An intriguing new species of dabbling duck (Aves: Anseriformes) from the middle Miocene of Austria

Zbigniew M. Bochenski, Johannes Happ, Grzegorz Salwa, and Teresa Tomek

ABSTRACT

Several dozen species of Miocene anatids are known worldwide, but few are known from abundant finds and even fewer from nearly complete specimens. Most fossil ducks have been described from very scant fragmentary remains, making it very difficult or impossible to compare them with one another. In Austria, only a few heavily damaged remains of Miocene anatids have been found so far. Here, we describe a new genus and species of a nearly complete medium-sized duck preserved on four slabs from the middle Miocene of Lavanttal, southern Austria. A number of features on various parts of the skeleton including the coracoid, humerus and pelvis indicate that it was a dabbling duck in an ecological sense, and exclude the option of it being a diving duck. The new species shows a unique mosaic of features typical of different groups of ducks and some features specific to it. Its more precise systematic position is uncertain, pending future finding of more fossil specimens.

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Key words: new species; new genus; Miocene; fossil dabbling duck; Anseriformes; Lavanttal, Austria

INTRODUCTION

The Lavanttal in Carinthia, southern Austria, is known for numerous and diverse middle Miocene fossils, which include plants, invertebrates and vertebrates representing terrestrial, marine and freshwater environments (e.g., Grímsson et al., 2015, 2020; Nolf and Brzobohatý, 2009; Prieto et al., 2019; Wank, 1991). Among these numerous finds are the remains of only two different passerine birds (Happ et al., 2022). Here, we describe a new genus and species of a medium-sized duck preserved on four slabs from this middle Miocene site.

The early evolution of the Anseriformes is poorly understood (Mayr, 2022); also the relationships and systematic division within the family Anatidae are constantly discussed and subject to change. The oldest definitely "duck-like" anseriforms are *Romainvillia stehlini* from the Late Eocene of France (Lebedinsky, 1927) and *Romainvillia kazakhstanensis* from Kazakhstan (Zelenkov, 2018). Romainvilliinae are also known from the Early Oligocene of Belgium (Mayr and Smith, 2001), England (Mayr 2008) and France (Mayr and De Pietri, 2013). The oldest representatives of the crown group Anatidae date back to the late Oligocene. These include the genera *Mionetta* and *Pinpanetta* from France and Australia, respectively (Mayr, 2022), and *Aminornis* and *Teleornis* from Argentina (Tambussi et al., 2023). In recent years, there have been a number of attempts to determine affinities among anatids (Worthy, 2009; Worthy and Lee, 2008; Worthy et al., 2022; Zelenkov et al., 2018), but this problem has still not been fully resolved (Mayr et al., 2022; Worthy et al., 2022; Zelenkov, 2020).

Worldwide, several dozen anatid species are known from the Miocene (Mlíkovský, 2002; Zelenkov, 2020, 2023b). Some Miocene anatids, such as *Mionetta blanchardi* from Europe or *Manuherikia lacustrina* from New Zealand, are known from abundant finds (Cheneval, 1987; Worthy et al., 2007). Sites rich in a diverse fauna of anseriforms are known from Europe (Mlíkovský, 2002), Asia (Gorobets, 2013; Zelenkov, 2011, 2012a, 2012b, 2020, 2023b; Zelenkov and Kurochkin, 2012), Australia and New Zealand (Worthy et al., 2007, 2022; Worthy, 2009). However, a number of fossil species have been described from very scant fragmentary remains, making it very difficult or impossible to compare them with one another (Mayr et al., 2022).

In Austria, only a few heavily damaged remains of Miocene anatids have been found so far. The oldest duck remains (Anatidae gen. and sp. indet.) come from the early Miocene of Oberdorf (Mlíkovský, 1998). Fragmentary remains of *"Dendronessa"* sp. from Götzendorf, and *Chenoanas* cf. *sansaniensis* and Anserinae indet. from Atzelsdorf are dated to the late Miocene (Mlíkovský, 1991 and Göhlich, 2009, respectively). Apart from the bone fragment of Anatidae indet. from the early Miocene, the new specimen described here is the oldest, most complete and best preserved duck from Austria, and one of the few near-complete ducks in the world.

MATERIAL AND METHODS

The nomenclature and classification of modern taxa follow Dickinson and Remsen (2013) and osteological terminology follows Baumel and Witmer (1993). Measurements are in millimeters.

The nearly complete specimen described here is preserved on four slabs (A-D) in the form of fossilized bones and their imprints. The thin layer of matrix covering some bone fragments was removed during the tedious, time-consuming preparation of the specimen by one of the coauthors (GS). Originally, the well-preserved right coracoid was visible on slab A in ventral view, which made it impossible to see the diagnostic features on its dorsal side. Taking advantage of the fact that this bone was not articulated with humerus, scapula or sternum, it was gently carved from the slab and the remnants of the surrounding rock were removed. Currently, it is a three-dimensional object and can be viewed from all sides.

The following extant species of the Anatidae were available for comparison in the osteological collection of the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences (ISEA PAS): Dendrocygninae: *Dendrocygna arborea, D. autumnalis, D. bicolor, D. eytoni, D. viduata.* Oxyurinae: *Oxyura jamaicensis.* Anserinae*: Anser albifrons, A. anser, A. caerulescens, A. canagicus, A. erythropus, A. fabalis, A. indicus, Branta bernicla, B. canadensis, B. leucopsis, B. ruficollis, B. sandvicensis, Cereopsis novaehollandiae, Coscoroba coscoroba, Cygnus atratus, C. columbianus, C. cygnus, C. melanocoryphus, C. olor.* Anatinae:

Mergini: *Bucephala clangula, B. islandica, Clangula hyemalis, Lophodytes cucullatus, Melanitta fusca, M. nigra, Mergellus albellus, Mergus merganser, M. serrator, Somateria mollissima, S. spectabilis.* Tadornini: *Alopochen aegyptiaca, Chloephaga picta, Tadorna ferruginea, T. tadorna, T. variegata.* Aythyni: *Aythya ferina, A. fuligula, A. marila, A. nyroca, Netta rufina.* Anatini: *Amazonetta brasiliensis, Anas acuta, A. bahamensis, A. capensis, A. crecca, A. formosa, A. gibberifrons, A. platyrhynchos, A. poecilorhyncha, A. rubripes, A. superciliosa, Malacorhynchus membranaceus, Mareca strepera, M. falcata, M. penelope, M. sibilatrix, Spatula clypeata, S. cyanoptera, S. discors, S. querquedula, S. rhynchotis.* Genera incertae sedis: *Aix galericulata, A. sponsa, Biziura lobata, Cairina moschata, Callonetta leucophrys, Chenonetta jubata, Nettapus auritus, N. coromandelianus, N. pulchellus, Stictonetta naevosa.*

In the case of Miocene ducks, in addition to original papers describing a given taxon, other publications describing features and/or containing informative illustrations were also used for comparisons. These additional publications, if any, are listed here in square brackets after the taxonomic authorities of the species: *Dunstanetta* Worthy, Tennyson, Jones, McNamara, and Douglas, 2007 [Worthy, 2009; Worthy and Lee, 2008; Worthy et al., 2008, 2022]; *Manuherikia* Worthy, Tennyson, Jones, McNamara, and Douglas, 2007 [Worthy, 2009; Worthy and Lee, 2008; Worthy et al., 2008, 2022]; *Mionetta blanchardi* (Milne-Edwards, 1863) [Cheneval, 1983; Howard, 1964; Livezey and Martin, 1988; Milne-Edwards, 1867-1868; Canterbury Museum's account on www.sketchfab.com; Worthy and Lee, 2008]; *Mionetta consobrina* (Milne-Edwards, 1867–1868) [Lambrecht, 1933; Howard, 1964; Cheneval, 1983]; *Mionetta natator* (Milne-Edwards, 1867-1868) [Lambrecht, 1933; Švec, 1981; Cheneval, 1983; Göhlich, 2002]; *Pinpanetta* Worthy, 2009 [Worthy et al., 2022]; *Aythya denesi* (Kessler, 2013) [Zelenkov 2016]; *Aythya molesta* (Kurochkin, 1985) [Zelenkov, 2012a, 2016]; *Aythya shihuibas* Hou, 1985 [Stidham, 2015]; *Miotadorna sanctibathansi* Worthy, Tennyson, Jones, McNamara, and Douglas, 2007 [Worthy and Lee, 2008]; *Anas kurochkini* Zelenkov et Panteleyev, 2015 [Zelenkov, unpublished photo]; *Matanas enrighti* Worthy, Tennyson, Jones, McNamara and Douglas, 2007; *Mioquerquedula minutissima* Zelenkov and Kurochkin, 2012 [Zelenkov, 2023a]; *Mioquerquedula soporata* (Kurochkin, 1976) [Zelenkov, 2023a; Zelenkov and Kurochkin, 2012]; *Bambolinietta lignitifila* (Portis, 1884) [Mayr and

Pavia, 2014]; *Chenoanas asiatica* Zelenkov, Stidham, Martynovich, Volkova, Li, Qui, 2018; *Chenoanas deserta* Zelenkov, 2012b [Zelenkov et al., 2018]; *Chenoanas sansaniensis* (Milne-Edwards, 1867–1868) [Göhlich, 2009; Zelenkov et al., 2018]; *Aix praeclara* Zelenkov and Kurochkin, 2012; *Nogusunna conflictoides* Zelenkov, 2011; *Protomelanitta gracilis* Zelenkov, 2011 [Zelenkov, 2023a]; *Protomelanitta velox* (Milne-Edwards, 1867-1868) [Švec, 1981; Zelenkov, 2023a; Zelenkov and Kurochkin, 2012]; *Sharganetta mongolica* Zelenkov, 2011.

Three ratios between skeletal elements were calculated: humerus length/ulna length (brachial index), humerus length/carpometacarpus length, and carpometacarpus length/coracoid medial length.

SYSTEMATIC PALAEONTOLOGY

Class AVES Linnaeus, 1758
Order ANSERIFORMES Wagler, 1831
Family ANATIDAE Leach, 1819
Genus *LAVANTTALORNIS* gen. nov.

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Type species. *Lavanttalornis hassleri* gen. et sp. nov.

Etymology. After the Lavanttal valley where the specimen was found, added to the Ancient Greek ὄρνις (órnis) meaning "bird".

Taxonomic remarks. The new species resembles Anatidae in overall morphology and a unique combination of the following characters: the end of the beak bears foramina neurovascularia; the shape and proportions of the pelvis correspond to those of anatids; the coracoid bears a deeply concave cotyla scapularis of a rounded-triangular shape, short processus procoracoideus, and laterally protruding facies articularis humeralis; the humerus bears the facet of the tuberculum supracondylare ventrale that is cranially buttressed and tilted distally, and there is no prominent tuberculum supracondylare dorsale; in tibiotarsus, the condylus medialis projects much medially in relations to distal shaft, and lateral side of distal shaft forms a sharp edge that slants anteriorly towards condylus lateralis.

Differential diagnosis. *Lavanttalornis hassleri* gen. et sp. nov. is distinguished from:

* *Mionetta blanchardi* (Milne-Edwards, 1863), from the late Oligocene to middle Miocene of Europe, in: coracoid with medial margin of the omal section of the shaft strongly inclined medially and almost straight, processus acro-

coracoideus hardly protruding beyond the medial margin of shaft, and facies articularis sternalis almost straight, humerus with roundish condylus ventralis, and distal end expanded little ventrally, and relatively wide phalanx proximalis digiti majoris with bulging caudal edge;

* *Mionetta consobrina* (Milne-Edwards, 1867–1868), from the early Miocene of Europe, in: coracoid with medial margin of the omal section of the shaft strongly inclined medially and almost straight, and processus acrocoracoideus hardly protruding beyond the medial margin of shaft;

* *Mionetta natator* (Milne-Edwards, 1867–1868), from the late Oligocene to early Miocene of Europe, in: coracoid with medial margin of the omal section of the shaft strongly inclined medially and almost straight, processus acrocoracoideus hardly protruding beyond the medial margin of shaft, and facies articularis sternalis almost straight;

* *Miotadorna sanctibathansi* Worthy, Tennyson, Jones, McNamara, and Douglas, 2007, from the early middle Miocene of New Zealand, in: coracoid with facies articularis sternalis almost straight, and humerus with distal end expanded little ventrally;

* *Manuherikia* Worthy, Tennyson, Jones, McNamara, and Douglas, 2007, and *Dunstanetta* Worthy, Tennyson, Jones, McNamara, and Douglas, 2007, from the early middle Miocene of New Zealand, in: coracoid with medial margin of the omal section of the shaft strongly inclined medially and almost straight, and humerus with relatively thick shaft that does not narrow distally;

* *Pinpanetta* Worthy, 2009, from the late Oligocene/early Miocene of Australia, in: coracoid with medial margin of the omal section of the shaft strongly inclined medially and almost straight, and processus acrocoracoideus hardly protruding beyond the medial margin of shaft;

* *Sharganetta mongolica* Zelenkov, 2011, *Nogusunna conflictoides* Zelenkov, 2011, and *Protomelanitta gracilis* Zelenkov, 2011, from the middle Miocene of Mongolia, in: humerus with shallow notch of incisura capitis in proximal outline of the bone, and distal end expanded little ventrally;

* *Chenoanas deserta* Zelenkov, 2012b, and *Chenoanas asiatica* Zelenkov, Stidham, Martynovich, Volkova, Li, Qui, 2018, both from the middle Miocene of eastern Russia and Mongolia, *Chenoanas sansaniensis* (Milne-Edwards, 1867–1868), from the early to middle Miocene of Europe, eastern Russia and Mongolia, *Aix praeclara* Zelenkov et Kurochkin, 2012, *Mioquerquedula soporata* (Kurochkin, 1976), and *Mioquerquedula minutissima* Zelenkov et Kurochkin, 2012, all from the middle Miocene of Mongolia, and *Protomelanitta velox* (Milne-Edwards, 1867), from the middle Miocene of France, in: coracoid with medial margin of the omal section of the shaft strongly inclined medially and almost straight, and processus acrocoracoideus hardly protruding beyond the medial margin of shaft;

* *Aythya denesi* (Kessler, 2013) from the late Miocene of Hungary, and *Bambolinetta lignitifila* (Portis, 1884) from the late Miocene of Italy, in: humerus with relatively thick shaft that does not narrow distally;

* *Aythya shihuibas* Hou, 1985, from the late Miocene of China, and *Aythya molesta* (Kurochkin, 1985), from the late Miocene of Mongolia, in: humerus with shallow notch of incisura capitis in proximal outline of the bone;

* *Matanas enrighti* Worthy, Tennyson, Jones, McNamara and Douglas, 2007, from the early-middle Miocene of New Zealand, in: coracoid with processus acrocoracoideus hardly protruding beyond the medial margin of shaft;

* *Anas kurochkini* Zelenkov et Panteleyev, 2015, from the late Miocene of northeastern Sea of Azov region, Russia, in: coracoid with medial margin of the omal section of the shaft strongly inclined medially and almost straight, thick crista acrocoracoidea, facies articularis humeralis with acute cranial angle and projecting little laterally, and facies articularis sternalis almost straight;

* all extant ducks by a unique combination of characters: coracoid with medial margin of the omal section of the shaft strongly inclined medially and almost straight, ventral plane of processus acrocoracoideus subparallel to the ventral plane of the extremitas sternalis, processus acrocoracoideus hardly protruding beyond the medial margin of shaft, and facies articularis sternalis almost straight, humerus

with distal end expanded little ventrally, and relatively wide phalanx proximalis digiti majoris with bulging caudal edge.

Lavanttalornis hassleri sp. nov.
Figures 1, 2, 3A-E, 4, 5A, 6A

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Etymology. The species is named after the finder of the specimen, Dr. Andreas Hassler of Sankt Andrä, a veterinarian by profession but a paleontologist by passion.

Holotype. LMK-Pal 7453a+a'+b+c+d (Figures 1, 2, 3A-E, 4, 5A, 6A), partly articulated nearly complete skeleton on four slabs from which the right coracoid has been removed, cleaned and is visible as a 3D object; housed at the paleontological collection of the Landesmuseum Kärnten (LMK-Pal), Klagenfurt, Austria.

Type locality and horizon. A site near the village of Schaßbach, about 50 km northeast of Klagenfurt in the Lavanttal, Carinthia, southern Austria. GPS coordinates using WGS 84 datum: 46.79752°N 14.80676°E at an altitude of 471 m above sea level. The specimen is dated to the Upper Sarmatian s. s. (upper middle Miocene), ca 12 Ma. It was found in freshwater sediments that contain two coal seams lying above the Middle Sarmatian layers (Reischenbacher et al., 2007).

Diagnosis. As for the genus.

Measurements. Measurements (in mm) including total length (TL) and others, taken from slabs A, B or C: coracoid (A, dext) TL, 47.6, medial length, 42.4, sternal width, 17.7; scapula (A, sin) articular height, 11.2; humerus (A, sin) TL, 75.5, proximal width, 18.7, distal width, 10.6, least shaft width, 6.3; radius (B, dext) TL, 62.6; ulna (B, dext) TL, 69.5; carpometacarpus (B, dext) TL, 46.4, proximal width, 11.9; phalanx proximalis dig. majoris (B, dext) TL, 19.6; phalanx dig. minoris (B, dext) TL=9.6; pelvis (C) TL, 64.4, width between antitrochanters, 30.5.

Description and Comparison

Skull. The skull, visible in lateral view on slabs C and D, is partly an imprint and partly fossilized bone remains (Figures 2, 6A). As in *Mionetta blanchardi*, the length of the beak is approximately the same as that of the skull. The braincase is too damaged for meaningful comparisons which also applies to the preserved small fragment of ramus mandibulae. As in extant anseriforms, the foramina neurovascularia are visible at the end of the beak. The caudal part of the nostril is elongated and tapered, while in the Miocene *Mioquerquedula* sp.,

Bambolinietta lignitifila and extant anseriforms, the caudal part of the nostril is rounded.

Coracoid. The well-preserved right coracoid removed from slab A (Figures 1, 3A-E) shows a very thick, massive shaft that is somewhat similar to that of the Miocene *Anas kurochkini*, *Mionetta blanchardi* and extant *Anas*, *Spatula*, *Mareca*, and *Melanitta*; *Mionetta natator* and extant species of the genera *Aythya*, *Bucephala,* and *Mergus* have much slender shafts. A feature specific to *Lavanttalornis hassleri* is the medial margin of the omal section of the shaft, which is strongly inclined medially and almost straight. In *Chenoanas*, medial margin of shaft is also straight but it does not incline medially, whereas in *Mionetta blanchardi, Mionetta consobrina, Mionetta natator, Aix praeclara, Mioquerquedula minutissima, Mioquerquedula soporata, Anas kurochkini, Pinpanetta, Manuherikia, Dunstanetta, Protomelanitta velox,* and most extant taxa (e.g., *Aix, Anas, Spatula, Mareca, Aythya, Clangula, Melanitta)* the medial margin of shaft is much less medially inclined, and is usually slightly arched. As, for example, in the extant genus *Anas* s.l., the ventral plane of the processus acrocoracoideus is subparallel to the ventral plane of the extremitas sternalis (Worthy and Lee, 2008: character 45). The processus acrocoracoideus hardly protrudes beyond the medial margin of the shaft. This distinguishes it from the genera *Chenoanas* and *Pinpanetta, Matanas enrighti, Aix praeclara, Mioquerquedula minutissima, Mioquerquedula soporata, Protomelanitta velox, Mionetta consobrina, Mionetta natator,* and to a lesser extent from *Mionetta blanchardi* and many extant taxa (e.g., *Aix, Anas, Mareca, Spatula, Clangula).* The tuberculum brachiale (name by Zelenkov and Kurochkin, 2012; Zelenkov and Panteleyev, 2015) is concave and slightly wider dorsoventrally than craniocaudally high. As in extant species of the genus *Anas* but unlike the extinct *Anas kurochkini*, the crista acrocoracoidea (name by Elzanowski et al., 2012) is thick. As in all anatids, the margin of the facies articularis humeralis projects laterally, although not as far as in *Anas kurochkini*, and in lateral view it has an acute cranial angle. The sulcus m. acrocoracoidei is deeply excavated near the facies articularis humeralis, which is observed in taxa from various groups. As in many ducks, the processus proccoracoideus is relatively short, projecting craniomedially, and the cotyla scapularis is deeply concave of a rounded-triangular shape. The angulus medialis is short, blunt ended, and its short cranial edge is almost perpendicular to the shaft; in *Mionetta blanchardi*
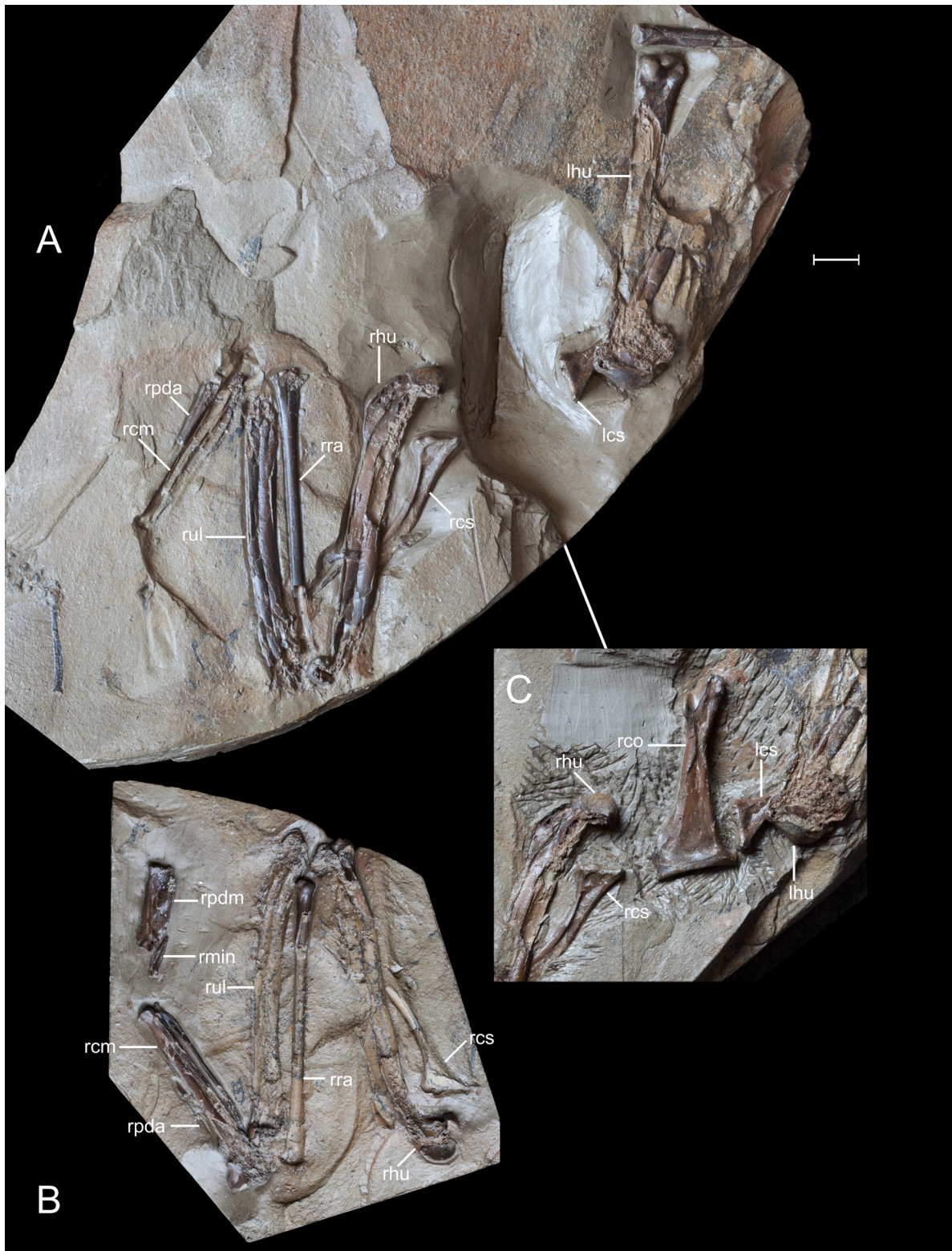
FIGURE 1. *Lavanttalornis hassleri* gen. et sp. nov., holotype, specimen LMK-Pal 7453a+b from Lavanttal, Austria, middle Miocene. A, slab A after exposing all the bones and removing the coracoid; B, slab B (counterslab of the wing bones visible on slab A); C, fragment of slab A before removal of the coracoid. Abbreviations: lcs, left scapula; lhu, left humerus; rcm, right carpometacarpus; rco, right coracoid; rcs, right scapula; rhu, right humerus; rmin, right phalanx digiti minoris; rpda, right phalanx digiti alulae; rpdm, right phalanx proximalis digiti majoris; rra, right radius; rul, right ulna. Scale bar equals 10 mm.
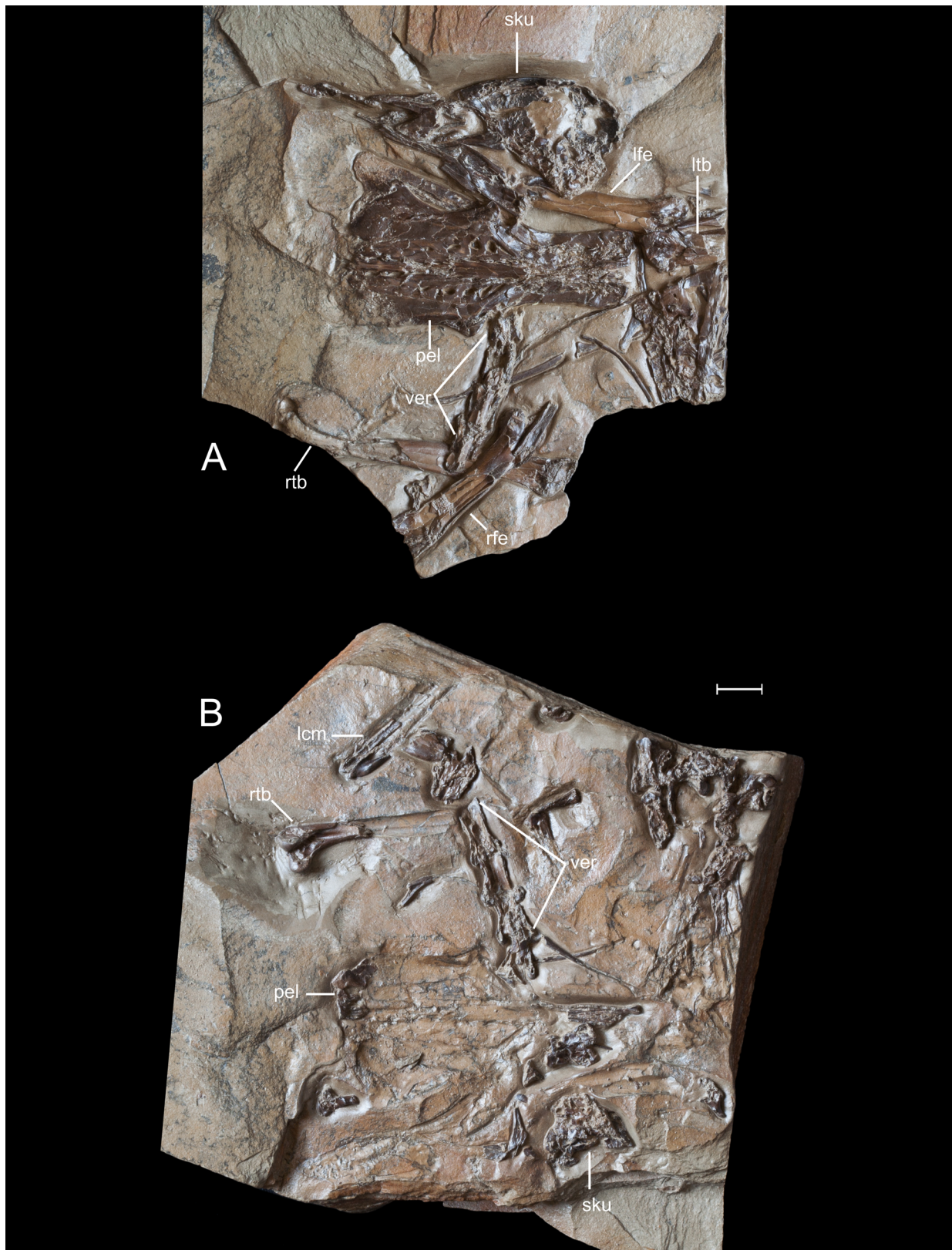
FIGURE 2. *Lavanttalornis hassleri* gen. et sp. nov., holotype, specimen LMK-Pal 7453c+d from Lavanttal, Austria, middle Miocene. A, slab C; B, slab D (counterslab of slab C). Abbreviations: lcm, left carpometacarpus; lfe, left femur; ltb, left tibiotarsus; pel, pelvis; rfe, right femur; rtb, right tibiotarsus; sku, skull; ver, vertebrae. Scale bar equals 10 mm.

the angulus medialis merges with the shaft gradually, in *Pinpanetta* a distinct flange of various shape extends cranially along the medial shaft margin, and in *Protomelanitta velox, Manuherikia,* and *Miotadorna sanctibathansi* the angulus medialis is acute. In ventral view, the edge of the facies articularis sternalis is almost straight, whereas in *Mionetta blanchardi, Mionetta natator, Anas kurochkini, Mioquerquedula minutissima, Manuherikia lacustrina,* and *Miotadorna sanctibathansi* it arches sternally.

Scapula. Articular parts with small fragments of the shaft of the left and right scapula are visible on slab A in medial (costal) view; slab B has an imprint of the right scapula (Figures 1, 4A). As in *Mionetta blanchardi* and some extant taxa (e.g., *Anas acuta, A.platyrhynchos, Spatula quercquedula, S. clypeata, Melanitta fusca),* the acromion deviates very slightly dorsally; its dorsal edge forms an almost straight line with the margo dorsalis of the corpus scapulae. In many other species (e.g., *Aix galericulata, Anas crecca, Mareca strepera, Aythya ferina, A.fuligula, Clangula hyemalis, Bucephala clangula, Mergellus albellus),* the acromion is much more dorsally curved.

Humerus. The left humerus is visible on slab A in cranial view and the right humerus in cranioventral view. Slab B shows an imprint of the dorsocaudal side of the right bone with a preserved tuberculum ventrale (Figures 1, 4A-C, F). As in the Miocene *Aythya denesi,* the notch of incisura capitis in proximal outline of the humerus is shallow (Worthy and Lee, 2008: character 59) whereas in the late Oligocene *Pinpanetta* from Australia as well as in extant dendrocygnines, anserines and tadornines it is (almost) missing. The notch is more pronounced in *Mionetta blanchardi, Sharganetta mongolica, Nogusunna conflictoides, Protomelanitta gracilis, Aythya molesta, A. shihuibas, Manuherikia,* and *Dunstanetta*. Extant species of such genera as *Aix, Anas, Spatula, Mareca, Aythya, Melanitta,* or *Mergellus* also show a more pronounced notch. The tuberculum ventrale is directed caudo-cranially so its distal margin is approximately at right angles to the fossorial plane (Worthy and Lee, 2008: character 57). A similarly directed tuberculum ventrale is found in *Pinpanetta, Aythya shihuibas* and *Aythya denesi,* whereas in *Miotadorna sanctibathansi, Mionetta,* and the genus *Chenoanas,* the tuberculum ventrale is proximally oriented. As in extant *Aix galericulata, Anas crecca, Spatula clypeata, Spatula querquedula,* the tuberculum ventrale is narrow (forms a narrow ridge); the tuberculum is wide in many other extant taxa including *Anas platyrhyn-*

chos, *Anas acuta, Aythya ferina, Aythya fuligula, Bucephala clangula, Clangula hyemalis, Melanitta*. The length of the crista deltopectoralis is comparable with the proximal width of the humerus. Other details of the crista deltopectoralis as well as details of the remaining structures of the proximal humerus, including tuberculum dorsale, crista bicipitalis, fossa pneumotricipitalis and capital shaft ridge, are not visible. As in *Pinpanetta fromensis, Pinpanetta vickersrichae* and *Mionetta blanchardi* the shaft is relatively thick, and it does not narrow distally but its sides are essentially parallel to each other (Worthy and Lee, 2008: character 61). The humerus of *Bambolinetta lignitifila* was definitely even more robust and stouter. In *Aythya denesi, Manuherikia* and *Dunstanetta, Pinpanetta tedfordi* and the similarly sized extant species, the shaft narrows distally. The shaft is s-shaped, in dorsal view. A similarly bent shaft is found in many extant taxa, including *Aix galericulata, Anas crecca, Anas acuta, Anas platyrhynchos, Mareca strepera, Mareca penelope, Spatula clypeata, Spatula querquedula, Bucephala clangula,* and *Clangula hyemalis*. In contrast, the shaft is more straight in such species as *Aythya fuligula* or *Mergellus albellus*. As in *Mionetta, Manuherikia, Dunstanetta, Malacorhynchus, Stictonetta, Nomonyx,* and *Pinpanetta,* the facet of the tuberculum supracondylare ventrale (attachment of the anterior articular ligament) is cranially buttressed (Worthy and Lee, 2008: character 65), whereas the unbuttressed facet is observed in *Anseranas, Thalassornis, Biziura,* and *Oxyura*. Moreover, in *Lavanttalornis hassleri,* the facet is tilted distally. As in Miocene *Mionetta blanchardi* and extant species such as *Aix galericulata* or *Aythya fuligula,* but unlike e.g., *Spatula clypeata,* fossa m. brachialis (brachial fossa) is large, well-defined and forms a marked depression (Worthy and Lee, 2008: character 68). It differs from that in *Pinpanetta,* where it is elongate and dorsal margin barely extends past midshaft width. As in *Mionetta blanchardi,* the processus flexorius extends roughly as far distally as condylus dorsalis (Worthy, 2009: character 63). As in Miocene *Mionetta blanchardi* and *Sharganetta mongolica,* and extant Anatinae, there is no prominent tuberculum supracondylare dorsale (ectepicondylar prominence) (Worthy and Lee 2008, character 64). A distinct ectepicondylar prominence is present in the Miocene *Pinpanetta* as well as in extant anserines. Contrary to *Mionetta blanchardi, Pinpanetta, Miotadorna sanctibathansi, Sharganetta mongolica, Nogusunna conflictoides,* and *Protomelanitta gracilis,* the distal end of the humerus is little expanded

FIGURE 3. Comparison of the right coracoid. A–E, *Lavanttalornis hassleri* gen. et sp. nov., holotype, specimen LMK-Pal 7453a' from Lavanttal, Austria, middle Miocene (removed from slab A) in ventral, dorsal, lateral, medial and dorso-medial views; F–G, *Dendrocygna bicolor* (Dendrocygninae); H–I, *Oxyura jamacensis* (Oxyurinae); J–K, *Melanitta nigra* (Anatinae: Mergini); L–M, *Aix galericulata* (incerte sedis); N–O, *Aythya fuligula* (Anatinae: Aythyni); P–R, *Anas platyrhynchos* (Anatinae: Anatini); S–T, *Tadorna tadorna* (Anatinae: Tadornini). Extant specimens are shown in ventral (left) and dorsal (right) views. Abbreviations: agm, angulus medialis; csc, cotyla scapularis; car, crista acrocoracoidea; fah, facies articularis humeralis; fas, facies articularis sternalis; pac, processus acrocoracoideus; ppc, processus procoracoideus; sac, sulcus m. acrocoracoidei; tbr, tuberculum brachiale. Scale bars equal 10 mm.

ventrally, and the condylus ventralis is roundish (more oblong in *Mionetta, Pinpanetta,* and *Sharganetta* but also roundish in *Protomelanitta* and *Miotadorna*).

Ulna. The right ulna is visible on plate A in ventral view, and its imprint is on plate B. The bone is clearly less stout and relatively longer than that of *Bambolinetta lignitifila*. Its length is in the range of *Mionetta blanchardi*; ulna of *M. consorbina* was longer, and that of *M. natator* was shorter. The proximal and distal parts are crushed, preventing meaningful comparisons.

Radius. The right proximal radius is visible on plate B in anterior view, and its distal posterior side is imprinted there. Plate A shows the distal right radius with a large portion of shaft in posterior view, and an imprint of the anterior proximal part (Figures 1, 4F-G). The bone differs significantly from that of *Bambolinetta lignitifila*, from which it is clearly less stout and relatively longer. As in *Mionetta blanchardi*, the shaft is more straight than, for example, in extant *Spatula clypeata*. As in *Spatula clypeata*, the capital tuberosity (name used by Howard, 1929) is roundish but clearly larger than in *Spatula*, whereas in some other extant species, such as *Aythya ferina* or *Melanitta nigra* the tuberculum is more oval. As in *Mionetta blanchardi* and *Spatula clypeata*, the tuberculum aponeurosis ventralis is proximodistally relatively short, whereas in some extant species, such as *Clangula hyemalis* or *Melanitta fusca* the tuberculum is significantly longer.

Carpometacarpus. The right carpometacarpus is visible on slab B in dorsal view, and its imprint is preserved on slab A. Moreover, the distal part of the left bone is visible on slab D in dorsal view (Figures 2, 4D). As in *Mionetta blanchardi* and such modern taxa as *Anas, Spatula, Mareca* or *Bucephala*, the processus extensorius is broad proximodistally and a distinct arcuate indentation separates it from the processus alularis; in *Clangula hyemalis*, the indentation is very small. Also as in *Mionetta blanchardi* and such extant taxa as *Aix galericulata, Anas acuta, Anas crecca, A. platyrhynchos, Spatula clypeata, Spatula querquedula, Mareca penelope, Mareca strepera, Aythya fuligula,* and *A. ferrina,* the symphysis metacarpalis distalis is long in relation to the carpometacarpus width measured just distad of spatium intermetacarpale (Worthy and Lee, 2008: character 84). The symphysis is relatively shorter in many other species (e.g., *Bucephala clangula, Clangula hyemalis, Melanitta fusca, M.nigra, Mergellus albellus.* There is a distinct nodule in the distal dorsal side of the os metacarpale majus. A similar nodule is in extant *Anas platyrhynchos, Anas acuta, Anas crecca, Mareca penelope, Mareca strepera, Spatula querquedula, Spatula clypeata, Aythya fuligula, Aythya ferina,* and *Clangula hyemalis*. In *Bucephala clangula, Melanitta fusca, M.nigra, Mergus merganser, Mergus serrator* the nodule is small or absent.

Phalanx proximalis digiti majoris. The right phalanx, detached from the carpometacarpus, is visible on slab B in dorsal view, and its imprint is preserved on slab A (Figures 1, 5). For a duck, the phalanx is relatively wide in relation to its length, which is the result of a bulging of the caudal edge. In this respect, it differs from *Mionetta blanchardi* and most extant duck species whose phalanx is narrower and its caudal and cranial edges are often almost parallel to each other. One of the few taxa with a similarly wide phalanx is *Anas platyrhynchos*, but other members of the Anatini, such as *Spatula clypeata*, have narrower phalanges. A broad phalanx is also found e.g., in *Aix galericulata* of uncertain systematic affiliation. In the proximal part of the phalanx there is a nodule clearly raised both above the dorsal surface and the pila cranialis. A similar nodule is found in species of the genus *Anas* s.l. Other modern ducks either do not have such a nodule, or if they do, it is less pronounced, especially in relation to pila cranialis.

Pelvis. Pelvis is visible on slab C in dorsal view, and its imprint is preserved on slab D (Figures 2, 6). The overall proportions of the pelvis, that is, length to width between antitrochanters and to width of the ala preacetabularis ilii, are similar to that of *Anas platyrhynchos*; some of the extant genera, e.g., *Netta, Aythya, Oxyura* or *Biziura* have a much narrower pelvis. *Mionetta blanchardi* also had a narrower pelvis, especially for ala preacetabularis ilii. Also as in *Anas platyrhynchos, Spatula clypeata* or *Aix gallericulata*, the pre-acetabular and post-acetabular parts are of similar length. In *Aythya, Netta, Oxyura, Bucephala,* or *Biziura*, the post-acetabular region is elongated to varying degrees. As in *Mionetta blanchardi* and many extant taxa including *Aix, Anas, Aythya, Bucephala,* and *Melanitta*, the caudal edges of the ala ischii and ala postacetabularis ilii extend roughly equally far caudally; in *Dendrocygna*, the ala ischii reaches further caudally. As in all Anatidae, foramina intertransversaria can be discerned.

Femur. Portions of the left and right femur are visible on slab C, and their imprints are on slab D. The bones are too damaged to allow meaningful comparisons.

FIGURE 4. *Lavanttalornis hassleri* gen. et sp. nov., holotype, specimen LMK-Pal 7453a+b+d from Lavanttal, Austria, middle Miocene. A, proximal left humerus in cranial view and proximal left scapula in medial view (preserved on slab A); B, proximal right humerus in dorsocaudal view (preserved on slab B); C, distal left humerus in cranial view (preserved on slab A); D, right carpometacarpus in dorsal view (preserved on slab B); E, distal right tibiotarsus in antero-lateral view (preserved on slab D); F, right proximal radius in anterior view (preserved on slab B); G, right distal radius in posterior view (preserved on slab A). Abbreviations: acr, acromion; cdd, condylus dorsalis; cdv, condylus ventralis; cla, condylus lateralis; cme, condylus medialis; ctu, capital tuberosity; fbr, fossa m. brachialis; fts - facet of the tuberculum supracondylare ventrale (attachment of the anterior articular ligament); ica, incisura capitis; ini, incisura intercondylaris; oma, os metacarpale majus; pal, processus alularis; pex, processus extensorius; pfl, processus flexorius; psu, pons supratendineus; se, sharp edge; syd, symphysis metacarpalis distalis; tav, tuberculum aponeurosis ventralis; tdo, tuberculum dorsale; tve, tuberculum ventrale. Scale bar equals 10 mm.

Tibiotarsus. The distal part of the right tibiotarsus is visible on slab D in anterolateral view and its imprint is on slab C. Portions of the left tibiotarsus and their imprints are on both slabs (Figures 2, 4E). As in *Mionetta blanchardi* and extant Anatidae, the condylus medialis projects much medially in relations to distal shaft and the lateral side of distal shaft forms a sharp edge that slants anteriorly towards condylus lateralis (Bochenski and Tomek, 2009: characters 7a, 7b and 14'b). The pons supratendineus is located in the middle of the shaft and opens into the incisura intercondylaris, which is also typical of anseriforms. In contrast to the Miocene genus *Chenoanas*, the lateral margin of the condylus lateralis is medially inclined (in *Chenoanas*, it is positioned in line with the lateral margin of the shaft), and condyli lateralis and medialis are proximodistally long (in *Chenoanas*, the condyli are shorter than the width of the incisura intercondylaris).

Ratios between selected skeletal elements. For *Lavanttalornis hassleri*, the brachial index (humerus length/ulna length) is 1.1; similar values of this ratio are also observed in some extant species in all other groups of Anatinae (Appendix 1). Slightly lower values (approx. 1.0) are typical for all Dendrocygninae and parts of Tadornini, and slightly higher values (approx. 1.2) occur in various groups. The ratio humerus length/carpometacarpus length for *Lavanttalornis hassleri* is 1.6, and similar values were most often recorded in extant Anatini (in 15 species out of 20 examined) and in several species of Mergini, Tadornini and genera incertae sedis. It is true that higher values of this ratio (1.7–2.2) were recorded in some species among all taxonomic groups examined, but only in Dendrocygninae, Oxyurinae, and Aythyni, i.e., in the groups of good divers, all species showed these higher values. The ratio of carpometacarpus length/coracoid medial length for *Lavanttalornis*

FIGURE 5 (to right). Comparison of the right phalanx proximalis digiti majoris in dorsal view. A, *Lavanttalornis hassleri* gen. et sp. nov., holotype, specimen LMK-Pal 7453b from Lavanttal, Austria, middle Miocene (preserved on slab B); B, *Dendrocygna bicolor* (Dendrocygninae); C, *Oxyura jamacensis* (Oxyurinae); D, *Melanitta nigra* (Anatinae: Mergini); E, *Tadorna ferruginea* (Anatinae: Tadornini); F, *Aythya ferrina* (Anatinae: Aythyni); G, *Anas platyrhynchos* (Anatinae: Anatini); H, *Spatula clypeata* (Anatinae: Anatini); I, *Aix galericulata* (incerte sedis). The phalanges of extant species are shown in the same size as the fossil phalanx to facilitate comparison. Abbreviations: pcr, pila cranialis. Scale bars equal 10 mm.
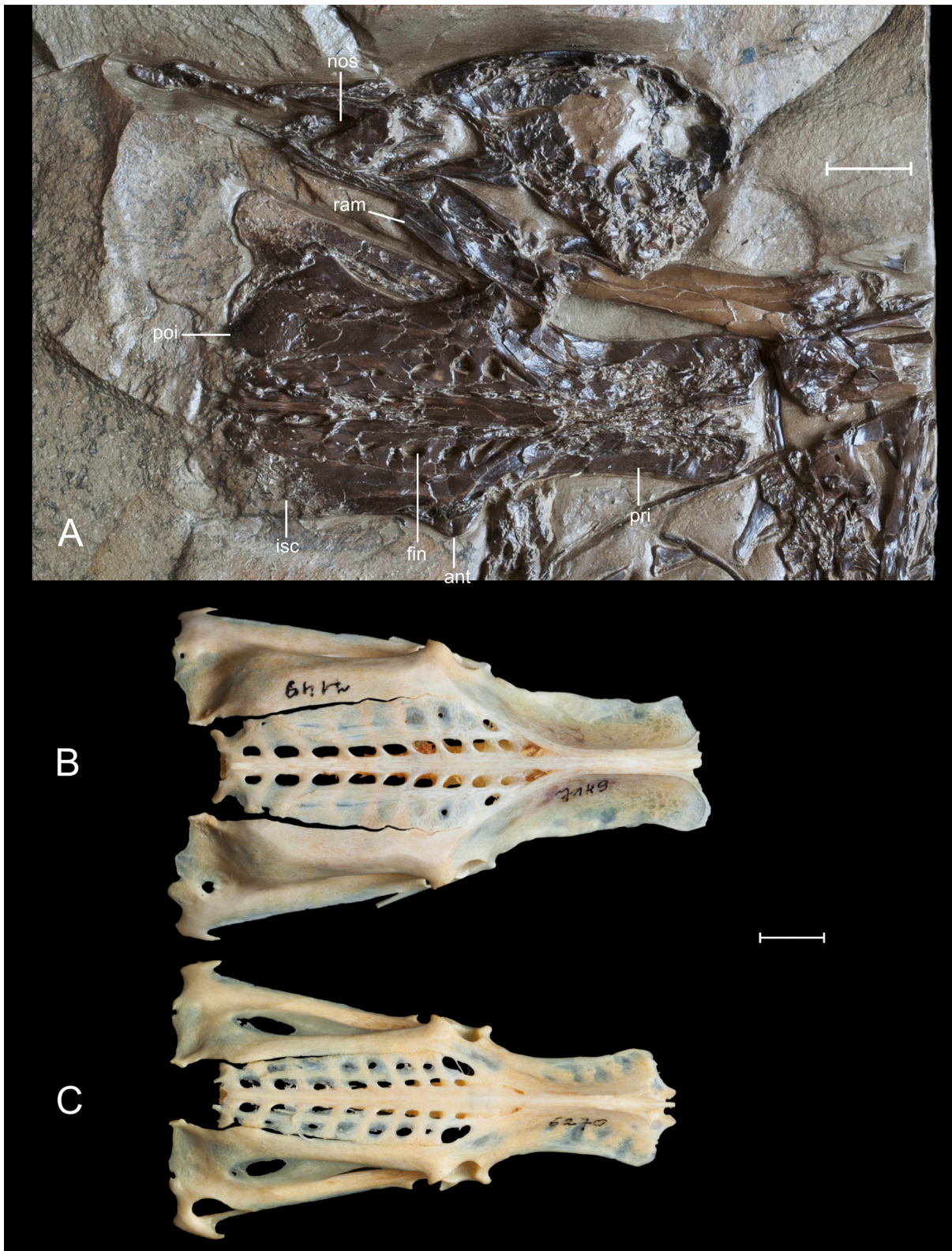
FIGURE 6. A, skull and pelvis of *Lavanttalornis hassleri* gen. et sp. nov., holotype, specimen LMK-Pal 7453c from Lavanttal, Austria, middle Miocene (preserved on slab C); B, pelvis of *Anas platyrhynchos* (Anatinae: Anatini); C, pelvis of *Aythya fuligula* (Anatinae: Aythyni). Abbreviations: ant, antitrochanter; fin, foramina intertransversaria; isc, ala ischii; nos, nostril; poi, ala postacetabularis ilii; pri, ala preacetabularis ilii; ram, ramus mandibulae (inside surface of right branch). Scale bars equal 10 mm.

hassleri is 1.1, and similar values were recorded in most of the examined Anatini (12 species out of 18), and most of the examined species of uncertain taxonomic position (incertae sedis: 7 out of 10). Again, the most homogeneous groups with different values of this ratio than in *Lavanttalornis* were Dendrocygninae and Tadornini, in which all species showed higher values (1.2--1.4). In other species that dive for food, including Aythyni (4 out of 5), Mergini (6 out of 9) and *Oxyura jamacensis*, these values were lower (0.9--1.0).

DISCUSSION

A number of features on various parts of the skeleton can be used to infer about the duck's way of life. In the examined specimen, such features are preserved mainly on three skeletal elements. In coracoid, the ventral plane of the processus acrocoracoideus is not much deviated from (lies sub-parallel to) the ventral plane of the extremitas sternalis, which is a usual condition in dabbling ducks; in Dendrocygninae, Oxyurinae, Aythyni, and Mergini, i.e., in ducks that dive while feeding, the ventral plane of the processus acrocoracoideus is more inclined (more perpendicular to) the ventral plane of the extremitas sternalis (Zelenkov, 2011; Zelenkov and Panteleyev, 2015; Worthy and Lee, 2008: character 45). In addition, the acute cranial angle of the facies articularis humeralis is also typical of dabbling ducks (Zelenkov and Panteleyev, 2015). Also, the distally tilted facet of the tuberculum supracondylare ventrale (distal humerus) is a usual condition in dabbling ducks whereas a medial rotation of the facet is common to all divers (McCracken et al., 1999; Worthy, 2009). Finally, the broad pelvis and its unextended post-acetabular part are also typical of dabbling ducks. Ducks that dive while foraging, such as *Oxyura, Biziura,* or *Aythya*, usually have a much narrower pelvis with extended post-acetabular section, which is interpreted as an adaptation to this type of activity (Raikow, 1970, 1971; Worthy and Lee, 2008). Although none of the three studied ratios gives a clear answer as to the ecology of *Lavanttalornis hassleri*, certain trends are clearly visible. It appears that the brachial index is relatively the least diverse among different groups of anatids, which is probably related to similar wing kinematics in all ducks (Nudds et al., 2007). The other two ratios (humerus length/carpometacarpus length and carpometacarpus length/coracoid medial length) seem to do a somewhat better job of dividing extant ducks into different groups. In both cases, *Lavanttalornis* is found in one group with most extant species of Anatini and other non-diving ducks. Species from good-diving groups (Dendrocygninae and Aythyni) have different proportions of bones examined. These preliminary results are promising but should be treated with caution because only one specimen per species was examined and not all species of anatids were included. More detailed analyses of the proportions of individual skeletal elements in all anatids are beyond the scope of the current study; they may be the subject of separate research. The above arguments taken together indicate unequivocally that *Lavanttalornis hassleri* was not a diving duck. Many osteological features are similar to those of dabbling ducks in an ecological sense.

Most of the new species of Miocene anatids have been described in new genera specially created for them (Mayr et al., 2022). Modern genera of ducks begin to dominate only in the late Miocene (Zelenkov, 2020). Given the unique mosaic of features typical of different ducks as well as features specific to *Lavanttalornis hassleri*, and the fact that it is of middle Miocene age, we decided to describe it in a new genus. Many features indicate that ducks that dive for food, including Dendrocygninae, Oxyurinae, and Aythyni can be excluded from the groups to which *Lavanttalornis* could belong, and Tadornini can probably be excluded from among non-diving ducks. It is more difficult to indicate the taxonomic group to which *Lavanttalornis* could belong. The similarity to Anatini is supported by many features but may be superficial, and considering the large number of ducks of uncertain systematic affiliation (genera incertae sedis) and the fact that the caudal side of humerus with significant phylogenetic features has not been preserved, it is difficult to draw more precise conclusions about the systematic affiliations of *Lavanttalornis*.

Most skeletal elements are preserved in articulation, but some bones, including both scapulae, the right coracoid, the left humerus, and the right phalanx proximalis digiti majoris, are no longer connected to the adjacent bones, but lie close to them. This indicates that the carcass was exposed to natural decomposition agents, including putrefaction gases, for some time before being buried in sediments, in a calm environment without much underwater turbulences that could stimulate its disarticulation and loss of skeletal elements (Schäfer, 1972; Bienkowska-Wasiluk, 2010). This was also the case with the passerine bird described earlier from the same site (Happ et al., 2022).

Many Miocene ducks are known from very few finds, sometimes even single incomplete

bones (e.g., Boev, 2007, 2020; Gál et al., 2000; Göhlich, 2009; Kessler and Venczel, 2009). This makes it very difficult or even impossible to compare such specimens with those previously described. Only occasionally can they be identified as previously described taxa; just as rarely they may be references to fossil specimens to be described in the future. *Lavanttalornis hassleri* does not suffer from this defect. The unique feature of specimens preserved on slabs is the certainty that all skeletal elements come from the same individual (species). This is not only helpful in identifying fossil specimens, but can also be helpful in comparative, ecomorphological and phylogenetic analyses.

Typical habitats of modern dabbling ducks, in the ecological sense of the word, are shallow freshwater and estuaries. Compared to diving ducks, dabblers have relatively larger wings with a more elliptical shape, which enables them to rocket upwards out of the water and land even on small bodies of water that are spatially broken up by surrounding or emergent vegetation (Raikow, 1973). In the middle Miocene in Lavanttal, lowland wetland forests covered the shores of lakes, rivers, streams, marshes, and floodplains, with a warm and humid climate in the basin and dryer environmental conditions in the surrounding lowlands, highlands and mountains (Grímsson et al, 2015,

2020). The paleogeographic and ecological setting must have been a suitable environment for *Lavanttalornis hassleri*.

The remains of three birds were found at this site, all very well preserved. In addition to the duck described here, an almost complete passerine bird and a perfectly preserved sternum of another passerine were also found there (Happ et al., 2022). This may be a coincidence but it may also indicate a particular form of Lagerstaette. There is also the question of whether the birds died as a result of a single event and were buried at the same time, or whether they were deposited at different intervals and why, then, they were in the same place and in such a good state of preservation. The site was closed for environmental reasons shortly after these discoveries, so no more bird fossils have been found. But it will be reopened in the near future, which gives hope for further discoveries.

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APPENDIX 1

Length of selected bones (in mm) and their ratios, rounded to one decimal place to avoid giving a false impression of the accuracy of this preliminary analysis. Abbreviations: hum, humerus; cmc, carpometacarpus; cor, coracoid. Extant specimen numbers are those of the osteological collection of the ISEA PAS. Classification of modern taxa follow Dickinson and Remsen (2013). (Available for download at https://palaeo-electronica.org/content/2023/4027-a-miocene-dabbling-duck)