New specimens of the earliest European passeriform bird

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Mayr, G. and Manegold, A. 2006. New specimens of the earliest European passeriform bird. *Acta Palaeontologica Polonica* 51 (2): 315–323.

We describe new specimens of the oldest European passeriform bird from the early Oligocene of Germany. This bird has hitherto been known only from a poorly preserved skeleton and we report here a second slab of the same specimen and an additional fragmentary skull. The new specimens allow the description of a new species, *Wieslochia weissi* gen. et. sp. nov., which lacks apomorphies of crown group Oscines, the taxon including most extant and all European passeriform species. In overall osteology, *Wieslochia* most closely resembles extant Suboscines but these similarities may be plesiomorphic for Passeriformes. *W. weissi* differs from the stem species pattern hypothesized for Eupasseres in the morphology of the distal carpometacarpus, the absence of a hooked processus acrocoracoideus (coracoid), and the presence of furrows instead of certain canals on the hypotarsus, and may even be outside crown group Eupasseres, the clade including Oscines and Suboscines. Because the earliest European fossil record of oscine passerines is from the late Oligocene, passerines outside crown group Oscines may have colonized Europe before the arrival of Oscines from the Australian continental plate.

Key words: Aves, Passeriformes, *Wieslochia* gen. nov., Oligocene, Frauenweiler.

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Introduction

Passeriformes (passerines or perching birds) are osteologically very uniform birds, which include more than half of all extant avian species. Recent molecular analyses provided a phylogenetic framework for the major clades, and according to these studies New Zealand wrens (Acanthisittidae) are the sister taxon of all other extant passerines, the Eupasseres, which comprise Suboscines and Oscines (Ericson et al. 2003; Barker et al. 2004). Today, only Oscines (songbirds) occur in Europe whereas Suboscines are mainly restricted to the New World, their sole Old World representatives being pittas (Pittidae) and broadbills and asities (Eurylaimidae). Fossil Suboscines, however, were reported from the early Miocene of Germany and France (Ballmann 1969; Cheneval 2000), although identification of woodcreepers (Furnariidae, Dendrocolaptinae) in the early Miocene of France needs to be corroborated by additional material. It is assumed that Oscines originated on the Australian continental plate from where they dispersed into Europe (Barker et al. 2002; Ericson et al. 2002).

The earliest fossils of passeriform birds are very fragmentary remains of uncertain affinities from the early Eocene of Australia (Boles 1995, 1997). Until recently, the only other published Paleogene (pre-Miocene) specimens were few bones of Oscines from the late Oligocene of France (Mourer-Chauviré et al. 1989), but Mayr and Manegold (2004) described a dissociated skeleton of a passeriform bird from the early Oligocene of Wiesloch-Frauenweiler in Germany. This specimen, which was donated by a private collector to Forschungsinstitut Senckenberg, is very poorly preserved, and most skeletal elements are casts of an impression in the original matrix, thus preventing detailed comparisons. Shortly after our study was published, however, we learned that a second slab of the same specimen with exquisitely preserved bones exists in the collections of the Staatliches Museum für Naturkunde in Karlsruhe. Both slabs were prepared with the resin transfer method (Kühne 1961) and the Karlsruhe slab completely separated from the original matrix without further preparation, leaving an impression with few adhering bones. To secure these bones, a second transfer specimen was made producing the Senckenberg slab described by Mayr and Manegold (2004). Unfortunately, both slabs ended in different institutions, which prevented their description in a single study.

Here we describe the Karlsruhe slab, which provides many new details of the osteology of this oldest European passerine. In addition, we report on a second specimen (cranium and mandible) of this species from the same locality and evaluate the phylogenetic affinities of the Frauenweiler passerine.

Material and methods

Anatomical terminology follows Baumel and Witmer (1993), if not indicated otherwise. We examined 84 extant species belonging to 37 family-taxa. For full taxonomic details (author names and original descriptions) of all the extant comparative material (listed in Appendix 1) see Peters (1931–1987). The term Pan-Passeriformes denotes the total

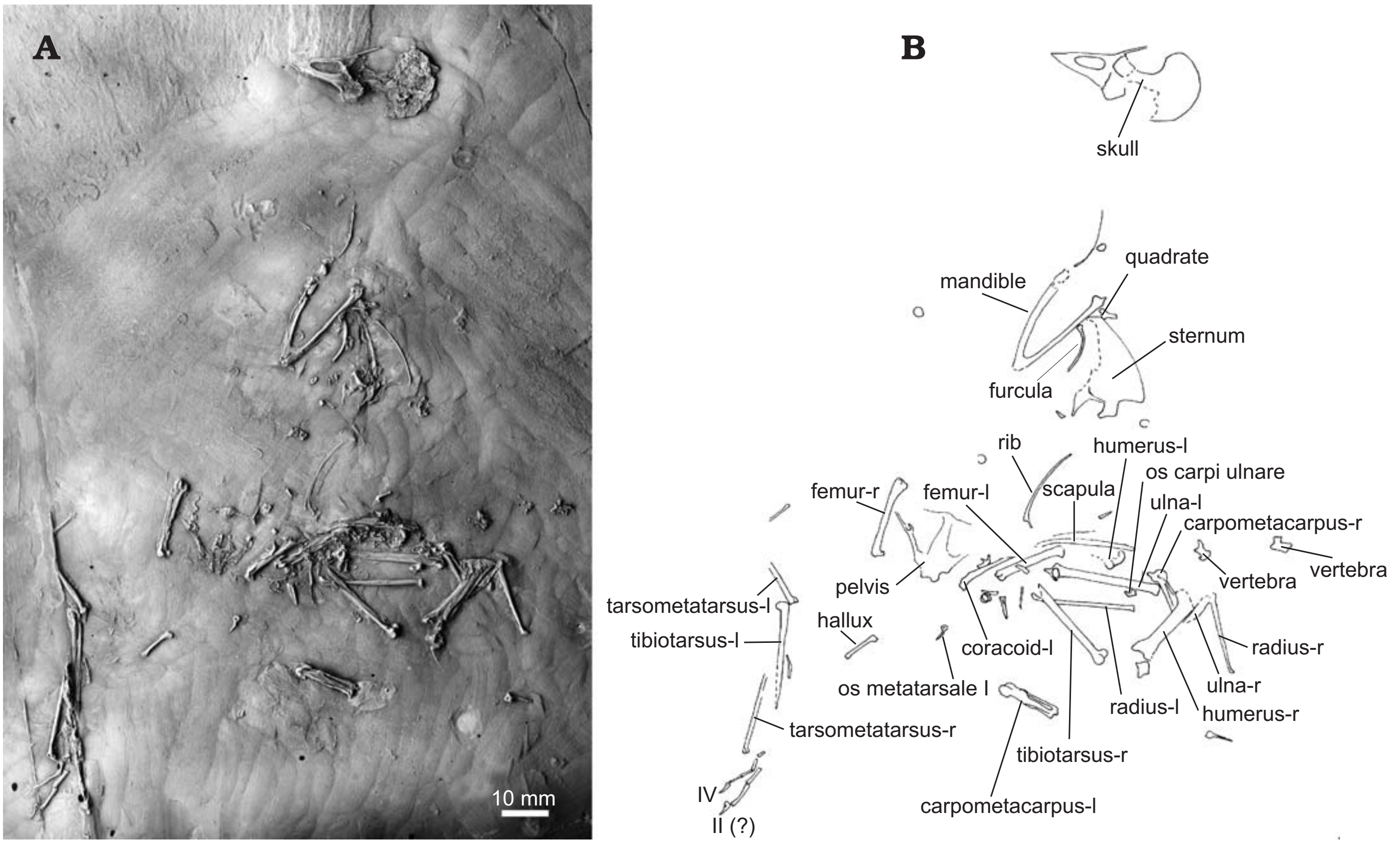

Fig. 1. *Wieslochia weissi* gen. et sp. nov., holotype, specimen SMNK-PAL.3980 from Frauenweiler near Wiesloch, Germany, early Oligocene (**A**) and interpretative drawing (**B**). Left (l) and right (r) elements are indicated. The toes of the right foot are numbered. Fossil coated with ammonium chloride.

group, i.e., the clade including stem group and crown group Passeriformes.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; MNHN, Muséum national d'Histoire naturelle, Paris, France; SMF, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; SMNK, Staatliches Museum für Naturkunde, Karlsruhe, Germany; YPM, Yale Peabody Museum, New Haven, USA.

Systematic paleontology

Aves Linnaeus, 1758

Pan-Passeriformes (Linnaeus, 1758)

Genus *Wieslochia* nov.

Type species: *Wieslochia weissi* sp. nov.

Derivation of the name: The genus name refers to the type locality, Wiesloch-Frauenweiler.

Diagnosis.—Small passerine, approximately the size of a House Sparrow, *Passer domesticus* (Passeridae), which is distinguished from all other passeriform taxa by the combination of the following characters: (1) coracoid with well-developed processus procoracoideus and (2) lacking hooked processus acromialis; (3) ulna with proximal end with well-developed tuberculum ligamenti collateralis ventralis; (4) carpometacarpus with os metacarpale minus not protruding as far distally as facies articularis digitalis minor; (5) hypotarsus with open canals for medial plantar tendons (including musculus flexor digitorum longus). Characters (1)–(5) distinguish the new taxon from all Oscines; character (2) distinguishes it from all examined Suboscines except *Phytotoma rara* (Cotingidae). Among numerous other differences, it is distinguished from *P. rara* and Acanthisittidae by character (5).

Wieslochia weissi gen. et sp. nov.

Derivation of the name: The species is named after Klaus Weiß, who collected and prepared the holotype.

Holotype: SMNK-PAL.3980 (main slab, Fig. 1), SMF Av 497 (specimen described by Mayr and Manegold 2004); dissociated skeleton on two slabs.

Type locality and horizon: Frauenweiler south of Wiesloch (Baden-Württemberg, Germany), former clay pit of the Bott-Eder GmbH ("Grube Unterfeld"); Rupelian, early Oligocene (MP 21–25; Micklich and Parin 1996; Legendre and Lévêque 1997; Trunkó and Munk 1998; Mayr 2000, 2004a, b, 2005; Mayr et al. 2002).

Diagnosis.—As for the genus.

Measurements (SMNK-PAL.3980, maximum length in mm).—Skull, 31.7; rostrum, from naso-frontal hinge to tip, 12.5; mandible, 24.0; sternum, 21.5; right humerus, 17.7 (note that

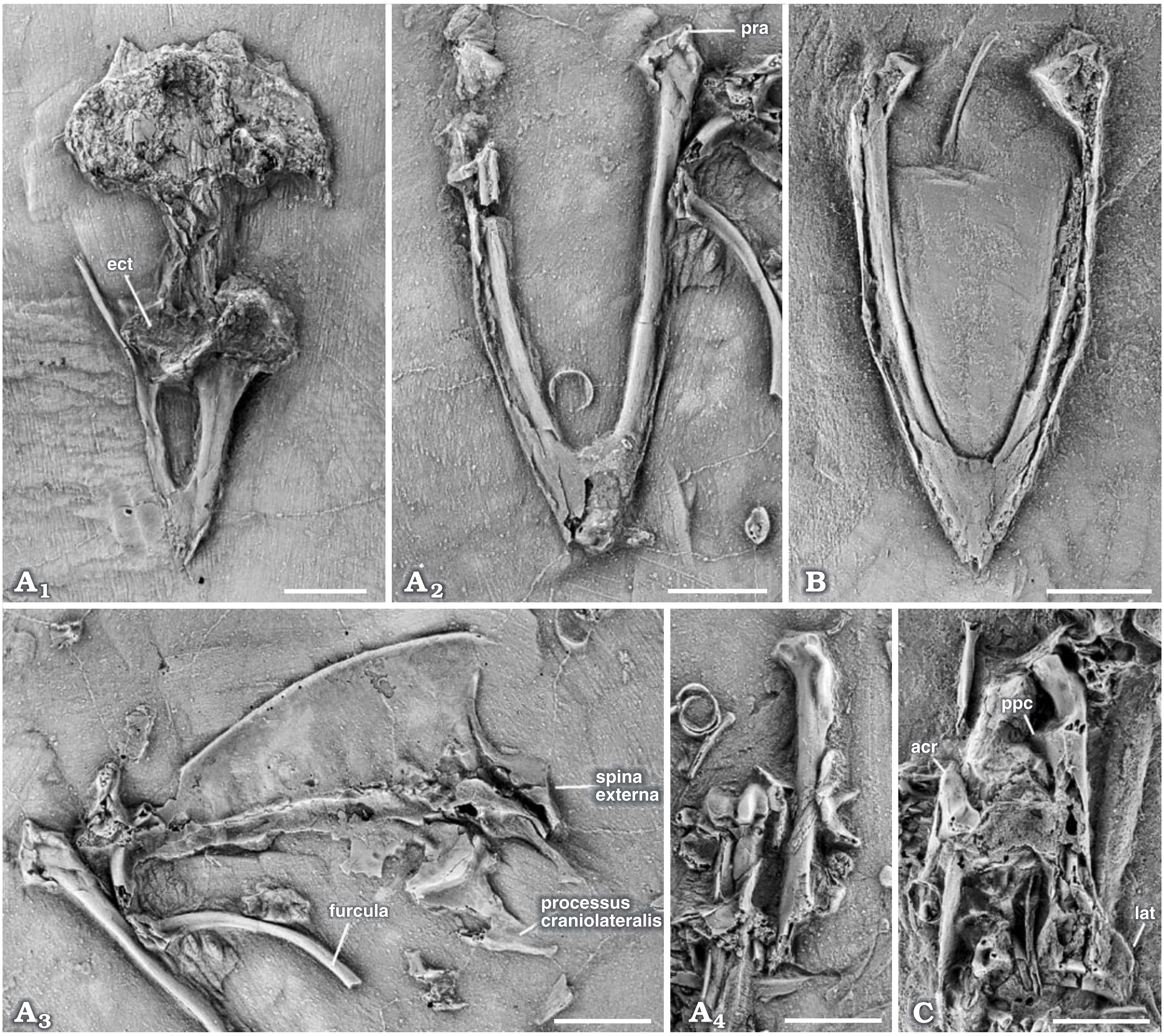

Fig. 2. *Wieslochia weissi* gen. et sp. nov. from Frauenweiler near Wiesloch, Germany, early Oligocene. **A**. Holotype, specimen SMNK-PAL.3980. **B**. Referred specimen SMF Av 501. **C**. Holotype, specimen SMF Av 497. Skull (A_1), mandible (A_2, B), sternum (A_3), left coracoid in ventral view (A_4), right coracoid in dorsal view and acromion of scapula (C). Abbreviations: acr, acromion of scapula; ect, os ectethmoidale; lat, processus lateralis of extremitas sternalis; ppc, processus procoracoideus of coracoid; pra, processus retroarticularis. Coated with ammonium chloride. Scale bars 5 mm.

the value for SMF Av 497 in Mayr and Manegold 2004 is incorrect and should read 18.1, not 28.1); left ulna, 23.8; left carpometacarpus, ~13.4; right femur, 17.3; left femur, 16.5; right tarsometatarsus (incomplete, length as preserved), 17.4.

Referred specimen.—SMF Av 501; cranium and mandible from the type locality and horizon (Fig. 2).

Description and comparison.—Mayr and Manegold (2004) considered the short beak of *Wieslochia* to be finch-like, but the new specimen SMNK-PAL.3980 shows that it more closely resembles the flatter beak of *Bombycilla* spp. (Bombycillidae) or *Pipra* spp. (Pipridae). The narial openings are large and oval shaped (Fig. $2A_1$); an ossified nasal septum appears to be absent. The os ectethmoidale is large and plate-like, as in many extant Passeriformes. The caudal end of the mandible resembles that of extant Passeriformes. As noted by Mayr and Manegold (2004), there is a small but distinct, caudally protruding processus retroarticularis (Fig. $2A_2$), which is also found in many extant passerines [e.g., *Menura* (Menuridae), *Corvus* (Corvidae)]. The processus medialis is short as in some Cracticidae and Artamidae (e.g., *Gymnorhina*, *Artamus*) and Pardalotidae (*Pardalotus*), whereas it is distinctly longer in most other Passeriformes. A fenestra mandibulae cannot be discerned and is therefore either absent or very small (SMF Av

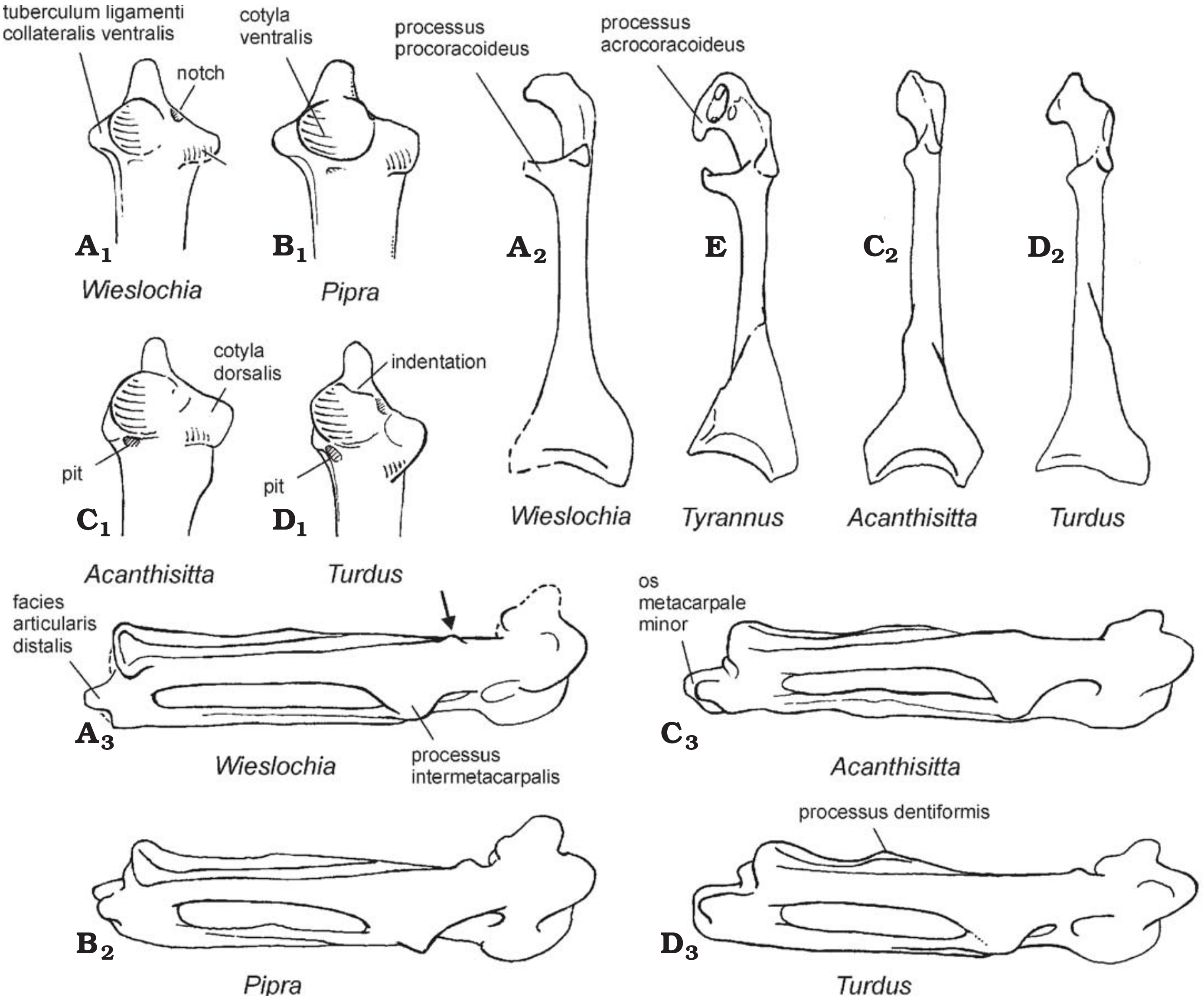

Fig. 3. Comparison of ulna (A_1, B_1, C_1, D_1), coracoid (A_2, E, C_2, D_2), and carpometacarpus (A_3, C_3, B_2, D_3) in *Wieslochia weissi* gen. et sp. nov. to the corresponding elements of extant passerines. **A**. *Wieslochia weissi* gen. et sp. nov. **B**. *Pipra rubrocapilla* (Pipridae). **C**. *Acanthisitta chloris* (Acanthisittidae). **D**. *Turdus merula* (Turdidae). **E**. *Tyrannus tyrannus* (Tyrannidae). The arrow indicates the process at the proximal end of the sulcus tendineus. Not to scale.

501). This fenestra is small in Acanthisittidae and most Suboscines but large in Oscines. The pars symphysialis is wide and flat, similar to that of Eurylaimidae and many Tyrannidae (tyrant flycatchers). The quadratum (SMNK-PAL.3980 and SMF Av 501), unfortunately, is too poorly preserved for meaningful comparisons.

The sternum of *Wieslochia* (Fig. 2A_3) has already been described by Mayr and Manegold (2004). SMNK-PAL.3980 provides new details on the shape of the processus craniolaterales, which are long and pointed as in Acanthisittidae, most Suboscines, and some Oscines (e.g., *Picathartes*, *Eopsaltria*). The spina externa is blade-like and bifurcated as in all extant Passeriformes except most Eurylaimidae (*Smithornis* is the exception) and some Cotingidae (e.g., *Procnias nudicollis*) (Olson 1971; Prum 1993). The caudal margin of the sternum is damaged but it can be seen that there was a single pair of incisions and a wide trabecula mediana as in most extant passerines, except Rhinocryptidae and some Grallariidae (*Pittasoma*, *Grallaria*, and *Myrmothera*) which have two pairs of incisions (Heimerdinger and Ames 1967, and own observations).

Mayr and Manegold (2004) noted that the processus procoracoideus of the coracoid of *Wieslochia*, visible only in SMF Av 497, is unusually large for a passeriform bird. In Acanthisittidae and Oscines the processus procoracoideus is greatly reduced, but we have now learned that a similarly-sized process does occur in several Suboscines [e.g., *Tyrannus tyrannus* (Tyrannidae, Fig. 3E), *Sittasomus* (Dendrocolaptinae), *Phytotoma rara* (Cotingidae), and Pipridae]. In SMNK-PAL. 3980 for the first time the shape of the extre-

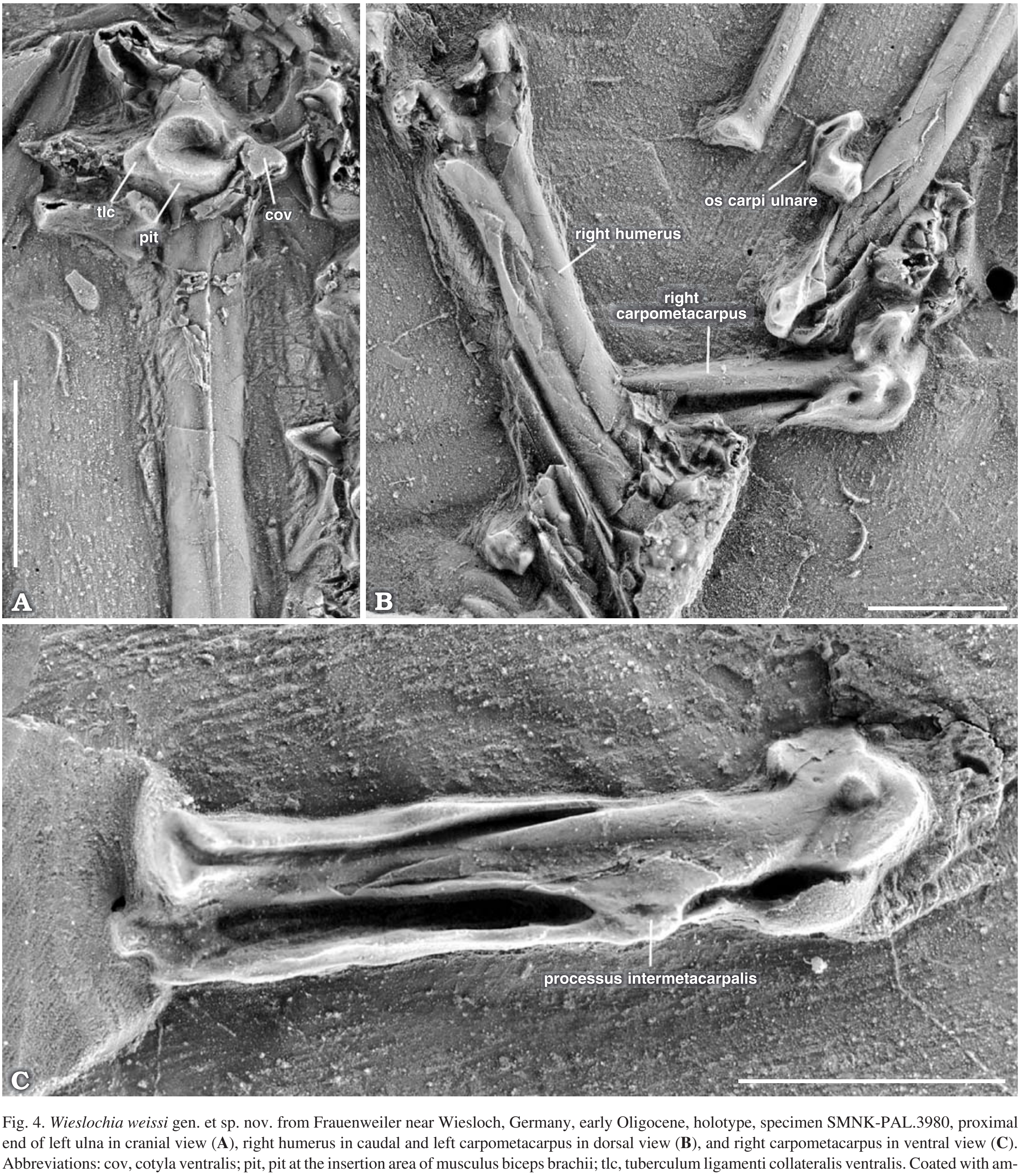

Fig. 4. *Wieslochia weissi* gen. et sp. nov. from Frauenweiler near Wiesloch, Germany, early Oligocene, holotype, specimen SMNK-PAL.3980, proximal end of left ulna in cranial view (**A**), right humerus in caudal and left carpometacarpus in dorsal view (**B**), and right carpometacarpus in ventral view (**C**). Abbreviations: cov, cotyla ventralis; pit, pit at the insertion area of musculus biceps brachii; tlc, tuberculum ligamenti collateralis ventralis. Coated with ammonium chloride. Scale bars 5 mm.

mitas omalis of the coracoid is visible and, most notably, the processus acrocoracoideus resembles that of *Phytotoma rara* in its shape and is not hooked as in other Eupasseres; within Passeriformes, the processus acrocoracoideus is even more rounded in Acanthisittidae (Fig. 3C$_2$) and *Atrichornis clamosus* (Atrichornithidae).

The acromion of the scapula (Fig. 2C) resembles that of Suboscines and is not bifurcated, with an additional ventro-

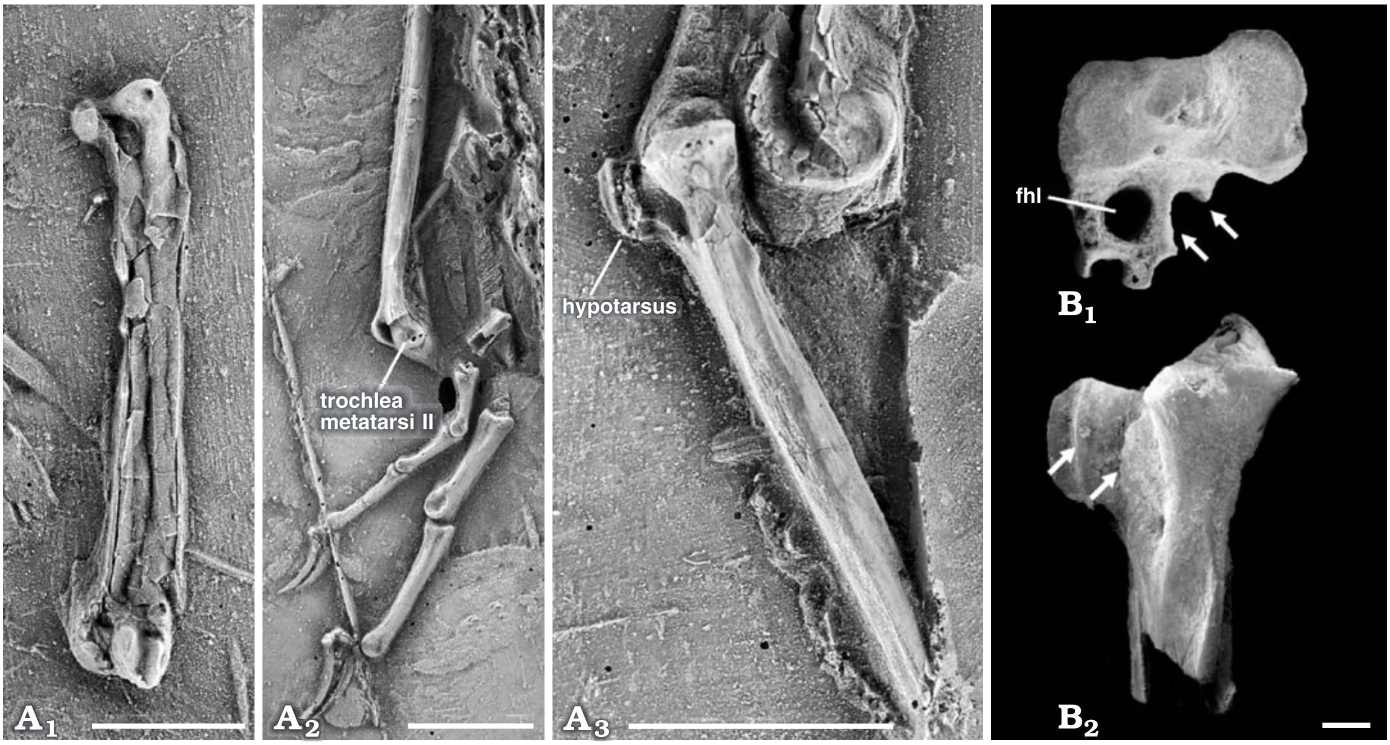

Fig. 5. **A**. *Wieslochia weissi* gen. et sp. nov., holotype, SMNK-PAL.3980, from Frauenweiler near Wiesloch, Germany, early Oligocene; right femur (A_1), distal end of right foot (A_2), and medial view of left hypotarsus (A_3). **B**. Proximal end of a left tarsometatarsus, MNHN SA 1263c, from the middle Miocene of Sansan, France, in proximal (B_1) and medial (B_2) views. The arrows indicate the bony ridges that border the canal for the tendon of musculus flexor digitorum longus. Abbreviation: fhl, ossified canal for tendon of musculus flexor hallucis longus. Coated with ammonium chloride. Scale bars 5 mm.

medial process, as in Oscines. The caudal part of the corpus scapulae is slightly angled.

Only a fragment of the furcula is preserved, which bears a damaged extremitas omalis (Fig. $2A_3$).

The humerus (Fig. 4B) is of similar proportions to that of thrushes *Turdus* spp. (Turdidae). A second fossa pneumotricipitalis, a characteristic feature of many Oscines, appears to be absent. Unfortunately the dorsal margin of the distal end is broken, and the shape of the processus supracondylaris dorsalis cannot be discerned. As in extant Passeriformes, the processus flexorius is strongly distally protruding.

The proximal end of the ulna (Fig. 4A) is very similar to that of Suboscines but differs markedly from the corresponding element of oscine passerines (Fig. $3D_1$). Unlike the latter but in concordance with suboscine passerines, there is a well-developed tuberculum ligamenti collateralis ventralis (Figs. 3, 4). Additionally, there is only a very shallow pit at the insertion area of musculus biceps brachii (Figs. 3, 4). This pit, which was considered to be a characteristic feature of passeriform birds by Ballmann (1969), is very distinct in Oscines but shallow or absent in most examined Suboscines except *Conopophaga* (Conopophagidae) and some Eurylaimidae (*Cymbirhynchus* and *Psarisomus*). Within Acanthisittidae, a marked pit is present in *Xenicus gilviventris* but absent in one of the two examined specimens of *Acanthisitta chloris* (YPM 110797, present in AMNH 27327). Unlike the condition in most Oscines, the cotyla dorsalis of *Wieslochia* is proximodistally short (Figs. 3, 4). The proximal rim of the cotyla ventralis is rounded, not indented as in Oscines (Figs. 3, 4). Also on the cranial surface of the proximal end, there is a marked notch between the cotylae ventralis et dorsalis (Figs. 3, 4), which appears to be part of the stem species pattern of Passeriformes, i.e. present in the last common ancestor of crown group Passeriformes. The distal ulna is too badly crushed to allow the recognition of phylogenetically informative details.

The carpometacarpus (Fig. 4C) exhibits the characteristic passeriform morphology in that there is a large processus intermetacarpalis that fuses with the os metacarpale minus and a marked facies ligamentalis interna (terminology after Ballmann 1969). The bone further exhibits a small process at the proximal end of the sulcus tendineus (Fig. $3A_3$), which is an apomorphy of either Passeriformes (Mayr 1998: 46) or the clade (Passeriformes + (Bucerotes + Piciformes)) (Manegold 2005). The facies articularis digitalis minor forms a marked projection which is set off from the os metacarpale minus but, contrary to all extant Passeriformes, the os metacarpale minus itself does not protrude distally (Figs. 3, 4). In Acanthisittidae and Oscines the os metacarpale minus reaches much farther distally than the os metacarpale majus and, together with the facies articularis digitalis minor, forms a marked square projection (Fig. 3); in Suboscines it forms a point that reaches as far distally as the facies articularis digitalis minor (Mourer-Chauviré et al. 1989; Manegold 2005).

As in other passeriform birds there is a processus dentiformis on the cranial margin of the bone, although this structure is not nearly as marked as in most Oscines (Fig. 3; Mourer-Chauviré et al. 1989).

Crus breve and crus longum of the os carpi ulnare (Fig. 4B) are of about equal size, as is the case in Acanthisittidae, Suboscines and basal oscine taxa (e.g., *Menura*), whereas the crus longum is greatly reduced in many Oscines (e.g., *Chloropsis*, *Turdus*).

The poorly preserved pelvis appears to have been approximately as long as wide and is similar in its proportions to the pelvis of *Tyrannus tyrannus* (Tyrannidae).

The femur (Fig. $5A_1$) is slender with similar proportions to the corresponding bone of *Cosmopsarus regius* (Sturnidae) and most other extant passerines.

The preservation of the tibiotarsus does not allow meaningful comparisons with that of extant Passeriformes. The distal end resembles the distal tibiotarsus of the extant taxa, which show only little variation with respect to this bone.

The tarsometatarsus (Fig. 5) is not completely preserved in the specimen (the distal end of the left and the proximal end of the right one are lacking) but appears to have been long, at least reaching the length of the humerus, as in most extant passerines. Whether there was an ossified arcus extensorius on the proximal end as in extant passerines is not clearly visible. The tuberositas musculi tibialis cranialis is marked and situated at the medial margin of the bone. The left hypotarsus is visible in medial view and, unlike the condition in most extant Passeriformes, there is no bony canal for the tendon of the M. flexor digitorum longus (Fig. $5A_3$, see also Manegold et al. 2004: fig. 1). In addition, and as in Acanthisittidae and few other extant Passeriformes (Manegold et al. 2004), the tendons for at least the medial of the most plantarly lying flexor tendons run through furrows instead of bony canals. The hypotarsus of *Wieslochia* thus resembles a passerine hypotarsus from the early Miocene of France figured by Manegold et al. (2004: fig. 2) in which the canals for musculus flexor digitorum longus, musculus flexor perforatus digiti 2 and musculus flexor perforans et perforatus digiti 2 et 3 are incompletely closed. This bird was considered to be outside crown group Eupasseres by Manegold et al. (2004). Most Eupasseres, by contrast, are characterized by the presence of six separate bony canals in the hypotarsus for the set of seven flexor tendons (six-canal-pattern). A crista plantaris lateralis, present in all extant Passeriformes, cannot be discerned in the specimen; however, this may be an artifact of preservation. The distal tarsometatarsus, of which only the medial section is visible, is similar to that of *Pitta sordida* (Pittidae). The trochlea metatarsi II is narrow, reaches farther distally than the trochlea metatarsi III, and is slightly plantarly deflected; the incisura intertrochlearis medialis is narrow. The fossa metatarsi I is large.

As in all other passeriform birds, the os metatarsale I exhibits a cylindrical trochlea metatarsi I. The proximal phalanx of the hallux is greatly elongated as in all extant Passeriformes. Its proximal end bears a lateral protrusion that also occurs in some extant passerines, such as *Paradisaea* (Paradisaeidae). The claws show only little curvature and the tubercula flexoria are weakly developed.

Discussion

Mayr and Manegold (2004) cited the well-developed processus procoracoideus as possible evidence for a position of *Wieslochia weissi* outside crown group Eupasseres. Occurrence of this character in several Suboscines (see above), however, does not allow such a conclusion to be drawn from this feature alone.

W. weissi can be clearly shown to be outside crown group Oscines by the absence of a bifurcated acromion on the scapula and the presence of a well-developed tuberculum ligamenti collateralis ventralis on the ulna. It is, however, more difficult to further delimit the phylogenetic affinities of the new fossil taxon which still could be on the stem lineage of Oscines, on the stem lineage or within the crown group of Suboscines, or outside crown group Eupasseres or even Passeriformes (for geographical reasons we consider a closer relationship to New Zealand Acanthisittidae to be very unlikely).

In overall osteology, *Wieslochia* most closely resembles extant Suboscines, but because the sister taxon of Passeriformes is uncertain (e.g., Mayr et al. 2003), it is difficult to decide whether these similarities are plesiomorphic or apomorphic. For example, *Wieslochia* agrees with suboscine passerines but is distinguished from Oscines and Acanthisittidae by the absence of a marked pit at the insertion area of musculus biceps brachii on the ulna (Fig. 3). Such a marked pit does not occur in any non-passeriform bird. If Acanthisittidae indeed are the sister taxon of all other extant Passeriformes (see introduction), it may be part of the stem species pattern of Passeriformes. Its absence or weak development in *Wieslochia* and most extant Suboscines would then be a derived reversal into the primitive condition. However, it is equally parsimonious to assume that a marked pit convergently evolved in the aforementioned taxa, in which case its absence in *Wieslochia* and Suboscines would be primarily plesiomorphic and thus not indicative of a closer relationship.

Wieslochia further agrees with extant Suboscines but differs from Acanthisittidae and Oscines by the presence of a well-developed tuberculum ligamenti collateralis ventralis on the ulna. Again, outgroup comparison with Acanthisittidae suggests that a well developed tuberculum is an apomorphy of Suboscines. However, this character also occurs in upupiform birds (hoopoes and wood-hoopoes), which have been considered to be among the closest extant relatives of passerines by some authors (e.g., Olson 1985; Manegold 2005), and thus may also be plesiomorphic for passeriform birds.

In addition, there are some features that may support a position of *Wieslochia* outside at least crown group Eupasseres as hypothesized by Mayr and Manegold (2004). Most notable among these is the fact that the os metacarpale minus of the carpometacarpus is short and does not protrude as far distally as the facies articularis digitalis minor (Fig. 3). If not an artifact of preservation (the ventral surface of the bone is embedded in the slab and may possibly be damaged), this feature distinguishes *Wieslochia* from all extant Passeriformes.

Wieslochia also differs from all extant passerines except Acanthisittidae, Atrichornithidae and *Phytotoma* (Suboscines, Cotingidae) by the absence of a hooked processus acrocoracoideus of the coracoid (Fig. 3), although it is again uncertain whether this feature is an apomorphy of *Wieslochia* or plesiomorphic for passeriform birds.

Another feature which may support position of *Wieslochia* outside crown group Eupasseres is the presence on the hypotarsus of furrows instead of canals for the most plantar medial tendons (of musculus flexor perforatus digiti 2 and musculus flexor perforans et perforatus digiti 2 et 3) (Fig. 5). Manegold et al. (2004) considered this character to be evidence for a position of some Miocene passerines outside crown group Eupasseres; note, however, that an open canal for the tendon of musculus flexor digitorum longus is likely to be an apomorphy of the fossil taxon.

The evidence discussed above is conflicting and at present it is not possible to convincingly show whether *Wieslochia* is a suboscine passerine (in which case it would be the earliest fossil record of this passeriform clade) or is outside crown group Eupasseres. We thus consider the phylogenetic affinities of *Wieslochia* uncertain pending on the discovery of additional specimens.

Wieslochia is the only passeriform taxon reported from the Frauenweiler deposits and is known from two specimens, a disarticulated skeleton and a cranium with mandible. Bird skeletons are rare in the Frauenweiler deposits, and beside the two passeriform specimens described here, only about a dozen other bird remains have been reported (Mayr 2000, 2004a, b, 2005; Mayr et al. 2002). If there is any correlation between the abundance of a species and the probability that individuals became fossilized and are found, *Wieslochia* was thus among the more abundant land bird species in this area.

Because the earliest European fossil record of oscine passerines is from the late Oligocene (Mourer-Chauviré et al. 1989), non-oscine passerines may have colonized Europe before the arrival of Oscines from the Australian continental plate. Future studies will have to show when exactly non-oscine passerines became extinct in Europe and whether climatic or ecological changes were the major reasons for this.

Acknowledgements

We thank Klaus Weiß and Manfred Keller for donating the fossil specimens to SMNK and SMF respectively, and Wolfgang Munk (SMNK) for the loan of the main slab. We further thank Sven Tränkner (SMF) for taking the photographs, and Paul Sweet (AMNH), Sara Bertelli (AMNH), Joanne Cooper (NHM), and Mark Adams (NHM) for access to skeletons of extant passerines. Andrzej Elżanowski (Wrocław University, Poland) and Walter Boles (Australian Museum, Sydney) provided helpful comments on the manuscript. This study is part of a project supported by Deutsche Forschungsgemeinschaft (MA 2328/3-1).

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Appendix

We examined skeletons of the following extant taxa in the collections of Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; Natural History Museum, London/Tring, United Kingdom; American Museum of Natural History, New York, United States; Yale Peabody Museum, New Haven, United States, and Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand.

Species are listed following the higher-level passerine sequence of Dickinson (2003) concerning Oscines and Ericson et al. (2003) concerning Acanthisittidae and Suboscines:

Acanthisittidae: *Acanthisitta chloris*, *Xenicus gilviventris*.

Suboscines: Pittidae: *Pitta guajana*, *P. sordida*, *P. granatina*. Eurylaimidae: *Calyptomena viridis*, *Cymbirhynchus macrorhynchus*, *Psarisomus dalhousiae*, *Smithornis capensis*. Thamnophilidae: *Thamnophilus caerulescens*, *Th. ruficapillus*. Conopophagidae: *Conopophaga aurita*. Grallariidae: *Myrmothera simplex*. Rhinocryptidae: *Scytalopus magellanicus*. Formicariidae: *Formicarius colma*. Furnariidae: *Campylorhamphus trochilirostris*, *Dendrocincla fuliginosa*, *D. merula*, *Furnarius rufus*, *Lepidocolaptes angustirostrum*, *L. fuscus*, *Leptasthenura aegithaloides*, *Sittasomus griseicapillus*. Cotingidae: *Phytotoma rara*, *Procnias nudicollis*, *Pyroderus scutatus*, *Rupicola peruviana*, *Xipholena punicea*. Oxyruncidae: *Oxyruncus cristatus*. Pipridae: *Chiroxiphia caudata*, *Pipra rubrocapilla*, *Lepidothrix nattereri*. Tyrannidae: *Megarhynchus pitangua*, *Tyrannus melancholicus*, *T. tyrannus*, *Pitangus sulphuratus*, *Xolmis irrupero*.

Oscines: Menuridae: *Menura novaehollandiae*. Atrichornithidae: *Atrichornis clamosus* (casts). Climacteridae: *Climacteris picumnus*. Maluridae: *Malurus leucopterus*. Meliphagidae: *Lichenostumus fuscus*. Pardalotidae: *Pardalotus striatus*. Pomatostomidae: *Pomatostomus isidori*. Melanocharitidae: *Oedistoma iliolophum*, *Paramythia montium*. Eupetidae: *Ptilorrhoa castanonota*. Vangidae: *Falculea palliata*. Cracticidae: *Cracticus* sp., *Gymnorhina tibicen*, *Strepera versicolor*, *S. graculina*. Artamidae: *Artamus leucorynchus*. Aegithinidae: *Aegithina tiphia*. Laniidae: *Laniarius ferrugineus*. Vireonidae: *Vireo philadelphicus*. Oriolidae: *Oriolus oriolus*. Dicruridae: *Dicrurus forficatus*. Corvidae: *Corvus corone*. Paradisaeidae: *Paradisaea apoda*. Petroicidae: *Eopsaltria australis, Tregellasia leucops*. Picathartidae: *Picathartes oreas*. Bombycillidae: *Bombycilla garrulus*. Paridae: *Parus inornatus*. Alaudidae: *Alauda arvensis*, *Lullula arborea*. Pycnonotidae: *Bleda syndactyla*, *Pycnonotus virens*. Irenidae: *Chloropsis cochinchinensis*, *Irena puella*. Regulidae: *Regulus satrapa*. Sturnidae: *Aplonis metallica*, *Lamprotornis regius*, *Gracula religiosa*. Turdidae: *Turdus merula*. Cinclidae: *Cinclus cinclus*. Nectariniidae: *Dicaeum celebicum*. Passeridae: *Passer domesticus*. Ploceidae: *Ploceus nigerrimus*. Fringillidae: *Fringilla teydea*, *Pinicola enucleator*. Icteridae: *Psarocolius montezuma*, *Sturnella bellicosa*.