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# ZOOTAXA

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**Systematics, morphology, and ecological history of the Mascarene starlings  
(Aves: Sturnidae) with the description of a new genus and species from Mauritius**

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**Systematics, morphology, and ecological history of the Mascarene starlings (Aves: Sturnidae) with the description of a new genus and species from Mauritius**

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## Table of contents

|   |    |
|---|----|
| Abstract  | 3  |
| Introduction  | 3  |
| Material and methods  | 5  |
| Systematics   | 8  |
| Class Aves  | 8  |
| Order Passeriformes   | 8  |
| Family Sturnidae  | 8  |
| Genus <i>Fregilupus</i> Lesson, 1831  | 8  |
| †Réunion Crested Starling, Huppe or Hoopoe Starling <i>Fregilupus varius</i> (Boddaert, 1783) | 10 |
| Genus <i>Necropsar</i> Günther & Newton 1879  | 44 |
| †Rodrigues Starling <i>Necropsar rodericanus</i> Günther & Newton, 1879                       | 45 |
| Genus <i>Cryptopsar</i> gen. nov.   | 51 |
| †Mauritius Starling <i>Cryptopsar ischyrrhynchus</i> sp. nov.                                 | 52 |
| Conclusions   | 55 |
| Acknowledgements  | 59 |
| References  | 59 |
| Appendix  | 65 |

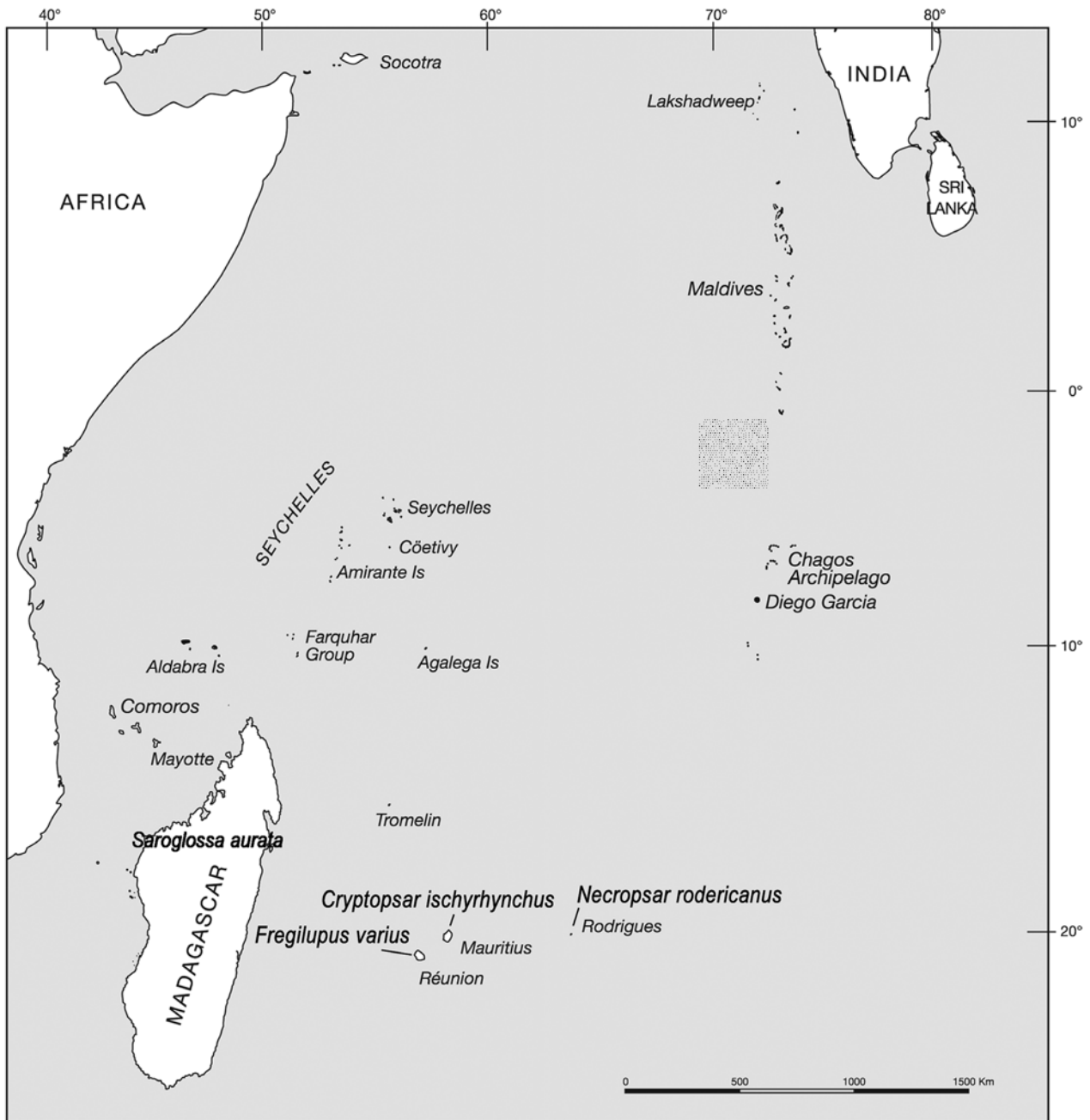
## Abstract

Two endemic starlings, both extinct, have been described from the Mascarene Islands of Réunion and Rodrigues: the Hoopoe Starling, Huppe or Réunion Crested Starling *Fregilupus varius*, which is known from 19 skins and a single Holocene proximal end of a fossil femur, and the Rodrigues Starling *Necropsar rodericanus*, which is known as specimens only from fossils of most skeletal elements. Both were recorded alive in early accounts of Mascarene faunas. A third species of starling *Cryptopsar ischyrrhynchus* **gen. nov. sp. nov.** is described herein from fossils from Mauritius, but was never reported in the early literature. This paper provides an analysis of the Sturnidae of the Mascarene Islands based on newly discovered fossil remains, and details historical reports and accounts. Their ecology and extinction are interpreted from historical evidence. *Necropsar*, *Cryptopsar* and *Fregilupus* clearly form part of the same clade, but morphological analysis shows that *Necropsar* and *Cryptopsar* are more closely related to each other than to *Fregilupus* and may have been part of a different colonisation event. All three genera appear to have their origins in SE Asia and have morphological similarities with the SE Asian sturnid genera, *Sturnia* and *Gracupica*, so they presumably colonised the islands via island-hopping during lower sea level stands.

**Key words:** Mascarene starlings, Sturnidae, *Fregilupus*, *Necropsar*, *Cryptopsar*, extinction, affinities, ecology

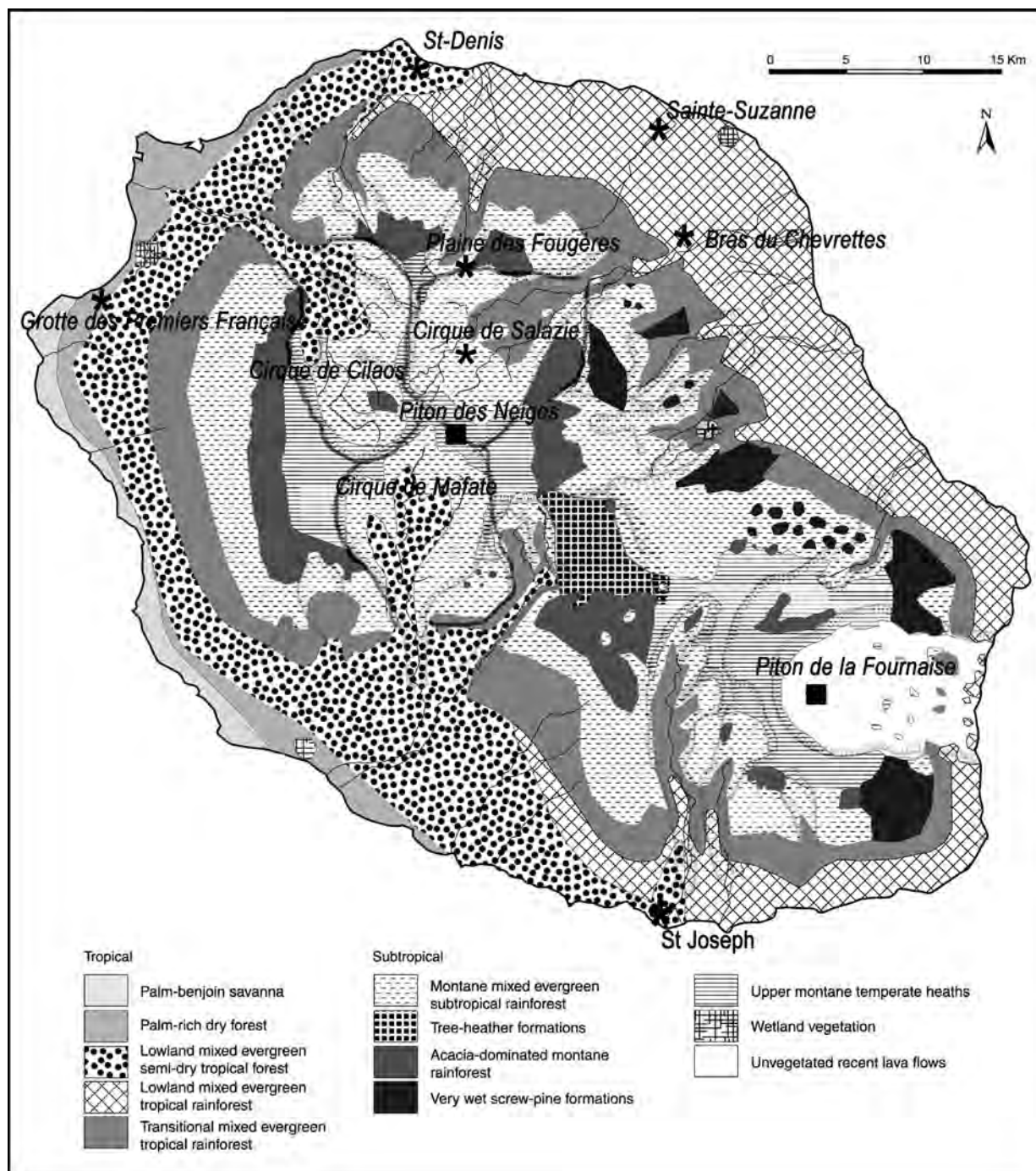
## Introduction

The starlings are a wide-ranging group of birds restricted to the Old World and have been divided into 32 genera (Craig & Feare 2009). They are extremely varied in plumage colouration and morphology, and some species are strikingly sexually dichromatic. The greatest diversity occurs in the Indo-Malayan and Afro-tropical regions, whereas only a few genera have colonised the Southwest Indian Ocean islands (Fig. 1). Two distinct, but now extinct starlings were described from the Mascarene Islands of Réunion (21° S, 55.5° E) (Fig. 2) and Rodrigues (19.75° S, 63.5° E) (Fig. 3). A third species of starling, endemic to Mauritius (20.25° S, 57.5° E) (Fig. 4), is described herein. The Réunion Crested Starling (or Bourbon Crested Starling, after the former name of the island), Hoopoe Starling, or Huppe, *Fregilupus varius* Boddaert, 1783 (Figs. 5, 6, 7, 8), last reported c.1860, is known from 19 museum skins and from a single fragment of fossil femur collected from a cave deposit on Réunion (Mourer-Chauviré *et al.* 1999). The Rodrigues Starling, *Necropsar rodericanus* Günther & Newton, 1879, last reported 1725–26, was described from subfossil remains collected by George Jenner and Henry. H. Slater during the 1860s and early 1870s (Günther & Newton 1879). The Réunion Crested Starling was mentioned a number of times by early visitors to the island (Cheke & Hume 2008), whereas the Rodrigues Starling was described only once (Hume & Walters 2012). The Mauritius Starling is known from Holocene fossil remains only.



**FIGURE 1.** Islands of the western Indian Ocean showing the Mascarene Islands of Réunion, Mauritius and Rodrigues and Madagascar with the distribution of starlings.

This paper synthesizes data from all available sources on Mascarene sturnids, including historical observations and accounts, and palaeontological material. Comparisons using morphometric data based on osteology and external morphology are also presented here. As *Fregilupus* and *Necropsar* are known from historical records, the texts of relevant historical accounts that mention them are included, particularly those for which no previous English translations exist. *Fregilupus varius* is known from numerous skins, but because their collecting history is complex, they will be dealt with elsewhere (Hume & Violani in prep).



**FIGURE 2.** Detail of Réunion and original vegetation, showing the place names mentioned in the text, and the historical distribution of *Fregilupus*\* based on early accounts (adapted from Cheke & Hume 2008).

## Material and methods

**Abbreviations.** Institutions: AMNH, American Museum of Natural History, New York; FLMR Francois Leguat Museum, Rodrigues; NHMUK, Natural History Museum, London and Tring, (formerly BMNH, British Museum (Natural History)); WML Liverpool World Museum; MCZH Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MNHN, Muséum National d’Histoire Naturelle, Paris, with the prefix MAD for Madagascar, e.g. MNHN MAD7142; MU, Mauritius Institute; MHNT Muséum d’histoire naturelle de Troyes; RMNH Naturalis, Leiden; UMZC, University Museum of Zoology, Cambridge, England; UCB, Université Claude-Bernard-Lyon I; USNM, National Museum of Natural History, Washington, D. C.

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.

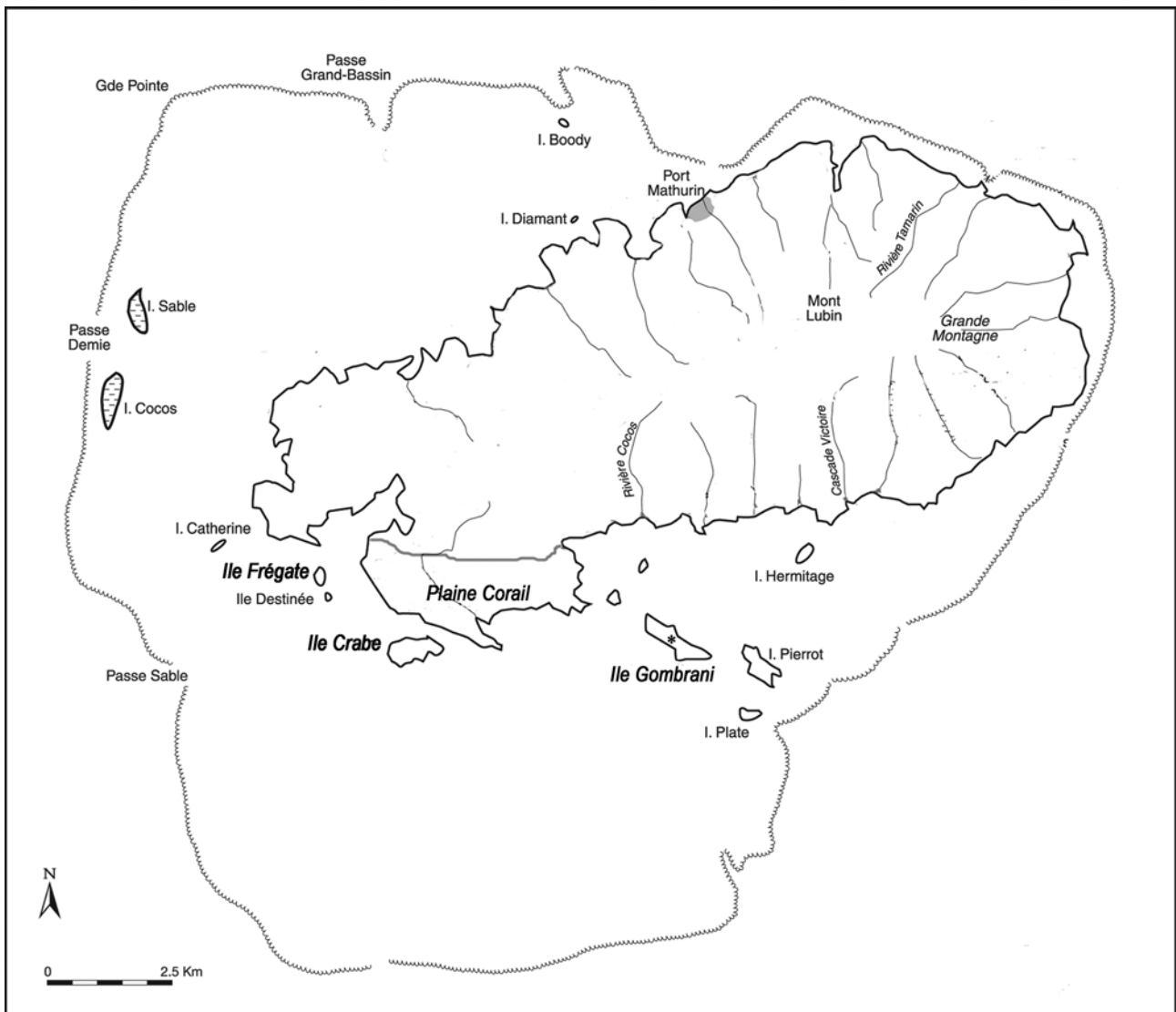
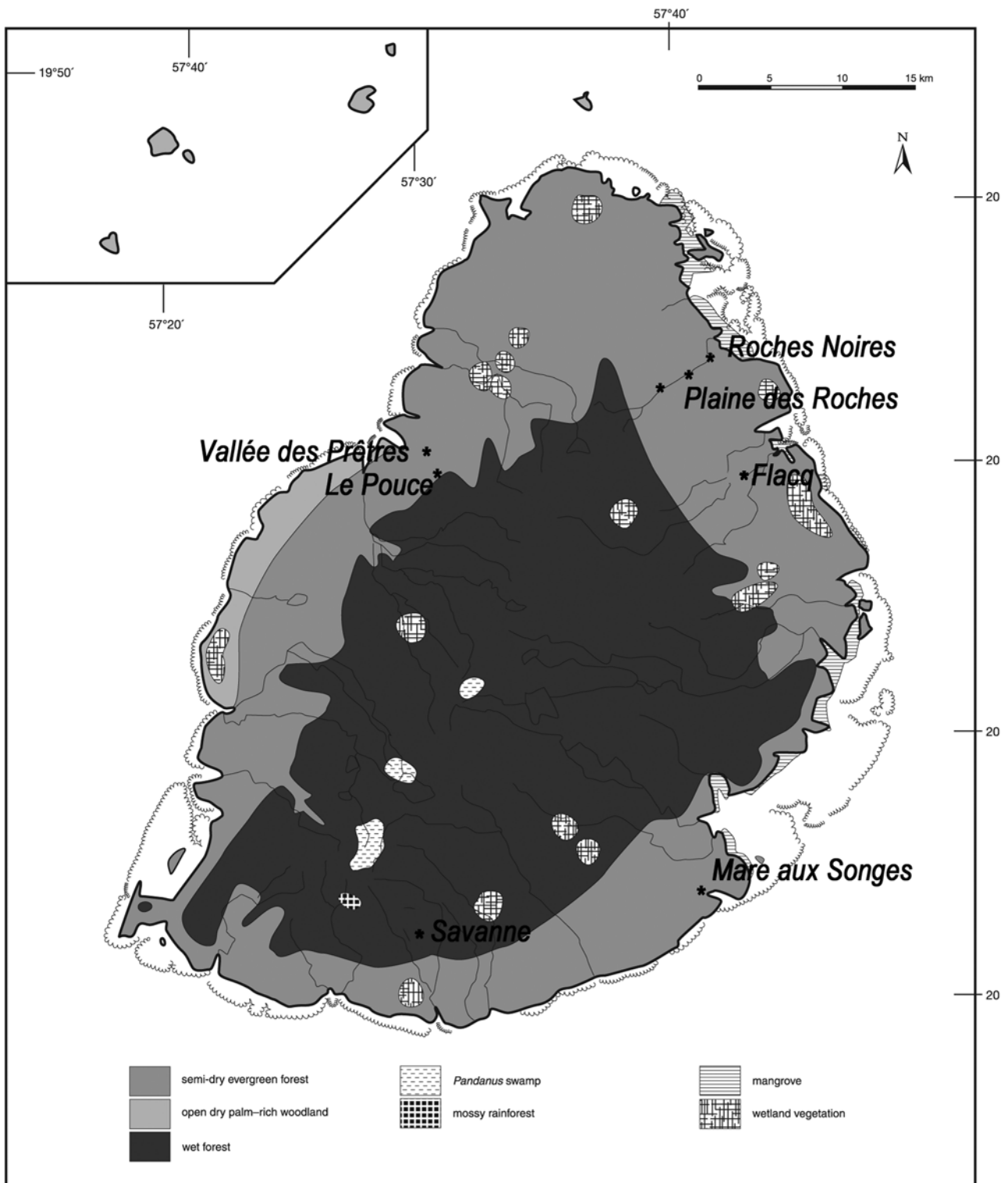


FIGURE 3. Detail of Rodrigues, showing the place names mentioned in the text (adapted from Cheke & Hume 2008).

**Comparative material examined.** The starling genera *Saroglossa*, *Sturnia*, *Gracupica* and *Leucopsar* were used in the comparative analysis, as they represent either biogeographically closely related species, *Saroglossa aurata* of Madagascar, or are from Southeast Asia, the likely founding source of the Mascarene starlings. *Acridotheres tristis* was also compared as it has been introduced to all three Mascarene Islands and some of its post-cranial skeletal elements can be confused with the endemic starling genera. The Eurasian Hoopoe *Upupa epops* was used for comparisons with *Fregilupus varius*, as the latter species was often considered to be related.

The following skeletal specimens were used, all held in the AMNH, UMZC and NHMUK bird skeleton collections, with registration number and sex provided for each. No skeleton of the Madagascan Starling *Saroglossa aurata* was available, so a specimen of the closely related Spot-winged Starling *S. spiloptera* was used instead for comparative purposes. Nomenclature follows Dickinson (2003), Lovette et al (2008) and Zuccon et al (2008): *Upupa epops* NHMUK S/1968.6.8 ♂; NHMUK S/1961.13.6 ♂; *Fregilupus varius* AMNH 23858 ♂; UMZC 448.cc u/s; *Gracupica nigricollis* NHMUK 1869.10.19.15 u/s; *Gracupica contra* AMNH 23006 ♂; *Saroglossa spiloptera* NHMUK S/1956.15.1 ♂; *Sturnia malabarica* NHMUK S/2004.21.1 u/s; NHMUK S/1987.15.15 u/s; NHMUK S1987.15.14 u/s; *Sturnia sinensis* NHMUK S/2007.119.1 u/s; *Acridotheres burmannicus leucocephalus* AMNH 3562 u/s; *Acridotheres melanopterus* AMNH 5893 u/s; *Acridotheres tristis* NHMUK S/1998.92.28 ♀; NHMUK S/1957.15.10 u/s; NHMUK S/1957.15.9 u/s; NHMUK S/1973.66.151 u/s; NHMUK S/

1980.8.2 ♀; NHMUK S/1986.75.53 u/s; NHMUK S/1986.75.52 u/s; NHMUK S/1986.75.51 u/s; *Leucopsar rothschildi* AMNH 23127 u/s; AMNH 22721 ♂; NHMUK S/1982.13.2 u/s; NHMUK S/1982.150.2 ♀; *Sturnus vulgaris* NHMUK S/1973.29.14 ♂.



**FIGURE 4.** Detail of Mauritius and original vegetation, showing the place names mentioned in the text (adapted from Cheke & Hume 2008). The district of Flacq (near NE coast) is where Desjardins maintained his aviary with captive *Fregilupus* from Réunion, and Savanne (bottom centre) is where an escapee from Desjardins aviary was taken in late 1836, the last unequivocal specimen record.

The following skin specimens were used, all held in the NHMUK, MNHN, and MHNT bird collections, with registration number and sex provided for each: *Sturnia erythropygia andamanensis* NHMUK 1955.6.3.28 ♂; NHMUK 1955.6.3.27 ♀; *Sturnia erythropygia erythropygia* NHMUK 1898.4.28.38 ♂; NHMUK 1898.4.28.40 ♀; *Acridotheres melanopterus melanopterus* NHMUK 1959.28.8 ♂; NHMUK 1959.28.11 ♀; *Leucopsar rothschildi* NHMUK 1969.41.8.20 ♂; NHMUK 1937.11.4.1 ♀; NHMUK 1937.11.4.1 juvenile u/s; *Gracupica nigricollis* NHMUK 1915.12.18.105 ♂; NHMUK 1955.1.3651 ♀; *Fregilupus varius* NHMUK 1889.5.30.15 u/s; MNHN 2000-755 u/s; MNHN 2000-756 u/s; MNHN 3709 u/s; MNHN u/s; MHNT O2647 u/s; MHNT O2648 u/s; MHNT O2649 u/s; MHNT O2650 u/s.

**Measurements.** All measurements were made using dial calipers and rounded to the nearest 0.1mm. TL = total length: cranium, from naso-frontal hinge to margin of crista occipital in a median plane; rostrum, from naso-frontal hinge to tip of rostrum maxillare in dorsal aspect; 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; sternum, from anterior tip of spina externa to margo caudalis in a median plane; humerus, radius and ulna, measured in dorsal aspect, carpometacarpus, measured in ventral aspect; pelvis, from anterior edge of ala preacetabularis to posterior edge of ala postacetabularis ilii; femur and tibiotarsus, measured in cranial aspect; tarsometatarsus, measured in dorsal aspect. WNF = width of naso-frontal hinge. PML = premaxilla length, measured in ventral aspect; LN = length of nasal opening, taken in lateral view. RMW = rostrum mandibulae width, taken in a lateromedial plane at the anterior point of the nasal opening. RMD = rostrum mandibulae depth, taken in a dorsoventral plane at the anterior point of the nasal opening. RML = rostrum mandibulae length, taken in a dorsoventral plane at the anterior point of the nasal opening to tip. LC = greatest length of carina sterni, from apex carinae to margo caudalis of sternum. DK = greatest depth of keel, taken from facies muscularis sterni to apex carinae. LW = least width; pelvis, measured between ala preacetabularis ilii anterior to sulcus antitrochantericus. PW = proximal width; taken in a lateromedial plane: mandible, taken 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; pelvis, taken between ala postacetabularis ilii. GD = greatest depth: cranium from medial point of parietal to medial ventral surface; pelvis, taken between ventral surface of processus terminalis ischii and posterior dorsal surface. PD = proximal depth, taken in a dorsoventral plane; carpometacarpus, proximal end from processus extensorius to caudal margin of trochlea carpalis; pelvis, taken between crista iliaca dorsalis and extremitas cranialis synsacri; 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 & Witmer (1993).

**Etymology.** Etymologies of Mascarene sturnids are given in their entirety, either from Jobling (1991, 2009) or from lexicographical sources for fossil species.

## Systematics

### Class Aves

### Order Passeriformes

### Family Sturnidae

### Genus *Fregilupus* Lesson, 1831.

*Fregilupus* Lesson, 1831, p.324. Type (by monotypy): *Upupa capensis* Gmelin = *Upupa varia* Boddaert.  
*Lophopsarus* Sundeval, 1872, p.40. Type: *Upupa varia* Boddaert.

**Etymology.** A composite word from the old genus *Fregilus* Cuvier, 1817, chough (now *Pyrrhocorax*), and *Upupa* Linnaeus, 1758, hoopoe), from the curved bill of the Réunion crested starling, which by early settlers on the island was called *Huppe* (hoopoe) from its crest and stout curved bill.

**Revised Diagnosis.** Only the relevant skeletal elements of *Fregilupus* are described here. For further



descriptions of cranial and post-cranial material, see Murie (1874), Milne-Edwards & Oustalet (1893), Berger (1957), Bock (1962) and Morioka (1996). *Fregilupus* is distinguished from other Mascarene sturnids by the following characters:

*Cranium*: in dorsal view, rounded, somewhat bulbous posteriorly; frontal narrow; in posterior view, crista nuchalis transversa rounded with distinct prominentia cerebellaris; foramen magnum large; in lateral view, foramen. n. optici small, almost equal in size to fonticuli orbitocraniales; processus postorbitalis elongate.

*Rostrum*: long and narrow with narrow, oval-shaped narial openings; rostrum maxillare narrow and strongly decurved.

*Mandible*: rostrum mandibulae narrow and sharply pointed; processus mandibulae medialis small; processus retroarticularis distinct; single large fenestra rostralis mandibulae.

*Sternum*: short and wide, particularly at caudal end; processus cranio-lateralis long and blade-like; spina externa bifurcated, projections narrow; in lateral view, apex carinae reduced; carina sterni shallow; in dorsal view, trabecula intermedia the same distal extent as margo caudalis; fenestra medialis reduced.

*Coracoid*: comparatively reduced in total length; shaft robust.

*Humerus*: robust with straight shaft; proximal and distal ends cranio-caudally flattened; tuberculum ventrale reduced; two pneumatic fossae; pneumatic fossa II completely enclosed and separated from pneumatic fossa I by medial bar; small circular depression on proximal side of tuberculum ventrale; processus supracondylaris dorsalis small with little proximad extension; crista deltopectoralis reduced, shallow in dorsal view.

*Radius*: robust; facies articularis radiocarpalis distinctly indented.

*Ulna*: impressio brachialis reduced.

*Carpometacarpus*: processus extensorius blunt.

*Pelvis*: extremely robust; ala preacetabularis ilii narrow; ala ischii broad; fenestra ischiopubica large and oval-shaped.

*Femur*: robust, particularly at proximal and distal ends; shaft straight with little expansion proximad and distad of mid-length; sulcus intercondylaris deeply excavated; facies articularis acetabularis large; in cranial aspect, sulcus patellaris indistinct proximal to condyles.

*Tibiotarsus*: long and robust; shaft broad and expanded, particularly near distal end; tuberculum retinaculi m. fibularis indistinct; crista cnemialis cranialis broad and expanded; impressio ligamenti collateralis medialis deep emphasising a ridge distal to crista cnemialis cranialis.

*Tarsometatarsus*: long and robust; shaft comparatively straight; trochleae not expanded lateromedially; impressio retinaculi extensorii with small bridge; crista medialis hypotarsi large and expanded distad; foramen vasculare distale large and distinct; in dorsal aspect, distinct proximal ridge on facies dorsalis; proximal extension of fossa metatarsi I lacking medial ridge; in plantar view, trochlea metatarsi III distinctly larger than trochlea metatarsi II; fossa parahypotarsalis medialis not situated in deep groove.

**Remarks.** There has been considerable confusion over the affinities and provenance of *Fregilupus*. The first account supposedly to mention the bird was penned by Flacourt (1658: 166) in his list of birds of Madagascar, where he described a bird called the Tivouch (Tiuouch). He merely stated: "Tivouch is the hoopoe, it is speckled black and grey, and has a beautiful feathered crest (my translation)." Newton (in Murie 1874) doubted that this was referable to *Fregilupus*, and considered it to be a description of a true *Upupa*, the Madagascar Hoopoe *Upupa epops marginata*, which is barely distinct from the Eurasian nominate, *Upupa e. epops*. *Fregilupus* was also called the Huppe (=Hoopoe) by the local inhabitants of Réunion, due to its morphological similarities with the Eurasian hoopoe (long, decurved bill and crest). That *Fregilupus* was thought to occur in the Cape and Madagascar is based in part on mistakes by De Montbeillard (in Buffon 1779: 463) and Levaillant (1807: 43), who both believed that the Tivouch was referable to *Fregilupus*. This erroneous provenance was followed by all subsequent authors, until Vinson (1868: 627) asserted that *Fregilupus* was restricted to Réunion. Therefore, as a result of this misidentification, *Fregilupus varius* was placed in *Upupa* by a number of authorities. However, it was also variously placed amongst birds of paradise and bee-eaters (Levaillant 1807: 43), choughs (Vieillot 1817: 3; Lesson 1831: 324), cow-birds or Pastors (Wagler 1827: 90) and Icteridae (Gray 1870: 28).

Although *Fregilupus* had been long considered a member of Upupidae, it differs markedly in osteology from *Upupa epops*. The latter species differs from *Fregilupus* by the following key diagnostic characters and also in morphometrics (see appendix 1):

*Cranium*: in dorsal view, less bulbous posteriorly; frontal wide; in posterior view, crista nuchalis transversa

small with less distinct prominentia cerebellaris; in lateral view, foramen. n. optici extremely reduced compared with large fonticuli orbitocraniales.

*Rostrum*: extremely long and narrow, about 2.5 times cranium length, with very small narial openings; rostrum maxillare narrow and strongly decurved.

*Mandible*: rostrum mandibulae long and narrow; processus retroarticularis lacks medial projections; single reduced fenestra rostralis mandibulae.

*Sternum*: short and narrow, particularly at caudal end; spina externa not bifurcated; in lateral view, apex carinae rounded, not projecting beyond spina externa; carina sterni deep; in dorsal view, trabecula intermedia shorter than margo caudalis.

*Coracoid*: processus lateralis extends further laterally; sulcus m. supracoracoidei enclosed with a bony bridge.

*Scapula*: short and straight.

*Humerus*: robust with curved shaft; processus supracondylaris dorsalis small with little proximad extension; crista deltopectoralis distinctly triangular and extends further distad; fossa pneumotricipitalis indistinct; processus supracondylaris dorsalis lacks proximal projection; caput humeri reduced.

*Radius*: distinct tuberculum bicipitale radialis.

*Ulna*: more pronounced extension of olecranon.

*Carpometacarpus*: os metacarpale minus extends further distally from os metacarpale majus; processus extensorius sharply pointed, not rounded.

*Pelvis*: less robust; ala preacetabularis ilii and ala postacetabularis ilii narrow; more numerous foramina intertransversaria.

*Femur*: comparatively robust, with thick shaft and little expansion at distal end; sulcus intercondylaris shallow; facies articularis acetabularis reduced.

*Tibiotarsus*: short and straight; greatly expanded distal end; shaft broad and expanded, particularly proximal to distal end; crista cnemialis cranialis not extended laterally into a hook; pons supratendineus absent.

*Tarsometatarsus*: short and gracile; trochleae metatarsi II expanded medially; impressio retinaculi extensorii without bridge; crista medialis hypotarsi large and expanded distad; single enclosed sulcus hypotarsi.

Schlegel (1857: 338), albeit briefly, was the first person to suggest the sturnid affinities of *Fregilupus*, followed by Hartlaub (1861: 53), who made a detailed study of the skin and placed it alongside the monotypic Madagascar starling genus, *Hartlaubius* (now *Saroglossa*). Based on this evidence, Sundeval (1872: 40) proposed the generic name *Lophopsarus* (=crested starling), but according to the rules of the International Commission on Zoological Nomenclature (1999), this more appropriate name remains a junior synonym of *Fregilupus*.

Murie (1874) made a detailed anatomical study of the only known skeleton of *Fregilupus* held at the UMZC, which confirmed its sturnid affinities. There were originally two spirit specimens of *Fregilupus* deposited at the MNHN by the natural historian, Julien Desjardins (see below); one was exchanged with the MCZH, and the other was exchanged with the AMNH (Jouanin 1962). Miller (1941) partly dissected the MCZH *Fregilupus* spirit specimen, and based on the comparative study of the pelvic and pectoral girdles and the syrinx, concluded that it differed little from Eurasian Starling *Sturnus vulgaris*. Despite the earlier conclusions, Amadon (1943) had reservations about the relationships of *Fregilupus*, suggesting that it might belong to Vangidae, but that more data were needed. He disregarded this view after examining skin specimens, and considered it to be a starling, noting morphological similarities with SE Asian *Sturnus* (Amadon 1956). Berger (1957) dissected the AMNH spirit specimen and cast some doubt on a sturnid relationship, although he provided little evidence in support of an alternative. He further remarked on suggestions made by Amadon and Ernst Mayr therein, that there might be a possible relationship with prionopid shrikes (Prionopidae), so it appears that Amadon was still uncertain about the relationships of *Fregilupus*. As Dorst (1960a, b) also proposed that *Fregilupus* might be related to vangas, Morioka (1996) compared cranial osteology with the Sickie-billed Vanga *Falcoelea palliata* and concluded that there was no direct relationship. MtDNA analysis has since confirmed that the affinities of *Fregilupus* lie within Sturnidae and that it is distantly related to SE Asian genera (Zuccon *et al.* 2008; see below).

### †Réunion Crested Starling, Huppe or Hoopoe Starling *Fregilupus varius* (Boddaert, 1783)

Huppe, Vachet, 1671, in Lougnon, 2005, p.72; de Lespinay, 1671, in Barré *et al.* 1996, p.38; Boureau-Deslandes, 1674, in

Lougnon, 2005, p.140; Bernardin, 1687, in Probst & Brial 2002, p.81; Borghesi, 1703, in Barré *et al.* 1996, p.39; Desforges-Boucher, 1704, in Probst & Brial 2002, p.81; Feuillet, 1705, in Lougnon, 1939, p.40; Cossigny, 1732, in Probst & Brial 2002, p.81; Renoyal de Lescouble, 1822, in Probst & Brial 2002, p.81; Legras, 1861, p.81; Vinson, 1877, p.327.

Huppes or callendres, Dubois, 1674, p.172.

La Huppe noire et blanche, du Cap de Bonne Espérance, De Montbeillard, in Buffon, 1779, vol. 6, p.463.

Madagascar Hoopoe, Latham, 1782, vol. 1, pt. 2, p.690.

Huppe du Cap de Bon Espérance, De Montbeillard, 1783 (in Daubenton, 1771-86), vol. 6, pl.697.

*Upupa varia* Boddaert, 1783, p.43 (no locality = Réunion Island).

*Upupa capensis* J.F. Gmelin, 1788, vol. 1, p.466 (Madagascar and Bourbon = Réunion); Cuvier, 1817, vol. 1, p.407.

La Huppe grise, Audebert & Vieillot, 1802, vol. 1, p.15, pl.3.

Le Mérops Huppé, Levaillant, 1807, vol. 3, p.43, pl.18.

*Upupa madagascariensis*: Shaw, 1812, vol. 8, p.140 (Madagascar).

*Coracia cristata*: Le Coracias tivouch Vieillot, 1817: in Vieillot, 1817, vol. 8, p.3 (Madagascar, Cape of Africa and Bourbon = Réunion).

*Pastor upupa*: Wagler, 1827, p. 90, sp.13 (St. Transcisco [=Francisco?], Bourbon and Madagascar).

*Fregilupus capensis*: (J. F. Gmelin); Lesson, 1831, p.324; Bonaparte, 1858, p.88; Maillard, 1862, p.162; Morel, 1863, p.175; Coquerel, 1863b, p.15.

*Fregilupus madagascariensis*: (Shaw); Reichenbach, 1851, p.321, t.596, fig.4039; Hartlaub, 1861, p.53; Schlegel & Pollen, 1868, p.104; Murie, 1873, p.200.

*Coracia tinouch* Hartlaub, 1861, p. 53 (lapsus).

*Sturnus capensis*: Schlegel, 1872, p.181 (Madagascar and Bourbon = Réunion).

*Coracias tivouch* Murie, 1874, p. 476 (unjustified amendment).

*Fregilupus borbonicus*: Vinson, 1868, p.627 (Réunion); Giebel, 1874, p.627.

*Lophopsarus varius* (Boddaert); Sundeval, 1872, p.40.

*Fregilupus varia* (Boddaert): Gray, 1870, p.28, no.6398.

*Fregilupus varius* (Boddaert): Murie, 1874, p.474, pls. 61,62; A. Newton, 1875, p.41; Salvadori, 1876, p.482; Hartlaub, 1877, p.203; Funaro & Angelini, 1883, p.230; Sharpe, 1889a, 40. p.177, 1889b, 13, p.310; Anon (W.M.), 1889, Sep 7; Sharpe, 1890, p.194; Oustalet [attrib.], 1890, p.49; Milne-Edwards & Oustalet, 1893, p.21, pl.2; A. Newton, 1893, p.217, fig. I; Oustalet, 1897 [1896], p.7, fig.1; Forbes, 1898, p.30; Renshaw, 1905, 9, p.418; Rothschild, 1907a, p.198; Rothschild, 1907b, p.3, pl.I; Brasil, 1911, 23, p.33; Brasil, 1912, p.15, pl.II,III; Angelini, 1912, p.261; Salvadori, 1912, p.159; Demandre, 1913, p.3, pl. I,II; Ménégaux, 1914, p.337; Renshaw, 1922, p.80; Legendre, 1929, p.645; Miller, 1941, p.586; Amadon, 1943, p.10; Berlioz, 1946, p.10; Mayr & Amadon, 1951, p.30; Hachisuka, 1953, p.213; Amadon, 1956, p.4; Greenway, 1958, p.129.

**Holotype:** Boddaert's (1783: 43) names were intended to provide Linnaean binomials for the plates in the works of Buffon, hence the holotype is Buffon's plate of "La Huppe noire et blanche, du Cap de Bonne Espérance" of De Montbeillard (in Buffon 1779: 463, pl. 697). Technically, according to Article 73.1.4. "Designation of an illustration of a single specimen as a holotype is to be treated as designation of the specimen illustrated; the fact that the specimen no longer exists or cannot be traced does not of itself invalidate the designation." (ICZN 1999). Although it is possible that one of the specimens in the Paris Museum (MNHN) could have been the basis for Buffon's plate (Oustalet 1896), this cannot be determined with certainty, so the plate itself must be considered the holotype.

The MNHN originally held at least five skins. MNHN 2000-755 is one of two birds seen by Levaillant (1807: 44) in the Paris Museum, the other was exchanged with Stockholm in 1833 (Legendre 1929), and so either of these could conceivably have been the type specimen. Of the three other Paris skins, a third skin (MNHN 2000-756) arrived in 1833 (Milne-Edwards & Oustalet 1893), whereas the two above-mentioned Desjardins aviary birds arrived in 1839 (Oustalet 1897). MNHN 2000-756 has been described and illustrated more than any other, but the crest in this specimen, which formed the basis for the well-known illustrations by John Gerard Keulemans (in Milne-Edwards & Oustalet 1893: pl. II; Rothschild 1907b: pl. 1), has been artificially trimmed (Christian Jouanin pers. comm., August 1996; Fig. 6), giving the false impression that this ornamentation was neatly semi-circular in life. The illustration in De Montbeillard (in Buffon 1779: pl. 697) also shows this feature (Fig. 8a).

**Measurements.** See Appendix 1.

**Type locality.** Réunion, Mascarenes.

**Distribution.** Réunion, Mascarenes.

**Etymology.** Latin, *varius* variegated, in reference to the black and white coloration of the "Huppe noire et blanche du Cap de Bonne Espérance".



**FIGURE 5.** Adult male? *Fregilupus varius* NHMUK 1889.5.30.15.



**FIGURE 6.** Head images of selected *Fregilupus varius* museum skins (top to bottom); MHNT O2647 (Adult male?); MHNT O2650 ( Juvenile); MNHN 2000-756 (Adult female?) (not to scale).



**FIGURE 7.** A pencil sketch of *Fregilupus varius* by Paul Philippe Sauguin de Jossigny c.1770 (in Oustalet 1897). This is the only unequivocal illustration of the bird drawn from life

**Referred skin material.** There are 19 surviving specimens of *Fregilupus varius* in the following museums (one skin unless otherwise stated): Brussels; Cambridge, England (skeleton); Cambridge, Massachusetts (partially dissected, originally a Paris (Desjardins) spirit specimen; see below); Florence; Genoa; Lausanne; Leiden; Mauritius; New York (skeleton, originally a Paris (Desjardins) spirit specimen; see below); Paris (2 skins); Pisa; Réunion; Stockholm; Tring; and Troyes (4 skins). A skin originally held in Turin and another in the Livorno Lyceum museum were lost during the Second World War (Tortonese 1957; Violani *et al.* 1999). There were originally three skins in Réunion (Milne-Edwards & Oustalet 1893) and at least three in Mauritius (Carié in Legendre 1929), but only a single specimen is present in each of those museums today (pers. obs). Another skin that was formerly in Caen (Brasil 1911), appears to have been destroyed during World War II.

**Referred fossil material:** The distal end of a left femur (registration number MNHN LAC1993-57), the only fossil specimen known (Mourer-Chauviré *et al.* 2006), was collected in the Grotte des Premiers Français in 1993 (see Mourer-Chauviré *et al.* 1999). The cave is situated near the coast and 1.5 km from the centre of Saint-Paul, on the northwest side of the island, and the femoral fragment was found in sediments between 800 and 1005 mm below the cave floor. The deposit contained no introduced animals or any signs of human occupation, which suggests that the deposit was laid down prior to human arrival on the island (*ibid*).

**Revised diagnosis.** As for genus.

**Description and comparison.** *Fregilupus* was the largest Mascarene starling and differs from Mascarene and other sturnids by the following character states:

*Cranium:* in *Necropsar*, cranium more dorso-ventrally compressed; overall more robust with wider naso-frontal hinge; crista nuchalis transversus less rounded, extending farther dorsad forming a distinct ridge, especially on lower part; prominentia cerebellaris larger; foramen n. optici larger than fonticuli orbitocraniales; in *Saroglossa*, in dorsal view, cranium less bulbous and dorso-ventrally compressed; frontal wider; in posterior view, crista nuchalis transversa rounded with indistinct prominentia cerebellaris; foramen. n. optici equal in size to fonticuli orbitocraniales; in *Leucopsar*, in lateral view, processus postorbitalis more reduced; in posterior view, crista nuchalis transversa smaller with indistinct prominentia cerebellaris; foramen magnum smaller; otherwise morphologically similar; in *Gracupica*, in dorsal view, cranium less rounded, more dorso-ventrally flattened; frontal narrower; in posterior view, foramen magnum smaller; in lateral view, foramen. n. optici larger than fonticuli orbitocraniales; processus postorbitalis less elongate; in *Sturnia*, in posterior view, crista nuchalis transversa with indistinct prominentia cerebellaris; less dorso-ventrally flattened; in *Acridotheres*, foramen

magnum smaller; less distinct crista nuchalis transversus, which extends more dorsad; processus postorbitalis less elongate (Figs. 9, 10, 11, 12).

*Rostrum*: in *Necropsar*, less decurved, shorter and more robust; narial openings longer; in *Saroglossa*, shorter and broader; in *Leucopsar*, shorter and wider, narial openings less elongate, more ovoid; in *Gracupica*, shorter, slightly wider with large ovoid narial openings; rostrum maxillare narrow and strongly decurved; in *Sturnia*, shorter and wider, narial openings elongate, almost half the length of rostrum; in *Acridotheres*, much shorter; narial openings smaller and shorter; in dorsal view, maxilla narrower but more pronounced angular surface on os nasale (Figs. 9, 10).



**FIGURE 8a.** *Fregilupus varius* by François-Nicolas Martinet (in Daubenton 1771–1786, pl. 697).



FIGURE 8b. by Jacques Barraband (in Levaillant 1807).





A. Roussin del. et lith.

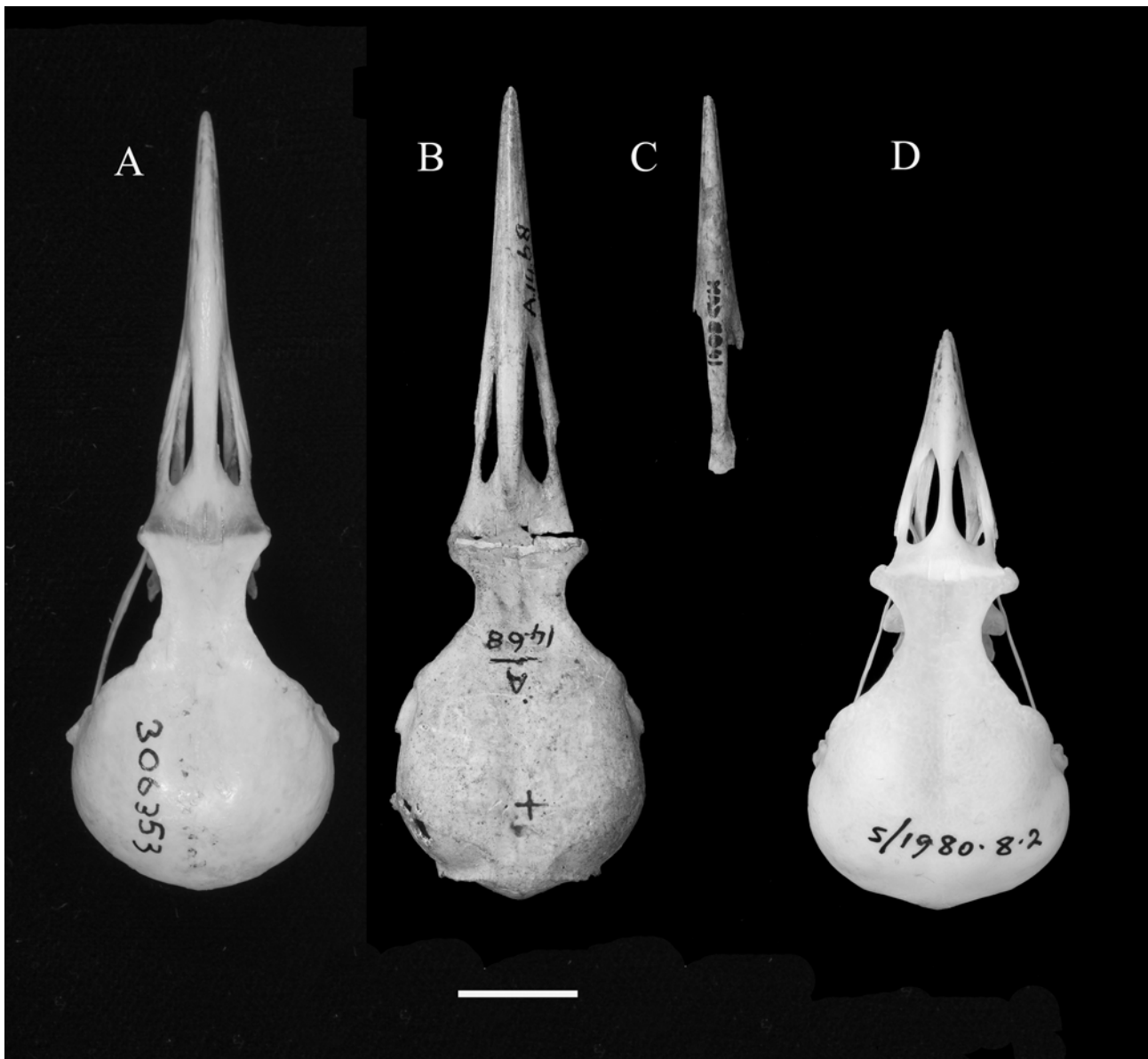
Déc. 1864.

Imp. A. R. Réunion.

HUPPE DE BOURBON

*Grave huppe fregilupus Capensis* LESS. —  $\frac{1}{2}$  de grandeur nat.<sup>elle</sup>

FIGURE 8c. by Albert Roussin (1860–68).



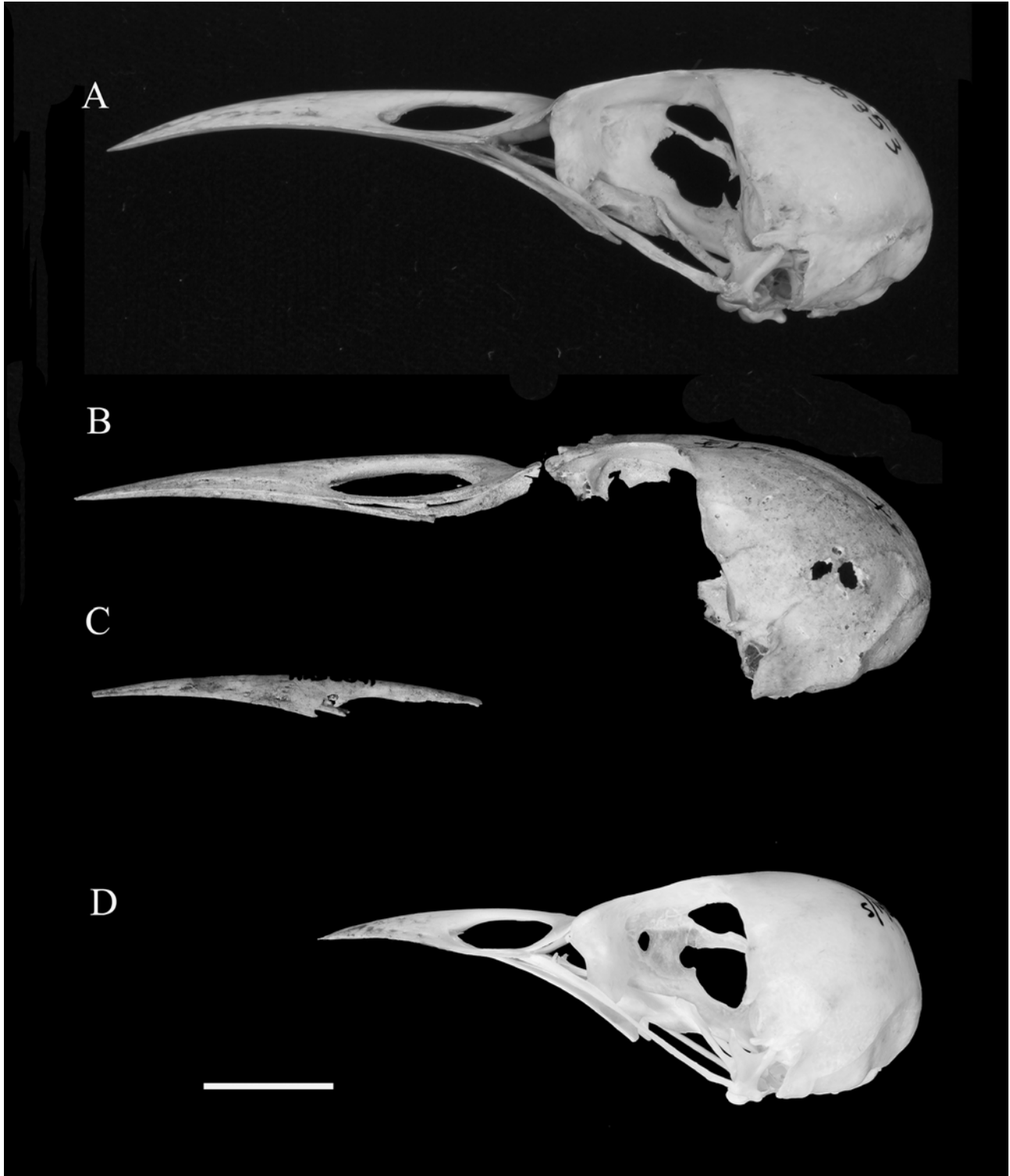
**FIGURE 9.** Comparison of crania and rostra of Mascarene starlings with *Acridotheres tristis*, dorsal view. **A.** AMNH 306353 *Fregilupus varius* ♂; **B.** NHMUK A9050 (lectotype; formerly A1468) *Necropsar rodericanus* u/s; **C.** MNHN MAD8041 *Cryptopsar ischyrhynchus* gen.nov. sp.nov. u/s. **D.** NHMUK S/1980.8.2 *Acridotheres tristis* ♀. Scale bar = 10mm.

*Mandible:* in *Necropsar*, less curved and more robust, in dorsal view, processus retroarticularis larger and deeper; processus mandibulae medialis larger, broader and inflected more medially; rostrum mandibulae wider; in *Saroglossa*, processus retroarticularis indistinct with no posterior projection; in *Leucopsar*, shorter; in dorsal view, no extension of processus retroarticularis; in lateral view, fenestra rostralis mandibulae comparatively larger; in *Gracupica*, no extension of processus retroarticularis; crista transversa fossae broader; less medial projection of processus mandibulae medialis; in lateral view, overall straighter; in *Sturnia*, processus retroarticularis indistinct with no posterior projection; fenestra rostralis mandibulae comparatively larger; in *Acridotheres*, overall shorter and wider, processus retroarticularis much smaller, less robust (Figs. 13, 14).

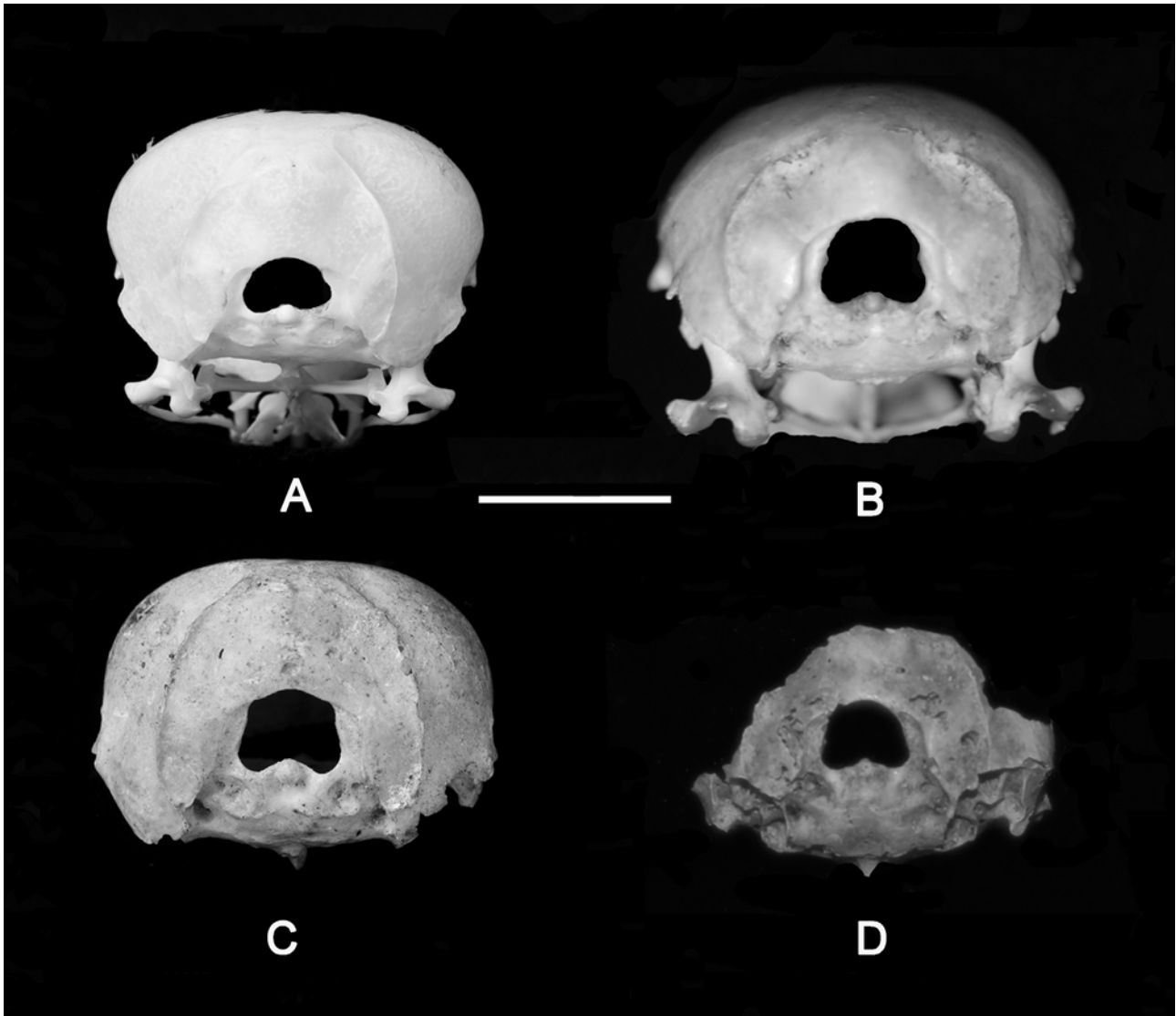
*Coracoid:* in *Necropsar*, shaft and proximal end less robust; angulus medialis deflected less medially; in *Saroglossa*, processus lateralis extends more laterally, less ventrally; in *Leucopsar* and *Sturnia*, less proximal extension of processus lateralis; in *Gracupica*, comparatively more gracile; in *Acridotheres*, overall less robust, but longer; more expanded at distal end (Fig. 15).

*Sternum:* in *Necropsar*, overall smaller, but spina externa larger; processus craniolateralis long, blade-like and deflected caudally, not laterally; in lateral view, carina sterni more reduced, with less cranially directed apex

carinae; in *Saroglossa*, in lateral view, apex carinae distinct extending beyond spina externa; carina sterni deep; in *Leucopsar*, in lateral view, spina externa longer; carina sterni larger, with more cranially directed apex carinae, otherwise morphologically similar; in *Gracupica*, in lateral view, apex carinae not reduced; carina sterni deep; in dorsal view, fenestra medialis completely enclosed; in *Sturnia*, overall narrower, in lateral view, carina sterni comparatively larger, with more cranially directed apex carinae, almost equaling extension of spina externa; in *Acridotheres*, comparatively larger, especially the carina sterni, otherwise morphologically similar (Figs. 16, 17).



**FIGURE 10.** Comparison of crania and rostra of Mascarene starlings with *Acridotheres tristis*, dorsal view. lateral view. **A.** AMNH 306353 *Fregilupus varius* ♂; **B.** NHMUK A9050 (lectotype; formerly A1468) *Necropsar rodericanus* u/s; **C.** MNHN MAD8041 *Cryptopsar ischyrrhynchus* gen.nov. sp.nov. u/s. **D.** NHMUK S/1980.8.2 *Acridotheres tristis* ♀. Scale bar = 10mm.

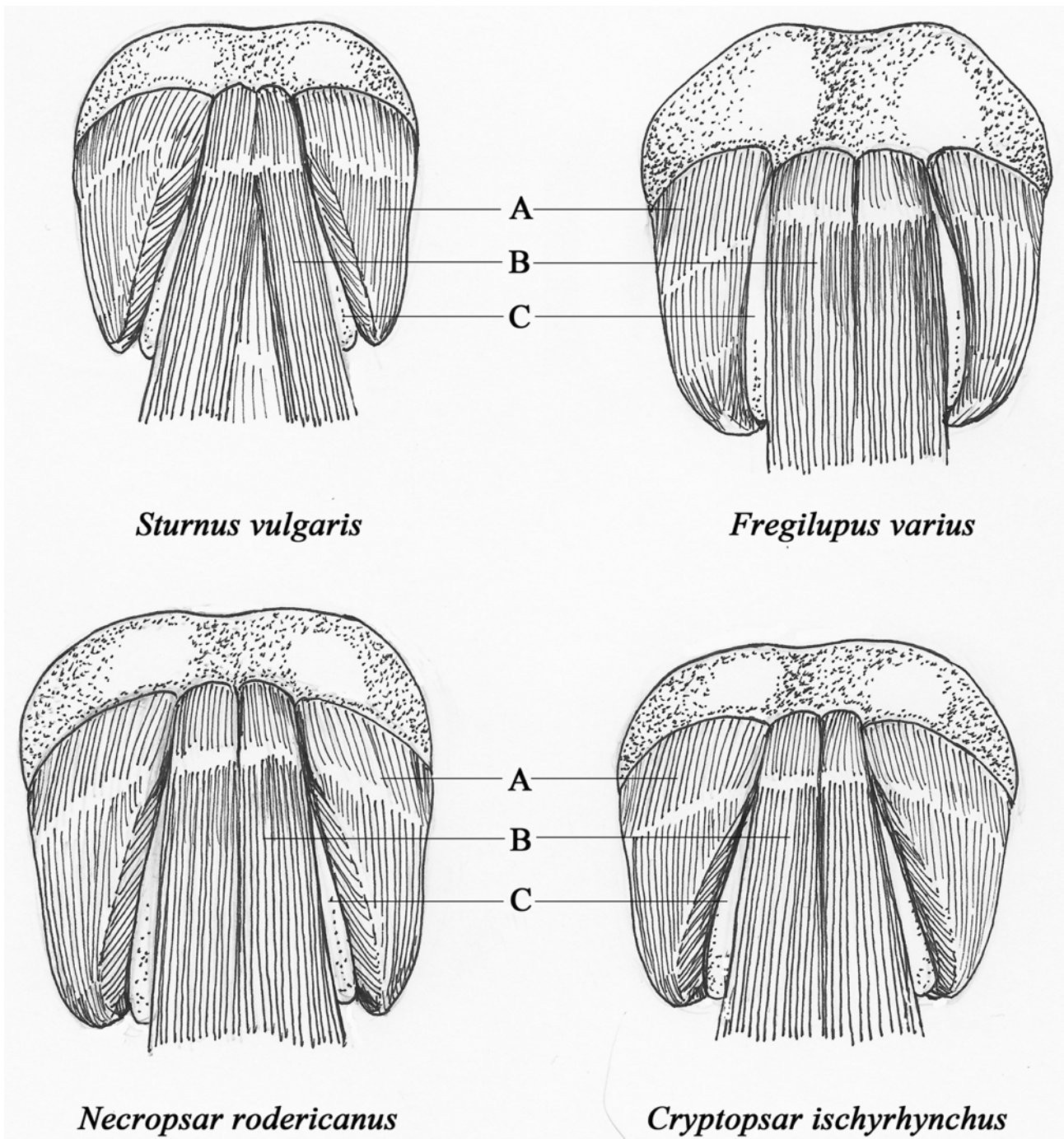


**FIGURE 11.** Comparison of crania of Mascarene starlings with *Acridotheres tristis*, posterior view; **A.** AMNH 306353 *Fregilupus varius* ♂; **B.** MNHN MADu/r u/s *Cryptopsar ischyrrhynchus* gen.nov. sp.nov. u/s; **C.** NHMUK A9050 (lectotype; formerly A1468) *Necropsar rodericanus* u/s; **D.** NHMUK S/1980.8.2 *Acridotheres tristis* ♀. Scale bar = 10mm.

*Humerus*: in *Necropsar*, less robust; shaft more curved; in caudal view, lacks circular depression on proximal side of tuberculum ventrale; two tricipital fossae; tricipital fossa II not completely enclosed and separated from tricipital fossa I by medial bar; tricipital fossa I open distally communicating with tricipital fossa II; medial bar much less developed; incisura capitis shallower; in *Saroglossa*, tuberculum ventrale directed more ventrally; crista deltopectoralis more reduced, otherwise morphologically similar; in *Leucopsar* and *Sturnia*, in caudal view, caput humeri more prominent, less rounded; medial ridge much less distinct, barely separating tricipital fossae; in *Gracupica*, medial ridge more distinct; less proximal extension of processus supracondylaris dorsalis; crista deltopectoralis more triangular; in *Acridotheres*, more expanded at proximal and distal ends; shaft less straight; incisura capitis less deeply excavated; crista deltopectoralis extends less distad (Fig. 18).

*Ulna*: in *Necropsar*, morphologically similar but smaller, less robust; in *Saroglossa*, less extension of condylus ventralis ulnae; in *Leucopsar*, in ventral aspect, olecranon straighter, directed less mediad; tuberculum ventrale more distinct, directed further mediad; in *Gracupica*, processus cotylaris dorsalis extends less dorsad; in *Sturnia*, comparatively more gracile, otherwise similar; in *Acridotheres*, longer, but comparatively less robust (Fig. 19).

*Carpometacarpus*: in *Necropsar*, smaller, more pronounced processus extensorius, otherwise similar; in *Saroglossa*, *Leucopsar* and *Sturnia*, more pronounced processus extensorius; *Gracupica* similar; in *Acridotheres*; larger, more robust (Fig. 20).



**FIGURE 12.** Authors scaled illustration of jaw myology of Mascarene starlings compared with *Sturnus vulgaris*, posterior view, showing the relative development of M. depressor mandibulae. **A.** M. depressor mandibulae; **B.** biventer cervicis; **C.** hyoid bone. *Sturnus vulgaris* and *Fregilupus varius* are adapted from Berger (1957), the musculature of *Necropsar rodericanus* and *Cryptopsar ischyrrhynchus* gen.nov. **sp. nov.** is illustrated hypothetically and based on morphometrics of the cranium.

*Pelvis:* in *Saroglossa*, less robust; larger number of foramina intransversaria; spina dorsolateralis illi less extended caudally; in *Leucopsar*, in dorsal view, narrower, less lateral extension of ala ischii; sulcus antitrochantericus less pronounced, not directed laterally; in *Gracupica*, narrower caudally otherwise similar; in *Sturnia*, in dorsal view, sulcus antitrochantericus less pronounced, not directed laterally; in lateral view, ala ischii and apex pubis joined forming two foramen; in *Acridotheres*, overall smaller, narrower and less robust; cranial end less constricted; sulcus antitrochantericus less pronounced, not directed laterally; apex pubis extends less caudally; in lateral view, fenestra ischiopubica much smaller with apex pubis deflected less ventrally (Fig. 21).



**FIGURE 13.** Comparison of mandibles of Mascarene starlings with *Acridotheres tristis*, dorsal view; **A.** AMNH 306353 *Fregilupus varius* ♂; **B.** MNHN MAD6931 *Cryptopsar ischyrynychus* gen.nov. sp.nov. u/s; **C.** NHMUK A1468 *Necropsar rodericanus* u/s; **D.** NHMUK S/1980.8.2 *Acridotheres tristis* ♀. Scale bar = 10mm.

*Femur*: in *Necropsar*, proximal end less expanded; facies articularis acetabularis smaller, less pronounced, otherwise similar; in *Saroglossa*, less robust, facies articularis acetabularis less bulbous; in *Leucopsar*, overall more robust; *Gracupica* similar; in *Sturnia*, comparatively more gracile; in *Acridotheres*, proximal and distal ends less robust, otherwise similar (Fig. 22).

*Tibiotarsus*: in *Necropsar*, shaft more expanded distad; sulcus extensorius more deeply excavated; pons supratendineus larger; in *Saroglossa*, shorter, shaft narrower, less expanded at proximal and distal ends; tuberculum retinaculi m. fibularis distinct; sulcus extensorius deflected laterally; in *Leucopsar*, comparatively less robust; tuberculum retinaculi m. fibularis more distinct; pons supratendineus smaller; in *Gracupica*, long and comparatively gracile; shaft not expanded proximal to distal end; tuberculum retinaculi m. fibularis distinct; pons supratendineus deeper; in *Sturnia*, comparatively less robust; tuberculum retinaculi m. fibularis more distinct; pons supratendineus comparatively larger; in *Acridotheres*, overall less robust; crista fibularis longer, situated less proximad; pons supratendineus deflected less laterally (Fig. 23).

*Tarsometatarsus*: in *Necropsar*, shorter, but more robust; more expanded proximal and distal ends, otherwise morphologically similar; in *Saroglossa*, trochleae less widely spaced; foramen vasculare distale smaller; in *Leucopsar*, shorter, less robust; trochleae less widely spaced; foramen vasculare distale comparatively smaller; in *Gracupica*, shaft distinctly narrower with broad expansion of proximal and distal ends; trochlea metatarsi II deflected medially; impressio retinaculi extensorii without bridge; in *Sturnia*, comparatively more gracile; trochleae less widely spaced; otherwise similar; in *Acridotheres*, shorter, but more robust; trochlea more expanded medio-laterally; foramen vasculare distale comparatively smaller, situated less proximad; ridge bordering facies subcutanea lateralis more defined; in plantar aspect, crista medialis hypotarsi shorter (Fig. 24. For myology, see Miller (1941) and Berger (1957).



**FIGURE 14.** Comparison of mandibles of Mascarene starlings with *Acridotheres tristis*, lateral view. **A.** AMNH 306353 *Fregilupus varius* ♂; **B.** MNHN MAD6931 *Cryptopsar ischyrynychus* gen.nov. sp.nov. u/s; **C.** NHMUK A1468 *Necropsar rodericanus* u/s; **D.** NHMUK S/1980.8.2 *Acridotheres tristis* ♀. Scale bar = 10mm.

**Plumage:** In the adult (male?) (NHMUK 1889.5.30.15) (Figs. 5, 6, 25), the forehead, crown, nape, hindneck and cheeks are light ash-grey, almost pale buff on the hind-neck, and the elongate crest is light-ash-grey with white shafts. The mantle, back, rump, upper tail-coverts are tail are ash-brown, the wings darker with a greyish wash, with the rump and upper-tail coverts washed rufous. The primary coverts are white with brown tips. The superciliary stripe, lores, chin, throat and rest of undersides are white and variably washed pale rufous on flanks and under-tail coverts. The beak, legs and feet are lemon-yellow (Levaillant 1807) with the claws yellowish-brown. There is bare skin that extends into a small triangle behind the eye and was probably yellowish in the live bird. The irides have been described or depicted as brown, yellow or orange, but De Montbeillard (in Buffon 1779) and Morel (1863) describe them as bluish-brown in adults. There is some variation in specimens (see Hartlaub 1877), particularly in the extent of the light rufous on the underside and thighs, and in some individuals the primary coverts have brown bases rather than brown tips.

In the adult (female?) MNHN 2000-756) (Fig. 6), the crest is supposedly smaller, the bill is shorter and straighter, less decurved, and the primary coverts are more reduced. The juvenile differs from the adult in having the crest, superciliary stripe and lores washed brown, not light ash-grey, the mantle and lower back light brown, not ash brown, and having smaller primary coverts and crest (Figs. 6, 25).



**FIGURE 15.** Comparison of coracoids of Mascarene starlings with *Acridotheres tristis*, ventral aspect, left side. **A.** AMNH 306353 *Fregilupus varius* ♂; **B.** MNHN MAD7131 u/s *Cryptopsar ischyrynychus* gen.nov. sp.nov.; **C.** NHMUK u/r *Necropsar rodericanus* u/s; **D.** NHMUK S/1980.8.2 *Acridotheres tristis* ♀. Scale bar = 10mm.

**Viscera and tongue:** Milne-Edwards and Oustalet (1893) dissected one of the pickled MNHN specimens supplied by Desjardins before they were exchanged, and provided some details about the viscera and tongue. Because their account included information not available elsewhere, I have translated it in its entirety:

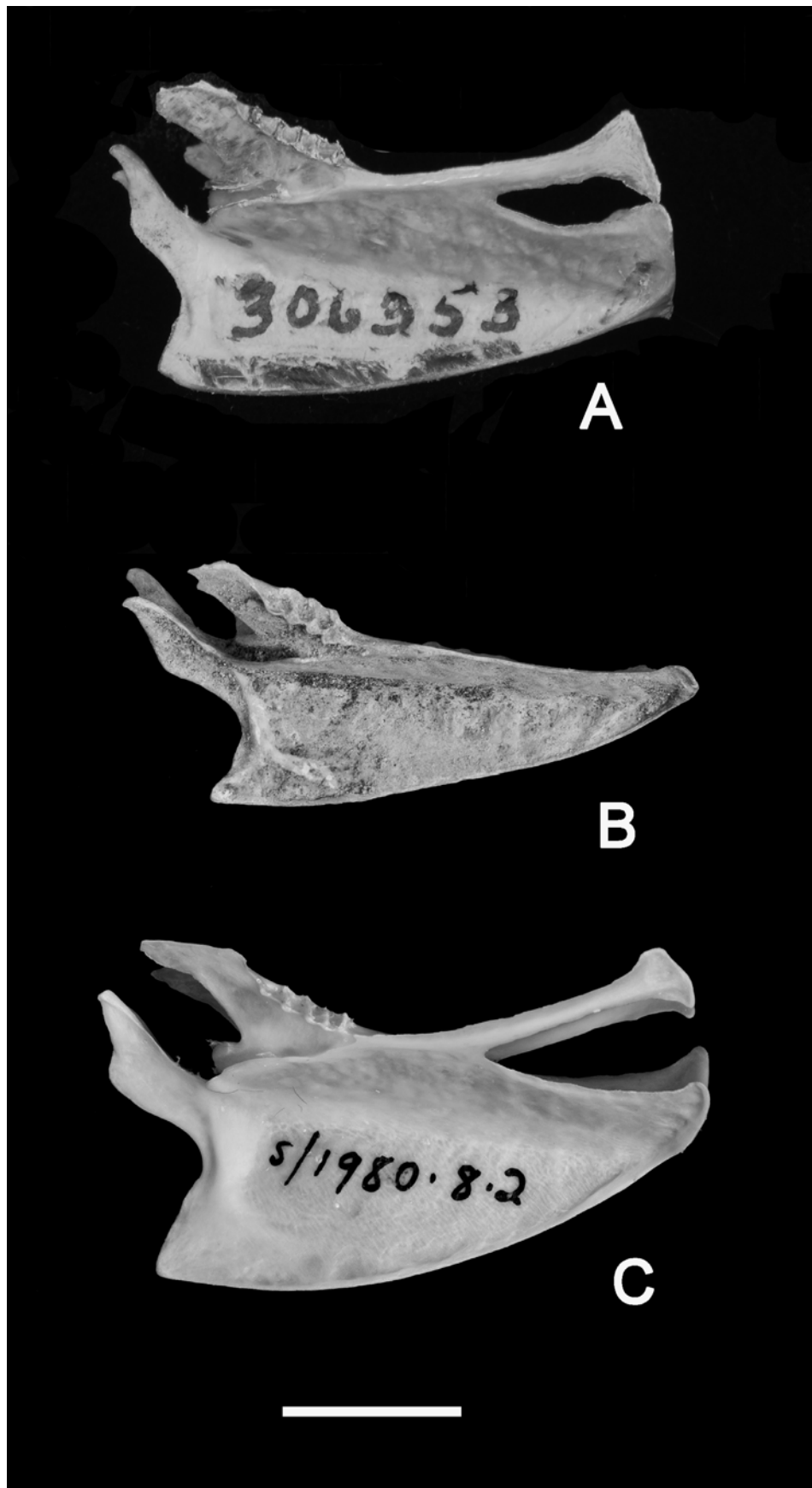
The digestive tract of *Fregilupus varius*, of which we could unfortunately only make a quick study and summary of an individual preserved in alcohol, seemed quite similar overall to that of *Falculia* [sic] *palliata* and *Hartlaubius madagascariensis* [*Saroglossa aurata*]. The proventriculus is not clearly separated from the esophagus, which seems to be a simple dilation. The gizzard is globular; the very strong and muscular walls are lined inside with a thick stratum corneum, with wrinkles corresponding to those of the underlying muscle layer.

On the upper two thirds of the height of the gizzard, the folds create a zigzag effect and become confluent, giving this section the roughness of a nutshell. The intestine, of a size approximately uniform over the greater part of its extent, is approximately 0 m. 25 [250 mm] long. The caeca barely exist and are represented only by two small extensions reaching up to 0 m, 001 [1 mm], that is to say, as rudimentary as in the *Falculia palliata* and slightly more marked than in *Hartlaubius madagascariensis*; we had great difficulty in finding evidence of these extensions due to it being an autopsy on a specimen preserved in alcohol.

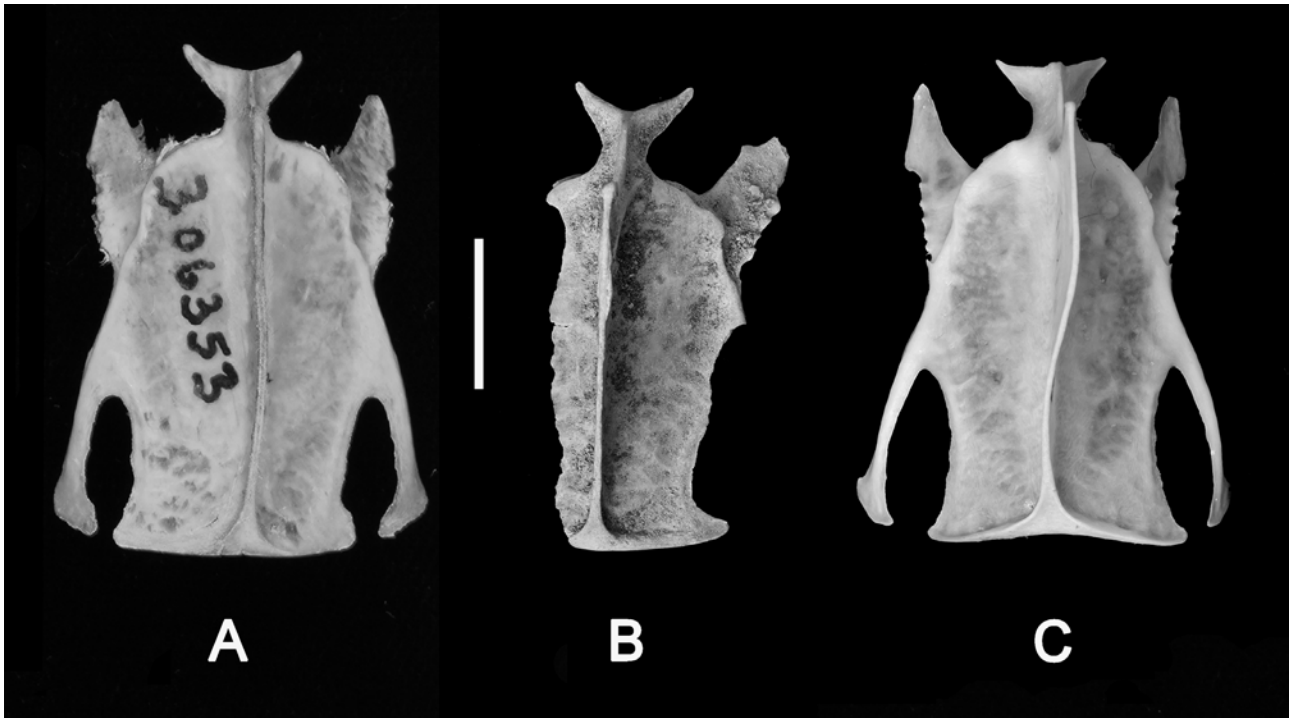
The tongue looks exactly like that of *Hartlaubius madagascariensis*. It is not immediately divided into several threads in its end portion, as said by Guéneau de Montbeillard [De Montbeillard (in Buffon 1779)], but it is divided at the top by a slight incision into two sharp lobes, themselves being frayed on the edges. It is a fairly rigid, triangular-shaped blade and fairly long, not exceeding half of that of the lower mandible. The trachea is medium-sized and almost uniform, without convolutions, and the lower larynx or syrinx has its lower end portion hidden beneath long elevator muscles, forming two contiguous masses, as in *Falculia* and in *Hartlaubius*.

Berger (1957), after dissection of the AMNH male specimen, added that the right testis measured 1.0 x 2.5 mm, and the left testis 1.5 x 3.0 mm. The right lobe of the liver was approximately three times the size of the left; the gall bladder was large and saccular, measuring 15 mm in length and 7 mm in diameter. The stomach, as reported by Milne-Edwards and Oustalet (1893), was empty. The spleen was a cylindrical mass, drawn to a point at





**FIGURE 16.** Comparison of sterna of Mascarene starlings with *Acridotheres tristis*, lateral view; **A.** AMNH 306353 *Fregilupus varius* ♂. **B.** FLMR 9 *Necropsar rodericanus* u/s; **C.** NHMUK S/1980.8.2 *Acridotheres tristis* ♀. Note the reduced sterna of *F. varius* and *N. rodericanus* compared with the smaller species, *A. tristis*. Scale bar = 10mm.



**FIGURE 17.** Comparison of sterna of Mascarene starlings with *Acridotheres tristis*, ventral view. **A.** AMNH 306353 *Fregilupus varius* ♂; **B.** FLMR 9 *Necropsar rodericanus* u/s; **C.** NHMUK S/1980.8.2 *Acridotheres tristis* ♀. Scale bar = 10mm.



**FIGURE 18.** Comparison of humeri (right side) of Mascarene starlings with *Acridotheres tristis*, caudal aspect. **A.** AMNH 306353 *Fregilupus varius* ♂; **B.** MNHN MAD6481 *Cryptopsar ischyrrhynchus* gen.nov. sp.nov. u/s; **C.** NHMUK A1470 *Necropsar rodericanus* u/s (left side reversed); **D.** MNHN MAD 7137 *Acridotheres tristis* u/s. Scale bar = 10mm.

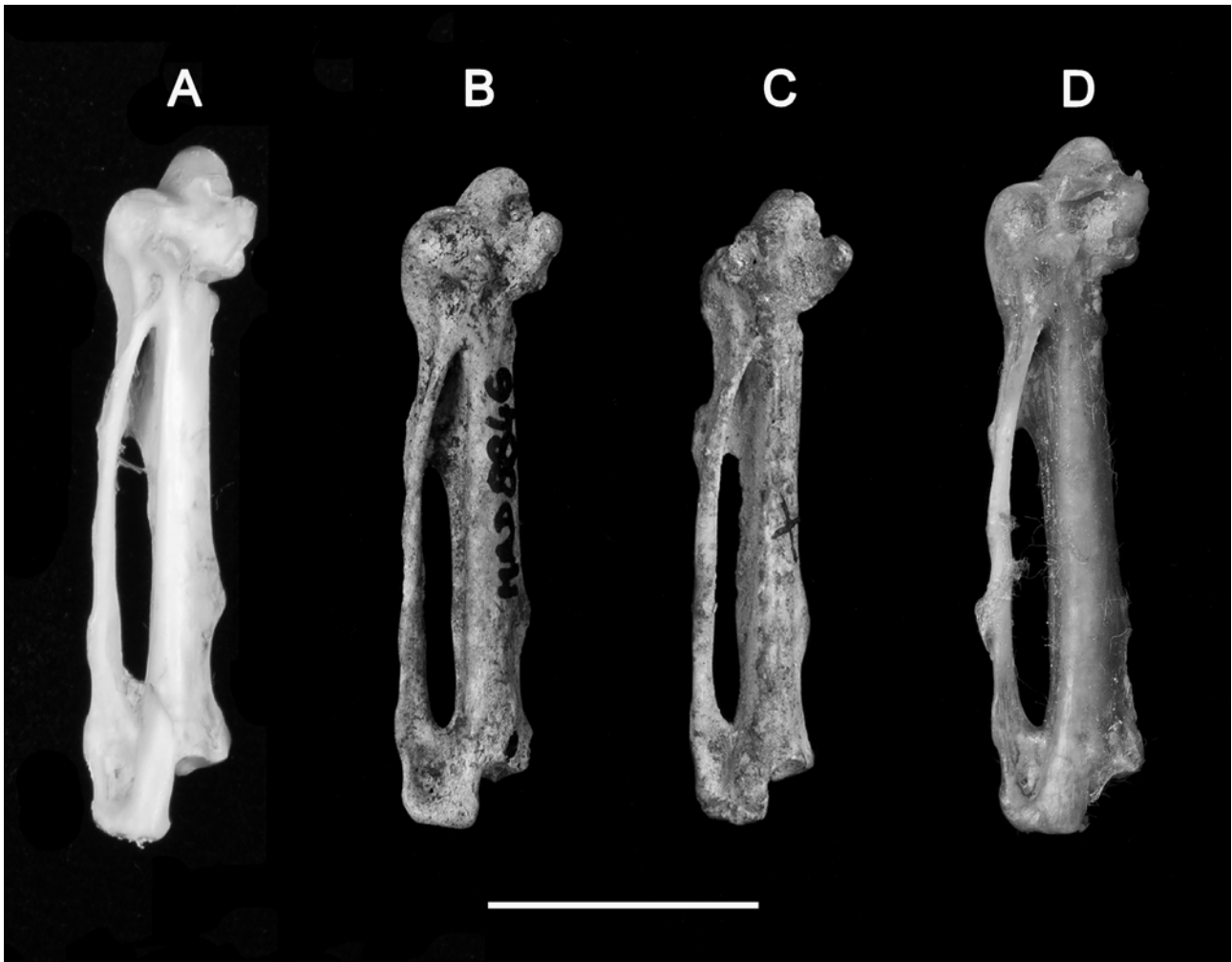


**FIGURE 19.** Comparison of ulnae (left side) of Mascarene starlings with *Acridotheres tristis*, ventral aspect. **A.** AMNH 306353 *Fregilupus varius* ♂; **B.** MNHN MAD8859 *Cryptopsar ischyrrhynchus* gen.nov. sp.nov. u/s (right side reversed); **C.** NHMUK A1471 *Necropsar rodericanus* u/s; **D.** NHMUK S/1957.15.9 *Acridotheres tristis* u/s. Scale bar = 10mm.

each end, and measured 10 mm in length, and 2.5 mm in maximum diameter. The pancreas appeared to be single, not bilobed, and was 33 mm long. The caeca were each 5 mm in length and about 1.5 mm in diameter at the attachment to the side of the intestine, about 20 mm anterior to the anal opening.

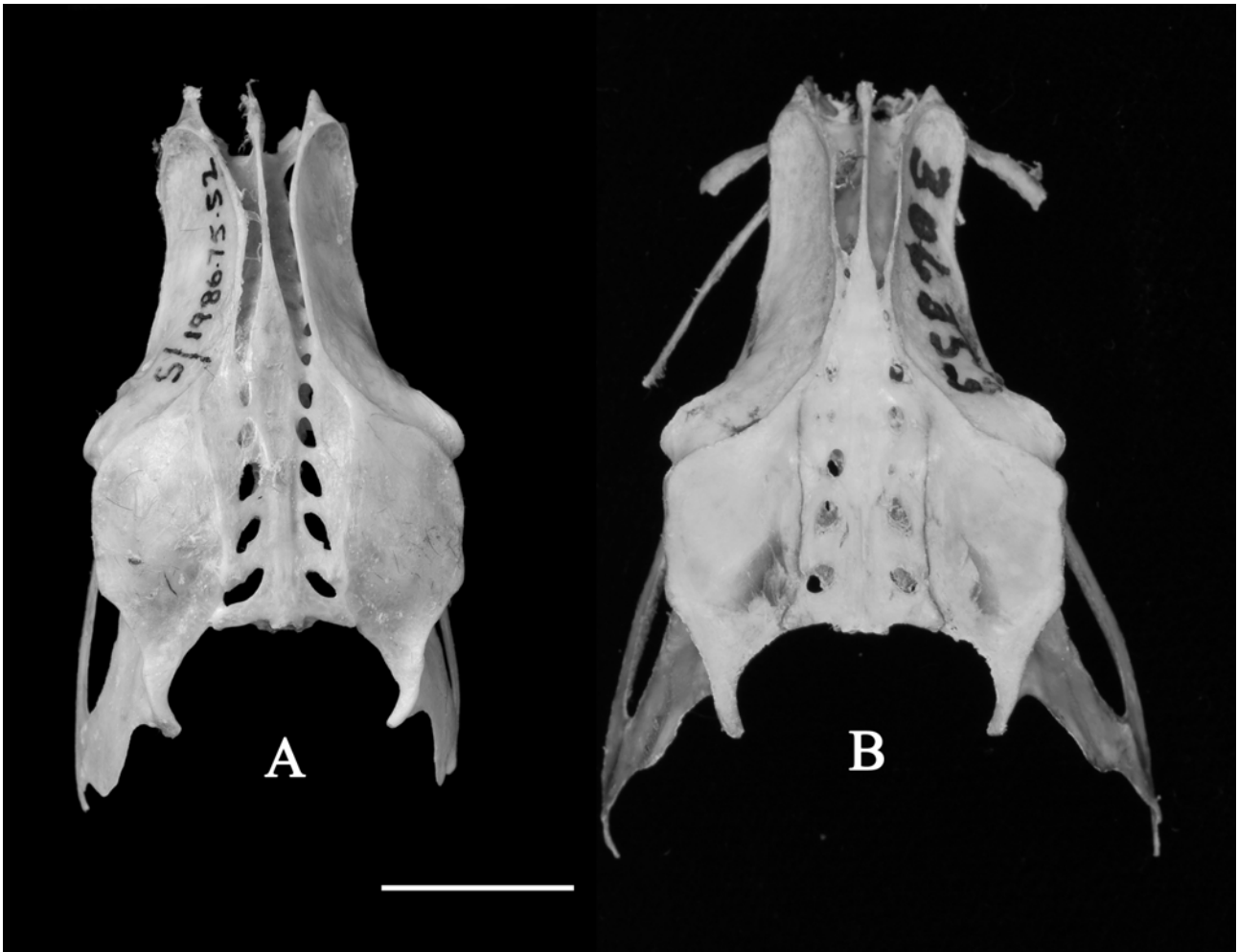
**Jaw anatomy and function:** In most birds, the adductor muscles that close the bill are stronger than the protractor muscles that open it, but in a few starling genera, especially *Sturnus vulgaris*, this character is reversed (Beecher 1978). Zusi (1959) showed that in *Sturnus*, the adductor, M. depressor mandibulae, and the protractor, M. protractor quadrati et pterygoidei, are both extremely large (Fig. 12). However, the depressor mandibulae had no effect on closing the upper jaw, which was accomplished by the protractor quadrati; this muscle in particular is extremely well developed in *Sturnus*. Furthermore, Berger (1957) and Zusi (1959, 1967) noted that the hypertrophy of M. depressor mandibulae has a direct relationship with the increased length of the processus retroarticularis; this large, posterior projection increases the area of insertion of the muscle as well as its leverage capabilities (Zusi 1959; Beecher 1978). All of these anatomical adaptations are associated with gaping. Gaping birds forage by inserting their bill into substrate such as soil, rotting wood or leaf litter and open it, to widen the hole and extract food items (See Beecher 1951, 1978; Burton 1974, 1984). Beecher (1978) further noted that the anterior region of the skull in *Sturnus vulgaris* is modified to assist forward vision along the long axis of the bill, which greatly

improves the starling's ability to locate prey once a hole has been opened up. This adaptation resulted in further modifications to the skull, most notably a reduction in the os ectethmoidale and the pinching in of the arcus jugalis (*ibid*), which can also be seen in *Fregilupus* and *Necropsar* (Fig. 9). The distinct crista nuchalis transversus, the crest which separates the nuchal plane of the supraoccipital bone for the attachment of *M. depressor mandibulae* and other neck muscles (Baumel & Witmer 1993; Fig. 11), combined with increased extension of the processus retroarticularis, shows that *Fregilupus* was a powerful gaper, although the musculature, as reported by Berger (1957), was not as developed as in *Sturnus vulgaris* (Fig. 12). These modifications are also found in *Necropsar* (see below), which had evolved a greater gaping ability than that of *Fregilupus*.



**FIGURE 20.** Comparison of carpometacarpal (left side) of Mascarene starlings with *Acridotheres tristis*, ventral aspect. **A.** AMNH 306353 *Fregilupus varius* ♂; **B.** MNHN MAD8846 *Cryptopsar ischyrrhynchus* gen.nov. sp.nov. u/s; **C.** NHMUK u/r *Necropsar rodericanus* u/s(right side reversed); **D.** NHMUK S/1957.15.9 *Acridotheres tristis* u/s. Scale bar = 10mm.

**Humerus in Sturnidae:** Bock (1962) described the humeral head in *Sturnus* as having two fossae, the first he termed “pneumatic fossa” and the other as “second pneumatic fossa, separated by a “medial bar.” This terminology is now considered antiquated as the fossae are frequently non-pneumatic in birds. The fossa is now generally termed the “tricipital fossa,” as this identifies the muscle involved, and the “medial bar” is better interpreted as a septum. In *Sturnus* and *Fregilupus*, and as noted by Berger (1957: 240), there is a small circular depression on the proximal side of the tuberculum ventrale, and the second tricipital fossa is completely enclosed and separated from the first tricipital fossa by the septum. In *Necropsar* and *Cryptopsar* the humeral head differs from *Fregilupus* in the absence of a circular depression on the proximal side of the tuberculum ventrale, and that the second tricipital fossa is not completely enclosed and separated from the first tricipital fossa by a septum, being open distally. The septum is also much less developed in these genera than in *Fregilupus* (Fig. 18).



**FIGURE 21.** Comparison of pelvises of *Fregilupus varius* with *Acridotheres tristis*, dorsal aspect. **A.** NHMUK S/1986.75.52 *Acridotheres tristis* u/s; **B.** AMNH 306353 *Fregilupus varius* ♂. Scale bar = 10mm.

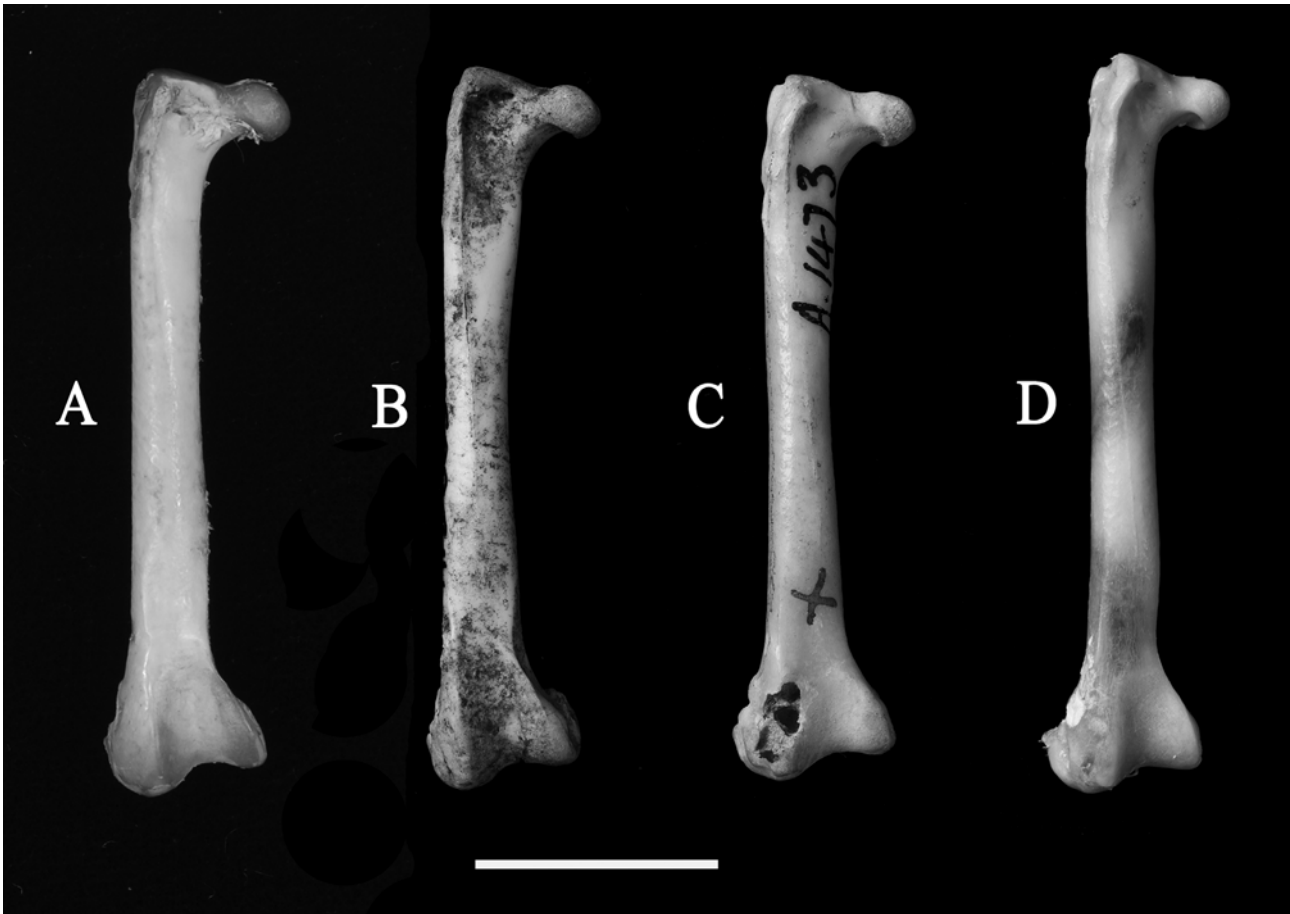
However, caution should be applied when determining these characters, especially with such a small number of fossil specimens, as the humerus in Sturnidae can show much variation. For example, in the most primitive condition exhibited in the genera, *Aplonis*, *Mino*, *Streptositta*, *Sarcops* and *Gracula*, there is a single, pneumatic tricripital fossa. In the more derived condition, e.g. *Sturnus*, *Sturnia*, *Saraglossa*, *Gracupica* and *Acridotheres*, there are two non-pneumatic tricripital fossae divided by a septum. The African genera, *Lamprotornis* and *Spreo* exhibit an intermediate condition, where a single or double pneumatic tricripital fossa is present.

Molecular work has shown that the genus *Sturnia* is distantly related to *Fregilupus* (Zuccon et al 2008; see below) and probably to the other Mascarene starlings as well, and like *Sturnia*, the Mascarene genera clearly exhibit the derived condition.

**Remarks.** The Réunion Crested Starling was mentioned in a number of accounts, but few provide any details. The species was first noted by a Père Vachet (1671; see Lougnon 2005) in 1669, who listed the bird along with other Réunion avifauna, but it was Dubois (1674) in 1671–2 who gave the first detailed description:

Hoopoes or calandres, with a white tuft on the head, the rest of the plumage white and grey, a long beak, and feet like a bird of prey. They are a little smaller than young pigeons. It is another good game [to eat] when fat [my translation].

Early accounts of *Fregilupus* all concur that the bird was tame and numerous and could easily be killed with sticks. The birds appeared to be able to tolerate this persecution, but even as early as 1704 Feuilley (1705), who was sent from France to make a detailed report about the island (Cheke & Hume 2008), noted their vulnerability to cats which were introduced a year before (Mourer-Chauviré et al. 2006):



**FIGURE 22.** Comparison of femora (right side) of Mascarene starlings with *Acridotheres tristis* cranial aspect. **A.** AMNH 306353 *Fregilupus varius* ♂; **B.** MNHN MAD8850 *Cryptopsar ischyrhynchus* gen.nov. sp.nov. u/s; **C.** NHMUK A1473 *Necropsar rodericanus* u/s; **D.** NHMUK S/1957.15.9 *Acridotheres tristis* u/s. Scale bar = 10mm.

Hoopoes and merles [*Hypsipetes borbonicus*] are the same fatness as those in France, and are of a marvellous taste, which are fat at the same time as parrots, living on the same foods. In order to catch them, hunting was done with staffs or long thin poles from six to seven feet in length, though this hunt is infrequently seen. The marrons [feral or perhaps escaped] cats destroy many. These birds allow themselves to be approached very closely, so the cats take them without leaving their places [my translation].

For the next century or so, nothing more was recorded about *Fregilupus* on Réunion; even the natural historian Bory de St. Vincent (1804), who wrote a lengthy and detailed report about the island and its fauna, failed to mention it. However, specimens began to arrive in Europe in the second half of the 18th century.

It is not at all clear how many specimens arrived in Europe during this time or which specimen or specimens provided the basis for descriptions and models; most surviving skins of *Fregilupus* were collected during the first half of the 19th century. Legendre (1929) made an extensive study of the skin specimens, but he found that the date when registered by the various museums did not always reflect the actual date of receipt of the specimen in the museum. There has been a suggestion that one of the surviving skins in Paris, which was acquired along with other specimens by Louis Dufresne in the late 18th century (see Jouanin 1962), may be the same specimen on which De Montbeillard (in Buffon 1779), followed by Boddaert (1783), had based their description (Oustalet 1897), hence the type specimen, but confirming data are lacking (see also Holotype). The botanist Philibert Commerson probably supplied the skin and Oustalet (*ibid*) thought that it was the same bird drawn by the artist, Paul Philippe Sauguin de Jossigny (see below). However, this also remains in doubt (Legendre 1929).

The individual drawn by Jossigny in the early 1770s was probably a live specimen (Fig. 7). My examination of Jossigny's *Fregilupus* drawing revealed that he had written and signed a note in pencil on the bottom of the original sketch (Archives Nationales, Paris, manuscript no: 282 (II)), which states: "For the greatest accuracy it is necessary that the engraver represents the crest of the bird not as straight up but at an angle going forward across the front of

the head [my translation].” This recommendation was followed by Daubenton in his coloured depiction of *Fregilupus* (De Montbeillard in Buffon 1779) (Fig. 8a), which strongly indicates that Daubenton had based his illustration on Jossigny’s rendition. The bird is also figured on the ground, rather than on a perch, which prompted Oustalet (1897) and Legendre (1929) to suggest that this was indicative of terrestrial habits. The robust pelvic elements of *Fregilupus* would certainly support this assumption. It is not clear whether Jossigny drew the undated illustration of *Fregilupus* while on Réunion from December 1770 to December 1771, when he accompanied Commerson to the island (Ly-Tio-Fane 1976), or at a later date. Jossigny executed two drawings of a live Rodrigues Parakeet *Psittacula exsul*, the only known illustrations of the bird in life, which had been sent to him while on Mauritius around 1772 (Hume 2007). It is therefore possible that he drew a captive *Fregilupus* on Mauritius. Murie (1874) thought that only two illustrations could be considered original and probably based on live birds (he was unaware of the Jossigny illustration), those being the coloured renditions by Daubenton (De Montbeillard in Buffon 1779) (Fig. 8a) and by Barraband (in Levaillant 1807) (Fig. 8b). Another illustration of note is one by Roussin (1860–68) (Fig. 8c), which accompanied the account of *Fregilupus* by Morel (1863). However, all of these appear to have been based on stuffed individuals, or in the case of Daubenton, a modification of Jossigny’s image. It is more likely that no live specimen ever left the Mascarenes, and that only Jossigny’s depiction was based on a live bird.

De Montbeillard was given information about a dissected specimen by a local resident, probably Commerson, who, along with other overseas naturalists, was a usual source of information for the 18th century French encyclopaedists (Cheke 2009), and noted that:

In its stomach are found seeds, berries of *pseudobuxus*: its weight [the bird’s presumably, not the stomach] is four ounces [113 gr]; but this must vary a lot and be more considerable in June and July, at which time the bird is very fat [my translation].

“*Pseudobuxus*” was probably the small forest tree or bush, *Eugenia buxifolia* (Myrtaceae) (Cheke & Hume 2008), which has conspicuous, orange, sweet-tasting berries that are 10–20 mm in diameter. It can reach a height of 10 m and is found in all types of forest from the coast up to 1800 m elevation (Pailler *et al.* 1998). Levaillant (1807) did not make it clear whether or not he had a live specimen when he wrote his account, but he managed to obtain information about *Fregilupus* from a local inhabitant on Réunion:

Buffon assures that this bird is in the île de France [Mauritius], in Madagascar, and in the Cape of Good Hope; but what is certain in this regard is that I encountered it in none of the districts of the continent of Africa through which I travelled, and that an inhabitant of l’île Bourbon assured me that the species was very abundant there, living in large flocks and frequenting the humid places and marshes; that they named it Martin, and that it caused great damage to coffee trees of which it was very greedy for the fruit [my translation].

The introduced Indian myna *Acridotheres tristis* and *Fregilupus* were both called ‘Martins’ by the inhabitants, and it is a name that is still used for *Acridotheres* on Réunion. Lesson (1831), having placed *Fregilupus* amongst the Corvidae, stated that they “have the manners and habits of crows [my translation]” but gave no indication as to where he got such information. The above accounts were the last to mention any details about the habits of *Fregilupus* while it was extant.

**Transportation of specimens.** During the first half of the 19th century, *Fregilupus* was a popular cagebird, both on Réunion and on Mauritius, with some being taken to the latter island by visiting Mauritians. Bouton (1878) wrote to Edward Newton at Cambridge about a pair of transported *Fregilupus* in 1817 (and here repeated verbatim), but noted that they were by then already becoming scarce:

When I came back from Bourbon in 1817—one of the passengers had in a cage two of the birds alive—therefore they were still existing at that time—he bought them as far I can recollect at the bazaar of St. Denis—but that he was told that they became rather scarce.

Renoyal (Probst & Brial 2002) reported the capture of two birds in March 1822 in the Bras du Chevrettes (Fig. 2), of which one died in April, and in November of the same year, Renoyal also noted that four hoopoes were intended for sale and destined for Mauritius (*ibid*). The natural historian, Julien Desjardins, who had an aviary at Flacq in the mid-east of Mauritius (Fig. 4), received four live birds in 1835 (in Milne-Edwards and Oustalet 1893), and stated:

My friend, Marcelin Sauzier, has sent me four alive from Bourbon in May, 1835. They eat everything. Two have escaped some months afterwards, and it might well happen that they will stock our forests [translation from Cheke & Hume 2008].



**FIGURE 23.** Comparison of tibiotarsi (left side) of Mascarene starlings compared with *Acridotheres tristis*, cranial aspect. **A.** AMNH 306353 *Fregilupus varius* ♂; **B.** MNHN MAD6830 *Cryptopsar ischyrrhynchus* gen.nov. sp.nov. u/s; **C.** NHMUK A1474 *Necropsar rodericanus* u/s; **D.** MNHN MAD6964 *Acridotheres tristis* u/s. Scale bar = 10mm.

Desjardins had written a manuscript entitled 'History of Mauritius' in preparation for publication (Oustalet 1897; Toussaint 1972), but the manuscript was never published and is now lost (see Hume 2011). Fortunately, Milne-Edwards & Oustalet (1893) and Oustalet (1897) published extracts from it before its disappearance. Desjardins (1837) further stated that:

We are not afraid to say today that the Huppe, which lives in the forests of Bourbon and are raised in cages, may have become naturalised in Mauritius. Mr. Autard presented one to us that had just been killed in the district of Savane [Savanne], and we ourselves had 4 which our colleague the elder Mr. Sauzier, long term correspondent in Bourbon, had brought us from that neighboring island and which, after a few months of captivity, took off and headed into the woods now so rare in the district of Flacq [my translation].



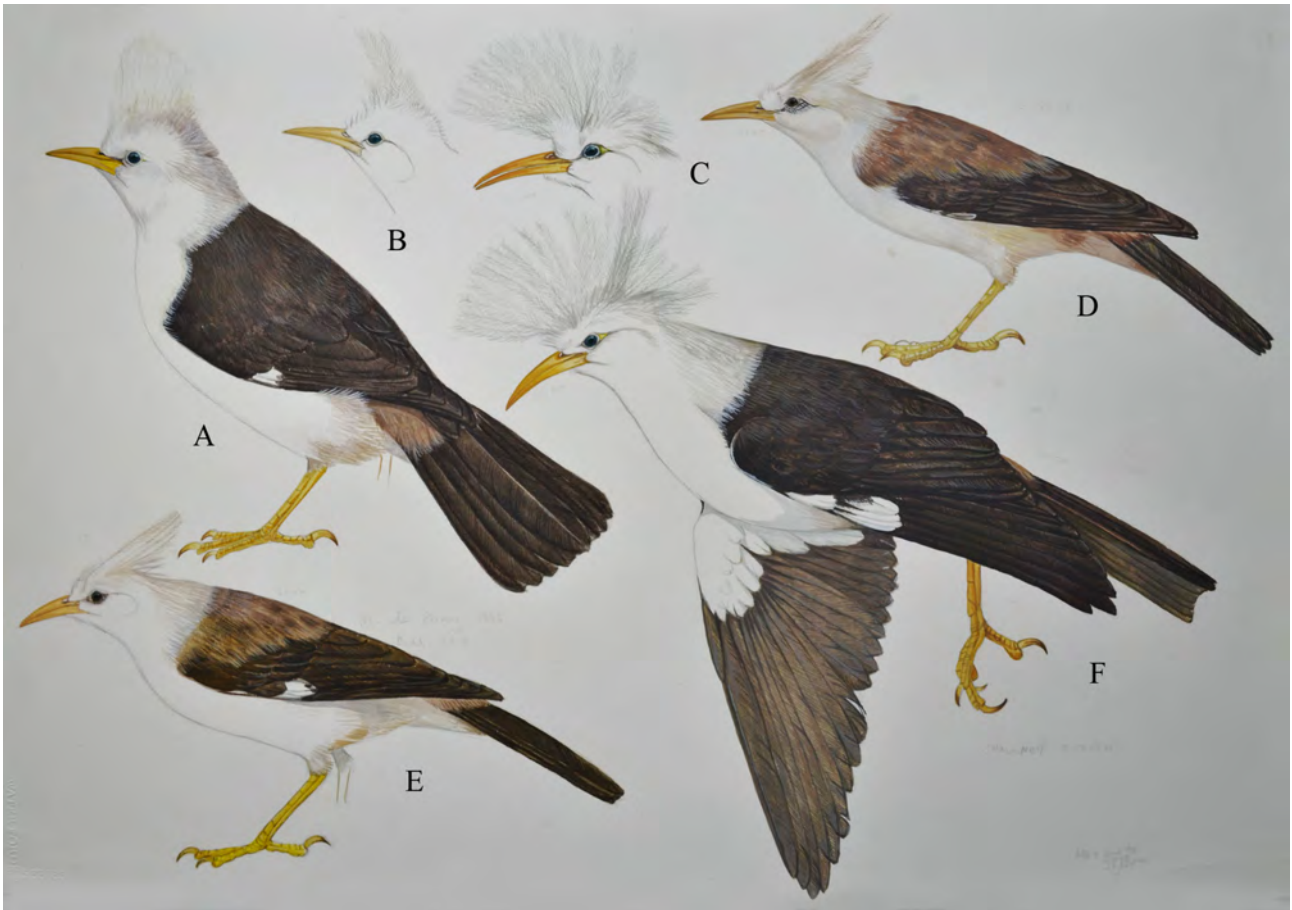


**FIGURE 24.** Comparison of tarsometatarsi (right side) of Mascarene starlings with *Acridotheres tristis*, dorsal aspect. **A.** AMNH 306353 *Fregilupus varius* ♂; **B.** MNHN MAD6486 *Cryptopsar ischyrrhynchus* gen.nov. sp.nov. u/s; **C.** NHMUK A1475 *Necropsar rodericanus* u/s; **D.** NHMUK S/1957.15.9 *Acridotheres tristis* u/s. Scale bar = 10mm.

The specimen killed in the District of Savanne was presented stuffed by the natural historian, François Liénard, at the 5 January 1837 session of the Mauritius Natural History Society (Milne-Edwards & Oustalet 1893), which implies that it had been shot in late 1836 (Cheke & Hume 2008). Liénard obtained it from a Mr Gustave Autard de Bragard, who remarked that he had often seen “considerable flocks” of them. As Desjardins reported that *Fregilupus* did not exist on Mauritius in 1826, Milne-Edwards & Oustalet (1893) thought Autard’s 1837 observation confirmed that a feral population had become established from Desjardin’s birds which had escaped in 1835. It is not known if there were earlier introductions of *Fregilupus* from elsewhere that were then breeding, but Legendre (1929) questioned the fact that only one escaped pair could generate considerable flocks of birds in less than two years. The district of Savanne is situated in south Mauritius, approximately 35 km south of the District of Flacq, where Desjardins kept his aviary (Fig. 4). Therefore at least one of the escapees had seemingly made it some distance from the original source. Regardless of the numbers of escaped birds, the feral population of *Fregilupus varius* on Mauritius, if indeed it was ever a population, lasted less than a decade. In 1839, Desjardins returned to Paris and presented the museum with his manuscript and two pickled *Fregilupus* specimens (Milne-Edwards & Oustalet 1897; Legendre 1929), presumably the two remaining birds from his aviary. It is possible that the surviving skin in the MU is the specimen shot by Autard (Cheke & Hume 2008), but the museum once had at least three specimens (Carié in Legendre 1929); two of which have now disappeared (pers. obs).



**FIGURE 25.** *Fregilupus varius* MHNT O2647 (Adult male?) (right), MHNT O2650 (juvenile) (left). Note the great difference in size.



**FIGURE 26.** Author's scaled illustration of *Fregilupus varius* skins held in the MNHN and MNHNT collections. **A.** MNHN 2000-756 u/s (adult female?); **B.** MNHN 2000-755 (juvenile?); **C.** MHNT O2647 u/s (adult male?); **D.** MHNT O2650 u/s (juvenile); **E.** MHNT O2649 u/s (juvenile); **F.** MNHNT O2648 u/s (adult male?).



**FIGURE 27.** A selection of skins of Southeast Asian black and white Sturnidae. From left to right: *Gracupica nigricollis* NHMUK 1915.12.18.105 ♂; NHMUK 1955.1.3651 ♀; *Leucopsar rothschildi* NHMUK 1969.41.820 ♀; NHMUK 1936.1.1.6 ♂; NHMUK 1937.11.4.1 ♀ juvenile; *Acridotheres melanopterus* NHMUK 1959.28.8 ♂; NHMUK 1959.28.11 ♀.

In the 1830s, it was still possible to secure skin specimens of *Fregilupus* on Réunion. In 1832, the naturalist and dealer Jules Verreaux personally shot an individual (now the skeleton at UMZC) (Murie 1874), but noted that by this time it had become so rare that his specimen may have been the last of the species (Renshaw 1922). However, in the same year, four specimens arrived at the Troyes Muséum (Demandre 1913; Ménégaux 1914), which included two juveniles (Figs. 26D, 26E). This important collection was presented by one M. Chaumet, who was born in Troyes and had been a physician on Réunion (Demandre 1913). In 1833 M. de Nivoy presented a skin (MNHN 2000-756) to Paris, and around the same time, another specimen became part of the Count de Riocour collection, which was later purchased for Rothchild's Tring Museum (Sharpe 1889a, 1889b). Milne-Edwards and Oustalet (1893) reported that a mounted specimen was sent from Réunion by M. Lepervanche-Mézières in June 1834. Lepervanche-Mézières was a member of the Société d'histoire naturelle de l'île Maurice (*ibid*), so presumably the skin was sent to Mauritius. A Corsican parish priest by the name of Lombardi sent at least six or seven skins of *Fregilupus* to his nephew, who was a student at the University of Pisa (Violani *et al.* 1999). These in turn were given to Paolo Savi, then professor and director of the natural history museum at the university, who distributed specimens to other Italian museums in 1844 (Salvadori 1876; Funaro & Angelini 1883; Salvadori 1912; Violani *et al.* 1999). Unfortunately, it is not known where Lombardi worked on the island or the precise dates when he collected the specimens, and this can be said for almost all of the above mentioned skins; only Verreaux's specimen and the four sent to Mauritius have precise years of collection. The British had taken control of Réunion from 1810–15, but by 1816 the island had been returned to French rule (Toussaint 1972). Almost immediately, the Congrégation du Saint-Esprit (spiritains) was founded, who were the only order providing priests in Réunion during this time (see Cheke & Hume 2008). It is very likely that Lombardi was a member of that order and had been sent to Réunion sometime prior to 1844. Therefore, the birds could have been collected anytime between 1816 and 1844.

Although the Réunion starling taken on Mauritius in late 1836 by Autard de Bragard was the last unequivocal date of collection, it is clear from the available evidence that specimens of *Fregilupus* could still be obtained during the 1830s, albeit as a rarity, and possibly the early 1840s, at least around Saint-Denis or from bird markets within. This was to change drastically over the next two decades.

**Extinction.** During the first half of the 19th century, changes were taking place on Réunion that were to have a grave negative impact on the avifauna. While populations of some birds such as *Hypsipetes* were in decline, those of *Fregilupus* appear to have crashed suddenly. Milne-Edwards and Oustalet (1893) and Legendre (1929) thought that competition for food with introduced mynas *Acridotheres tristis* was partly to blame for the extinction of *Fregilupus*. Mynas had been first introduced to Réunion in 1759 by Boucher Desforges, Governor General, to control locusts, but with limited success (Cheke & Hume 2008). They were subsequently persecuted by colonists in the mistaken belief that they were taking sown grain, and within the same year had either become rare or completely disappeared. A second successful introduction took place around 1762, after which the birds benefitted from edicts protecting them in 1767, 1774 and 1786 (Maillard 1862; Vinson 1867; Cheke 1987). As a result of protective legislation, the mynas had become extremely abundant and pests themselves, raiding fruit crops and robbing domestic pigeons of their squabs (Cheke & Hume 2008). In 1820, in order to control the birds, the authorities encouraged people to eat them, but this was not successful (Vinson 1867). However, within the next few decades their numbers were to plummet again due to persecution (Legras 1861; Milne-Edwards & Oustalet 1893). Therefore, *Fregilupus* had survived alongside mynas for nearly a century, so direct competition is unlikely to have been the cause. Furthermore, *Acridotheres* did not occur in the same habitat as *Fregilupus* (Oliver 1897), so competition, especially for insect food, was almost certainly not a factor.

Neville Manders (1911) was studying mimicry in Mascarene and Sri Lankan butterflies and questioned why this phenomenon had evolved on the islands. Most fortunately, he wrote in 1910 to his friend, Eugène Jacob de Cordemoy, a long-term resident on Réunion, asking for information about potential predators of butterflies. According to Manders, Cordemoy was in his 90th year, although in fact he was born in 1835, making him 75 years old at the time (Cheke & Hume 2008). Regardless, he was almost certainly the last living person at that time to have observed *Fregilupus* in life, and provided more information about the bird than any other observer:

I have known the bird you ask me about since childhood, namely the *Fregilupus varius* (old writers called it *F. capensis*), which has in fact entirely disappeared....

When I was a boy this bird lived in the forests of the interior of the island and never set foot nor wing in towns or inhabited places. It remained faithful to the forests where it bred, which it enlivened with its clear notes. I used to

hunt it then at an age when one is pitiless. I can see it now, a little larger than the white blackbird [merle blanc = *Coracina newtoni*], with a white crest on the head in the case of the male, the wings a blackish grey on the upper surface, the beak and feet yellowish. By no means shy, it was not frightened even by the sound of firearms, and after a regular slaughter one went off with dozens of these poor victims in one's game-bag.

After ten years spent in Paris I did not find a single one in the forests where formerly they flew about in flocks. All ruthlessly destroyed. I shall never forgive myself for the part, slight though it was, which I took in the matter. I lost my taste for sport and the best bag would not tempt me... We will now consider the feeding habits of this bird. Having raised several in the aviary, I can risk talking about it though I never saw one feeding in the wild state. In my aviary its food consisted of bananas, potatoes, and choux-choux, *Sechium edule* (boiled). But when left to its own instincts, it must, like the other winged denizens of the forest, have eaten insects as is done by its companion in the forests, the Bourbon Blackbird (*Hypsipetes olivaceous* [sic]) [now *H. borbonicus*], and as is the habits of most fruit-eating birds (from Manders 1911).

There has been much speculation about the seemingly almost instantaneous disappearance of *Fregilupus*. Cheke (1987) concluded that Cordemoy returned to Réunion around 1860–61, so the time he was referring to was the late 1840s or early 1850s, and that the bird was still common at that time. Cordemoy was born and probably brought up in St-André, near the entrance to Salazie, with the nearest forests on the eastern slopes of the Plaine des Fougères (Cheke & Hume 2008; Fig. 2). This was near the locality where Renoyal caught his *Fregilupus* specimens in 1822 (Renoyal 1811–38 in Probst 2000; Cheke & Hume 2008). It is not clear how far Cordemoy had to travel to reach the forests mentioned in his youth; a journey to the cirques was lengthy and arduous, but he seems to imply that he returned to the same, intact forest upon his return from Paris.

*Fregilupus* had survived alongside rats, cats, and a host of anthropogenic changes for two centuries, yet it apparently disappeared within a decade of Cordemoy's observation. Brasil (1912) was the first person to suggest that disease, introduced by mynas, was the probable reason for their rapid disappearance. Mason (1921) supposedly discovered two species of exotic ticks on museum skins of the extinct Huia *Heteralocha acutirostris* of New Zealand, which had arrived with the Indian Myna, *Acridotheres tristis*, the same species of myna introduced to Réunion. Based on this evidence it was thought that the ticks may have spread a disease fatal to the Huia (Hume & Walters 2012), and therefore a disease may have also been fatal to *Fregilupus* (Brasil 1912; Mason 1921; Cheke 1987; Cooper 1993; Wikelski *et al.* 2004; Smith *et al.* 2006; Cheke & Hume 2008; Hume & Walters 2012). However, recent work (Ricardo Palma and Trevor Worthy *pers. comm.* 2013) have shown that Mason had misidentified the ticks. They were in fact referable to the cattle tick, *Haemaphysalis longicornis* Neumann, 1901, a species not known to carry any avian disease. But this still does not rule out the possibility that introduced avian diseases were a factor in the extinction of Mascarene birds, just as they were in the Hawaiian Islands (Warner 1968; van Riper & Scott 2001; van Riper *et al.* 2002; Smith *et al.* 2006; Hume & Walters 2012).

The accidental introduction of rats has also been implicated in the extinction of *Fregilupus*. The Black Rat *Rattus rattus* arrived between 1672 and 1676, because by 1676 they had reached plague proportions (Cheke & Hume 2008). The Brown Rat *Rattus norvegicus* arrived in 1735, and together they wreaked havoc on the inhabitants' crops and preyed on their domestic animals (*ibid.*). Legendre (1929), quoting from an anonymous source about black rat numbers in the forests, remarked:

These rodents would have been able to destroy the nests of birds [i.e. *Fregilupus*] and easily take a good many incubating hens, because *Fregilupus* nested in the trunks of trees, similarly to that of Hoopoes [*Upupa epops*] and Starlings. We know that at the time of the disappearance of *Fregilupus*, rats lived in the forests of l'île Réunion in considerable numbers. They took shelter and nested in numerous families in the holes of the trees where they accumulated [food] supplies; and it was easy to find trunks of trees containing more than fifty individuals [my translation].

It is difficult to attribute rats as a major factor in the extinction of *Fregilupus*, as the birds had survived their presence even longer than that of mynas. No doubt rats would have preyed on the birds' eggs and young, and perhaps competed for food, but other species of starlings, e.g. Polynesian Starling *Aplonis tabuensis*, can tolerate heavy rat predation and also nest in tree cavities (Hume 2002).

It has been suggested that the extinction of the Réunion Slit-eared Skink *Gongylomorphus borbonicus*, which had succumbed to predation from the introduced Wolf Snake *Lycodon aulicum* between 1840 and 1860, and competition from introduced mynas for large insects, may have seriously affected the remaining populations of *Fregilupus* (Cheke & Hume 2008). The Mauritian passerine genera *Hypsipetes* and *Coracina* feed their young on

lizards, especially *Phelsuma* day-geckos (Safford 1996; Cheke & Hume 2008); therefore, *Fregilupus* may have lost an important food source during the raising of young. However, Réunion has two extant *Phelsuma* day-geckos and a *Cryptoblepharus* skink. Being an omnivore, and reported to “eat anything” in captivity, it is unlikely that *Fregilupus* declined as result of the extinction of a skink when other prey items were evidently still available.

But other factors seem likely to have been equally or more significant. The decline of *Fregilupus* coincided with a massive increase in deforestation from the 1830s, especially as coffee plantations began to give way to sugar cane. Coffee plantations would have provided at least some form of substitute evergreen forest for *Fregilupus*, and the birds certainly ate the coffee beans (Levaillant 1807). Cordemoy mentioned that *Fregilupus* never occurred near settlements or inhabited places, so the emancipation of the slave population from 1848 (Toussaint 1972) must also have had an impact on the numbers of birds. The cirques of Salazie, Cilaos and Mafate are volcanic calderas formed from the collapse of the Piton des Neiges shield volcano (Rivals 1989; Fig. 2), and due to their isolation, they remained comparatively pristine until the early 19th century. However, the rush to cultivate the cirques by the ex-slaves and white peasantry left Salazie largely ruined by 1850, followed by Cilaos and Mafate in 1868 (Cheke & Hume 2008); Salazie in particular was a stronghold for *Fregilupus* (Vinson 1888). Between 1848 and 1880, the forest had been cleared up to 500 m on the windward side and to 700–800 m in the west (Cheke & Hume 2008), which may have forced *Fregilupus* into marginal, less suitable habitat at the limits of its altitudinal range. Furthermore *Fregilupus* nested in tree holes (Legendre 1929), which is common to most starlings (Feare & Craig 1999; Craig & Feare 2009), therefore the loss of suitable nesting trees may have made *Fregilupus* increasingly vulnerable.

The significance of over-hunting has generally been over-looked, but in my opinion this was probably the primary cause for the rapid extinction of *Fregilupus*, once the forests were opened up. There was a large-scale increase in the human population during the first half of the 19th century, which had more than doubled in number between the 1830s and 1870s. Over 30,000 ex-slaves and large numbers of the white peasantry established small-holdings during this period (Toussaint 1972), which resulted in the occupation and degradation of formerly undisturbed forest regions, especially the mountain cirques. In 1704, the population of Réunion numbered 734 inhabitants, which increased to 61,000 by 1789, and 101,000 by 1830. Between 1850 and 1870 the human population had reached 212,000 (Legendre 1929; INSEE 2012). Human population declined to 163,000 by 1887 (INSEE 2012), after the opening of the Suez Canal, because the island was no longer considered a suitable staging post en route to the East Indies (Leguen 1993). Legendre (1929) made important notes about the effects of over-hunting in the 19th century on Réunion:

Natives and settlers, with their more sophisticated weapons, and advancing deeper into the country, must have made a merciless war on this bird, which could very well be presented on the table as small game. Besides, the bird came for food in plantations, and Levaillant had learned from an inhabitant of the island that *Fregilupus* lived in big flocks and caused great damage to coffee trees. It should be noted that at the time of the disappearance of the bird, the island was well inhabited, the prosperous businessmen and Frenchmen were also very numerous, and all were hunters [my translation].

A law was implemented in 1821 ordering the extermination of any birds that destroyed food-grain (Delabarre de Nanteuil 1844; Cheke & Hume 2008). *Fregilupus* was already known for its destructive capabilities in coffee plantations, so no doubt at this time it was heavily persecuted. Bouton (1878) was told by a local resident that by 1817 the bird had already become scarce, and in 1832 Jules Verreaux thought that he may have shot the last one (Renshaw 1922). There were also sharp declines in other species of birds. In 1834, Renoyal (in Probst 2000) noted that while hunting the mountain forests of Sainte-Suzanne, he saw only two merles or *Hypsipetes* bulbuls when a decade before several dozen could be shot in a day. The former distribution of *Fregilupus* is unknown, as few accounts provide any details. However, it is likely that by the 1830s populations had become isolated due to over-hunting and deforestation. It appears that *Fregilupus* was not favoured by some of the inhabitants as a game bird, because Vinson (1877) noted that the creoles would not eat them. On the other hand, Milne-Edwards & Oustalet (1893) thought that the settlers exterminated them in part for their flesh, as the mynas had been almost hunted out for the same reason. No doubt *Fregilupus* would certainly have been shot at every opportunity because of its pest status; they were obviously easy targets and could be killed en masse.

Being a conspicuous and confiding bird, living in large flocks and with no fear of humans, it is not unreasonable to suggest that two decades of intense human hunting pressure on an already declining population could easily have been the *coup de grâce* for *Fregilupus varius*.

*Fregilupus* was thought still to exist in the 1860s, but was considered rare. Legras (1861) records its decline and the increasing rarity of other birds, but provides no exact date for his observation, which was presumably in the 1850s:

The Huppe has become so rare that we have scarcely seen a dozen in our travels to discover birds; we were even grieved to search in vain for a specimen in our museum. Merles [*Hypsipetes borbonicus*] do no more than sparsely inhabit the more distant forests, the martins [*Acridotheres tristis*] cannot be counted by the hundreds as before, and one sees the number destroyed every day, it is feared that we'll see them disappear entirely [my translation].

Legras (1861) and Maillard (1862, 1863) recorded *Fregilupus* as rare, Morel (1863) that it “becomes rarer every day” and Coquerel (1864) that it was “very rare today.” Vinson (1868) declared that it was currently becoming “rarer by the day,” and even in the 1870s Lantz (in Hartlaub 1877) thought the bird was not extinct and that he might be able to procure a specimen. As late as 1877, Vinson (1877) clung to the belief that *Fregilupus* still survived, despite noting that forest fires may have finished off the last remaining birds:

Two formidable fires, which our great forests have fallen victim to in days of extreme drought, have completed their annihilation, and today, as I write these lines, perhaps there is not a single one left in the entire island. And it really is irreparable damage [my translation].

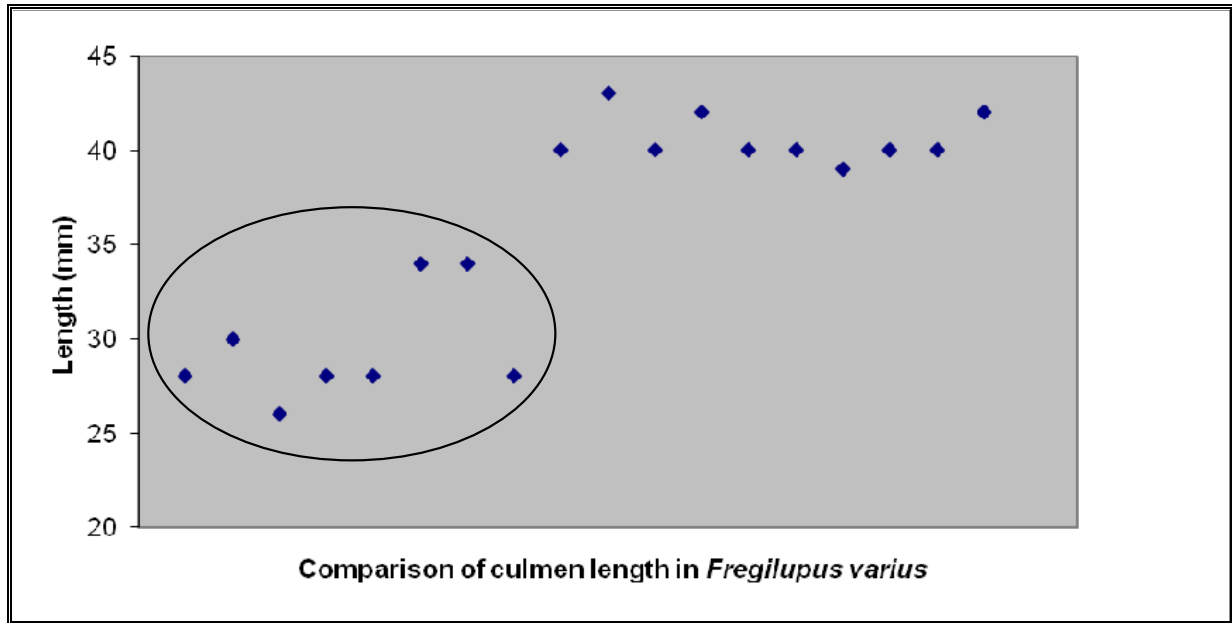
The accounts from the above mentioned Réunionnais authors, Legras (1861) and Morel (1863), appeared in a five-volume encyclopedia on the island's history, culture and natural history by Albert Roussin (1862–68), which included an illustration of *Fregilupus* (Fig. 8c). In a second edition (Roussin 1879–83), Montforand (1880), while deploring the disappearance of the native fauna on Réunion, stated that “The Huppe, which one does not encounter more than a few samples in the most remote places [my translation],” which suggests that *Fregilupus* may have survived until the 1870s. However, Legendre (1929) noted that the dates of publication in this work did not reflect the actual time that the events took place. Regardless of the dates, all of the accounts that appeared in Roussin's work, as well as those of Maillard (1863), Coquerel (1863a, 1863b, 1864) and Vinson (1868, 1877), are almost certainly based on hearsay. It is a great pity that as *Fregilupus* headed towards extinction, there was no attempt by any of these naturalists to study its ecology, to document the causes of its decline, or to bring birds into captivity. It was the Dutchman, François Pollen (Schlegel & Pollen 1868), while collecting specimens with D. C. van Dam for the natural history museum at Leiden (RMNH), who provided a more realistic and certainly the last detailed account of the birds' status:

This species has become so rare that one has not heard them mentioned for the past ten years. It has been destroyed in all coastal parts, and even in the mountains not far from the coast. Trustworthy persons, however, have assured me that they must still exist in the forests of the interior, near St. Joseph. The old Créoles I consulted told me that, in their youth, these birds were still common, and that they were so stupid they could kill them with sticks. The Créoles of the island give this bird the name, Hoopoe [my translation].

It is very likely that *Fregilupus* had completely disappeared by 1860, or even earlier, perhaps two decades before.

**Ecology and behaviour.** Little was recorded about the ecology and behaviour of *Fregilupus*. From the meagre information available, we know that it lived in large flocks, inhabited marshy areas and humid lowland and montane forests (Levaillant 1807), and nested in tree cavities (Legendre 1929). *Fregilupus* was omnivorous, as are most starlings, and fed on fruit, seeds, vegetable matter and insects (De Montbeillard in Buffon 1779; Vinson 1877; Cordemoy in Manders 1911). The strong jaw musculature, the robust pelvic elements and large feet and claws suggest that *Fregilupus* was an opportunistic forager in all types of forest, and clearly capable of utilising the forest understorey and canopy, as well as ground substrates. Morioka (1996) examined the skull of *Fregilupus* and concluded that its feeding technique was probably the same as that of the Hoopoe *Upupa epops*, which feeds in soft substrate using a combination of probing and gaping. The greater development of the processus retroarticularis and associated musculature would make the jaws of *Fregilupus* more powerful than those of *Upupa*, however.

The tongue of *Fregilupus* was sharp and arrow-shaped, with a shallow-grooved horny body, the end slightly bifurcated, and frayed on the edges towards the tip (Levaillant 1807; Murie 1874; Milne-Edwards & Oustalet 1893). It was also long and slender, nearly reaching the tip of the beak (Levaillant 1807) or reaching halfway (Milne-Edwards & Oustalet 1893). Due to the ventral surface being convex and longitudinally furrowed, Murie (1874: 483) suggested that the associated musculature enabled its rapid protrusion and withdrawal. This may have been an adaptation for feeding on soft fruit, nectar and pollen or a tool for extracting invertebrates when gaping.



**FIGURE 28.** Comparison of culmen length in *Fregilupus varius*. The shorter, straighter-billed specimens (circled) are here interpreted as probable females, and suggest that the species was sexually dimorphic.



**FIGURE 29.** The southern islets of Rodrigues. View looking south.





**FIGURE 30a.** Ile Gombrani, with Ile Pierrot in the distance. View looking south.



**FIGURE 30b.** View from the centre of Ile Gombrani. The vegetation today is dominated by introduced trees and shrubs.

Despite his long familiarity with *Fregilupus*, Vinson (1877) provided little extra information about the habits of the bird:

Now these daughters of the wood, when they were numerous, flew in flocks and went thus in the rain forests, while deviating little from one another, as good companions or as nymphs taking a bath: they lived on berries, seeds and insects, and the créoles, disgusted by the latter fact, held them for an impure game.

Sometimes, coming from the woods to the littoral [coast], always flying and leaping from tree to tree, branch to branch, they often alighted in swarms on coffee trees in bloom, and there was in the past the testimony of an inhabitant of the Island of Bourbon, said the naturalist Levaillant, that they caused big damage in coffee trees by making the flowers fall prematurely.

But it is not the white flowers of coffee that the hoopoes were searching for and thus behaving so, it was for the caterpillars and insects that devoured them; and in this they made an important service to the silviculture of the Island of Bourbon and the rich coffee plantations, with which this land was then covered, the golden age of the country! [my translation].

The forests that once formed the prime habitat of *Fregilupus* were largely destroyed or seriously degraded by the 1880s (Cheke & Hume 2008). Vinson (1888; Cheke & Hume 2008), writing about his childhood 57 years after the event, described the forests of Salazie in 1831, where *Fregilupus* was once abundant. This is the only account that gives any insight into the natural habitat of the bird:

We passed through the shadiest coverts, next to the most magnificent trees, through dense refreshing thickets where the soil disappeared under a carpet of green moss as if an emerald coat spangled with strawberries as red as rubies. . . . On the plateau where today exists the true village of Salazie—the village of Petit Sable—there was a thick forest, frequented by clouds of black and white huppés the size of a pigeon. This powerful insectivore, whose unique habitat was Réunion, has today completely disappeared from creation. Around the Mare à Poules d’Eau it was still virgin forest and its thousand streams, the forest always full throughout with black parrots [introduced *Coracopsis* sp.] of which one can no longer find a single pair in the whole island [translation from Cheke & Hume 2008].

The song of *Fregilupus* was inadequately described, but presumably was loud and complex, as in other starlings (Feare & Craig 1998; Craig & Feare 2009). Only three accounts provide any details. Vinson (in Roussin 1860–68; Cheke & Hume 2008) retold the exploits of local hunters who described “the monotonous bleating of the merles, the song of the huppe, and the murmurings of a few birds scattered in the foliage [translation from Cheke & Hume 2008]. Vinson (1877), while lamenting about the fact that *Fregilupus* was probably extinct, stated that “the bright and cheerful whistle will no more be heard in the middle of our woods [my translation],” and Cordemoy (in Manders 1911) that *Fregilupus* made “clear notes.”

Vinson’s (1877) remark that *Fregilupus* travelled from the woods to the coast is almost certainly due to intra-island movement, notably vertical migration. Dubois (1674) in March 1671–September 1672 stated that a number of Réunion bird species, including *Fregilupus*, spent six months in the lowlands and six months in the mountains. Boyer (in Loughnon 2005) in May 1671 was more specific, and noted that the pigeons descended to the lowlands from November until May and the parrots from March until November (see Hume 2011). The latter dates correspond with the cool austral winter, which initiates a food shortage in the highlands (Vaughan & Wiehe 1937; Jones 1987), forcing the birds to descend to the lowlands to feed. The birds were particularly sought after by the inhabitants during this time, as they were at their fattest and best to eat (Boyer in Loughnon 2005; Hume 2011). De Montbeillard (in Buffon 1779) recorded that *Fregilupus* was “very fat” in June and July, and Feuilley (1705) in May 1704–April 1705 that it was very fat after eating the same foods as the parrots. These observations suggest that *Fregilupus* undertook vertical migration at the same time as the parrots, descending to the lowlands from March to November (austral winter), and feeding on the same type of food. Furthermore, almost all Mascarene birds breed during the austral summer (November–June) (Cheke 1987; Jones 1987; Impey *et al.* 2002), so it is likely that during that time *Fregilupus* returned to the mountain forests to breed. It is also possible that as *Fregilupus* was an adaptable species, and presumably quite capable of surviving in the lowlands year-round, vertical migration may have only involved adult breeding birds and not the entire population.

**Sexual and age dimorphism.** Milne-Edwards & Oustalet (1893) and Hartert in Rothschild (1907b) suggested that *Fregilupus* was sexually dimorphic, the males being larger than females, having a longer and slightly more decurved bill with a bigger crest (Figs. 6, 26). However, Brasil (1912) and Legendre (1929) were both cautious about making such determination, especially as only three individuals were sexed, all of them males, and that no consideration of age or individual variation was taken into account. The size differences were based in part on the four Troyes specimens, the two smaller having been variously labelled as juveniles (Sharpe 1890) or females (Hartert in Rothschild 1907b). The plumage colouration of the two smaller Troyes (MHNT) specimens differs from adults, and I concur with Sharpe that they represent juvenile birds (Figs. 25, 26D, 26E). Sharpe (1890: 194) refers to a juvenile skin or skins held at the “Paris Museum” (MNHN), but the specimen that he was most likely referring to (MNHN2000-755), does not exhibit the same degree of juvenile characteristics as those of the Troyes skins. The juveniles of some SE Asian, predominantly black and white starlings are also browner, especially *S. erythropygia*, Bali Starling *Leucopsar rothschildi*, Black-winged Myna *Acridotheres melanopterus* and Black-collared Myna *Gracupica nigricollis* (Fig. 27).

My analysis of the two juvenile *Fregilupus* shows further intraspecific differences, which suggests that either one is younger than the other or that they represent juvenile male and female (Fig. 26). Adult birds measure around 300 mm in total length, whereas the smaller “juvenile” specimen (MHNT O2650) measures 240 mm in total length and the larger (MHNT O2649) measures 260 mm. The smaller one also differs from the larger one in being more rufous on the back, the light rufous more extensive on the underside, the white primary coverts browner and much less distinct, and the bill slightly deeper, which suggests that the smaller bird was younger.

Measurements of culmen length from Salvadori (1876), Funaro and Angelini (1883), Angelini (1912), Brasil (1912) and Legendre (1929), taken with my own data, suggest that there were sexual differences in bill length and shape in *Fregilupus* (Fig. 28). Out of 20 skins, including the two lost Italian specimens, from which only the measurement of culmen length and shape can be ascertained, 10 have a longer, more decurved bill (Hume & Violani in prep). Furthermore, the primary coverts in these 10 birds are larger and more distinct than in the straighter-billed specimens (*ibid*). Brasil (1911) suggested that either two races or two sexes were involved. The different bill shapes certainly appear to represent sexual dimorphism, but dimorphism in other factors, e.g. total length and crest size, are much less evident.

Rather confusingly, Cordemoy (in Manders 1911; see above) stated that a white crest only occurred in the male. Legendre (1929) was puzzled by this remark, as it suggested that only males had been collected, but as

Cordemoy was reciting observations made over 50 years earlier, it is likely that his remark was erroneous. Furthermore, almost all museum skins of *Fregilupus* were mounted with an erect crest, suggesting that this was its natural position in life (e.g. Sharpe 1890). Vinson (1877) resolved this issue when he eloquently described the natural position and function of the crest in a living bird:

But what especially is this marvel of simplicity and elegance; it is a beautiful white crest composed of feathers of various lengths but higher in the middle, very flexible, barbs disunited, mobile, which curl forward as in a crest of a cockatoo. When anxious, happy, surprised or angry, the bird erects them to his liking: these feathers, which all combine to form the crest, go down as if bowing, and are shortest towards the midline. Their exquisite lightness, their charming tenuity is such that they resemble those, fine and delicate, also disunited, that compose the rich and splendid tail of a Bird of Paradise [presumably *Paradisaea*] [my translation].

## Genus *Necropsar* Günther & Newton 1879

*Necropsar* Günther & Newton, 1879 (ex Slater MS) 168: 427, type species *Necropsar rodericanus*.

*Testudophaga* Hachisuka, 1937, p. 212, type species *T. bicolor* Hachisuka (= *Necropsar rodericanus*)

*Rodriguites* (Cowles) in Strahm, 1989b, p. 39. *nomen nudum*, type species *R. microcarina* (Cowles) *nomen nudum*.

**Etymology.** Greek *nekros*, dead and *psar*, starling, in reference to the starling being known only from fossils.

**Revised diagnosis.** *Necropsar* is distinguished from other Mascarene sturnids by the following characters:

**Cranium:** comparatively dorso-ventrally compressed; frontal wide; crista nuchalis transversus oval-shaped with distinct protruding prominentia cerebellaris; foramen n. optici large, larger than fonticuli orbitocraniales, which is divided into two in one specimen.

**Rostrum:** long and comparatively wide, with a large oval nasal opening; dorsal os nasale wide; os premaxillare robust and comparatively straight.

**Mandible:** rostrum mandibulae wide and sharp; processus mandibulae medialis small; single small fenestra rostralis mandibulae; rostrum mandibulae deeply excavated; in lateral view, proximal ends comparatively deep and robust; processus retroarticularis robust, extended and directed medially. **Coracoid:** small and comparatively gracile.

**Sternum:** processus craniolateralis long and blade-like and deflected laterally; spina externa broadly bifurcated; apex carinae extremely reduced with little extension anterior to pila carinae; carinae sterni shallow; fenestra medialis reduced.

**Humerus:** gracile; shaft curved; tuberculum ventrale small; two tricipital fossae; tricipital fossa II not completely enclosed and separated from tricipital fossa I by medial bar; tricipital fossa I open distally communicating with tricipital fossa II; processus supracondylaris dorsalis reduced, with little proximal extension; crista deltopectoralis reduced, shallow in dorsal view.

**Ulna:** small and comparatively gracile.

**Carpometacarpus:** small; pronounced processus extensorius; no extension of os metacarpale minus distal to os metacarpale majus.

**Femur:** large and robust, particularly at proximal and distal ends; shaft straight with proximal and distal expansion; sulcus intercondylaris deeply excavated; facies articularis acetabularis comparatively large; in caudal aspect, sulcus patellaris shallow proximal to condyles.

**Tibiotarsus:** large and robust; shaft broad and expanded, particularly proximal to distal end; tuberculum retinaculi m. fibularis distinct; sulcus extensorius deeply excavated; pons supratendineus large; crista cnemialis cranialis broad and expanded; impressio ligamenti collateralis medialis deep emphasising a ridge distal to crista cnemialis cranialis.

**Tarsometatarsus:** long and robust; shaft comparatively straight; trochleae expanded; impressio retinaculi extensorii generally without bridge, but present in one specimen (NHMUK A1475); crista medialis hypotarsi large and square-shaped; foramen vasculare distale deeply excavated; distinct ridge along facies dorsalis; fossa metatarsi I extends further proximad, with indistinct medial ridge; in ventral view, trochlea metatarsi III wide and indistinctly larger than trochlea metatarsi II; fossa parahypotarsalis medialis not situated in distinct groove.

## †Rodrigues Starling *Necropsar rodericanus* Günther & Newton, 1879

*Necropsar rodericanus* Günther & Newton, (ex Slater MS) 1879, 168: 427 (Rodrigues).

*Testudophaga bicolor* Hachisuka, 1937, p. 212 (Ile au Mât = Ile Gombrani).

Babbler, **sp. nov.** Cowles, 1987b: p. 99 (Rodrigues).

*Rodrigues microcarina* (Cowles) in Strahm, 1989b, p. 39. *nomen nudum*.

**Lectotype:** Henry H. Slater had written a manuscript describing the Rodrigues starling (Slater *c.*1874), which presumably was to appear in volume 168 of the Philosophical Transactions of the Royal Society in 1879 (see below). Slater assigned the name, *Necropsar rodericanus*, to a large series of skeletal specimens, which was subsequently used by Günther & Newton (1879: 427) to formally describe the bird. Slater's starling bones were deposited in the NHMUK, but Günther and Newton also used Rodrigues starling material held at the UMZC. Günther & Newton (1879: figs. A–G) figured cranial and postcranial bones of *Necropsar rodericanus* in their original description, but failed to designate a holotype. The specimens they referred to are housed at the UMZC and NHMUK. I have studied both collections and conclude that only three individual fossil specimens can be recognised as clearly being the same as illustrated and described by Günther & Newton. These are the NHMUK cranium (Günther & Newton 1879: Pl. 42, Fig. A = NHMUK A9050) (Figs. 9, 10), rostrum (Günther & Newton 1879: Pl. 42, Fig. A = NHMUK A1468) (Figs. 9, 10), and an incomplete mandible (Günther & Newton 1879: Pl. 42, Fig. Aa) (= UMZC 566). As Günther & Newton (1879: 423) erroneously referred some post cranial specimens of *Necropsar rodericanus* from the syntype series to *Acridotheres tristis* (e.g. NHMUK A1474 right tibiotarsus; NHMUK A1475 right tarsometatarsus), I therefore designate the most diagnostic specimen (cranium NHMUK A9050; formerly NHMUK A1468) as the lectotype. This particular specimen was illustrated in Günther & Newton (1879: Pl. 42, Fig. A) (Figs. 9, 10), and was collected by Henry H. Slater between September 14 and December 15, 1874, from an unspecified cave on the Plaine Corail, an extensive limestone plain in southwest Rodrigues (Fig. 3).

**Certain paralectotypes (former syntypes):** As Günther & Newton also figured the above-mentioned rostrum (1879: Pl. 42, Fig. A) (=NHMUK A1468) (Figs. 9, 10) and incomplete mandible (Günther & Newton 1879: Pl. 42, Fig. Aa) (= UMZC 566) in their original description and were clearly part of the syntype series, therefore, I designate them as paralectotypes. The NHMUK rostrum was collected at the same time as the lectotype by Slater. The UMZC mandible was collected by the Rodrigues police magistrate, George Jenner, in either August to October 1866 or January 15 to February 15, 1871 (Hume *et al.* 2014).

**Probable paralectotypes (former syntypes):** Although it is now difficult to establish with any certainty which fossil specimens, other than the lectotypes and paralectotypes, Günther & Newton (1879) were specifically referring to, this section includes all probable paralectotype material collected by the Rodrigues police magistrate, George Jenner, in August, September and October, 1866 and January 15–February 15, 1871, and by reverend Henry H. Slater in 1874 (Hume *et al.* 2014). *Cranium*, UMZC 566; NHMUK A1468; NHMUK u/r (Caverne l’Affouche); FLMR 142 (Caverne Tortue); *rostrum*, NHMUK A1468; UMZC 566; *mandible*, NHMUK A1468; UMZC 566; UMZC 566 (missing left articular end); *coracoid*, NHMUK 1469 (R); *humerus*, NHMUK A1470 (L); NHMUK A1470 (L); NHMUK A1470 (L); NHMUK A1470 (R); *ulna*, NHMUK A1471 (R); NHMUK A1471 (L); NHMUK A1471 (L); NHMUK A1471 (L); *femur*, NHMUK A1473 (R); NHMUK A1473 (R); *tibiotarsus*, NHMUK A1474 (L); NHMUK A1474 (L); NHMUK A1474 (L); NHMUK A1474 (L); NHMUK A1474 (L); NHMUK A1474 (L); NHMUK A1474 (L); NHMUK A1474 (R); NHMUK A1474 (R); NHMUK A1474 (Ld); NHMUK A1474 (Ld); NHMUK A1474 (Lp); *tarsometatarsus*, NHMUK A1475 (R); NHMUK A1475 (R); NHMUK A1475 (R); NHMUK A1475 (L); NHMUK A1475 (L); NHMUK A1475 (L); NHMUK A1475 (Rd); NHMUK A1475 (Lp).

**Subsequent collected material:** This fossil material was collected between 1974 and 2013 by myself and others in caves on the Plaine Corail. The bones obtained in Caverne l’Affouche, Caverne Gastonia and Caverne Bambara I were found at depths ranging from 200–700 mm in gently fining upwards coral sands and silts interspersed with cave roof collapse breccia (>10–100mm). In Caverne Poule Rouge specimens were found on the surface of large lower chamber approximately 3 m from the entrance, and a cranium (FLMR 142) was found on the surface and near the entrance in Caverne Tortue. A rostrum (FLMR 428.1) was found at 30 mm depth against the north-west cave wall in Caverne Bambara I, and found in association with giant tortoise *Cylindraspis* sp. carapace fragments and a partially associated White-tailed Tropic Bird *Phaethon lepturus*. My excavation with palaeontologist Lorna Steel, in Caverne Bambara I in April 2013 resulted in the discovery of more bones at

200–700 mm, found in association with giant tortoises *Cylindraspis* sp., Solitaire *Pezophaps solitaria*, Rodrigues Night Heron *Nycticorax megalcephalus* and white-tailed tropic bird. The top 200 mm contained the remains of introduced mammal bones, especially sheep, and recent organic material. A humerus (FLMR 33) was found in Caverne l’Affouche in a small scree slope with unassociated remains of Rodrigues Parrot *Necropsittacus rodericanus*, solitaire, white-tailed tropic bird, Rodrigues Fruit Bat *Pteropus rodricensis*, giant tortoise *Cylindraspis* sp., and Newton’s Day Gecko *Phelsuma edwardnewtoni*. *Cranium*, NHMUK u/r (Caverne l’Affouche); FLMR 142 (Caverne Tortue); *rostrum*, NHMUK u/r (Caverne Gastonia); NHMUK u/r (Caverne Gastonia); NHMUK u/r; FLMR 220 (Caverne l’Affouche); FLMR 428.1 (Caverne Bambara I); FLMR 484 (Caverne Bambara I); FLMR 425 (Caverne Bambara I); FLMR 1 (Caverne Poule Rouge); *mandible*, NHMUK u/r; NHMUK u/r (Caverne Gastonia); FLMR 428 (Caverne Bambara 3); FLMR 425 (Caverne Bambara I); FLMR 1 (Caverne Poule Rouge); UMZC 566; UMZC 566 (missing left proximal end); *sternum*, NHMUK u/r; FLMR 9 (Caverne Poule Rouge); *coracoid*, NHMUK S/1978.14.62 (R); NHMUK S/1978.14.62 (R); NHMUK S/1978.14.62 (R); *humerus*, NHMUK u/r (L) (Caverne l’Affouche); NHMUK u/r (L) (Caverne l’Affouche); NHMUK u/r (L) (Caverne l’Affouche); FLMR 33 (L) Caverne l’Affouche); *ulna*, NHMUK S/1978.14.64 (R); NHMUK u/r (L); NHMUK u/r (L); NHMUK A1471 (Ld); NHMUK u/r (L) (Caverne l’Affouche); NHMUK u/r (R) (Caverne l’Affouche); NHMUK u/r (Ld) (Caverne l’Affouche); NHMUK u/r (Rp) (Caverne l’Affouche); *carpometacarpus*, NHMUK S/1978.14.66 (L); NHMUK u/r (R) (Caverne Gastonia); *femur*, NHMUK u/r (R) (Caverne l’Affouche); FLMR 1 (R) (Caverne Poule Rouge); NHMUK u/r (L) (Caverne Bambara I); *tibiotarsus*, NHMUK S/1978.14.63 (Lp); FLMR 1 (Rd) (Caverne Poule Rouge); FLMR 1 (Lp) (Caverne Poule Rouge); *tarsometatarsus*, NHMUK S/1978.14.65 (R); FLMR 476 (Rd) (Caverne Bambara I).

**Measurements.** See Appendix 1.

**Type locality.** Rodrigues, Mascarenes.

**Distribution.** Rodrigues, Mascarenes.

**Etymology.** A Latinized version (*rodericanus*) of the name of the island of Rodrigues, Mascarenes, Indian Ocean.

**Revised diagnosis.** As for genus.

**Description and comparison.** *Necropsar* differs from other sturnids used in the comparisons by the following character states that are given for *Necropsar*. For description and comparison with *Fregilupus*, see *Fregilupus* above:

*Cranium*: in *Saraglossa*, cranium more rounded, more bulbous and less dorso-ventrally flattened; frontal wider; in lateral view, fonticuli orbitocraniales slightly larger than foramen. n. optici; in posterior view, crista nuchalis transversa more rounded with indistinct prominentia cerebellaris; in *Leucopsar*, more rounded, more bulbous and less dorso-ventrally flattened; in lateral view, fonticuli orbitocraniales slightly larger than foramen. n. optici; in posterior view, foramen magnum smaller; nuchalis transversa more rounded with indistinct prominentia cerebellaris; in *Gracupica*, larger; more bulbous, less dorso-ventrally compressed; in lateral view, fonticuli orbitocraniales smaller than foramen. n. optici; in posterior view, foramen magnum smaller; crista nuchalis transversus more rounded with less distinct prominentia cerebellaris; in *Sturnia*, more bulbous, less dorso-ventrally compressed; in lateral view, fonticuli orbitocraniales equal in size with foramen. n. optici; in posterior view, crista nuchalis transversus more rounded extended less dorsad, with less distinct prominentia cerebellaris; in *Acridotheres*, less dorso-ventrally compressed, more bulbous; in posterior view, foramen magnum smaller; crista nuchalis transversus more rounded, extends less dorsad (Figs. 9, 10).

*Rostrum*: in *Saraglossa*, *Leucopsar*, *Gracupica*, *Sturnia* and *Acridotheres*, rostrum shorter, wider and more decurved; narial openings and os nasale wider; in dorsal view, less pronounced angular surface on os nasale (Figs. 9, 10).

*Mandible*: in *Saraglossa*, in dorsal view, reduced processus retroarticularis and processus mandibulae medialis; in lateral view, rostrum mandibulae less deeply excavated; in *Leucopsar*, in dorsal view, no posterior extension of processus retroarticularis; in lateral view, fenestra rostralis mandibulae larger; in *Gracupica*, in dorsal view, wider; no posterior extension of processus retroarticularis; processus mandibulae medialis less distinct; in *Sturnia*, less posterior extension of processus retroarticularis; comparatively larger fenestra rostralis mandibulae; in *Acridotheres*, wider, more curved; processus extensorius less robust; rostrum mandibulae shorter; fenestra rostralis mandibulae larger (Figs. 13, 14).



**FIGURE 31.** Comparison of rostra of *Necropsar rodericanus* showing possible sexual dimorphism. **A–B**, lateral view, **C–D**, dorsal view. **A, D**. NHMUK u/r; **B, C**. NHMUK A1468 u/s. Note the shorter, deeper and wider bill in A and D, and here interpreted as female. Scale bar = 10mm.

*Coracoid*: in *Saraglossa*, processus lateralis extends more laterally, less ventrally; in *Leucopsar*, shorter, but comparatively more robust; in *Gracupica*, more robust, more pronounced processus procoracoideus; in *Sturnia*, facies articularis comparatively larger, otherwise similar; in *Acridotheres*, larger, more robust, otherwise similar (Fig. 15).

*Sternum*: in *Saraglossa*, in lateral view, apex carinae extends anteriorly beyond spina externa; carina sterni deep; in *Leucopsar*, in dorsal view, spina externa much more reduced; processus craniolateralis shorter, narrower and deflected less laterally; in *Gracupica*, much larger, spina externa longer, but less robust; carina sterni not reduced; anterior extension of apex carinae almost equal with spina externa; in *Sturnia*, in dorsal view, spina externa longer, but much smaller; processus craniolateralis deflected less laterally; in lateral view, anterior extension of apex carinae equal or beyond spina externa; in *Acridotheres*, larger; processus craniolateralis shorter, narrower and deflected less laterally; carina sterni not reduced (Figs. 16, 17).

*Humerus*: in *Saraglossa*, tuberculum ventrale directed less ventrally; medial ridge less pronounced; crista delto pectoralis more pronounced; in *Leucopsar*, smaller, in caudal aspect, medial ridge less distinct; tricripital fossa I less deeply excavated; in cranial aspect, tuberculum supracondylare ventrale more excavated; in *Gracupica*, in caudal

aspect, distinct depression on crista deltopectoralis; medial bar wider; no distal connection between tricipital fossae I and II; in *Sturnia*, in caudal aspect, tricipital fossa I less deeply excavated; medial bar reduced; crista deltopectoralis extends less distad; in *Acridotheres*, larger, more robust; in caudal aspect, tricipital fossa I less deeply excavated; in cranial aspect, sulcus ligamenti transversus and fossa m. brachialis more excavated (Fig. 18).

*Ulna*: *Saraglossa* and *Sturnia* similar; in *Leucopsar*, shorter, but proximal end comparatively more robust; in *Gracupica*, larger, more robust; olecranon extension situated more ventrally; in *Acridotheres*, much larger, more robust, otherwise similar (Fig. 19).

*Carpometacarpus*: *Saraglossa*, *Leucopsar*, *Gracupica* and *Sturnia* similar; in *Acridotheres*; slightly larger, more robust (Fig. 20).

*Femur*: in *Saraglossa* and *Sturnia*, less robust, facies articularis acetabularis less bulbous; in *Leucopsar*, much less robust; facies articularis acetabularis deflected more proximad; in *Gracupica*, facies articularis acetabularis deflected more proximad; otherwise similar; in *Acridotheres*; much less robust, especially in shaft and distal end; in cranial aspect, sulcus patellaris less deeply excavated; crista trochanteris more clearly defined (Fig. 22).

*Tibiotarsus*: in *Saraglossa*, shorter, shaft less robust with less expanded proximal and distal ends; tuberculum retinaculi m. fibularis distinct; sulcus extensorius not deflected mediad; comparatively larger pons supratendineus; in *Leucopsar*, overall comparatively less robust, otherwise similar; in *Gracupica*, comparatively more robust on proximal end, otherwise similar; in *Sturnia*, pons supratendineus not deflected mediad; otherwise similar; in *Acridotheres*; overall less robust; less expanded distal end; crista cnemialis lateralis smaller, more hooked, extends less laterally; pons supratendineus not deflected mediad (Fig. 23).

*Tarsometatarsus*: in *Saraglossa*, impressio retinaculi extensorii with small bridge; in *Leucopsar*, less robust; trochlea less widely spaced; foramen vasculare distale smaller; in *Gracupica*, much longer, but shaft comparatively narrower; impressio retinaculi extensorii with small bridge; trochlea more widely spaced; foramen vasculare distale smaller; in *Sturnia*, trochlea less widely spaced; impressio retinaculi extensorii with small bridge; in *Acridotheres*, morphologically similar, but comparatively less robust; foramen vasculare distale smaller; facies subcutanea lateralis less deeply excavated; in plantar aspect, fossa metatarsi I less deeply excavated, situated less proximad (Fig. 24).

**Remarks.** It is not clear why Slater's manuscript (Slater c.1874) describing *Necropsar* was not published (see Hume *et al.* 2014), as sections of it were used verbatim by Günther & Newton (1879) in their formal description of the bird. As the manuscript proved extremely difficult to locate and was never published, I repeat Slater's original description verbatim and in its entirety:

P.24.

*Necropsar rodericanus*: sp: nov:

Prof: Newton prophesied, as it were, the existence of this bird (P.Z.S: /aug 19./75) when alluding to a bird mentioned in the Archives de la Marine [Tafforet's account, see below] aforesaid, he said " I am at a loss to conjecture what these birds were, unless possibly some form allied to *Fregilupus*."

It is with great pleasure that I lay before you the description of this new form. If it were a mammal I would not make a separate genus of it, but as it is a bird, I think I cannot do less. It is most closely allied to *Fregilupus* (lately described by Dr Murie; of which the only [skeletal] specimen belongs to Cambridge Museum) with which I have carefully compared it.

*Necropsar* is altogether a smaller bird than *Fregilupus*. My specimens include the cranium with upper and lower mandible, coracoid, humerus, ulna, metacarpus, femur, tibia and metatarsus.

P.25.

Comparative measurements of *Necropsar* and *Fregilupus*.

**Head** : Total length *Necropsar* 2 6/10 in [66 mm]: *Fregilupus* 2 7/10 [68 mm]: ridge of occipital arch less prominent in *Fregilupus* : measuring the distance horizontally between the right and left sides of the occipital arch across the foramen magnum, the *Fregilupus* has considerable advantage : breadth of skull at parietals in *Necropsar* 8/10 in [20.3 mm]: in *Fregilupus* 9/10 [22.8 mm]: interorbital part of frontal in *Necropsar* 1/20 in [1.2 mm]: broader than in *Fregilupus*, and 1/10 [2.5 mm] shorter.

Upper mandible less curved in *Necropsar*; its total length 1 5½ /10 in [39.3 mm] *Necropsar*; exactly the same as in *Fregilupus* : length of nares 1/10 in [2.5 mm]: greater in *Necropsar*.



Lower jaw : length in *Necropsar* 2 1/10 [53.3 mm], in *Fregilupus* 2 3/10 [58.4 mm]: *Fregilupus* has this advantage in the dentary portion, the articulating portions being equal in length: the articulation of the lower jaw peculiar to the Sturnidae, is much more pronounced in *Necropsar* than in *Fregilupus*.

Coracoid : greatest length in *Necropsar* 1 1/10 in [27.9 mm]: in *Fregilupus* 1 1/2/10 in [29.2 mm]; this bone is slenderer and straighter in *Necropsar*.

Humerus : length in *Necropsar* 1 3 2/3/10 in [34.6 mm]: in *Fregilupus* 1 4/2/10 in [36.8 mm]: they are much alike in appearance.

P.26.

Ulna length in *Necropsar* 1 6/10 [40.6 mm]; in *Fregilupus* 1 7 1/3/10 [44 mm]

Metacarpus length 9/10 in [22.8 mm]: in *Necropsar*, in *Fregilupus* 1 inch [25.4 mm].

Femur : in *Necropsar* 1 3/10 in [33 mm]: long : in *Fregilupus* 1 3 1/2/10 [34.2 mm].

Tibia in *Necropsar* 2 2 1/2/10 [57.1 mm]–2 3/10 [58.4 mm] long : in *Fregilupus* 2 6/10 [66 mm]: there is a great difference in these bones, that of *Necropsar* being much slenderer in proportion.

Metatarsus in *Necropsar*, length 1 4 1/2/10 [36.8 mm]–1 5 1/3/10 [38.9 mm]; in *Fregilupus* 1 7 1/2/10 [44.4 mm]: this bone is stouter in proportion in *Necropsar*, and has its anterior ridge more prominent.

The presumption of a supposed second species of starling from Rodrigues, *Necropsar leguati*, arose from a skin specimen that was purchased in 1850 by the 13th Earl of Derby from Jules Verreaux (Fisher 2002; Olson *et al.* 2005), the same person who personally shot a *Fregilupus* in 1832. The skin of *Necropsar leguati* was transferred to the Liverpool Museum (now NML) in 1851 (Fisher 2002), where Forbes (1898) located it in 1897 and formally described it, believing its provenance to be Rodrigues Island. This belief was based in part on the specimen being linked with the account of Tafforet, who had described a black and white bird on one of the southern islets, Ile au Mât [=Ile Gombrani], off Rodrigues (see below). The specimen was labelled “Madagascar,” by Verreaux, which was interpreted by Forbes as meaning any part of the Mascarene region. However, Verreaux was notorious for mislabelling specimens (Olson *et al.* 2005). The skin was indeed predominantly white with darker wings and tail, but the supposed dark colouration on the wings was asymmetrical and more likely due to staining (*ibid*). Regardless of the dubious provenance and aberrant colouration, Forbes concluded that *Necropsar leguati* differed from *N. rodericanus* in its smaller tarsus and other minor details, therefore warranting it specific recognition. Hachisuka (1953: 204) further confounded the issue, considering the differences sufficiently diagnostic to erect a new genus, *Orphanopsar*, but stated that the provenance was “probably Mauritius.” Olson *et al.* (2005) made a detailed study of *N. leguati*, and using x-radiographs and mtDNA analysis concluded that the specimen was an albinistic West Indian trembler, most closely related to *Cinlocerthia gutteralis*, and nothing to do with starlings or the Mascarene Islands at all.

Because Hachisuka (1937: 212) believed that Tafforet’s Ile au Mât bird could not be *Orphanopsar* (as he had already suggested Mauritius as the provenance) or referable to a starling because of its flesh-eating ability (see below), he named it as a new genus and species of aberrant cough, *Testudophaga bicolor*, placing it in the Corvidae. This taxon was later doubted by most authorities (e.g. Greenway 1958: 113; Vinson 1964: 268; Gill 1967: 383; Bourne 1968: 342; Staub 1973: 31; Hume & Walters 2012: 433). That one dubious skin and a single account has caused so much taxonomic confusion epitomises the overzealous approach of certain writers when birds of the Mascarenes are concerned.

Greenway (1958: 129), rather confusingly, listed *Necropsar rodericanus* as a junior synonym of *Fregilupus varius*, then maintained it as a valid species (1958: 130), and finally suggested that *Necropsar* should be placed in *Fregilupus* (1958: 131). Cowles (1987a, b: 99) assigned an incomplete sternum collected in a cave on the Plaine Corail, Rodrigues, to a new genus and species of babbler, provisionally placing it in the subfamily Timaliinae, and had prepared a manuscript for publication. He described it as thrush-sized, and having “unique characters, which differ greatly from those of other genera examined.” Regardless of its status, Strahm (1989b: 39) inadvertently published the name without description, thus making it a nomen nudum. My examination of Cowles’ specimen has confirmed that it is referable to *Necropsar rodericanus*. A second sternum collected in 2004 supports this assignment (Figs. 16, 17). Cowles used the specific name ‘*microcarina*’ to indicate the reduced carina sterni but this is characteristic of *Necropsar*, as well as other Mascarene birds, including parrots, pigeons and *Fregilupus varius* (see Hume 2007, 2011; also this paper, Appendix 1, Table 6).

*Necropsar* was about the same size as *Fregilupus* in the cranial elements (see Appendix 1), but smaller postcranially, being approximately 280 mm in total length. *Necropsar* differed from *Fregilupus* mainly in characters of the skull, jaws and sternum. Günther & Newton noted that the crista nuchalis sagittalis was more developed (Figs. 11, 12), which suggests that the neck muscles were stronger, as were those of the bill. The maxilla is shorter and less curved, less slender at the tip than in *Fregilupus*, and the mandible stouter. The greater development of the processus retroarticularis suggests that *Necropsar* was able to exploit a broad range of substrates and use an even greater force than *Fregilupus* when foraging. The sternum of *Fregilupus*, apart from overall size and shallow depth of the carina sterni, most resembles that of *Acridotheres* (Figs. 16, 17) and other SE Asian starling genera, which is in direct contrast with the distinct sternum of *Necropsar*. Although *Necropsar* was clearly volant, the greater reduction in size of the sternum may have been related to the small size and gentle topography of Rodrigues, as the starling may no longer have required powerful or sustained flight.

*Necropsar* was described in life only once, by the Réunionnais mariner, Julien Tafforet, who was accidentally marooned on Rodrigues for 9 months in 1725–1726 (Tafforet 1725–26; North-Coombes 1971). Tafforet had been sent to survey the island to report on its potential for French occupation, and he was an astute and careful observer. Tafforet had a copy of a book by François Leguat (1708; North-Coombes 1971), who had also been marooned on Rodrigues from 1691–1693 with a group of Huguenot refugees (North-Coombes 1971). Leguat had written a detailed account about the island and its fauna, but unlike Tafforet, he had no boat and was unable to reach the lagoonal islets. On Ile Gombrani, one of the large southern islets (Figs. 29, 30), Tafforet made the only known observation of the Rodrigues Starling in life:

There is a small bird that is not very widespread, because it is not on the mainland; one sees it on the islet du Mât [=Ile Gombrani], which is south of the main island; and I believe that it is on this island because of the birds of prey on the mainland, and also to live with more facility on the eggs of the fishing birds which lay there, because they do not eat anything other than eggs or a few turtles dead of hunger that they know well enough to tear. These birds are a little larger than a blackbird [*Hypsipetes borbonicus*] and have a white plumage, a part of the wings and tail black, a yellow beak as well as the legs, and have a wonderful song. I say a song though they have several, and all different, and each is of the most beautiful. We fed some with finely-chopped cooked meat that they ate in preference to seeds of forest trees [my translation from the original manuscript].

Tafforet was familiar with the fauna and flora on Réunion, as he made direct comparisons between those and similar species on Rodrigues (Strahm 1989a; Cheke & Hume 2008). He made no mention of a crest in *Necropsar*, and he would certainly have been aware of the crested *Fregilupus*, so *Necropsar* clearly lacked that ornamentation, but it did have similar black and white plumage and yellow bill, legs and feet. Tafforet never saw the starling on the main island of Rodrigues. Ile Gombrani and nearby Ile Pierrot are the largest of the southern islets (Figs. 30a, 30b); both are waterless, and were originally covered with open, stunted forest (Tafforet, in Oliver 1891), thus providing refuge for the birds. The largest Rodrigues islet, Crabe Island, is situated about 4 km to the west of Ile Gombrani, and another large islet, Ile Frégate, lies about 2 km to the northwest of Crabe (Fig. 3), but Tafforet made no mention of starlings on those, so they may have been confined to the southern group at that time. Leguat (1708) noted that the pigeons only bred on the southern islets due to rat persecution, and Tafforet recorded that the pigeons and parrots were coming to the mainland from them only to drink water (Hume 2007, 2011). It is likely therefore that the starling was doing the same. *Necropsar* was either absent or very rare on mainland Rodrigues in 1726, and when Pingré (in Alby & Serviable 1993) visited Rodrigues, including the islets, to observe the Transit of Venus in 1761, the starling was extinct.

Leguat (1708) noted that rats occurred in huge numbers on Rodrigues. They could have arrived nearly a century before Leguat's visit in 1691–93, as at least one Dutch fleet surveyed the island in 1601 (Moree 2001), and a number of other visits had taken place (see Bertuchi 1923; North-Coombes 1971; Chan Low 2001; Cheke & Hume 2008), which may have allowed these rodents to escape. Rodrigues once harboured the densest populations of giant tortoises *Cylindraspis* sp. in the world (Arnold 1979), and also large populations of marine turtles (Cheke & Hume 2008). This resulted in the first official exploitation of giant tortoises in 1717 (North-Coombes 1971), which reached its peak in the 1740s, when around 10,000 tortoises were exported annually (North-Coombes 1971, 1994). Cats were introduced c.1745 to rid the island of rats but, after decimating the native birds, turned their attentions to turtle and tortoise hatchlings (Cheke & Hume 2008). However, this was already two decades after *Necropsar* was confined to the islets, so it is very likely that the extinction of the Rodrigues starling was largely or entirely due to rat predation (see also Bourne 1968). The southern islets provided the final refuge, but when rats

eventually colonised them, the birds were quickly exterminated. Rats now occur on all but the smallest of the Rodrigues lagoonal islets (pers. obs).

**Ecology and behaviour.** Little is known about the habits of *Necropsar*, but it is possible to make a number of inferences from Tafforet's account. He reported that *Necropsar* had the ability to tear the flesh of dead turtles or tortoises, and a strong gape would have been useful for this purpose. Vast colonies of seabirds and giant land tortoises *Cylindraspis* spp. occurred on all of the larger islets, along with breeding populations of Green Turtle *Chelonia mydas* and Hawksbill Turtle *Eretmochelys imbricata* (see Cheke & Hume 2008), so there would have been an ample food supply, at least during the seabird and turtle breeding seasons. The robust limbs and strong gape suggests that *Necropsar* was a terrestrial foraging species, and it may have preyed on the diverse snail and invertebrate fauna of Rodrigues, as well as scavenging carcasses, eggs and chicks in the seabird colonies and tortoise and turtle breeding areas. Tafforet's description of vocalisation suggests the song of *Necropsar* was loud and complex. It is likely that *Necropsar* once had a wide distribution on mainland Rodrigues, with perhaps seasonal occurrence on the islets.

Tafforet was marooned on Rodrigues from September 1725 to June 1726, through a period of time (austral summer) when many of the Mascarene birds breed, including the two surviving terrestrial birds of Rodrigues, Rodrigues Fody *Foudia flavicans* (September–June) and Rodrigues Warbler *Acrocephalus rodericana* (September–March) (Cheke 1987; Jones 1987; Impey *et al.* 2002). It is likely therefore that *Necropsar* also bred during the same period, as Tafforet was able to procure what were presumably juvenile birds from a probable breeding population on Ile Gombrani and take them back to the mainland for hand-rearing.

Like *Fregilupus*, *Necropsar* may have been sexually dimorphic in bill shape and length. The differences between the longest and shortest bones of the three most numerous bone series (Appendix 1) of ulna 36.4–40.1 mm (n=9; SD 1.49), tibiotarsus 53.4–59.3 mm (n=9; SD 2.56) and tarsometatarsus 36.1–40.8 mm (n=8; SD 3.50) indicate significant size variation, but might merely represent individual variation. This is further supported by the continuous variation in long bone measurements which do not fall into large or small size classes. However, there is a clearly discernible difference in the bill length and shape between two of the available subfossil specimens (Fig. 31), which does suggest that *Necropsar* was sexually dimorphic. This may have been accentuated in the rhamphotheca, but unfortunately, the overall degree of bill dimorphism in *Necropsar* may never be known as no rhamphotheca has as yet been discovered.

## Genus *Cryptopsar* gen. nov.

**Type species:** *Cryptopsar ischyrrhynchus* sp. nov.

**Etymology.** Greek *kryptós*, hidden, concealed, and *psar*, starling, in reference to the bones of this species being hidden in a museum drawer for over 100 years, concealing the evidence of a third species of sturnid on the Mascarenes. The gender is masculine.

**Diagnosis.** *Cryptopsar* is distinguished from other Mascarene sturnids by the following suite of characters:

*Cranium:* crista nuchalis transversus oval-shaped and narrow; tuba audivita communis deeply excavated; processus paroccipitalis elevated, enhancing depression below; lamina parasphenoidalis slightly excavated.

*Rostrum:* sharp and decurved; os nasale narrow.

*Mandible:* in dorsal view, rostrum mandibulae deeply excavated; processus mandibulae medialis inflected posteriorly and sharply pointed; in lateral view, processus retroarticularis extremely long and distinctly triangular; single, small fenestra rostralis mandibulae; articular ends comparatively shallow.

*Coracoid:* comparatively gracile.

*Humerus:* gracile; shaft curved; tuberculum ventrale small; two tricipital fossae; tricipital fossa II not completely enclosed and separated from tricipital fossa I by medial bar; tricipital fossa I open distally communicating with tricipital fossa II; processus supracondylaris dorsalis reduced, with little proximal extension; crista deltopectoralis reduced, shallow in dorsal view.

*Ulna:* impressio brachialis deeply excavated; olecranon prominent.

*Carpometacarpus:* processus extensorius reduced.

*Femur:* facies articularis acetabularis deflected slightly proximad; linea internus cranialis distinctly ridged;

sulcus patellaris deeply excavated; in caudal aspect, deep excavation distal to facies articularis acetabularis.

*Tibiotarsus*: tuberculum retinaculi m. fibularis distinct; crista lateralis cranialis distinctally hooked; pons supratendineus narrow with deep canalis extensorius.

*Tarsometatarsus*: comparatively short and robust; trochleae expanded; no bridge linking impressiones retinaculi extensorii; crista medialis hypotarsi not expanded distally; on proximal end, cotyla medialis projects dorsad; foramen vasculare distale extends proximad; distinct ridge on facies dorsalis; fossa metatarsi I with increased proximal extension and distinct medial ridge; in ventral view, trochlea metatarsi III wide and indistinctly larger than trochlea metatarsi II; fossa parahypotarsalis medialis forms a distinct groove.

**Remarks.** Rothschild (1907b:6), followed by Hachisuka (1953: 204), were convinced that *Necropsar* (*Orphanopsar*) *leguati* could not have occurred on Rodrigues alongside *N. rodericamus* (contra Forbes 1898), so its provenance must have been Mauritius. They completely erred in this context, but were inadvertently correct in the fact that a species of starling, closely related to *Necropsar* and *Fregilupus*, did once occur on Mauritius.

### †Mauritius Starling *Cryptopsar ischyrrhynchus* sp. nov.

**Holotype:** MNHN MAD6931 complete mandible. Collected by Etienne Thirioux around 1904 at an undisclosed cave or boulder field locality in the Vallée des Prêtres, central-west Mauritius. This is one of a series of mandibles with the same registration number, but it is the only complete specimen.

**Measurements.** See Appendix 1.

**Type locality.** Mauritius, Mascarenes.

**Distribution.** Mauritius, Mascarenes.

**Etymology.** Greek *iskhuros*, strong, powerful, and *rhunkhos*, bill, in reference to the powerful gaping ability of this species. The gender is masculine.

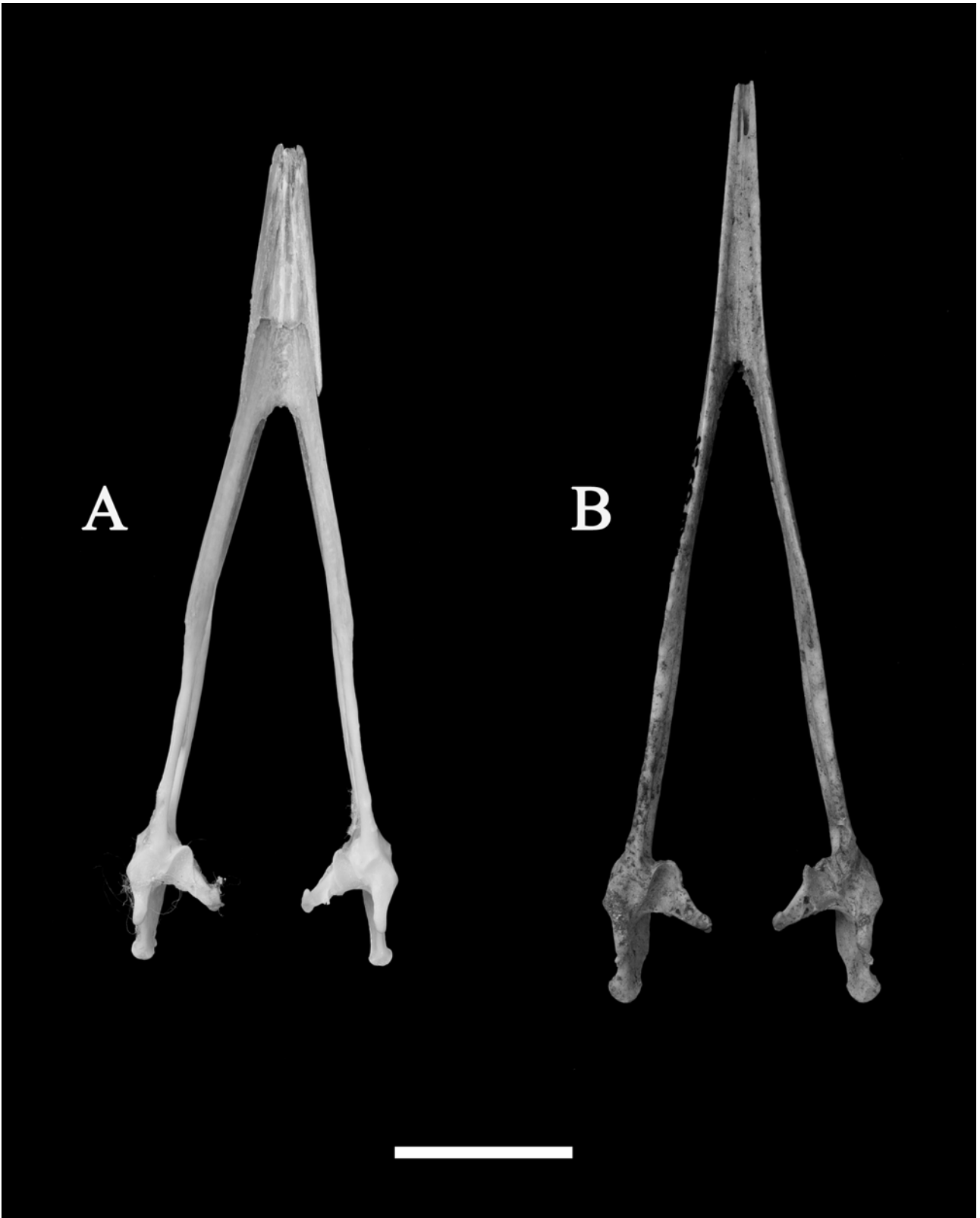
**Paratypes:** The partial rostrum (NHMUK u/r) was collected by the author, Lorna Steel and Greg Middleton in a limestone cave (area D, 150–200 mm depth) at Vieux Grand Port, southeast Mauritius. It was found in lightly compacted fining-upwards silt/sand intermixed with cave roof collapse debris >10 mm, and in association with fragmentary elements of Mauritius Red Rail *Aphanapteryx bonasia*, Mauritius Blue Pigeon *Alectroenas nitidissima*, Mauritius Bulbul *Hypsipetes olivaceous*, Mauritius Fody *Foudia rubra* and Lesser Mauritian Fruit Bat *Pteropus subniger*.

*Cranium*, MNHN MADu/r small cranial fragment comprising part of parasphenoidalis and occipital region, lacking fossa temporalis; *rostrum*, MNHN MAD8041 (d); MNHN MAD8843 (d); MNHN MAD8839 (d); MNHN MAD8840 (d); UMZC 448.cc (Mare aux Songes); NHMUK u/r (Vieux Grand Port); *mandible*, MNHN MAD6931 (d); MNHN MAD6931 (d); MNHN MAD6931 (d); MNHN MAD6931 (d); MNHN MAD6931 (d); MNHN MAD6931 (Rp); MNHN MAD8843 (Rp); MNHN u/r (Rp); MNHN u/r (Lp); MNHN u/r (Lp); *Coracoid*, MNHN MAD7131 (R); *humerus*, MNHN MAD6481 (R); MNHN MAD7127 (L); MNHN MAD8852 (L); *ulna*, MNHN MAD8837 (R); *carpometacarpus*, MNHN MAD8846; *femur*, MNHN MAD8850 (R); *tibiotarsus*, MNHN MAD6830 (R); MNHN MAD6830 (L); *tarsometatarsus*, MNHN MAD6486 (R).

**Diagnosis.** As for genus.

**Description and comparison:** *Cryptopsar* differs from the Mascarene and other sturnids by the following characters:

*Cranium*: in *Fregilupus*, wider crista nuchalis transversus; lamina parasphenoidalis not excavated (slightly excavated in *Cryptopsar*); prominentia cerebellaris less distinct; foramen magnum larger; in *Necropsar*, more distinct prominentia cerebellaris and narrower crista nuchalis transversus; lamina parasphenoidalis not excavated; foramen magnum larger; in *Saroglossa*, crista nuchalis transversus smaller, more heart-shaped with less distinct protruding prominentia cerebellaris; in *Leucopsar*, in posterior view, crista nuchalis transversa more rounded with indistinct prominentia cerebellaris; larger foramen magnum; in *Gracupica*, overall smaller, but foramen magnum slightly larger, otherwise similar; in *Sturnia*, in posterior view, crista nuchalis transversa more rounded with indistinct prominentia cerebellaris; in *Acridotheres*, wider crista nuchalis transversus; lamina parasphenoidalis not excavated; crista nuchalis transversus and prominentia cerebellaris less distinct; processus paroccipitalis less elevated (Figs. 9, 10, 11).



**FIGURE 32.** Comparison of mandibles of **A.** NHMUK S/1973.29.14 *Sturnus vulgaris* and **B.** MNHN MAD6931 *Cryptopsar ischyrrhynchus* gen.nov. sp.nov. The mandible of *S. vulgaris*, a powerful gaping species, most closely resembles that of *Cryptopsar*. Scale bar = 10mm.



**FIGURE 33.** Skins of the two subspecies of *Sturnia erythropygia*, the Southeast Asian starling species that most closely resembles *Fregilupus varius* in colouration. From left to right, dorsal view, lateral view: *Sturnia erythropygia erythropygia* NHMUK 1898.4.28.38 ♂; NHMUK 1898.4.28.40 ♀; *Sturnia erythropygia andamanensis* NHMUK 1955.6.3.28 ♂; NHMUK 1955.6.3.27 ♀.

*Rostrum*: differs from all sturnids studied in being sharper and narrower (Figs. 9, 10).

*Mandible*: in *Fregilupus*, longer, less extension of the processus retroarticularis; rostrum mandibulae shorter and less excavated; fenestra rostralis mandibulae larger; in *Necropsar*, more robust, less decurved; less extension of processus retroarticularis; processus mandibulae medialis projects less posteriorly, more medially; in lateral view, fenestra rostralis mandibulae larger; processus retroarticularis indistinctly triangular, pointed at base; in *Saroglossa*, in dorsal view, rostrum mandibulae less deeply excavated; processus mandibulae medialis and processus retroarticularis weakly developed; in *Acridotheres*, shorter, distinctly wider; in dorsal view, rostrum mandibulae shorter; less extension of processus retroarticularis; processus mandibulae medialis projects less posteriorly, more medially; in lateral view, fenestra rostralis mandibulae larger; processus retroarticularis indistinctly triangular, more square-shaped (Figs. 13, 14).

*Coracoid*: in *Fregilupus*, more robust; processus procoracoideus more pronounced; in *Necropsar* and *Acridotheres*, processus lateralis extends further proximad; otherwise similar; in *Saroglossa*, comparatively more robust, especially at proximal end; processus procoracoideus more pronounced; in *Leucopsar* and *Gracupica*, more robust, otherwise similar; in *Sturnia*, shaft comparatively narrower, otherwise similar (Fig. 15).

*Humerus*: in *Fregilupus*, overall more robust, especially in shaft; circular depression on proximal side of tuberculum ventrale; tricipital fossa II completely enclosed and separated from tricipital fossa I by medial bar; medial bar much more developed; in *Necropsar*, shaft and distal end more robust, otherwise similar; in *Saroglossa*, medial ridge more distinct; crista delto pectoralis larger; in *Leucopsar*, larger, with circular depression on crista deltopectoralis; in *Gracupica* and *Sturnia*, circular depression on crista deltopectoralis; less distinct medial bar; tricipital fossae I and II connected laterally; in *Acridotheres*, dimensions overall larger, more robust; caput humeri more bulbous; fossa pneumotricipitalis less deeply excavated; tuberculum ventrale situated less laterally; processus flexorius comparatively short (Fig. 18).

*Ulna*: in *Fregilupus*, much larger, more robust; in *Necropsar*, comparatively larger cotyla dorsalis, olecranon smaller, less prominent; impressio brachialis less deeply excavated; in *Saroglossa*, olecranon more prominent, extends further proximad; processus cotylaris dorsalis directed more proximad; in *Leucopsar* and *Gracupica*, comparatively more robust, otherwise similar; in *Sturnia*, less pronounced cotyla dorsalis, otherwise similar; in *Acridotheres*, olecranon less prominent; tuberculum carpalis less reduced (Fig. 19).

*Carpometacarpus*: in *Fregilupus*, larger; processus extensorius comparatively smaller; *Necropsar*, *Leucopsar*, *Gracupica* and *Sturnia* similar; in *Acridotheres*, larger, more robust (Fig. 20).

*Femur*: in *Fregilupus*, facies articularis acetabularis more bulbous, deflected less distad; sulcus patellaris less deeply excavated; otherwise similar; in *Necropsar*, condylus medialis larger and deflected less medially; in cranial

aspect, sulcus patellaris less deeply excavated; in *Saroglossa*, facies articularis acetabularis less bulbous, much less robust, especially in shaft and at distal end; in *Leucopsar*, less robust, in cranial aspect, sulcus intercondylaris less deeply excavated; in *Gracupica*, more robust; facies articularis acetabularis not deflected proximad; in *Sturnia*, shaft less expanded at proximal and distal ends; in *Acridotheres*, much less robust, especially in shaft and at distal end (Fig. 22).

*Tibiotarsus*: in *Fregilupus*, less extension of crista fibularis; less expanded distal end, especially proximal to condyles; pons supratendineus wider; in *Necropsar*, overall more robust, especially at distal end; crista fibularis more pronounced; pons supratendineus wider and situated less distad; in *Saroglossa*, shorter, shaft less robust, less expansion at proximal and distal ends; tuberculum retinaculi m. fibularis more distinct; sulcus extensorius not deflected mediad; pons supratendineus comparatively larger; in *Leucopsar*, less robust, shaft wider at distal end; tuberculum retinaculi m. fibularis more distinct; in *Gracupica*, longer, tuberculum retinaculi m. fibularis more distinct; otherwise similar; in *Sturnia*, pons supratendineus comparatively larger; otherwise similar; in *Acridotheres*, distal end not medially deflected; less expansion of distal end; pons supratendineus wider and situated less distad (Fig. 23).

*Tarsometatarsus*: in *Fregilupus*, longer, overall less robust; facies subcutanea lateralis less deeply excavated; trochlea less widely spaced; in plantar aspect, foramen vasculare distale smaller; in *Necropsar*, overall less robust; foramen vasculare distale smaller; in plantar aspect, fossa supratrochlearis plantaris less deeply excavated; in *Saroglossa* and *Sturnia*, trochlea less widely spaced; impressio retinaculi extensorii with small bridge; in *Leucopsar*, less robust; trochlea less widely spaced; in plantar aspect, sulcus flexorius less deeply excavated; on proximal end, hypotarsi rectangular, not square-shaped; in *Gracupica*, longer, but shaft comparatively narrower; in dorsal aspect, foramen vasculare distale larger; on proximal end, hypotarsi rectangular, not square-shaped; in *Acridotheres*, overall much less robust, but longer in total length; cotyla medialis with indistinct dorsal extension; facies subcutanea lateralis less deeply excavated; foramen vasculare distale smaller and situated less distad; in plantar aspect, hypotarsi less square-shaped, more rectangular; fossa supratrochlearis plantaris less deeply excavated and extends less proximad (Fig. 24).

**Remarks.** The Mauritius Starling was never reported in the early literature, which suggests that it had either disappeared before humans arrived on Mauritius or, less likely, that it was not clearly distinguishable from the other larger Mauritian passerines. It was the smallest of the Mascarene sturnids, being approximately 260 mm in total length (see Appendix 1). The processus retroarticularis is extremely well developed in *Cryptopsar*, more so than in the other Mascarene starlings, and the mandible most closely resembles that of *Sturnus vulgaris* (Fig. 32). However, this is due entirely to convergence, both species being powerful gapers but with no close relationship. The strong, robust limbs and powerful gaping ability suggests that the Mauritius starling was probably carnivorous and a terrestrial forager, even more adapted to this niche than *Fregilupus* or *Necropsar*. *Cryptopsar* probably fed on small reptiles and invertebrates, raided the nests of forest birds and scavenged turtle, tortoise and sea bird breeding areas. Subfossil remains of the Mauritius Starling have been found in caves and boulder scree in the valleys around Le Pouce Mountain and the Vallée des Prêtres in the central-west, and Plaine des Roches and Roches Noires in the central-east (Hume 2005), and a single premaxilla was collected from the Mare aux Songes marsh and a cave at Vieux Grand Port in the southeast. The remains of *Cryptopsar* were all found in what was originally semi-dry evergreen forest (Fig. 4), which may have been the preferred habitat, but no doubt it had a wide distribution over the island before humans arrived. The black rat arrived on Mauritius during the 14th century (Hume 2013), almost certainly introduced by Arab traders, and may have exterminated the bird long before the arrival of the Dutch, who left the first descriptions of the fauna in 1598 (Moree 1998). Like *Necropsar*, it is very likely that rats were solely to blame for its extinction.

## Conclusions

**Affinities.** It is apparent from similarities in plumage that *Fregilupus* was related to SE Asian sturnids, and not to the Madagascar Starling *Saroglossa aurata* or to any of the African genera. MtDNA analysis has confirmed a distant relationship with a clade of SE Asian starlings (Zuccon et al 2008), which contains both black-and-white and crested species. Of this clade, *Leucopsar rothschildi* has a distinct, erectile crest, but Lovette et al (2008) showed that it has no close extant allies. Lovette et al failed to extract DNA from the MCZH *Fregilupus* specimen,

probably due to its long immersion in spirit, but concluded that the predominantly black and white *Sturnornis albofrontata*, *Sturnia sinensis* and *Sturnia (Temenachus) malabarica* comprise a well-supported clade, with *Sturnia (Temenachus) erythropygia* sister to *S. malabarica*. They hypothesise that *S. erythropygia* arose from an early representative of the *malabarica* lineage, colonising the remote Andaman and Nicobar Islands in the Indian Ocean. Of all SE Asian sturnids, the White-headed Starling *Sturnia erythropygia* most closely resembles *Fregilupus* in colouration (Fig. 33), so it is reasonable to suggest that an ancestral member of that clade was the most likely candidate to colonise the Mascarenes. *Necropsar* and *Cryptopsar* are clearly related to *Fregilupus* (Fig. 34) and form part of the same clade, but in terms of morphology *Necropsar* and *Cryptopsar* are more closely related to each other than to *Fregilupus*, especially in characters of the skull, sternum and humerus. *Fregilupus* has more morphological similarities with *Sturnia* and *Gracupica*, which suggests that it may have been a more recent colonist than *Necropsar* and *Cryptopsar*, therefore, there may have been at least two Mascarene sturnid colonisation events. Zuccon et al (2008) estimated a divergence time of 4 Ma for the origin of the *Fregilupus* lineage, long before Réunion emerged above the sea around 2.1 Ma. This suggests that this lineage arrived at a later date on Réunion, further supporting a second colonisation event, and that it had evolved as it crossed the Indian Ocean during low sea level stands, when now submerged seamounts and plateaus would have provided numerous, large and long-term island stepping-stones. This scenario is mirrored by a number of other Mascarene endemic landbird genera (Shapiro et al. 2002; Groombridge et al. 2004; Hume 2007, 2011; Cheke & Hume 2008; Warren et al. 2010).

There is a paucity of sturnids on islands in the southwest Indian Ocean; other than the Mascarenes, only the micro-continent of Madagascar has a single endemic species, *Saroglossa aurata*, which is not closely related genetically (Lovette & Rubenstein 2007) or morphologically (this paper). That three endemic genera occurred on the comparatively small Mascarene Islands is probably a result of those islands' long isolation and their varied topography and vegetation regions. However, it is somewhat perplexing in terms of biogeography that starlings are not recorded from other southwestern Indian Ocean islands, especially the granitic Seychelles, which is an archipelago that shares a number of avian taxa with the Mascarenes (Cheke & Hume 2008; Warren et al. 2010).

#### Extinction

At least five other species of starling, all Pacific island taxa of *Aplonis*, have become extinct in recent times (Hume & Walters 2012), and they were almost all victims, in part at least, of introduced rats (Olson 1986; Steadman 1989; Hume 2002; Hume & Walters 2012).

It is therefore not surprising that at least two of the Mascarene sturnids appear to have disappeared for the same reason. By 1725–26, rats seemingly had eliminated *Necropsar* from mainland Rodrigues, the southern and then rat-free islets providing the only refuge, on which it appears that the entire population was breeding. But rats are adept at crossing open-water (Russell et al. 2005), and once they reached the starling's last stronghold, its fate was sealed. The Rodrigues Starling had certainly disappeared by 1761. *Cryptopsar* seems likely to have been an early casualty on Mauritius, becoming extinct at some point after the late 14th or early 15th centuries, when rats first colonised the island (Hume unpubl. data). West-Zanen (in Soeteboom 1648: 19), who was on Mauritius in 1602, made an extensive list of the avifauna, including passerines, and mentioned "thrushes and sparrows." Had a starling still been in existence, West-Zanen may well have mentioned it, but there is a possibility that his "thrushes" included both starlings and *Hypsipetes* bulbuls, especially if they looked superficially similar. The morphology of *Cryptopsar* suggests a more terrestrial mode of existence, and if it was as vulnerable to rat predation as was *Necropsar* on Rodrigues and the extinct *Aplonis* starlings were in the Pacific, it probably disappeared extremely rapidly once rats had become established.

In contrast and somewhat inexplicably, *Fregilupus* was able to survive alongside rats, cats and a host of other introduced animals for centuries. It was persecuted for crop damage and large numbers could easily be killed with guns and sticks. The survival of *Fregilupus* against all of these odds was probably due to the Réunion's rugged topography and that it was subject to vertical migration, remaining in the highlands for six months of the year, which included the breeding season. This must have given it at least some respite from the human-induced destructive events that took place in the lowlands. *Fregilupus* was reported as being scarce as early as 1817 (Bouton 1878), and also in the early 1830s (Renshaw 1922), but specimens could still be secured during the following few years, after which time the numbers collapsed. Large-scale deforestation occurred during this period, which probably made *Fregilupus* highly vulnerable to hunting once the remnant forests were opened up. It is very likely that over-hunting finished off the birds.





**FIGURE 34.** Author's scaled illustration showing the morphologies of the endemic Mascarene starlings. *Fregilupus varius* (above); *Necropsar rodericanus* (centre); *Cryptopsar ischyryhynchus* gen.nov. sp.nov. (below).

The Mascarene Islands remained pristine until comparatively recently, but upon arrival of humans and their commensal animals the islands were irreparably devastated (Cheke & Hume 2008). This resulted in the extinction of all Mascarene sturnids within a few centuries. A number of early accounts provide some indication about their ecology, but little mention was made about the reasons why they had disappeared. The fate of the Réunion birds is best attested by Antoine Boucher, the French East India Company's store keeper and treasurer. Around 40 years after the first settlement, he condemned the actions of the company's management of the island (Boucher 1710; Cheke & Hume 2008), especially for the wanton destruction of the birds and giant tortoises. The fact that *Fregilupus* managed to survive for nearly a century and a half after Boucher's account is testament to its adaptability, as at the time of writing almost all of Réunion's endemic birds, including most of those that Boucher had listed, were already extinct:

What has become, sirs, from your glorious reign, of the quantity prodigious and innumerable of game such as flamingos, pigeons, doves, teal, water-hens, geese and wild ducks, whimbrels, waders, snipe, merles, huppés and others whose details would be too long [to enumerate], not mentioning an infinity of other game from this country whose names are unknown in France. The abundance of those I have mentioned as well as the others was such that they ate one another and darkened the air. All this has much changed; one now finds just the feeble remnants which have managed to escape your insatiable gluttony [translation from Cheke & Hume 2008].

**TABLE 1.** Some key distinguishing characters of Mascarene sturnids used in the Systematics.

|                 | <i>Fregilupus</i>  | <i>Necropsar</i>   | <i>Cryptopsar</i>   |
|-----------------|--|--|---|
| Cranium         | overall robust; no dorso-ventral compression; distinct crista nuchalis transversus; foramen. n. optici small, almost equal in size to fonticuli orbitocraniales                                      | very robust; dorso-ventral compression; very distinct crista nuchalis transversus; foramen n. optici large, larger than fonticuli orbitocraniales  | very distinct crista nuchalis transversus   |
| Rostrum         | long; robust; decurved; narial openings shorter  | long; robust; straighter; narial openings longer   | long; narrow and sharp; decurved  |
| Mandible        | long; decurved; processus retroarticularis large   | long; straighter; processus retroarticularis larger and greatly extended   | shorter; decurved; processus retroarticularis extremely large and greatly extended  |
| Coracoid        | robust   | less robust, especially in shaft and on sternal end  | less robust   |
| Sternum         | comparatively small; reduced carina sterni; spina externa small; processus cranio-lateralis long and narrow, deflected cranially   | comparatively very small; carina sterni extremely reduced; spina externa larger; processus cranio-lateralis long and wide, deflected laterally   | Not known   |
| Humerus         | robust with straight shaft; two tricipital fossae; fossa II completely enclosed and separated from tricipital fossa I by a septum; small circular depression on proximal side of tuberculum ventrale | less robust; shaft more curved; two tricipital fossae; pneumatic fossa II not completely enclosed and separated from tricipital fossa I by a septum; tricipital fossa I open distally communicating with tricipital fossa II | smaller; less robust; shaft curved; two tricipital fossae; tricipital fossa II not completely enclosed and separated from tricipital fossa I by a septum; tricipital fossa I open distally communicating with tricipital fossa II |
| Ulna            | larger, comparatively robust   | smaller; less robust   | smaller, less robust  |
| Carpometacarpus | larger; comparatively small processus extensorius  | smaller; comparatively large processus extensorius   | smaller; comparatively large processus extensorius  |
| Femur           | robust; proximal end more expanded; facies articularis acetabularis larger   | robust; proximal end less expanded; facies articularis acetabularis smaller, less pronounced   | robust; facies articularis acetabularis smaller   |
| Tibiotarsus     | comparatively long and robust; less distal expansion of shaft; sulcus extensorius less deeply excavated; pons supratendineus small   | comparatively long and robust; shaft more expanded at distal end; sulcus extensorius more deeply excavated; pons supratendineus larger   | comparatively long and robust; distal end more expanded; pons supratendineus narrower, situated further distad  |
| Tarsometatarsus | comparatively long; robust; less expanded proximal and distal ends   | comparatively long, but shorter, more robust; greater expansion of proximal and distal ends  | comparatively long and robust, but shortest; foramen vasculare distale larger; greater expansion of distal end  |

**TABLE 2.** Nomenclatural status of real and supposed Mascarene starlings.

| Species   | Distribution | Types of evidence   |
|---|--------------|---|
| † <i>Fregilupus varius</i>                        | Réunion      | Skins, fossil record, contemporary illustrations and accounts   |
| † <i>Cryptopsar ischyrrhynchus</i> nov.gen. & sp. | Mauritius    | Fossil record   |
| † <i>Necropsar rodericanus</i>                    | Rodrigues    | Fossil record, single contemporary account  |
| <i>Necropsar leguati</i>                          | Rodrigues    | Skin. Based on misidentification and erroneous provenance. Synonymised under <i>Cinlocerthia gutturalis</i> (Olson <i>et al.</i> 2005)      |
| <i>Orphanopsar leguati</i>                        | Mauritius    | Based on misinterpretation of account and erroneous provenance. Synonymised under <i>Cinlocerthia gutturalis</i> (Olson <i>et al.</i> 2005) |
| <i>Testudophaga bicolor</i>                       | Rodrigues    | Based on misinterpretation of account. Synonymised under <i>Necropsar rodericanus</i>   |

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**APPENDIX 1.** Measurements . The starling genera *Saroglossa*, *Sturnia*, *Gracupica* and *Leucopsar* were used in the comparative analysis, as they either represent biogeographically closely related species (*Saroglossa aurata* of Madagascar), or are from Southeast Asia, the likely founding source of the Mascarene starlings. *Acridotheres tristis* was also compared as it has been introduced to all three Mascarene Islands and some of its post-cranial skeletal elements can be confused with the endemic starling genera. The Eurasian Hoopoe *Upupa epops* was used for comparisons with *Fregilupus varius*, as the two were once considered to be related.

**TABLE 1.** Measurements (mm) of the cranium of Mascarene starlings compared with other sturnids and *Upupa epops*. For abbreviations, see Methods.

| Species                                       | TL (n) range  | TL (m) SD     | GW (n) range  | GW (m) SD     | WNF (n) range | WNF (m) SD    | GD (n) range  | GD (m) SD     |
|---|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|
| <i>Upupa epops</i>                            | (2) 21.3–21.8 | (21.5) (0.35) | (2) 16.9–17.4 | (17.1) (0.35) | (2) 13.9–15.6 | (14.7) (1.20) | (2) 12.9–15.9 | (14.4) (2.12) |
| <i>Fregilupus varius</i>                      | (2) 29.2–30.1 | (29.6) (0.63) | (2) 22.0–22.5 | (22.2) (0.35) | (2) 10.7–11.7 | (11.2) (0.70) | (2) 16.2–17.8 | (17.0) (1.13) |
| <i>Necropsar rodericanus</i>                  | (4) 31.3–31.8 | (31.4) (0.23) | (4) 21.2–21.6 | (21.4) (0.18) | (3) 11.7–12.4 | (12.1) (0.40) | (4) 15.3–16.7 | (16.0) (0.70) |
| <i>Acridotheres tristis</i>                   | (8) 26.8–30.0 | (28.4) (1.09) | (8) 20.7–22.9 | (21.7) (0.82) | (7) 11.3–13.7 | (12.5) (0.73) | (8) 16.7–18.6 | (17.7) (0.60) |
| <i>Acridotheres burmannicus leucocephalus</i> | (1) 27.0      | (27.0)        | (1) 19.7      | (19.7)        | (1) 11.3      | (11.3)        | (1) 16.4      | (16.4)        |
| <i>Acridotheres melanopterus</i>              | (1) 26.7      | (26.7)        | (1) 19.4      | (19.4)        | (1) 13.1      | (13.1)        | (1) 15.3      | (15.3)        |
| <i>Gracupica contra</i>                       | (1) 26.8      | (26.8)        | (1) 19.8      | (19.8)        | (1) 12.3      | (12.3)        | (1) 15.9      | (15.9)        |
| <i>Gracupica nigricollis</i>                  | (1) 31.5      | (31.5)        | (1) 23.6      | (23.6)        | (1) 13.4      | (13.4)        | (1) 17.9      | (17.9)        |
| <i>Leucopsar rothschildi</i>                  | (4) 26.9–29.0 | (28.1) (0.89) | (3) 21.0–21.4 | (21.3) (0.26) | (4) 10.6–11.1 | (10.7) (0.29) | (4) 16.3–17.6 | (16.9) (0.58) |
| <i>Saroglossa spiloptera</i>                  | (1) 21.7      | (21.7)        | (1) 17.3      | (17.3)        | (1) 11.4      | (11.4)        | (1) 13.9      | (13.9)        |
| <i>Sturnia malabarica</i>                     | (3) 22.3–22.8 | (22.6) (0.28) | (3) 17.0–17.7 | (17.4) (0.37) | (3) 8.8–9.7   | (9.2) (0.45)  | (3) 13.4–14.1 | (13.8) (0.40) |
| <i>Sturnia sinensis</i>                       | (1) 23.2      | (23.2)        | (1) 16.7      | (16.7)        | (1) 9.7       | (9.7)         | (1) 14.9      | (14.9)        |

**TABLE 2.** Measurements (mm) of the rostrum of Mascarene starlings compared with other sturnids and *Upupa epops*. For abbreviations, see Methods.

| Species                          | TL (n)<br>range  | TL (m)<br>SD     | PW (n)<br>range         | PW (m)<br>SD     | PD (n)<br>range          | PD (m)<br>SD                   | LN (n)<br>range            | LN (m)<br>SD     | PML (n)<br>range               | PML (m)<br>SD  | PMW (n)<br>range | PMW (m)<br>SD | PMD (n)<br>range | PMD (m)<br>SD |
|----------------------------------|------------------|------------------|-------------------------|------------------|--------------------------|--------------------------------|----------------------------|------------------|--------------------------------|--|------------------|---------------|------------------|---------------|
| <i>Upupa epops</i>               | (2)<br>47.3–58.8 | (53.0)<br>(8.13) | (2)<br>10.0–11.0        | (10.5)<br>(0.70) | (2) 6.5<br>(6.5)         | (2) 2.7–3.2<br>(2.9)<br>(0.35) | (2)<br>37.9–49.6           | (43.7)<br>(8.27) | (2) 3.2–3.9<br>(3.5)<br>(0.49) | (2) 4.9–5.2<br>(5.0)<br>(0.21)                                   |                  |               |                  |               |
| <i>Fregilupus varius</i>         | (2)<br>37.5–40.0 | (38.7)<br>(1.76) | (2)<br>10.8–11.7        | (11.2)<br>(0.63) | (1) 5.9<br>(5.9)         | (2)<br>10.6–11.3<br>(0.49)     | (1) 21.3<br>(21.3)         | (1) 3.7<br>(3.7) | (1) 3.4<br>(3.4)               |  |                  |               |                  |               |
| <i>Necropsar rodericanus</i>     | (7)<br>33.0–39.0 | (36.4)<br>(2.41) | (2) 9.5–9.9<br>-        | (9.7)<br>(0.28)  | (4)<br>4.5–4.9           | (4)<br>11.6–12.1<br>(0.26)     | (6)<br>17.2–22.0<br>(3)    | (18.9)<br>(16.6) | (3.8)<br>(3.6)                 | (8) 3.0–5.0<br>(4) 3.0–3.6<br>(3.5)<br>(0.52)<br>(3.1)<br>(0.30) |                  |               |                  |               |
| <i>Cryptopsar ischyrynchus</i>   | -                | -                | -                       | -                | -                        | -                              | 16.3–18.2<br>(7)           | (14.7)<br>(12.4) | (0.07)<br>(5.0)                | (0.30)<br>(11.6)   |                  |               |                  |               |
| <i>Acridotheres tristis</i>      | (7)<br>21.4–26.5 | (24.1)<br>(1.84) | (7)<br>9.1–11.0         | (10.2)<br>(0.63) | (7)<br>5.1–7.6<br>(0.89) | (8) 7.3–9.2<br>(8.4)<br>(0.60) | (7)<br>8.4–15.0<br>(2.11)  | (12.4)<br>(2.11) | (5.0)<br>(0.53)                | (7)<br>8.4–13.7<br>(1.81)  |                  |               |                  |               |
| <i>Acridotheres burmannicus</i>  | (1) 22.1         | (22.1)           | (1) 8.3                 | (8.3)            | (1) 5.3                  | (1) 8.9                        | (1) 11.2                   | (11.2)           | -                              | -  | -                | -             |                  |               |
| <i>leucocephalus</i>             | (1) 33.2         | (33.2)           | (1) 8.5                 | (8.5)            | (1) 4.2                  | (1) 10.3                       | (1) 20.0                   | (20.0)           | -                              | -  | -                | -             |                  |               |
| <i>Acridotheres melanopterus</i> | (1) 27.8         | (27.8)           | (1) 8.8                 | (8.8)            | (1) 5.2                  | (1) 9.7                        | (1) 16.6                   | (16.6)           | -                              | -  | -                | -             |                  |               |
| <i>Gracupica contra</i>          | (1) 29.9         | (29.9)           | (1) 10.4                | (10.4)           | (1) 6.0                  | (1) 9.9                        | (1) 15.6                   | (15.6)           | (1) 5.5                        | (5.5)  | (1) 4.3          | (4.3)         |                  |               |
| <i>Gracupica nigricollis</i>     | (4)<br>27.8–29.5 | (28.7)<br>(0.71) | (4) 7.6–8.6<br>(1) 10.4 | (8.1)<br>(0.43)  | (4)<br>5.7–6.9<br>(0.51) | (4) 8.7–9.2<br>(8.8)<br>(0.23) | (4)<br>14.2–15.7<br>(0.67) | (15.2)<br>(0.70) | (2) 4.6–5.6<br>(5.1)<br>(0.70) | (2) 5.6–5.9<br>(5.7)<br>(0.21)                                   |                  |               |                  |               |
| <i>Leucopsar rothschildi</i>     | (1) 20.2         | (20.2)           | (1) 10.4                | (10.4)           | (1) 4.1                  | (1) 7.0                        | (1) 10.7                   | (10.7)           | (1) 4.1                        | (4.1)  | (1) 2.6          | (2.6)         |                  |               |
| <i>Saroglossa spiloptera</i>     | (3)<br>19.0–19.7 | (19.3)<br>(0.35) | (3) 7.2–7.6<br>(1) 10.4 | (7.4)<br>(0.20)  | (3)<br>3.5–3.9<br>(0.23) | (3) 6.4–7.4<br>(6.9)<br>(0.50) | (3)<br>9.9–11.3<br>(0.70)  | (10.6)<br>(0.70) | (3) 3.7–5.1<br>(4.2)<br>(0.75) | (3) 2.0–2.4<br>(2.1)<br>(0.20)                                   |                  |               |                  |               |
| <i>Sturnia malabarica</i>        | (1) 20.2         | (20.2)           | (1) 10.4                | (10.4)           | (1) 4.1                  | (1) 7.0                        | (1) 10.7                   | (10.7)           | (1) 4.3                        | (4.3)  | (1) 2.4          | (2.4)         |                  |               |

TABLE 3. Measurements (mm) of the mandible of Mascarene starlings compared with other sturnids and *Upupa epops*. For abbreviations, see Methods.

| Species                          | TL (n)<br>range  | TL (m)<br>SD     | PW(n)<br>range | PW (m)<br>SD    | PD (n)<br>range | PD (m)<br>SD     | RMW (n)<br>range | RMW (m)<br>SD   | RMD (n)<br>range | RMD (m)<br>SD   | RML (n)<br>range | RML (m)<br>SD    |
|----------------------------------|------------------|------------------|----------------|-----------------|-----------------|------------------|------------------|-----------------|------------------|-----------------|------------------|------------------|
| <i>Upupa epops</i>               | (2)<br>68.9–71.4 | (70.1)<br>(1.76) | (2)<br>5.0–5.3 | (5.1)<br>(0.21) | (2)<br>3.6–4.3  | (3.9)<br>(0.49)  | (2) 2.5–4.2      | (3.3)<br>(1.20) | (2)<br>1.8–2.5   | (2.1)<br>(0.49) | (2)<br>33.9–43.7 | (38.8)<br>(6.92) |
| <i>Fregilupus varius</i>         | (2)<br>54.9–58.8 | (56.8)<br>(2.75) | (1) 6.2        | (6.2)           | (2)<br>3.2–4.5  | (3.8)<br>(0.91)  | (1) 3.1          | (3.1)           | (1) 2.7          | (2.7)           | (1) 17.2         | (17.2)           |
| <i>Necropsar rodericanus</i>     | (5)<br>49.6–58.6 | (52.9)<br>(3.43) | (5)<br>6.2–7.8 | (6.8)<br>(0.68) | (5)<br>4.8–4.9  | (4.8)<br>(0.04)  | (7) 3.1–4.5      | (3.8)<br>(0.46) | (7)<br>2.0–2.9   | (2.3)<br>(0.33) | (7)<br>13.0–16.7 | (14.0)<br>(1.25) |
| <i>Cryptopsar ischyrynchus</i>   | (1) 51.7         | (51.7)           | (6)<br>5.6–6.4 | (6.0)<br>(0.32) | (7)<br>3.1–3.6  | (3.3)<br>(0.19)  | (6) 3.0–3.7      | (3.2)<br>(0.27) | (6)<br>2.1–2.6   | (2.3)<br>(0.16) | (3)<br>15.3–17.3 | (16.1)<br>(1.05) |
| <i>Acridotheres tristis</i>      | (9)<br>38.4–43.5 | (41.1)<br>(1.85) | (9)<br>5.3–6.4 | (5.9)<br>(0.42) | (9)<br>3.2–3.9  | (3.96)<br>(0.21) | (9) 2.9–4.8      | (3.9)<br>(0.66) | (9)<br>1.9–2.7   | (2.4)<br>(0.28) | (9)<br>6.9–12.0  | (10.0)<br>(1.75) |
| <i>Acridotheres burmannicus</i>  | (1) 36.9         | (36.9)           | (1) 5.4        | (5.4)           | (1) 3.3         | (3.3)            | (1) 3.0          | (3.0)           | (1) 2.0          | (2.0)           | (1) 7.8          | (7.8)            |
| <i>leucocephalus</i>             | (1) 49.6         | (49.6)           | (1) 5.7        | (5.7)           | (1) 3.8         | (3.8)            | (1) 4.9          | (4.9)           | (1) 2.8          | (2.8)           | (1) 19.5         | (19.5)           |
| <i>Acridotheres melanopterus</i> | (1) 42.7         | (42.7)           | (1) 5.9        | (5.9)           | (1) 4.5         | (4.5)            | (1) 4.9          | (4.9)           | (1) 2.0          | (2.0)           | (1) 11.9         | (11.9)           |
| <i>Gracupica contra</i>          | (1) 46.2         | (46.2)           | (1) 7.0        | (7.0)           | (1) 5.0         | (5.0)            | (1) 4.1          | (4.1)           | (1) 2.3          | 2.3             | (1) 11.4         | (11.4)           |
| <i>Gracupica nigricollis</i>     | (4)<br>40.4–44.9 | (43.0)<br>(1.88) | (4)<br>5.9–6.4 | (6.1)<br>(0.20) | (4)<br>3.4–3.7  | (3.5)<br>(0.12)  | (4) 4.1–4.6      | (4.4)<br>(0.23) | (4)<br>2.4–3.0   | (2.7)<br>(0.30) | (4)<br>9.7–11.9  | (11.5)<br>(1.37) |
| <i>Leucopsar rothschildi</i>     | (1) 31.8         | (31.8)           | (1) 4.2        | (4.2)           | (1) 2.2         | (2.2)            | (1) 3.5          | (3.5)           | (1) 1.5          | (1.5)           | (1) 7.2          | (7.2)            |
| <i>Saroglossa spiloptera</i>     | (3)<br>32.0–33.5 | (32.7)<br>(0.75) | (3)<br>4.2–4.4 | (4.3)<br>(0.10) | (3)<br>2.4–2.6  | (2.5)<br>(0.10)  | (3) 3.4–3.8      | (3.6)<br>(0.20) | (3)<br>1.6–1.8   | (1.7)<br>(0.10) | (3)<br>8.4–8.7   | (8.5)<br>(0.15)  |
| <i>Sturnia malabarica</i>        | (1) 31.6         | (31.6)           | (1) 4.3        | (4.3)           | (1) 2.9         | (2.9)            | (1) 3.4          | (3.4)           | (1) 1.6          | (1.6)           | (1) 7.4          | (7.4)            |

**TABLE 4.** Measurements (mm) of the coracoid of Mascarene starlings compared with other sturnids and *Upupa epops*. For abbreviations, see Methods.

| Species                                       | TL (n) range  | TL (m) SD     | SW (n) range | SW (m) SD    | SD (n) range | SD (m) SD    | DW (n) range | DW (m) SD    |
|---|---------------|---------------|--------------|--------------|--------------|--------------|--------------|--------------|
| <i>Upupa epops</i>                            | (2) 21.3–21.5 | (21.4) (0.14) | (2) 1.6      | (1.6)        | (2) 1.9–2.0  | (1.9) (0.07) | (2) 7.2–8.3  | (7.7) (0.77) |
| <i>Fregilupus varius</i>                      | (2) 25.8–29.8 | (27.8) (2.82) | (1) 1.7      | (1.7)        | (1) 1.7      | (1.7)        | (2) 7.5–8.1  | (8.1) (0.84) |
| <i>Necropsar rodericanus</i>                  | (4) 23.3–25.9 | (25.2) (1.27) | (4) 1.7–1.9  | (1.7) (0.09) | (4) 1.7–1.8  | (1.7) (0.32) | (3) 5.9–6.5  | (6.2) (0.32) |
| <i>Cryptopsar ischyryhynchus</i>              | (4) 24.6–24.9 | (24.7) (0.15) | (4) 1.5–1.7  | (1.6) (0.10) | (4) 1.8–2.0  | (1.9) (0.11) | (4) 5.7–6.0  | (5.9) (0.17) |
| <i>Acridotheres tristis</i>                   | (8) 25.6–29.5 | (27.9) (1.24) | (8) 1.6–1.9  | (1.7) (0.13) | (8) 1.7–2.2  | (1.8) (0.14) | (8) 6.3–7.6  | (6.9) (0.43) |
| <i>Acridotheres burmannicus leucocephalus</i> | (1) 26.8      | (26.8)        | (1) 1.6      | (1.6)        | (1) 1.9      | (1.9)        | (1) 7.0      | (7.0)        |
| <i>Acridotheres melanopterus</i>              | (1) 27.3      | (27.3)        | (1) 1.8      | (1.8)        | (1) 1.9      | (1.9)        | (1) 7.6      | (7.6)        |
| <i>Gracupica contra</i>                       | (1) 26.5      | (26.5)        | (1) 1.4      | (1.4)        | (1) 1.8      | (1.8)        | (1) 6.4      | (6.4)        |
| <i>Gracupica nigricollis</i>                  | (1) 31.8      | (31.8)        | (1) 2.0      | (2.0)        | (1) 1.9      | (1.9)        | (1) 7.8      | (7.8)        |
| <i>Leucopsar rothschildi</i>                  | (3) 25.3–26.0 | (25.5) (0.37) | (3) 1.5–1.7  | (1.6) (0.11) | (3) 1.6–1.7  | (1.6) (0.05) | (3) 6.6–6.7  | (6.6) (0.05) |
| <i>Saroglossa spiloptera</i>                  | (1) 21.9      | (21.9)        | (1) 1.6      | (1.6)        | (1) 1.5      | (1.5)        | (1) 6.0      | (6.0)        |
| <i>Sturnia malabarica</i>                     | (3) 21.5–21.9 | (21.7) (0.23) | (3) 1.3–1.5  | (1.3) (0.11) | (3) 1.2–1.5  | (1.4) (0.17) | (3) 5.6–5.7  | (5.6) (0.05) |
| <i>Sturnia sinensis</i>                       | (1) 21.7      | (21.7)        | (1) 1.3      | (1.3)        | (1) 1.3      | (1.3)        | (1) 5.5      | (5.5)        |

**TABLE 5.** Measurements (mm) of the scapula of Mascarene starlings compared with other sturnids and *Upupa epops*. For abbreviations, see Methods.

| Species                                       | TL (n) range  | TL (m) SD     | PW (n) range | PW (m) SD    | PD (n) range | PD (m) SD    |
|---|---------------|---------------|--------------|--------------|--------------|--------------|
| <i>Upupa epops</i>                            | (2) 25.2–26.8 | (26.0) (1.13) | (2) 5.4–5.6  | (5.5) (0.14) | (2) 2.8      | (2.8)        |
| <i>Fregilupus varius</i>                      | (2) 31.1–33.0 | (32.0) (1.34) | (1) 5.7      | (5.7)        | (1) 3.4      | (3.4)        |
| <i>Acridotheres tristis</i>                   | (8) 29.7–35.8 | (33.2) (2.13) | (8) 5.2–6.9  | (6.2) (0.65) | (8) 2.5–3.4  | (3.0) (0.32) |
| <i>Acridotheres burmannicus leucocephalus</i> | (1) 30.2      | (30.2)        | (1) 6.6      | (6.6)        | (1) 2.0      | (2.0)        |
| <i>Acridotheres melanopterus</i>              | (1) 28.7      | (28.7)        | (1) 5.4      | (5.4)        | (1) 1.8      | (1.8)        |
| <i>Gracupica contra</i>                       | (1) 30.7      | (30.7)        | (1) 4.7      | (4.7)        | –            | –            |
| <i>Gracupica nigricollis</i>                  | (1) 37.0      | (37.0)        | (1) 7.3      | (7.3)        | (1) 2.5      | (2.5)        |
| <i>Leucopsar rothschildi</i>                  | (4) 30.3–33.0 | (31.6) (1.11) | (4) 4.7–5.8  | (5.3) (0.46) | (4) 3.2–3.7  | (3.4) (3.73) |
| <i>Saroglossa spiloptera</i>                  | (1) 25.6      | (25.6)        | (1) 5.2      | (5.2)        | (1) 2.5      | (2.5)        |
| <i>Sturnia malabarica</i>                     | (3) 23.0–25.0 | (24.0) (1.00) | (3) 4.3–4.5  | (4.4) (0.10) | (3) 2.4–2.6  | (2.5) (0.10) |
| <i>Sturnia sinensis</i>                       | (1) 25.7      | (25.7)        | (1) 4.2      | (4.2)        | (1) 2.9      | (2.9)        |

TABLE 6. Measurements (mm) of the sternum of Mascarene starlings compared with other sturnids and *Upupa epops*. For abbreviations, see Methods.

| Species                          | TL (n)<br>range  | TL (m) SD        | GW (n)<br>range  | GW (m)<br>SD     | LW (n)<br>range  | LW (m)<br>SD     | KL (n)<br>range  | KL (m) SD        | KD (n)<br>range  | KD (m)<br>SD     |
|----------------------------------|------------------|------------------|------------------|------------------|------------------|------------------|------------------|------------------|------------------|------------------|
| <i>Upupa epops</i>               | (2)<br>33.1–33.4 | (33.2)<br>(0.21) | (2)<br>14.0–15.0 | (14.5)<br>(0.70) | (2)<br>11.2–11.8 | (11.5)<br>(0.42) | (2)<br>31.7–31.9 | (31.8)<br>(0.14) | (2)<br>11.7–12.5 | (12.1)<br>(0.56) |
| <i>Fregilupus varius</i>         | (2) 33.6         | (33.6)           | (2)              | (19.1)           | (1) 16.2         | (16.2)           | (2)              | (31.0)           | (2) 8.6–9.1      | (8.8)            |
| <i>Necropsar rodericanus</i>     | (2)              | (34.6)           | (2)              | (18.9)           | (1) 15.7         | (15.7)           | (2)              | (30.7)           | (2) 7.7–8.6      | (8.1)            |
| <i>Acridotheres tristis</i>      | (8)<br>32.2–37.0 | (3.39)<br>(35.1) | (7)<br>18.7–19.2 | (0.35)<br>(17.7) | (8)              | (14.8)           | (6)              | (4.59)<br>(33.1) | (7) 9.8–12.0     | (0.63)<br>(10.8) |
| <i>Acridotheres burmannicus</i>  | (1) 31.7         | (3.68)<br>(31.7) | (1) 15.4         | (0.87)<br>(15.4) | (1) 12.7         | (12.7)           | (1) 32.1         | (2.24)<br>(32.1) | (1) 9.7          | (0.76)<br>(9.7)  |
| <i>leucocephalus</i>             | (1) 34.2         | (34.2)           | (1) 17.0         | (17.0)           | (1) 13.8         | (13.8)           | (1) 28.0         | (28.0)           | (1) 9.7          | (9.7)            |
| <i>Acridotheres melanopterus</i> | (1) 30.8         | (30.8)           | (1) 15.9         | (15.9)           | (1) 14.0         | (14.0)           | (1) 27.9         | (27.9)           | (1) 10.0         | (10.0)           |
| <i>Gracupica contra</i>          | (1) 38.8         | (38.8)           | (1) 18.8         | (18.8)           | (1) 14.6         | (14.6)           | (1) 36.6         | (36.6)           | (1) 10.5         | (10.5)           |
| <i>Gracupica nigricollis</i>     | (3)              | (31.8)           | (2)              | (16.9)           | (4)              | (13.9)           | (4)              | (27.9)           | (4) 7.6–8.6      | (8.1)            |
| <i>Leucopsar rothschildi</i>     | (1) 26.1         | (26.1)           | (1) 13.6         | (13.6)           | (1) 12.1         | (12.1)           | (1) 27.4         | (27.4)           | (1) 7.1          | (7.1)            |
| <i>Saroglossa spiloptera</i>     | (3)              | (26.6)           | (3)              | (15.1)           | (3)              | (11.3)           | (3)              | (25.2)           | (3) 7.1–8.0      | (7.4)            |
| <i>Sturnia malabarica</i>        | (1) 26.3         | (26.3)           | (1) 17.0         | (17.0)           | (1) 11.0         | (11.0)           | (1) 26.8         | (26.8)           | (1) 7.7          | (7.7)            |
| <i>Sturnia sinensis</i>          | (1) 26.3         | (26.3)           | (1) 17.0         | (17.0)           | (1) 11.0         | (11.0)           | (1) 26.8         | (26.8)           | (1) 7.7          | (7.7)            |

**TABLE 7.** Measurements (mm) of the humerus of Mascarene starlings compared with other sturmds and *Upupa epops*. For abbreviations, see Methods.

| Species                          | TL (n)           | TL (m)           | PW (n)         | PW (m)          | PD (n)         | PD (m)          | SW (n)         | SW (m)          | SD (n)         | SD (m)          | DW (n)          | DW (m)          | DD (n)         | DD (m)          |
|----------------------------------|------------------|------------------|----------------|-----------------|----------------|-----------------|----------------|-----------------|----------------|-----------------|-----------------|-----------------|----------------|-----------------|
|                                  | range            | SD               | range          | SD              | range          | SD              | range          | SD              | range          | SD              | range           | SD              | range          | SD              |
| <i>Upupa epops</i>               | (2)<br>33.0–33.3 | (33.1)<br>(0.21) | (2)<br>8.6–8.8 | (8.7)<br>(0.14) | (2)<br>4.1–4.3 | (4.2)<br>(0.14) | (2)<br>3.2–3.3 | (3.2)<br>(0.07) | (2)<br>2.5–2.7 | (2.6)<br>(0.14) | (2)<br>8.0–8.1  | (8.0)<br>(0.07) | (2)<br>4.0–4.1 | (4.0)<br>(0.07) |
| <i>Fregilupus varius</i>         | (2)<br>35.9–37.6 | (36.7)<br>(1.20) | (2)<br>9.1–9.2 | (9.1)<br>(0.07) | (2)<br>3.8–3.9 | (3.8)<br>(0.07) | (2)<br>3.0–3.3 | (3.1)<br>(0.21) | (2)<br>2.8–2.9 | (2.8)<br>(0.07) | (2)<br>8.1–9.0  | (8.5)<br>(0.63) | (2)<br>4.1–4.7 | (4.4)<br>(0.42) |
| <i>Necropsar rodericanus</i>     | (8)<br>32.1–35.0 | (33.6)<br>(1.14) | (6)<br>8.0–8.7 | (8.3)<br>(0.25) | (7)<br>3.7–3.8 | (3.7)<br>(0.05) | (8)<br>2.5–3.0 | (2.7)<br>(0.15) | (8)<br>2.1–2.5 | (2.3)<br>(0.11) | (8)<br>7.1–8.1  | (7.4)<br>(0.36) | (7)<br>3.6–4.0 | (3.8)<br>(0.14) |
| <i>Cryptopsar ischyrynchus</i>   | (3)<br>32.5–34.5 | (33.5)<br>(1.00) | (3)<br>7.9–8.4 | (8.2)<br>(0.28) | (3)<br>3.8–4.5 | (4.3)<br>(0.43) | (3)<br>2.5–2.7 | (2.5)<br>(0.11) | (3)<br>2.2–2.3 | (2.2)<br>(0.05) | (3)<br>6.9–10.4 | (8.1)<br>(2.01) | (3)<br>3.9–4.3 | (4.0)<br>(0.20) |
| <i>Acridotheres tristis</i>      | (8)<br>31.6–37.6 | (34.8)<br>(1.77) | (8)<br>8.4–9.5 | (8.7)<br>(0.35) | (8)<br>3.4–4.2 | (3.8)<br>(0.26) | (8)<br>2.5–3.0 | (2.8)<br>(0.16) | (8)<br>2.2–2.6 | (2.4)<br>(0.13) | (8)<br>6.8–8.0  | (7.4)<br>(0.43) | (8)<br>3.7–4.6 | (4.2)<br>(0.29) |
| <i>Acridotheres burmannicus</i>  | (1) 31.2         | (31.2)           | (1) 9.8        | (9.8)           | (1) 4.6        | (4.6)           | (1) 3.3        | (3.3)           | (1) 2.8        | (2.8)           | (1) 8.5         | (8.5)           | (1) 4.6        | (4.6)           |
| <i>Leucocephalus</i>             |                  |                  |                |                 |                |                 |                |                 |                |                 |                 |                 |                |                 |
| <i>Acridotheres melanopterus</i> | (1) 31.5         | (31.5)           | (1) 7.8        | (7.8)           | (1) 4.0        | (4.0)           | (1) 2.6        | (2.6)           | (1) 2.3        | (2.3)           | (1) 6.4         | (6.4)           | (1) 4.3        | (4.3)           |
| <i>Gracupica contra</i>          | (1) 31.0         | (31.0)           | (1) 7.8        | (7.8)           | (1) 3.7        | (3.7)           | (1) 2.7        | (2.7)           | (1) 2.5        | (2.5)           | (1) 7.1         | (7.1)           | (1) 3.8        | (3.8)           |
| <i>Gracupica nigricollis</i>     | (1) 39.0         | (39.0)           | (1) 9.8        | (9.8)           | (1) 4.6        | (4.6)           | (1) 3.3        | (3.3)           | (1) 2.8        | (2.8)           | (1) 8.5         | (8.5)           | (1) 4.6        | (4.6)           |
| <i>Leucopsar rothschildi</i>     | (4)<br>30.6–32.6 | (31.4)<br>(0.85) | (4)<br>7.9–8.6 | (8.1)<br>(0.32) | (4)<br>3.4–4.0 | (3.8)<br>(0.28) | (4)<br>2.5–2.7 | (2.5)<br>(0.09) | (4)<br>2.1–2.3 | (2.2)<br>(0.08) | (4)<br>6.9–7.3  | (7.0)<br>(0.20) | (4)<br>3.8–3.9 | (3.8)<br>(0.05) |
| <i>Saroglossa spiloptera</i>     | (1) 24.3         | (24.3)           | (1) 6.6        | (6.6)           | (1) 3.3        | (3.3)           | (1) 2.3        | 2.3             | (1) 1.9        | (1.9)           | (1) 5.6         | (5.6)           | (1) 3.3        | (3.3)           |
| <i>Sturnia malabarica</i>        | (3)<br>22.8–23.7 | (23.3)<br>(0.49) | (3)<br>6.4–6.5 | (6.4)<br>(0.05) | (3)<br>2.9–3.3 | (3.1)<br>(0.20) | (3)<br>2.1–2.3 | (2.2)<br>(0.10) | (3)<br>1.9–2.0 | (1.9)<br>0.05)  | (3)<br>4.9–5.9  | (5.5)<br>(0.52) | (3)<br>3.0–3.2 | (3.1)<br>(0.10) |
| <i>Sturnia sinensis</i>          | (1) 23.2         | (23.2)           | (1) 6.1        | (6.1)           | (3) 3.3        | (3.3)           | (1) 2.2        | (2.2)           | (1) 1.8        | (1.8)           | (1) 5.6         | (5.6)           | (1) 3.2        | (3.2)           |

**TABLE 8.** Measurements (mm) of the radius of Mascarene starlings compared with other sturnids and *Upupa epops*. For abbreviations, see Methods.

| Species                                       | TL (n) range     | TL (m) SD        | PW (n) range | PW (m) SD     | PW (m) SD   | SW (n) range | SW (m) SD   | SW (m) SD    | SD (n) range | SD (m) SD    | DW (n) range | DW (m) SD |
|---|------------------|------------------|--------------|---------------|-------------|--------------|-------------|--------------|--------------|--------------|--------------|-----------|
| <i>Upupa epops</i>                            | (2)<br>40.0–42.2 | (41.1)<br>(1.55) | (2) 2.0–2.7  | (2.3) (0.49)  | (2) 2.4–2.8 | (2.6) (0.28) | (2) 0.9–1.5 | (1.2) (0.42) | (2) 2.6–2.7  | (2.6) (0.07) |              |           |
| <i>Fregilupus varius</i>                      | (1) 37.0         | (37.0)           | (1) 2.3      | (2.3)         | (1) 1.3     | (1.3)        | (1) 1.0     | (1.0)        | (1) 3.3      | (3.3)        |              |           |
| <i>Acridotheres tristis</i>                   | (7)<br>32.4–38.3 | (35.9)<br>(2.13) | (7) 1.6–1.9  | (1.17) (0.15) | (8) 0.9–1.5 | (0.9) (0.11) | (8) 0.8–1.2 | (0.9) (0.11) | (8) 2.9–3.4  | (3.0) (0.18) |              |           |
| <i>Acridotheres burmannicus leucocephalus</i> | (1) 32.8         | (32.8)           | (1) 2.1      | (2.1)         | (1) 1.3     | (1.3)        | (1) 0.8     | (0.8)        | (1) 2.8      | (2.8)        |              |           |
| <i>Acridotheres melanopterus</i>              | (1) 32.1         | (32.1)           | –            | –             | –           | –            | (1) 0.8     | (0.8)        | (1) 3.1      | (3.1)        |              |           |
| <i>Gracupica contra</i>                       | (1) 32.8         | (32.8)           | (1) 1.7      | (1.7)         | (1) 1.0     | (1.0)        | (1) 1.1     | (1.1)        | (1) 2.9      | (2.9)        |              |           |
| <i>Gracupica nigricollis</i>                  | (1) 40.7         | (40.7)           | (1) 2.5      | (2.5)         | (1) 1.3     | (1.3)        | (1) 0.9     | (0.9)        | (1) 3.3      | (3.3)        |              |           |
| <i>Leucopsar rothschildi</i>                  | (4)<br>30.0–33.8 | (31.8)<br>(1.55) | (4) 1.8–2.1  | (1.9) (0.14)  | (4) 1.0–1.1 | (1.0) (0.05) | (4) 0.9–1.2 | (1.0) (0.15) | (4) 2.8–3.1  | (2.9) (0.14) |              |           |
| <i>Saroglossa spiloptera</i>                  | (1) 26.9         | (26.9)           | (1) 1.7      | (1.7)         | (1) 1.8     | (1.8)        | (1) 0.9     | (0.9)        | (1) 2.4      | (2.4)        |              |           |
| <i>Sturnia malabarica</i>                     | (3)<br>24.1–25.1 | (24.6)<br>(0.50) | (3) 0.8–1.3  | (1.1) (0.28)  | (3) 0.8–1.9 | (1.2) (0.60) | (3) 0.5–1.0 | (0.7) (0.26) | (1) 2.2–2.3  | (2.2) (0.05) |              |           |
| <i>Sturnia sinensis</i>                       | (1) 24.8         | (24.8)           | (1) 1.5      | (1.5)         | (1) 0.9     | (0.9)        | (1) 0.7     | (0.7)        | (1) 2.4      | (2.4)        |              |           |

**TABLE 9.** Measurements (mm) of the ulna of Mascarene starlings compared with other sturnids and *Upupa epops*. For abbreviations, see Methods.

| Species                                       | TL (n) range     | TL (m) SD        | PW (n) range | PW (m) SD | PW (m) SD | PD (n) range | PD (m) SD | PD (m) SD | SW (n) range | SW (m) SD | SW (m) SD | SD (n) range | SD (m) SD | DW (n) range | DW (m) SD    |
|---|------------------|------------------|--------------|-----------|-----------|--------------|-----------|-----------|--------------|-----------|-----------|--------------|-----------|--------------|--------------|
| <i>Upupa epops</i>                            | (2)<br>43.9–46.5 | (45.2)<br>(1.83) | (2) 5.7      | (5.7)     | (2) 5.7   | (2)          | (3.8)     | (3.8)     | (2) 2.5      | (2.5)     | (2) 2.5   | (2)          | (2.4)     | (2) 4.8      | (4.8)        |
| <i>Fregilupus varius</i>                      | (2)<br>41.2–43.6 | (42.4)<br>(1.69) | (2)          | (6.5)     | (2) 4.0   | (2) 4.0      | (4.0)     | (4.0)     | (2)          | (2.7)     | (2.7)     | (2)          | (2.9)     | (2)          | (5.4) (0.14) |
| <i>Necropsar rodericanus</i>                  | (9)<br>36.1–40.1 | (38.0)<br>(1.49) | (9) 5.9–7.1  | (0.84)    | (11)      | (11)         | (3.5)     | (3.5)     | 2.6–2.8      | (0.14)    | (0.14)    | 2.6–3.3      | (0.49)    | 5.3–5.5      | (4.5) (0.21) |
| <i>Cryptopsar ischyrynchus</i>                | (1) 36.0         | (36.0)           | (1) 4.9      | (4.9)     | (1) 3.6   | (3.6)        | (3.6)     | (3.6)     | 2.0–2.4      | (0.12)    | (0.12)    | 2.2–2.6      | (0.12)    | 4.1–4.8      | (4.6)        |
| <i>Acridotheres tristis</i>                   | (8)<br>36.1–43.3 | (40.5)<br>(2.30) | (8) 5.0–6.2  | (0.39)    | (8)       | (8)          | (3.9)     | (3.9)     | (1) 2.3      | (2.3)     | (2.3)     | (1) 2.4      | (2.4)     | (1) 4.6      | (4.9) (0.36) |
| <i>Acridotheres burmannicus leucocephalus</i> | (1) 35.9         | (35.9)           | (1) 4.8      | (4.8)     | (1) 3.6   | (3.6)        | (3.6)     | (3.6)     | 2.2–2.4      | (0.09)    | (0.09)    | 2.3–3.1      | (0.25)    | 4.2–5.4      | (4.4)        |
| <i>Acridotheres melanopterus</i>              | (1) 36.5         | (36.5)           | (1) 4.7      | (4.7)     | –         | –            | –         | –         | (1) 1.9      | (1.9)     | (1.9)     | (1) 2.1      | (2.1)     | –            | –            |
| <i>Gracupica contra</i>                       | (1) 36.3         | (36.3)           | (1) 4.9      | (4.9)     | (1) 3.6   | (3.6)        | (3.6)     | (3.6)     | (1) 2.3      | (2.3)     | (2.3)     | (1) 2.3      | (2.3)     | (1) 4.4      | (4.4)        |
| <i>Gracupica nigricollis</i>                  | (1) 45.3         | (45.3)           | (1) 5.9      | (5.9)     | (1) 4.3   | (4.3)        | (4.3)     | (4.3)     | (1) 2.5      | (2.5)     | (2.5)     | (1) 2.7      | (2.7)     | (1) 5.5      | (5.5)        |
| <i>Leucopsar rothschildi</i>                  | (4)<br>34.5–37.8 | (36.1)<br>(1.34) | (4) 4.8–4.9  | (0.05)    | (4)       | (4)          | (3.9)     | (3.9)     | (4)          | (2.1)     | (2.1)     | (4)          | (2.3)     | (4)          | (4.6) (0.09) |
| <i>Saroglossa spiloptera</i>                  | (1) 30.6         | (30.6)           | (1) 4.1      | (4.1)     | (1) 2.8   | (2.8)        | (2.8)     | (2.8)     | (1) 1.9      | (1.9)     | (1.9)     | (1) 2.0      | (2.0)     | (1) 3.8      | (3.8)        |
| <i>Sturnia malabarica</i>                     | (3)<br>27.1–28.2 | (27.7)<br>(0.56) | (3) 3.7–3.8  | (0.05)    | (3)       | (3)          | (2.6)     | (2.6)     | (3)          | (1.7)     | (1.7)     | (3)          | (1.8)     | (3)          | (3.3) (0.20) |
| <i>Sturnia sinensis</i>                       | (1) 28.1         | (28.1)           | (1) 3.7      | (3.7)     | (1) 2.7   | (2.7)        | (2.7)     | (2.7)     | 1.7–1.9      | (0.11)    | (0.11)    | 1.7–2.0      | (0.15)    | 3.2–3.6      | (3.5)        |

**TABLE 10.** Measurements (mm) of the carpometaecarpus of Mascarene starlings compared with other sturnids and *Upupa epops*. For abbreviations, see Methods.

| Species                                       | TL (n) range            | TL (m) range | PW (n) range | PW (m) range | PD(n) range | PD (m) range | SW (n) range | SW (m) range | SD (n) range | SD (m) range | DD (n) range | DD (m) range |
|---|-------------------------|--------------|--------------|--------------|-------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|
| <i>Upupa epops</i>                            | (2) 20.3–21.4<br>(0.77) | (20.8)       | (2)          | (5.6)        | (2)         | (3.6)        | (2)          | (1.7)        | (2) 2.1      | (2.1)        | (2) 2.4      | (2.4)        |
| <i>Fregilupus varius</i>                      | (2) 24.1–26.0<br>(1.34) | (25.0)       | (1) 5.9      | (0.28)       | (1) 3.7     | (0.14)       | (1) 2.3      | (0.07)       | (1) 1.9      | (1.9)        | (1) 2.9      | (2.9)        |
| <i>Necropsar rodericanus</i>                  | (1) 22.6                | (22.6)       | (1) 5.4      | (5.4)        | (1) 3.3     | (3.3)        | (1) 1.7      | (1.7)        | (1) 1.9      | (1.9)        | (1) 2.2      | (2.2)        |
| <i>Cryptopsar ischyrynchus</i>                | (1) 23.1                | (23.1)       | (1) 5.6      | (5.6)        | (1) 3.2     | (3.2)        | (1) 2.3      | (2.3)        | (1) 1.9      | (1.9)        | (1) 2.1      | (2.1)        |
| <i>Acridotheres tristis</i>                   | (10)                    | (23.6)       | (10)         | (5.5)        | (10)        | (3.1)        | (10)         | (2.1)        | (10)         | (2.0)        | (10)         | (2.3) (0.30) |
|   | 21.4–25.0               | (1.03)       | 4.9–6.0      | (0.31)       | 2.7–3.7     | (0.37)       | 1.9–2.5      | (0.19)       | 1.9–2.6      | (0.20)       | 2.0–3.1      |              |
| <i>Acridotheres burmannicus leucocephalus</i> | (1) 20.0                | (20.0)       | (1) 5.1      | (5.1)        | (1) 3.1     | (3.1)        | (1) 1.8      | (1.8)        | (1) 1.7      | (1.7)        | (1) 1.9      | (1.9)        |
| <i>Acridotheres melanopterus</i>              | (1) 21.0                | (21.0)       | (1) 6.6      | (6.6)        | (1) 3.2     | (3.2)        | (1) 1.9      | (1.9)        | (1) 1.8      | (1.8)        | (1) 2.1      | (2.1)        |
| <i>Gracupica contra</i>                       | (1) 20.7                | (20.7)       | (1) 5.2      | (5.2)        | (1) 3.1     | (3.1)        | (1) 2.0      | (2.0)        | (1) 1.9      | (1.9)        | (1) 2.0      | (2.0)        |
| <i>Gracupica nigricollis</i>                  | (1) 26.3                | (26.3)       | (1) 6.3      | (6.3)        | (1) 3.4     | (3.4)        | (1) 2.2      | (2.2)        | (1) 2.2      | (2.2)        | (1) 2.1      | (2.1)        |
| <i>Leucopsar rothschildi</i>                  | (4) 20.0–21.4           | (20.5)       | (4)          | (5.3)        | (4)         | (2.9)        | (4)          | (1.9)        | (4)          | (1.7)        | (4)          | (2.0) (0.05) |
|   | (0.60)                  | (0.60)       | 5.3–5.8      | (0.31)       | 2.9–3.1     | (0.09)       | 1.7–2.0      | (0.14)       | 1.7–1.8      | (0.09)       | 2.0–2.1      |              |
| <i>Saroglossa spiloptera</i>                  | (1) 18.0                | (18.0)       | (1) 5.7      | (5.7)        | (1) 2.7     | (2.7)        | (1) 1.8      | (1.8)        | (1) 1.5      | (1.5)        | (1) 1.8      | (1.8)        |
| <i>Sturnia malabarica</i>                     | (3) 15.6–16.8           | (16.2)       | (3)          | (3.8)        | (3)         | (2.4)        | (3)          | (1.6)        | (3)          | (1.4)        | (1)          | (1.6) (0.05) |
|   | (0.60)                  | (0.60)       | 3.6–4.1      | (0.25)       | 2.3–2.5     | (0.10)       | 1.6–1.7      | (0.05)       | 1.4–1.5      | (0.05)       | 1.6–1.7      |              |
| <i>Sturnia sinensis</i>                       | (1) 16.4                | (16.4)       | (1) 3.9      | (3.9)        | (1) 2.4     | (2.4)        | (1) 1.7      | (1.7)        | (1) 1.4      | (1.4)        | (1) 1.6      | (1.6)        |

**TABLE 11.** Measurements (mm) of the pelvis of Mascarene starlings compared with other sturnids and *Upupa epops*. For abbreviations, see Methods.

| Species                                       | TL (n) range            | TL (m) range | TL (m) SD | GW (n) range | GW (m) range | GD (n) range | GD (m) range | PD (n) range | PD (m) range | LW (n) range  | LW (m) range  |
|---|-------------------------|--------------|-----------|--------------|--------------|--------------|--------------|--------------|--------------|---------------|---------------|
| <i>Upupa epops</i>                            | (2) 25.4–29.7<br>(3.04) | (27.5)       | (2)       | (17.9)       | (17.9)       | (2)          | (13.9)       | (2) 4.9–5.1  | (5.0) (0.14) | (2) 10.9–11.7 | (11.3) (0.56) |
| <i>Fregilupus varius</i>                      | (1) 34.3                | (34.3)       | (1) 19.7  | (19.7)       | (1) 17.4     | (17.4)       | (1) 17.4     | (1) 6.4      | (6.4)        | (1) 9.6       | (9.6)         |
| <i>Acridotheres tristis</i>                   | (8) 29.7–33.9<br>(31.5) | (31.5)       | (7)       | (18.9)       | (18.9)       | (8)          | (14.3)       | (8) 5.9–7.0  | (6.4) (0.38) | (8) 8.5–9.9   | (9.1) (0.59)  |
|   | (1.41)                  | (1.41)       | 17.5–20.6 | (1.04)       | 12.0–15.7    | (1.35)       |              |              |              |               |               |
| <i>Acridotheres burmannicus leucocephalus</i> | (1) 28.8                | (28.8)       | (1) 17.4  | (17.4)       | (1) 11.7     | (11.7)       | (1) 11.7     | (1) 5.1      | (5.1)        | (1) 8.6       | (8.6)         |
| <i>Acridotheres melanopterus</i>              | (1) 28.4                | (28.4)       | (1) 15.6  | (15.6)       | (1) 13.0     | (13.0)       | (1) 13.0     | (1) 5.8      | (5.8)        | –             | –             |
| <i>Gracupica contra</i>                       | (1) 28.2                | (28.2)       | (1) 17.7  | (17.7)       | (1) 11.9     | (11.9)       | (1) 11.9     | (1) 5.4      | (5.4)        | (1) 9.3       | (9.3)         |
| <i>Gracupica nigricollis</i>                  | (1) 36.7                | (36.7)       | (1) 21.3  | (21.3)       | (1) 16.9     | (16.9)       | (1) 16.9     | (1) 7.3      | (7.3)        | (1) 9.6       | (9.6)         |
| <i>Leucopsar rothschildi</i>                  | (4) 28.3–29.5<br>(0.64) | (29.5)       | (4)       | (18.1)       | (18.1)       | (4)          | (12.8)       | (4) 5.8–6.1  | (5.9) (0.15) | (4) 9.2–9.9   | (9.5) (0.29)  |
|   | (1) 21.3                | (21.3)       | 17.1–18.8 | (0.72)       | 11.2–13.6    | (1.12)       |              |              |              |               |               |
| <i>Saroglossa spiloptera</i>                  | (1) 21.3                | (21.3)       | (1) 15.1  | (15.1)       | (1) 8.9      | (8.9)        | (1) 8.9      | (1) 4.1      | (4.1)        | (1) 7.3       | (7.3)         |
| <i>Sturnia malabarica</i>                     | (3) 21.6–22.8<br>(0.64) | (22.3)       | (3)       | (13.8)       | (13.8)       | (3)          | (9.4–11.5)   | (3) 3.9–4.6  | (4.2) (0.35) | (3) 7.1–7.7   | (7.4) (0.32)  |
|   | (1) 23.6                | (23.6)       | 13.4–14.3 | (0.45)       |              |              |              |              |              |               |               |
| <i>Sturnia sinensis</i>                       | (1) 23.6                | (23.6)       | (1) 14.3  | (14.3)       | (1) 11.0     | (11.0)       | (1) 11.0     | (1) 5.0      | (5.0)        | (1) 7.5       | (7.5)         |



**TABLE 12.** Measurements (mm) of the femur of Mascarene starlings compared with other sturnids and *Upupa epops*. For abbreviations, see Methods.

| Species                          | TL (n)    |        | TL (m)  |        | PW (n)  |        | PW (m)  |        | PD (n)  |        | PD (m)  |        | SW (n)  |        | SW (m)  |        | DW (n) |     | DW (m) |     | DD (n) |     | DD (m) |       |
|----------------------------------|-----------|--------|---------|--------|---------|--------|---------|--------|---------|--------|---------|--------|---------|--------|---------|--------|--------|-----|--------|-----|--------|-----|--------|-------|
|                                  | range     | SD     | range   | SD     | range   | SD     | range   | SD     | range   | SD     | range   | SD     | range   | SD     | range   | SD     | range  | SD  | range  | SD  | range  | SD  | range  | SD    |
| <i>Upupa epops</i>               | (2)       | (23.3) | (2)     | (4.5)  | (2)     | (3.3)  | (2)     | (2.2)  | (2)     | (2)    | (2)     | (1.9)  | (2)     | (2)    | (4.4)   | (2)    | (2)    | (2) | (2)    | (2) | (2)    | (2) | (2)    | (3.6) |
|                                  | 23.2–23.4 | (0.14) | 4.5–4.6 | (0.07) | 3.1–3.5 | (0.28) | 2.1–2.3 | (0.14) | 1.8–2.0 | (0.14) | 1.8–2.0 | (0.14) | 1.8–2.0 | (0.14) | 3.6–3.7 | (0.07) |        |     |        |     |        |     |        |       |
| <i>Fregilupus varius</i>         | (2)       | (33.8) | (2)     | (7.0)  | (2)     | (3.9)  | (2)     | (3.0)  | (2)     | (2)    | (2)     | (2.8)  | (2)     | (2)    | (7.1)   | (2)    | (2)    | (2) | (2)    | (2) | (2)    | (2) | (2)    | (5.1) |
|                                  | 32.7–34.9 | (1.55) | 6.7–7.3 | (0.42) | 3.7–4.2 | (0.35) | 2.9–3.1 | (0.14) | 2.6–3.0 | (0.28) | 2.6–3.0 | (0.28) | 2.6–3.0 | (0.28) | 4.8–5.4 | (0.42) |        |     |        |     |        |     |        |       |
| <i>Necropsar rodericanus</i>     | (5)       | (32.9) | (5)     | (6.4)  | (5)     | (3.9)  | (5)     | (2.7)  | (5)     | (5)    | (5)     | (2.6)  | (5)     | (5)    | (6.6)   | (5)    | (5)    | (5) | (5)    | (5) | (5)    | (5) | (5)    | (5.2) |
|                                  | 32.1–33.7 | (0.56) | 6.4–6.7 | (0.13) | 3.6–4.3 | (0.25) | 2.6–3.1 | (0.23) | 2.4–3.3 | (0.38) | 2.4–3.3 | (0.38) | 2.4–3.3 | (0.38) | 4.9–5.9 | (0.46) |        |     |        |     |        |     |        |       |
| <i>Cryptopsar ischyrynchus</i>   | (1)       | (33.8) | (1)     | (6.4)  | (1)     | (3.5)  | (1)     | (2.6)  | (1)     | (2.6)  | (1)     | (2.5)  | (1)     | (2.5)  | (1)     | (6.5)  | (1)    | (1) | (1)    | (1) | (1)    | (1) | (1)    | (4.3) |
| <i>Acridotheres tristis</i>      | (8)       | (32.3) | (8)     | (6.0)  | (8)     | (3.4)  | (8)     | (2.4)  | (8)     | (8)    | (8)     | (2.2)  | (8)     | (8)    | (5.8)   | (8)    | (8)    | (8) | (8)    | (8) | (8)    | (8) | (8)    | (4.8) |
|                                  | 29.8–34.3 | (1.31) | 5.5–6.5 | (0.34) | 3.0–3.7 | (0.22) | 2.4–2.6 | (0.07) | 2.1–2.4 | (0.10) | 2.1–2.4 | (0.10) | 2.1–2.4 | (0.10) | 4.5–5.2 | (0.26) |        |     |        |     |        |     |        |       |
| <i>Acridotheres burmannicus</i>  | (1)       | (29.6) | (1)     | (5.3)  | (1)     | (3.1)  | (1)     | (2.3)  | (1)     | (2.3)  | (1)     | (2.1)  | (1)     | (2.1)  | (1)     | (4.4)  | (1)    | (1) | (1)    | (1) | (1)    | (1) | (1)    | (4.4) |
| <i>leucocephalus</i>             |           |        |         |        |         |        |         |        |         |        |         |        |         |        |         |        |        |     |        |     |        |     |        |       |
| <i>Acridotheres melanopterus</i> | (1)       | (28.6) | (1)     | (5.2)  | (1)     | (3.2)  | (1)     | (2.1)  | (1)     | (2.1)  | (1)     | (2.1)  | (1)     | (2.1)  | (1)     | (4.0)  | (1)    | (1) | (1)    | (1) | (1)    | (1) | (1)    | (4.0) |
| <i>Gracupica contra</i>          | (1)       | (27.8) | (1)     | (5.1)  | (1)     | (3.4)  | (1)     | (2.2)  | (1)     | (2.2)  | (1)     | (2.3)  | (1)     | (2.3)  | (1)     | (4.0)  | (1)    | (1) | (1)    | (1) | (1)    | (1) | (1)    | (4.0) |
| <i>Gracupica nigricollis</i>     | (1)       | (34.4) | (1)     | (6.4)  | (1)     | (3.4)  | (1)     | (2.6)  | (1)     | (2.6)  | (1)     | (2.6)  | (1)     | (2.6)  | (1)     | (5.2)  | (1)    | (1) | (1)    | (1) | (1)    | (1) | (1)    | (5.2) |
| <i>Leucopsar rothschildi</i>     | (3)       | (31.0) | (3)     | (5.8)  | (3)     | (3.4)  | (3)     | (2.3)  | (3)     | (3)    | (3)     | (2.2)  | (3)     | (3)    | (6.0)   | (3)    | (3)    | (3) | (3)    | (3) | (3)    | (3) | (3)    | (4.7) |
|                                  | 30.6–31.5 | (0.45) | 5.7–6.0 | (0.15) | 3.3–3.7 | (0.23) | 2.3–2.4 | (0.05) | 2.1–2.3 | (0.11) | 2.1–2.3 | (0.11) | 2.1–2.3 | (0.11) | 5.8–6.3 | (0.26) |        |     |        |     |        |     |        |       |
| <i>Saroglossa spiloptera</i>     | (1)       | (20.7) | (1)     | (4.2)  | (1)     | (2.3)  | (1)     | (1.6)  | (1)     | (1.6)  | (1)     | (1.5)  | (1)     | (1.5)  | (1)     | (3.1)  | (1)    | (1) | (1)    | (1) | (1)    | (1) | (1)    | (3.1) |
| <i>Sturnia malabarica</i>        | (3)       | (21.7) | (3)     | (3.9)  | (3)     | (2.5)  | (3)     | (1.7)  | (3)     | (3)    | (3)     | (1.7)  | (3)     | (3)    | (3.9)   | (3)    | (3)    | (3) | (3)    | (3) | (3)    | (3) | (3)    | (3.2) |
|                                  | 21.1–22.3 | (0.60) | 3.8–4.1 | (0.15) | 2.3–2.7 | (0.20) | 1.7–1.8 | (0.05) | 1.6–1.8 | (0.10) | 1.6–1.8 | (0.10) | 1.6–1.8 | (0.10) | 3.2–3.3 | (0.05) |        |     |        |     |        |     |        |       |
| <i>Sturnia sinensis</i>          | (1)       | (22.8) | (1)     | (4.0)  | (1)     | (2.5)  | (1)     | (1.7)  | (1)     | (1.7)  | (1)     | (1.7)  | (1)     | (1.7)  | (1)     | (3.4)  | (1)    | (1) | (1)    | (1) | (1)    | (1) | (1)    | (3.4) |

TABLE 13. Measurements (mm) of the tibiotarsus of Mascarene starlings compared with other sturnids and *Upupa epops*. For abbreviations, see Methods.

| Species                          | TL (n)           | TL (m)           | PW (n)          | PW (m)          | PD (n)          | PD (m)          | SW (n)          | SW (m)          | SD (n)          | SD (m)          | DW (n)          | DW (m)          | DD (n)          | DD (m)          |
|----------------------------------|------------------|------------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
|                                  | range            | SD               | range           | SD              | range           | SD              | range           | SD              | range           | SD              | range           | SD              | range           | SD              |
| <i>Upupa epops</i>               | (2)<br>33.0–36.3 | (34.6)<br>(2.33) | (2)<br>4.0–4.1  | (4.0)<br>(0.07) | (2)<br>4.2–4.5  | (4.3)<br>(0.21) | (2)<br>1.6      | (1.6)           | (2)<br>1.6      | (1.6)           | (2)<br>3.6–3.7  | (3.6)<br>(0.07) | (2)<br>3.4–3.8  | (3.6)<br>(0.28) |
| <i>Fregilupus varius</i>         | (2)<br>58.7–64.5 | (61.6)<br>(4.10) | (2)<br>7.5–9.3  | (7.5)<br>(1.27) | (2)<br>8.2–8.3  | (8.2)<br>(0.07) | (2)<br>2.8–3.1  | (2.9)<br>(0.21) | (2)<br>2.2–2.3  | (2.2)<br>(0.07) | (2)<br>5.5–5.9  | (5.7)<br>(0.28) | (2)<br>5.5–6.0  | (5.7)<br>(0.35) |
| <i>Necropsar rodericanus</i>     | (9)<br>53.4–59.3 | (57.0)<br>(2.56) | (11)<br>5.9–7.4 | (6.7)<br>(1.00) | (11)<br>5.7–7.8 | (7.1)<br>(1.37) | (14)<br>2.3–3.0 | (2.6)<br>(0.32) | (14)<br>2.1–2.7 | (2.2)<br>(0.35) | (12)<br>4.8–5.5 | (5.2)<br>(0.50) | (12)<br>4.8–5.5 | (5.2)<br>(0.32) |
| <i>Cryptopsar ischyrynchus</i>   | (2)<br>56.2–56.3 | (56.2)<br>(0.07) | (1)<br>6.0      | (6.0)<br>(6.0)  | (1)<br>6.7      | (6.7)<br>(6.7)  | (2)<br>2.4      | (2.4)           | (2)<br>2.5      | (2.5)           | (2)<br>5.2–5.3  | (5.2)<br>(0.07) | (2)<br>4.7–4.8  | (4.7)<br>(0.07) |
| <i>Acridotheres tristis</i>      | (8)<br>51.9–59.2 | (56.1)<br>(2.50) | (8)<br>5.2–5.9  | (5.4)<br>(0.21) | (8)<br>6.1–7.8  | (7.1)<br>(0.55) | (8)<br>2.3–2.6  | (2.4)<br>(0.10) | (8)<br>2.1–2.3  | (2.2)<br>(0.07) | (8)<br>4.8–6.0  | (5.1)<br>(0.39) | (8)<br>4.7–5.3  | (4.9)<br>(0.21) |
| <i>Acridotheres burmannicus</i>  | (1)<br>50.9      | (50.9)           | (1)<br>5.1      | (5.1)           | (1)<br>6.5      | (6.5)           | (1)<br>2.0      | (2.0)           | (1)<br>1.9      | (1.9)           | (1)<br>4.3      | (4.3)           | (1)<br>4.1      | (4.1)           |
| <i>Acridotheres melanopterus</i> | (1)<br>49.1      | (49.1)           | (1)<br>6.0      | (6.0)           | (1)<br>5.2      | (5.2)           | (1)<br>1.9      | (1.9)           | (1)<br>2.0      | (2.0)           | (1)<br>4.4      | (4.4)           | (1)<br>4.2      | (4.2)           |
| <i>Gracupica contra</i>          | (1)<br>47.3      | (47.3)           | (1)<br>5.9      | (5.9)           | (1)<br>6.2      | (6.2)           | (1)<br>2.0      | (2.0)           | (1)<br>1.8      | (1.8)           | (1)<br>4.4      | (4.4)           | (1)<br>4.3      | (4.3)           |
| <i>Gracupica nigricollis</i>     | (1)<br>61.4      | (61.4)           | (1)<br>6.9      | (6.9)           | (1)<br>8.1      | (8.1)           | (1)<br>2.4      | (2.4)           | (1)<br>2.4      | (2.4)           | (1)<br>5.4      | (5.4)           | (1)<br>5.5      | (5.5)           |
| <i>Leucopsar rothschildi</i>     | (4)<br>46.6–53.6 | (50.6)<br>(2.92) | (4)<br>5.6–6.2  | (5.9)<br>(0.25) | (4)<br>6.1–6.7  | (6.5)<br>(0.27) | (4)<br>2.1–2.2  | (2.1)<br>(0.05) | (4)<br>1.9–2.2  | (2.0)<br>(0.12) | (4)<br>4.9–5.4  | (5.0)<br>(0.23) | (4)<br>4.4–4.6  | (4.5)<br>(0.09) |
| <i>Saroglossa spiloptera</i>     | (1)<br>34.5      | (34.5)           | (1)<br>4.0      | (4.0)           | (1)<br>4.8      | (4.8)           | (1)<br>1.6      | (1.6)           | (1)<br>1.4      | (1.4)           | (1)<br>3.3      | (3.3)           | (1)<br>3.2      | (3.2)           |
| <i>Sturnia malabarica</i>        | (3)<br>36.4–37.3 | (36.8)<br>(0.45) | (3)<br>3.9–4.3  | (4.0)<br>(0.20) | (3)<br>4.6–4.8  | (4.7)<br>(0.10) | (3)<br>1.5–1.6  | (1.5)<br>(0.05) | (3)<br>1.3–1.4  | (1.3)<br>(0.05) | (3)<br>3.1–3.4  | (3.2)<br>(0.15) | (3)<br>3.1–3.2  | (3.1)<br>(0.05) |
| <i>Sturnia sinensis</i>          | (1)<br>38.9      | (38.9)           | (1)<br>3.9      | (3.9)           | (1)<br>5.1      | (5.1)           | (1)<br>1.7      | (1.7)           | (1)<br>1.5      | (1.5)           | (1)<br>3.2      | (3.2)           | (1)<br>3.3      | (3.3)           |

**TABLE 14.** Measurements (mm) of the tarsometatarsus of Mascarene starlings compared with other sturnids and *Upupa epops*. For abbreviations, see Methods.

| Species                          | TL (n)<br>range  | TL (m)<br>SD     | PW (n)<br>range | PW (m)<br>SD | PD (n)<br>range | PD (m)<br>SD | SW (n)<br>range | SW (m)<br>SD | SD (n)<br>range | SD (m)<br>SD | DW (n)<br>range | DW (m)<br>SD | DD (n)<br>range | DD (m)<br>SD |
|----------------------------------|------------------|------------------|-----------------|--------------|-----------------|--------------|-----------------|--------------|-----------------|--------------|-----------------|--------------|-----------------|--------------|
| <i>Upupa epops</i>               | (2)<br>20.5–23.3 | (21.9)<br>(1.97) | (2) 4.2         | (4.2)        | (2)             | (3.9)        | (2)             | (1.6)        | (2) 1.7         | (1.7)        | (2)             | (3.7)        | (2)             | (2.1)        |
| <i>Fregilupus varius</i>         | (2)<br>41.9–45.8 | (43.8)<br>(2.75) | (2)             | (6.1)        | (2)             | (5.9)        | (2)             | (2.4)        | (2)             | (3.0)        | (2)             | (4.5)        | (2)             | (3.0)        |
| <i>Necropsar rodericanus</i>     | (8)<br>36.1–40.8 | (38.4)<br>(3.50) | (9)             | (5.8)        | (7)             | (5.7)        | (10)            | (2.3)        | (10)            | (2.7)        | (8)             | (4.5)        | (8)             | (2.5)        |
| <i>Cryptopsar ischyrylynchus</i> | (1) 39.0         | (39.0)           | (1) 5.9         | (5.9)        | (1) 5.9         | (5.9)        | (1) 2.4         | (2.4)        | (1) 3.4         | (3.4)        | (1) 4.8         | (4.8)        | (1) 2.7         | (2.7)        |
| <i>Acridoheres tristis</i>       | (8)<br>35.3–41.5 | (39.0)<br>(2.15) | (8)             | (5.5)        | (8)             | (5.7)        | (8)             | (2.2)        | (8)             | (2.5)        | (8)             | (4.4)        | (8)             | (2.6)        |
| <i>Acridoheres burmannicus</i>   | (1) 35.2         | (35.2)           | (1) 4.8         | (4.8)        | (1) 4.5         | (4.5)        | (1) 1.6         | (1.6)        | (1) 1.8         | (1.8)        | (1) 3.7         | (3.7)        | (1) 2.3         | (2.3)        |
| <i>Leucocephalus</i>             |                  |                  |                 |              |                 |              |                 |              |                 |              |                 |              |                 |              |
| <i>Acridoheres melanopterus</i>  | (1) 35.3         | (35.3)           | (1) 4.9         | (4.9)        | (1) 4.8         | (4.8)        | (1) 1.9         | (1.9)        | (1) 2.7         | (2.7)        | (1) 4.2         | (4.2)        | (1) 2.5         | (2.5)        |
| <i>Gracupica contra</i>          | (1) 32.5         | (32.5)           | (1) 5.0         | (5.0)        | (1) 5.1         | (5.1)        | (1) 1.9         | (1.9)        | (1) 2.6         | (2.6)        | (1) 3.9         | (3.9)        | (1) 2.3         | (2.3)        |
| <i>Gracupica nigricollis</i>     | (1) 42.7         | (42.7)           | (1) 6.2         | (6.2)        | (1) 6.8         | (6.8)        | (1) 18.0        | (18.0)       | (1) 2.6         | (2.6)        | (1) 5.6         | (5.6)        | (1) 3.3         | (3.3)        |
| <i>Leucopsar rothschildi</i>     | (4)<br>29.4–36.2 | (33.7)<br>(2.97) | (4)             | (5.3)        | (4)             | (5.2)        | (4)             | (1.9)        | (4)             | (2.6)        | (4)             | (4.1)        | (4)             | (2.4)        |
| <i>Saroglossa spiloptera</i>     | (1) 21.4         | (21.4)           | (1) 3.7         | (3.7)        | (1) 3.5         | (3.5)        | (1) 1.6         | (1.6)        | (1) 1.8         | (1.8)        | (1) 2.6         | (2.6)        | (1) 1.7         | (1.7)        |
| <i>Sturnia malabarica</i>        | (3)<br>23.7–24.9 | (24.1)<br>(0.64) | (3)             | (3.6)        | (3)             | (3.5)        | (3)             | (1.5)        | (3)             | (2.0)        | (3)             | (2.9)        | (3)             | (1.7)        |
| <i>Sturnia sinensis</i>          | (1) 25.0         | (25.0)           | (1) 3.7         | (3.7)        | (1) 3.7         | (3.7)        | (1) 1.4         | (1.4)        | (1) 2.0         | (2.0)        | (1) 3.0         | (3.0)        | (1) 1.8         | (1.8)        |