Taylor & Francis
Taylor & Francis Group

Historical Biology
An International Journal of Paleobiology

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/ghbi20

Nearly complete leg of an unusual, shelduck-sized anseriform bird from the earliest late Miocene hominid locality Hammerschmiede (Germany)

Gerald Mayr, Thomas Lechner & Madelaine Böhme

To cite this article: Gerald Mayr, Thomas Lechner & Madelaine Böhme (2022): Nearly complete leg of an unusual, shelduck-sized anseriform bird from the earliest late Miocene hominid locality Hammerschmiede (Germany), Historical Biology, DOI: 10.1080/08912963.2022.2045285

To link to this article: https://doi.org/10.1080/08912963.2022.2045285

HISTORICAL BIOLOGY
https://doi.org/10.1080/08912963.2022.2045285

Taylor & Francis
Taylor & Francis Group

OPEN ACCESS Check for updates

Nearly complete leg of an unusual, shelduck-sized anseriform bird from the earliest late Miocene hominid locality Hammerschmiede (Germany)

Gerald Mayr[a], Thomas Lechner[b] and Madelaine Böhme[b]

[a]Ornithological Section, Senckenberg Research Institute and Natural History Museum Frankfurt, Frankfurt Am Main, Germany; [b]Senckenberg Centre for Human Evolution and Palaeoenvironment (HEP), Eberhard Karls University Tübingen, Institute for Geoscience, Tübingen, Germany

ABSTRACT

We describe leg bones of a larger-sized representative of the Anatidae from the Tortonian of the Hammerschmiede clay pit in southwestern Germany. *Allgoviachen tortonica*, n. gen. et sp. differs from most other representatives of the Anatidae in tarsometatarsus characters. The holotype is among the most substantial records of an anatid from this stratigraphic period in Central Europe and shows unusual morphological features that impede a straightforward phylogenetic assignment. In overall proportions, the tarsometatarsus resembles that of the extant taxon *Sarkidiornis* and some Tadornini, whereas the hypotarsus morphology differs from all extant Anatidae. Because of its resemblance to the early Miocene taxa *Paranyroca* and *Cygnopterus*, the new species may be a stem group representative of the Anatidae, but more osteological data are required for a firm phylogenetic placement. We show that anseriform birds exhibit a previously unnoticed diversity of the ungual phalanges of the pedal digits, and the curved unguals of the fossil indicate a predominantly non-aquatic way of living. The Hammerschmiede avifauna also includes a very small anseriform, which may belong to the extinct taxon *Mioquerquedula*; equally small species of the Anatidae are today restricted to tropical and subtropical regions.

ARTICLE HISTORY
Received 1 November 2021
Accepted 18 February 2022

KEYWORDS
Allgoviachen tortonica, n. gen. et. sp.; Anatidae; Aves; fossil birds; Hammerschmiede locality; Tortonian

Introduction

Extant Anseriformes include the South American Anhimidae (screamers) and the Australo-Papuan Anseranatidae (magpie-geese), which are successive sister taxa of the globally distributed Anatidae (ducks and allies). The latter are the most species-rich group of waterfowl and the only one that occurs in Europe today. The phylogenetic interrelationships and evolutionary history of anatids are not well understood. There exists a consensus that the Dendrocygninae (whistling ducks or tree ducks) are the sister taxon of a clade including the Anserinae (geese and swans) and the Anatinae (ducks and allies). Otherwise, however, molecular analyses yield conflicting tree topologies concerning the interrelationships of anatids (Donne-Goussé et al. 2002; Gonzalez et al. 2009; Sun et al. 2017; Buckner et al. 2018).

Taxonomically diverse assemblages of Miocene anseriforms are known from Europe (Mlíkovský 2002), Australia and New Zealand (Worthy et al. 2007; Worthy 2009) as well as Central Asia (Zelenkov 2011, 2012a, b, 2020; Zelenkov and Kurochkin 2012). In Europe, the earliest unambiguously identified anatids occur towards the late Eocene and earliest Oligocene, and these are also the oldest fossils of the Anatidae on a global scale (Mayr in press). Fossils of the anatid taxon *Mionetta* are fairly abundant in some early Miocene European sites (Cheneval 1987), whereas the middle and late Miocene record of the Anatidae is much scarcer (Mlíkovský 2002; Zelenkov 2020). The affinities of most fossil taxa are furthermore poorly constrained. Earlier authors assigned small duck-like anatids to the taxon *Anas*, whereas larger species were often classified into *Anser* (Mlíkovský 2002). In fact, however, these extant taxa appear to have diverged quite recently (Sun et al. 2017). Miocene anatids often represent distinctive morphologies and virtually all of the described taxa belong to extinct genus-level taxa (Worthy et al. 2007; Worthy 2009; Mayr and Pavia 2014; Zelenkov 2011, 2012a, b, 2020; Zelenkov and Kurochkin 2012, 2015; contra Mlíkovský 2002). Even the affinities of the well-represented *Mionetta* are controversially resolved, and the taxon has either been assigned to the Dendrocygninae (Cheneval 1983), resulted as a basal representative of the clade formed by Anserinae and Anatinae (Livezey and Martin 1988), or was found nested within the Anatinae (Worthy and Lee 2008). In the early Miocene, there still appear to have existed some stem group representatives of the Anatidae, such as the taxa *Paranyroca* and *Cygnopterus* (Cheneval 1984; Mayr and Smith 2017), whereas late Miocene Anseriformes were considered to be of essentially modern aspect (Zelenkov 2020).

A major obstacle impeding an understanding of the evolution of waterfowl from a fossil perspective is the fact that many extinct taxa are only known from fragmentary bones, and often there is no overlap of the holotype material of the various species described. This is particularly true for larger, shelduck- or goose-sized species, of which few fossils have been described so far, most of which are based on isolated fragmentary bones.

One of the best-represented species is *Anserobranta tarabukini* from the early late Miocene (MN 9) of Moldova. The holotype of this species is a partial carpometacarpus, but in the original description (Kurochkin and Ganea 1972) other wing bones and the distal end of a tarsometatarsus were also referred to *A. tarabukini*; a largely complete humerus was furthermore reported by Kessler (1984). Mainly based on a similar size and geological age, the distal end of a humerus from the middle Miocene (MN 6) of Sansan in France, described as *Anas robusta* by Milne-Edwards (1867–1869), was tentatively assigned to *Anserobranta* by Cheneval (2000). A record of '*Anas*' cf. *robusta* from the early middle Miocene (MN 5) locality of Regensburg-Dechbetten (Germany) is likewise based on the distal

CONTACT Gerald Mayr Gerald.Mayr@senckenberg.de Senckenberg Research Institute and Natural History Museum Frankfurt, Ornithological Section, Senckenberganlage 25, D-60325 Frankfurt Am Main, Germany.

end of a humerus (von Ammon 1918). A similar-sized anatid, '*Anser*' *oeningensis* from the middle Miocene (MN 7) of Öhningen in Germany (von Meyer 1865) is represented by crushed wing and pectoral girdle bones on a slab. Two larger species of the Anatidae, *Heteroanser vicinus* and *Bonibernicla ponderosa*, were furthermore described from the late Miocene (MN 13) of Hyargas Nuur 2 in Mongolia and are known from a proximal tarsometatarsus and a distal humerus, respectively (Zelenkov 2012a).

Here, we report a leg of a larger-sized anseriform bird, as well as the bones of a very small duck from the Hammerschmiede clay pit near Pforzen (Allgäu region, Bavaria, Germany). The fossiliferous sediments of this locality stem from the middle to late Miocene transition (MN 8) and the local stratigraphic level HAM 4, which yielded most of the described bones, is dated to the earliest Tortonian, at 11.44 Ma (Kirscher et al. 2016). The HAM 4 level represents a large-sized, fluvial, and meandering channel filled with cross-bedded fine sand. The somewhat older level HAM 5 is dated to 11.62 Ma and stems from a smaller-sized channel (Kirscher et al. 2016). The Hammerschmiede locality yielded a diversified vertebrate fauna, and as yet more than 120 non-avian species have been reported, most of which are represented by isolated bones or fragments thereof (Böhme et al. 2019). Previously described bird fossils from the Hammerschmiede site include bones of a large-sized darter (Mayr et al. 2020a) and a partial skull of a crane (Mayr et al. 2020b), but the site also yielded remains of various other undescribed avian taxa.

Material and methods

The examined fossil and extant material is stored in the Palaeontological Collection of the University of Tübingen, Germany (GPIT) and is labelled with both GPIT (for Hammerschmiede fossils excavated until 2019) and SNSB-BSPG (Staatliche Naturwissenschaftliche Sammlungen Bayerns – Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; for excavations of 2020). All measurements are in millimetres.

Skeletons of the following species of the Anatidae were examined in the collection of the Senckenberg Research Institute Frankfurt (SMF; the nomenclature follows the IOC World Bird List at https://www.worldbirdnames.org; the classification follows Carboneras 1992; Gonzalez et al. 2009): Dendrocygninae: *Dendrocygna arborea, D. autumnalis, D. bicolor, D. eytoni, D. guttata, D. viduata, Thalassornis leuconotus*. Anserinae: *Anser albifrons, A. anser, A. brachyrhynchos, A. canagicus, A. cygnoides, A. erythropus, A. fabalis, A. indicus, A. rossii, Branta bernicla, B. canadensis, B. leucopsis, B. ruficollis, B. sandvicensis, Coscoroba coscoroba, Cygnus atratus, C. cygnus, C. melanocoryphus, C. olor*. Cereopsini: *Cereopsis novaehollandiae*. Anatinae: Stictonettini: *Stictonetta naevosa*. Tadornini: *Alopochen aegyptiaca, Chloephaga melanoptera, Ch. picta, Ch. poliocephala, Ch. rubidiceps, Cyanochen cyanopterus, Neochen jubata, Radjah radjah, Tadorna cana, T. ferruginea, T. tadorna, T. tadornoides, T. variegata*. Tachyerini: *Tachyeres magellanicus, T. pteneres*. 'Cairinini': *Aix galericulata, A. sponsa, Amazonetta brasiliensis, Asarcornis scutulata, Cairina moschata, Callonetta leucophrys, Chenonetta jubata, Nettapus auritus, N. coromandelianus, N. pulchellus, Plectropterus gambensis, Pteronetta hartlaubi*. Merganettini: *Merganetta armata*. Anatini: *Anas acuta, A. bahamensis, A. bernieri, A. capensis, A. castanea, A. crecca, A. erythrorhyncha, A. flavirostris, A. formosa, A. gibberifrons, A. luzonica, A. melleri, A. platyrhynchos, A. sparsa, A. superciliosa, Hymenolaimus malacorhynchus, Malacorhynchus membranaceus, Mareca americana, M. strepera, M. falcata, M. penelope, M. sibilatrix, Marmaronetta angustirostris, Spatula clypeata, S. cyanoptera, S. discors, S. hottentota, S. platalea, S. puna, S. querquedula, S. versicolor, Speculanas specularis*. Aythyini: *Aythya ferina, A. fuligula, A. marila, A. nyroca, Netta peposaca, N. rufina*. Mergini: *Bucephala albeola, B. clangula, B. islandica, Clangula hyemalis, Histrionicus histrionicus, Lophodytes cucullatus, Melanitta fusca, M. nigra, Mergellus albellus, Mergus merganser, M. serrator, M. squamatus, Polysticta stelleri, Somateria fischeri, S. mollissima, S. spectabilis*. Oxyurini: *Heteronetta atricapilla, Oxyura jamaicensis, O. leucocephala, O. vittata*.

Systematic palaeontology

Aves Linnaeus, 1758
Anseriformes Wagler, 1831
Anatidae Leach, 1820
Allgoviachen, n. gen.

Type species

Allgoviachen tortonica, n. sp.

Diagnosis

Characterised by tarsometatarsus (1) fairly long and slender, with (2) deep fossa infracotylaris dorsalis, (3) prominent and mediolaterally narrow eminentia intercotylaris; (4) proximal articular surface deep with fossa between cotyla medialis and cotyla lateralis; (5) dorsomedial side of shaft with marked furrow for musculus extensor hallucis longus; (6) hypotarsus without canal for tendon of musculus flexor digitorum longus and (7) with plantarly prominent and proximodistally long crista medialis; (8) trochlea metatarsi II short, reaching only to middle of trochlea metatarsi IV; (9) fossa metatarsi I absent; (10) ungual phalanges with well developed and proximally situated tuberculum flexorium.

Differential diagnosis

The new species differs from:

- all extant taxa of the Anatidae in the plantarly more prominent and proximodistally longer crista medialis, the narrower and more pointed eminentia intercotylaris, and the deeper fossa infracotylaris dorsalis.

- the Oligo-Miocene *Cygnopterus* Lambrecht, 1931 in: tarsometatarsus shaft somewhat stouter in its distal section; cotyla medialis more strongly medially protruding; eminentia intercotylaris more projected; crista medialis hypotarsi less laterally deflected; trochlea metatarsi II proportionally larger; plantar articular surface of trochlea metatarsi IV proportionally longer.

- the early Miocene *Paranyroca* Miller and Compton, 1939 in: fossa infracotylaris dorsalis deeper; hypotarsus with sulcus for tendon of musculus flexor perforatus digiti 2; crista medialis more prominent.

- the late Miocene *Anserobranta* (Kurochkin and Ganea 1972) in: tarsometatarsus shaft stouter and trochlea metatarsi II proportionally larger.

- the late Miocene *Heteroanser* (Zelenkov 2012a) in: eminentia intercotylaris narrower and more pointed; crista medialis hypotarsi proximodistally longer.

Taxonomic remarks

Owing to a lack of overlap in the known bones, the new taxon cannot be differentiated from *Bonibernicla* (Zelenkov 2012a).

Etymology

From allgovia (Lat.: Allgäu), in reference to the geographic provenance of the fossil, and chen (Gr.: goose).

Allgoviachen tortonica, n. gen. et sp.

Holotype

SNSB-BSPG 2020 XCIV 1058: left leg including the distal portion of the femur as well as the tibiotarsus, tarsometatarsus and most pedal phalanges (Figures 1,2).

Etymology

The species epithet refers to the stratigraphic age of the new species.

Diagnosis

As for genus.

Referred specimen

GPIT/AV/00143: fragmentary distal portion of left tarsometatarsus (HAM 5).

Type locality and horizon

Hammerschmiede clay pit near Pforzen (Allgäu region, Bavaria, Germany); stratigraphic horizon HAM 4, earliest late Miocene, Tortonian (MN 8, 11.44 Ma).

Measurements

Tibiotarsus, length, 125.8; distal width, 14.1. Tarsometatarsus, length, 74.1; proximal width, 14.7; width of trochlea metatarsi III, ~6.2. Pedal phalanges: I1, 14.1; I2, 6.1; II1, 33.3; II2, 26.5; II3, >11.0; III1, 33.5; III2, >23.4; IV1, 27.1; IV2, 18.7; IV3, >12.7; IV4, 16.7; IV5, >8.4.

Description and comparisons

Owing to the fragmentary condition of GPIT/AV/00143, the following description is based on the partial leg SNSB-BSPG 2020 XCIV 1058, which was found in articulation (Figure 1). The bones belong to a species about the size of the extant *Anser indicus* (Anserinae) and *Alopochen aegyptiaca* (Anatinae), which are medium-sized anatids with body masses of about two kilograms (Carboneras 1992). Of the femur, only the crushed distalmost portion is preserved, which is attached to the proximal end of the tibiotarsus (Figure 2(c-d)) and does not allow a meaningful description. Tibiotarsus, tarsometatarsus, and the pedal phalanges, however, are nearly complete.

The crista cnemialis cranialis of the tibiotarsus has a similar shape to that of, e.g., *Anser indicus*, whereas it is proximodistally shorter in, e.g., *Alopochen aegyptiaca*. The distal end of the bone is medially inflected, even though the curvature appears more pronounced than it actually was owing to the fact that the distalmost portion is broken and displaced. Condylus medialis and condylus lateralis are of similar size and separated by a wide incisura intercondylaris. The epicondylus medialis is only weakly protruding.

In its proportions, the tarsometatarsus corresponds to that of some Tadornini (Figure 3) and the taxon *Sarkidiornis* (which is more closely related to the Aythyini and Anatini; Gonzalez et al. 2009; Sun et al. 2017; Buckner et al. 2018). Compared with other fossil taxa, the bone most closely resembles the tarsometatarsus of the Oligo-Miocene *Cygnopterus* and *Paranyroca* (Figure 4; Mayr and Smith 2017). As in *Heteroanser* from the late Miocene of Mongolia (Zelenkov 2012a) but unlike most extant Anatidae, the fossa infracotylaris dorsalis is very deep. The eminentia intercotylaris is more pointed and mediolaterally narrower than in crown group Anatidae. The cotyla medialis is mediolaterally wide, as it is in extant Anserinae and some Anatinae (e.g., *Alopochen*), whereas this cotyla is proportionally narrower in other Anatinae and the Dendrocygninae (Figure 3(h), (i)). Unlike in crown group Anatidae, there is a fossa between the cotyla medialis and the cotyla lateralis, in the plantar portion of the proximal articular surface of

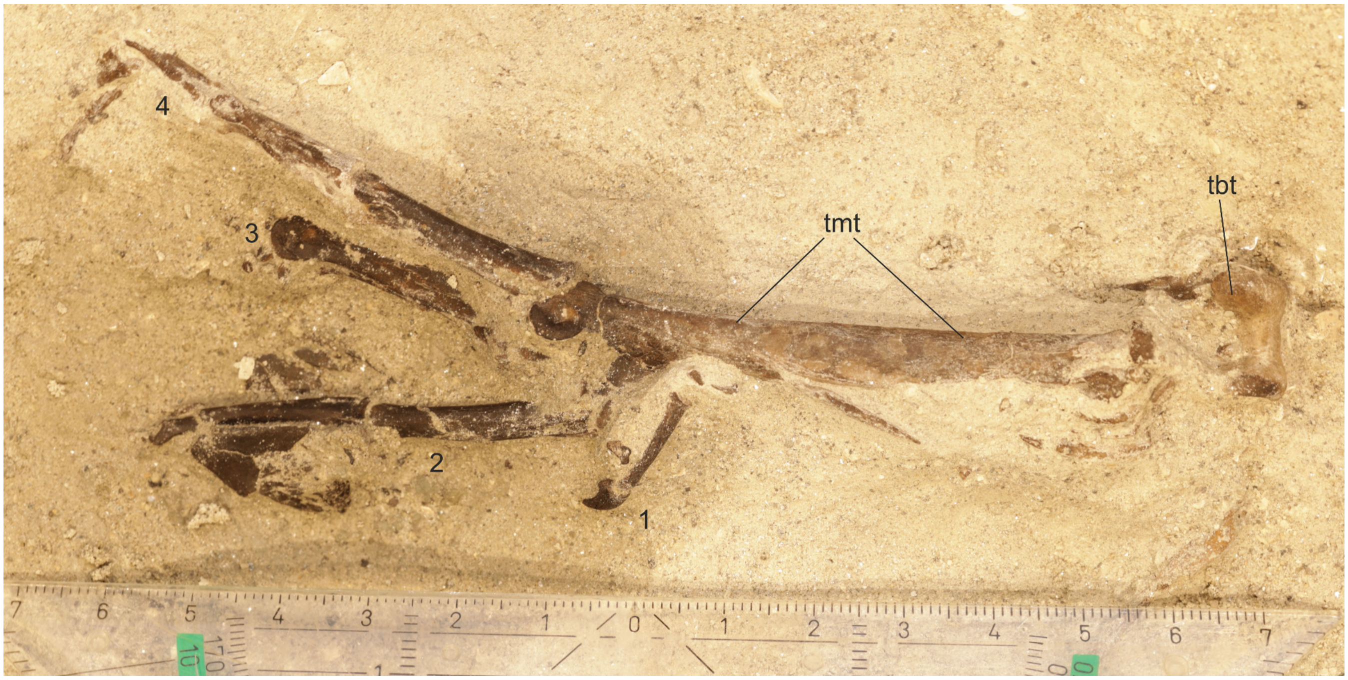

Figure 1. In-situ photo of the partial leg of *Allgoviachen tortonica*, n. gen. et sp. from the earliest late Miocene (Tortonian) of the Hammerschmiede clay pit (holotype, SNSB-BSPG 2020 XCIV 1058). Abbreviations: tbt, tibiotarsus; tmt, tarsometatarsus. The toes are numbered. Photo by Henrik Stöhr. [Colour online].

Figure 2. Partial leg of *Allgoviachen tortonica*, n. gen. et sp. from the earliest late Miocene (Tortonian) of the Hammerschmiede clay pit (holotype, SNSB-BSPG 2020 XCIV 1058). (a) – (d) Left tibiotarsus in (a) cranial, (b) medial, (c) caudal, and (d) lateral view, with details of the distal end in (e) cranial and (f) distal view. (g)– (j) Left tarsometatarsus in (g) dorsal, (h) medial, (i) plantar, and (j) lateral view. (k) Pedal phalanges. Abbreviations: brg, breakage; ccc, crista cnemialis cranialis; cdl, condylus lateralis; cdm, condylus medialis; crf, crista fibularis; fib, fibula; ito, intratendinous ossification; pst, pons supratendineus. Scale bars equal 10 mm. [Colour online].

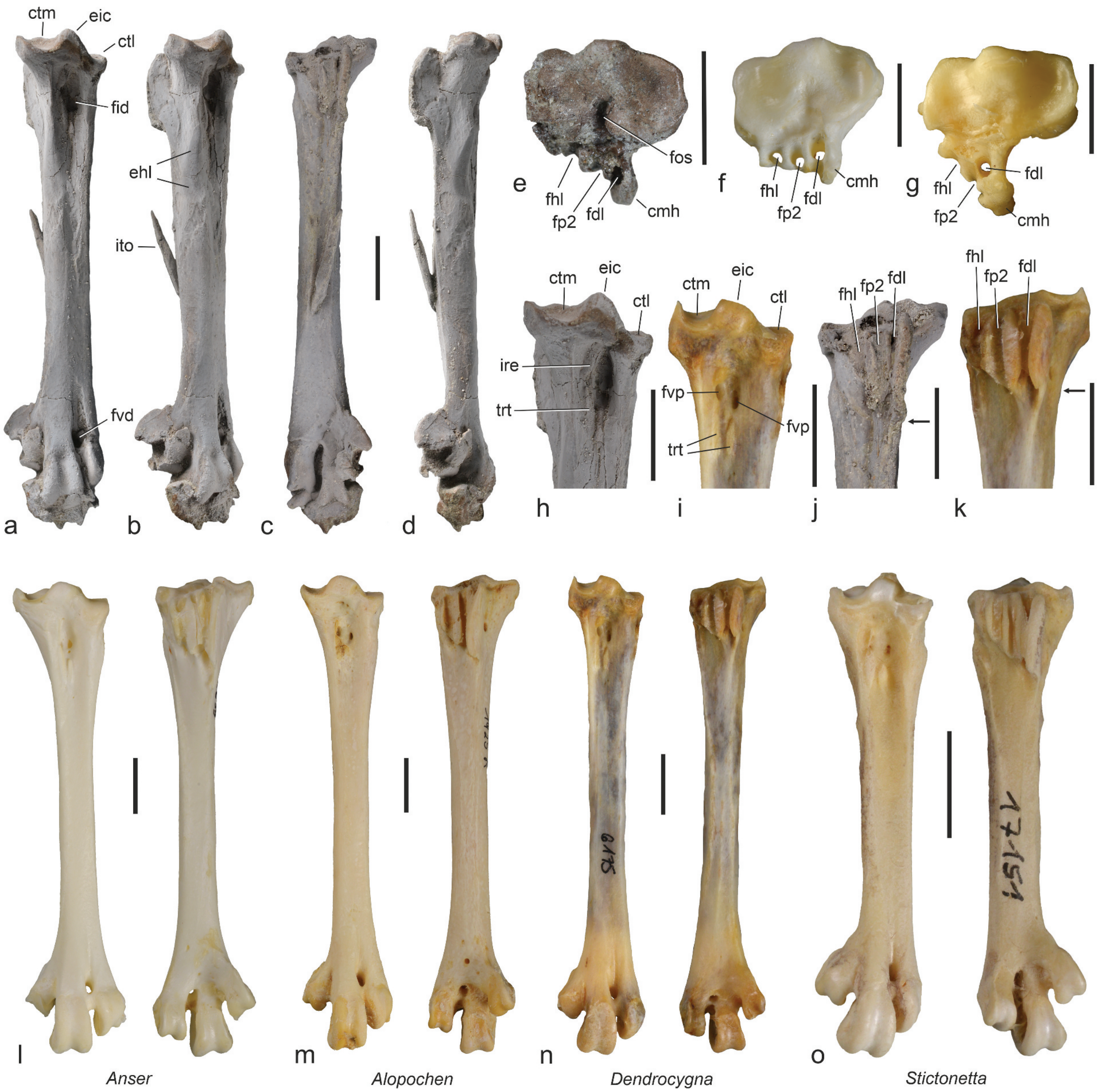

Figure 3. (a–e) Left tarsometatarsus of *Allgoviachen tortonica*, n. gen. et sp. from the Hammerschmiede locality (holotype, SNSB-BSPG 2020 XCIV 1058) in (a) dorsal, (b) dorsomedial, (c) plantar, (d) medial, and (e) proximal view; the specimen was coated with ammonium chloride. (f) Proximal tarsometatarsus (proximal view) of *Anser indicus* (Anserinae; SMF 19855). (g) Proximal tarsometatarsus (proximal view) of *Anseranas semipalmata* (Anseranatidae; SMF 11276). (h), (j) Detail of the proximal tarsometatarsus of SNSB-BSPG 2020 XCIV 1058 in (h) dorsal and (j) plantar view. (i), (k) Proximal tarsometatarsus of *Dendrocygna arborea* (Dendrocygninae; SMF 6175) in (i) dorsal and (k) plantar view. Left tarsometatarsi (left: dorsal view, right: plantar view) of (l) *Anser indicus* (Anserinae; SMF 19855), (m) *Alopochen aegyptiaca* (Anatinae; SMF 1925), (n) *Dendrocygna arborea* (Dendrocygninae; SMF 6175), and (o) *Stictonetta naevosa* (Anatinae; SMF 17151). The small arrows in (j) and (k) indicate the distal extent of the crista medialis hypotarsi. Abbreviations: cmh, crista medialis hypotarsi; ehl, furrow for musculus extensor hallucis longus; eic, eminentia intercotylaris; fdl, hypotarsal sulcus/canal for tendon of musculus flexor digitorum longus; fhl, hypotarsal sulcus for tendon of musculus flexor hallucis longus; fid, fossa infracotylaris dorsalis; fos, fossa between cotyla medialis and cotyla lateralis; fp2, hypotarsal sulcus for tendon of musculus flexor perforatus digiti 2; fvd, foramen vasculare distale; fvp, foramen vasculare proximale; ire, impressio retinaculi extensorii; ito, intratendinous ossification; trt, tuberositas retinaculi musculi tibialis. Scale bars equal 10 mm. [Colour online].

the bone (Figure 3(e)). As in crown group Anatidae, the tuberositas retinaculi musculi tibialis is bipartite, with the longer, medially situated ridge being aligned with the lateral impressio retinaculi extensorii. Of the foramina vascularia proximalia, only the medial one is clearly visible and situated between the medial ridge of the tuberositas retinaculi musculi tibialis and the lateral impressio retinaculi extensorii.

As in extant Anatidae, the hypotarsus appears to have formed three sulci for the tendons of musculus flexor digitorum longus, musculus flexor perforatus digiti 2, and musculus flexor hallucis longus, but the most lateral hypotarsal crest is broken, so that only the two medial sulci (for m. flexor digitorum longus and m. flexor perforatus digiti 2) are well delimited (Figure 3(e), (j)). Otherwise, however, the hypotarsus has a distinctive morphology, which shows a resemblance to the hypotarsus of *Cygnopterus alphonsi* (Figure 4 (i)) but is different from that of all other Anatidae, of which the hypotarsus is known. In particular, the crista medialis hypotarsi is much more plantarly prominent than in extant Anatidae (Figure 3 (e), (f)) and the hypotarsal crest between the sulci for m. flexor digitorum longus and m. flexor perforatus digiti 2 is proximodistally shorter and mediolaterally less wide (Figure 3(j), (k)). Even though the tarsometatarsus is slightly crushed, the unusual

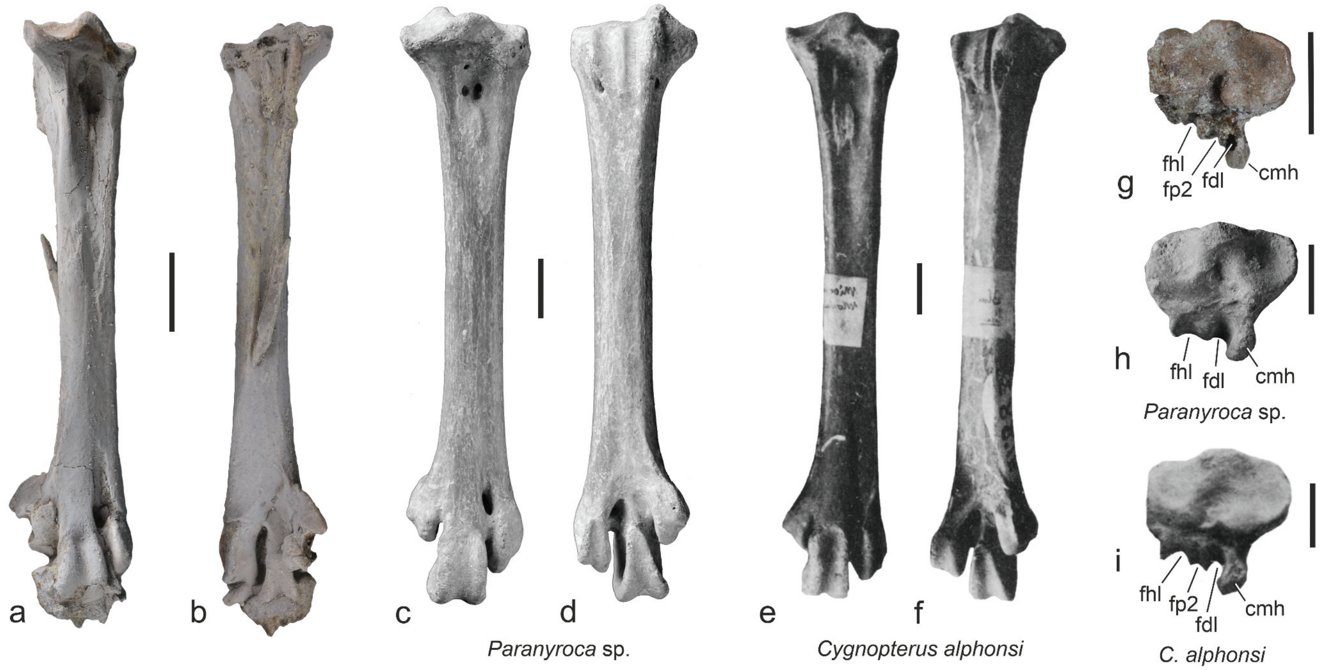

Figure 4. Tarsometatarsi of (a), (b), (g) *Allgoviachen tortonica*, n. gen. et sp. from the Hammerschmiede locality (holotype, SNSB-BSPG 2020 XCIV 1058), (c), (d), (h) *Paracygnopterus* sp. from the early Miocene of the Saint-Gérand-le-Puy area in France (University of Leuven, Department of Earth and Environmental Sciences, Leuven, Belgium; PLV 1988/17–1), and (e), (f), (i) *Cygnopterus alphonsi* from Saint-Gérand-le-Puy (from Cheneval 1983: pl. 9; mirrored to ease comparisons). Abbreviations: cmh, crista medialis hypotarsi; fdl, hypotarsal sulcus/canal for tendon of musculus flexor digitorum longus; fhl, hypotarsal sulcus for tendon of musculus flexor hallucis longus; fp2, hypotarsal sulcus for tendon of musculus flexor perforatus digiti 2. Scale bars equal 10 mm. [Colour online].

morphology of the hypotarsal crests does not seem to be an artefact of preservation, and the two medial crests are fully preserved, with their morphologies being unaltered by breakage or compression. With regard to the plantar prominence of the crista medialis, the hypotarsus of the Hammerschmiede anatid resembles that of extant Anseranatidae (Figure 3(g)). Unlike in the latter and crown group Anatidae, however, there appears to be no canal for the tendon of musculus flexor digitorum longus, even though an assessment of this feature is less ambiguous and the osseous bridge connecting the two medial hypotarsal crests may be broken in the fossil.

On the dorsomedial side of the shaft, there is a marked furrow for musculus extensor hallucis longus (Figure 3(b)), which is less developed in most crown group Anatidae. A splint on the plantar surface of the bone represents an intratendinous ossification (Figure 2(h)).

The distal end of the tarsometatarsus is not medially inflected, as it is in most extant Anatini. The dorsal opening of the foramen vasculare distale is situated at the end of a marked sulcus extensorius; as in extant Anatidae, the plantar opening is recessed. A fossa metatarsi I is absent. Adhering matrix and bone fragments obscure the shapes of the trochleae. The trochlea metatarsi II is short and reaches distally only to the middle of the trochlea metatarsi III. Its plantar surface bears a prominent lobe, similar to *Alopochen*. Unfortunately, the distomedial portion of the trochlea is damaged so that it is not possible to discern whether there was a groove on the trochlea metatarsi II (which is absent in the Anseranatidae and the dendrocygnine taxon *Dendrocygna* but present in *Thalassornis*, the Anserinae, and the Anatinae). The plantar articular surface of the trochlea metatarsi III tapers proximally and has a subtriangular shape. The trochlea metatarsi IV is mediolaterally narrow and its lateral plantar rim reaches farther proximally than the medial one.

The processus articularis tarsometatarsalis of the os metatarsale I (Figure 5(a)) is of similar shape to that in *Alopochen aegyptiaca*, whereas it is wider in many other extant Anatidae. The fossil lacks the two distalmost phalanges of the third toe. The pedal digits are of similar proportions to those of extant Anatidae. The hallux is quite short and its first phalanx is shorter than the second phalanx of the fourth toe, whereas both phalanges are of equal length in many Anatinae (e.g., Figure 6(b-d)). As in most extant Dendrocygninae and Anatinae, but unlike some terrestrial Anserinae (e.g., *Anser indicus*, Figure 6(c)), the fourth toe is much longer than the second. The ungual phalanges of the Hammerschmiede anseriform correspond to those of extant Anseranatidae, the dendrocygnine taxon *Dendrocygna* (Figure 5(e)), the anserine *Cereopsis* (Figure 5(d)), and some Tadornini and Cairinini in that the tuberculum flexorium is prominent and proximally located, as it is in most other neornithine birds. In highly aquatic anatids, by contrast, the unguals are straighter, and the tuberculum flexorium is proximodistally stretched and low Figure 5(c), (f), (h).

Discussion

Allgoviachen tortonica, n. gen. et sp. is identified as a representative of the Anatidae by the short trochlea metatarsi II (which reaches only to the middle of the trochlea metatarsi IV) and the absence of a fossa metatarsi I. Unfortunately, the fossil bones do not show unambiguous character evidence for a well-founded further phylogenetic placement. The proximal end of the tarsometatarsus differs from all extant Anatidae in the very deep fossa infracotylaris dorsalis, the mediolaterally narrower eminentia intercotylaris, the more plantarly protruding crista medialis of the hypotarsus, and – possibly (see above) – the absence of a hypotarsal canal for the tendon of musculus flexor digitorum longus. The latter character (absence of a hypotarsal canal for

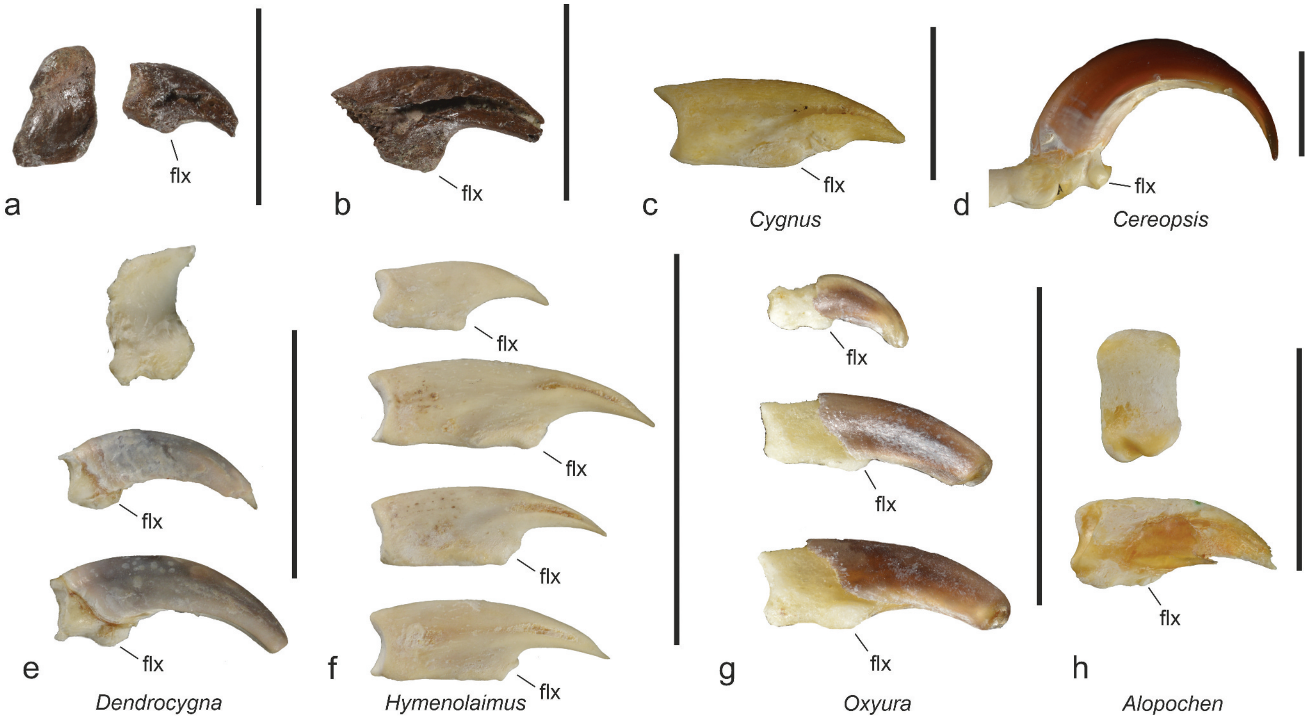

Figure 5. (a) Left os metatarsale I and ungual phalanx of the hallux of *Allgoviachen tortonica*, n. gen. et sp. from the Hammerschmiede locality (holotype, SNSB-BSPG 2020 XCIV 1058). (b) Ungual phalanx of the second toe of *A. tortonica* (holotype, SNSB-BSPG 2020 XCIV 1058). (c) Ungual phalanx of *Cygnus atratus* (Anserinae; SMF 3423). (d) Ungual phalanx of the second toe of *Cereopsis novaehollandiae* (Anserinae; SMF 19923). (e) Left os metatarsale I and ungual phalanges of the hallux and second toe (left side) of *Dendrocygna viduata* (Dendrocygninae; SMF 2271). (f) Four ungual phalanges of *Hymenolaimus malacorhynchus* (Anatinae; SMF 10257). (g) Ungual phalanx of the hallux (top) and two other ungual phalanges of *Oxyura jamaicensis* (Oxyurini; SMF 10472). (h) Left os metatarsale I and ungual phalanx of the second toe of *Alopochen aegyptiaca* (Anatinae; SMF 1925). Abbreviation: flx, tuberculum flexorium. Scale bars equal 10 mm. [Colour online].

musculus flexor digitorum longus) may be plesiomorphic for the Anatidae, but its occurrence in the new species needs to be verified by future specimens. The resemblance to the taxa *Paranyroca* and *Cygnopterus* potentially also indicates that *A. tortonica* is a stem group representative of the Anatidae (see Mayr and Smith 2017 for a discussion of the affinities of the latter two taxa). However, more data on the osteology of the new species are required for a robust phylogenetic placement, and the above-listed characteristics do not allow a well-supported assignment to any anatid subtaxon.

With regard to the shape of the ungual phalanges, *A. tortonica* resembles extant Dendrocygninae (*Dendrocygna* spp., but not *Thalassornis leuconotus*), the anserine *Cereopsis*, and some Tadornini (shelducks, e.g. *Tadorna, Alopochen*, and *Chloephaga*). Most other extant Anatidae have less curved ungual phalanges, in which the tuberculum flexorium is hardly protruding and more distally situated Figure 5(c), (f). To the best of our knowledge, no surveys of the different shapes of the ungual phalanges of extant Anatidae exist, and the marked variability appears to have been unnoticed before. Outgroup comparisons with the Anhimidae, Anseranatidae, and other neornithine birds suggest that a low and distally situated tuberculum flexorium represents a derived morphology, which evolved several times independently, in the Dendrocygninae (*Thalassornis*), Anserinae (Cygnini and Anserini), and Anatinae (Anatini). This derived morphology is found in highly aquatic anatids, and the plesiomorphic shape of the ungual phalanges of *A. tortonica* indicates a predominantly non-aquatic and more terrestrial species, which – in analogy to the extant *Dendrocygna* – may have had perching capabilities.

Concerning the deep fossa infracotylaris dorsalis, *A. tortonica* agrees with *Heteroanser vicinus* from Mongolia (Zelenkov 2012a), but otherwise there are distinct differences (see differential diagnosis). Owing to a lack of overlap in the known bones, *A. tortonica* cannot be differentiated from '*Anser*' *oeningensis*, '*Anas*' *robusta*, and *Bonibernicla ponderosa*. These three species are from strata that are either slightly older ('*A.*' *oeningensis*, '*A.*' *robusta*) or somewhat younger (*B. ponderosa*) than those yielding the specimens from the Hammerschmiede site. Well-founded morphological comparisons will, however, only be possible on the basis of the eventual future discovery of further fossils.

Irrespective of its exact phylogenetic affinities, the holotype of *A. tortonica* is of interest from a taphonomic point of view, because it constitutes the only skeletal remains of a bird from the Hammerschmiede clay pit that were found in articulation. Even though some bones of the large darter *Anhinga pannonica* from the Hammerschmiede locality may belong to a single individual (Mayr et al. 2020a), these were scattered over a larger area owing to transport of the disarticulated bones in the flow direction of the river channel in which they were deposited. The preservation of the anseriform leg indicates a rapid burial in the sediment without subsequent reworking, and the fact that the femur lacks the proximal portion suggests that the specimen represents the feeding remains of a scavenger or predator. Isolated legs or feet are commonly found in the Eocene fossil locality Messel, where they were interpreted as feeding remains of crocodilians (Mayr 2016). Crocodilians no longer existed in the late Miocene of Central Europe (Böhme 2003), but snapping turtles (Chelydridae) are commonly found in the Hammerschmiede locality (Kirscher et al. 2016) and may have scavenged bird carcases.

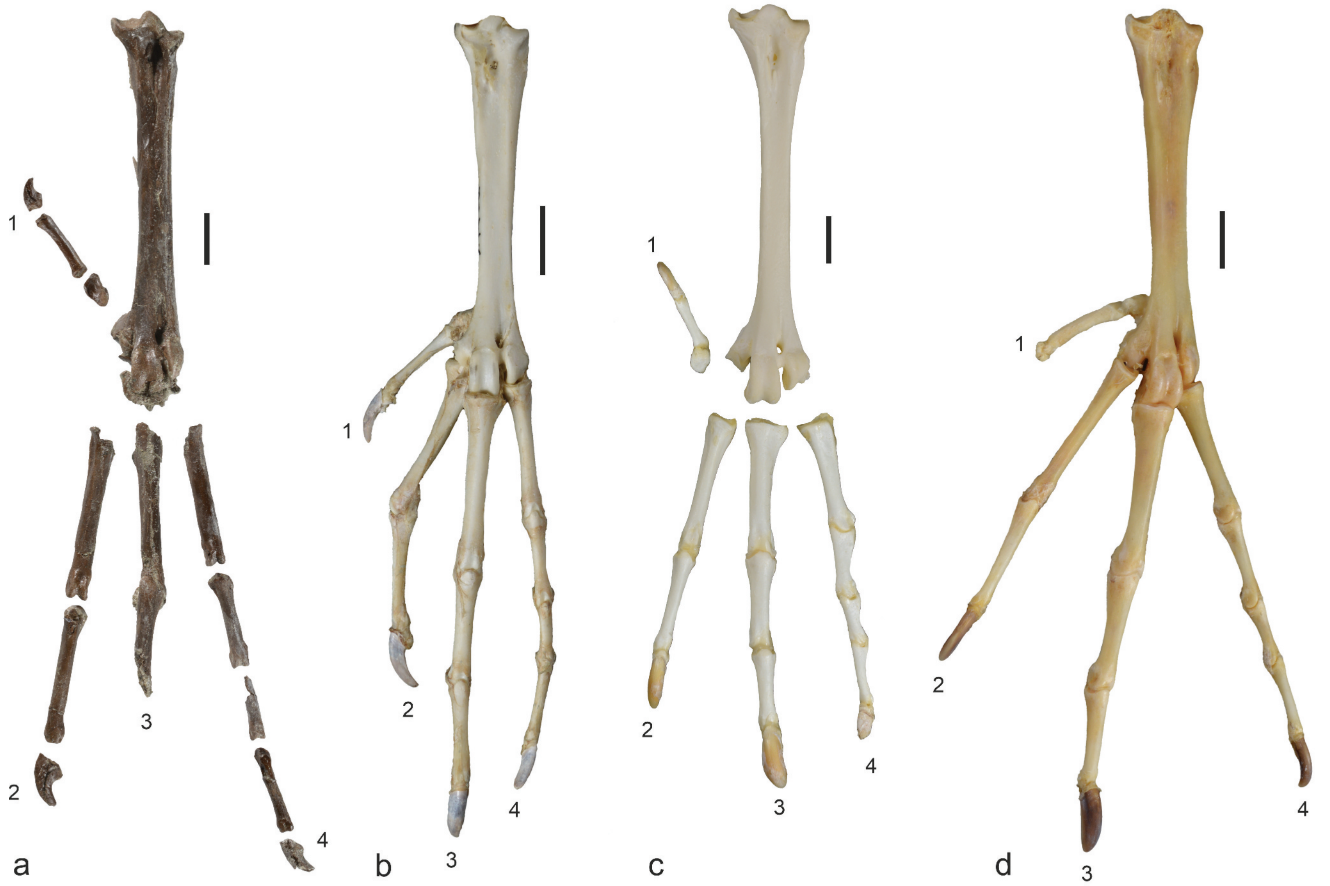

Figure 6. Left feet of (a) *Allgoviachen tortonica*, n. gen. et sp. from the earliest late Miocene (Tortonian) of the Hammerschmiede clay pit (holotype, SNSB-BSPG 2020 XCIV 1058), (b) *Dendrocygna viduata* (Dendrocygninae; right foot, mirrored; SMF 2271), (c) *Anser indicus* (Anserinae; SMF 19855), and (d) *Sarkidiornis melanotos* (Anatinae; ungual phalanx of hallux truncated; SMF 19912). The toes are numbered. Scale bars equal 10 mm. [Colour online].

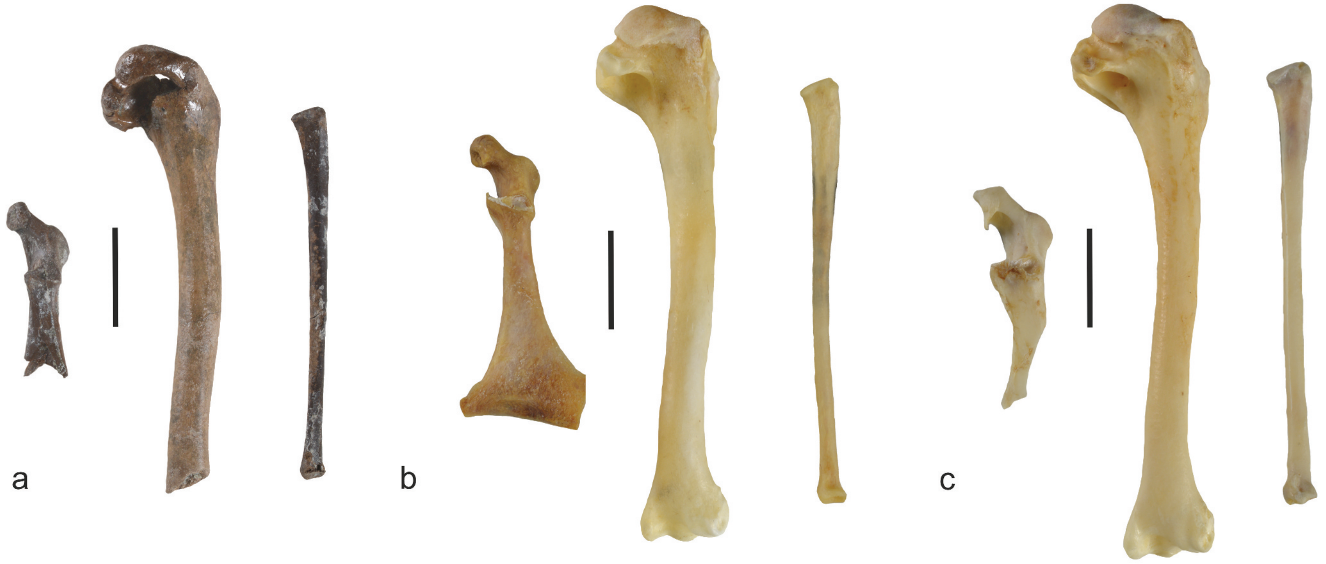

Figure 7. (a) Omal extremity of right coracoid (GPIT/AV/00236; dorsal view), right humerus lacking distal end (GPIT/AV/00232; caudal view), and right radius (GPIT/AV/00213; ventral view) of a very small anatid from the Hammerschmiede clay pit (cf. *Mioquerquedula*). (b) Right coracoid, humerus, and radius of the extant *Spatula hottentota* (SMF 5794). (c) Omal extremity of right coracoid as well as right humerus and right radius of the extant *Nettapus auritus* (SMF 255). Scale bars equal 10 mm. [Colour online].

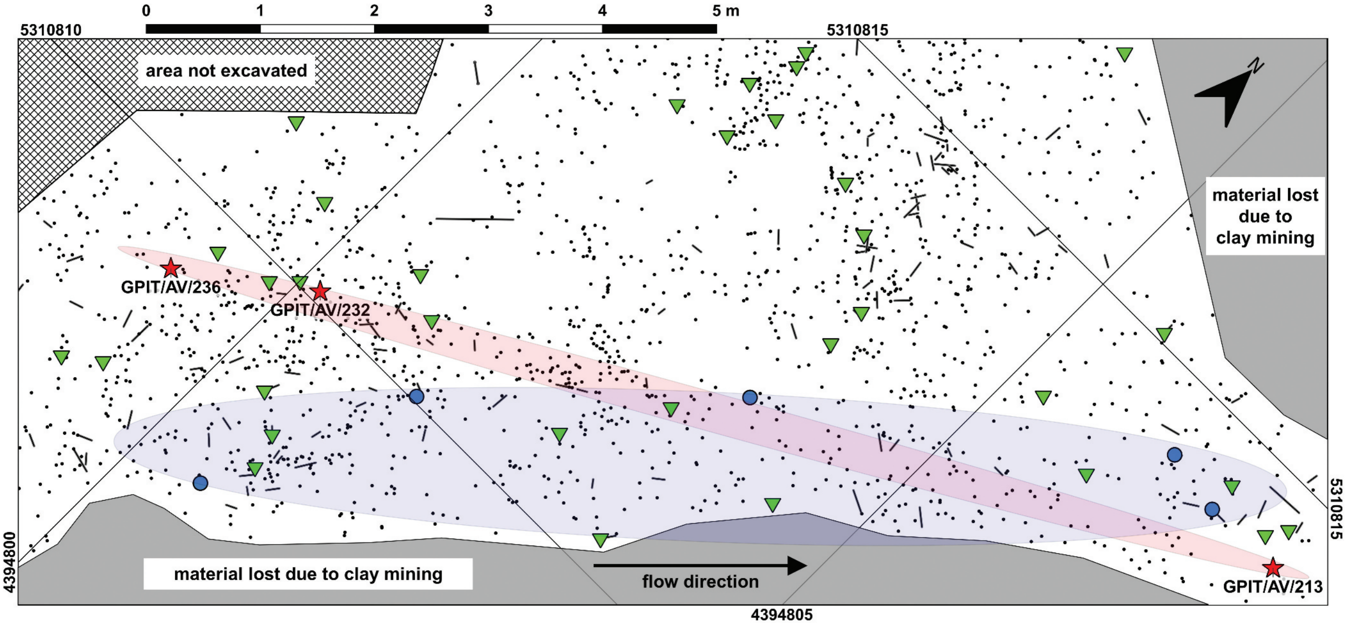

Figure 8. Section of the excavation plan Hammerschmiede level HAM 4 (excavation years 2019–2021). Black dots represent vertebrate fossils, black stripes denote the orientation of elongated objects. Bird bones are indicated by green triangles, cf. *Mioquerquedula* bones (likely belonging to the same individual) are highlighted with red stars, and bones that probably belong to a single individual of the large-sized darter *Anhinga pannonica* are shown with blue circles. The three wing and pectoral girdle bones that likely belong to a single individual of cf. *Mioquerquedula* are scattered over a distance of ten metres in an area (red field) of similar length to that containing putatively associated bones of *A. pannonica* (blue field). Coordinates correspond to a Gauss-Krüger Zone 4 grid with values in metres. Modified after Mayr et al. (2020a). [Colour online].

The Hammerschmiede clay pit also yielded remains of further anseriform taxa. Most notable among these are four bones of a very small species, which was even smaller than the smallest extant anatids, *Spatula hottentota* and *Nettapus auritus* (Figure 7). The material includes the omal extremities of two right coracoids (GPIT/AV/00236 and GPIT/AV/00245) as well as a right humerus lacking the distal end (GPIT/AV/00232) and a right radius (GPIT/AV/00213). These bones, all of which stem from the local stratigraphic level HAM 4, are likely to belong to the taxon *Mioquerquedula*. The type species of this taxon, *M. minutissima*, was described from the middle Miocene Sharga locality of Mongolia (Zelenkov and Kurochkin 2012). *Mioquerquedula* seems to have been quite common during the middle and early late Miocene in Eurasia, between approximately 14 and 10 Ma. Another species, *M. velox* occurs in the middle Miocene of France (Sansan locality, Zelenkov and Kurochkin 2012). A tentative record of *Mioquerquedula* was furthermore reported from the middle Miocene (Volhynian) of the northern Caucasus near Tsurevsky in the Krasnodar region of Russia (Zelenkov 2017a), and the taxon was also identified in the late Miocene (MN 9) of Rudabanya, Hungary (Zelenkov 2017b).

The specimens of this very small dabbling duck are also of interest from a taphonomic point of view. Due to the presence of duplicate coracoids from the same body side, a minimal number of two individuals is obvious. Judging from the presumed direction of transport and the spatial data of the finds, three specimens – a right coracoid (GPIT/AV/00236), a right proximal humerus (GPIT/AV/00232) and a right radius (GPIT/AV/00213) – are likely to belong to the same individual (the other coracoid, GPIT/AV/00245, was gathered without spatial data several metres NNW in the deeper parts of the HAM 4 channel). These three bones were discovered within a distance of ten metres and were scattered in accordance with the reconstructed flow direction (SSW-NNE) (Figure 8). The specimens are anatomically sorted from proximal (SSW) to distal bones (NNE), and their spatial distribution within the 150 cm thick fossiliferous profile of the HAM 4 layer is within a range of 23 cm only. This observation is consistent with a similar taphonomic event regarding the scattered bones of a darter (*Anhinga pannonica*). The latter are also likely to stem from a single individual and were dispersed in a stray field with a similar direction and expansion to the closely adjacent one of the small dabbling duck (Mayr et al. 2020a). The small-scale transport and redeposition of the wing and pectoral girdle bones of the small duck (cf. *Mioquerquedula*) sharply contrasts with the preservation of the articulated leg of *A. tortonica*.

In conclusion, the anseriform assemblage of the Hammerschmiede clay pit, and that of the HAM 4 level in particular, is represented by four species: *Allgoviachen tortonica*, cf. *Mioquerquedula*, and two so far undetermined medium-sized anatids. This association shows notable differences to extant anseriform faunas from Central Europe. *A. tortonica* represents an unusual morphotype unknown from extant avifaunas, which places a caveat on attempts to shoehorn Miocene anseriforms into extant genus-level taxa (e.g., Mlíkovský 2002). Today, very small-sized Anatidae are only found in the tropical and subtropical regions and their occurrence at the Hammerschmiede site, and elsewhere in Eurasia, is likely to be due to a warmer paleoenvironment, which featured mean annual temperatures above 20°C in the Hammerschmiede locality (Mayr et al. 2020a). Climatic cooling after the late Miocene was also hypothesised to have accounted for the disappearance of other taxa found in the Hammerschmiede locality, that is, the large-sized darter *Anhinga pannonica* (Anhingidae) and a very large crane (Mayr et al. 2020a, b). Currently, early late Miocene avifaunas remain poorly studied, and it is to be hoped that future finds from the Hammerschmiede clay pit and coeval sites will add to our understanding of the avifaunas of this time period.

Acknowledgments

We thank the members of the Hammerschmiede excavation team from 2020 for their invaluable assistance in the field. This excavation was supported by the Bavarian State Ministry of Research and the Arts, and by the Bavarian Natural History Collections (SNSB). We furthermore thank Sven Tränkner (Frankfurt) for taking the photographs and Henrik Stöhr (Tübingen) for the preparation of the fossil. Comments from an anonymous reviewer improved the manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

ORCID

Gerald Mayr http://orcid.org/0000-0001-9808-748X

References

Böhme M. 2003. The Miocene Climatic Optimum: evidence from ectothermic vertebrates of Central Europe. Palaeogeogr, Palaeoclimatol, Palaeoecol. 195 (3–4):389–401. doi:10.1016/S0031-0182(03)00367-5.

Böhme M, Spassov N, Fuss J, Tröscher A, Deane AS, Prieto J, Kirscher U, Lechner T, Begun DR. 2019. A new Miocene ape and locomotion in the ancestor of great apes and humans. Nature. 575:489–493.

Buckner JC, Ellingson R, Gold DA, Jones TL, Jacobs DK. 2018. Mitogenomics supports an unexpected taxonomic relationship for the extinct diving duck *Chendytes lawi* and definitively places the extinct Labrador Duck. Mol Phylogenet Evol. 122:102–109.

Carboneras C. 1992. Family Anatidae (ducks, geese, and swans). In: Del Hoyo J, Elliott A, Sargatal J, editors. Handbook of the Birds of the World (Vol. 1). Barcelona: Lynx Edicions; p. 536–628.

Cheneval J. 1983. Les Anatidae (Aves, Anseriformes) du gisement Aquitanien de Saint-Gerand-le-Puy (Allier, France). In: Buffetaut E, Mazin JM, Salmon E, editors. Actes du symposium paleontologique Georges Cuvier. Montbéliard: la Ville; p. 85–98.

Cheneval J. 1984. Les oiseaux aquatiques (Gaviiformes à Ansériformes) du gisement aquitanien de Saint-Gérand-le-Puy (Allier, France): révision systématique. Palaeovertebr. 14:33–115.

Cheneval J. 1987. Les Anatidae (Aves, Anseriformes) du Miocène de France. Révision systématique et évolution. Doc Lab Géol (Lyon). 99:137–157.

Cheneval J. 2000. L'avifaune de Sansan. In: Ginsburg L, editor. La faune miocène de Sansan et son environnement, Vol. 183. Mém Mus natl Hist nat.; p. 321–388.

Donne-Goussé C, Laudet V, Hänni C. 2002. A molecular phylogeny of anseriformes based on mitochondrial DNA analysis. Mol Phylogenet Evol. 23:339–356.

Gonzalez J, Düttmann H, Wink M. 2009. Phylogenetic relationships based on two mitochondrial genes and hybridization patterns in Anatidae. J Zool. 279 (3):310–318. doi:10.1111/j.1469-7998.2009.00622.x.

Kessler E. 1984. Noi contribuţii privind studiul avifaunelor din Paratethys [New contributions to the study of the avifauna in the Paratethys]. Crisia. 14: 521–532. in Romanian.

Kirscher U, Prieto J, Bachtadse V, Aziz HA, Doppler G, Hagmaier M, Böhme M. 2016. A biochronologic tie-point for the base of the Tortonian stage in European terrestrial settings: magnetostratigraphy of the topmost Upper Freshwater Molasse sediments of the North Alpine Foreland Basin in Bavaria (Germany). Newslett Stratigr. 49(3):445–467. doi:10.1127/nos/2016/0288.

Kurochkin EN, Ganea IM. 1972. Birds of the Middle Sarmatian of Moldavia. In: David AI, editor. Neogene and Pleistocene Vertebrates of Moldavia. Kishniev: Akademiya Nauk Moldavskoy SSR. [in Russian]; p. 45–70.

Livezey BC, Martin LD. 1988. The systematic position of the Miocene anatid *Anas* [?] *blanchardi* Milne-Edwards. J Vertebr Paleontol. 8:196–211.

Mayr G. 2016. Avian feet, crocodilian food and the diversity of larger birds in the early Eocene of Messel. Palaeobiodiv Palaeoenviron. 96:601–609.

Mayr G. in press. Paleogene fossil birds. 2nd edition ed. Heidelberg: Springer.

Mayr G, Lechner T, Böhme M. 2020a. The large-sized darter *Anhinga pannonica* (Aves, Anhingidae) from the late Miocene hominid Hammerschmiede locality in Southern Germany. PLoS ONE. 15(5):e0232179. doi:10.1371/journal.pone.0232179.

Mayr G, Lechner T, Böhme M. 2020b. A skull of a very large crane from the late Miocene of Southern Germany, with notes on the phylogenetic interrelationships of extant Gruinae. J Ornithol. 161:923–933.

Mayr G, Pavia M. 2014. On the true affinities of *Chenornis graculoides* Portis, 1884 and *Anas lignitifila* Portis, 1884 – an albatross and an unusual duck from the Miocene of Italy. J Vertebr Paleontol. 34:914–923.

Mayr G, Smith T. 2017. First Old World record of the poorly known, swan-sized anseriform bird *Paranyroca* from the late Oligocene/early Miocene of France. N Jb Geol Paläontol, Abh. 286:349–354.

Milne-Edwards A. 1867–1869. Recherches anatomiques et paléontologiques pour servir à l'histoire des oiseaux fossiles de la France, vol, Vol. 1. Paris: Victor Masson et fils.

Mlíkovský J. 2002. Cenozoic Birds of the World, Vol. Part 1. Europe: Ninox Press, Praha.

Sun Z, Pan T, Hu C, Sun L, Ding H, Wang H, Zhang C, Jin H, Chang Q, Kan X, et al. 2017. Rapid and recent diversification patterns in Anseriformes birds: inferred from molecular phylogeny and diversification analyses. PLoS ONE. 12(9):e0184529. doi:10.1371/journal.pone.0184529.

von Ammon L. 1918. Tertiäre Vogelreste von Regensburg und die jungmiocäne Vogelwelt. Abh naturwiss Ver Regensburg. 12:1–69.

von Meyer H. 1865. Fossile Vögel von Radoboy und Oehningen. Palaeontogr. 14:125–131.

Worthy TH. 2009. Descriptions and phylogenetic relationships of two new genera and four new species of Oligo-Miocene waterfowl (Aves: anatidae) from Australia. Zool J Linn Soc. 156(2):411–454. doi:10.1111/j.1096-3642.2008.00483.x.

Worthy TH, Lee MS. 2008. Affinities of Miocene waterfowl (Anatidae: *manuherikia, Dunstanetta* and *Miotadorna*) from the St Bathans Fauna, New Zealand. Palaeontol. 51:677–708.

Worthy TH, Tennyson AJ, Jones C, McNamara JA, Douglas BJ. 2007. Miocene waterfowl and other birds from Central Otago, New Zealand. J Syst Palaeontol. 5:1–39.

Zelenkov NV. 2011. Diving ducks from the middle Miocene of western Mongolia. Paleontol J. 45:191–199.

Zelenkov NV. 2012a. Neogene geese and ducks (Aves: anatidae) from localities of the Great Lakes Depression, western Mongolia. Paleontol J. 46:607–619.

Zelenkov NV. 2012b. A new duck from the Middle Miocene of Mongolia, with comments on Miocene evolution of ducks. Paleontol J. 46:520–530.

Zelenkov NV. 2017a. Finds of fragmentary bird skeletons in the Middle Miocene of the northern Caucasus. Dokl Biol Sci. 477:223–226.

Zelenkov NV. 2017b. The revised avian fauna of Rudabanya (Hungary, Late Miocene). Paleontología y evolución de las Aves. Contrib Museo Argentino Cienc Nat 7:253–266.

Zelenkov NV. 2020. Cenozoic evolution of Eurasian anatids (Aves: anatidae s.l.). Biol Bull Rev. 10(5):417–426. doi:10.1134/S2079086420050096.

Zelenkov NV, Kurochkin EN. 2012. Dabbling ducks (Aves: anatidae) from the middle Miocene of Mongolia. Paleontol J. 46:421–429.

Zelenkov NV, Kurochkin EN. 2015. Class Aves. In: Kurochkin EN, Lopatin AV, Zelenkov NV, editors. Fossil vertebrates of Russia and adjacent countries, Fossil reptiles and birds, part 3. Moscow: Geos; p. 86–290. in Russian.