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ABSTRACT

Knowledge of the Palaeogene avifauna of East Asia is scarce, and only a few fossils have been described thus far. A tarsometatarsus from the upper Eocene Na Duong Basin represents the first Palaeogene fossil bird from Vietnam. The fossiliferous sediments in the Na Duong Basin originated from an aquatic ecosystem but also yielded terrestrial animal and plant remains suggesting a dense forest habitat surrounding an ancient lake. In accordance, the Na Duong Basin tarsometatarsus is compared with extant aquatic, terrestrial and arboreal bird species, but because of diagenetic compression and fragmentary preservation, it is difficult to classify the bone. Nevertheless, the specimen exhibits a distinctive morphology and is potentially referable to an endemic neognath unknown from other Palaeogene localities outside of Vietnam.

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Tobias Massonne [tobias.massonne@uni-tuebingen.de], Senckenberg Center of Human Evolution and Palaeoecology, Tübingen, Germany; Department of Geosciences, Eberhard-Karls-Universität Tübingen, Tübingen, Germany; Madelaine Böhme [m.boehme@ifg.uni-tuebingen.de], Senckenberg Center of Human Evolution and Palaeoecology, Tübingen, Germany; Department of Geosciences, Eberhard-Karls-Universität Tübingen, Tübingen, Germany; Gerald Mayr [gerald.mayr@senckenberg.de], Senckenberg Research Institute and Natural History Museum Frankfurt, Ornithological Section, Frankfurt am Main, Germany.

WHILE there is a rich fossil record of birds from the Cretaceous of East Asia, current knowledge of Palaeocene and Eocene avifaunas from southern and eastern Asia is scarce (Kurochkin 1976, Rich *et al.* 1986, Nessov 1992, Hou 2003, Mayr 2009, 2022, Zelenkov & Kurochkin 2015, Hood *et al.* 2019). More substantial fossils are mainly documented from the Palaeocene and Eocene of India, Mongolia and China and include, among others, species that were assigned to the Anseriformes, Galliformes, Mirandornithes, Gruiformes, and Strigiformes (e.g., Hwang *et al.* 2010, Mayr *et al.* 2010, Kurochkin & Dyke 2011, Wang *et al.* 2012, Mayr *et al.* 2013, Stidham & Ni 2014, Zhao *et al.* 2015, Hood *et al.* 2019, Zelenkov 2021a, 2021b). Fossil remains referred to Gastornithiformes are known from the early Eocene of China (Buffetaut 2013), and there is a specimen of the suliform clade Protoplotidae from Sumatra (Lambrecht 1931), and a putative record of Threskiornithidae from the upper Eocene Pondaung Formation of Myanmar (Stidham *et al.* 2005). In addition, late Eocene and early Oligocene fossils attributed to Eogruidae and Ergilornithidae have been reported from Mongolian localities (Clarke *et al.* 2005, Hood *et al.* 2019, Mayr & Zelenkov 2021, Mayr 2022).

In this study, we describe an avian tarsometatarsus from the Na Duong Basin in Northern Vietnam, that was excavated in 2011 (Böhme *et al.* 2013). The bone represents the first record of fossil birds from the Na Duong Basin, and it is also the first evidence of bird remains from the Eocene of Vietnam. As such, it improves our knowledge of the east Asian avifaunas as a whole and Vietnam in particular. Furthermore, the specimen adds to the significance of the Na Duong Basin as a Lagerstätte from the Eocene of East Asia.

Palaeogene bird fossils from Vietnam have not been previously described, but a comprehensive Pleistocene avifauna has been recently published (Boev 2022). This latter study reported various species that no longer occur in Vietnam, but all represent modern taxa, and in most cases, the identification of fragmentary remains requires corroboration with more material.

Geological setting

The Na Duong Basin is located in northern Vietnam near the Chinese border (Fig. 1). It represents one of only a few areas in East and Southeast Asia with a complete sequence of continental sediments from the middle Eocene to lower Oligocene (Böhme *et al.* 2013). The basin is part of the Cao Bang-Tien Yen fault system and covers an area of 45 km^2. The middle to upper Eocene (late Bartonian–Priabonian) Na Duong Formation is 240 m thick with the upper 140 m section being exposed in the Na Duong open cast coal mine. Böhme *et al.* (2013) biochronologically correlated the fossil mammals from Na Duong (layer 80) with the Chinese Naduan land mammal age (= Ulangochuian stage: Wang *et al.* 2019), and provided an 39–34 Ma age estimate.

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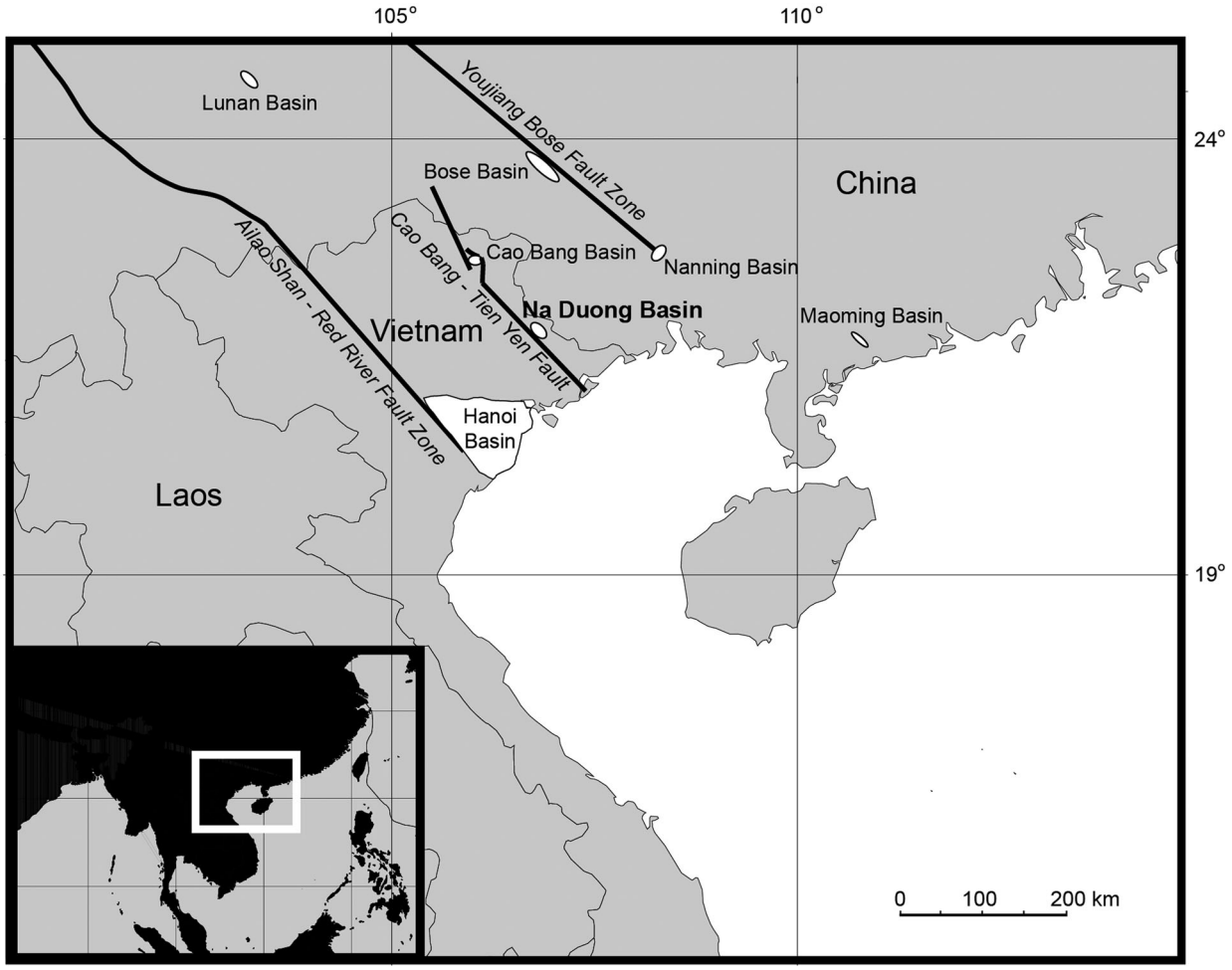

Figure. 1. Map of northern Southeast Asia showing the Na Duong Basin in northeast Vietnam (after Böhme *et al.* 2013).

Palaeomagnetic data calibrate the Ulangochuian at between 40 and 37 Ma (Wang *et al.* 2019).

The tarsometatarsus described herein was excavated within the transition zone between the coaly shale of the main seam and the underlying dark-brown claystone (layer 80).

The layer 80 sediments are lacustrine lignitic shales that were deposited at a time of tropical to warm-subtropical climate. The region was also undergoing a transition from shallow pond systems to a large anoxic lake (Böhme *et al.* 2013, Garbin *et al.* 2019). This fossil ecosystem has yielded both aquatic and terrestrial faunal elements. The bird specimen occurred sympatrically with two species of crocodile (*Orientalosuchus naduongensis* Massonne, Vasilyan, Rabi & Böhme, 2019 and *Maomingosuchus acutirostris* Massonne, Augustin, Matzke, Weber & Böhme, 2021), the anthracothere *Bakalovia orientalis* Böhme, Aiglstorfer, Antoine, Appel, Halvik, Métais, Phug, Schneider, Setzer, Tappert, Tran, Uhl & Prieto, 2013, the rhinocerotine *Epiaceratherium naduongense* Böhme, Aiglstorfer, Antoine, Appel, Havlik, Métais, Phug, Schneider, Setzer, Tappert, Tran, Uhl & Prieto, 2013, a strepsirrhine (Chavasseau *et al.* 2019), fishes representing the families Amiidae and Cyprinidae, and at least two species of turtle (Böhme *et al.* 2013, Garbin *et al.* 2019).

Materials and methods

Osteological terminology is based on Baumel & Witmer (1993). Micro-CT (μCT) scanning was undertaken on a Nikon (Minato, Tokyo, Japan) XTH 320 μCT scanner in the 3D Imaging Lab of the Senckenberg Centre for Human Evolution and Palaeoenvironment (SHEP) and University of Tübingen (UT), Germany. This used an X-ray tube containing a multi metal reflection target with a maximum acceleration voltage of 225 kV. Scan parameters included 210 kV and 90 μA with a voxel size of 27.31305 mm, and utilization of a 0.1 mm thick copper filter. Segmentation used threshold and brush tools in Amira v.2021.1 (Thermo Fisher, Waltham, Massachusetts, USA), with the surface mesh exported as a STL file. The 3D-Model is provided in Supplementary Data 1.

Institutional abbreviations

GPIT, Geologisch-Paläontologisches Institut Tübingen, Tübingen, Germany. NMNH, National Museum of Natural History, Washington, DC, USA; SMF, Senckenberg Museum, Frankfurt am Main, Germany.

Systematic palaeontology

Aves Linnaeus, 1758

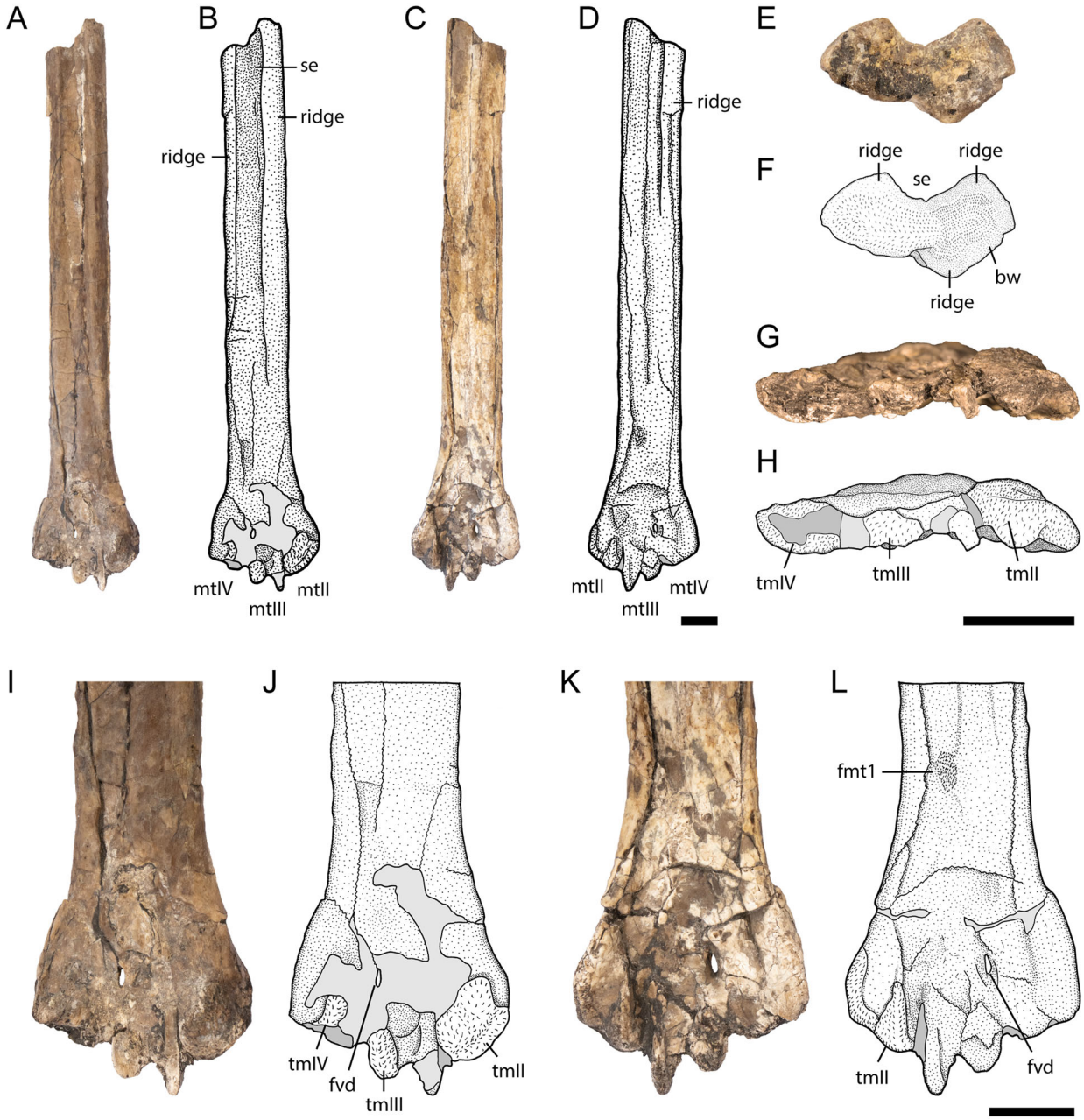

Figure. 2. Neognathae *incertae sedis* (GPIT-PV-122865). Tarsometatarsus in **A, B**, dorsal view; **C, D**, plantar view; **E, F**, cross-section of the proximal end of the shaft; **G, H**, distal view; **I, J**, enlargement of the distal end in dorsal view; **K, L**, enlargement of the distal end in plantar view. Abbreviations: bw, bone wall; fmt1, fossa metatarsi 1; fvd, foramen vasculare distale; mt, metatarsale; se, sulcus extensorius; tm, trochlea metatarsi. Scale bar = 5 mm.

Neognathae *incertae sedis*
(Fig. 2)

Referred material. GPIT-PV-122865, a partial right tarsometatarsus.

Locality, unit and age. Layer 80 of the Na Duong coal mine in northern Vietnam (21°42.2′N, 106°58.6′E); Na Duong Formation (Na Duong Basin), late Bartonian to Priabonian (late Eocene), 39–35 Ma (Böhme *et al.* 2013).

Description. GPIT-PV-122865 represents the distal part of a right tarsometatarsus with a shaft approximately covering half to two-third of its original length (Fig. 2). Distal width = 15.2 mm; trochlea metatarsi III width = 5.0 mm; shaft width = 8.3 mm; foramen vasculare distale length = 1.5 mm. Diagenetic compression has flattened the bone dorsoplantarly, and both its plantar surface and the dorsal surface of the distal end are weathered.

The shaft is elongate with an equal width over the preserved length, but it is much wider than the trochlea metatarsi III. In dorsal view (Fig. 2A, B), GPIT-PV-122865 has a deep sulcus extensorius that is proximally bordered by prominent ridges; the shaft becomes flat and smooth towards the distal one-third of the bone (see Supplementary Data 1). On the plantar surface (Fig. 2C, D), a sulcus is bordered by a prominent latera ridge. The fossa metatarsi I is

situated on the plantar surface medial to the midline of the bone, and appears to be oval in outline but is poorly preserved (Fig. 2K, L).

The foramen vasculare distale is very small and oval-shaped. The canalis interosseus distalis cannot be discerned. The incisurae intertrochleares lateralis and medialis are not evident due to mediolateral flattening, as well as the dorsoplantar compression (Fig. 2G–L, S1).

The trochlea metatarsi II is shorter than the trochlea metatarsi III and has a medially slanting distal margin; although it does not form a plantarly directed projection. A broad sulcus on the plantar surface is bounded by two proximodistally oriented large ridges. The distal portion of the trochlea metatarsi III is damaged with ~50% being lost. The narrow plantar rims are widely separated by a large furrow, which is likely to be a taphonomic artefact. The trochlea metatarsi IV is mediolaterally broad, but its distal portion is damaged. It also lacks a distinct trochlear furrow on the preserved surface and appears to be slightly larger than the other trochleae (Fig. 2G–L, S1). The bone wall is thick in cross-section (Fig. 2E, F).

Discussion

Extant bird species can be separated into two higher-level clades: Palaeognathae and Neognathae. GPIT-PV-122865 is most likely a representative of the latter group. The only long-legged palaeognaths present during the Eocene in Eurasia are members of the Palaeotididae and Eogruidae (Mayr 2022). Although GPIT-PV-122865 shares with the latter taxa a long shaft, and the presence of a trochlea metatarsi III that reaches further distally than the trochleae metatarsorum II and IV, it differs in many other characteristics. For example, GPIT-PV-122865 has a more robust shaft, smaller foramen vasculare distale, narrower incisurae intertrochleares lateralis and medialis, and equally-sized trochleae metatarsorum. This character combination precludes referral to either Palaeotididae or Eogruidae.

The Na Duong Basin late Eocene palaeoenvironment was characterized by a transition from shallow ponds to a large anoxic lake supporting rich aquatic and terrestrial faunas (Böhme *et al.* 2013, Garbin *et al.* 2019). We therefore compared GPIT-PV-122865 with extant aquatic and semi-aquatic members of Aequornithes and Gruiformes, together with terrestrial representatives of Galliformes, and arboreal members of Coliiformes, which have similar tarsometatarsal morphologies (Fig. 3). The distal width of GPIT-PV-122865 is comparable to *Gallus gallus* Linnaeus, 1758 (Fig. 3B, H), which exhibits a trochlea metatarsi III reaching further distal than the trochleae metatarsorum II and IV, and trochleae that are subequal in size. The common presence of a small rectangular process on the medial flank of the trochlea metatarsi II is also visible in ventral view. By contrast, the shaft in GPIT-PV-122865 is longer than that of *G. gallus* and has an elongate extensor sulcus along its dorsal surface as well as a plantar ridge (absent in *G. gallus*). In addition, the foramen vasculare distale is much smaller in GPIT-PV-122865, and the incisura intertrochlearis lateralis is nearly closed (otherwise much wider in *G. gallus*). Finally, the trochleae metatarsorum II and IV reach an equal distal distance in GPIT-PV-122865, whereas the trochlea metatarsi II is further proximally oriented in *G. gallus*.

Birds with elongate tarsometatarsi that may have occurred in the Na Duong Basin palaeoenvironment include members of the Ardeidae (herons), Ciconiidae (storks and allies), and Gruidae (cranes). We therefore used *Ardea herodias* Linnaeus, 1758 (Ardeidae; Fig. 3C, I), *Mycteria americana* Linnaeus, 1758 (Ciconiidae; Fig. 3D, J) and *Antigone canadensis* (Linnaeus, 1758; Gruidae; Fig. 3E, K) for comparisons. These taxa share an elongate tarsometatarsal shaft, although GPIT-PV-122865 has a more marked sulcus extensorius along the dorsal surface of the shaft and a plantar ridge on the ventral surface, and broader shaft proportions, as well as a smaller foramen vasculare distale. GPIT-PV-122865 specifically shares equally-sized trochleae metatarsorum and relatively narrow incisurae intertrochleares lateralis and medialis, together with a small plantar opening of the foramen vasculare distale with *A. herodias*. GPIT-PV-122865 otherwise differs in its much smaller dorsal opening for the foramen vasculare distale, and a more distally projected trochlea metatarsi III.

Similarities with *M. americana* include a relatively narrow incisurae intertrochleares lateralis and medialis, and a trochlea metatarsi III that is more distally projected than the trochlea metatarsorum II and IV. Conversely, GPIT-PV-122865 lacks a proximally positioned canal leading into the foramen vasculare distale, and the trochlea metatarsi III is subequal to the size of the trochleae metatarsorum II and IV.

GPIT-PV-122865 shares the possession of a trochlea metatarsi III that reaches further distally than the trochleae metatarsorum II and IV with *A. canadensis*. However, GPIT-PV-122865 differs in having narrower incisurae intertrochleares lateralis and medialis, the trochlea metatarsi II having the same distal extent as the trochlea metatarsi IV, and the trochleae metatarsorum being of equal size.

Amongst arboreal birds, GPIT-PV-122865 is comparable to *Colius striatus* Gmelin, 1789 (Fig. 3F, L) in overall tarsometatarsus shape, the robust shaft, small foramen vasculare distale, equally sized trochleae metatarsorum, and narrow incisurae intertrochleares lateralis and medialis. By contrast, GPIT-PV-122865 has a more marked sulcus extensorius along the dorsal surface of the shaft and a plantar ridge along its ventral surface, as well as the trochlea metatarsi III that projects further distally than the trochleae metatarsorum II and IV. In addition, the general size difference is substantial.

Well-studied Palaeogene avian fossil assemblages from the Palearctic region also include stem group representatives of Strigiformes (owls) and Psittacopasseres (parrots and passerines); however, the tarsometatarsus of these lineages differs significantly in proportions and morphology of the distal extremity compared to GPIT-PV-122865 (Mayr 2022).

The lacustrine palaeohabitat of the Na Duong Basin was surrounded by a dense dipterocarpacean swamp forest, as indicated by preserved leaves, woods and resin (Böhme

Figure. 3. Tarsometatarsi comparisons. Neognathae *incertae sedis* (GPIT-PV-122865) in **A**, dorsal and **G**, plantar views; *Gallus gallus* (Galliformes) (GPIT-PV-122866) in **B**, dorsal and **H**, plantar views; *Ardea herodias* (Pelecaniformes) (NMNH 555715) in **C**, dorsal and **I**, plantar views; *Mycteria americana* (Ciconiiformes) (NMNH 16295) in **D**, dorsal and **J**, plantar views; *Antigone canadensis* (Gruiformes) (NMNH 432705) in **E**, dorsal and **K**, plantar views; *Colius striatus* (Coliiformes) (SMF 8019) in **F**, dorsal and **L**, plantar views. Images of NMNH 555715, NMNH 16295 and NMNH 432705 obtained from the open-access database of the Smithsonian Institution, Washington DC, USA: https://collections.nmnh.si.edu/search/birds/. Scale bar = 5 mm.

et al. 2013). Estimates of tree density and canopy height suggest ~600 individual trees/ha and a maximum canopy height of around 35 m, which is compatible with swamp forests found in Southeast Asia today (Böhme *et al.* 2013). Like these modern settings, we expect that the avian fauna was diverse and incorporated a range of arboreal, ground-dwelling, aquatic or semi-aquatic species. Unfortunately, because of the poor preservation, GPIT-PV-122865 cannot be identified beyond Neognathae *incertae sedis*. Nonetheless, GPIT-PV-122865 does provide the first insight into the Na Duong Basin bird assemblage and offers a novel Palaeogene avifaunal occurrence for East Asia.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

ORCID

Tobias Massonne http://orcid.org/0000-0002-6782-5280
Gerald Mayr http://orcid.org/0000-0001-9808-748X

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