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In Focus

The cover picture shows SMF ME-3495, undetermined "ptychogasterid", Middle Eocene (Lutetian, MP11), Messel Pit Formation, Germany. Photographs in ventral/external (top) and dorsal/visceral (bottom) views.

See the paper by **Ascarrunz E**, **Joyce WG** "A plastron fragment reveals a previously unrecorded turtle species in the Eocene of Messel Pit, Germany".



Fossil Record An International Journal of Palaeontology

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PENSOFT,



The first Permian Diaphanopterodea (Insecta, Megasecopteromorpha) from China

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Abstract

A new Diaphanopterodea (Insecta, Palaeoptera, Megasecopteromorpha), *Sinoelmoa yangquanensis* gen. et sp. nov., is described based on a single specimen discovered from the Shuiquan Gully locality (Shanxi Formation; Permian, Cisuralian, Asselian; China). A broad comparative analysis of the wing venation of the known members of the diaphanopterodean families Parelmoidae and Elmoidae allowed assigning the new taxon to the former family. This new occurrence represents the first record of a Permian Diaphanopterodea from China, and both the earliest and most oriental record for the Parelmoidae. It sheds new light on the distribution and diversity of these extinct taxa.

Key Words

Asselian, Cisuralian, China, Diaphanopterodea, Fossil insect, North China Block, Parelmoidae

Introduction

The insect order Diaphanopterodea, a member of the broader taxon Megasecopteromorpha Béthoux, 2020 in Yang et al. (2020), is a particular member of Late Palaeozoic faunas. Compared with other megasecopteromorphan lineages, it is represented by fewer species and fossil specimens. The capacity of these insects to hold wings backwards, along the abdomen, at rest ('neoptery') has long been considered a distinctive feature of the group (Carpenter 1992). Different opinions emerged as to whether the occurrence of this ability, in such ancient insects, should be regarded as the ancestral condition for the entire winged insects, or should be accounted for by convergent acquisitions, within Megasecopteromorpha and within Neoptera (Yang et al. 2020; and references therein). The latter hypothesis is now generally accepted. Also, in the course of their 75 million years of evolution, the group evolved very small forms, with a very reduced wing venation (Carpenter 1992) reminiscent of that of Hymenoptera.

One of the best documented families is the Parelmoidae Rohdendorf, 1962, composed of various Cisuralian (i.e. lower Permian) genera and species from Czech Republic (Obora; Sakmarian), USA (Elmo & Midco; Artinskian), France (Lodève; Kungurian) and Russian Federation (Chekarda; Kungurian). Here, we describe a new, isolated wing discovered from the Shuiquan Gully, Shanxi Formation (China; Asselian), which can be confidently assigned to this family. Our broad comparative analysis suggests that it belongs to a previously unknown genus and species. It constitutes the first record of Permian Diaphanopterodea from China.

Material and method

Geological setting

The new material (specimen YQZYW 15) was collected from the siltstone layer of the middle Shanxi Fm., in a rock profile at Duanjiabei District, Yanquan, Shanxi Province,

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North China (Fig. 1A-C). The Shanxi Fm. (also spelled 'Shansi' in some accounts) is a set of deposits of continental-oceanic interaction facies, mainly consisting of coal, mudstone, siltstone, and sandstone, which conformably overlies the Taiyuan Fm. and conformably underlies the Xiashihezi Fm. (Fig. 1D). The upper part of the fossiliferous layer is blackish grey and contains some invertebrates, such as brachiopods and gastropods, while the lower part is grey with abundant plant fossils, including Neuropteris ovata, Pecopteris orientalis, Pecopteris linsiana, Pecopteris sp., Sphenopteris nystroemii, Sphenopteris sp. and Cordaites sp. (Fig. 1D) (Wu 1997). The newly described insect specimen was collected from the lower layer. Based on lithological characters, this layer likely belongs to the Shanxi Fm., which is Asselian in age (Permian, Cisuralian; Shen S. et al. 2020; Shen B. et al. 2022).

Documentation of fossil material

The new material (specimen YQZYW 15) is housed at Yangquan City Planning and Natural Resources Bureau (Geological Specimen Room). It was photographed using a Nikon SMZ25, and a Canon 5DS coupled with a Canon MP-E 65 mm macro lens, under both dry and ethanol conditions. Photographs of this specimen reproduced herein are the result of a combination of photographs taken under both dry (best-preserved side) and ethanol conditions (both sides) ('eth-eth-dry' composite).

New photographs of material housed at the Museum of Comparative Zoology (MCZ; Cambridge, MA, USA) were provided by the MCZ staff. A photograph of the specimen PIN 1700/492 (Paleontological Institute, Academy of Sciences; Moscow, Russia; part of Fig. 2F) was provided by Anastasia Felker. All photographs were optimized using Adobe Photoshop CS6 (Adobe Systems, San Jose, California, USA).

New photographic data on the specimen Ld LAP 365 (Musée of Lodève, France) were also collected. Two reflectance transformation imaging (RTI) files were generated based on photographs taken using a ~30 cm diameter, automated light dome driving a Canon EOS 5DS digital camera, itself coupled to a Canon MP-E 65 mm macro lens. The first file provides an overview of the side Ld LAP 365a, while the second file is focused on the wing base of the side Ld LAP 365b (each based on a set of 42 photographs). Original photographs were optimized using Adobe Photoshop CS6 prior to RTI processing, itself achieved using the RTI builder software (Cultural Heritage Imaging). We provide an online Dryad dataset (Yang et al. 2024, forthcoming) containing these RTI files. Images (other than drawings) reproduced on Fig. 5 were extracted from the overview RTI file, the second item having been obtained using the 'normals visualisation' mode, which assigns a colour code to each pixel according to the orientation of the vector perpendicular to the plane tangent to the object at the corresponding point. This extract was optimized for contrast.

In addition to photographs, hand-drafted drawings were also produced. For the MCZ material such drawings were prepared using an unspecified dissecting microscope equipped with a drawing tube; for the specimen Ld LAP 365, hand-drafted drawings were prepared using a Zeiss SteREO Discovery V8 Stereomicroscope equipped with a pair of W-PL $10\times/23$ eye pieces, a Plan Apo S $1.\times$ FWD objective, and a drawing tube (Jena, Germany); and for the specimen YQZYW 15, hand-drafted drawings were prepared using a Leica MZ75 equipped with a drawing tube. Final drawings were then prepared using both draft drawings and photographs. For the specimen PIN 1700/492, a drawing was derived from photographs only.

Terminology

We follow the serial insect wing venation groundplan and the associated wing venation nomenclature (Lameere 1922, 1923; Kukalová-Peck 1991). Abbreviations are repeated for convenience: ScA, Subcosta anterior; ScP, Subcosta posterior; R, Radius; RA, Radius anterior; RP, Radius posterior; M, Media; MA, Media anterior; MP, Media posterior; Cu, Cubitus; CuA, Cubitus anterior; CuP, Cubitus posterior; AA, Analis anterior; AP, Analis posterior. The identification of AP veins must be regarded as tentative, as the corresponding veins are convex.

Systematic Palaeontology

Class Insecta Linnaeus, 1758 Taxon Rostropalaeoptera Kukalová-Peck, 2000 in Wootton & Kukalová-Peck (2000) Taxon Megasecopteromorpha Béthoux, 2020 in Yang et al. (2020)

Order Diaphanopterodea Handlirsch, 1906

Remarks. Commonly among Megasecopteromorpha, and more particularly in Diaphanopterodea, MA shows some degree of connection with RP. It ranges from a connection via a strong cross-vein, shortly after the origin of MA, to a full fusion with R, then continuing along RP, from which MA diverges at some stage. Because Diaphanopterodea also exhibit oblique crossveins, it can sometimes be difficult to determine whether an oblique structure occurring between RP and MP is the genuine MA or a cross-vein. Unlike previous authors (Carpenter 1963, 1992; Béthoux and Nel 2003), Prokop and Kukalová-Peck (2017) suggested that a full fusion of MA with R/RP occurred in Diaphanoptera Brongniart, 1893, the type-genus of the family from which the names of the order derives. These authors based their interpretation on vein elevation as observed in the specimen MNHN.F.R51214, holotype of Diaphanoptera munieri Brongniart, 1893. However, our observation reveals that rock compression this particular specimen



Figure 1. Geographic and stratigraphic information on the Shuiquan Gully locality (red triangle). **A–C.** Location of the collecting site, on **A.** The palaeogeographic map of early Permian (Cisuralien); **B.** The map of Shanxi Province, China; **C.** The map of Shuiquan Gully locality, Yangquan City. **D.** Chronological framework of the Early Permian strata according to Shen S. et al. (2020), Shen B. et al. (2022) and Sun et al. (2022), with indication of the fossil horizon (abbreviations: HSL, Houshi Limestone; QSL, Qianshi Limestone; SJSL, Sijieshi Limestone). Scale bars: 150 km (**B**); 1 km (**C**). The palaeogeographic map of early Permian (Cisuralien), redrawn by A. Lethiers (CR2P, Paris, from reconstruction by R. Blakey. All Chinese maps data source, Tianditu (www.tianditu.gov.cn, 2024/05/08).



Figure 2. Wing venation of representatives of Parelmoidae Rohdendorf, 1962. A–D. Representatives of the genus *Parelmoa* Carpenter, 1947. A. *Parelmoa revelata* Carpenter, 1947, holotype, specimen MCZ 4822, drawing of right forewing and photograph (positive imprint, light-mirrored). B, C. *Parelmoa radialis* Carpenter, 1947. B. Holotype, specimen MCZ 4825, drawing of left forewing and photograph (negative imprint, flipped horizontally, light-mirrored). C. Paratype, specimen MCZ 4824, drawing of left forewing and photograph (negative imprint, flipped horizontally). D. *Parelmoa obtusa* Carpenter, 1947, holotype, specimen MCZ 4823, drawing of left forewing and photograph (negative imprint, flipped horizontally). D. *Parelmoa obtusa* Carpenter, 1947, holotype, specimen MCZ 4826, drawing of left forewing and photograph (negative imprint), flipped horizontally). E. *Pseudelmoa ampla* Carpenter, 1947, holotype, specimen MCZ 4826, drawing of right forewing and photograph (composite of both sides). E. *Pseudelmoa ampla* Carpenter, 1947, holotype, specimen MCZ 4826, drawing of right forewing and photograph (positive imprint). F. *Permuralia maculata* (Kukalová-Peck & Sinichenkova, 1992), paratype, specimen PIN 1700/492, drawing of right forewing and photograph (negative imprint). Photographs of MCZ material, Museum of Comparative Zoology, Harvard University, ©President and Fellows of Harvard College, CC BY-NC-SA 4.0; photograph of PIN specimen, courtesy A. Felker.

experienced (like several other Commentry specimens) makes it impossible to derive a solid inference on the elevation of elements attributable to MA. In contrast, the specimen MNHN.F.R51196 [considered conspecific to the specimen MNHN.F.R51214 by Béthoux and Nel (2003)] is better preserved in that respect. Our observation revealed that the structure regarded as the base of MA by Béthoux and Nel (2003) and as a cross-vein by Prokop and Kukalová-Peck (2017) is indeed concave, while MA is convex distal to the point where it diverges from RP. This difference in elevation underlies the argument by Prokop and Kukalová-Peck (2017). However, an elevation shift, applying to both MA and CuA, is a general feature of the broader taxon Rostropalaeoptera (Béthoux 2008). Most decisively, in Eukulojidae, whose wings lack cross-venation, the then undisputable bases of MA and CuA are both concave for a short distance before turning convex, after having approached RP and M, respectively (Béthoux 2008: fig. 3). The assumption that MA is fused very early with R/RP in Diaphanoptera is therefore unsubstantiated.

Family Parelmoidae Rohdendorf, 1962

Type genus. Parelmoa Carpenter, 1947.

Included genera. Diapha Kukalová-Peck, 1974; Elmodiapha Kukalová-Peck, 1974; Paradiapha Kukalová-Peck, 1974; Permelmoa Prokop & Nel, 2011; Permodiapha Kukalová-Peck, 1974; Permuralia Sinichenkova & Kukalová-Peck, 1997; Protodiapha Kukalová-Peck, 1974; Pseudelmoa Carpenter, 1947; Stenodiapha Kukalová-Peck, 1974; Sinoelmoa gen. nov.

Commented diagnosis. ScP long, ending beyond the first fork of RP (plesiomorphy within Diaphanopterodea); near wing base, shortly after its origin, CuA fused for some distance with, or running closely along, R+M (apomorphy; as currently documented, shared with all Diaphanopterodea except Sinodiaphidae, in which CuA is connected with M by a short cross-vein, and Diaphanopteridae, in which the connection of CuA and M is very brief); first cross-vein in the CuA-CuP area very short and oblique, with CuA displaying a clear inflexion at the point of connection with this cross-vein [also present in Diaphanopteridae, Carrizodiaphanoptera and, to some extent, Elmoidae (Fig. 3); possibly an apomorphy of the entire Diaphanopterodea -except for Sinodiaphidae, in which this state is primarily absent-, and with presumed secondary losses in various families, such as Martynoviidae]; MP branched (plesiomorphy within Diaphanopterodea); CuP with 1-3 distal branches (plesiomorphy within Diaphanopterodea); developed anal area (putative apomorphy for the family).

Remarks. The combination of (i) an overall rich venation, (ii) a long fusion of CuA with R+M (or, CuA running very close to R+M for some distance), and (iii) a cua-cup cross-vein very short, is generally used to identify members of the Parelmoidae. The Pennsylvanian

Diaphanopteridae differ from this family only by lacking character state (ii) (see Béthoux and Nel 2003). Given the polarity of several character states listed as diagnostic of the family, it is not excluded that this taxonomic concept might represent a paraphyletic entity, to include other Diaphanopterodea families, such as Elmoidae.

Carpenter (1992) considered the six genera and 10 species reported from the Obora locality (Permian, Cisuralian, Sakmarian), and originally assigned to the Elmoidae or Parelmoidae (Kukalová-Peck 1974), as of uncertain familial affinities. Addressing aspects of species delimitation, and the systematics of these species, is made difficult by post-depositional deformations this material endured. Nevertheless, wing venation character states they display tend to indicate a placement to the family Parelmoidae as delimited above, in particular the well-developed anal area. Also, despite deformation, this comparatively large sample allows appreciating variation in character states variability (in other words, how the extent of variability varies within families), likely to differ among (and within) the closely related families Diaphanopteridae, Parelmoidae and Elmoidae (see below and Kukalová-Peck and Sinichenkova 1992).

Notably, a distal fork of CuP is common in the Obora material, with some specimens displaying an early fork, and even a 3-branched CuP. The relation between RP and MA is also very variable across the corresponding species, ranging from a complete lack of fusion to a long one. In contrast, species of the genus Parelmoa Carpenter, 1947 (Fig. 2A–D) show more stable venational features (CuP simple; MA and RP connected by a short crossvein). Among other Parelmoidae, the monotypic genera Pseudelmoa Carpenter 1947 (Fig. 2E) and Permuralia Sinichenkova & Kukalová-Peck, 1997 (Fig. 2F) remain similar to Parelmoa spp. in most of their venational features. Also, Elmoa trisecta Tillyard, 1937 (Elmoidae; Fig. 3) shows rather stable venational features, with a consistent occurrence of a (i) distally forked CuP and (ii) a MA distinct from RP, with a cross-vein connecting the two veins shortly after the origin of the latter. The Obora material is therefore unusual in several respects. Instead of attempting to finely resolve relationships between the corresponding taxa, whose variability in many aspects cannot be properly appreciated, we believe it is more sensible to use the Parelmoidae as a broad taxonomic concept, possibly paraphyletic (i.e., a grade), to include the Obora material.

Genus *Sinoelmoa* Yang, Cui, Xu & Béthoux, gen. nov. https://zoobank.org/3FA908E9-C520-454C-8FE0-1A4F1909C0BF

Type species. *Sinoelmoa yangquanensis* Yang, Cui, Xu & Béthoux, sp. nov.

Etymology. Named after the ancient Greek prefix Sino- (China), and the genus *Elmoa*.

Species included. Type species only.

Diagnosis. By monotypy, same as for the type species.



Figure 3. Wing venation of *Elmoa trisecta* Tillyard, 1937 (Elmoidae Tillyard, 1937). **A.** Specimen MCZ 4590, drawing of left forewing and photograph (negative imprint, reversed, light-mirrored). **B.** Specimen MCZ 4593, drawing of right forewing and photograph (negative imprint, light-mirrored). **C.** Specimen MCZ 4606, drawing of right forewing and photograph (negative imprint, flipped horizontally). **D.** Specimen MCZ 4592, drawing of right forewing (positive imprint). **E.** Specimen MCZ 4591, drawing of wings and photograph (positive imprint). **F.** Specimen MCZ 4594, drawing of left forewing and photograph (positive imprint). Abbreviations: LFW, left forewing; LHW, left hind wing; RFW, right forewing; RHW, right hind wing. All photographs, Museum of Comparative Zoology, Harvard University, ©President and Fellows of Harvard College, CC BY-NC-SA 4.0.

Sinoelmoa yangquanensis Yang, Cui, Xu & Béthoux, sp. nov.

https://zoobank.org/541893E5-C3B2-42FB-A772-14B700882B0D Fig. 4

Type material. YQZYW 15, part and counterpart.

Etymology. Named after the Yangquan city where the Shuiquan Gully locality is located.

Type locality. The specimen was collected at the Shuiquan Gully locality; Shanxi Formation, Permian, Cisuralian, Asselian (Shen S. et al. 2020; Shen B. et al. 2022); near Yangquan City, Shanxi Province, China.

Diagnosis. Area between anterior wing margin and R/RA dark; ScP vanishing in the area between anterior margin and R/RA; MA/MP split opposite the RA/RP split (as opposed to MA/MP split well distal of RA/RP split); CuP forked; AA long (as opposed to AA short), ending on posterior margin beyond wing mid-length.

Description. Positive and negative imprints of a right forewing, distal part missing; dark area between anterior margin and R/RA; near wing base, preserved anterior wing margin very oblique, suggestive of the presence of a short portion of ScA distinct from the anterior wing margin (see Fig. 4A); ScP vanishing in the area between the anterior wing margin and RA, just beyond the brief RP-MA connection; stem of R+M convex, with a distinct inflexion opposite the point of separation of R and M (located about 3.6 mm distal from wing base); RA convex, simple and strong, parallel to anterior wing margin; RP posteriorly pectinate, with 3 simple branches preserved; MA/MP split opposite the RA/RP split; MA diverging anteriorly and then shortly connected with RP; MA simple; MP forked distally; short Cu stem visible; CuA diverging anteriorly from Cu, then close and parallel to R+M stem for some distance, suddenly diverging posteriorly, slightly basal to the R/M split; CuA simple; CuP forked distally; CuA-CuP area narrow until the first cross-vein occurring in this area, which is short and strong, located slightly distal to MA/MP split; anal area very well-developed, with a total of eight terminal branches (anterior-most branch, presumably AA, with 3 terminal branches); cross-veins difficult to observe, evenly distributed over the whole wing, forming two gradate series.

Measurements. Preserved wing length 15.4 mm, width 5.5 mm.

Systematic placement. The presence of a very short cua-cup cross-vein allows assigning the new specimen to the Diaphanopterodea and, within this taxon, allows excluding affinities with the Sinodiaphidae. Furthermore, the derived state 'long fusion of CuA with R+M (or, CuA running very close to R+M for some distance)' allows excluding the new material from the Diaphanopteridae. Then, an assignment to the Parelmoidae as delimited above is straightforward. Nevertheless, a possible assignment to the family Elmoidae was also considered. Two main character states allow distinguishing members of this family (Fig. 3) from the Parelmoidae (Fig. 2), namely (1)

an anal area narrow, with a simple AA (Fig. 3A, B, C, E), sometimes with a short AP-like vein (Fig. 3D, F) (as opposed to a well-developed anal area, with numerous long veins, in Parelmoidae); and (2) ScP terminating on RA near the basal third of the wing length (as opposed to distal to the wing mid-length, in Parelmoidae). Even though the termination of ScP is not visible in the new material, it is clearly not directed towards RA at the point where it vanishes, which is already distal to the point where it reaches RA in Elmoidae. The assignment of our new material to the Elmoidae can therefore be excluded.

Within the Parelmoidae, the extent of the AA area is a useful character to consider first. This area is distinctively long in the new material, a state shared with Elmodiapha (see Kukalová-Peck 1974, text-figs 1, 2), from Obora (Czech Republic; Cisuralian, Sakmarian), and Parelmoa (Fig. 2A-D) and Pseudelmoa (Fig. 2E), from the Elmo & Midco localities (Kansas, Oklahoma, USA; Cisuralian, Artinskian). However, the MA/MP split is located well distal of the RA/RP split in these three genera, whereas they are at the same level in new material. The new material further differs from Parelmoa, Pseudelmoa and Elmodiapha by the brief connection of RP and MA (the two veins are distinct in the three genera) and the presence of a forked CuP (this vein is simple in the three genera). Incidentally, in addition to differences in the extent of the AA area, the same characters allow excluding affinities with the genus Permuralia (Fig. 2F; Chekarda, Russian Federation; Cisuralian, Kungurian; and see Kukalová-Peck and Sinichenkova 1992), in which RP and MA are fused for a more or less long distance, and CuP is simple.

Permelmoa magnifica Prokop & Nel, 2011, from the Lodève locality (France; Cisuralian, Kungurian), is also currently assigned to Parelmoidae. To better assess the affinities of the new material we carried out new observations of the material of this species (Fig. 5; and see Yang et al. 2024). In contrast with Prokop and Nel (2011), we observed that (i) RP has four branches (as opposed to three); that (ii) CuA runs close to (or is fused with) R+M for a short distance, and then sharply diverge posteriorly from the R+M stem, just basal of the first split of this stem, a character generally occurring in Parelmoidae (Fig. 2) and Elmoidae (Fig. 3) (and see Carpenter 1943, 1947, 1992); that (iii) the first fork of MP is located distally [the basal portion of the stem regarded by Prokop and Nel (2011) as the first posterior stem of MP (long dotted line on Fig. 5A) is herein regarded as a twin, shifted impression of CuA, because (i) the apical part of the wing is preserved as a shifted impression, on a layer different from the rest of the wing (Fig. 5A), (ii) the elevation of this vein portion is inconsistent with an assignment to MP and (iii) such twin imprints have already been documented for Lodève material (Béthoux et al. 2007: p. 185; and O.B. pers. obs.) but also from other fossil localities (e.g., see Béthoux 2015); it may be the consequence of delamination and then shifting of the two epidermic layers composing the wing, or of multiple impressions implying a release from the



Figure 4. *Sinoelmoa yangquanensis* gen. et sp. nov., holotype, specimen YQZYW 15. **A.** Overview, drawing and photograph (dryeth-eth composite; dashed line delimiting the area missing on side a) of right forewing. **B.** Detail of the course of CuA, drawing and photograph (eth-eth-dry composite), as located in **A**.



Figure 5. Wing venation of *Permelmoa magnifica* Prokop & Nel, 2011 (Parelmoidae Rohdendorf, 1962), holotype specimen Ld LAP 365, right forewing. **A.** Interpretative drawing under interpretation favoured herein (dotted line, twin imprints of vein sections; and see text), photograph (RTI extract), and normals visualization (RTI extract). **B, C.** Detail of the radial and median systems, as located in **A**, under the interpretation followed by Prokop and Nel (2011) (**B**) and the interpretation favoured herein (**C**).

sediment, displacement, and second impression of a single wing, a phenomenon yet to be demonstrated experimentally], this being consistent with previous reports on the wing morphology of Parelmoidae and Elmoidae (Figs 2, 3; and see Kukalová-Peck 1974); and (iv) despite a very incomplete preservation, it can be assessed that CuA and CuP, distal to their respective origins, approximate each other before departing, and are therefore most likely connected by a short, oblique cua-cup cross-vein known in Diaphanopteridae, Parelmoidae and Elmoidae (see above). Additionally, we propose homology conjectures alternative to those followed by Prokop and Nel (2011) regarding the MA/ MP split. These authors adopted a traditional interpretation (Fig. 5B) involving a free stem of M splitting into MA and MP near the origin of RP. However, this implies the presence of a very strong, oblique crossvein between RA and RP (* on Fig. 5B), unknown in other Parelmoidea and Elmoidae. A possible alternative interpretation (Fig. 5C) predicts that the MA/MP split occurs at the point where R and M diverge, and that MA runs fused with R for some distance. The 'strong oblique cross-vein' can then be interpreted as the base of RP (* in Fig. 5C). Incidentally, RP and MA are then connected by a strong cross-vein, as is commonly the case in Parelmoidae and Elmoidae. However, the first cross-vein in the MA-MP area is then located in a more basal position than is usually the case in these families, but this can be legitimately related to the more basal position of the MA/MP split. It must be emphasized that a R+MA common stem has already been advocated for Permuralia sharovi (Kukalová-Peck and Sinichenkova 1992) (although a free base of MA is still present) and is admitted for several other members of the order Diaphanopterodea (see Prokop and Kukalová-Peck 2017: text-figs 4, 6; and in Asthenohymenidae Tillyard, 1924 and Martynoviidae Tillyard, 1932). Following this interpretation, and in conjunction with a very long ScP, Permelmoa magnifica stands out as a very unique Parelmoidae. Regardless of the favoured interpretation on the course of MA, the new material differs from Permelmoa magnifica in many respects, including the respective position of the RA/RP and MA/MP split, the extent of ScP, and the extent of the AA area.

In summary, it is legitimate to erect a new genus and species for the new material.

Discussion

Thanks to its good preservation, the material of *Sinoelmoa yangquanensis* gen. et sp. nov. allows addressing some uncertainty of the course of main veins near the wing base in Diaphanopterodea. Except for the Sinodiaphidae and Diaphanopteridae, the area between the Cu stem and R+M is very narrow in these insects; and, concurrently, the distal free portion of CuA clearly diverge in the close vicinity of the split of R+M (into R and M). Up to now,

this situation made it difficult to clearly assess whether the entire stem of Cu, or CuA only, fuses with R+M (and, if so, at which point the (R+M)+CuA fusion takes place). In the newly described specimen a Cu stem independent from R+M is clearly visible; and a simple CuA diverges from it, runs along R+M for some distance, and then diverges abruptly opposite the bending of R+M, just basal of the R/M split (Fig. 4B). This new observation overturns the assumption of the occurrence of a R+M+Cu/CuA early common stem (or, of a CuA/CuP split located at the wing base) in these insects, and instead corroborates previous observations of a more or less brief connection of CuA with R+M (or M alone; see Kukalová-Peck 1974: fig. 10; Kukalová-Peck and Sinichenkova 1992). Furthermore, it suggests that the CuA/CuP split being located opposite the point where CuP patently diverges posteriorly is a general feature of Diaphanopterodea (except for Sinodiaphidae and Diaphanopteridae), and is likely the case in more specialized families in which R+M and Cu cannot be easily distinguished, such as Martynoviidae and Asthenohymenidae. It can be reasonably assumed that it is also the case in the megasecopteran family Protohymenidae, which acquired an 'Astenohymenidae' habitus convergently.

The discovery of *Sinoelmoa yangquanensis* gen. et sp. nov. has also relevance regarding the age and distribution of the Parelmoidae. Being Asselian in age, it composes the earliest occurrence of the family, but also the most oriental one, along the eastern margin of the Palaeothetys, on the North China Block. This new record suggests that these rather infrequent insects may have had a large distribution, at least along the lower latitudes of the Northern Hemisphere.

Author Contributions

Conceptualization, Y.C., D.R. and O.B.; investigation, N.Y., Z.X., Y.X. and O.B.; resources, D.R.; writing—original draft preparation, Y.C., N.Y. and O.B.; writing—review and editing, Y.C., N.Y., D.R. and O.B.; visualization, Y.C., N.Y., Z.X. and O.B.; supervision, Y.C.; project administration, Y.C.; funding acquisition, Y.C., D.R. All authors have read and agreed to the published version of the manuscript.

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<u>» PENSOFT.</u>



A plastron fragment reveals a previously unrecorded turtle species in the Eocene of Messel Pit, Germany

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Abstract

Depending on taxonomic opinion, between four and five turtle species are well attested for the Middle Eocene Messel Pit formation of Germany. Here, we describe specimen SMF ME-3495 from the Messel collection of the Senckenberg Museum in Frankfurt, which unambiguously corresponds to an additional turtle species. The specimen consists of a partial anterior plastral lobe that can be distinguished from other Messel turtle taxa on the basis of the presence of gular tubercles, an extensive epiplastral lip, narrow gulars that lap onto the entoplastron, and a sinuous gulo-humeral sulcus. The fragment is not sufficient to diagnose another contemporary European turtle taxon, but its epiplastral lip morphology is reminiscent of "ptychogasterid" geoemydids (Cryptodira). We also remark on bone corrosion consistent with "shell disease" and distinctive coloration.

Key Words

Geoemydidae, Gunnellichnus, pathology, Ptychogasteridae, shell disease, Testudines

Introduction

The Messel Pit quarry is a major Konservat-Lagerstätte with a rich sub-tropical flora and fauna preserved in black oil shale from the Middle Eocene (Lutetian, MP11) in the State of Hesse, Germany (Smith et al. 2018). An abundant fossil record of at least four turtle species is recognized for this site (Cadena et al. 2018). There is broad taxonomic agreement about three: the podoc-nemidid *Neochelys franzeni* Schleich, 1993 (Cadena 2015), the trionychid *Palaeoamyda messeliana* (Reinach, 1900) (Cadena 2016) and the carettochelyid *Allaeochelys crassesculpta* (Harrassowitz, 1922) (Joyce et al. 2012).

The taxonomy of the geoemydid turtles (Testudinoidea) from Messel is far more contentious: the number of potentially attested species ranges between one and four. A major cause for the divergence of opinions is the extensive intraspecific variation present in geoemydids in particular (Garbin et al. 2018), and in testudinoids in general (Joyce and Bell 2004). Two morphotypes of geoemydids were first considered as two species called *Ocadia messeliana* Staesche, 1928 and *Ocadia kehreri* Staesche, 1928, and later attributed by Hervet (2004a) to her new genera *Francellia* and *Euroemys*, respectively. Claude and Tong (2004) proposed a systematic treatment that synonymizes Hervet's genera into *Palaeoemys* and considers the two morphotypes as juvenile and adult forms of a single species: *Palaeoemys messeliana*. As some other authors before us (e.g., Cadena et al. 2018), we follow the latter assessment in this contribution, but the matter remains unsettled (Ascarrunz et al. 2021).

Other proposed geoemydids from Messel are more dubious. Hervet (2004a) identified as *Borkenia* aff. oschkinisi the Messel specimens SMNS 54849, SMNK 395, and IRSBN IG28502. However, those identifications were founded on subtle differences that could feasibly be encompassed in the extensive variation of the *Palaeoemys kehreri* morphotype. Indeed, Claude and Tong (2004) even posited that *Borkenia* as a whole is a possible junior synonym of *Palaeoemys*. In similar fashion, Hervet (2004a) tentatively referred the specimens HLMD-ME 7448 and BMNH R10869 to the geoemydid *Juvemys* sp., but this genus was also contested by Claude and Tong (2004) as a

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junior synonym of *Palaeoemys*, and HLMD-ME 7448 is a small juvenile, which is difficult to contextualize due to the poorly understood ontogenetic variation of these taxa.

Here, we describe the Messel specimen SMF ME-3495, a partial anterior plastral lobe consisting of much of the epiplastra and the entoplastron. This limited material displays distinctive features that clearly lie outside the ranges of variation considered by previous authors for turtles from this site. Thus, SMF ME-3495 can be safely said to represent a distinct turtle species not previously recorded for Messel.

Institutional abbreviations

BMNH, Natural History Museum, London (UK); **HLMD**, Hessiches Landesmuseum Darmstadt (Germany); **IRSNB**, Institut Royal des Sciences Naturelles de Belgique (Belgium); **SMNK**, Staatliches Museum für Naturkunde Karlsruhe (Germany); **SMF**, Senckenberg Museum Frankfurt (Germany); **SMNS**, Staatliches Museum für Naturkunde Stuttgart (Germany).

Material

SMF ME-3495 (Fig. 1) is housed at the Senckenberg Museum, Frankfurt. It was found under the marker horizon *alpha* (Felder and Harms 2004) at the boundary between cells G8 and G9 of the site grid of Schaal and Rabenstein (2012), close to the "Turtle Hill," where numerous other turtle fossils have been collected. It was catalogued on the 9th of September 1999. In comparison to fragmentary, historic material, which was often collected as float from the surface, this specimen was collected directly from the sediments under controlled conditions. Its partial nature is therefore not a result of recent weathering, but rather of decay and disarticulation prior to deposition.



Figure 1. SMF ME-3495, undetermined "ptychogasterid", Middle Eocene (Lutetian, MP11), Messel Pit Formation, Germany. Photographs in ventral/external (**A**) and dorsal/visceral (**B**) views, with matching illustrations (**C** and **D**, respectively). Abbreviations: el, epiplastral lip; ent, entoplastron; epi, epiplastron; gt, gular tubercle; GU, gular scute; HU, humeral scute; le, large shell disease lesion; PE, pectoral scute; pi, pitting; vc, visceral coat. Colored areas correspond to light cream coloration discussed in the text.

PE

Description

SMF ME-3495 (Fig. 1) is a fragment of the anterior plastral lobe, consisting of much of the epiplastra and the entoplastron, preserved in a muted brown color like that of other Messel turtle material of similar size. The right epiplastron appears almost intact: cancellous bone is only exposed in gaps along the suture with the entoplastron and along the edge corresponding to the contact with the missing hyoplastron. The epi-hyoplastral suture is well-preserved, showing only some wear near the contact with the entoplastron. This suture displays a slight sinuous shape seen in many extant turtles (viz. Geoemyda spengleri, Mauremys annamensis, Malayemys spp.; pers. obs.) and its jagged edge is consistent with small sutural interdigitations. Sutural interdigitations are more salient on the visceral side. The left epiplastron preserves the entire region corresponding to the gular scute, but it is broken off, preserving only about a third of the region corresponding to the humeral scute.

On the ventral side, there is evidence of a large lesion in the humeral scute region encompassing the left epiplastron and a small semicircular portion of the entoplastron. The cortical bone is uniformly corroded away, beginning to expose a finely porous layer of cancellous bone. The affected area displays a light cream coloration and has smooth, well-defined boundaries. This kind of damage is consistent with a variety of "shell disease" pathologies (also informally known as "shell rot") caused by bacterial or fungal infections. Similar lesions have been reported for numerous other fossil turtles (e.g., Hutchison and Frye 2001; Guerrero and Pérez-García 2021, 2022, 2023, 2024; Zonneveld and Bartels 2023) and were recently grouped into the ichnotaxon *Gunnellichnus moghraensis* Zonneveld et al., 2022.

Other minor lesions are also present on the ventral face of the entoplastron: two small pits to the right of the inter-humeral sulcus and another to the left, and four small patches of cortical bone corrosion that display the same coloration as the large lesion, but are more superficial and have more jagged boundaries. The small pit on the left side of the entoplastron resembles the ichnotaxon *Karethraichnus* Zonneveld et al., 2022. Zonneveld and Bartels (2023) ascribed *Karethraichnus* to the action of ectoparasitic invertebrates such as ticks or leeches. Irregular whitish patches are scattered on the ventral and visceral sides of the epiplastra. They are faint at the center and more opaque at the periphery. These are likely taphonomic discolorations not associated with bone corrosion.

In ventral view, the anterior margins of the gular regions of the epiplastra are straight and form an angle of about 160° at the midline meeting point. In frontal view, these margins form a slight concavity that would have accommodated the head. In lateral view, there is an angle of about 150° between the planes of the entoplastron and the epiplastra. The latter are gently curved upwards.

The entoplastron appears complete on the right side. As with the epi-hyoplastral suture, the suture lines in the anterior and right regions of the entoplastron are well preserved considering that their overall shape is consistent with attested turtle anatomy and the appearance of its edges is consistent with interdigitations. The posterior edge of the entoplastron is overall well preserved as well, but some interdigitations are less pronounced and some wear cannot be ruled out. The left part of the entoplastron is broken off laterally. Slightly more than half of its medial side is preserved.

In ventral view, the gular scutes are about 1.2 times longer (= length of the inter-gular sulcus) than they are wide (= distance between the external end of the intergular sulcus and the external end of the gulo-humeral sulcus), and they clearly lap onto the entoplastron. They bear small tubercles at the margin with the humeral scutes, which accentuate the overall quasi-triangular shape of the scutes in ventral view. The gulo-humeral sulcus has a sinuous shape. At the level slightly anterior to half the medial length of the epiplastra, it distinctly bows into the gular, but more posteriorly, it bows more gently into the humeral, crossing the ento-hyoplastral suture. The curvature is such that the left and right gulo-humeral sulci meet the inter-gular sulcus at near-straight angles, forming together a parabolic section over the entoplastron.

The humero-pectoral sulcus crosses the entoplastron very near to its posterior edge. It is straight and forms an angle slightly smaller than 90° with the inter-humeral sulcus.

The anterior border of the visceral face of the plastron was also covered by the gular and humeral scutes, as is common in most testudinoids. This border is quite extensive, encompassing over 50% of the epiplastra. The part that is covered by the gular scutes is distinctly raised, forming a shelf or "epiplastral lip" (Fig. 1). This lip spans about 70% of the inter-epiplastral suture at the midline. The posterior border of the visceral face of the gular scutes is longer than the anterior border, defining a roughly trapezoidal outline. The anterolateral tubercles formed by the gular are visible in this view as well. The visceral area is covered by a material that forms a thin and patchy coat, irregularly colored in light cream and more orangish tones ("visceral coat" in Fig. 1). The posterior half of the entoplastron is textured by numerous fine foramina.

Discussions

Taxonomic status

Any affinities of SMF ME-3495 with the Messel pan-trionychians *Palaeoamyda messeliana* and *Allaeochelys crassesculpta* can be easily ruled out, because these softshelled turtles feature highly apomorphic plastral bone configurations with characteristic ornamentation and no plastral scute sulci (Joyce et al. 2012; Cadena 2016).

The Messel pleurodiran *Neochelys franzeni* differs from SMF ME-3495 (Fig. 2A) by the presence of extragular scutes, a single median gular, and a more anteriorly located humero-pectoral sulcus relative to the contact between the epi-hyoplastral suture with the entoplastron (Cadena 2015).



Figure 2. Anterior plastral lobes of select turtle taxa from the Eocene of western Europe. The pleurodire *Neochelys franzeni* (SMF ME1091, Messel Pit, Middle Eocene) in ventral aspect (**A**), based on Cadena (2015). The geoemydid *Palaeoemys "messeliana"* (HLMD ME13437, Messel Pit, Middle Eocene) in ventral aspect (**B**). The geoemydid *Palaeoemys "kehreri"* (SMF ME11389, Messel Pit, Middle Eocene) in ventral (**C**) and visceral (**D**) aspect. Hervet's (2006) reconstruction of the "ptychogasterid" *Merovemys ploegi* (northern France, Early Eocene) in ventral (**E**) and visceral (**F**) aspect. The "ptychogastrid" *Geiselemys ptychogastroides* (GM XXVI-204/62, Geiseltal, Middle Eocene) in ventral (**G**) and visceral (**H**) aspect. Grey lines and shading represent breakage lines or regions covered by other structures.

SMF ME-3495 differs markedly from the Messel geoemydid morphs Palaeoemys messeliana and P. kehreri (Fig. 2B–D) as described in a recent paper (Ascarrunz et al. 2021). The new specimen's gular scutes are longer than wide, clearly lap onto the entoplastron, and form a sinuous sulcus with the humeral. This contrasts the gulars of both P. messeliana and P. kehreri, which are broader than long, do not lap or barely onto the entoplastron, and form a straight sulcus with the humeral. The overall shape of the gulars in SMF ME-3495 makes the gular tubercles more distinct than in P. messeliana and P. kehreri. Lastly, while SMF ME-3495 displays a distinct epiplastral lip on the visceral side of anterior plastral lobe, this character is incipient to absent in P. kehreri (SMF-ME 3774 and SMF-ME 11389, Fig. 2D). The relevant area cannot be observed in P. messeliana.

The distinct epiplastral lip with lateral swellings and gular tubercles of SMF ME-3495 are consistent with the diagnosis of the putative clade "Ptychogasteridae" De Stefano, 1903 (Hervet 2004b, 2006). Among Eocene "ptychogasterids", SMF ME-3495 stands out by the presence of a markedly sinuous gulo-humeral sulcus, but the shape and dimensions of the epiplastral lip are within the range of variation of the group without clearly matching any particular figured specimen (Hervet 2004b, 2006; Schäfer 2012; Bourque 2022). The two spatially and temporally closest named "ptychogasterids" are *Merovemys ploegi* Hervet, 2006 from the Early Eocene (Ypresian, MP 7; Fig. 2E, F) of France (Hervet 2006) and Geiselemvs ptychogastroides (Hummel, 1935) from the Middle Eocene of Geiseltal (Lutetian, MP 11-13; Fig. 2G, H). SMF ME-3495 somewhat bridges the morphological gap between Merovemys ploegi and Geiselemys ptychogastroides by having a more expanded anterior plastral lobe with widely spaced gular tubercles, unlike Merovemys ploegi, but not yet having achieved the extremely long epiplastral lip, as seen in Geiselemys ptychogastroides. Still, the erection of a new species for SMF ME-3495 is unwarranted on the basis of the scant material, also given that, as figured by Schäfer (2012), "ptychogasterids" display extensive intraspecific variation of the epiplastral lip character complex in particular, likely also during ontogeny. Thus, we tentatively identify SMF ME-3495 as an indeterminate "ptychogasterid". Given the great amount of interspecific variability that is apparent to the development of the gular scutes among geoemydids in general and the Messel geoemydids in particular (Ascarrunz et al. 2021), combined with the poor preservation of many Messel turtles, we cannot rule out that this taxon is known from other specimens, but until the epiplastral lip of additional specimens with unclear characters favoring identity as Palaeoemys kehreri or P. messeliana have been exposed, either mechanically or radiographically, SMF ME-3495 is the only specimen available from Messel with likely "ptychogasterid" affinities. The taxonomy of "Ptychogasteridae" itself remains an open problem.

Biogeography and paleoecology

A comparison of the rich Messel Pit turtle fauna to roughly coeval faunas in France and Germany suggest a strong taxonomic bias at this site. More than 250 individuals held in the three largest collections (HLMD, IRSBN, and SMF) document a dominance of the carettochelyid *Allaeochelys crassesculpta* (N \approx 100) and the geoemydid *Palaeoemys kehreri/messeliana* (N \approx 100), followed by the less common trionychid *Palaeoamyda messeliana* (N \approx 40) and the rare pleurodire *Neochelys franzeni* (N \approx 6). The notable absence of terrestrially adapted tortoises, which are common across France and Germany at that time (Lapparent de Broin 2001), suggests a strong bias towards aquatic turtles at Messel. Prior to this publication, possible "ptychogasterids" were unknown for Messel.

There is evidence that at least some "ptychogasterids" were terrestrial. In Geiseltal, G. ptychogastroides is most commonly found in localities called "Trichter" (funnels). These are holes in the forest floor, a kind of doline that is filled up with vertebrate remains. True aquatic turtles (e.g., trionychids) are never found there, but tortoises and G. ptychogastroides are common (Krumbiegel 1962; Krumbiegel et al. 1983). An interpretation of SMF ME-3495 as a terrestrial "ptychogasterid" would account for its unusual preservation as an isolated anterior plastral lobe, in contrast to a complete skeleton, as this suggests transport from the outside into Messel lake. Although some extant tortoises and terrestrial geoemydids live in mountainous terrain today (e.g., Geoemyda spengleri, Manouria impressa; Ernst and Barbour 1989), their absence from Messel may suggest that they did not live in the volcanic slopes that likely surrounded the Messel lake, but rather favored flat terrain beyond this volcanic Maar lake.

Alternatively, a preference for an aquatic habitat would be consistent with the presence of bone corrosion lesions on SMF ME-3495, as they strongly resemble shell disease lesions common in continental aquatic taxa (J.-P. Zonneveld, pers. comm.; Zonneveld and Bartels 2023). The "shell diseases" characteristic of terrestrial turtle taxa are cutaneous dyskeratosis and necrotizing scute disease, both of which primarily cause lesions on the epidermis with minimal effect on bone (Zonneveld and Bartels 2023). Even if SMF ME-3495 is indeed a "ptychogasterid", it is not certain that all "ptychogasterids" must have been terrestrial. Unlike the clade of tortoises (Testudinidae), which is uniformly terrestrial, the geoemydid clades *Cuora, Heosemys, Rhinoclemmys*, and *Melanochelys* all contain both aquatic and terrestrial species.

Pathology and preservation

Other hard-shelled turtles from Messel are similarly affected by shell bone lesions, although none of them quite replicate the features of the large lesion on the humeral scute of SMF ME-3495, which has well-defined boundaries, lighter coloration, and is uniformly corroded. In most other specimens that display pitting and bone corrosion, when large patches (relative to scute size) of bone corrosion occur, the necrosis tends to be deeper and very irregular, and the color is not different from the rest of the bone (e.g. *N. franzeni* SMF-ME 1267, *Palaeoemys kehreri* HLMD-ME 7229 and HLMD-ME 8877). Shell lesions with lighter coloration do occur in the *P. messeliana* specimen HLMD-ME 10477 and, possibly, in the *P. messeliana* specimen HLMD-ME 9051, albeit the lesion borders are not well-defined. That the precise lesion of SMF ME-3495 is not replicated in other specimens is perhaps not surprising, as pathologies can have different susceptibilities and manifestations in different species.

The cream-orange colored coat on the visceral aspect of the specimen is circumscribed to the surface of the plastron that walled the body cavity. It is interesting that changes in coloration correspond to areas that were never protected by scutes on the visceral side, and to the lesion surface on the ventral side, where the scute either had necrosed or flaked off. In other Messel turtles, similar coloration is not observed on exposed visceral surfaces of the plastra, or even on preserved internal organs (Gaßner et al. 2001). The taphonomic significance of the coloration patterns is not immediately clear, but it could be a reflection of different depositional conditions, perhaps due to behavior, habitat, or some other factors.

Conclusions

SMF ME-3495 displays a unique combination of characters that may well be indicative of a currently unrecognized species with affinities to "ptychogasterid" geoemydids. Yet, these characters are largely quantitative and known to present high variation. On the basis of the present material, a diagnosis is unlikely to be robust enough to warrant the erection of a new species. Nonetheless, the other turtle species hitherto described for the Eocene of Messel are sufficiently well characterized to recognize SMF ME-3495 as distinct.

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<u> PENSOFT</u>,



Oligocene vertebrate footprints from the Lower Red Formation, Central Iran

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Abstract

The Lower Red Formation (LRF) in Central Iran consists of the alternation of red-brown terrigenous sediments, marls and evaporites with basalt intercalations, exposed under the Chattian-Burdigalian Qom Formation and deposited on Eocene volcaniclastic sediments. The LRF is considered Rupelian in age. In the Deh Nar area, between Qom and Kashan cities, the LRF includes a basal conglomerate, alternations of brown-red sandstone and shale, colored marls with evaporite diapirs and top eroded red sandstone, with dark gray and green basalt lava intercalations. These sedimentary rocks are deposited in fluvial and playa environments, influenced by volcanic activities. Lower sandstone layers of the LRF in Deh Nar contain numerous vertebrate footprints, mostly preserved as convex hyporeliefs. Bird footprints are identified as *Ardeipeda egretta*, *Aviadactyla vialovi*, *Avipeda phoenix* and *Gruipeda dominguensis*. Small bird footprints are attributed to small, incumbent anisodactyl shoreline birds, such as sandpipers, and the larger of them to Gruiformes and Ciconiiformes, such as Ardeidae and Ciconiidae. Mammal footprints include *Dehnaripus incognitus* **ign. nov.** and **ign. nov.**, *Lophiopus* isp., *Moropopus elongatus*, *Moropopus kashanensis* **isp. nov.**, *Platykopus stuartjohnstoni*, and *Zanclonychopus* isp.

Dehnaripus incognitus is large circular manus and pes imprints; usually, they show unorganized, large, radial surface wrinkles and their digital or metatarsal/ metacarpal imprints are ambiguous. *Moropopus kashanensis* is tridactyl mammal pes and manus imprints and is distinguished by sharp, claw-like imprints in lateral digits of the manus from *Moropopus elongatus*. Most probably, the mammal tridactyl footprints of Deh Nar made by three toed, medium- to large sized terrestrial herbivores perissodactyls such as Tapiroidea. *Platykopus* and *Zanclonychopus*, however, were remained by large carnivores such as Amphicyonidae or Ursidae. Trackmakers of footprints in the LRF of Deh Nar area lived under hot and dry conditions of terrestrial and evaporitic environments, after cool and dry conditions of the Early Oligocene.

Key Words

Iran, Kashan, Lower Red Formation, Paleogene, Vertebrate track

Introduction

Most reports of Cenozoic vertebrate footprints from Iran, are related to the Eocene and Miocene series (Abbassi 2022). There are, however, many other formations in the Iranian Plateau with terrestrial facies (Rahimzadeh 1994; Aghanabati 2004), which have a high potential for the preservation of vertebrate footprints in this part of the Middle East. Only one vertebrate tracksite has been reported from the Oligocene sediments of Iran (Abbassi et al. 2015), which belong to the continental sediments of the Eastern Mountains Zone of Iran. On the other hand,

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the Lower Red Formation (LRF) of the Oligocene of Central Iran, similar to the Miocene Upper Red Formation (URF), is a good candidate for vertebrate footprint investigations. Continental deposits of the LRF and URF were originally identified to thick, red-bed formations in the Qom-Kashan area of Central Iran, where these formations lie, respectively, below and above the marine Oligo-Miocene Qom Formation (Gansser 1955; NIOC 1959; Abaie et al. 1964; Rahimzadeh 1994). Based on stratigraphical position, the LRF is Oligocene (Rupelian) in age and the URF was attributed to the Middle to Late Miocene. Unlike the URF, which has numerous Miocene vertebrate tracksites in Central Iran (summarized in Abbassi 2022, table 2), vertebrate footprints have not been reported from the LRF. During the geological mapping of the Cenozoic outcrops of Kashan area by geologists of the Geological Survey of Iran in September 2023, numerous bird and mammal footprints were discovered in the lower part of the LRF, by two of us (MST and MGD). The field studies were performed in March and April 2024, and paleontological and stratigraphical data were collected by three others (NA and SSh, and AE). This tracksite is located in 3 km northwest of Deh Nar village, about 55 km southeast of Qom and 53 km northwest of Kashan, and located in the Esfahan Province (Fig. 1A-C). The significance of this report is the introduction of the second Oligocene tracksite from Iran and the first record of vertebrate tracks from the LRF of Central Iran, and from the Esfahan Province.

Materials and methods

The study of the LRF footprints included two main phases of field and laboratory studies. Most data have been collected during the field studies, and they include stratigraphical information or paleontological data, stratigraphic position of the footprints, and preparation of adequate photos by use of digital cameras. A Canon EOS M2 camera (EF-M 18–55 mm, 1:3.5–5.6) was used to take photographs of the footprints from multiple viewpoints.

The track-bearing, large, untransferable slabs were studied in the field and 12 slabs of bird and mammal footprints were sampled. Four plaster molds were prepared from two large mammal trackways (three molds from footprints) of one trackway and one mold from two other footprints). Bird footprints include numerous footprints (more than 160 footprints) and more than dozen trackways were identified. Mammal footprints include 19 footprints in the 8 trackways. These samples and plaster molds were deposited in the private collection of one of us (NA), under the collection numbers IFMI-680 to IFMI-688. The personal collection materials were authorized by the Iranian Cultural, Handicraft and Tourism Organization (ICHTO), with registered catalog numbers (IFMI, Ichnofossil Museum of Iran, under planned, proposed to ICHTO).

Geometrical studies of the photos of tracks and samples were carried out in the laboratory. Geometrical data were used for ichnotaxonomical identification of the footprints. We used standard methods for the geometry of bird and mammal footprints (e.g., Leonardi 1987). The measurement of footprints includes, stride (S) and pace (P) length, footprints width (FW), footprint length (FL), length of digits (DL, include digit I in bird tetrapods), digit width (DW), and main angle between digits, including II-III (= α 1) and III-IV (= α 2). Photographic analysis and sketches of outlines of the footprints were useful in visualization of the geometry of the studied footprints. Digital three-dimensional photos of footprints were obtained by high-resolution digital photogrammetry, according to a standard protocol for ichnological studies (Falkingham 2012; Falkingham et al. 2018). The package Agisoft Photo Scan Professional (Educational License) software, and Cloud Compare software were used for this method.

Geological setting

The Iranian Middle Plateau is defined as a part of the geological territory of Iran, which is surrounded by the main suture lines of paleo-Tethys in the north and neo-Tethys in the south (Stöcklin 1968, 1974; Berberian and King 1981; Aghanabati 2004). This plateau comprises the anticlinorium Alborz Mountains to the north, mosaic blocks of Central Iran in the middle and the metamorphism belt of the Sanandaj-Sirjan zone to the south. Central Iran consists of three north-south oriented crustal domains, called the Lut, Tabas and Yazd blocks, and is separated by N-S faults from the Eastern Mountains Zone and other adjacent geological zones (Aghanabati 2004; Nadimi 2007; Masoodi et al. 2013). This part of Iran continues toward the northwest of Iran and transverse faults and Mesozoic ophiolite belts separate it from the Alborz Mountains in the north and the Sanandaj-Sirjan zone in the south (Stöcklin 1968, 1974; Moghadam et al. 2014). Since the Cenozoic, shortening related to the Arabia-Eurasia convergence has been taken up mainly by the Alborz and Sanandaj-Sirjan thrustand-fold belts, whereas Central Iran seems to show little internal deformation (Allen et al. 2004; Agard et al. 2005; Kargaranbafghi et al. 2011; Ballato et al. 2011; Mousavi et al. 2023). Extensive orogenic magmatic activity started in the Paleocene and reached a climax during the Eocene, causing creation of the NW-SE oriented Urumieh-Dokhtar Magmatic Arc (UDMA) along the southern part of Central Iran (Honarmand et al. 2013; Yeganehfar et al. 2013; Kazemi et al. 2019). These magmatic activities continued during the Late Eocene-Oligocene (Torabi 2010; Pang et al. 2013; Kazemi et al. 2019), and Miocene (Lechmann et al. 2018; Azizi et al. 2021; Zheira et al. 2020) and some suggest that this magmatic activity has not yet ended (Kazemi et al. 2019).

Most estimates show that the collision between the Arabian and Eurasian continents occurred between ca. 35 and 20 Ma (McQuarrie and van Hinsbergen 2013; Song et al. 2023), and this collision caused the closure of

the Tethyan seaway, uplifting of blocks, and finally caused prevailing continental conditions in Central Iran during the Early Oligocene, and probably in the Late Oligocene. Actually, the LRF deposited in this regional tectonic regime, includes both continental red beds and volcanic lavas that originated from the UDMA. Gansser (1955) surveyed terrestrial dominated facies of the Oligocene of central Iran and named it as LRF in the Qom area, without introducing a type section. The thickness of the LRF ranges from a few meters around the paleo-reliefs to more than a few hundred meters in the central part of the basin, so that its thickness reaches more than 800 m in the southern part of the Great Kavir desert in north Central Iran. The LRF consists of alternations of conglomerate, sandstone, marl and gypsum, mostly with red and brown colors. The LRF, however, includes mafic lavas and volcaniclastic intercalations in the southern outcrops of the Qom and Kashan areas and mostly near the UDMA (Rahimzadeh 1994). There are no fossil indexes in the LRF, and, usually, the LRF is considered Rupelian in age, according to its stratigraphic position: over the Eocene volcaniclastics and under the Chattian basal carbonates of the Qom Formation.

The LRF in Deh Nar

The Oligocene rock units of the Qom-Kashan district are known as the LRF, consisting of terrigenous sediments with evaporite diapirs and basalt intercalations (Amini and Emami 1996). The LRF in the Deh Nar area is about 1550 m in thickness, regardless of basalt lavas (Fig. 1D), which covers Eocene volcaniclastic rocks on an erosional surface and is overlain by the Oligo-Miocene Qom Formation. The LRF includes the following lithostratigraphic subunits in the Deh Nar area:

The LRF begins with basal conglomerate layers (300 m), as a gray to brown paraconglomerate with sandy matrix and carbonate cement with sandstone intercalations. The Eocene igneous clasts are the main grains of the conglomerate.

Alternations of red to brown sandstones, interbedded with brown siltstones and shales (550 m). This part of the LRF contains numerous vertebrate footprints. Ripple marks, various cross laminations, and mud crack casts are common non-biogenic structures in sandstone layers. There are tuffaceous and mafic interbeds between the layers.

Colored marls and marly sandstones with gypsum and salt intercalations (620 m) make up the next rock unit of the LRF in the Deh Nar area, with eroded lowland geomorphology. In parts, this subunit is accompanied by alkaline basalts and cut by alkaline diabase dykes.

The final rock unit of the LRF is poorly cemented, erodible brownish red sandstone (80 m).

The LRF of Deh Nar has two distinct lithofacies: first, tuffite and basalt intercalations, which indicate continuation of Eocene magmatic activities, which most probably were sourced from the UDMB, and second, particular lithofacies of the LRF in Deh Nar is seen in outcrops of abundant diapirs of salt and gypsum deposits in the colored marls, with an unknown source.

Systematic Paleoichnology

Bird and mammal footprints were identified in this study. Here, we document four bird ichnogenera, with four ichnospecies, and six mammal ichnogenera with seven ichnospecies. Among these ichnotaxa, one monospecific new ichnogenus and one new ichnospecies of mammal footprints are introduced. Tables 1, 2 show the geometric data of the tracks.

 Table 1. Mean of measurements of bird footprints in the studied samples (in millimeter).

Ichnogenus (Number measured)	FL	FW	DL			DW	Interdigital angle		Р	S	
			Ι	Π	Ш	IV		α,	α		
Ardeipeda egretta (3)	44	42	11	20	27	21	4	46	70	99	125
Aviadactyla vialovi (1)	22	27	_	13	14	10	1	50	50	-	-
Avipeda phoenix (4)	67	83	_	30	55	40	8	247	-	72	69
Gruipeda	26	23	6	11	16	11	1	55	48	45	89
dominguensis (20)											

Table 2. Means of measurements of mammal footprints in the studied samples (in millimeter).

Ichnogenus		FL	FW			DL			DW	Р	S
(Number measured)				Ι	Π	III	IV	V			
Dehnaripus incognitus (7)	m	120	116	-	-	-	-	-	-	_	-
	р	98	103	-	-	-	-	-	-		
Lophiopus isp. (1)		59	67	_	39	34	47	_	10	-	-
Moropopus elongatus (3)		132	103	-	52	88	58	-	32	420	-
Moropopus	m	75	50	_	20	40	28	_	18	200	-
kashanensis (2)	р	71	62	-	-	42	28	-	18		
Platykopus stuartjohnstoni	(4)	81	83	15	18	20	19	15	20	30	57.5
Zanclonychopus isp. (2)	m	141	115	42	48	48	54	42	10	_	-
	р	>90	110	40	40	64	48	-	12		

Bird footprints

Cenozoic bird footprints comprise diverse morphotypes, which are classified as numerous ichnotaxa. The size of footprints, number of digits, presence or absence of web imprint between digits, digit imprint width, quality of tip of digit preservations, with or without claw imprint, and the quality of connection of digit and metatarsal imprints, are the main ichnotaxonomic criteria in bird footprint studies. A total 36 ichnogenera have been recorded for Paleogene/ Neogene bird footprints. Some of these footprints, however, are similar in morphology. Recently, bird footprints were revised to 25 valid ichnogenera by Abbassi et al. (in press). Among the bird footprint ichnotaxa, ichnogenus Gruipeda is a common record with 15 ichnospecies and has extensive distribution in northern (North America, Europe and Asia) and southern (Argentina and South Africa) hemispheres (Lucas et al. 2023). Deh Nar bird footprints include Ardeipeda, Aviadactvla, Avipeda and Gruipeda. Gruipeda is common and abundant bird footprint in the Deh Nar tracksite.



Figure 1. Geography and geology map of studied area. **A.** Studied area in the north Esfahan Province, central Iran; **B.** Outcrops of the LRF, Qom Formation and URF in the Qom-Kashan district (Modified from Amini and Emamai 1996); **C.** Location of studied section in the northwest Deh Nar; studied section is marked by red star; **D.** Stratigraphic column of LRF in the Deh Nar area, and position of track-bearing layers in the lower part of the section.

Ichnogenus Ardeipeda Panin & Avram, 1962

Type ichnospecies. Ardeipeda egretta Panin & Avram, 1962.

Revised diagnosis. Avian footprints showing four digits, three (II to IV) directed forward and large, the fourth (digit I) backward and somewhat smaller. The interdigital angles between digits II and III and between digits III and IV are less than 70°. The axis of digit I corresponds, or almost corresponds, with that of digit III, the interdigital angle between digits I and II being almost equal to that between digits I and IV. Webbing absent (emended from Sarjeant and Langston 1994).

Discussion. Numerous tetradactyl non-webbed small to large footprints have been named from the Mesozoic and Cenozoic deposits, and include:

Cenozoic

Alaripeda Sarjeant & Reynolds, 2001. *Antarctichnus* Covacevich & Lamperein, 1970. *Archaeornithipus* Fuentes Vidarte, 1996. *Ardeipeda* Panin & Avram, 1962. Charadriipeda Panin & Avram, 1962. Gruipeda Panin & Avram, 1962. Iranipeda Lambrecht, 1938. Leptoptilostipus Payros et al., 2000. Pavoformipes Lockley & Delgado, 2007. Tetraornithopeda Kordos, 1985 (nomen nudum).

Mesozoic

Jindongornipes Lockley et al., 1992. Koreanaornis Kim, 1969. Pullornipes Lockley et al., 2006. Pulchravipes Demathieu et al., 1984. Trisauropodiscus Ellenberger, 1972.

The characteristics for identification of this group of bird footprints are based on the morphology and size of footprint or digit imprints. These ichnotaxa may simply be extramorphological (substrate-related) variations of others and therefore are not valid, thus some of these ichnogenera are not sufficiently distinct to be regarded as new ichnogenera. The last revision of bird ichnogenera (by Melchor in Abbassi et al. in press) shows that *Alaripeda*



Figure 2. A, B. Ardeipeda egretta, trackway a1–a3 and Gruipeda dominguensis (b), sampled specimen, IFMI-680; **C, D.** Aviadactyla vialovi trackway b1 and Gruipeda dominguensis, trackway a1–a4; mcc – mud crack cast; nvs – non-vertebrate structures; sampled specimen, IFMI-681.

lofgreni Sarjeant and Reynolds (2001) is considered a taphotaxon and *A. bristolia*, is considered comparable with *Gruipeda dominguensis*. *Antarctichnus* Covacevich and Lamperein (1970) was synonymized under *Gruipeda* by de Valais and Melchor (2008), and *Tetraornithopeda* Kordos (1985) is a *nomen nudum*. *Pulchravipes* is monospecific and *P. magnificus* was considered as the junior synonym of *Gruipeda becassi* (Abbassi et al. in press).

Ichnospecies *Ardeipeda egretta* Panin & Avram, 1962 Fig. 2A, B

Materials. Three footprints in one trackway, sampled specimen, IFMI-680.

Revised diagnosis. Avian tracks of moderate size, exhibiting four digits, II to IV directed forward and I backward. All digits are slender and relatively long; digit

III is longest, II and IV about four-fifths the length of digit III, digit I about three-fifths the length of digit III. Digit I forms a backward prolongation to the axis of III; the interdigital angle between digits III and IV is greater than that between digits II and III. The digits are united proximally. Trackway moderate; stride moderate in size (emended from Sarjeant and Langston 1994).

Description. This trackway includes three small tetradactyl footprints, preserved as hyporeliefs on the lower bedding plane of fine-grained sandstone (Fig. 2, trackway a_1-a_3). Three-digit imprints (II-IV) directed forward and a relatively shorter fourth digit (I) directed backward. Digit I imprint is not completely prolonged to the axis of III. Digit imprints are straight, slender, with sharp tips, no claw imprint is visible. Digit imprints connected to each other in the heel imprint. Interdigital angles of II-III and IV-III are not symmetrical, and the angle between digits II-III is closer than that between digit III-IV (Table 1).

Discussion. The studied small bird footprints show slender digit imprints with sharp tips, imprints of digit II and IV are slightly asymmetric relative to the digit III axis, and show a lower interdigital angle II-III compared that of IV-III, thus we considered it as Ardeipeda egretta. Panin and Avram (1962) established Ardeipeda for small to large tetradactyl bird footprints with three ichnospecies, A. egretta, A. gigantea, and A. incerta. These ichnospecies have slender digit imprints with sharp tips. Usually, the digit I imprint is large and directed along the digit III axis, and mostly closer to digit II. Digit IV and II imprints are not symmetrical with respect to the digit III axis, and the interdigital angle II-III is smaller than that of digit III-IV. A. gigantea is a larger footprint with sharp digit tips and relatively thicker digit imprints compared to A. egretta. Ratios of FL/FW and FL/DL, of A. incerta are the same as these ratios in A. egretta, and both footprints have similar morphology, thus A. incerta is considered a junior synonym of A. egretta (Abbassi et al. in press). Lockley and Harris (2010) suggested the replacement of Avipeda filiportatis under Ardeipeda, but Avipeda filiportatis shows distinctive heel imprints and digit I imprint is not as clearly impressed as the imprints of the other three, so it is not considered to belong to Ardeipeda here. Ardeipeda is attributed to herons (Abbassi 2022).

Ichnogenus Aviadactyla Kordos, 1985

Type ichnospecies. Aviadactyla media Kordos, 1985.

Diagnosis. Bird footprint of small to medium size consisting of three toes. The prints of all three toes are thin, stick-like, shallowly imprinted. Longest is the middle toe, to be followed by the gradually shorter inner and outer toes. The distal end of the inner toe print is, in the normal case, farther away from the basic line (the line normal to the middle toe) than the end of the middle toe print. Consequently, it is slightly asymmetrical (Kordos 1985).

Emended diagnosis. Avian footprints of small to moderate size, composed of three digital impressions.

Digits of slender to moderate width, tapering distally and sometimes exhibiting distinct, slender claws but typically without, or with only feeble, indication of digital pads or interpad spaces. Length of central digit (III) less than 25% greater than that of the lateral digits. Total interdigital span exceeds 95°. Digits convergent proximally but usually isolated (though digit II may have a minimal contact with digit III). No indication of a metatarsal pad or of webbing between digits (by Sarjeant and Reynolds 2001).

Discussion. At first, ichnotaxonomically unwebbed small bird footprints were named as Charadriipeda by Panin and Avram (1962) and Avipeda by Vialov (1965). These names were used for both tetra- and tridactyl footprints. The diagnosis of these ichnogenera was not clarified by authors, and later tridactyl bird footprints introduced by Kordos (1983), including Aviadactyla, Ornithotarnocia, and Passeripedia. Footprints of Aviadactyla show thin digit imprints, usually unconnected, and slightly asymmetrical digits II and IV imprints. The type material of Ornithotarnocia shows thick asymmetrical digit imprints with rounded digit tips (Kordos 1983, text fig. 1, no. 12), although some others have thinner, unconnected digit imprints with sharp digit tips. These thick digit imprints were the ichnotaxonomic base for identifying Ornithotarnocia for Miocene bird footprints California by Sarjeant and Reynolds (2001). Passeripedia includes small tridactyl unconnected bird footprints and differs from Aviadactyla by its smaller size. Sarjeant and Langstone (1994) revised Passeripedia ipolyensis Kordos (1983) and transferred it to Avipeda ipolyensis. Melchor in a strict revision (Melchor in Abbassi et al. in press) consider Aviadactyla as a junior synonym of Ornithotarnocia and Passeripedia as nomen dubium. We, however, would rather regard Aviadactyla as valid and report the studied footprints as Aviadactyla, in the comparison with other found footprints in the studied section.

Ichnospecies *Aviadactyla vialovi* Kordos in Kordos and Prakfalvi 1990

Fig. 2C, D

Materials. One footprint in the sampled specimen (IFMI-681, partim).

Revised diagnosis. Avian footprints of small to moderate size, having slender and flexible digits (II to IV) with slender claws whose inclination is only slightly divergent from the digit axis. The digits lack interpad spaces. Interdigital span variable according to pace and substrate, ranging from about 80° to over 155°. The interdigital angle between digits II and III is slightly less than between digits III and IV. Proximally the digits converge, with digit II sometimes in slight contact with digit III; but digit IV is always separate and neither webbing nor a metatarsal pad are present. The digits are of comparable length, with digit III slightly the longest. Trackway of moderate width; stride of moderate length (emended by Sarjeant and Reynolds 2001).

Description. Specimen IFMI-681 (Fig. 2B, track b) includes one tridactyl imprint, preserved as convex hyporelief, and consists of slender unconnected three-digit imprints. Digit III is relatively longer and slenderer than the lateral digits. Tips of the digits are sharp and no digit pads are visible.

Discussion. Tridactyl unconnected footprints usually left by digitigrade track makers. The substrate conditions such as moisture and plasticity of sediments affect the quality of footprint preservation. Ichnospecies of *Aviadactyla*, and some *Avipeda* ichnospecies of (*A. adunca*, *A. ipolyensis*), and *Koreanaornis* (*K. hamanensis K. dodsoni*, *K. lii*) traces do not join digits proximally. *Aviadactyla vialovi* shows more slender digit imprints than *A. media* and *A. panini* and the digit imprints are slightly joined proximally.

Ichnogenus Avipeda Vialov, 1965

Type ichnospecies. Avipeda phoenix Vialov, 1965.

Revised diagnosis. Avian footprints of small size (footprint length < 30 mm), showing three short, thick digits, with distinct claws. Length of central digit (III) less than 25% greater than that of the lateral digits. Total interdigital span 95° or more. Digits closely convergent or united proximally; webbing lacking or limited to the most proximal part of the interdigital angles (modified from Sarjeant and Langston 1994).

Discussion. At first, *Avipeda* was the general name for tridactyl unwebbed bird footprints which was proposed by Vialov (1965). Later, varieties of bird footprints were considered as ichnospecies of *Avipeda* with different size or morphologies showing similarities to several existing ichnogenera. Thus, Sarjeant and Langston (1994) emended the diagnosis and designated *Avipeda phoenix* (Vialov 1965) as the type ichnospecies.

Ichnospecies *Avipeda phoenix* Vialov, 1965 Fig. 3

Materials. Four footprints preserved in three slabs (IFMI-682/1-3).

Diagnosis. Small, tridactyl tracks up to 1.6 cm long, digits short, relatively broad, angle (Vialov 1965; translated by Lucas 2007).

Description. Slab IFMI-682/1 (Fig. 3A, B) includes medium-sized, tridactyl footprints, preserved as concave epirelief on the upper bedding plane of fine-grained, ripple-mark-bearing, brown sandstone. Digit imprints are straight, with sharp tips, slightly deformed by reliefs of ripple marks, and connected to each other in the heel part. The digit III imprint is thicker and larger than the lateral digits, and wider in the front part of the digits; one digital pad is visible in the distal part of digit III. Slab IFMI-682/2 comprises one medium-sized tridactyl footprint, preserved as convex hyporelief in a lower bedding plane of thin-bedded, fine-grained brown sandstone (Fig. 3C).

Digit III is longer than the lateral digits, and the interdigital angle between digit II and IV is wide. The metapodium imprint is an eminence, and the digits are connected to the metapodium. Proximal outline of the footprints slightly convex, without digit I imprint. Small slab no. IFMI-682/3 includes one tridactyl bird footprint, preserved as concave epirelief on the fine-grained brown sandstone, filled by fine-grained, lighter, silt-size sediments (Fig. 3D). Similar to previous slabs, it shows a digit III imprint larger than the lateral digits. One of the lateral digits (here considered as digit IV) is thicker than the other. The tips of the digits are round or slightly sharp in the footprint slabs of IFMI-682.

Discussion. Vialov (1965) established Avipeda with three ichnospecies Avipeda phoenix, A. sirin, and A. filiportatis. Later, other new ichnospecies were added or recombined with Avipeda. Sarjeant and Langstone (1994) recombined Passeripedia ipolyensis Kordos (1985) as Avipeda ipolyensis but Abbassi et al. (in press) believe that the diagnosis of P. ipolyensis lacks any distinctive feature, and there is no description and considered Passeripedia ipolyensis as a nomen dubium. On the other hand, Abbassi et al. (in press) considered A. sirin as a junior synonym of A. phoenix, and Sarjeant and Langston (1994) recombined A. filiportatis as Gruipeda filiportatis. Thus, the valid ichnospecies of Avipeda include:

Avipeda adunca Sarjeant & Langston, 1994. Avipeda circumontis Lockley et al., 2022. Avipeda gryponyx Sarjeant & Reynolds, 2001. Avipeda phoenix Vialov, 1965. Avipeda rastini Abbassi, 2022.

Avipeda thrinax Sarjeant & Reynolds, 2001.

The studied materials of the Deh Nar section, show similar shape to the type materials of *A. phoenix*, mainly with its wide lateral digit angle, although the Den Nar materials are larger.

Ichnogenus Gruipeda Panin & Avram, 1962

Type ichnospecies. *Gruipeda maxima* Panin & Avram (1962)

Revised diagnosis. Footprints showing four-digit imprints, three of which (II to IV) are directed forward and larger, the fourth (I), directed backward, spur-like and short. The interdigital angle between digits II and III and between digits III and IV are commonly less than 70°. The hallux imprint is posteromedially directed; the interdigital angle between digits I and II being smaller than that between digits I and IV. When present, digital pad traces display the relationship I: 2, II: 2, III: 3, IV: 4. Webbing trace absent (emended from de Valais and Cónsole-Gonella 2019).

Discussion. *Gruipeda* is a well-known bird footprint, and mostly reported as tetradactyl from the Cenozoic sediments. Panin and Avram (1962) established *Gruipeda*



Figure 3. *Avipeda phoenix.* **A. B.** Preserved as concave epirelief on the ripple mark-bearing surface of sandstone (sampled IFMI-682/1); **C, D.** Preserved as convex hyporeliefs (sampled specimen, IFMI-682/2-3).

for tetradactyl small bird footprints with a short description and without type materials. Sarjeant and Langston (1994) emended its diagnosis and considered number, position and shape of digit imprints, and interdigital angel, as main characteristics of *Gruipeda*. de Valais and Cónsole-Gonella (2019) however followed Sarjeant and Langston (1994) and reformulated the diagnosis of *Gruipeda* by extending the description of interdigital angles and number of digital pad traces. Numerous ichnospecies have been introduced for *Gruipeda* based on original type materials or by new recombination from other ichnogenera. Abbassi et al. (2015, *in press*) listed the following ichnospecies:

Gruipeda maxima Panin & Avram, 1962. Gruipeda becassi Panin & Avram, 1962. Gruipeda disjuncta Panin & Avram, 1962. Gruipeda minor Panin, 1965. Gruipeda intermedia Panin, 1965. Gruipeda filiportatis Vialov, 1965. Gruipeda grus Panin et al., 1966. Gruipeda abeli Lambrecht, 1938. Gruipeda calcarifera Sarjeant & Langston, 1994. Gruipeda diabloensis Remeika, 1999. Gruipeda lambrechti Mirzaie Ataabadi & Khazaee, 2004. Gruipeda dominguensis de Valais & Melchor, 2008. Gruipeda fuenzalidae Covacevich & Lamperein, 1970. Gruipeda vegrandiunus Fiorillo et al., 2011. Gruipeda limosa Rădan & Brustur, 1993.

Panin and Avram (1962) established Charadriipeda disjuncta as a tridactyl bird footprint lacking a digit I imprint. Sarjeant and Langston (1994) recombined it as Gruipeda disjuncta. Because Charadriipeda disjuncta is a true tridactyl this recombination is not confirmed. Based on this reason, the recombination of Charadriipeda (Panin, 1965) as Gruipeda minor by Sarjeant and Langston (1994) is not correct. Avipeda filiportatis Vialov (1965) was recombined as Gruipeda filiportatis by Sarjeant and Langston (1994) but later replaced under Ardeipeda by Lockley and Harris (2010). Sarjeant and Langston (1994) considered Iranipeda abeli (Lambrecht, 1938) as Gruipeda abeli but Abbassi et al. (2016) and Abbassi et al. (2024) reevaluated its taxonomic position and considered Iranipeda abeli as valid. Melchor in Abbassi et al. (in press) listed Gruipeda grus, Gruipeda diabloensis, Gruipeda limosa as nomina dubia and Gruipeda minor and Gruipeda vegrandiunus equal to Avipeda. He classified Gruipeda into three groups of ichnospecies considering the footprint length (including the hallux): 1) G. lambrechti, G. intermedia, G. filipor*tatis* and *G. maxima* that are large ($FL_{h} = 120-172 \text{ mm}$); 2) G. becassi and G. limosa have an intermediate size (FL_b = 55–65 mm); and 3) G. fuenzalidae, G. calcarifera, G. dominguensis and G. diabloensis that are small $(FL_{h} = 27 - 35 \text{ mm}).$

Ichnospecies *Gruipeda dominguensis* de Valais & Melchor, 2008

Figs 2, 4

Materials. Numerous footprints studied in the field (more than 140 footprints) and one specimen sampled (IFMI-681).

Revised diagnosis. *Gruipeda* preserved as tridactyl or tetradactyl footprints, commonly with a footprint length smaller than 50 mm, and a length/width ratio of 0.7–0.9. Bipedal trackways displaying a zero to inward rotation with relation to the midline, pace angulation ranging from 150° to 182°, and a stride length from 2.5 to 5 times the footprint length. Footprints slightly asymmetrical, typically with the angle between digits II-III larger than those of digits III-IV, and a large divarication of digits III-IV in the range 90°–135°. Relative digit length is I < II < IV < III. Hallux impression present in almost half of the footprints with a posterior to posteromedial position. Occasional rhomboid to rounded sole.

Description. Small tetradactyl footprints well to poorly preserved as convex hyporeliefs on the lower

bedding plane of medium- to thick-bedded, dark brown to brown, fine-grained sandstone layers. In the well-preserved footprints, all digit imprints are visible, and digit I is smallest, has slightly inward rotation and is not along the longitudinal axis of the footprints. Digit II and IV imprints have the same size but are not symmetrical around the longitudinal axis of footprint. Digit III imprint is the longest, straight, or slightly curved and is more bulged. Usually, all digit imprints are connected with each other proximally by the metatarsal pad imprint. In other imprints, digit I-II-III-IV imprints are preserved as not connected imprints without metatarsal imprints. Footprints have outward orientation on the trackway axis. Some trackways show higher relief digit III imprints with indistinct lateral digit imprints. Three to four digital pad imprints are visible in several footprints, and usually the tip of the digits is sharp.

Discussion. The studied small bird footprints were preserved with different quality, and in the well-preserved setting they are attributable to *Gruipeda dominguensis*. These footprints are smaller than *Gruipeda becassi* and differ from *Charadriipeda minima* by its smaller digit I imprint and orientation of digit II and III imprints.

Mammal footprints

Ichnogenus Dehnaripus igen. nov.

https://zoobank.org/C9451ED2-C738-4E93-A752-E001E463F428

Type ichnospecies. Dehnaripus incognitus

Etymology. From village Deh Nar, where the footprints were discovered, and pus meaning foot.

Diagnosis. Large, circular footprints consisting of manus and pes imprints (> 10 cm). Manus imprint is larger than the pes, deeper in epirelief preservation. Usually, footprints show unorganized radial large wrinkles, and digital and metatarsal/metacarpal position are ambiguous. The technical imaging shows five thick digits in the manus with large metacarpal imprints, and three-digit imprints in the digitigrade pes imprint. Outlines of digit imprints in pes and manus are unclear.

Discussion. Morphology and quality of the preservation of footprints are controlled by numerous factors, partly related to sedimentological features of the substrate and others by the biological characteristics of the track-maker and, finally, preservational conditions. Some reports of vertebrate tracks include ambiguous footprints with unusual morphology; these mostly were reported from the dinosaur tracks (e.g., Harris and Lacovara 2004). There are a few documents about enigmatic footprints from the Cenozoic (e.g., Mayoral et al. 2023). Demathieu et al. (1984) reported mammal enigmatic small footprints from the Oligocene of southern France. These footprints are pentadactyl with forwarded three-digit imprints (II-III-IV) and set backward two digits (I-V). They were named as Sarcotherichnus enigmaticus and attributed to canids or felids. Dehnaripus differs



Figure 4. A, B. *Gruipeda dominguensis* trackways in the lower bedding plane of a large dislocated block with numerous mud cracks; C–H. *Gruipeda dominguensis* trackways in the dislocated slabs.

from *Sarcotherichnus* by larger size and unclear digit imprints, on the other hand, preservation quality of specimens of *Dehnaripus* is well, so that it shows even fine wrinkles. *Aenigmatipodus* Mayoral et al. (2023) comprises series of tracks that are grouped in sets of three tracks or triads, each track constituting a subunit of the whole set and consisting of a depression or cleft formed by a central body and two bodies placed at the ends (Mayoral et al. 2023). *Dehnaripus* differs from *Aenigmatipodus* by its morphology, so that *Dehnaripus* is mound-shaped, with circular outline, and *Aenigmatipodus*, however, is a depression formed by a central body that is three times as long as it is wide, with two shorter bodies placed at the ends.

There are other non-biogenic mound shape structures, which may look similar to *Dehnaripus*; for example, sand-volcano occurs on upper bedding surfaces, and result from liquefied sand being extruded through a local vent at the sediment surface (Collinson and Mountney 2019). Sedimentary biogenic structures, such as stromatolites, have mound shapes on the carbonate platforms. Essentially, these structures differ from *Dehnaripus*, not only by their morphologies but also by their lithofacies. Although there are no complete and convincing trackways, we would rather consider *Dehnaripus* as a new ichnotaxon, because of:

- a. The extramorphology of *Dehnaripus* is not the result of substrate conditions, because it was found in the different horizons of the lower rock units of LRF. It is difficult to conclude that the same extramorphologically conditions were repeated in different lithohorizons. On the other hand, the preservation of *Dehnaripus* is good so that fine wrinkles were preserved, which shows the unusual morphology of the sole of pes or manus.
- b. The extramorphology of Dehnaripus is related to the unusual morphology of the sole of the track makers. In comparison, the pentadactyl toes of proboscideans, embedded by digital thick cushions and their broad sole, are flat and full of wrinkles. The impressions of these feet are large oval to subcircular imprints, with large and flat sole surfaces either ornamented or smooth. The digit impressions may point anteriorly (Panin and Avram 1962; Neto de Carvalho et al. 2021). These footprints are completely different from the skeletal anatomy of proboscideans. Like this, Dehnaripus shows the morphology of the sole of the track maker as radial unorganized thick wrinkles. These ornamentations could be formed by thick, unorganized and disordered radial cushions or hooves.

Ichnospecies Dehnaripus incognitus isp. nov.

https://zoobank.org/C4A7A7B1-260D-4E8F-8F1C-4ACBF1522C47 Figs 5, 6

Materials. Seven pes and manus footprints of five trackways, in three slabs, sampled (IFMI-683/1-3).

Holotype. Specimen No. IFMI-683/2 includes pes and manus imprints.

Etymology. From Latin incognitus, meaning unknown.

Type-locality. Iran, Esfahan (= Isfahan) province, Kashan township, west Ab Shirin, northwest Deh Nar, 34°19'N–38°46'N, 51°12'E.

Type horizon. lower Oligocene (Rupelian).

Diagnosis. As for ichnogenus.

Description. Footprints preserved as mound-shaped convex hyporeliefs in the lower bedding plane of dark brown, thin to thick, fine-grained sandstone. Usually, the surface of footprints is marked by radial wrinkles, and identifying digit imprints is difficult; hence, measuring digital geometry is impossible. In special imaging, however, five-digit imprints in the manus and three-digit imprints in the pes are distinguishable.

Dehnaripus incognitus was found in three slabs. Slab 1 was studied in the field, comprising two large footprints (Fig. 5A). The pes imprint in this slab is smaller, with three large and thick digit imprints, a small metatarsal imprint, and numerous radial wrinkles preserved in the proximal part of the pes imprint (Fig. 5B). The manus imprint is larger, showing five short digit imprints, completely connected to a large, circular metacarpal imprint. No claw imprints are visible in the digits, and the tips of digits are round (Fig. 5C). Slab 2 (IFMI-683/1) includes one manus imprint as a large mound-shape with large, radial five-digit imprints. The metacarpal imprint is not developed in the footprint (Fig. 5D, E). It is preserved as radial wrinkles and a rough imprint. Slab 3 includes two pairs of pes and manus imprints, belonging to separate trackways (Fig. 6A). One of them is slightly smaller (Holotype, IFMI-683/2, Fig. 6B, C), and has large manus imprints, with short digit imprints and unclear outlines of digit imprints. It shows a large, circular metacarpal imprint. The pes imprint includes three-digit circular imprints without a clear metatarsal imprint. Another pes-manus set is larger and comprises pes and manus imprints (IFMI-683/3). Pes imprints show three-digit imprints without metatarsal imprints, and the manus is larger and has unclear outlines of digit imprints, but five-digit imprints are distinguishable (Fig. 6D, E).

Discussion. Quality of preservation contributes to the unusual morphology of Dehnaripus incognitus, as circular imprints and unclear digit imprints. Definitely, the footprints are traces of the outer morphology of the feet, and the final morphology of a footprint is affected by trackmaker behavior, autopodia anatomy and substrate features (Melchor 2015; Marchetti et al. 2019). The anatomical characteristics of the "heel," control the sole morphology, thus controlling the morphology of footprints. Dehnaripus incognitus shows distinctive morphology, and we would rather consider it as a new ichnotaxon. Dehnaripus incognitus differs from Proboscipeda enigmatica by its smaller size and radial wrinkles and number of digit imprints. Dehnaripus incognitus differs from Glyptodontichnus pehuencoensis Aramayo et al. (2015) and Platykopus maxima (Kordos 1985) by its number of unclear digit imprints.

Ichnogenus Lophiopus Ellenberger, 1980

Type ichnospecies. Lophiopus rapidus Ellenberger, 1980.

Revised diagnosis. Footprint of small perissodactyls, imprints belong to three-toed foot that shows a longer middle digit, which supports the entire pedal sole on the ground. The footprint is small. The lateral digit II and IV imprints are symmetrical to each other, and are set farther back from the middle digit III. These digit imprints end distally in sharp tips. The trackway is narrow, which denotes a much faster and lighter mode of locomotion (translated and adapted by Abbassi et al. in press).



Figure 5. *Dehnaripus incognitus* nov. **A–C.** Mound shaped footprints preserved as convex hyporeliefs in lower bedding plane of large slab, front footprints considered as pes and footprints behind as manus imprints; **D**, **E**. Preserved as convex hyporelief and including photogrammetric false-color depth map, sampled specimen, IFMI-683/1.

Discussion. Ellenberger (1980) introduced *Lophiopus* from the Eocene of France for tridactyl footprints with symmetrical lateral digits. *Lophiopus* latus is the most similar to *Plagiolophustipus*, and Santamaria et al. (1989–1990) distinguish *Plagiolophustipus* from *Lophiopus* by a little larger and its thick lateral digits.

The report of *Lophiopus* from the Eocene of Alborz Mountain of north Iran lacked adequate figures and description (Davoodi et al. 2016) and that report needs further investigation (Abbassi et al. in press). *Lophiopus* of Deh Nar is the second record of *Lophiopus* from the Tethyan realm.



—5 cm

Figure 6. *Dehnaripus incognitus* nov. in the studied block (A) and sampled parts of slab; **B**, **C**. Holotypes of pes and manus imprints with their photogrammetry photo (IFMI-683/2); **D**, **E**. Other pes and manus imprints and including photogrammetric false-color depth map their photogrammetry photo (IFMI-683/3).

Ichnospecies Lophiopus isp.

Fig. 7A-C

Material. One specimen, collected (IFMI-684).

Description. One tridactyl footprint preserved as convex hyporelief in the lower bedding plane of the fine-grained, dark-brown sandstone. This bedding plane comprises flute and groove casts. The surface of the

footprint is not smooth, and erosional structures encompass the footprint. One of the lateral digits shows three digital pad imprints, and digit III and the other lateral digit imprint are thick and lacking digital pad. The tips of the digits are sharp, the proximal rim of the footprint is curved and the sole imprint is not developed.

Discussion. Ellenberger, 1980 considered two ichnospecies for Lophiopus, L. lalus and L. rapidus. L. lalus has



Figure 7. A–C. *Lophiopus* isp. preserved as convex hyporelief with its photogrammetry photo and outline sketch, sampled (IFMI-684); D–F. *Moropopus elongatus* preserved as convex hyporelief, including photogrammetric false-color depth map, sampled (IFMI-685); *Moropopus elongatus* in lower bedding plane of large slab full of mud crack casts (G); H–I. Close up view of behind footprints with outline sketch; J–K. Front footprint with outline sketch.

a marked "heel mark" and an elongate digit III, whereas *L. rapidus* is wider, and its lateral or central digits are more rounded along the tips. No digital pads were mentioned for ichnospecies of *Lophiopus*. The studied footprints of the Deh Nar area show similar morphology to *Lophiopus* in their round proximal outline, undeveloped sole imprint and distinct lateral digit imprints.

Ichnogenus *Moropopus* Abbassi, Alinasiri & Lucas, 2017

Type ichnospecies. *Moropopus elongatus* Abbassi, Alinasiri & Lucas, 2017.

Emended diagnosis. Medium-sized tridactyl footprints with elongated oval to ellipsoidal to fusiform digit imprints. Two digital pads may be present in lateral digits. Digit imprints connect to metatarsus by a narrower proximal imprint. Lateral digits (digit II and IV) are smaller than the middle digit (digit III) and are curved toward the front. Digit III imprint is wider in the front. Digit III tip is completely curved, and the tips of lateral digits may curve or end in elongate sharp tips, like the claw imprints. Metatarsus imprints include two metatarsal pads with a complete rounded back, or with two lobes.

Discussion. The narrow proximal part of digit imprints is a distinctive feature of *Moropopus*, which distinguishes it from the other tridactyl ichnogenera of perissodactyls. The presence of sharp tips on the lateral digits of the pes imprint of the Deh Nar footprints caused an emended diagnosis of *Moropopus* and introduced a second ichnospecies of *Moropopus*.

In Asia, mammal tridactyl ungulate footprints have been reported from Early Tertiary of China (Lockley et al. 1999), Oligoene of India (Rajkumar and Klein 2014) and Eocene-Oligocene of Iran (Abbassi et al. 2015, 2017). Oligoene tridactyl footprints of India strongly resemble those described from China (Rajkumar and Klein 2014) and differ from Iran's Oligocene tridactyl footprints in morphology and size. Demathieu et al. (1984) reported Ronzotherichnus with short digit imprints not connected to the metatarsus imprint and thus differing from Moropopus. Usually, tridactyl footprints in perissodactyls show round outlines in the distal part of digits, however some ichnogenera of tridactyls have sharp tips in the lateral digits, such as Plagiolophustipus Santamaria et al. (1989–1990). Moropopus differs from Plagiolophustipus by its narrow digit III imprint.

Ichnospecies *Moropopus elongatus* Abbassi, Alinasiri & Lucas, 2017

Fig. 7D–K

Materials. One footprint sampled (IFMI-685) and two footprints of a trackway studied in the field.

Emended diagnosis. Tridactyl footprints with elongated digit imprints. Digit imprints are proximally narrower and

distally ellipsoidal and inflated. Digit tips are completely curved without claw imprints. Metatarsus imprints include two metatarsal pads with a complete rounded back.

Description. Tridactyl footprints preserved as convex hyporeliefs in lower bedding plane of the fine-grained sandstones. Sampled footprint (Fig. 7D-F, IFMI-685) includes circular digit imprints, lateral digits are fat with one digit pad, and middle digit (III) is incomplete. All digits connected by narrower imprint to metatarsal/ metapodial imprint. The metatarsal/metapodial imprint is oval with three proximal lobes. The unsampled two footprints belong to one trackway, preserved as convex hyporelief in a lower bedding plane of thick-bedded, dark brown sandstone. This bedding plane has abundant mud crack casts that interact with the footprints. These footprints comprise one to two fat circular digital pads, which connect by narrower imprints to metatarsal/metapodial imprints. The tips of the digits are round. The proximal parts of the metatarsal/metapodial imprints are round.

Discussion. *Moropopus* was established as monotypy from the Late Eocene of Iran (Abbassi et al. 2017), and by discovery of new *Moropopus* from Oligocene of Central Iran, with new morphological features, we prefer to establish a new ichnospecies for *Moropopus* and emended the diagnosis of *Moropopus elongatus*.

Ichnospecies Moropopus kashanensis isp. nov.

https://zoobank.org/0E24AF8D-52D9-4C29-A514-4FF98C339401 Fig. 8

Materials. Two footprints of one trackway, sampled (IFMI-686/1-2).

Holotype. specimen IFMI-686.

Etymology. *kashanensis* refers to Kashan city where the traces were found.

Type-locality. Iran, Esfahan (= Isfahan) province, Kashan township, west Ab Shirin, northwest Deh Nar, 34°19'N, 51°12'E.

Type horizon. lower Oligocene (Rupelian).

Diagnosis. *Moropopus* with tridactyl footprint in pes and manus imprints. Pes has elongated digit imprints; digit III is larger than the lateral digits II and IV. Tips of digits are completely round. The manus imprint has a digit III that is longer than the lateral digits. The tip of digit III is round, but lateral digits end with a distally sharp claw-like imprint.

Description. The smaller posterior footprint is considered as a pes imprint and it includes two digit imprints and one of the lateral digit and most parts of the metapodial imprints are omitted by weathering. Digits include one pedal circular imprint with round tips, and connect by a narrower imprint to the metapodial imprint. The anterior larger imprint is the manus imprint and it is distinguished by the sharp tip of the lateral digit imprints and it seems that the middle digit imprint has a round tip. The metacarpal imprint is circular, with a round proximal outline.

Discussion. The general morphology of *Moropopus* with elongated distally swollen digit imprints is traceable

in these footprints, but the distinctive feature is the sharp tips of lateral digits. Usually, perissodactyls have round distal outlines in hooves, and there are no records of sharp tips. The skeletal remains of pes and manus of perissodactyls anatomically comprise distally round phalanges (ungula) with or without medial fissure and covered by fat digital pads or round unguals. Instead, the unguals of artiodactyls usually have sharp tips.

Moropopus kashanensis however shows strongly sharp tips in lateral digits of the manus imprint. No secondary deformations such as drag marks or combination with non-biogenic structures were included in the detailed analysis of the tips of *Moropopus kashanensis*. Thus, we believe these footprints are a new ichnospecies of *Moropopus*.

Ichnogenus *Platykopus* Sarjeant, Reynolds & Kissell-Jones, 2002

Type ichnospecies. *Platykopus ilycalcator* Sarjeant, Reynolds and Kissell-Jones (2002).

Diagnosis. Large plantigrade footprints with digits close to manual/pedal pad. Manus width is similar to that of the pes, with the pes being slightly narrower and elongated due to a metatarsal pad. Five digits on manus and pes are clawed, and digits II–V are of equal length on a quadratic manus with digit I offset. Digits I–V form a symmetrical arc around the pes, with digits I and V being shorter than II and IV.

Discussion. Sarjeant et al. (2002) introduced Platykopus from Late Miocene of Nevada for large plantigrade footprints with digits close to manual/pedial pad and compared its tracks to those of creodonts and amphycyonids. Recently, Platykopus has been identified by ichnologists for medium to large, pentadactyl plantigrade footprints with an undeveloped metatarsus imprint in manus. Abbassi (2010) attributed footprints that are semiplantigrade with five short digits with distinct digit V from the Miocene of Iran to Platykopus, and he reported Platykopus from the Oligocene of the Eastern Mountains of Iran (Abbassi et al. 2015). Botfalvai et al. (2023) re-examined large pentadactyl footprints from the Miocene Ipolytarnóc of Hungary by 3D methods and concluded that footprints previously defined as Bestiopeda maxima should be reclassified under the Platykopus ichnogenus as Platykopus maxima. Platykopus differs from Zanclonychopus Sarjeant and Langston (1994) by larger width and shorter digit imprints.

Ichnospecies *Platykopus stuartjohnstoni* Lucas & Schultz, 2007

Fig. 9

Materials. Three footprints of a trackway, molded by plaster (IFMI-687/1-3).

Diagnosis. Footprints of an ursid that differ from *Platykopus ilycalcator* in having: manus narrower than pes,



Figure 8. *Moropopus kashanensis* nov. in the studied slab (**A**); **B–D.** Holotype of pes imprint with outline sketch and photogrammetry photo (IFMI-686/1); **E–I.** Holotype of manus imprint with its outline sketch (**F**) and photogrammetric false-color depth maps, (**G**, **H**) and closeup of digit claw imprint (**I** arrow), (IFMI-686/2).



Figure 9. *Platykopus stuartjohnstoni* in the studied slab (A), and closeup view of footprints (B, E, H), with photos of plaster molds (C, F, I IFMI-687/1-3) and photogrammetric false-color depth maps (D, G, J).

clear separation of metatarsal/metacarpal pads from digital pads, digits II-V of subequal size on the pes, metatarsal pad on pes wide and short and only four pes digit imprints.

Description. Three footprints of a trackway were poorly preserved as concave epireliefs on the upper bedding plane of dislocated, thick bedded large sandstone slab. Imprints of pes and manus are not distinguishable and it seems that one set of footprints of the trackway has been preserved. The first footprint is circular in outline, and no digit imprints are visible (Fig. 9B, D). Footprint 2 includes five-digit imprints that are visible in the 3D image as short and having sharp tips. Metatarsal imprint is short and has a straight proximal outline (Fig. 9E–G). The third footprint shows round, small digit imprints without a claw imprint and includes a circular outline in the metatarsal imprint (Fig. 9H–J).

Discussion. Platykopus has been attributed to large trackmakers such as Amphicyonidae or Ursidae by its main feature as large plantigrade footprints, with all five digits, close to the manual/pedial pad. Dietrich (2011) named the large cave bear footprints Ursichnus europaeus and noted that Ursichnus have all digital pads spaced from the metatarsal/metapodial imprints, as an anatomical feature and differs from *Platykopus*. Platykopus includes three ichnospecies: P. ilycalcator Sarjeant et al. (2002) (type ichnospecies of the ichnogenus; Late Miocene, Nevada USA), P. stuartjohnstoni Lucas and Schultz (2007) (Upper Miocene, Texas, USA), and P. maxima (Kordos, 1985) (Miocene, Hungary, new combination by Botfalvai et al. 2023). The studied footprints from the Deh Nar area show triangular digit imprints without distinct claws in the tips of digits; this indicates a difference from P. ilycalcator and P. maxima. These imprints are closely similar to P. stuartjohnstoni. Usually, Platykopus was preserved as pentadactyl imprints, and the type materials of P. stuartjohnstoni is tetradactyl. Lucas and Schultz (2007) believed that tetradactyly of P. stuartjohnstoni is an extramorphological feature that may reflect either an extremely small pes digit I or a walking pattern in which digit I was not impressed. The studied footprints of Deh Nar are poorly preserved and the pes and manus imprint are not distinguishable.

Ichnogenus Zanclonychopus Sarjeant & Langston, 1994

Type ichnospecies. *Zanclonychopus cinicalcator* Sarjeant and Langston (1994).

Diagnosis. Plantigrade footprints, with manus and pes of similar size and with all digits strongly clawed. Digits II to IV most deeply impressed and forming, with palm or sole, an approximately oval shape (more marked in the pes); digit I set off to one side and impressed lightly or not at all. Tips and claws of inner digits curving outward, of outer digits curving inward. Inner phalangeal pads of pes fused; those of manus free.

Discussion. Sarjeant and Langston (1994) considered Creodonta as the trackmaker for *Zanclonychopus*, and compared it with American black bear for large footprints. The modern bears have large metatarsal and short metacarpal imprints with one pedal digit and distinctive long claws imprints. *Zanclonychopus* have the same sizes in the metatarsal and metacarpal imprints with long two to three pedal imprints. Exactly, *Zanclonychopus* differs from *Ursichnus* Diedrich (2011) by its position of digit I, shorter digit imprints and absence of claw imprints. *Hirpexipes* Sarjeant et al. (2002) is known as semidigitigrade to semiplantigrade footprints with all digits long and with sharp claws. *Zanclonychopus* has stocky and shorter digit imprints.

Ichnospecies Zanclonychopus isp. Fig. 10

Material. Two footprints of a trackway, molded by plaster (IFMI-688).

Description. These footprints belong to manus and pes imprints of a trackway, preserved as convex hyporelief on the lower bedding plane of a large, thick slab of sandstone (Fig. 10A–C). Half of the pes imprint is preserved, and the manus imprint is complete. Pes and manus are separated and do not overlap. Based on the size and depth of penetration, the smaller front footprint was considered as pes and the larger one behind as a manus imprint; usually, mammals have a larger manus footprint. The metatarsal/metacarpal are the deepest



Figure 10. *Zanclonychopus* isp. in the studied slab (A), and its plaster mold (B IFMI-688), with sketch (C) and close up view, sharp tips of digit imprints are distinct (D). Photogrammetric false-color depth maps in perpendicular and lateral views (E, F).

part of the footprints, and digit imprints are not clear in footprints; the claw imprints, however, are distinct as a drop-shape slightly curved with sharp tips (Fig. 10D). Four digit and claw imprints are visible in the manus with an unclear digit V imprint. The pes imprint is not deeper than the manus and comprises unclear digit imprints (Fig. 10E, F). It seems that trackway width is larger, and the manus has more inward orientation than the pes.

Discussion. Zanclonychopus was recorded as a large carnivore footprint with monotypy and has not previously been reported outside of North America. The studied footprints from Deh Nar have indistinct digit imprints, but one side has inclined claw imprints that are clear. Based on the size and morphology of the studied footprints, Zanclonychopus is the nearest ichnogenus name for the Deh Nar footprints, and this is the first report of Zanclonychopus outside of North America.

Discussions

The report of vertebrate tracks from the Oligocene LRF of Central Iran is a new step in the detection of paleobiogeography of the Iranian Plateau. This reconstruction is important, because the Arabian-Eurasian collision was a unique opportunity for the creation of a natural land bridge in the Middle East region, and caused the migration and amalgamation of terrestrial vertebrates of two sides of the Tethys Ocean, between Gondwana and Eurasia. Paleogene-Neogene tracksites of the Iranian Plateau are key areas for the study of the evolution of the Middle East ichnofauna during this era. A total of 19 different tracksites have been described in the Eocene to Quaternary of the Middle East (Abbassi and Dashtban 2021; Abbassi 2022), and 14 of them located in the Iranian territory. Abbassi (2022, table 2; and references therein) summarized Cenozoic vertebrate ichnites from

	Bird	Mammal	Reptile
Quaternary	No report	Chiropterichnus scabens	No report
		Chiropterichnus garmabensis	
Pliocene	No report	No report	No report
Miocene	Anatipeda recurvirostra	Bifidipes velox	Crocodylopodus isp.
	Antarctichnus fuenzalidae	Canipeda longigriffa	Gandopodichnus caesellum
	Ardeipeda filiportatis	Creodontipus isp.	Hatcherichnus sanjuanensis
	Ardeipeda incerta	Felipeda isp.	Merthykhuwaripus conicus
	Aviadactyla media	Felipeda lynxi	Batrachichnus salamandroides
	Aviadactyla vialovi	Pazhanipeda kiyani	Lunichnium isp.
	Avidactyla isp.	Pecoripeda gazella	Sauripes isp.
	Avipeda gryponyx	Pecoripeda malphaea	
	Avipeda isp.	Platykopus isp.	
	Avipeda rastini	Proboscipeda enigmatica	
	cf.Ornithotarnocia lambrechti	Lamaichnum alfi	
	Charadriipeda disjuncta	Lamaichnum isp.	
	Charadriipeda isp.	Pecoripeda satyri	
	Culcitapeda incerta	Pecoripeda isp.	
	Culcitapeda isp.	Bifidipes velox,	
	Fuscinapeda texana	Lamaichnum guanicoe,	
	Gruipeda dominguensis	Pecoripeda amalphaea,	
	Gruipeda intermedia	Pecoripeda isp.	
	Gruipeda isp.	Canipeda isp.	
	Iranipeda abeli	Felipeda isp.	
	Koreanaornis hamanensis		
	Persiavipes gulfi		
	Sarjeantopodus clinodactylus		
Oligocene	Ardeipeda egretta	Dehnaripus incognitus	No report
	Aviadactyla vialovi	Khafipus khadari	
	Avipeda phoenix	Lophiopus isp.	
	Gruipeda dominguensis	Moropopus elongatus	
	Gruipeda intermedia	Moropopus kashanensis	
		Palaeotheriipus isp.	
		Platykopus isp.	
		Platykopus stuartjohnstoni	
		Zanclonychopus isp.	
Eocene	Avipeda isp.	Diplatriopus isp.	No report
	cf. Charadriipeda isp.	Gambapes hastatus	
	Gruipeda lambrechti	Lophiopus isp.	
		Moropopus elongatus	
		Musaltipes taromi	
		Palaeotheriipus isp.	
		Palaeotheriipus sarjeanti	
		Proboscipeda enigmatica	
		cf. Proboscipeda isp.	
		Pycnodactylopus cf. achras	
Paleocene	No report	No report	No report

Table 3. Cenozoic vertebrate ichnotaxa in the Iranian Plateau.

the main geological zones of Iran (Table 3, updated here): while no body fossils of mammals have been so far reported from the Eocene of Iran, several Eocene vertebrate footprints were reported from Iran, which includes footprints of birds, perissodactyls (proboscidean, tridactyl mammals, like tapirs and rhinos), small artiodactyls, carnivores (Felidae, Mesonychidae), and hopping, rodent-like mammals.

Composition of the Oligocene biotas of Iran, restricted to bird and mammal footprints, includes ursine-like animals with plantigrade pentadactyl footprints, tridactyl perissodactyls and avian footprints. The Miocene deposits, however, comprise diverse and abundant footprints of birds, mammals and reptiles. This ichnodiversity is not only caused by the large amount of surveying of Miocene deposits, but also resulted from extensive outcrops of Miocene terrestrial sediments in this country. There are no reports about Paleocene and Pliocene footprints, and Quaternary vertebrate ichnites include bats ichnites, preserved as subfossils in the cave sediments. The Oligocene Deh Nar tracksite shows numerous ichnotaxa of bird and mammal footprints, and some of them are in common with previous reports:

Ardeipeda egretta Aviadactyla vialovi Avipeda phoenix Gruipeda dominguensis Dehnaripus incognitus Lophiopus isp. Moropopus elongatus Moropopus kashanensis Platykopus stuartjohnstoni Zanclonychopus isp.

Eocene and Oligocene bird footprints belong to small to medium size, tri- to tetradactyl birds with low ichnotaxonomic diversity; Miocene deposits, however, show a large variety of bird footprints and include small to large webbed and unwebbed bird footprints. The increase is traceable in mammal footprints also, and, of course, the appearance of reptile footprints, also; so that eight mammal ichnogenera were identified from the Eocene and Oligocene of Iran, increasing to 15 ichnogenera reported from the Miocene of Iran. If we attribute these changes to trackmaker variations, thus succession of faunas of Paleogene to Neogene forms, was accompanied by increase of biodiversity. This biodiversity resulted from the confluence of Gondwanan and Eurasian faunas, after the collision between the Gondwanan and Eurasian continents by the Arabian-Iranian plateaus, which occurred between the early Oligoene to early Miocene (McQuarrie and van Hinsbergen 2013; Song et al. 2023). Among the studied footprints, the small bird footprints are attributed to small, incumbent anisodactyl shoreline birds, such as sandpipers, and the larger of them to Gruiformes and Ciconiiformes. Most probably, the mammal tridactyl footprints of Deh Nar made by three toed, medium- to large sized terrestrial herbivores perissodactyls such as Tapiroidea. *Platykopus* and *Zanclonychopus*, however were remained by large carnivores such as Amphicyonidae or Ursidae.

There are some endemic ichnogenera of herbivore footprints (*Moropopus*) and common carnivore footprints in the Paleogene are *Platykopus*, changing in the Neogene to abundant artiodactyl footprints with the appearance of felids and canids (Abbassi 2022).

Outside the Iranian Plateau, Mesci et al. (2019) reported mammal tracks from late Oligocene sediments of the Sivas basin, central Türkiye, and attributed them to ungulates. These footprints are poorly preserved in the clayey sediments of Karayün Formation, and details of the tracks are not clear. However, numerous artiodactyls and proboscideans were identified. The ichnoassemblage of Karayün Formation is different from Deh Nar and mostly similar to Miocene ichnites of Central Iran.

Researchers have usually believed that the Cenozoic Era was a time of very substantial rise in global biodiversity, especially at the lower taxonomic levels of species and genus, and Cenozoic diversification was concentrated in low-latitude and tropical regions, where the climate was warmer (Crame and Rosen 2002). After the Middle Eocene Climatic Optimum (MECO, ~40 Ma) as a warming event (Zachos et al. 2001, 2005; Bohaty et al. 2009), the Eocene-Oligocene transition (ca. 33.5 Ma) is known as the first major decline in Cenozoic global temperatures, and interpreted as a time of drastic global cooling and associated drying (Zachos et al. 2001; DeConto and Pollard 2003). Eocene-Oligocene climate changes are associated with continuous Neo-Tethyan seaway closure during the Eurasia and India-Arabia-Africa convergence and growth of the Alpine-Himalayan Mountain belt, accompanied by a shift towards modern patterns of ocean currents (McQuarrie et al. 2003; Allen and Armstrong 2008). Cool and dry conditions during the beginning of the Early Oligocene gradually changed to warm conditions of the Late Oligocene, and caused deposition of extensive terrestrial red beds facies, such as LRF, in west and central Asia (Sun et al. 2010; Kargaranbafghi and Neubauer 2018; Wu et al. 2018; Jenny et al. 2024). Late Oligocene terrestrial conditions of Central Iran did not last long-term and shifted to shallow marine carbonate seaways of the Qom Formation (Daneshian and Ramezani Dana 2007; Reuter et al. 2009; Mohammadi et al. 2013, 2024). The Eocene-Oligocene cooling was coeval with an extinction event and faunal turnover between 33.9 and 33.4 million years ago, long known as the "Grande Coupure" corresponding to a major turnover in mammalian faunas, and to an important change in mammalian community structure (Legendre and Hartenberger 1992; Costa et al. 2011; Pélissié et al. 2021). It may be possible to evaluate the "Grande Coupure" event in the Iranian Plateau, so that there are increases in the size of bird tracks, but decreasing size of mammal footprints. Retallack (1983) associated fossil mammal remains from the Cretaceous

to Oligocene with decreasing mammal size. On the other hand, there is the appearance of new trackmakers with an increasing number of carnivore trackmakers in the Oligocene compared to the Eocene, and the appearance of felids in the Miocene, confirmed by abundant footprints in Central Iran.

Conclusion

The LRF is a good reference for terrestrial vertebrate ichnology of the Oligocene in Central Iran. It includes alternations of red beds of siliciclastic sediments that were deposited under warm evaporitic conditions. The discovery of vertebrate footprints in the LRF in the Deh Nar area, near Kashan, Central Iran, is an effective step for completing vertebrate distribution in the Cenozoic of the Iranian Plateau. Footprints comprise bird and mammal footprints. Small to large bird footprints were attributed to Ardeipeda egretta, Aviadactyla vialovi, Avipeda phoenix and Gruipeda dominguensis. Mammal footprints are identified as Dehnaripus incognitus, Lophiopus isp., Moropopus elongatus, Moropopus kashanensis, Palaeotheriipus isp., Platykopus stuartjohnstoni and Zanclonychopus isp. Among these footprints, Dehnaripus incognitus and Moropopus kashanensis are new ichnotaxa, and Zanclonychopus isp. is reported for the first time from Iran.

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