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A new subfossil bulbul (Aves: Passerines: Pycnonotidae) from Rodrigues Island, Mascarenes, south-western Indian Ocean

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The Hypsipetes bulbuls (Pycnonotidae) occur on Madagascar and oceanic islands throughout the Indian Ocean, as well as continental Asia. Endemic species are found on the Mascarene Islands of Mauritius and Réunion, but the genus was purportedly never reported from Rodrigues, the smallest and most isolated of the Mascarene group, which was somewhat anomalous considering present avian biogeography. Based on recently discovered subfossil remains, this paper describes a new Hypsipetes bulbul from Rodrigues Island, which presumably became extinct historically, thus filling in the biogeographical gap. This discovery further emphasises the need for palaeontological surveys in situations in which unexpected bird species distribution patterns occur, before robust biogeographical conclusions can be ascertained.


Keywords: biogeography, extinction, Hypsipetes cowlesi, Rodrigues Bulbul

Introduction

The Hypsipetes bulbuls (Pycnonotidae) are widely distributed, with endemic species occurring on Madagascar and a number of isolated islands and island archipelagos throughout the Indian Ocean (Figure 1), as well in continental Asia. Indian Ocean island species occur on the Seychelles H. crassirostris E. Newton, 1867, nominate H. madagascariensis (Statius Müller, 1776) on Madagascar and Comoros with a subspecies on Aldabra, H. parvirostris Milne-Edwards & Oustalet, 1885 on Grande Comore, and H. moheliensis (Benson, 1960) on Mohéli (Warren et al. 2005; Safford and Hawkins 2013). The Mascarene islands of Mauritius and Réunion each have a distinct, endemic species, whereas the genus was reputedly unknown on Rodrigues, the smallest and most isolated of the Mascarene group. This was somewhat perplexing in terms of avian biogeography. Based on recently discovered subfossil remains, this paper describes a new Hypsipetes bulbul from Rodrigues Island, which presumably became extinct historically, thus filling in the biogeographical gap. This discovery further emphasises the need for palaeontological surveys in situations in which unexpected bird species distribution patterns occur, before robust biogeographical conclusions can be ascertained.


Keywords: biogeography, extinction, Hypsipetes cowlesi, Rodrigues Bulbul

Materials and methods

Institutions: American Museum of Natural History, New York (AMNH); Francois Leguat Museum, Rodrigues (FLMR); Muséum National d’Histoire Naturelle, Paris (MNHN), with the prefix MAD for Madagascar, e.g. MNHN MAD8849; Natural History Museum, London and Tring (NHMUK) (formerly British Museum (Natural History) [BMNH]); University Museum of Zoology, Cambridge, UK (UMZC); National Museum of Natural History, Washington, DC (USNM).

Abbreviations: 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. † indicates an extinct taxon.


Comparative material examined

The following skeletal specimens were used, all held in the NHMUK and USNM bird skeleton collections, with registration number and sex provided for each. Because
of the rarity of Mascarene passerine skeletons in museum collections, a genetically closely related Black-winged Cuckoo-shrike *Coracina melaschistos* Hodgson, 1836 (Jønsson et al. 2010) was used instead of a Mascarene-endemic species. Where some elements were lacking in the latter, e.g. cranium, wing and leg bones, a Madagascar Cuckoo-shrike *Coracina cinerea* was used for comparison. Only one continental *Hypsipetes* partial skeleton was available for comparison, *H. leucocephalus psaroides* Vigors, 1831, and as no modern *H. olivaceus* was available, subfossil remains were used for comparative purposes (see Systematic Palaeontology): *Coracina cinerea* NHMUK 1897.5.10.56 u/s; *Coracina melaschistos* NHMUK 1845.1.2.117.175 u/s; *Hypsipetes borbonicus* USNM 488426 ♀; *Hypsipetes crassirostris* USNM 488421 ♀; *Hypsipetes madagascariensis* NHMUK 1897.5.10.6 u/s; NHMUK 1897.5.10.42 u/s; *Hypsipetes leucocephalus psaroides* NHMUK 1845.1.12.109 (trunk only) u/s; *Hypsipetes leucocephalus concolor* NHMUK 1895.7.14.1243♀.

Measurements

All measurements were made using dial calipers and rounded to the nearest 0.1 mm. TL = total length; cranium, from naso-frontal hinge to margin of crista occipitalis in a median plane; mandible, from processus retroarticularis to rostrum mandibulae in dorsal aspect; coracoid, measured on the medial side; scapula, from facies articularis clavicularis to extremitas caudalis in lateral plane; humerus and ulna, measured in dorsal aspect; carpometacarpus, measured in ventral aspect; tarsometatarsus, measured in dorsal aspect. WNF = width of naso-frontal hinge. PML = premaxilla length, measured in ventral aspect; PW = proximal width; taken in a lateromedial plane: mandible, from processus mandibulae medialis to cotyla medialis; femur, from the femoral head through mid-depth point of the neck to lateral side; GW = greatest width, taken in a dorsoventral plane: cranium, taken between processus postorbitales; GD = greatest depth: cranium from medial point of parietal to medial ventral surface; PD = proximal depth, taken in a dorsoventral plane; carpometacarpus,
proximal end from processus extensorius to caudal margin of trochlea carpalis; SW = shaft width, in lateromedial plane. SD = shaft depth, in dorsoventral plane. DW = distal width, in lateromedial plane; coracoid, taken from angulus medialis to processus lateralis; ulna, taken in dorsal aspect. DD = distal depth, in dorsoventral plane. Anatomical nomenclature follows Baumel and Witmer (1993).

**Systematic palaeontology**

Passeriformes Linnaeus, 1758  
Pyconnotidae G.R. Gray, 1840  

**Etymology**

From Greek; *hupsi*, on high, and *petes*, flyer.

**Diagnosis**

*Hypsipetes* is distinguished by the following characters:  
*Cranium* (Figure 3): in dorsal view, rounded, somewhat bulbous posteriorly; frontal wide; in posterior view, crista nuchalis transversa oval-shaped with indistinct prominentia cerebellaris; foramen magnum comparatively large; in lateral view, two foramen. n. optici, much smaller than fonticuli orbitocraniales; processus postorbitalis elongate and wide.  
*Rostrum*: relatively long and wide with large, oval-shaped narial openings; os nasale narrow; rostrum maxillare sharp and slightly decurved.  
*Mandible* (Figure 4): rostrum mandibulae wide and sharply pointed; processus mandibulae medialis sharply deflected dorsally; processus retroarticulпарис reduced; single large fenestra rostralis mandibulae.  
*Scapula* (Figure 5a): extremitas caudalis strongly decurved; almost no expansion of margo dorsalis.  
*Coracoid* (Figure 5b): in dorsal surface, shaft narrow with
Figure 3: Comparison of crania of Hypsipetes bulbuls, dorsal view (left), lateral view (right). (a and b) NHMUK1897.5.10.6 Hypsipetes madagascariensis u/s; (c and d) FLMR 273 (holotype) Hypsipetes cowlesi sp. nov. u/s. Scale bar = 10 mm

Figure 4: Comparison of mandibles of Hypsipetes bulbuls, dorsal view. (a) MNHN MAD6931 Hypsipetes olivaceus u/s; (b) FLMR 600 Hypsipetes cowlesi sp. nov. u/s; (c) NHMUK1897.5.10.6 Hypsipetes madagascariensis u/s. Scale bar = 10 mm
sharp lateral edge to processus lateralis; facies articularis clavicularis sharply hooked.

**Humerus** (Figure 6): comparatively gracile with straight shaft; caput humeri distinct and bulbous; tuberculum ventrale reduced; one pneumatic fossae; pneumatic fossa II connects with pneumatic fossa I; crista deltopectoralis with little distal extension; incisura capitis deeply excavated.

**Ulna** (Figure 7): olecranon distinct and sharply pointed; impressio brachialis deeply excavated; papillae remigales caudae sharply defined; incisura tuberculi carpalis deeply excavated.

**Radius**: facies articularis ulnaris with distinct laterally deflected expansion; lineae intermuscularis forms a prominent ridge proximad on dorsal surface.

**Carpometacarpus** (Figure 8): processus pisiformis distinct; processus intermetacarpale extensive connecting to os metacarpale minus ventrally; os metacarpale majus dorso-ventrally flattened, with raised ridge running from processus pisiformis to distal end of os metacarpale minus; os metacarpale minus narrow, not offset from os metacarpale majus, extending much further distad; sulcus interrosseus deeply incised.

**Femur**: robust, particularly at proximal and distal ends; in cranial aspect, sulcus patellaris narrow and deeply excavated; facies articularis acetabularis large; in caudal aspect, condylus lateralis strongly directed caudally.

**Tibiotarsus**: robust, especially at proximal and distal ends;

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**Figure 5a**: Comparison of scapulae (right side) of *Hypsipetes* bulbuls, dorsal view. (a) NHMUK u/r Hypsipetes cowlesi sp. nov. u/s; (b) NHMUK1897.5.10.6 Hypsipetes madagascariensis u/s. Scale bar = 10 mm

**Figure 5b**: Comparison of coracoids (left side) of *Hypsipetes* bulbuls, ventral aspect. (a) MNHN MAD8849 Hypsipetes olivaceus u/s; (b) NHMUK S/1978.14.61 Hypsipetes cowlesi sp. nov. u/s; (c) NHMUK1897.5.10.6 Hypsipetes madagascariensis u/s. Scale bar = 10 mm
Hume

in cranial aspect, crista cnemialis lateralis distinctly hooked; tuberculum retinaculi m. fibularis distinct; pons supratendineus large.

Tarsometatarsus (Figure 9): comparatively short and robust; trochlea not expanded lateromedially; foramen vasculare distale large and distinct; in dorsal aspect, distinct proximal ridge on facies dorsalis; in plantar view, trochlea. metatarsi III distinctly larger than trochlea. metatarsi II; on proximal end, four enclosed canali hypotarsi.

The Mascarene and Seychelles taxa differ from some of the continental Hypsipetes species generally in their larger size, and are significantly larger when compared with H. madagascariensis. The Himalayan Black Bulbul H. l. psaroides is larger in the coracoid and femur, the subspecies H. l. concolor is smaller in the rostrum, mandible and leg elements, the tarsometatarsus especially so, whereas the Seychelles species, H. crassirostris, is the largest of the Indian Ocean genera (see Table 1).

Description and comparison

Hypsipetes differs from the other Mascarene passerine genera Foudia, Zosterops, Acrocephalus, Terpsiphone and Saxicola by much larger size; conversely, smaller than the Mascarene sturnids, Fregilupus, Necropsar and Mauritius starling (JPH unpublished data). It is similar in size to Coracina, but the latter species differs from it by the following characters:

Cranium: larger and less rounded; in dorsal view, frontal much narrower between orbits and more deeply excavated at nasofrontal hinge; in posterior view, crista nuchalis transversa less oval-shaped; foramen magnum comparatively much smaller; in lateral view, one foramen n. optici, equal in size with fonticuli orbitocraniales; and processus postorbitalis sharply pointed.

Rostrum: much wider, narial openings more circular; os nasale comparative narrower.

Mandible: narrower, processus retroarticularis more distinct; and fenestra rostralis mandibulae much smaller.

Scapula: longer with more expansion of margo dorsalis; facies articularis clavicularis extends further dorsad.

Coracoid: overall much more robust, processus lateralis more expanded; facies articularis clavicularis less sharply hooked; in dorsal surface, processus procoracoideus less distinct.

Humerus: more robust with more curved shaft; caput humeri less bulbous; tuberculum ventrale more reduced; one pneumatic fossae; pneumatic fossa I separated from pneumatic fossa II by a septum; crista deltopectoralis extends further distad; incisura capitis less deeply excavated.

Figure 6: Comparison of humeri (right side, except for H. olivaceus, left side reversed) of Hypsipetes bulbul, caudal aspect. (a) MNHN MAD7127 Hypsipetes olivaceus u/s; (b) FLMR 569 Hypsipetes cowlesi sp. nov. u/s; (c) NHMUK1897.5.10.6 Hypsipetes madagascariensis u/s. Scale bar = 10 mm
Ulna: similar, but more expanded on proximal end; papillae remigales caudales less sharply defined.

Radius: shorter, shaft more robust, ridge on lineae intermuscularis more distinct.

Carpometacarpus: processus extensorius longer and sharper; in ventral aspect, facies articularis digitalis major less pronounced.

Femur: shorter, less robust, particularly at proximal and distal ends; in caudal aspect, condylus lateralis much less directed caudally.

Tibiotarsus: much shorter and less robust, especially at proximal and distal ends, otherwise similar.

Tarsometatarsus: comparatively gracile, especially in shaft and distal end; foramen vasculare distale smaller, less distinct.

Figure 7: Comparison of ulnae (left side) of Hypsipetes bulbuls, ventral aspect. (a) MNHN MAD8856 Hypsipetes olivaceus u/s; (b) NHMUK S/1978.14.64 Hypsipetes cowlesi sp. nov. u/s; (c) NHMUK1897.5.10.6 Hypsipetes madagascariensis u/s. Scale bar = 10 mm
Mauritius Bulbul Hypsipetes olivaceus Jardine & Selby, 1837

Holotype
NHMUK 1886.6.24.254 unsexed.

Diagnosis
As for genus.

Type locality and horizon
Mauritius, Mascarene Islands, south-western Indian Ocean

Dimensions
See Table 1.

Etymology
From Latin olivaceus, olive-green, in reference to the colouration of the plumage.

Description and comparison
Hypsipetes olivaceus is morphologically similar to H. borbonicus of Réunion in the skeleton, but generally larger and more robust, especially in the femur, tibiotarsus and tarsometatarsus (Table 1). In the living bird, it is considerably larger and heavier, with a longer bill (Safford and Hawkins 2013). H. olivaceus is much larger and more robust in all skeletal elements compared with H. madagascariensis, and differs from H. crassirostris in being generally smaller in all cranial and post-cranial elements except the tarsometatarsus.

Referred fossil material
As no modern skeletal material of the Mauritius bulbul Hypsipetes olivaceus was available, subfossil remains collected by Etienne Thirioux in undisclosed caves and boulder scree in the valleys of Le Pouce and the Vallée des Prêtres, central-east Mauritius and in the Mare aux Songes fossil locality, south-east Mauritius (see Hume 2013) were used for comparative purposes: Rostrum, UMZC 593; Mandible, MNHN MAD6931; Coracoid, UMZC 593; MNHN MAD8839 (L); MNHN MAD8839 (L); MNHN MAD8839 (L); MNHN MAD8839 (L); MNHN MAD8839 (L); MNHN MAD8839 (L); MNHN MAD8839 (L); MNHN MAD8839 (L); MNHN MAD8839 (R); Humerus, MNHN MAD7127 (L); MNHN MAD7127 (L); MNHN MAD7127

Figure 8: Comparison of carpometacarpi (left side) of Hypsipetes bulbuls, ventral aspect. (a) NHMUK S/1978.14.60 Hypsipetes cowlesi sp. nov. u/s; (b) NHMUK1897.5.10.6 Hypsipetes madagascariensis u/s. Scale bar = 10mm
Remarks
The Mauritius Bulbul is presently restricted to the montane forests of south-east, central and south-west Mauritius (Safford and Hawkins 2013), and subfossil remains have been found in the mountain valleys of the central-east and in the Mare aux Songes fossil locality in the coastal south-east. It was formerly much more widespread (Cheke 1987; Cheke and Hume 2008); therefore, the present distribution is presumably an artefact of human interference, with surviving populations being restricted to the last remaining forest tracts.

Réunion Bulbul Hypsipetes borbonicus (J.R. Forster, 1781)

Holotype
Present whereabouts unknown.

Diagnosis
As for genus.

Type locality and horizon
Réunion, Mascarene Islands, south-western Indian Ocean

Dimensions
See Table 1.

Etymology
From borbonicus, Île de Bourbon (= Île de la Réunion = Réunion), after the island of Réunion. Bourbon was the original name of the island.
Table 1: Measurements of the subfossil remains of *Hypsipetes cowlesi* sp. nov. compared with other south-western Indian Ocean *Hypsipetes* taxa and continental *Hypsipetes leucocephalus* psaroides and *H. l. concolor*. For osteological measurement abbreviations, see Methods. For statistical abbreviations: *n* = number of specimens, *m* = mean, *SD* = standard deviation

(a) Measurements (mm) of the cranium of *Hypsipetes cowlesi* nov. sp. compared with other Indian Ocean island *Hypsipetes* bulbuls. For abbreviations, see Methods

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<th>Species</th>
<th>TL (n) range</th>
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<th>GW (n) range</th>
<th>GW (m) SD</th>
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<td>(14.7)</td>
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(b) Measurements (mm) of the mandible of *Hypsipetes cowlesi* nov. sp. compared with other Indian Ocean island *Hypsipetes* bulbuls. For abbreviations, see Methods

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(c) Measurements (mm) of the scapula of *Hypsipetes cowlesi* nov. sp. compared with other Indian Ocean island *Hypsipetes* bulbuls. For abbreviations, see Methods

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(d) Measurements (mm) of the coracoid of *Hypsipetes cowlesi* nov. sp. compared with other Indian Ocean island *Hypsipetes* bulbuls. For abbreviations, see Methods

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Table 1: (cont.)

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(g) Measurements (mm) of the radius of Hypsipetes cowlesi nov. sp. compared with other Indian Ocean island Hypsipetes bulbuls. For abbreviations, see Methods.

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<th>DW (m) range</th>
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(h) Measurements (mm) of the carpometacarpus of Hypsipetes cowlesi nov. sp. compared with other Indian Ocean island Hypsipetes bulbuls. For abbreviations, see Methods.

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<th>Species</th>
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<td>(2) 2.7 (2)</td>
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(i) Measurements (mm) of the tarsometatarsus of Hypsipetes cowlesi nov. sp. compared with other Indian Ocean island Hypsipetes bulbuls. For abbreviations, see Methods.

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<td>Hypsipetes olivaceus</td>
<td>(3) 26.5–27.4 (27.0)</td>
<td>(3) 1.9 (3)</td>
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<tr>
<td>Hypsipetes cowlesi</td>
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<td>(1) 1.9 (2)</td>
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</table>

Description and comparison

Hypsipetes borbonicus is smaller in both body size and weight (Safford and Hawkins 2013) in the living bird than H. olivaceus, and the skeletal elements average smaller, especially in the bones of the leg (Table 1). It is much smaller than H. crassirostris, being approximately equal in size cranially with H. madagascariensis, but differs from the latter in having longer wing elements and a much larger, more robust tarsometatarsus.

Referred fossil material

None known.

Remarks

Due to the paucity of fossil material on Réunion (Hume 2013), fossil remains of the bulbul have yet to be found. The Réunion species is presently considered not threatened (Safford and Hawkins 2013), and survives in numbers where the original forest still persists.
†Rodrigues Bulbul Hypsipetes cowlesi sp. nov.

Holotype
FLMR 273 cranium (Fig. 3), missing the right extremity of the nasofrontal ridge and os lacrimale, and right side of the frontal/squamosal.

Paratypes
Subfossil material collected from specified and unspecified caves: Mandible FLMR u/r; FLMR 517 (Caverne Bambara I); Scapula NHMUK u/r (Rp) (Caverne Gastonia); Coracoid FLMR 600 (R); NHMUK S/1978.14.61 (L); NHMUK S/1978.14.62 (L); NHMUK 1978.14.63 (R); Humerus FLMR 569 (R) (Caverne Bambara I); FLMR 435 (R) (Caverne de la Vierge); Ulna NHMUK S/1974.14.64 (L); NHMUK u/r (R); Radius NHMUK u/r (R) (Caverne l’Affouche); Carpometacarpus NHMUK S/1978.14.60 (L); FLMR 284 (R) (Level 2, Caverne Tortue); Tarsometatarsus FLMR 529 (Ld) (Caverne Bambara I); NHMUK u/r (L) (Caverne Bambara I).

Cowles (1987: 99) wrote that ‘bones representing a new species of extinct bulbul have been identified from collected material in 1974.’ This comprised the three coracoids, ulna and carpometacarpus NHMUK registrations listed above. The holotype was collected by the S.E.S.C.R. (Société d’Etudes Scientifiques des Cavernes de la Réunion) in Caverne Bambara I (see below). The proximal scapula fragment (NHMUK u/r, Figure 5a) was collected by the author in Caverne Gastonia on the surface approximately 5 m from the cave entrance. The humerus (FLMR 569; Figure 6) and tarsometatarsus (FLMR 529; Figure 9) were collected by the author and by palaeontologist Lorna Steel in Caverne Bambara I near the cave entrance in Square A2, and at a depth of 0–300 and 600–900 mm, respectively. They were found with the remains of White-tailed Tropic Bird Phaethon lepturus Daudin, 1802; Rodrigues Night Heron Nycticorax megacephalus (Milne-Edwards, 1874); Rodrigues Solitaire Pezophasus solitarius (Gmelin, 1788), Rodrigues Parakeet Psittacula exsul (Newton, 1872); Rodrigues Lizard Owl Mascarenornis murivorus (Milne-Edwards, 1874); Rodrigues Starling Nesophaerodrbericanus Günther & Newton, 1879; Rodrigues Fruit Bat Pteropus rodricensis Dobson, 1878; Saddleback Giant Tortoise Cylindraspis vosmaeri (Fitzinger, 1826); Rodrigues Day Gecko Phelsuma edwardnewtoni Vinson & Vinson, 1969; and various fish bones; the last-mentioned brought into the caves by nesting tropic birds.

Diagnosis
As for genus.

Type locality and horizon
Rodrigues Island, Mascarene Islands, south-western Indian Ocean. Collected in 1999 by S.E.S.C.R. in Caverne Bambara I (19°45.273’ S, 63°22.132’ E), Plaine Corail. Rodrigues is a basaltic island, but has a small covering of calcarenite (lithified calcareous sand dunes) called the Plaine Corail, covering an area of approximately 3 km² in the south-western corner of the island (Saddul 2002). There are at least 30 fossil-rich caves found within the Plaine Corail region (Hume 2005, Hume et al. 2015).

Dimensions of holotype
Cranium FLMR 273: total length 24.2 mm; greatest width ~19.0 mm; greatest depth 15.3 mm; width of nasofrontal hinge ~13.0 mm.

Dimensions of paratypes
See Table 1.

Etymology
Named after Graham S Cowles, former keeper of the bird collections at the Natural History Museum, Tring, who first brought this taxon to the attention of the ornithological community (Cowles 1987), and in honour of his work on Mascarene Island fossil birds (Cowles 1994).

Description and comparison
Hypsipetes cowlesi differs from Mascarene other south-western Indian Ocean Hypsipetes by the following characters:

Cranium (Figure 3): overall smaller than H. crassirostris; in dorsal view, similar to H. borbonicus but averages larger; differs from H. madagascariensis in nasofrontal hinge more deeply excavated; prominentia cerebellaris more prominent; in lateral view, processus postorbitalis more elongate.

Mandible (Figure 4): larger than H. madagascariensis; shorter in total length and less deep compared with Mascarene Hypsipetes and H. crassirostris; single fenestra rostralis mandibulae smaller.

Scapula (Figure 5a): morphologically similar, but smaller than H. crassirostris and H. borbonicus; facies articularis and facies articularis humeralis more robust than H. madagascariensis.

Coracoid (Figure 5b): similar in morphology and total length, but more gracile in shaft and distal width than all other Hypsipetes examined; much smaller than H. crassirostris.

Humerus (Figure 6): smaller than H. borbonicus and H. crassirostris, otherwise similar, larger than H. madagascariensis with shaft narrower proximal to distal end.

Radius (Figure 7): smaller than H. crassirostris and H. borbonicus, equal in size with H. olivaceus, otherwise similar; longer in total length than H. madagascariensis; olecranon sharper, less pronounced; incisura tuberculorum more deeply excavated; sulcus intercondylaris more deeply incised.

Radius: differs from H. crassirostris and H. borbonicus in its smaller size; equal in total length with H. madagascariensis, but overall less robust.

Carpometacarpus (Figure 8): much smaller than H. crassirostris, equal in size with H. olivaceus and H. borbonicus; slightly larger than H. madagascariensis; processus extensorius more rounded; os metacarpale minus extends less distal, otherwise similar.

Tarsometatarsus (Figure 9): smaller and less robust than H. crassirostris and H. olivaceus, similar in size to H. borbonicus; trocleae less expanded latero-medially;
foramen vasculare distale smaller; much larger and much more robust than *H. madagascariensis*.

**Discussion**

The two surviving *Hypsipetes* species on Mauritius and Réunion differ genetically (Warren et al. 2005), and significantly in size, weight and colouration (Cheke 1987; Safford and Hawkins 2013); thus they have been given full specific status (Dowsett and Forbes-Watson 1993). However, the size differences are much less striking when comparing the skeleton. Apart from the coracoid, humerus and ulna in *H. borbonicus* and the mandible and tarsometatarsus in *H. olivaceus*, *H. cowlesi* is approximately equal in skeletal element size (see Table 1), and therefore would have been approximately the same size as the other large Mascarene bulbuls in life at 22–24 cm in total length.

The Indian Ocean island greenish bulbuls form part of several independent colonisations that arose from a small grey ancestor from Asia within the last 2.6 My, followed by a rapid expansion across their current range (Louteau and Herremans 1985; Warren et al. 2005); therefore the greenish colouration exhibited in different species is due to convergence and not especially to close relationship. Furthermore, Warren et al (2005) have shown that the large body-sized, greenish *H. olivaceus* of Mauritius is sister to the small body-sized, grey Madagascar Bulbul *H. madagascariensis*, and not part of the same lineage that gave rise to the small body-sized, greenish *H. borbonicus* of Réunion. Based on the available evidence, therefore, it cannot be stated with any certainty as to which of the extant Mascarene bulbuls the Rodrigues Bulbul was more closely related.

**Ecology**

The Mascarene Islands were heavily forested before the arrival of humans in the late fifteenth century (Cheke and Hume 2008), which would have provided suitable habitat for bulbuls over much of the land surface area. The surviving Mascarene bulbuls are almost entirely arboreal, rarely obtaining food from the ground (Cheke 1987), and they generally forage in evergreen forest on fruits, insects and small vertebrates, especially *Phelsuma* geckos (Safford and Hawkins 2013); the last-named make up 30% of the diet on Mauritius (Safford 1996). Rodrigues once harboured a diverse geckonid fauna, including two large *Phelsuma* species, *Phelsuma gigas* (Liénard, 1842) and *P. edwardnewtoni*, the nocturnal Mourning Gecko *Lepidodactylus lugubris* (Duméril & Bibron, 1836), while a further four await description (Arnold 2000). Some of these would have provided abundant and suitable prey items for the Rodrigues bulbul. On Mauritius and Réunion, bulbuls take fruits from many species of forest trees, palms and shrubs, but they are especially fond of the fleshy fruit of the forest tree, fandamane *Aphloia theiformis* (*Aphloiceae*) (Cheke 1987; Safford and Hawkins 2013). Fandamane was once an abundant component of Rodrigues forests, growing on all substrates, but was last recorded there in 1949, after being considered rare for over a century (Balfour 1879; Strahm 1989).

**Extinction**

Bulbuls or merles, as they are known locally, were one of the few passerines mentioned in the early literature of the Mascarenes, primarily because of their culinary qualities (Cheke and Hume 2008). As a result they have been heavily persecuted as a food item, and have declined due to severe deforestation and predation by introduced mammals, particularly rats, the Mauritius Black Bulbul especially so (Cheke 1987; Cheke and Hume 2008; Safford and Hawkins 2013). The Black Rat *Rattus rattus* (Linnaeus, 1758) appears to be one of the main factors affecting all bulbul populations elsewhere in the Indian Ocean. For example, although the Aldabra Bulbul *H. madagascariensis rostratus* (Ridgway, 1893) remains common, breeding success is apparently extremely low with almost no young reaching adulthood (Safford and Hawkins 2013); this is almost certainly due to black rat predation (Prŷs-Jones and Diamond 1984). However, despite the threats facing other *Hypsipetes* bulbuls, *H. cowlesi* represents the only documented case of a *Hypsipetes* bulbul extinction in historical times.

The Rodrigues Bulbul was not mentioned by Francois Leguat in 1691–1693 (Leguat 1708) or Julien Tafforet in 1725–1726 (Tafforet c. 1725–1726), who both gave comprehensive accounts of the fauna. The black rat was already a pest at the time of their stay on Rodrigues, having been introduced c. 1675 or perhaps much earlier (Cheke and Hume 2008; Hume 2013), and both noted that some of the landbirds were restricted to offshore islands, coming to the mainland only to drink water (Hume 2007, 2011, 2014). Cats were introduced in c. 1745 to control rats, but turned their attention instead on the native birds and juvenile tortoises (Cheke and Hume 2008). However, it is very likely that rats solely eliminated the Rodrigues Bulbul either before the visit of Leguat in 1691–1693, or by the time of Tafforet’s visit in 1725–1726, as deforestation was still negligible at this time. However, had the Rodrigues Bulbul survived into the eighteenth century, the decline of fruiting trees such as fandamane, and the extinction of all Rodrigues native reptiles, may also have impacted on their numbers.

The discovery of subfossil remains of a *Hypsipetes* bulbul on Rodrigues fills in a hitherto perplexing biogeographical gap, as this genus occurs on the two neighbouring Mascarene Islands. This has important implications for our understanding of avian biogeography within the Malagasy region (see Hume 2013), and further exemplifies the need to investigate similar scenarios palaeontologically, before any robust biogeographical conclusions are attempted.

In general, *Hypsipetes* bulbuls have survived the negative impact of anthropogenic interference, and some have even adapted to human-modified habitats (Safford and Hawkins 2013), whereas the Rodrigues Bulbul probably became extinct within a comparatively short time. This is most likely due to the small size of the island and its comparatively flat topography. In contrast, the larger size and the higher mountain ranges of Mauritius and Réunion have provided long-term refugia for bulbuls, thus ensuring their continued survival.

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References


