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Source: Bulletin of the British Ornithologists' Club, 142(4) : 388-403

Published By: British Ornithologists' Club

URL: https://doi.org/10.25226/bboc.v142i4.2022.a2

A new subfossil ground thrush (Turdidae: *Geokichla*) from Mauritius, Mascarene Islands

by Julian P. Hume

Received 31 March 2021; revised 1 July 2022; published 7 December 2022

http://zoobank.org/urn:lsid:zoobank.org:pub:02FD1CC8-9A5D-45AC-AB2A-B1A05E10256A

Summary.—*Geokichla* ground thrushes (Turdidae) are widely distributed, in Siberia, South-East Asia, Indonesia, the Indian Subcontinent, Nicobar and Andaman Islands, and continental Africa. Based on recently discovered subfossil remains, I describe a *Geokichla* from Mauritius, a new genus for the Mascarene Islands, which presumably became extinct historically, although it seems never to have been reported in the literature. The new species appears closely related to the extant Orange-headed Thrush *G. citrina* of South-East Asia, so probably island-hopped via the Nicobar or Andaman Islands to Mauritius during low sea level stands, as did some other Mauritian endemic birds. Like *Geokichla* in general, the Mauritius species probably inhabited the understorey or forest floor, and as a result disappeared due to the introduction of invasive species, especially rats, by humans.

Divided into 15 genera and *c*.140 species (Dickinson & Christidis 2014), the true thrushes (subfamily Turdinae) are of worldwide distribution and occur on all continents as well as on a number of islands and archipelagos in the Indian, Atlantic and Pacific Oceans (Clement 2000, Collar 2005). They are small to medium-sized birds that predominantly forage on the ground, and their terrestrial habits have made them extremely vulnerable to introduced predators on islands, especially rats (Hume 2017). *Geokichla* ground thrushes, formerly listed in *Zoothera* (Voelker & Klicka 2008, Voelker & Outlaw 2008), occur in Siberia, South-East Asia, the Indian Subcontinent, as well as the Nicobar and Andaman Islands in the Indian Ocean, and continental Africa (Clement 2000, Collar 2005, Dickinson & Christidis 2014). Some *Geokichla* are threatened with extinction, primarily due to habitat destruction, collection for the aviculture trade and the effects of introduced animals (Collar 2005).

Situated in the south-west Indian Ocean (Fig. 1), the Mascarene Islands of Mauritius (20°25′S, 57°05′E) (Fig. 2), Réunion (21°00′S, 55°05′E) and Rodrigues (19°75′S, 63°05′E) were once inhabited by a number of endemic bird genera, best epitomised by the iconic Dodo *Raphus cucullatus* of Mauritius. Considered tame and easy to catch when first discovered by mariners and settlers, the birds disappeared rapidly due primarily to the introduction of predatory mammals, especially rats and cats, and over-hunting (Cheke & Hume 2008, Hume 2013, 2017). On Mauritius, descriptive (albeit generally inadequate) accounts of the larger terrestrial birds appeared in ships' logs and journals, but this was not true for passerines, Mauritius Bulbul *Hypsipetes olivaceus* Jardine & Selby, 1837, and Mauritius Fody *Foudia rubra* (J. F. Gmelin, 1789) being the only exceptions (Cheke & Hume 2008). Represented in the fossil record on Mauritius but not mentioned in the literature was an endemic starling *Cryptopsar ischyrhynchus* Hume, 2014, and at least three more undescribed passerines (Hume 2013, 2014a, 2017). Including these, it is likely that passerine diversity was greater on Mauritius and the other Mascarene Islands than presently known (Hume 2005, 2013).

Here I describe a new, fossil *Geokichla* ground thrush from Mauritius, which is a new genus for the Mascarenes, and provide a detailed morphometric and osteological

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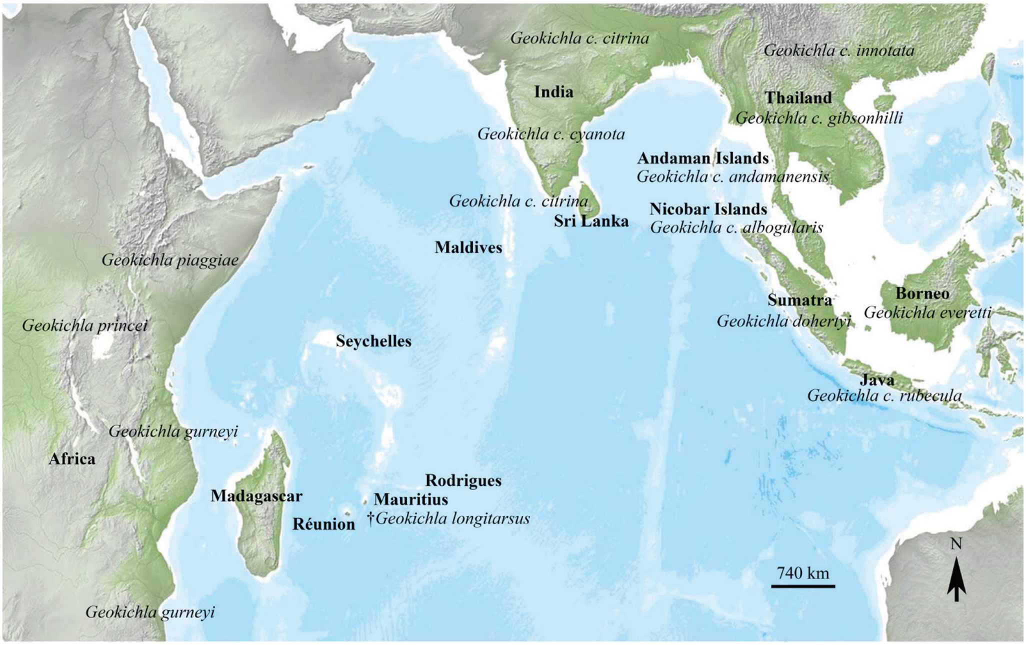

Figure 1. Geography of the Indian Ocean showing the islands mentioned in the text and distribution of selected *Geokichla* ground thrushes. It is likely that Mauritius was colonised from South-East Asia via southern India and Sri Lanka or from the Andaman and Nicobar Islands (adapted from https://www.freeworldmaps.net/physical.html).

comparison (see Appendix 1). I discuss its affinities and, although not known in life, suggest reasons why it became extinct. Despite molecular data showing that *Geokichla* and *Zoothera* are well-separated clades of Turdidae (Voelker & Klicka 2008, Voelker & Outlaw 2008), some *Geokichla* are osteologically closer to certain *Zoothera* than to other *Geokichla*, which suggests possible convergence, or that some species have not diverged as far from the ancestral condition as others. Either way this emphasises the great osteological variability in this group.

Methods

Abbreviations. Institutions.—AMNH, American Museum of Natural History, New York; NHMUK, Natural History Museum, London and Tring; MNHN, Muséum national d'Histoire naturelle, Paris, with the prefix MAD for Madagascar, e.g., MNHN MAD7142.

Listing of skeletal material: 'u/r' unregistered material, u/s = unsexed, left (L) or right (R) prefixed by 'p' proximal, 's' shaft or 'd' distal, juv. = juvenile. † = extinct taxon.

Comparative skeletal material. The following skeletal specimens were used, all held in the AMNH and NHMUK bird skeleton collections, with registration number and sex (M = male, F = female) for each: *Lalage melaschistos* NHMUK 1845.1.12.117.175 u/s; *Dicrurus paradiseus* NHMUK S/1969.1.163 M; *Hypsipetes madagascariensis* NHMUK 1897.5.10.6 u/s; *Cochoa viridis* NHMUK 1845.1.12.204 u/s (partial skeleton); *Zoothera dauma* AMNH 25556 F, AMNH 23245 M, AMNH 4016 M, NHMUK 1847.1.12.83 u/s, NHMUK 1847.1.12.84 u/s; *Z. talaseae* AMNH 29046 M; *Z. dixoni* AMNH 23246 F; *Z. marginata* AMNH 25557 F; *Z. monticola* NHMUK S/1952.2.632 u/s; *Geokichla princei* AMNH 17024 M; *G. interpres* AMNH 27568 F; *G. dohertyi* NHMUK S/2016.26.2 M, NHMUK S/2016.26.1 u/s, NHMUK S/2016.10.1

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M; *G. guttata* NHMUK 1902.2.2.6 u/s; *G. piaggiae* NHMUK S/2016.19.14 u/s; *G. c. citrina* AMNH 6331 u/s, NHMUK S/2003.4.8 M; *G. citrina rubecula* NHMUK 1850.8.15.86 u/s; *G. citrina cyanota* NHMUK S/2016.46.1 M, NHMUK S/1972.1.113 u/s; *Turdus poliocephalus erythropleurus* NHMUK 1898.9.16.80 F; *Copsychus sechellarum* NHMUK S/1998.30.1 u/s, NHMUK S/1996.59.52 u/s; *Gracupica nigricollis* NHMUK 1869.10.19.15 F; *Saroglossa spilopterus* NHMUK S/1956.15.1 M.

Black-breasted Fruithunter *Chlamydochaera jefferyi* Sharpe, 1887, an aberrant Turdidae endemic to Borneo, is unavailable for comparison, as no museum skeletons exist (see Wood & Schnell 1986). Similarly, of the four *Cochoa* species, only a partial skeleton of Green Cochoa *C. viridis* Hodgson, 1836, is available, which lacks the corresponding elements of the new *Geokichla*. Nevertheless, the restricted range and generally sedentary habits of *Chlamydochaera jefferyi*, and the restriction of two of the *Cochoa* species to continental Asia, with sedentary species on Java and Sumatra (Collar 2005), suggest these taxa are not potential candidates for colonising the Mascarenes. Other similar-sized Indian Ocean island passerine taxa *Lalage* (Campephagidae); *Dicrurus* (Dicruridae); *Hypsipetes* (Pycnonotidae); *Gracupica*; *Saraglossa* (Sturnidae) and *Copsychus* (Muscicapidae) were also compared in this study.

Measurements.—All measurements were made using dial callipers accurate to the nearest 0.1 mm. TL = total length: *humerus*, measured in dorsal aspect, *tibiotarsus*, measured in cranial aspect from articulating surfaces; *tarsometatarsus*, measured in dorsal aspect; GW = greatest width, on a lateromedial plane; GD = greatest depth, on a dorsoventral plane; PD = proximal depth, on a dorsoventral plane, including hypotarsus; LSW = least shaft width, on lateromedial plane; LSD = least shaft depth, in dorsoventral plane, anterocaudal for tibiotarsus; DW = distal width, in lateromedial plane; DD = distal depth, in dorsoventral plane, tarsometatarsus across trochleae metatarsorum III.

Anatomical nomenclature follows Baumel & Witmer (1993), with general abbreviations: m = musculus; n = nervus; Manegold *et al.* (2004) for hypotarsus. Avian nomenclature follows Dickinson & Christidis (2014).

Systematics

Class Aves

Order Passeriformes Linnaeus, 1758

Family Turdidae Rafinesque, 1815

Genus *Geokichla* S. Müller, 1836

Geokichla S. Müller, 1836, *Tijdschr. Nat. Gesch. Phys*. 2 ['1835'], pt. 3, pp. 348–349 = *Turdus citrinus* Latham, 1790, *Index Orn*., vol. 1, p. 350. Type by original designation.

Assignment to Turdidae. *Humerus*.—In caudal surface, fossa pneumotricipitalis with distinct dorsal and ventral parts separated by crus dorsale fossae, with dorsal part open distally, undercutting the caput humeri; fossa pneumotricipitalis dorsalis deeper than fossa pneumotricipitalis ventralis; crista pectoralis short compared to proximal width, so proximal end square-shaped; sulcus humerotricipitalis weakly excavated; margo caudalis narrow and straight with no medial deflection proximal to caput humeri; processus supracondylaris dorsalis undivided, more prominent and directed proximodorsad; in cranial surface, crista deltopectoralis long and marked with distinct narrow ridge, extending further distad than crista bicipitalis; tuberculum supracondylare ventrale deeply excavated and elongate in ventral view (see Wójcik 2001).

In *Gracupica* and *Saroglossa*, in caudal surface, tuberculum ventrale directed less ventro-mediad; fossa pneumotricipitalis dorsalis wider than fossa pneumotricipitalis ventralis; margo caudalis broader with medial deflection proximal to caput humeri; sulcus

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humerotricipitalis less excavated; in cranial surface, crista deltopectoralis with broad and flat ridge; tuberculum supracondylare ventrale less excavated.

In *Hypsipetes*, similar-sized but more robust; in caudal surface, caput humeri less bulbous; fossa pneumotricipitalis dorsalis shallower than fossa pneumotricipitalis ventralis; in cranial surface, crista deltopectoralis lacking ridge; condylus dorsalis smaller.

In *Lalage*, proportionately longer and more robust; in caudal surface, fossa pneumotricipitalis dorsalis much shallower than fossa pneumotricipitalis ventralis; tuberculum ventrale much larger; processus supracondylaris dorsalis less prominent, directed proximad, not proximodorsad; in cranial surface, impressio coracobrachialis shallower.

In *Copsychus*, in caudal surface, tuberculum ventrale smaller; processus flexorius proportionately larger.

In *Dicrurus*, in caudal surface, caput humeri smaller; tuberculum ventrale smaller, directed proximoventrad; processus supracondylaris dorsalis much reduced; processus flexorius proportionately smaller, extending less distad; in cranial surface, impressio coracobrachialis shallower; crista deltopectoralis flatter, not deflected craniad.

Tibiotarsus.—In cranial aspect, crista cnemialis lateralis sharply hooked distally; sulcus extensorius deeply excavated; pons supratendineus deflected slightly medioproximad relative to condyles with proximal margins of condyles approximately level with distal margin of pons supratendineus; condylus medialis and condylus lateralis equally sized and parallel, not curved laterally or medially; tuberculum retinaculi m. fibularis prominent; incisura intercondylaris deep; in caudal aspect, large, rectangular-shaped facies articularis lateralis; fossa flexoria shallow; trochlea cartilaginis tibialis deeply excavated; in proximal aspect, crista cnemialis cranialis and crista cnemialis lateralis long, forming a sharp, right-angled sulcus intercnemialis; facies articularis and incisura tibialis deeply excavated.

In *Gracupica* and *Saroglossa*, in cranial aspect, crista cnemialis cranialis extends less distally; pons supratendineus not deflected ventrolaterad; tuberculum retinaculi m. fibularis more prominent; in proximal aspect, facies articularis medialis oblong-shaped, less square-shaped; incisura tibialis more deeply excavated; crista cnemialis cranialis long, crista cnemialis lateralis short, forming an arched, not right-angled sulcus intercnemialis.

In *Hypsipetes*, shorter; distal end comparatively broader; in cranial aspect, crista cnemialis lateralis blunt, not sharply hooked distally; sulcus intercnemialis shallower; pons supratendineus deflected slightly ventro-laterad; in proximal aspect, crista cnemialis cranialis much shorter; facies articularis medialis and incisura tibialis shallower.

In *Lalage*, proportionately much shorter and more gracile; in cranial aspect, crista cnemialis lateralis blunt, not sharply hooked distally; condylus medialis slightly smaller than condylus lateralis; pons supratendineus not deflected medioproximad; in proximal aspect, facies articularis medialis oblong-shaped, less square-shaped; incisura tibialis shallow; crista cnemialis cranialis long, crista cnemialis lateralis short, forming a rounded, not right-angled sulcus intercnemialis.

In *Copsychus*, proportionately longer, but more gracile; in cranial surface, crista cnemialis lateralis deflected laterad; pons supratendineus not deflected ventrolaterad, with proximal margins of condyles approximately level with distal margin of pons supratendineus; in proximal aspect, facies articularis medialis strongly square-shaped; incisura tibialis more deeply excavated; crista cnemialis cranialis and crista cnemialis lateralis extremely long, forming a sharp, right-angled sulcus intercnemialis.

In *Dicrurus*, shorter but more robust; in cranial aspect, crista cnemialis cranialis extending less distad; condylus lateralis larger than condylus medialis; pons supratendineus deflected ventrolaterad; in proximal aspect, facies articularis medialis more square-shaped;

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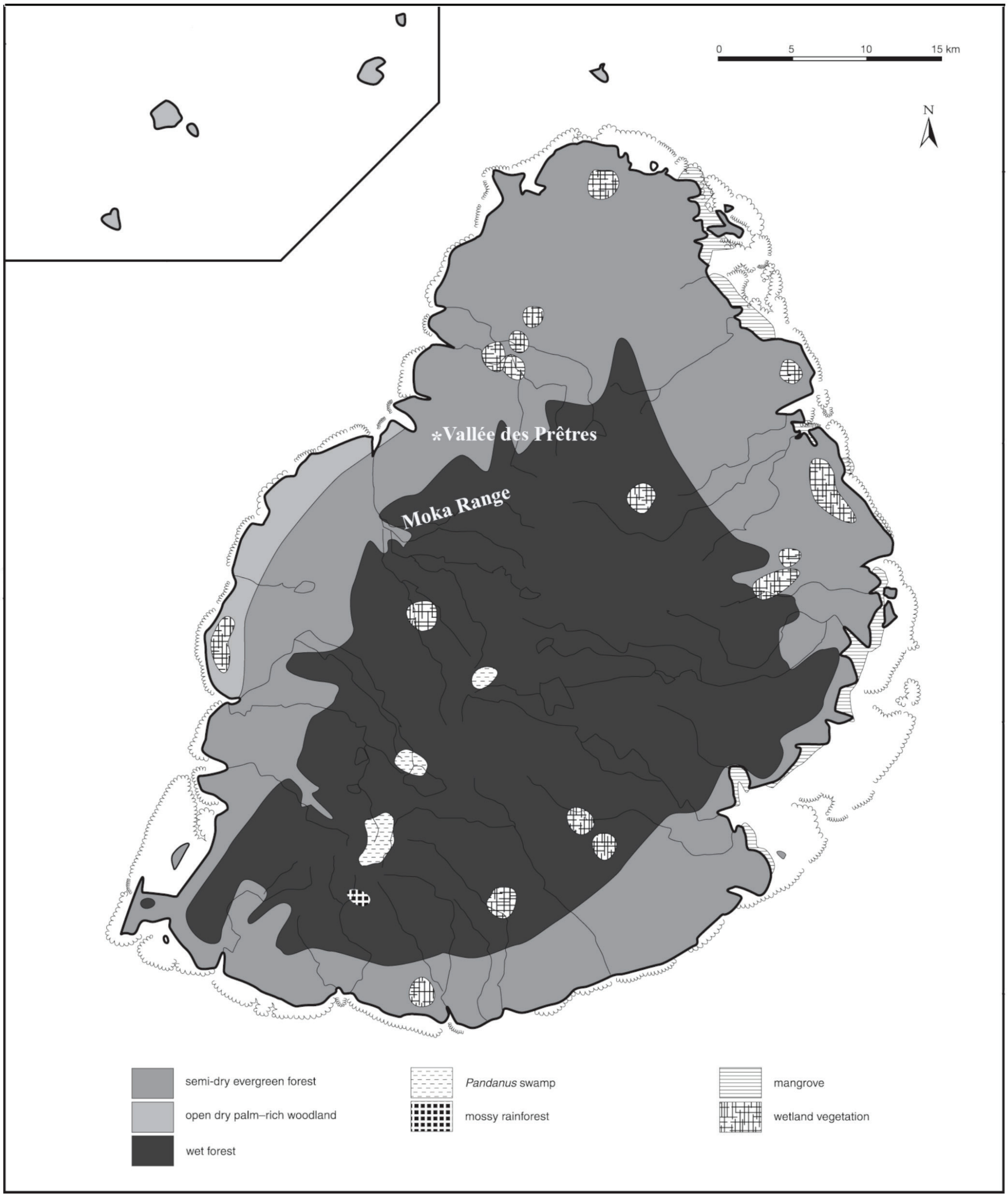

Figure 2. Detail of Mauritius and its original vegetation, showing the place names in the text (adapted from Cheke & Hume 2008).

incisura tibialis shallower; crista cnemialis cranialis short, crista cnemialis lateralis long, forming a sharp, right-angled sulcus intercnemialis.

Tarsometatarsus.—Extremely long in total length, *c*.8 times longer than proximal width; in dorsal aspect, eminentia intercotylaris extends strongly proximad of cotyla lateralis and cotyla medialis; sulcus extensorius extensive, extending to level of fossa metatarsi I, and deeply excavated; lateral foramen vasculare proximale slightly larger, unequally aligned and situated further proximodistad than lateral foramen vasculare proximale, with both foramina positioned proximal to tuberositas m. tibialis cranialis; shaft straight; trochleae metatarsorum II deflected slightly mediad and trochleae metatarsorum

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IV deflected slightly laterad, both shorter and much narrower than trochleae metatarsorum III; incisura intertrochlearis medialis equal in width with incisura intertrochlearis lateralis; trochleae metatarsorum III deeply incised; incisura intertrochlearis medialis and incisura intertrochlearis lateralis adjoin a deep sulcus extending to distal edge of foramen vasculare distale; foramen vasculare distale situated in a shallow sulcus dorsally; in medial profile, fossa metatarsi I creates a slight notch; in plantar aspect, hypotarsus short extending to lateral foramen vasculare proximale; sulcus flexorius deeply excavated with distinct, ridged crista plantares medialis that connects to hypotarsus; in proximal aspect, cotyla medialis projects dorsad to cotyla lateralis; eminentia intercotylaris with dorsolaterally situated incisura creating a slight notch; cotyla lateralis rounded to square-shaped.

In *Gracupica* and *Saroglossa*, much more robust at proximal and distal ends, with shaft proportionately narrower; in dorsal aspect, sulcus extensorius much less excavated extending less distad; incisura intertrochlearis medialis wider than incisura intertrochlearis lateralis; in plantar aspect, crista plantares medialis with more distinct ridge; in proximal aspect, eminentia intercotylaris less sharp, more rounded.

In *Hypsipetes*, approximately 2/3 less in total length; overall much more robust, especially on proximal end; in dorsal aspect, foramen vasculare distale situated in a deeper sulcus; incisura intertrochlearis medialis wider than incisura intertrochlearis lateralis; in lateral aspect, crista medialis hypotarsus more rounded with less pronounced hook; in proximal aspect, cotyla lateralis equal in size to cotyla medialis.

In *Lalage*, proportionately shorter and more gracile; in dorsal aspect, sulcus extensorius shallower, less extensive; in medial profile, fossa metatarsi I creates a more distinct notch; in plantar aspect, sulcus flexorius shallower; on proximal end, cotyla medialis smaller; in proximal aspect, cotyla lateralis much larger than cotyla medialis.

In *Copsychus*, proportionately longer and more robust; in dorsal aspect, foramen vasculare distale situated further proximad; incisura intertrochlearis medialis and incisura intertrochlearis lateralis much narrower; in medial profile, fossa metatarsi I shallow with indistinct notch; in proximal aspect, eminentia intercotylaris less sharp, more rounded and broader.

In *Dicrurus*, overall much shorter and more robust; in dorsal aspect, sulcus extensorius much less excavated extending less distad; incisura intertrochlearis medialis narrower than incisura intertrochlearis lateralis; in proximal aspect, eminentia intercotylaris more prominent, sharper.

Hypotarsus.—In proximal aspect, all six tendinal canals wholly enclosed: canal for musculus flexor hallucis longus (fhl) larger, more oval-shaped than that for musculus flexor digitorum longus (fdl), which is more circular; canal for fdl with an open connection to canal for musculus flexor perforans et perforatus (fpp2) and to canal for musculus flexor perforatus (fp2); canal for fp3 and fp4 larger than that for fpp3, all characteristic of Turdidae (see also Manegold *et al*. 2004). The above-mentioned numerals relate to the number of trochleae metatarsi supplied by the tendon.

In *Gracupica*, *Saraglossa*, *Hypsipetes*, *Lalage* and *Copsychus*, in proximal aspect, fhl larger than fdl, but not as large as that in Turdidae.

In *Dicrurus*, in proximal aspect, hypotarsus smaller with fhl and fdl situated more proximad to cotyla dorsalis and cotyla medialis.

In *Cochoa viridis*, only sternum, pelvis, coracoid and femur available. These elements differ in their much larger size and robustness compared to other Turdidae in this study, in particular, the sternum is distinct in being extremely broad distally, much wider than proximal end.

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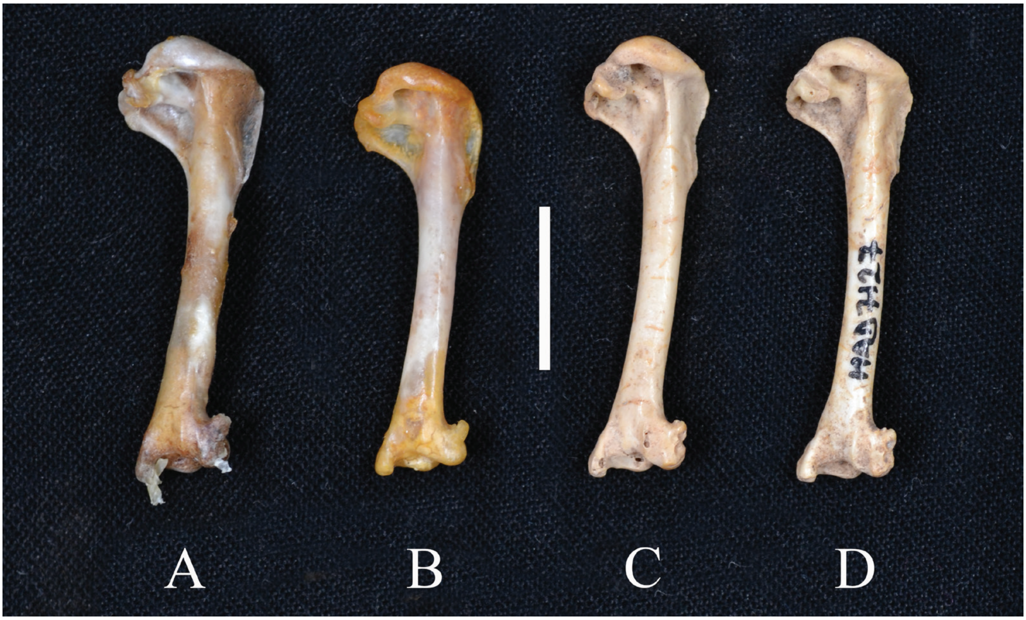

Figure 3. Comparison of humeri (right side, caudal aspect) of *Geokichla* ground thrushes with *G. longitarsus*. (A) *G. citrina cyanota* NHMUK S/2016.46.1 M; (B) *G. c. citrina* NHMUK S/2003.4.8 M; (C) *G. longitarsus* MNHN MAD 7127a u/s; (D) MNHN MAD 7127b u/s. Scale bar = 10 mm (Julian P. Hume)

Osteological diagnosis. The following characters in combination characterise the genus *Geokichla*.

Humerus (Fig. 3).—In caudal aspect, crista deltopectoralis extends further distad than crista bicipitalis; tuberculum ventrale rounded; in cranial aspect, sulcus ligamenti transversus deeply incised ventrally; tuberculum dorsale indistinct; impressio coracobrachialis deep; epicondylus ventralis projects further distad than condylus ventralis and condylus dorsalis.

In *Turdus*, overall more gracile, especially at the distal end, with narrower shaft; in cranial surface, caput humeri and tuberculum ventrale smaller; tuberculum supracondylare ventrale less deeply excavated; processus supracondylaris dorsalis more prominent.

In *Zoothera*, proportionately more robust in shaft and proximal end than *Geokichla*; processus supracondylaris dorsalis less prominent.

Tibiotarsus (Figs. 4–5).—In cranial aspect, crista cnemialis lateralis sharply hooked distad; sulcus extensorius deeply excavated; pons supratendineus deflected slightly medioproximad relative to condyles with proximal margins of condyles approximately level with distal margin of pons supratendineus; tuberculum retinaculi m. fibularis prominent; condyles equally sized and parallel; incisura intercondylaris deep; in caudal aspect, large rectangular-shaped, facies articularis lateralis; impressio ligamentum collateralis medialis prominent; fossa flexoria shallow; trochlea cartilaginis tibialis deeply excavated.

In *Turdus*, similar except in cranial aspect, crista cnemialis cranialis longer; in caudal aspect, impressio ligamentum collateralis medialis smaller, less extensive; in proximal surface, fossa retropatellaris shallower.

In *Zoothera*, overall longer and more robust; in cranial aspect, crista cnemialis cranialis extends further distad; in proximal aspect, crista cnemialis cranialis shorter; crista cnemialis lateralis longer, forming a sharp, right-angled sulcus intercnemialis; facies articularis and incisura tibialis more deeply excavated.

Hypotarsus.—*Geokichla* similar to *Turdus* and *Zoothera*.

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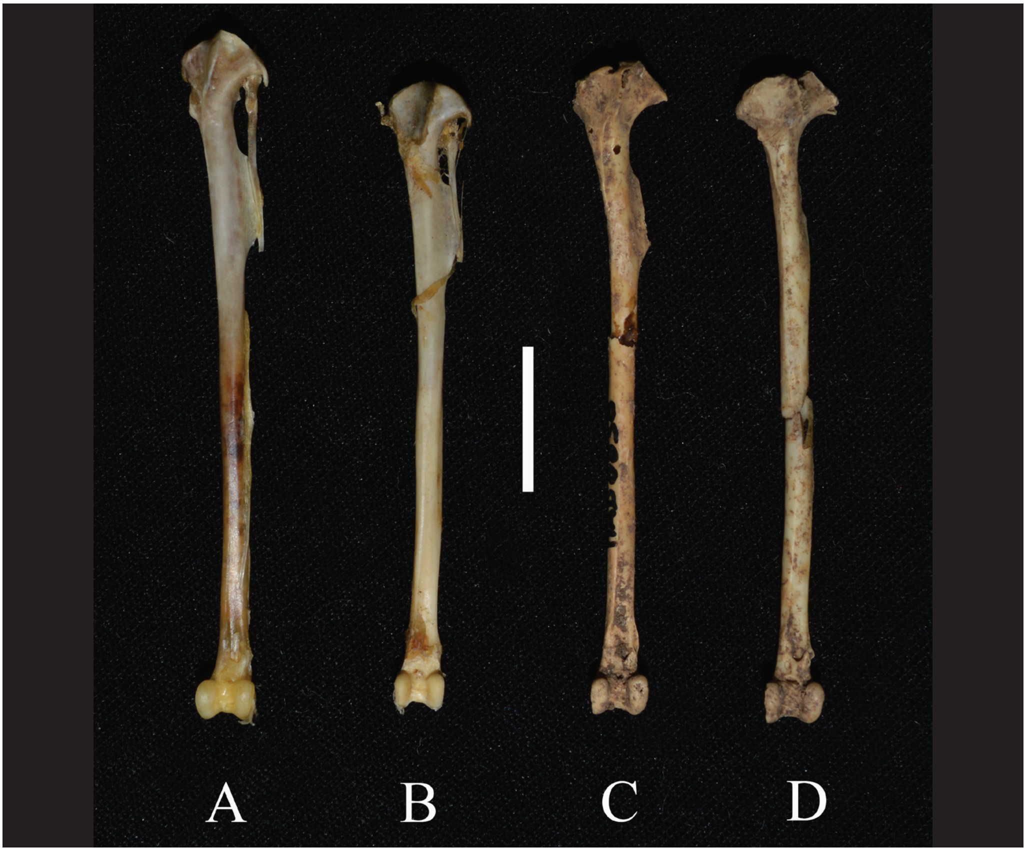

Figure 4. Comparison of tibiotarsi (left side, cranial aspect) of *Geokichla* ground thrushes with *G. longitarsus*. (A) *G. c. citrina* NHMUK S/2003.4.8 M; (B) *G. citrina cyanota* NHMUK S/2016.46.1 M; (C) *G. longitarsus* MNHN MAD 8850 u/s; (D) MNHN MAD 7172 u/s. Scale bar = 10 mm (Julian P. Hume)

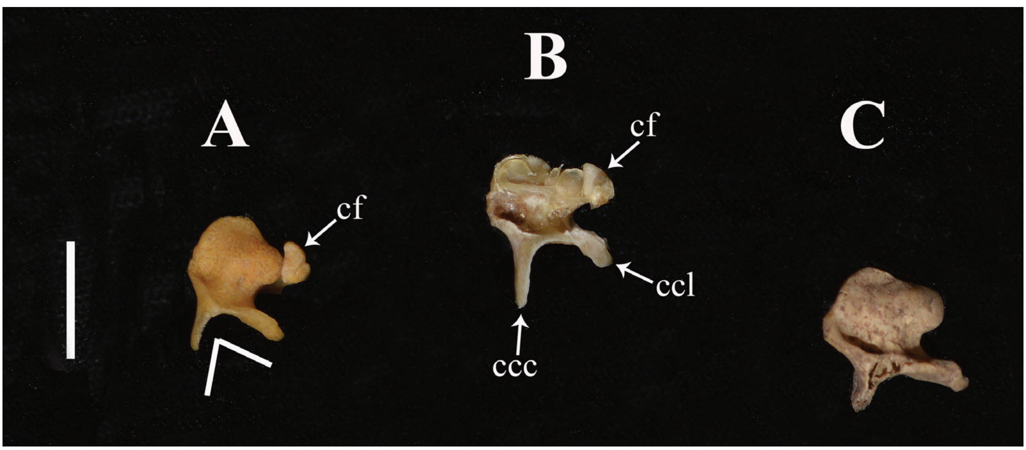

Figure 5. Comparison of tibiotarsi (left side, proximal articular surface) of *Geokichla* ground thrushes with *G. longitarsus*. (A) *G. citrina cyanota* NHMUK S/2016.46.1 M; (B) *G. c. citrina* NHMUK S/2003.4.8 M; (C) *G. longitarsus* MNHN MAD 7127 u/s. Osteological abbreviations: cf = caput fibulae (not preserved in paratype); ccc = crista cnemialis cranialis (distal end missing in paratype); ccl = crista cnemialis lateralis. Note angle between ccc and ccl as indicated in (A), a characteristic of Turdidae when compared to other similar-sized Indian Ocean passerine genera. Scale bar = 5 mm (Julian P. Hume)

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Figure 6. Comparison of tarsometatarsi (right side, above dorsal aspect; below, plantar aspect) of *Geokichla* ground thrushes with *G. longitarsus*. (A) *G. citrina cyanota* NHMUK S/2016.46.1 M; (B) *G. c. citrina* NHMUK S/2003.4.8 M; (C) holotype *Geokichla longitarsus* MNHN MAD 7127 u/s. Scale bar = 10 mm (Julian P. Hume)

Tarsometatarsus (Figs. 6–7).—Shaft straight; in dorsal aspect, eminentia intercotylaris extends strongly proximad of cotyla lateralis and cotyla medialis; sulcus extensorius extensive, extending to level of fossa metatarsi I, deflected slightly mediad and deeply excavated; deep sulcus adjoining incisura intertrochlearis medialis and incisura intertrochlearis lateralis proximally; in plantar aspect, large hypotarsus with sulcus hypotarsi completely enclosed; sulcus flexorius deeply excavated with high crista plantares lateralis that connects to hypotarsus; crista plantares medialis indistinct; foramen vasculare distale large; fossa metatarsi I shallow, but in medial profile creates a slight notch.

In *Turdus*, overall longer, slightly less robust; in dorsal aspect, sulcus extensorius less excavated proximad; trochlea metatarsi smaller with incisura intertrochlearis medialis and incisura intertrochlearis lateralis narrower; trochleae metatarsorum II deflected more mediad; in plantar aspect, crista plantares medialis less distinct; foramen vasculare distale smaller and less deeply situated; in proximal aspect, cotyla lateralis on same plane as cotyla medialis; eminentia intercotylaris smaller, less prominent.

In *Zoothera*, proportionately more robust, especially in proximal and distal ends; in medial profile, fossa metatarsi I creates a larger notch; in proximal aspect, cotyla lateralis on same plane as cotyla medialis; eminentia intercotylaris larger, less prominent.

Hypotarsus.—*Geokichla* similar to *Turdus* and *Zoothera*.

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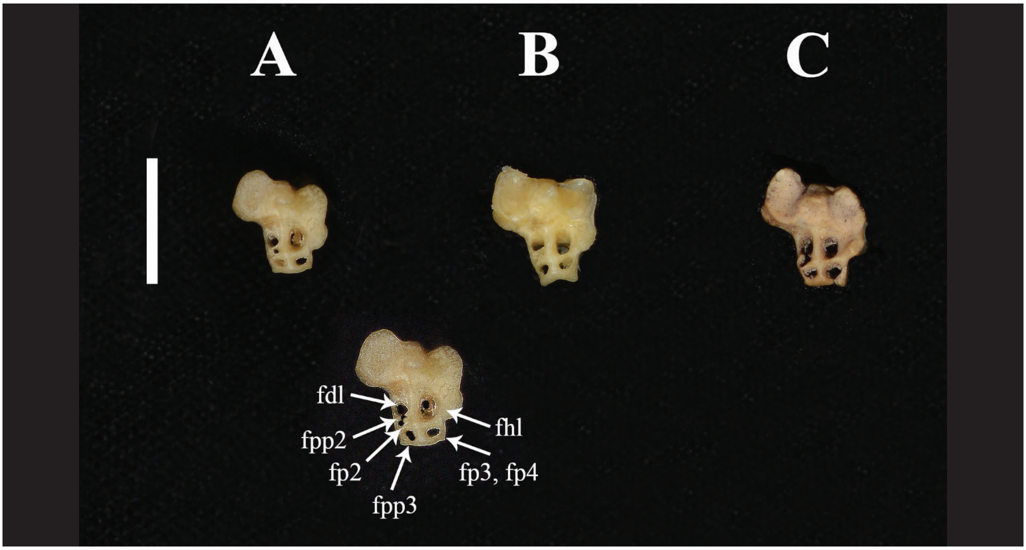

Figure 7. Comparison of hypotarsi (right side, proximal aspect) of *Geokichla* ground thrushes with *G. longitarsus*. (A) *G. citrina cyanota* NHMUK S/2016.46.1 M; (B) holotype *G. longitarsus* MNHN MAD 7127 u/s; (C) *G. c. citrina* NHMUK S/2003.4.8 M. Abbreviations of tendinal canals (after Manegold *et al*. 2004): fdl = musculus flexor digitorum longus; fhl = musculus flexor hallucis longus; fp = musculus flexor perforatus, fpp = musculus flexor perforans et perforatus; numerals 2–4 show the number of the toe supplied by the tendon. Note the open connection between fdl, fpp2 and fp2, characteristic of Turdidae. Scale bar = 5 mm (Julian P. Hume)

Species †*Geokichla longitarsus* sp. nov.

A 'long-legged finch' Hume 2013: 226; 2014b: 51

Holotype.—*Tarsometatarsus* MNHN MAD7127 (R) (Fig. 6c) collected by amateur Mauritian naturalist Etienne Thirioux in boulder scree at Vallée des Prêtres, Moka Range, central-west Mauritius. Similar sites in the Moka Range that contained fossils comprised fine silts interspersed by >5 mm igneous rock debris situated deep under boulders away from plant root intrusions (see Hume 2011).

Measurements of holotype.—Max. TL 35.4 mm, PW 4.3 mm, PD 4.1 mm, SW 1.7 mm, SD 2.1 mm, DW 3.5 mm, DD 1.9 mm. For abbreviations, see Methods.

Paratypes.—All collected by Etienne Thirioux at Vallée des Prêtres, Moka Range, central-west Mauritius (Fig. 2). Some of the following specimens are bulk-registered, so duplication of registration numbers exists. *Humerus*.—MNHN MAD7127a (R); MNHN MAD7127b (R); MNHN MAD u/r (R); MNHN MAD 7127 (L); *Tibiotarsus*.—MNHN MAD 7172 (L); MNHN MAD 8850 (L).

Diagnosis and comparison with Geokichla and other Mauritian passerines. Humerus (Fig. 3c–d).—On caudal surface, incisura capitis deeply grooved; fossa pneumotricipitalis deep, but shallow in one specimen (MNHN MAD7127b), so variable; tuberculum ventrale rounded; crista deltopectoralis indented, not forming a straight ridge, but possibly due to erosion; sulcus scapulotricipitalis deep. On cranial surface, sulcus ligamenti transversus deeply incised medially; tuberculum dorsale with slight incisura. In *Geokichla*, on caudal surface, incisura capitis less deeply grooved; fossa pneumotricipitalis shallower; tuberculum ventrale more rectangular; crista bicipitalis extends further distad; crista deltopectoralis forms a straight ridge, not indented. On cranial surface, sulcus ligamenti transversus less deeply incised medially; tuberculum dorsale without incisura.

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Larger than all other Mauritius passerines except *Hypsipetes olivaceus* and *Cryptopsar ischyrhynchus* and some generic characters are different from all other Mauritius passerines examined (see Assignment to Turdidae above; Hume 2014a for *Cryptopsar*).

Tibiotarsus (Fig. 4c–d).—In cranial aspect, crista cnemialis lateralis rounded, extending laterad well beyond crista fibularis; sulcus intercnemialis wide and deeply excavated; tuberculum retinaculi m. fibularis prominent; facies gastrocnemialis with shallow sulcus; incisura intercondylaris wide; sulcus extensorius deeply excavated. In caudal aspect, crista fibularis short; impressio ligamentum collateralis medialis prominent; in proximal surface (Fig. 5c), crista cnemialis lateralis and crista cnemialis cranialis long creating an almost square-shaped sulcus intercnemialis; facies articularis medialis square-shaped caudally.

In *Geokichla*, in cranial aspect, crista cnemialis lateralis more sharply hooked, extending less laterad; tuberculum retinaculi m. fibularis less prominent; incisura intercondylaris narrower; sulcus extensorius shallower. In caudal aspect, crista fibularis slightly longer, extending further distad; impressio ligamentum collateralis medialis more prominent. On proximal surface (Fig. 5a–b), facies articularis medialis more rounded caudally; crista cnemialis cranialis less robust; sulcus intercnemialis slightly less square-shaped, more triangular; fossa retropatellaris slightly deeper.

Other than *Cryptopsar* (see Hume 2014a), tibiotarsus longer, with some generic characters different from all other Mauritius passerines examined (see Assignment to Turdidae above).

Tarsometatarsus (Fig. 6c).—Extremely long relative to width; in dorsal aspect, two foramina vascularia proximalia, with lateral foramina more deeply situated; sulcus extensorius deep but not extending to level of fossa metatarsi I; incisura intertrochlearis medialis and incisura intertrochlearis lateralis wide with deep proximal sulci; trochleae metatarsorum II with no distal mediad deflection. In plantar aspect, hypotarsus reduced; foramen vasculare distale deeply situated. In proximal aspect, cotyla medialis with strong projection dorsad to cotyla lateralis; cotyla lateralis rounded, deeply excavated, and not directed laterad; eminentia intercotylaris prominent. In *Geokichla* (Figs. 6a–b), shaft narrower with less robust proximal and distal ends; in dorsal aspect, lateral and medial foramina vascularia proximalia less deeply situated, especially medial foramina; sulcus extensorius more extensive, extending to level of fossa metatarsi I; proximal sulci adjoining incisura intertrochlearis medialis and incisura intertrochlearis lateralis less deeply excavated; trochleae metatarsorum II with a slight distal deflection mediad. In plantar aspect, hypotarsus larger, extending further distad; foramen vasculare distale less deeply situated; in proximal aspect, cotyla lateralis shallower, less deeply excavated; cotyla medialis projects less dorsad to cotyla lateralis; eminentia intercotylaris smaller, less prominent.

Differs substantially from all other Mauritius passerines by its considerably longer total length and proportionately smaller proximal and distal ends.

Hypotarsus (Fig. 7c).—Comparable with all Turdidae examined herein, with six tendinal canals present, but differs from *Geokichla* (Figs. 7a–b) in musculus flexor hallucis longus (fhl) distinctly larger than musculus flexor digitorum longus (fdl). In passerines, the fhl and fdl both pass through the hypotarsus independently and emerge on the plantar surface of foot before branching to the digits, with the fhl inserting on the hallux (digit 1) alone (Garrod 1875, Berman & Raikow 1982). This provides a strong flex in the hallux, so the larger fhl tendinal canal in *Geokichla longitarsus* sp. nov. suggests even greater strength in this digit.

Distribution.—Mauritius, Mascarene Islands All specimens were found in boulder scree in the Vallée des Prêtres, north-west Mauritius, but the species undoubtedly occurred over much of the island in suitable habitat.

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Suggested vernacular name.—Mauritius Ground Thrush.

Etymology.—The specific name *longitarsus* is from Latin, *longus* long; Greek *tarsos* flat of the foot, in reference to the extremely long, slender tarsometatarsus, which separates this species from all other Mascarene passerines.

Discussion

The holotype tarsometatarsus, discovered among the hundreds of Mauritian passerine fossils collected by amateur natural historian Etienne Thirioux in the late 19th and early 20th centuries (Claessens & Hume 2015), was tentatively assigned to a 'long-legged finch' (Hume 2013: 226, 2014a: 51). However, a more detailed analysis of the specimen, as well as other material in the same collection, confirmed its true affinities. This also makes sense biogeographically (Fig. 1). It is similar proportionately and osteologically to several *Geokichla* (Appendix 1; Figs. 3–7), especially Orange-headed Thrush *G. citrina* (Latham, 1790), a species with ten subspecies in China, Thailand, Myanmar, Borneo and Java, as well as the Nicobars (*G. c. albogularis* Blyth, 1847) and Andamans (*G. c. andamanensis* Walden, 1874) in the north-east Indian Ocean (Dickinson & Christidis 2014) (Fig. 1). It is a non-breeding boreal winter visitor to India and Sri Lanka (Collar 2005). In size, *G. longitarsus* would have been slightly larger than *G. citrina* (Appendix 1), which is 23 cm in total length; the Andaman and Nicobar subspecies average smaller, *c*.21 and 22 cm, respectively (Clement 2000, Collar 2005).

Affinities.—*Geokichla* ground thrushes occur in South-East Asia as well as in Africa, meaning that the Mauritius species could derive from either source. However, it is more likely that South-East Asia was the origin and that the genus was able to colonise Mauritius during sea level lows. In the last five Ma, sea levels up to 50 m lower than present occurred (Miller *et al*. 2005), whereas in the last 650 Ka, sea level lows were sometimes up to 135 m lower than present and such periods persisted for up 50 Ka at a time (Warren *et al*. 2010). These events would have greatly increased the land-surface area of the Maldives, Seychelles and Mascarenes, and created subaerial island groups in the Chagos Archipelago, the Saya de Malha, Nazareth and St. Brandon (Cargados Carajos) banks (Hume 2013) (Fig. 1). This not only reduced distances between islands and continental landmasses, but also the inter-island crossings, and would have provided numerous, large and long-term island stepping-stones (Warren *et al*. 2010, Hume 2013). This scenario mirrors the affinities of many endemic Mascarene birds, including other passerines (Warren *et al*. 2005, 2006, Zuccon *et al*. 2008, Jønsson *et al*. 2010, Hume 2013, 2014b, 2015). In particular, in addition to being clearly genetically derived from South-East Asia starling genera (Zuccon *et al*. 2008), the endemic Mascarene Sturnidae are most similar in coloration to White-headed Starling *Sturnia erythropygia* (Blyth, 1846) of the Andaman and Nicobar Islands (Hume 2014b). As two *Geokichla citrina* subspecies occur on the latter islands, with the nominate in southern India and Sri Lanka, it is feasible that the Mauritian Ground Thrush and *G. citrina*, or a similar species, derive from the same common ancestor. Voelker & Outlaw (2008) demonstrated that *G. citrina* is sister to the South-East Asian *G. cinerea* clade, and both diverged early from a common ancestor, whilst speciation events that reached the neighbouring islands occurred rapidly. They further showed that initial diversification in this lineage occurred in the late Pliocene, with a pulse of speciation occurring during 2.09–1.74 Ma. Evolution of Mauritius shield-building volcanism was well underway by 8.9 Ma (Moore *et al*. 2011), providing evidence for long-term, subaerial land surface availability, despite fluctuating sea levels, so presumably the ancestral *Geokichla* was subject to allopatric speciation as it island-hopped to Mauritius during sea level low stands.

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Ecology.—Heavily forested before the arrival of human settlers in the early 17th century, and dominated by semi-dry evergreen forest at lower elevations and by wet forest in the highlands (Cheke & Hume 2008) (Fig. 2), the *G. longitarsus* fossil remains originated from what would have been semi-dry evergreen forest on Mauritius. This vegetational biome may have been the species' preferred habitat, and the relatively large size of Mauritius with an extensive covering of suitable forest suggests that this ground thrush had a wide range over the island prior to human arrival (Fig. 2).

Several *Geokichla* thrushes, including Orange-headed Thrush, occur in the understorey of moist deciduous and mixed evergreen secondary forest, often near running water in lower-elevation ravines, and generally forage on the ground in leaf litter under dense shrubbery, searching for food by tossing leaves aside (Clement 2000, Collar 2005). Although they will take terrestrial gastropods, worms and leeches, as well as berries, fruit and seeds, they are predominantly insectivorous (Clement 2000, Collar 2005). It is very likely that the Mauritius Ground Thrush had a similar ecology, feeding on insects and the diverse terrestrial gastropod fauna of Mauritius (see Griffiths & Florens 2006), as well as taking advantage of seasonal fruits and seeds. The long tarsi are indicative of a terrestrial lifestyle, so it probably fed on the forest floor and nested near the ground, as do some other *Geokichla* (Clement 2000, Collar 2005). The greater strength in the hallux due to a large musculus flexor hallucis longus tendon may have also been an adaptation to a terrestrial lifestyle.

Extinction.—The Mauritius Ground Thrush seemingly disappeared without mention in the literature. West-Zanen (*in* Soeteboom 1648: 19), who was on Mauritius in 1602, included 'thrushes and sparrows', in his extensive list of the avifauna, but it is likely that 'thrushes' refer to the *Hypsipetes* bulbul or merle, as known locally, and 'sparrows' to the endemic Mauritius Fody *Foudia rubra* (Cheke & Hume 2008). The predatory Black Rat *Rattus rattus* appears to have been the main cause of decline in many passerines on Indian Ocean islands (Safford & Hawkins 2013) and was probably to blame for the extinction of Mauritius Ground Thrush. Introduced by Arab traders, Black Rats arrived on Mauritius in the 14th century (Hume 2013) and may have exterminated the ground thrush before the arrival of the Dutch, who made the first descriptions of the fauna in 1598 (Moree 1998). A terrestrial thrush that had evolved without mammalian predators would have quickly succumbed to rat predation, especially if it nested near the ground. An endemic terrestrial starling, *Cryptopsar ischyrhynchus*, and two other, undescribed fossil passerines also probably disappeared due to rat predation (Hume 2013, 2017), and rats continue to threaten the extant Mauritian passerines, especially Mauritius Fody (Safford & Hawkins 2013).

The discovery of a new genus of passerine on Mauritius is not without consequence. It represents the only known extinction in *Geokichla*, although the closely related *Zoothera* thrushes have lost one species and one subspecies (Hume 2017) both endemic to Pacific islands. Furthermore, new fossil passerines have considerably increased the number of recognised human-caused extinctions on the Mascarenes (Hume 2014a, 2015, Cheke & Hume 2018, this paper), which has one of the highest avian extinction rates in the world (Safford & Hawkins 2013, Hume 2017). Mauritius has lost 19 of 28 endemic birds, or *c*.68% (Hume 2013), including four undescribed fossil taxa. Yet, this discovery also has important outcomes for avian biogeography, evolutionary history and phylogenetic relationships in the Malagasy region (see Hume 2013). Using molecular data from *Zoothera* and *Geokichla*, Voelker & Outlaw (2008) deliberated as to over-water dispersal vs. land-based vicariance in the Indian Ocean Basin (IOB). As ground thrushes had seemingly not colonised major Indian Ocean islands, they hypothesised that the absence of *Geokichla* in this region could be a function of extinction. As a result, they tentatively concluded that trans-IOB dispersal by *Geokichla* was unlikely to have occurred, and that vicariance better explains IOB perimeter

ISSN-2513-9894 (Online)

distributions in Africa and continental Asia. Therefore, the discovery of an endemic *Geokichla* on Mauritius succinctly closes the biogeographical gap.

In conclusion, the discovery of a now-extinct *Geokichla* on Mauritius, with other bird taxa awaiting description, and likely more awaiting detection, reinforces the necessity for detailed investigative palaeontological studies on such islands where unexpected bird genera demonstrably once occurred, before making defining biogeographical conclusions.

Acknowledgements

I thank Robert Prŷs-Jones, an anonymous referee and especially Trevor Worthy, whose comments improved the manuscript. I thank Ronan Allain and Claire Sagne (MNHN) for support and loan of Paris Thirioux fossil material; and Joel Cracraft and Paul Sweet (AMNH) for access to specimens in their care. A Collection Study Grant, from AMNH, in 2019, made this research possible.

References:

Baumel, J. J. & Witmer, L. M. 1993. Osteologica. Pp. 45–132 *in* Baumel, J. J., King, A. S., Breazile, J. E., Evans, H. E. & Vanden, B. J. (eds.) *Handbook of avian anatomy: nomina anatomica avium*. Second edn. Nuttall Orn. Cl., Cambridge, MA.

Berman, S. L. & Raikow, R. J. 1982. The hindlimb musculature of the mousebirds (Coliiformes). *Auk* 99: 41–57.

Cheke, A. S. & Hume, J. P. 2008. *Lost land of the Dodo: the ecological history of the Mascarene Islands.* A. & C. Black, London.

Cheke, A. S. & Hume, J. P. 2018. The Réunion Fody *Foudia delloni* Cheke & Hume and the validity of scientifically naming animals described without physical types. *Zootaxa* 4382: 592–600.

Claessens, L. & Hume, J. P. 2015. Provenance and history of the Thirioux Dodos. *J. Vert. Paleontol*. 35 (Suppl. 1): 21–28.

Clement, P. 2000. *Thrushes.* Christopher Helm, London.

Collar, N. J. 2005. Family Turdidae (thrushes). Pp. 514–807 *in* del Hoyo, J., Elliott, A. & Christie, D. A. (eds.) *Handbook of the birds of the world*, vol. 10. Lynx Edicions, Barcelona.

Dickinson, E. C. & Christidis, L. (eds.) 2014. *The Howard and Moore complete checklist of the birds of the world*, vol. 2. Fourth edn. Aves Press, Eastbourne.

Garrod, A. H. 1875. On the disposition of the deep plantar tendons in different birds. *Proc. Zool. Soc. Lond*. 1875: 339–348.

Griffiths, O. & Florens, F. B. V. 2006. *A field guide to the non-marine molluscs of the Mascarene Islands (Mauritius, Rodrigues and Réunion) and the northern dependencies of Mauritius*. Bioculture Press, Mauritius.

Hume, J. P. 2005. Contrasting taphofacies in ocean island settings: the fossil record of Mascarene vertebrates. Pp. 129–144 *in* Alcover, J. A. & Bover, P. (eds.) Proceedings of the International Symposium 'Insular vertebrate evolution: the palaeontological approach'. *Monogr. Soc. Hist. Nat. Balears* 12.

Hume, J. P. 2011. Systematics, morphology, and ecology of pigeons and doves (Aves: Columbidae) of the Mascarene Islands, with three new species. *Zootaxa* 3124: 1–62.

Hume, J. P. 2013. A synopsis of the pre-human avifauna of the Mascarene Islands. Pp. 195–237 *in* Göhlich, U. B. & Kroh, A. (eds.) *Proc. Eighth Intern. Meet. Soc. Avian Paleontol. Evol.* Naturhistorisches Museum, Wien.

Hume, J. P. 2014a. Systematics, morphology, and ecological history of the Mascarene starlings (Aves: Sturnidae) with the description of a new genus and species from Mauritius. *Zootaxa* 3849: 1–75.

Hume, J. P. 2014b. A review of the past and present bird fauna of the Mascarene Islands. *Proc. Roy. Soc. Arts Sci. Mauritius* 8: 17–82.

Hume, J. P. 2015. A new subfossil bulbul (Aves: Passerines: Pycnonotidae) from Rodrigues Island, Mascarenes, southwestern Indian Ocean. *Ostrich* 86: 247–260.

Hume, J. P. 2017. *Extinct birds*. Second edn. Christopher Helm, London.

Jønsson, K. A., Bowie, R. C. K., Nylander, J. A. A., Christidis, L., Norman, J. A. & Fjeldså, J. 2010. Biogeographical history of cuckoo-shrikes (Aves: Passeriformes): transoceanic colonization of Africa from Australo-Papua. *J. Biogeogr*. 37: 1767–1781.

Manegold, A., Mayr, G. & Mourer-Chauviré, C. 2004. Miocene songbirds and the composition of the European passeriform avifauna. *Auk* 121: 1155–1160.

Miller, K. G., Kominz, M. A., Browning, J. V., Wright, J. D., Mountain, G. S., Katz, M.E., Sugarman, P. J., Cramer, B. S., Christie-Blick, N. & Pekar, S. F. 2005. The Phanerozoic record of global sea-level change. *Science* 310: 1293–1298.

Moore, J., White, W. M., Debajyoti, P., Duncan, R. A., Abouchami, W. & Galer, S. J. G. 2011. Evolution of shield-building and rejuvenescent volcanism of Mauritius. *J. Vol. Geotherm. Res*. 207: 47–66.

Moree, P. J. 1998. *A concise history of Dutch Mauritius, 1598-1710*. Kegan Paul International, London & New York.

Safford, R. J. & Hawkins, A. F. A. (eds.) 2013. *The birds of Africa*, vol. 8. Christopher Helm, London.

ISSN-2513-9894 (Online)

Soeteboom, H. 1648. *Derde voomaemste Zeegetogt (der verbondene vrije Nederlanden) na de Oost-Indien*. Amsterdam.
Voelker, G. & Klicka, J. 2008. Systematics of *Zoothera* thrushes, and a synthesis of true thrush molecular systematic relationships. *Mol. Phylo. & Evol*. 49: 377–381.
Voelker, G. & Outlaw, R. K. 2008. Establishing a perimeter position: speciation around the Indian Ocean Basin. *J. Evol. Biol*. 21: 1779–1788.
Warren, B. H., Bermingham, E., Prŷs-Jones, R. & Thébaud, C. 2005. Tracking island colonization history and phenotypic shifts in Indian Ocean bulbuls (*Hypsipetes*: Pycnonotidae). *Biol. J. Linn. Soc*. 85: 271–287.
Warren, B. H., Bermingham, E., Prŷs-Jones, R. & Thébaud, C. 2006. Immigration, species radiation and extinction in a highly diverse songbird lineage: white-eyes on Indian Ocean islands. *Mol. Ecol*. 15: 3769–3786.
Warren, B. H., Strasberg, D., Brüggemann, J. H., Prŷs-Jones, R. P. & Thébaud, C. 2010. Why does the biota of the Madagascar region have such a strong Asiatic flavour? *Cladistics* 26: 526–538.
Wójcik, J. D. 2002. The comparative osteology of the humerus in European thrushes (Aves: *Turdus*) including a comparison with other similarly sized genera of passerine birds – preliminary results. Pp. 369–381 *in* Bocheński, Z. M., Bocheński, Z. & Stewart, J. R. (eds.) Proceedings of the Fourth Meeting of the ICAZ Bird Working Group Kraków, Poland, 11–15 September, 2001. *Acta Zool. Cracov* 45 (Spec. Iss.).
Wood, D. S. & Schnell, G. D. 1986. *Revised world inventory of avian skeletal specimens.* American Ornithologists' Union & Oklahoma Biological Survey, Norman, OK.
Zuccon, D., Pasquet, E. & Ericson, P. G. P. 2008. Phylogenetic relationships among Palearctic-Oriental starlings and mynas (genera *Sturnus* and *Acridotheres*: Sturnidae). *Zool. Scripta* 37: 469–481.

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Appendix 1: measurements (mm) of several *Zoothera*, one *Turdus* and multiple other *Geokichla* compared to *G. longitarsus*. For osteological measurement abbreviations, see Methods. Statistical abbreviations: *n* = no. of specimens; m = mean; R = range.

(a) Measurements of humerus

Species	*n*	TL m [R]	GW m [R]	GD m [R]	SW m [R]	SD m [R]	DW m [R]	DD m [R]
G. longitarsus	3	27.6 [27.5–27.7]	7.1 [7.0–7.2]	3.5 [3.2–3.7]	2.6 [2.3–2.4]	2.0 [1.9–2.1]	6.4 [6.2–6.7]	3.4 [3.3–3.6]
G. c. citrina	2	25.2 [25.0–25.4]	7.0 [6.8–7.2]	3.4 [3.4–3.5]	2.2 [2.2–2.3]	2.0 [2.1–2.2]	6.1 [6.1–6.2]	3.3 [3.3–3.4]
G. c. cyanota	2	24.8 [24.7–24.9]	6.9 [6.8–6.9]	3.2 [3.0–3.4]	2.2 [2.1–2.3]	2.1 [2.0–2.2]	5.9 [5.9–6.0]	3.5 [3.4–3.6]
G. princei	1	28.2	7.4	3.5	2.5	2.3	6.6	3.7
G. interpres	1	23.2	6.1	2.8	1.9	1.8	5.2	3.0
G. dohertyi	3	23.6 [23.2–23.9]	6.8 [6.3–7.1]	3.0 [3.0–3.2]	1.9 [1.9–2.0]	1.7 [1.7–1.8]	5.8 [5.7–6.1]	3.0 [2.9–3.2]
G. guttata	1	18.6	4.8	3.1	1.7	1.6	4.8	2.8
G. piaggiae	1	23.5	6.5	3.3	2.3	2.1	5.6	2.8
Zoothera monticola	1	33.1	9.7	4.5	3.2	2.9	8.4	4.3
Z. dauma	2	32.9 [31.2–34.5]	9.6 [8.9–10.3]	4.5 [4.2–4.7]	3.2 [3.1–3.4]	2.8 [2.7–3.0]	8.2 [7.7–8.6]	4.3 [4.0–4.5]
Z. talaseae	1	22.9	6.1	3.1	2.3	2.0	6.1	3.2
Z. dixoni	1	28.4	8.2	3.9	2.8	2.3	7.2	4.0
Z. marginata	1	29.8	8.9	4.0	2.9	2.5	7.2	4.0
Turdus poliocephalus erythropleurus	1	24.7	6.3	3.4	2.1	3.0	5.5	3.3

(b) Measurements of tibiotarsus

Species	n	TL m [R]	GW m [R]	GD m [R]	SW m [R]	SD m [R]	DW m [R]	DD m [R]
G. longitarsus	2	44.1 [44.1–44.2]	5.5 [5.2–5.8]	5.9 [5.8–6.1]	1.7	1.9 [1.8–2.0]	3.9 [3.8–4.0]	3.5 [3.2–3.8]
G. c. citrina	2	41.7 [41.7–42.4]	5.2 [5.2–5.3]	5.7 [5.6–5.9]	1.7	1.7	3.4 [3.3–3.4]	3.5

ISSN-2513-9894 (Online)

G. c. cyanota	2	40.7 [39.1–42.4]	4.7 [4.2–5.3]	5.8	1.7 [2.1–2.3]	2.1 [1.7–1.8]	3.4	3.4 [3.4–3.5]
G. princei	1	48.0	5.1	6.7	2.1	2.1	4.2	3.8
G. interpres	1	38.9	3.9	5.0	1.5	1.5	3.2	3.3
G. dohertyi	3	40.5 [39.8–41.4]	4.2 [4.1–4.5]	5.9 [5.7–6.0]	1.6 [1.6–1.7]	1.6 [1.6–1.7]	3.2 [3.2–3.3]	3.4 [3.4–3.6]
G. guttata	1	37.0	3.9	4.2	1.3	1.6	2.6	2.7
G. piaggiae	1	45.3	4.5	6.0	1.7	1.8	3.6	3.5
Zoothera monticola	1	50.4	6.0	7.6	2.6	2.3	4.8	4.9
Z. dauma	2	52.8 [50.3–55.5]	6.1 [5.8–6.7]	7.4 [6.9–7.8]	2.3 [2.3–2.5]	2.6 [2.5–2.8]	4.8 [4.4–5.2]	4.8 [4.2–5.2]
Z. talaseae	1	48.6	5.5	5.6	2.1	1.9	4.0	3.9
Z. dixoni	1	49.7	5.4	6.1	2.0	2.3	4.0	4.0
Z. marginata	1	42.9	5.3	6.2	2.0	2.2	4.5	4.1
Turdus poliocephalus erythropleurus	1	43.7	5.7	6.1	1.6	1.7	3.6	3.6

(c) Measurements of tarsometatarsus

Species	n	TL m [R]	GW m [R]	GD m [R]	LSW m [R]	LSD m [R]	DW m [R]	DD m [R]
G. longitarsus	1	35.4	4.3	4.1	1.7	2.1	3.5	1.9
G. c. citrina	2	30.8 [29.9–31.7]	3.8 [3.7–4.0]	4.0 [3.8–4.3]	1.4	1.6 [1.6–1.7]	3.1 [3.0–3.2]	1.8 [1.7–2.0]
G. c. cyanota	2	31.3 [30.7–32.0]	3.7 [3.5–3.9]	3.8	1.7 [1.7–1.8]	1.9 [1.9–2.0]	2.9 [2.7–3.1]	1.7 [1.7–1.8]
G. princei	1	36.6	4.5	4.3	2.0	2.2	4.0	2.4
G. interpres	1	29.2	3.6	3.8	1.5	1.8	2.9	1.8
G. dohertyi	3	30.0 [29.2–31.1]	3.7 [3.6–3.8]	3.7 [3.6–3.8]	1.5 [1.4–1.7]	1.7 [1.6–1.8]	2.9 [2.8–3.1]	1.8 [1.8–1.9]
G. guttata	1	29.7	2.9	2.1	1.2	1.3	2.2	1.3
G. piaggiae	1	34.3	3.9	3.8	1.6	1.8	3.3	1.7
Zoothera monticola	1	34.1	5.2	6.0	2.1	2.1	4.6	2.6
Z. dauma	2	35.2 [34.2–36.5]	5.4 [4.9–5.7]	5.9 [5.4–6.3]	2.1 [2.0–2.3]	2.5 [2.3–2.8]	4.6 [4.3–4.9]	2.4 [2.2–2.7]
Z. talaseae	1	37.8	4.8	4.7	1.7	2.2	3.9	1.9
Z. dixoni	1	36.2	4.4	4.7	1.7	2.0	3.6	2.1
Z. marginata	1	29.5	4.8	4.9	1.9	1.9	4.1	2.3
Turdus poliocephalus erythropleurus	1	31.3	3.9	3.9	1.5	1.7	3.3	1.8

ISSN-2513-9894 (Online)