supplementary data to this article can be found online at http://dx. doi.org/10.1016/j.palaeo.2014.08.031.

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