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Abstract

The parrots (Psittacidae: *Lophopsittacus, Psittacula, Necropsittacus, Mascarinus*) of the Mascarenes (Mauritius, Réunion, Rodrigues) have been relatively poorly studied. Most analyses have been based on a few skins, insufficient fossil material, and unreliable contemporary accounts and illustrations, which have led to erroneous interpretations. The discovery of new fossil remains of parrots and new interpretations of contemporary descriptions and illustrations has clarified many issues. One problematic species, *Lophopsittacus bensoni* is here removed to the genus *Psittacula*. A detailed comparative analysis of fossil skeletal elements indicates that the affinities of the Mascarene parrots lie within the Psittaculini, a wide ranging tribe of parrots that occurs mainly in Southeast Asia and Australasia. The Mascarenes are remote volcanic islands and biogeographical evidence presented here suggests that parrots reached this isolated group by island-hopping from India, probably during low sea level stands.

Key words: Mascarene parrots, extinction , affinities, morphology, ecology, biogeography, Psittaculini, *Psittacula bensoni* new comb

Introduction

The Mascarene Islands, comprising Mauritius, Réunion, and Rodrigues, lie on the southern edge of the tropics in the western Indian Ocean. The nearest large land mass is Madagascar, some 665 km to the west of Réunion, whilst the continental land mass of Australia is situated 4800 km east of Rodrigues. Mauritius (20.25° S 57.5°E) lies 164 km ENE of Réunion (21 S° 55.5°E) and Rodrigues (19.75°S 63.5°E) is situated 574 km to the east of Mauritius (Fig.1).

The isolation of the Mascarenes has resulted in high faunal endemism, although adaptive radiation, particularly among birds, is extremely low. Terrestrial mammals and amphibians are absent, but endemic reptiles (Arnold 1979; 2000; Bour 1981) and fruit bats of the genus *Pteropus* (Cheke & Dahl 1981; Cheke 1987) are diverse. Mascarene environments remained pristine until comparatively recently. The first serious human activity did not occur until the late 16th century (Moree 1998), so that early travellers were able to provide a number of contemporary accounts and illustrations (Cheke 1987), which, although generally crude, give some indication as to the original ecology. The subsequent discovery of fossil material has allowed some corroboration of species described in early accounts. Because parrots were considered 'preferred game' to early mariners visiting the islands, most accounts unfortunately refer only to the ease with which they could be taken for the pot (Strickland & Melville 1848; Cheke 1987). Intense hunting led to their depletion or rapid extinction so that most species of parrots disappeared before they could be described scientifically except from fossil remains (see Table 1). In attempting to determine the original composition of the Mascarene parrot fauna, some influential works (Rothschild 1907a, b; Hachisuka 1953) confused rather than clarified the situation, with some parrots being based on inadequate evidence. Nethertheless, the number of species is remarkable for such a small archipelago and endemism is high. Because of the paucity of fossil parrot remains, the number of species may well have been higher than recognised here.

TABLE 1. Parrots of the Mascarenes and their status.

Species	Distribution	Types of evidence
†*Lophopsittacus mauritianus*	Mauritius	Fossil record, contemporary illustrations and accounts
†*Necropsittacus rodericanus*	Rodrigues	Fossil record and contemporary accounts
†*Psittacula bensoni* new comb.	Mauritius	Fossil record, contemporary illustrations and accounts
†*Psittacula cf. bensoni*	Réunion	Based on reliable contemporary accounts
Psittacula echo	Mauritius	Extant. Skins, fossil record and contemporary accounts
†*Psittacula eques*	Réunion	Contemporary illustrations and accounts
†*Psittacula exsul*	Rodrigues	Skins, fossil record, contemporary illustrations and accounts
†*Mascarinus mascarinus*	Réunion	Skins, fossil record, contemporary illustrations and accounts
†*Necropsittacus(?) borbonicus*	Réunion	Hypothetical, based on one reliable account. Indeterminate genus.
†Necropsittacus francicus	Mauritius	Invalid taxon based on misinterpretation of accounts

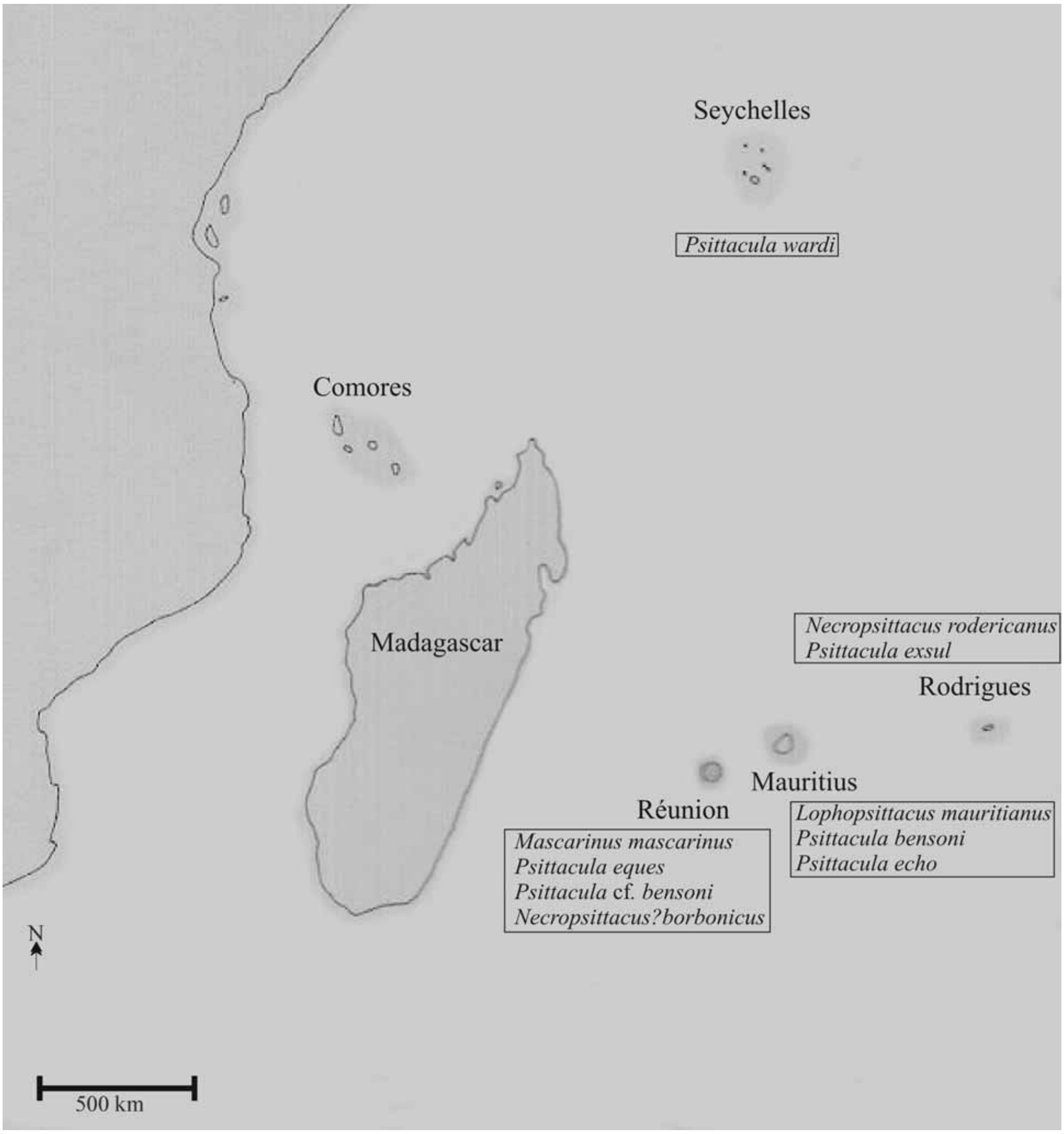

FIGURE 1. The Mascarene Islands of Réunion, Mauritius and Rodrigues with the distribution of Mascarene species of parrots (boxed).

This paper deals mainly with psittaciform osteological remains, but relevant historical accounts are also included, especially those where no English translations existed and the works had thus been ignored by other writers. The Seychelles Parakeet *Psittacula wardi* is also discussed, as it appears to be closely linked to the colonisation of the Mascarenes by other species of *Psittacula*.

The geological, palaeontological, and historical record

Although the Mascarenes are of similar volcanic origin (Courtillot 1999), the islands are strikingly different and have evolved in isolation, having never had connections among themselves or any connections to a continental landmass (Saddul 1995). Mauritius is the oldest island with rocks > 7 my; its youngest volcanics are dated at 20,000 BP (Saddul 1995). Réunion is still volcanically active, and its oldest rocks are only 3 my old (Rivals 1989; Saddul 1995). The supposed youthful age of Rodrigues, recorded as the youngest island at 1.5 MY (McDougall *et al.* 1965; Saddul 1995) is not supported by the nature of the biota as endemism at the familial and generic level in some taxa is higher than that of Mauritius or Réunion (Hume unpubl). Réunion and Mauritius, unlike Rodrigues, lack extensive limestone caverns and their main fossiliferous sites are in marshes, cliff undercuts, small caves, and boulder fields (Clark 1866; Slater 1879b; Cowles 1987; Mourer-Chauviré *et al.* 1999), all of which are scarce within the archipelago. Fossil assemblages are taphonomically biased, particularly in element type and species representation (Hume 2005). Bone preservation is generally poor to good on Mauritius and Réunion but may be excellent on Rodrigues. Parrot remains are generally rare at all fossil localities. Unlike Rodrigues, much of the avifauna of Réunion was derived from the older fauna, including parrots, pigeons, rails, and passerines.

Parrot remains have been discovered on Réunion in three different cave localities and have been referred to the extinct endemic species *Mascarinus mascarinus* (Mourer-Chauviré *et al.* 1999). At least three other species may have existed on Réunion (Dubois 1674), none of which is known from skins or fossils. On Mauritius, only the large extinct parrot species *Lophopsittacus mauritianus* has been recovered from the Mare aux Songes, a marsh situated in southeast Mauritius famous for harbouring the remains of almost all endemic Mauritian species (Owen 1866a; Clark 1866; Newton & Gadow 1893). The marsh sediments present today are black and peaty containing <30% fine to medium coral sand, but the original sedimentology cannot now be determined as all material was removed for agriculture (pers. obs). Furthermore, the marsh was infilled with basalt boulders by the British Armed Forces during the 1940s to control malaria, an act instigated by Dr Herman André, head of the Department of Health, Mauritius (P. André, British Veterinary Hospital Association, pers.comm., 20 July 2006). The marsh is inundated with fresh water for at least six months of the year but run-off is slow (Hume 2005). George Clark excavated the marsh during the mid 1860s and Théodore Sauzier further worked there under a Government commission in 1889–1890 (Newton and Gadow 1893; Koenig 1932). Paul Carié re-excavated the Mare aux Songes in the early 1900s and, along with Etienne Thirioux, discovered additional material in cave (boulder field?) deposits located at Le Pouce (northwest), Corps de Garde (central west) and Le Rouche (northeast) (Carié 1916; Koenig 1932; Florens 2002). At least three species of parrot once coexisted on Mauritius (Cheke 1987; Hume 1996), but no skin specimens of the extinct species are known. The only surviving Mauritian parrot, *Psittacula echo*, is critically endangered and now confined to the Black River Gorges in southwest Mauritius (Jones 1987), although, a successful captive breeding program has substantially increased the population (Thorsen & Jones 1998). Numerous fossil specimens referable to this species (see below), discovered by Thirioux in the Le Pouce and Corde de Garde locations, suggest a much greater distribution on the island than at present.

Rodrigues was once inhabited by at least two species of parrot, both now extinct. They are known from fossil remains found in cave deposits and one is represented as well by two skins collected in the early 1870s (Newton & Newton 1876). The Plaine Corail in southwest Rodrigues is an extensive limestone deposit (calcarenite) containing a complex network of caverns and caves carved out by the action of underground streams and percolating water (Caldwell 1875; Slater 1879b; Saddul 1995). Roof collapses and narrow entrances formed a natural trap for the original fauna. Most of the fossil material is perfectly preserved with many skeletal elements often in articulation. Despite the discovery of thousands of bird bones (Newton & Gadow 1893), parrots are extremely rare in these deposits.

Materials and methods

Comparative material examined

Skeletal material of the following species was examined, all at BMNH:

Cyanoramphus unicolor S/1955.5.57 (unsexed); *Cyanoramphus novaezelandiae* S/1992.62.1 ♀; S/1983.26.2 (unsexed); *Cyanoramphus novaezelandiae hochstetteri* (Antipodes) S/1952.3.163 ♂; *Tanygnathus* *megalorhynchus* S/1989.26.20 ♂; S/1983.26.2 ♀ *Psittacula krameri krameri* S/1993.15.1 ♂, S/1993.15.2 ♂, S/1993.15.3 ♂, S/1993.15.4 (unsexed), S/1993.15.5 ♀; S/1993.15.8 ♂, S/1993.15.8 ♂, S/1993.15.10 ♀; *Psittacula krameri borealis* S/1975.103.70 ♀; S/1975.103.62 ♂; S/1975.103.68 ♂; *Psittacula krameri manillensis* S/1952.2.442 (unsexed); S/1952.2.444 (unsexed); S/1973.66.111 ♀; *Psittacula echo* Juvenile (loan MWF) (unsexed); S/2000.44.1 ♀; *Psittacula eupatria* S/1999.11.5 ♂; S/1990.20.4 (unsexed); S/1994.61.4 ♀; S/1990.20.5 (unsexed); S/1990.20.3 (unsexed); S/1990.20.2 ♂; S/1990.20.1 (unsexed); S/199018.30 ♀; S/1990.18.28 ♂: S/1990.18.27 ♀; S/1990.18.26 ♂; S/1990.18.29 ♀; S/1990.18.25 ♀; *Coracopsis nigra* S/1972.1.83 (unsexed); 1897.5.10.45 (unsexed); *Coracopsis vasa* S/2002.4.3 ♂; S/1972.1.84 (unsexed); *Agapornis cana* 1876.3.16.1 (unsexed); *Psittrichas fulgidus* S/1983.74.1 (unsexed); S/2001.50.168 ♂; *Psittacus erithacus* S/1994.61.3 ♂; S/1997.32.1 ♀; *Psephotus pulcherrimus* 1868.4.15.4 ♂; *Geopsittacus occidentalis* 1868.4.15.3 ♂; *Eclectus roratus* S/1990.12.1 ♂; S/1991.44.6 ♀; *Calyptorhynchus magnificus magnificus* S/1969.4.22 ♂; S/1997.32.2 ♀; *Anodorhynchus hyacinthinus* S/1973.66.104 ♂; S/1955.22.9 (unsexed); *Probosciger aterrimus* S/1958.9.2 ♀; S/1989.26.5 ♂; *Nestor notabilis* 1862.5.13.1 (unsexed); S/1958.10.11 ♀; *Nestor meridionalis* S/1952.2.411 (unsexed); S/1952.3.12 (unsexed); *Strigops habroptilus* S/1972.1.71 (unsexed); S/1952.2.410 (unsexed); S/1955.5.27 (unsexed); 1881.1.17.71 (unsexed).

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 occipitalis in a median plane; rostrum, from tip of crista tomialis to nasofrontal hinge; mandible, from distal margin of rostrum mandibulae to furthest point on the proximal articulating surface; sternum, from cranial tip of spina externa to margo caudalis in a median plane; coracoid, measured on the medial side; ulna, measured in dorsal aspect. LIT = length inner trochlea; length from trochlea. metatarsi II to proximal end. GW = greatest width; cranium taken between processus postorbitales; mandible, greatest width taken across the mandible articulating surfaces; coracoid, proximal end from processus extensorius to facies articularis ulnacarpalis. GD = greatest depth; cranium from medial point of parietal to medial ventral surface; mandible, greatest depth of symphysis taken from angulus mandibulae to ventral surface of symphysis. NFW = naso-frontal width; width across naso frontal hinge. NW = nares width; width taken between medial edges of nares. LS = length of symphysis; mandible, greatest length of symphysis taken in a medial plane. WS = width of symphysis; mandible, symphysis width taken from internal lateral most edges. PL = palatine greatest length; ventral surface from proximal edge to distal edge of pars lateralis. PD = palatine greatest depth; taken from processus rostralus to ventral surface of pars lateralis. PW = proximal width; in lateromedial plane; femora, from the acetabulum through mid-depth point of the neck to lateral side. SW = shaft width; in lateromedial plane. SD = shaft depth; in dorsoventral plane. DW = distal width; in lateromedial plane; cranium, taken across width of the cranionasal hinge; ulna, taken in dorsal aspect. WSE = width of the sternal end of coracoid. DL = dorsal length; sternum excluding spina externa taken in medial plane. LC = greatest length of carina sterni; from apex carinae to margo caudalis of sternum. IC = intercostal width; sternum width taken across sternum between 2nd intercostals. LK = greatest depth of keel; taken from facies muscularis sterni to apex carinae.

Abbreviations

The following abbreviations are used: BMNH, The Natural History Museum, London (formerly the British Museum (Natural History)); UMZC, University Museum of Zoology, Cambridge; RMS, Royal Museum of Scotland; MNHN, Muséum National d'Histoire Naturelle, Paris; UCB, Université Claude Bernard-Lyon 1, France; NMW, Naturhistorisches Museum Wien; MWF, Mauritius Wildlife Foundation; FLMR, Francois Leguat Museum, Rodrigues.

In listing skeletal material, the following abbreviations are used: left (L) or right (R) prefixed by 'p' proximal,'s' shaft or'd' distal. † indicates an extinct genus or species. In Figs. 2 through 13, if unspecified, the sex of the specimen is indeterminate.

Anatomical nomenclature follows Baumel & Witmer (1993).

Etymology

In order to clarify nomenclature, the etymology of Mascarene parrots is presented here in its entirety and is taken from Jobling (1991), but where unavailable, etymology of fossil taxa is taken from the original description.

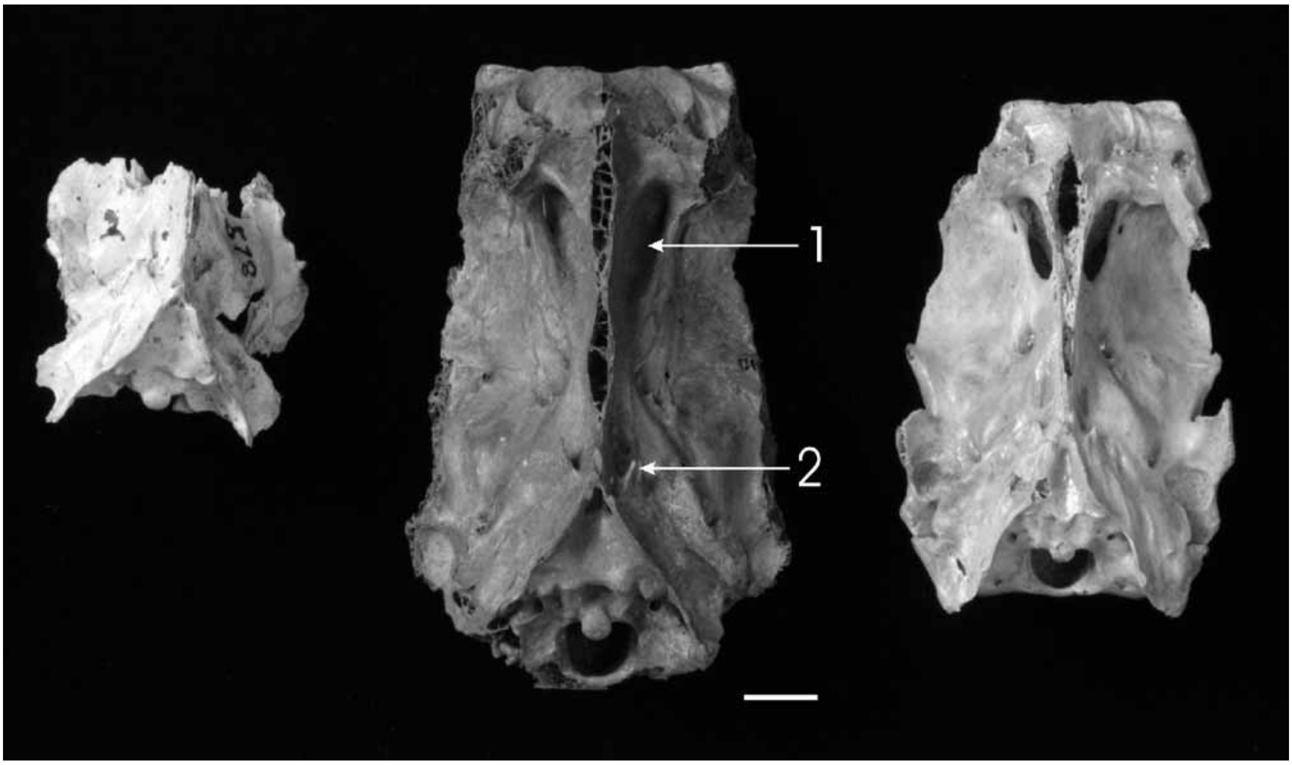

FIGURE 2. Crania of Mascarene parrots, ventral aspect. A, UMZC578 *Lophopsittacus mauritianus* (mis-identified as *Necropsittacus rodericanus*); B, UMZC1551 *Lophopsittacus mauritianus.* In 1., the fonticuli orbitocraniales form deep pits and are not connected to the cranial cavity by large openings and 2., the two triangular processes projecting ventroanteriorly. Both of these structures are particularly diagnostic in *Lophopsittacus*; C, UMZC562 *Necropsittacus rodericanus*. Scale bar = 10mm.

Species accounts

Class Aves

Order Psittaciformes

Family Psittacidae

Genus *Lophopsittacus* Newton, 1875: 349.

Psittacus (*Lophopsittacus*) *mauritianus*; Newton, 1875a: 349, Type (by original designation).

Etymology: From Greek *lophos*, crest and *psittakos*, a parrot, in reference to the distinct feathered crest.

Diagnosis: A monotypic genus with disproportionately large head and jaws, distinct frontal crest of feathers, broad rounded wings and long graduated tail, the two central tail feathers longer than the rest. Cranium dorso-ventrally flattened with distinct dorsal surface ridges confined to the frontal region; fonticuli orbitocraniales form deep pits and are not connected to the cranial cavity by large openings; in sternum, comparatively reduced with shallow carina sterni; pronounced flattening of the surface of facies muscularis sterni and anterior projection of the spina externa; in humerus, condylus dorsalis comparatively reduced and deflected less medially with a small proximal depression; in femur, impressiones iliotrochantericae markedly ridged and deeply excavated.

Raven Parrot; Broad-billed Parrot *Lophopsittacus mauritianus* (Owen, 1866)

Indische Raven, Het Tweede Boeck 1601; Begin en de voortgangh 1646:30; Soete-boom 1648:19; Granaet 1666., in Barnwell, 1948: 25. Visits and Despatches 1598–1948. Port Louis, Mauritius Standard Printing Establishment [Original not seen]; Hoffman 1680., in Grandidier & Grandidier. 1905, III, 374. Ouvrages ou extraits d'ouvrages anglais, hollandaise, portugais, espagnols et allemands, relatifs à anciens Madagascar (1640 à 1716) [Original not seen].
Psittacus mauritianus Owen, 1866a: 168; figs 1– 4; Owen, 1866b: 88; Milne-Edwards, 1866: 91.
Broad-billed parrot; Owen, 1869: 53.
Psittacus (*Lophopsittacus*) *mauritianus*; Newton, 1875a: 349, Type (by original designation).
Lophopsittacus mauritianus; Newton, 1875b: 732, figs. 44, 46.

Holotype: symphysis of mandible. The present location of this specimen is unknown.

Measurements: See Appendix 3, tables 1–11.

Type locality: Mare aux Songes, Mauritius. Holocene material collected in 1865 by George Clark. Further material collected by Théodore Sauzier in 1889–1890 (Newton & Gadow 1893).

Additional locality: Le Pouce, Mauritius. Specimens collected by Etienne Thirioux in the late 1890s and early 1900s and deposited in MNHN. The precise locality where Thirioux procured his specimens has not yet been determined, but Thirioux in correspondence with Alfred Newton held at UMZC states that it was at 2000 m on the side of Le Pouce valley.

Distribution: Mauritius, Mascarenes, Indian Ocean

Etymology: *mauritianus*, from the island of Mauritius, named in honour of Stadhouder Maurits, Prince of Orange (1567–1625).

Paratypes: None designated.

Referred material: Subfossil material collected from the Mare aux Songes and Le Pouce, Mauritius: cranium Type A ♂ BMNH 1551; mandible Type A ♂ UMZC 424AA, BMNH A3298, BMNH A3298, BMNH A3298, BMNH A3298, BMNH A3297, BMNH A3297, BMNH A3297, BMNH A3296, Type B ♀ BMNH A3296, BMNH A3297, BMNH A3298; palatine Type A ♂ BMNH 01(L); BMNH 02(R); BMNH 03(L); BMNH 04(L); BMNH 05(R); BMNH 06(R); BMNH 07(R); BMNH 08(R); BMNH 09(L); BMNH 10(R); BMNH 11(L); BMNH 12(L); BMNH 13(R); BMNH 14(L); BMNH 15(R); BMNH 16(R); BMNH 17(L); UMCZ A24AA(R); UMZC A24AA(R); UMZC A24AA(L); MNHN MAD4986; MNHN MAD4985; MNHN MAD4997(R); MNHNMAD4995(R); MNHN MAD4996; Type B ♀ BMNH A3300(L); BMNH A3300(R); BMNH A3300(L); BMNH A3300(L); sternum UMZC 424.AA; furcula UMZC 599; UMZC 599(p); coracoid UMCZ 599(L), UMZC 599(Ld); MNHN MAU496(R); MNHN MAU525(R); MNHN MAU767(L); humerus UMZC 596(L); UMZC 596(Lp); UMZC 596Rp); MNHN MAD6800(L); MNHN MAD7011(R); ulna Type A ♂ UMZC 600(R); UMZC 600(L); UMZC 601(Rp); Type B ♀ MNHN MAD6969(L); MNHN MAD7187(R); carpometacarpus MNHN MAU569; MNHN MAU539; MNHN MAU537; MNHN MAU597; MNHN MAU542; MNHN MAU378; femur Type A ♂ UMCZ 424AA(L), UMZC 424AA(R), UMZC 424AA(R); UMZC 600(Rs); MNHN u/c(L); MNHN u/c(R); MNHN MAU367(L); tibiotarsus Type A ♂ UMZC 424AA(L), UMZC 424AA(R), UMZC 424AA(L), UMZC 424AA(R), UMZC 424AA(R), UMZC 424AA(R), UMZC 424AA(L), UMZC 424AA(R); UMZC 424AA(L); BMNH A3301(L), BMNH A3301(R), BMNH A3301(Ld), BMNH 829B(L), BMNH A3299(Lp), BMNH A3299(Rd), BMNH A3299(Rd), BMNH A3299(Rd), BMNH A3299(Ld), BMNH A3299(Rd), BMNH A3299(Ld), BMNH A3299(Ld), BMNH

A3299(L), BMNH A3299(Rd), BMNH A3299(Ld), BMNH A3299(Ld), BMNH A3299(R), BMNH A3299(L), BMNH A3299(R); MNHN MAD6829(R); MNHN MAD6825(L); MNHN MAD5005(L); MNHN MAD6819(R); MNHN MAD5006(R); MNHN MAD6822(R); MNHN MAD6821(L); MNHN MAD6827(R); Type B ♀ UMZC 424AA(R); UMZC 600(R); UMZC 600(Lp); UMZC 600(Rp); UMZC 600(Ld); BMNH A3300(L), BMNH A3300(L), BMNH A3300(Ld), BMNH A3300(Rd), BMNH A3300(Rd), BMNH A3300(L), BMNH A3300(Lp), BMNH A3300(L), BMNH A3300(Rd), BMNH A3300(Rd), BMNH A3300(R); MNHN MA3299(R), MNHN A3299(Rs), MNHN MAU5671; tarsometatarsus Type A ♂ UMCZ 424AA(R), MNHN MAU368; MNHN MAU366, MNHN MAU507; Type B ♀ MNHN MAU557. The elements are derived from at least 28 individuals.

Additional referred specimen: Posterior part of a cranium UMZC 578 (Fig. 2A).This specimen, accessioned in 1908, was catalogued as *Necropsittacus rodericanus*, "collected on Rodrigues Island, by E. Thirioux, who died in 1918 on Rodrigues, aged 71. As far as known, Thirioux did not collect any fossil material on Rodrigues and the preservation of this specimen is similar to that of other cave material from Le Pouce on Mauritius collected by Thirioux and is almost certainly from the same source. It is similar in morphology to *Lophopsittacus mauritianus* from Mauritius. In comparison with *Necropsittacus*, the preserved ventral area is much broader, the articulations for the quadrates are larger, and the foramen magnum is most similar to that in *Lophopsittacus*, i.e., shaped like a figure eight with a prominent condylus occipitalis. It is also highly unlikely that two extremely large parrots coexisted along with *P. exsul* on Rodrigues. Therefore, I refer this specimen to *Lophopsittacus mauritianus* (only the second cranium known), collected on Le Pouce, Mauritius, by E. Thirioux between 1897 and 1908.

Description and comparison: See Appendix 2a.

Diagnosis: As for the genus.

Remarks: A detailed drawing of *Lophopsittacus* in life executed in 1601 illustrates a distinct crest confined to the frontal region (Hume 2003). No such adornment is known in any other Mascarene parrot. The ridges on the frontal region indicate that the crest was firmly attached to the cranium. This implies that the crest was not raised or lowered in life, but remained stiff and stationary as in all other crested parrots except the Cacatuinae. It is also apparent from subfossil remains and one account (Begin en de voortgangh 1646, p. 30) that size differences occurred in this species. Sexual dimorphism is difficult to determine from fossils when dealing with small samples, yet the material clearly falls into two size classes. Does this indicate separate species or different sexes? Smith (1975) and Forshaw (1989) state that many parrots are sexually dimorphic in color, and males have larger skeletons (Shine 1989). The kakapo *Strigops habroptilus* exhibits the greatest sexual dimorphism in any living parrot (Livezey 1992), with the males being much larger, but showing only marginal size differences in the skeleton, primarily in the cranium and bill, humerus, femur, and scapula.

The cranial elements of *Lophopsittacus* exhibit the greatest size difference, the largest in any psittaciform (Holyoak 1971), with the larger mandibles and palatines being approximately 21% and 19% greater in total length than the smaller ones, whereas post-cranial differences are less striking, e.g. 8% difference in total length of tibiotarsus. Hereafter, the larger fossil specimens are designated male (type A) and the smaller elements female (type B). Sexual dimorphism in bill size is also common to other parrot genera, with males of Palm Cockatoo *Probosciger aterrimus stenolophus* and North Island Kea *Nestor meridionalis septentrionalis* being 24.8% and 12.3% larger than female in exposed culmen length respectively (Moorehouse *et al.* 1999). The 21% size difference in the bony core of the mandible of *Lophopsittacus* would be increased if the rhamphotheca were preserved.

Measurements of *Lophopsittacus* indicate that although the cranial elements were comparable in size with those of the largest living parrots, the pelvic elements in the male were only equal in size to or slightly larger than in *Nestor notabilis*, whilst the pelvic elements of the female approximated those of *Nestor meridionalis*. However, the pectoral elements are very much more reduced. In *Lophopsittacus* the male would have been approximately 55–65 cm in total length, whilst the female may have been 45–55 cm. Both sexes had disproportionately larger heads and jaws than in *Nestor* and longer tails. The big-headedness of this species is readily apparent in the only known detailed drawing of the bird in life (Fig. 5a), executed by Joris Laerle in 1601 (Hume 2003), and in a reconstruction comparing *Lophopsittacus* with the largest living psittaciform, *Anodorhynchus hyacinthinus* (Fig. 3).

Using x-radiographs, Holyoak (1971) proposed that *L. mauritianus* had a weakly constructed mandible. This assumption was based on the internal trabeculae being widely spaced, the palatines narrow, and the supposition that the lack of preservation indicated such delicateness that none survived, as opposed to their simply not having been found. Smith (1975:33) questioned Holyoak's conclusion that the internal trabeculae could predict jaw strength, and in reference to the genera *Cyanorhamphus*, *Melopsittacus*, *Neophema* and *Psephotus* remarked:

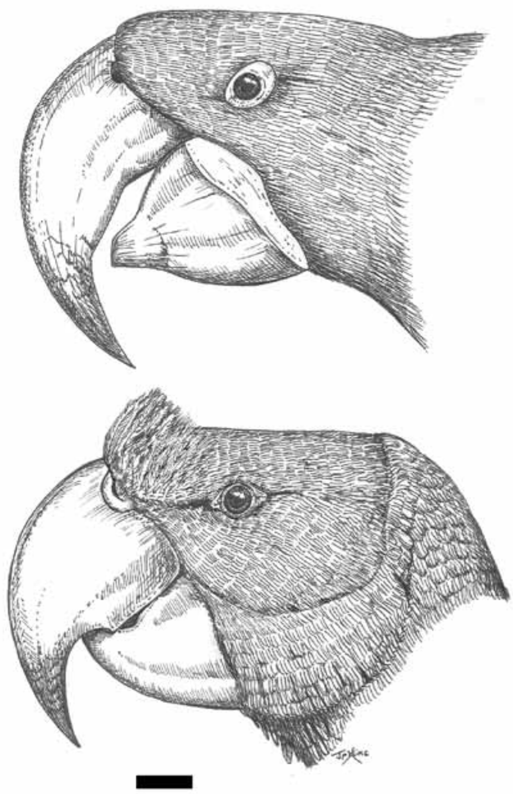

FIGURE 3. Author's reconstruction of the head of the Mauritian parrot *Lophopsittacus mauritianus* (below), compared with that of the largest living parrot *Anodorhynchus hyacinthinus* (above) from South America. Scale bar = 10mm.

> Holyoak's conclusion (1973b), following his examination of radiographs, that parrots of these four genera have 'strong beaks' is not borne out by experience of the live birds.

These genera are in fact extremely weak jawed in the hand (Smith 1975). Holyoak (1971) further concluded that *L. mauritianus* 'ate soft fruit or other such material'. These suggestions are incorrect due to a number of factors. Parrot jaws have a number of significant properties that allow great manipulative and physical pressure to be applied whilst feeding (Newton & Gadow 1893; Vlasblom 1953; Bock 1974; Homberger 1980,1986). The specialised synovial joints found between the craniofacial hinge and within the palatine and jugal bars in large parrots and macaws (Bühler 1981), as opposed to a narrow strip of bone or hinge in most birds, increase the flexibility and heavy biting forces of the upper jaw (Bock 1974; Bühler 1981). Jaw flexibility is further increased by limited vertical and forward/backward sliding movements via the quadratomandibular attachments of the mandible (Bühler 1981).

The palatines in *Lophopsittacus* are robust and in size equal to or greater than those of most large-jawed psittaciforms (*cf*. Holyoak 1971) (Figs. 20A and 6). Furthermore, the posterior expansion of the palatines provides large areas for attachment of L. mesethmopalatinum and the M. pterygoideus dorsalis lateralis. Their arrangement, however, inhibits the swallowing capability of parrots (Homberger 1981), thus the need for them to hold food in their feet and break the food down into manageable morsels. The jaws of the largest frugivorous parrots, e.g. Pesquet's parrot *Psittrichas fulgidus*, and the hawk-headed parrot *Deroptyus accipitrinus*, are far less massive, and their proportions of head to body length are 1:4 whilst in the granivorous *Anodorhynchus* and *Probosciger* they are 1:3. The palatines in *Psittrichas* (Fig. 6E) and *Deroptyus* are also reduced, hence the ability of *Psittrichas,* for example, to swallow large chunks of fruit (Homberger 1981). The bony core of the mandible is covered by a rhamphotheca with a chisel-like end, the gnathotheca (Fig. 3). The apical third part of the maxilla has a corrugated structure that acts as a sharpening implement for the gnathotheca during honing movements of the mandible (Homberger & Ziswiler 1972). The width of the gnathotheca is proportional to the size class of food consumed, i.e. the larger the gnathotheca, the larger the food size (Yamashita & Valle 1993). Therefore, the robust jaw of *Lophopsittacus* enabled this species, convergently with large macaws and cockatoos, to exploit large hard nuts and seeds (Fig.4) rather than soft fruit.
The cranial size dimorphism present in *Lophopsittacus* may have been a result of intraspecific sexual selection. It is now impossible to determine what ecological and behavioural factors were involved, but in other groups of birds, including parrots, with pronounced sexual differences in bill size, each sex prefers food items of different sizes (Selander 1972), has differing ecological requirements (Shine 1989), the males have bill-enhanced courtship or combat rituals (Trivers 1972), or each sex has specialised reproductive roles for nest-building and provisioning the offspring (see Moorehouse *et al.* 1999).

FIGURE 4. Examples of large, hard Mascarene seeds and fruits that may have been taken as food by *Lophopsittacus mauritianus*. **A,** Latan Palm *Latania loddigesii* Mart. (Arecaceae); **B,** Makak *Mimusops maxima* Vaughan (Sapotaceae); **C,** Tambalacoque *Sideroxylon grandiflorum* A. DC (Sapotaceae); **D,** Ebony *Diospyros egrettorium* Richardson (Ebenaceae); **E,** Screw Pine *Pandanus utilis* Bory (Pandanaceae). Scale bar = 10mm.

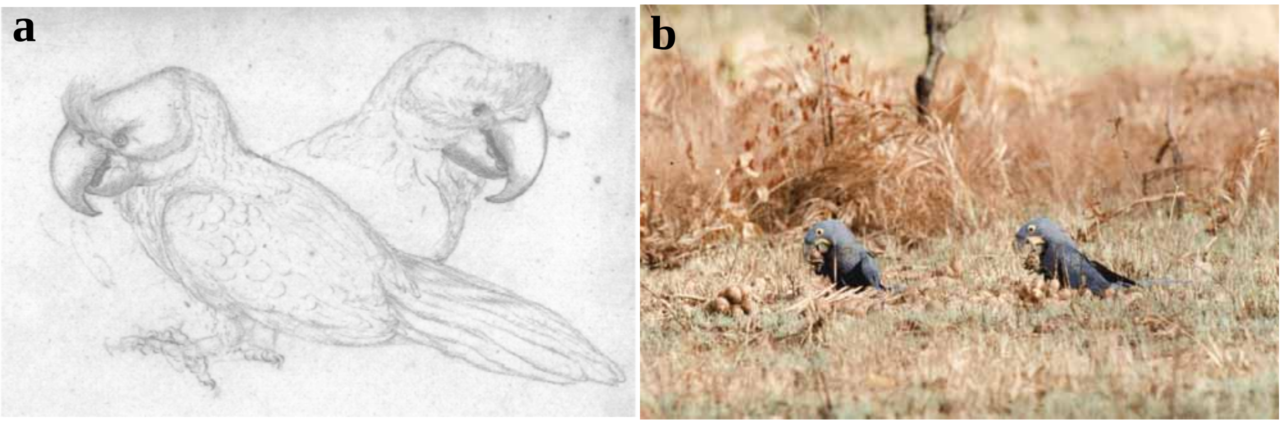

FIGURE 5a. *Lophopsittacus mauritianus* sketched by Joris Laerle in 1601 (from Moree 2001). Note the larger bird (possibly male) behind; **Figure 5b.** *Anodorhynchus hyacinthinus* feeding on palm fruit regurgitated by cattle. The cattle do not swallow the seeds but expel them after rumination. The macaws are attracted to this source of food. Photo courtesy of Carlos Yamashita**.** Note the kinetics of the rostrum and mandible during manipulation of food and the similar big-headiness and bill morphologies between this species and *Lophopsittacus mauritianus*.

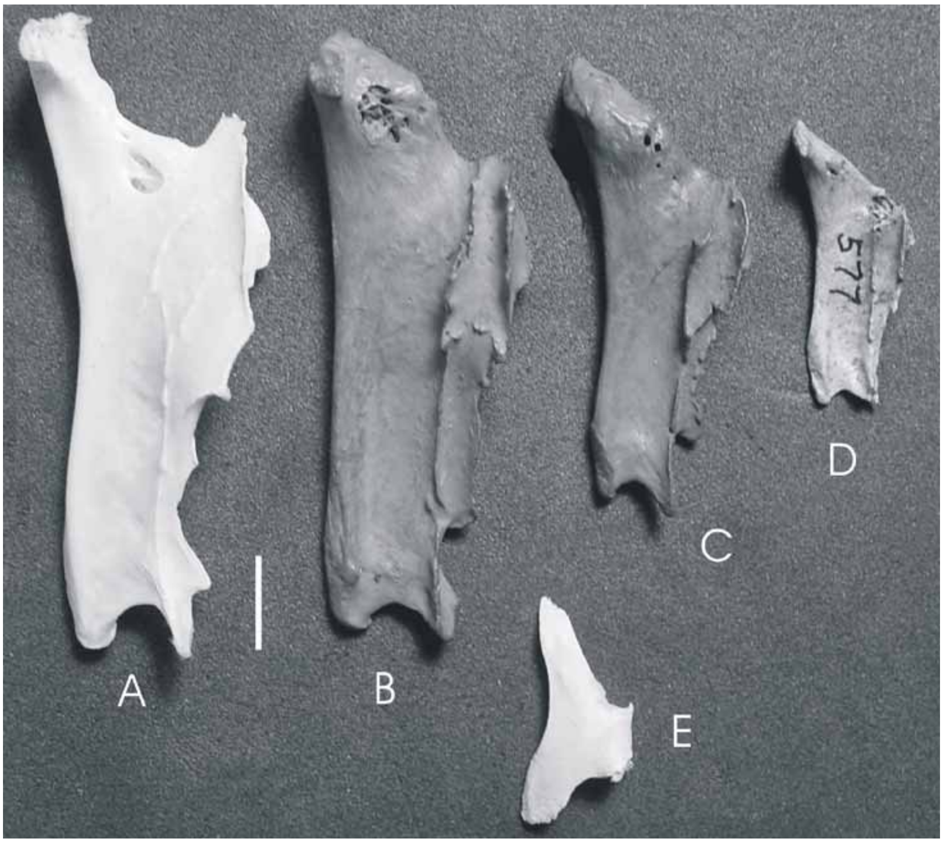

FIGURE 6. Comparison of palatines of Mauritian parrots, left lateral views, with typical granivorous and frugivorous species of parrots. **A,** BMNH S/1955.22.9; *Anodorhynchus hyacinthinus;* **B,** UMZCA24AA (type A) *Lophopsittacus mauritianus*; **C,** BMNH01 (type B) *Lophopsittacus mauritianus*; **D,** UMZC577 *Psittacula bensoni*, new comb.; **E,** BMNHS/1983.74.1; *Psittrichas fulgidus*. Scale bar = 10mm.

In addition to fossils, *Lophopsittacus* is known from three drawings and two written descriptions executed in the 17th century (Hume 2003). The assumption that this species was flightless originated in a pencil and ink sketch of a live bird drawn in 1601 and inferences (short wings, large size) made from this illustration by Newton & Newton (1876) and their followers (Newton & Gadow 1896; Rothschild 1905 [1907]; Hachisuka 1953; Holyoak 1971; Day 1981). The original drawing (Fig. 5a), however, reveals obscured pencil outlines beneath the finished ink that demonstrate that the wing to body length is not particularly short (Hume 2003). Furthermore, the wings of *Lophopsittacus* in the drawing appear broad rather than narrow, as also characteristic of *Psittacula echo* and commonly associated with forest-adapted species (Campbell & Lack 1985: 218–223; Jones 1987). A large alula is also more clearly defined in the underlying pencil sketch (Hume 2003), an adaptation that prevents stalling in slow-flying birds (Campbell & Lack 1985: 218–223, 654–656). The sternal keel is reduced in *Lophopsittacus* but not so much as to preclude flying, as Hoffman's account in 1673–75 (Grandidier & Grandidier 1905) indicates that *Lophopsittacus* could fly but with some difficulty. Parrots of the genus *Cyanoramphus*, which are adept and powerful fliers (Forshaw 1989, Livezey 1992), also have a reduced keel. Moreover, even with a nearly obsolete keel, the 'flightless' kakapo *Strigops habroptilus* is quite capable of sustained downward glides and short upward ascents (Merton 1985; Forshaw 1989; Livezey 1992).

In the flightless New Zealand kakapo, the tarsi are comparatively long, which is presumably an adaptation for a terrestrial existence. Most parrots are arboreal and have proportionately short and stout tarsi (Forshaw 1989), with the distal width being half the length (Table 11). In *Nestor* and *Strigops*, the tarsometatarsus is approximately 2.5 times as long as it is wide, whereas in *Cyanoramphus* it is 3 times as long as wide. Thus the volant but terrestrially adapted species of *Cyanoramphus* (along with *Pezoporus* and *Geopsittacus*; see Livezey 1992) have proportionately the longest tarsometatarsi of any parrots. It is apparent from its short and stout tarsometatarsus that *Lophopsittacus* retained arboreal characteristics even though it may have fed on the ground and been only weakly flighted. It appears that only on the ancient oceanic islands of New Zealand has a parrot (*Strigops*) become nearly functionally flightless.

In life, *Lophopsittacus* was probably a dull-coloured bird with at least two, and perhaps three, discernable colours (Het Tweede Boeck 1601), one of which was evidently a blue head as described by Hoffman (Grandidier & Grandidier 1905), and the remaining plumage possibly greyish or blackish. It was certainly not all blue as described by Newton and Gadow (1896), Rothschild (1907a, 1907b) and Hachisuka (1953). A grey/blue plumage is found in 50% of Mascarene genera of parrots (see Thirioux's Grey Parrot and Rodrigues Parakeet below), and occurs in other members of the Psittaculini. A number of other Indian Ocean parrots also exhibit dull dark colours, e.g. *Coracopsis* and *Mascarinus*, and it is common to other large, big-headed parrots such as *Anodorhynchus* and *Probosciger.* A bright red bill is diagnostic for the tribe Psittaculini (Forshaw 1989; Collar 1997; Juniper & Parr 1998), but unfortunately, not one account mentions the beak colour of *Lophopsittacus* or that of other endemic Mascarene parrots (*Necropsittacus* or *Psittacula bensoni*) for which no skins or coloured illustration exists. In 1673–75, Hoffman (Grandidier & Grandidier 1905) refers to *Lophopsittacus* as '*red crows with recurved beaks*', which may be a reference to beak colouration.

The ecology of *Lophopsittacus* is unknown, but species with similar morphologies may provide an insight into possible ecological traits. The hyacinth macaw *Anodorhynchus hyacinthinus* and palm cockatoo *Probosciger aterrimus* are reasonable analogues. *Anodorhynchus* is a habitual ground dweller that eats the extremely hard nuts of palms (Forshaw 1989; Yamashita & Valle 1993; Yamashita 1997). Yamashita noted that cattle provide a similar modern ecological analogue to the now extinct megaherbivores by amassing undigested endocarps (the extremely hard shell surrounding the kernel) in dung heaps. *Anodorhynchus* does not eat the fleshy and often fibrous pulp of the palm mesocarp but the nutritious kernels within the endocarp, and cattle provide macaws with a pre-prepared food source around which macaws concentrate (Fig. 5b), even when ripe, fruit-laden palms are available nearby (Yamashita 1997; Juniper & Parr 1998). *Probosciger aterrimus* also feeds on the undigested endocarps gleaned from the droppings of cassowaries *Casuarius* sp. (Mack & Wright 1996). On Mauritius, *Lophopsittacus* may well have had a similar ecological niche. Palms and palm-like plants are an important part of the Mascarene flora. The true palm genera *Hyophorbe*, *Dictyosperma*, *Latania* as well as the screw pines *Pandanus,* have evolved into a number of endemic species inhabiting montane bogs to coastal spray zones (Staub 1993). Palms and screw pines formerly dominated the lowland areas (Soete-boom 1648); they produce prodigious amounts of fruit (Staub 1993), which concentrate beneath the parent plants. An endemic genus of giant tortoise, *Cylindraspis*, occurred on Mauritius (2 species), Réunion (1 species) and Rodrigues (2 species) (Arnold 1979, 2000; Bour 1981), which may have had the densest populations of tortoises on earth (Arnold 2000). These tortoises may have been analogous to the large mammalian herbivores on continents. After eating the fruits of the endemic Mauritian Round Island bottle palm *Hyophorbe lagenicaulis* and ebony *Diospyros egretarrum*, captive Aldabran giant tortoises *Aldabrachelys gigantea* excrete the undigested endocarps, after which a high percentage of germination takes place (Owen Griffiths pers. Comm., 02.09.2005; Hume pers. obs). It is possible, therefore, that *Lophopsittacus* exploited this food source.

The notion that *Lophopsittacus* was a nocturnal species comes entirely from the fertile imagination of Hachisuka (1953). Although he stated that ”We have many reasons to believe that the Broad-billed Parrot was nocturnal in its habits”, he did not say what any of the reasons were and only analogized *Lophopsittacus* with two recent nocturnal ground parrots, the New Zealand kakapo *Strigops habroptilus* and the Australian night parrot *Geopsittacus occidentalis*. From the meager information available (see below) we can conclude that all observers found *Lophopsittacus* to be active during daylight hours and depicted or described it accordingly (see Strickland & Melville 1848; Hume 2003). Furthermore, although the only existing cranium of *Lophopsittacus* is incomplete, enough of the orbits remain to suggest that they were similar in size to other large parrots such as macaws and cockatoos, despite the dorso-ventral compression of the cranium. In the nocturnal Kakapo *Strigops habroptilus*, which lacks a dorso-ventrally compressed cranium, the orbits are comparatively reduced. In general, nocturnal birds have large orbits, so presumably flightlessness and the specialised ecology of *Strigops* resulted in atypical cranial morphology.

The broad-billed parrot was called the ‘Indian raven or crow’ from its discovery in 1598 until the last first-hand account in 1673–4. As these accounts are brief and some are not widely known, they are repeated here in their entirety. The first account stems from the voyage of Admiral Jacob Cornelis van Neck in 1598 (Het Tweede Boeck 1601) and his report reads:

> Is a bird which we called the Indian Crow, more than twice as big as the parroquets, of two or three colours (Strickland & Melville 1848: 123).

This account also includes the first, albeit poor, illustration of *Lophopsittacus* (see Hume 2003). The second mention stems from Captain Willem van West-Zanen (Soete-boom 1648) who first visited Mauritius under van Neck in 1598 and returned in 1602 to write an account of the island and its fauna that was published in 1648 (Soete-boom 1648:19):

> The birds (of which the island is full) are of all kinds: Doves, Parrots, Indian Crows, Sparrows, Hawks, Thrushes, Owls, Swallows, and many small birds; white and black Herons, Geese, Ducks, Dodos….[translation from Cheke & Hume in prep.].

Reyer Cornelisz remained on Mauritius for three months in 1602 (Begin en de voortgangh 1646, p. 30) and wrote a journal during his stay. He is the only observer to recognise size differences in *Lophopsittacus*:

In this country occur Tortoises, Wallichvogels [dodos], Flamingos, Geese, Ducks, Field-hens, large and small Indian Crows [=*Lophopsittacus*], Doves, some of which have red tails (by eating which many of the crew were made sick), grey and green Parrots with long tails, some of which were caught [Strickland & Melville 1848: 125].

Jacob Granaet was a bookkeeper who arrived in Mauritius on 30 July 1666. Although his account is rather vague, he mentions the large size of the ravens (=*Lophopsittacus*):

> Within the forests dwell parrots, turtle and other wild doves, mischievous and unusually large ravens, falcons, bats and other birds whose names I do not know, never having seen before [Barnwell 1948:25].

Granaet also mentions that cattle and pigs were found in most remote areas of forest. The last unequivocal account stems from Johann Christian Hoffman, who was appointed preacher to Commandeur Hugo from 1673–5 (Moree 1998). Hoffman's description in 1673–5 (Grandidier & Grandidier 1905) was better than that of any other observer, although even his account leaves much to be desired:

> There are also geese, flamingos, three species of pigeon of varied colours, mottled and green perroquets [=parakeets], red crows with recurved beaks and with blue heads, which fly with difficulty and have received from the Dutch the name of 'Indian crow' [my translation].

The terminology of 'Indian raven/crow' distinguished *Lophopsittacus* from the *perroquets, papegayen,* or *perruche*, names applied to the smaller grey and green parrots. The early observers, therefore, were seemingly impressed by the distinctiveness of *Lophopsittacus* insomuch that they clearly separated it from the other parrots. The reasons for this may have been its probable crow-like (raucous) call, some behavioural trait, or simply its dark colouration, which must have reminded the Dutch of another group of birds. As further evidence of the association of a corvine appellation with a parrot, South American macaws were also termed "Indian ravens" or Kakataws (=cockatoos) by the Dutch during the mid 17th century (Nieuhoff (1682: 315), as were southeast Asian hornbills (Bucerotidae) (Ray 1678: 126). Furthermore, the greatest French nature artist of the 17th century, Nicolas Robert (1614–1685), made a series of vélins (illustrations on fine vellum) for Gaston d'Orléans (Louis XIV's uncle) prior to 1660 (Jackson 1999). Robert included a Scarlet Macaw *Ara macao* which he labelled *Corbeau d'Inde* (Cecilé Mourer-Chauviré pers.comm. 08.08.2004). Some authors (Strickland & Melville 1848; Staub 1993) were convinced that 'Indian raven' referred to a ground hornbill *Bucorvus* sp. This assumption was based on the above-mentioned drawing of the Indian raven included in the account of the Dutch Admiral Jacob Cornelis van Neck (Het Tweede Boeck 1601). No hornbill bones have ever been discovered on the Mascarenes, and no hornbills occur on any other remote oceanic island except New Caledonia in the South Pacific (Steadman 2006).

Lophopsittacus must have provided a ready source of food for early mariners (Fig. 7a, and 7b). Its tame and confiding nature, large size, and reluctant or feeble flight, coupled with a possible nesting requirement of large tree cavities or even rocks (the Cuban Amazon *Amazona leucocephala bahamensis* nests in rock cavities on Abaco Bahamas---Juniper & Parr 1998) would have made this species extremely vulnerable to humans and introduced animals. No doubt rats and monkeys were particularly harmful to nesting birds.

The few records of *Lophopsittacus* are from the drier, leeward side of the island, the most easily accessible part of the island for people. The first mention of parrots was made by the crews of the fleet under Admiral van Neck in 1598. A junior merchant, Rochus Pieterzoon, led an expedition that went 8–10 miles inland from Vieue Grand Port on the southeast drier side of the island (Moree 1998; Payandee 2002). Interestingly, Pieterzoon noted that the nearer that they were to the coast, the richer was the bird life, therefore, it is not unreasonable to suggest that this zone harboured a more diverse and abundant fauna (see also Hume 2005). Hoffman's account of 1673–5 is the last record of *Lophopsittacus,* but the Dutch presence on Mauritius was extremely limited by this time (Moree 1998) and it is possible that this parrot persisted for some time after. Surprisingly, despite the fact that parrots were regularly transported from one place to another as pets, there is no record of a specimen of *Lophopsittacus* ever being taken out of Mauritius alive or dead, possibly an indication of stigmas associated with ravens.

Genus *Psittacula* Cuvier, 1800:
table with no pagination.

Etymology: From Latin *Psittacus* meaning parrot, and -*ula*, a diminutive suffix.

Diagnosis: Cranium moderately dorso-ventrally flattened, craniofrontal hinge medially concave, processus postorbitalis long but not fused to the lacrimal; mandible comparatively broad; diameter of nares greater than the width of internarial septum; tomium distinctly notched, with a concavity that abruptly indents the cranial border, creating a single tooth; spina externa prominent with an indistinct distal division. Species of *Psittacula* are large-billed, long-tailed parrots, the tail graduated with the attenuated central feathers longest. Red bills and neck rings are also common to the majority of taxa in this genus (see Forshaw 1989).

Thirioux's Grey Parrot *Psittacula bensoni* (Holyoak, 1973), new combination

Grauwe papegayan, Begin en de voortgangh 1646:30; Soete-boom 1648: 20, pl. 20v., with note.
Lophopsittacus bensoni Holyoak, 1973: 417.

Holotype: Although Holyoak (1973a:417) clearly designated mandibular symphysis UMZC 18/Psi/37/a/1 (now UMZC 577a) as the holotype and illustrated it in dorsal view (pl. 8a), he erroneously labeled a mandible in ventral view (pl. 8b) as also being the holotype, whereas the illustration actually shows a different specimen (Cowles 1987; Hume, pers. obs.). The latter (now UMZC 577b) is to be included among the various paratypes illustrated by Holyoak and listed below.

Measurements: See Appendix 3, tables 1–11.

Type locality: Le Pouce, Mauritius

Distribution: Mauritius and possibly Réunion Island, Mascarenes (see below)

Etymology: In honour of C. W. Benson (1909–1982).

Paratypes: Subfossil material collected from Le Pouce, Mauritius. The second symphysis of lower mandible (UMZC577b) (Holyoak pl. 8b); upper mandible (UMZC 577) (Holyoak pl. 8c, 8d and 8e); palatine (UMZC 577 (L)) (Holyoak pl. 8f and 8g); tarsometatarsus (UMZC 577(R) (Holyoak pl. 8i and 8o); (UMZC 577(R) (Holyoak pl. 8l and 8r); (UMZC 577(R) (Holyoak pl. 8m and 8s); (UMZC 577(Ld) (Holyoak pl. 8k and 8q). Two of the tarsi assigned by Holyoak to '*Lophopsittacus*' *bensoni* (UMZC 577) (Holyoak pl. 8h and 8n) and (UMZC 577) (Holyoak pl. 8j and 8p) are referable to another species (see *Psittacula echo*).

Referred material: Subfossil material collected from Le Pouce, Mauritius; mandible UMZC 577(d); UMZC 577 (d); rostrum UMZC 577 (d); UMZC 577(d); palatine UMZC 577(L); sternum UMZC 599(p); UMZC 599(p); UMZC 599(p); coracoid MNHN MAU566(L); MNHN MAU579(R); MNHN MAU576(L); humerus UMZC 596(L); UMZC 596(L); UMZC 596(R); UMZC 596(Rp); UMZC 600(Lp); UMZC 596(R); UMZC 596(L); MNHN MAU562(L); carpometacarpus MNHN MAU515; femur MNHN MAU556(R); MNHN MAU540(R); MNHN MAU549(L); tibiotarsus MNHN u/c(R); MNHN u/c(L); MNHN MAU514(R); MNHN MAU550(R); tarsometatarsus UMZC 594(Lp); UMZC 594(Ld); UMZC 594(R) (juv); MNHN u/c(L) (juv); MNHN u/c(R); MNHN MAU593(R); MNHN MAU368(R); MNHN MAU366(L); MNHN MAU527(R); MNHN 508(R); MNHN 553(L); MNHN 524(L).

Diagnosis: This species was previously placed in the genus *Lophopsittacus* (Holyoak 1973; Cowles 1987), but re-examination of the fossils now available indicates that it belongs in the genus *Psittacula*. Differs from *Lophopsittacus* and *Psittacula echo* by the following suite of characters: rostrum approximately 29% larger in total length than in *P. echo*; rami of mandible more laterally deflected indicating that this species had a comparatively broad bill; in sternum spina externa less anteriorly projected; incisura costalis more pronounced with the 5th deeply excavated; one anteriorly situated foramen pnematicum present; sulcus articularis coracoideus distinctly unequal; in humerus, processus flexorius distinct, emphasising the sulcus humerotricipitalis with fossa olecrani comparatively wide; crista bicipitalis merges sharply with the shaft distally, proximal fossa pneumotricipitalis circular and sulcus transversus deeply excavated; processus supracondylaris dorsalis prominent and a small depression occurs proximal to the condylus dorsalis; tuberculum ventrale deflected mediolaterally and distolateral edge of crista bicipitalis not angled as it merges with the shaft; in coracoid, processus procoracoideus short with shallow cotyla scapularis, and projects further medially; in tarsometatarsus, two canals formed by crista intermediae hypotarsi shallow; two foramina vascularia proximalia present. In life, *P. bensoni* was described as a long-tailed grey parrot.

Description and comparison: See Appendix 2b.

Remarks: As specimens of *P. bensoni* are known only from the fossil collections of Etienne Thirioux and the species was described in life as grey, to avoid further confusion with the green *Psittacula echo*, the English name Thirioux's grey parrot, honouring the collector and indicating the colouration, is proposed here. Holyoak (1973a) diffidently placed *bensoni* in *Lophopsittacus* and he separated it from *Lophopsittacus mauritianus* on size alone, although there are discernible generic differences that he did not discuss. The species is clearly derived from *Psittacula* stock and is similar to *Psittacula eupatria* but larger and more robust in some elements (Fig. 19). It also appears to have been atypical in colouration, being all grey, as the majority of species of *Psittacula* are green or partially green.

The the ease with which *P. bensoni* could be caught in abundance is reported by Willem van West-Zanen, who visited Mauritius in 1602. His account, published in 1648 (Soete-boom 1648), included the only known drawing of this species (Fig. 7b) and described the first encounter West-Zanen's crew had with parrots:

> ….some of the people went bird hunting. They could grab as many birds as they wished and could catch them by hand. It was an entertaining sight to see. The grey parrots are especially tame and if one is caught and made to cry out, soon hundreds of the birds fly around ones' ears, which were then hit to the ground with little sticks. Also just as tame are the pigeons and turtle doves, that let themselves be caught easily…..[my translation].

Admiral Steven van der Hagen visited Mauritius in 1606 and 1607 (Begin en de voortgangh 1646; Barnwell 1948). Der Hagen mentions again the ease with which the birds could be caught and that the catching of a single parrot ultimately could lead to the entire flock being taken:

> During all our time there, we lived on turtles, dodos, pigeons, doves, grey parrots, and other game, which we caught in the woods with our hands. Besides their usefulness to us, there was also much amusement to be got from them. Sometimes when we had caught a grey parrot, we made it call out, and at once hundreds more came flying around, and we were able to kill them with sticks [Barnwell 1948:17].

Thirioux's grey parrot was particularly sought after as game. Despite this persecution, grey parrots remained reasonably common until the 1750s, but the population must have crashed shortly afterwards as Cossigny's account in 1764 (Cheke 1987) is the last time that they were mentioned. It was during the 1730s that the French instigated large-scale slash and burn forest clearance (Toussaint 1972), which undoubtedly had a serious effect on cavity-nesting species such as parrots.

Réunion grey parrot *Psittacula* cf. *bensoni*

Perroquets gris; Dubois 1674: 172; Borghesi 1705., in Lougnon 1992: 187. Sous le Signe de la Tortue. Azalées Editions. [Original not seen]; Feuilley 1705: 129. Mission à I'lle Bourbon du Sieur Feuilley en 1704., in Recueil trimestriel de documents et travaux inédits pour servir á l'histoire des Mascareignes françaises. [Original not seen.]; Cossigny 1732: 168–96,205–82, 305–16, in Trieze letters de Cossigny á Reaumer. Recueil trimestriel de documents et travaux inédits pour servir á l'histoire des Mascareignes françaises. [Original not seen.].

FIGURE 7. a. The Dutch on Mauritius in 1598 (from De Bry, 1601). Note the ease with which parrots are depicted as being caught; **b.** Parrot catching on Mauritius in 1601 (from Soete-boom, 1648). One bird was captured and made to call out, which subsequently attracted other parrots, and an entire flock could be taken by the hunters.

Holotype: None.

Measurements: None.

Type locality: Réunion Island, Indian Ocean.

Distribution: Réunion Island, Indian Ocean.

Etymology: As for *Psittacula bensoni*.

Referred material: None.

Diagnosis: Presumably as for *Psittacula bensoni*.

Description & comparison: Described as larger in size than *Psittacula eques*.

Remarks: A grey parrot occurred on Réunion at least until 1732. It was first mentioned by Bontekoe (1646) as present in 1618 and, as with the population on Mauritius, was easily killed with sticks:

> Coming further inland we found [a] great number of geese, doves, grey parrots and other birds, also many land-turtles; seeing as many as twenty to twenty-five lying in the shade of a tree, so that we could have as many as we desired. The geese were not wise enough to fly up when we pursued them, and we beat them to death with sticks without their making a motion to fly……And what we most did marvel at, when we held one of the parrots and other birds and squeezed it till it screamed, there came all the others from thereabout as if they would free it and let themselves be caught as well, so we had enough of them to eat [translation from Bodde-Hodgkinson & Geyl 1929: 30].

Dubois (1674), in 1671–2, mentions the destructive nature of grey parrots toward crops and the altitudinal migration of the birds:

> Grey parrots, as good [to eat] as the pigeons…..All the birds of this island have their season at different times, being six months in the low country and six months in the mountains, when returning, they are very fat and good to eat. I exclude the river birds and the solitaires, the partridge and the blue birds [=Oiseaux bleu] that do not change…..There are caterpillars at certain seasons that are very irritating. The sparrows [=fodies *Foudia*], grey parrots, pigeons and other birds, bats [=flying foxes *Pteropus* sp.], cause plenty of damage, some to cereals others to fruit [my translation].

Feuilley (1705) in 1704 provides a more detailed account and confirms that at least 3 species of parrots were present on Réunion:

> There are several sorts of parrot, of different sizes and colours. Some are the size of a hen, grey, the beak red; others the same colour the size of a pigeon, and yet others, smaller, are green. There are great quantities, especially in the Sainte-Suzanne area and on the mountainsides. They are very good to eat, especially when they are fat, which is from the month of June until the month of September, because at that time the trees produce a certain wild seed that these birds eat [translation from Cheke and Hume in prep.].

The parrot described as being the size of a hen refers to *Mascarinus*, the pigeon-sized species is presumably the grey parrot and the third green species is *Psittacula eques*. According to Feuilley (1705), all species of parrot on Réunion were subject to a seasonal fat cycle, being particularly good to eat from June to September. It is apparent that grey parrots were particularly sought after as game, and coupled with their reputed damage to crops, were persecuted accordingly. A mention of unspecified Réunion parrots in 1754 may have included grey parrots (see Cheke 1987), but the last unequivocal mention of this bird was by Cossigny in 1732:

> The woods are full of parrots, either completely grey or completely green. They were eaten a lot formerly, the grey especially, but both are always lean and very tough whatever sauce one puts on them [my translation].

As with such birds as *Anas theodori* and *Fulica newtoni*, the Réunion grey parrot was possibly conspecific with a species that also occurred on Mauritius, in this case the grey parrot *Psittacula bensoni* (Cheke 1987; Hume & Cheke 2004). The Réunion grey parrot has sometimes been referred to the genus *Coracopsis*

(Coquerel 1864; Vinson 1868), but no fossils assignable to that genus or to *Psittacula* have been found (Mourer-Chauviré *et al.* 1999) to resolve its affinities. An indeterminate species of *Coracopsis* was introduced to Réunion sometime prior to 1800 (Newton and Newton 1876; Berlioz 1946; Cheke 1987), but did not become established.

Echo Parakeet *Psittacula echo* (Newton & Newton, 1876).

Perroquet vert, Cossigny, 1732: 168–96,205–82, 305–16., in Trieze letters de Cossigny á Reaumer. Recueil trimestriel de documents et travaux inédits pour servir á l'histoire des Mascareignes françaises. [Original not seen.]

Perruche; La Motte 1754, 1756., in Cheke 1987: 45. Mascarene Island Birds. Cambridge University Press. [Original not seen]

Palaeornis echo Newton & Newton, 1876: 284; Rothschild 1907: 68.

Palaeornis eques; Salvadori, 1891: 442; Meinertzhagen, 1912: 94.

Psittacula echo; Peters, 1937: 243.

Measurements: See Appendix 3.

Type locality: Mauritius, Mascarenes.

Distribution: Mauritius, Mascarenes.

Etymology: From Latin *echo*, meaning a woodnymph.

Syntypes*:* UMZC18/Psi/67/k/1-4. Collected on Mauritius, 2 immature males, Vacoa, 12 Apr and male and female on 31 Dec 1860 by C.E.Banks, Bois Sec, Oct 1873.

Referred material: Despite this species being known from at least 34 museum skins (Cheke 1987), their comparative use is limited therefore they are not included here. Trunk skeleton including sternum, pelvis, femora, and coracoids removed from spirit specimen of captive bird BMNH S/2000.44.1. Subfossil material collected by E. Thirioux, Le Pouce, Mauritius and elsewhere: rostrum MNHN MAU528; mandible MNHN MAU599; MNHN MAU509; MNHN 760; MNHN MAU602; MNHN MAU573 (juv); palatine MNHN MAU593(L); sternum UMZC 599(p); UMZC 599(p); UMZC 599(p); UMZC 599(p); UMZC 600(p); coracoid UMZC 600(R); UMZC 600(R); UMZC 600(R); UMZC 600(R); UMZC 600(R); UMZC 600(R); UMZC 600(R); UMZC 600(R); UMZC 600(L); MNHN MAU534(L); MNHN MAU516(L); MNHN MAU589(R); MNHN MAU578(R); MNHN MAU543(R); MNHN MAU504(L); MNHN MAU577(R); MNHN MAU545(R); MNHN MAU554(R); MNHN MAU588(R); humerus UMZC 600(L); UMZC 600(Lp); MNHN u/c(L); MNHN u/c(R); MNHN u/c(L); MNHN MAU505(L); MNHN MAU512(L); MNHN MAU586(R); MNHN MAU506(L); MNHN MAU517(R); MNHN MAU552(R); MNHN MAU498(L); MNHN MAU551(R); MNHN MAU7017(L); MNHN MAD7000(L); MNHN u/c(L); ulna UMZC 600(L); UMZC 600(R); MNHN MAU547(R); MNHN MAU495(R); MNHN MAU555(L); MNHN MAD7189(L); MNHN MAD7200(L); MNHN MAD7188(R); MNHN MAD7195(L); radius UMZC 600(L); carpometacarpus MNHN MAU500; MNHN MAU560; femur MNHN u/c(R); MNHN u/c(L); MNHN MAU570(L); MNHN MAU548(L); tibiotarsus MNHN u/c(L); MNHN u/c(L); MNHN MAU511(L); MNHN MAU601(R); MNHN MAU535(Rd); MNHN MAU529(Ld); MNHN MAU761(Rd); tarsometatarsus UMZC 594(Lp) (juv); UMZC 594(Lp) (juv); UMZC 594(Lp) (juv); UMZC 594(Lp) (juv); UMZC 594(Lp) (juv); UMZC 594(Lp) (juv); UMZC 594(Ld); UMZC 594(Ls); UMZC (Rp); UMZC (Rp); UMZC (Rp); UMZC 577(Rs); UMZC 593(Rs); UMZC 593(Rs); UMZC 593(Lp); UMZC 593(R); UMZC 593(L); MNHN u/c(L); MNHN 560(L); MNHN 582(L); MNHN 597(L); MNHN 546(R); MNHN 507(R); MNHN 579(R); MNHN 596(L); MNHN 758(R); MNHN 556(R); MNHN MAD6880(L); MNHN MAD6864(L); MNHN MAD6888(L) (juv).

Diagnosis: Apart from its distinctly smaller size, *Psittacula echo* may be distinguished from *P. bensoni* by the following suite of characters. Sternum; spina externa weakly bifurcated. Coracoid; lateral margin of angulus medialis pointed; proximal to facies articularis clavicularis, a small circular deeply excavated foramen present; processus procoracoideus short with a shallow cotyla scapularis.Humerus: shorter condylus dorsalis, distal end mediolaterally less expanded and fossa olecrani shallow.Tarsometatarsus: impressiones retinaculi extensorii less defined. Despite molecular evidence for a sister relationship between *P. echo* and the Indian *P. krameri* (*borealis)* (Groombridge *et al.* 2004), my morphological analysis indicates that *P. echo* is more closely related to *P. eupatria* than to *P. krameri*.

Description and comparison: See Appendix 2c, tables 1–11.

Remarks: This species, the last surviving Mascarene parrot, was reduced to fewer than 12 birds by the 1980s (Cheke 1987; Jones 1999), but has now recovered to 250+ after conservation efforts (Cheke and Hume in prep.). La Motte in 1754 & 1756 described their former abundance:

> One eats here [in Mauritius] a good number of long-tailed green parrots called perruches whose flesh is black and very good. A hunter can kill three or four dozen in a day. There is a time of year when these birds eat a seed that makes their flesh bitter and even dangerous [Cheke 1987: 45].

Unsurprisingly, the Echo Parakeet is very rare in skeletal collections and its osteology is known mainly from fossil remains. It is easily distinguishable from all other Mauritian parrots by size, all elements being much smaller and less robust. It is intermediate in size between *P. krameri* and *P. eupatria*. The Echo Parakeet is the smallest Mauritian parrot and the one most frequently found in cave fossil deposits, where both adult and juveniles are represented. Groombridge *et al*. (2004) concluded from a DNA analysis that *P. echo* is derived from the Indian Ring-necked Parakeet *Psittacula krameri borealis,* as opposed to the nominate subspecies *P. k. krameri* in Africa (Smith 1975). As no species of *Psittacula* occurs on Madagascar, it is reasonable to assume that *P. krameri* populated Africa via the Middle East and not the Indian Ocean islands.

The Echo Parakeet has been afforded species-level status, being stockier than *P. krameri* with shorter, more rounded wings, and a broader shorter tail (Jones 1987; Forshaw 1989; Low 1994; Juniper & Parr 1998), and has been reported to measure 25% larger in weight and body size than *P. krameri* (Low 1994). The size difference in the live bird is also particularly noticeable in the bill (Juniper & Parr 1998; Hume pers. obs.). Most available skeletal elements, when compared to its closest relative *Psittacula krameri borealis* (Groombridge *et al.* 2004), are similar in size except the hindlimb elements being 4.8% – 6.8% larger and the sternum 6.4% smaller. According to Glenny (1957), parrots generally have limited powers of flight compared to many other bird groups, but many are agile, swift fliers. *Psittacula echo* is an adept but not a long distance flier, and can rapidly maneuver between small openings in the forest canopy making clear observation of the birds difficult (pers. obs.). The reduction of the sternum thus appears to have had little affect on its flight capabilities. A similar proportional reduction in the sternum is found in the endemic Mauritian Pink Pigeon *Nesoenas mayeri*, when compared to similar-sized columbids (Hume unpubl.), also without any noticeable reduction in flight capabilities (Hume pers.obs.).

The Echo Parakeet feeds on buds, emergent shoots, leaves, flowers, berries, seeds, twigs and bark/sap, never descending on the ground to forage (Jones 1987; Jones & Owaddally 1988; Forshaw 1989). This behaviour is in direct contrast to *P.krameri*, which regularly feeds on the ground (Smith 1979) and is a bird of open areas, not dense forests (Forshaw, 1989). If the other species of parrot already established on the Mascarenes were adapted to a ground niche, the most recently arrived may have had to adjust its habits accordingly; therefore, the different morphology of *P.echo* may be linked to an arboreal habitat adjustment (Jones 1987).

Réunion ring-necked parakeet *Psittacula eques* Boddaert, 1783

Perroquets verts ayant un collier noir, Dubois, 1674:172.

Perroquets verts, Borghesi, 1705., in Lougnon 1992: 187. Sous le Signe de la Tortue. Azalées Editions. [Original not seen]; Feuilley 1705: 129., in Mission à I'lle Bourbon du Sieur Feuilley en 1704. Recueil trimestriel de documents et travaux inédits pour servir á l'histoire des Mascareignes françaises. [Original not seen.]; Cossigny 1732: 168–

96,205–82, 305–16., in Trieze letters de Cossigny á Reaumer. Recueil trimestriel de documents et travaux inédits pour servir á l'histoire des Mascareignes françaises. [Original not seen.].
Psittaca borbonica torquata Brisson, 1760: 328, pl. xxvii.
Psittacus alexandri var. Γ; Linnaeus, 1766: 142.
Perruche à double collier, Buffon, 1779: 143.
Alexandrine Parakeet var. C, Latham, 1781: 326.
Perruche à double collier de I'Isle de Bourbon, Daubenton, 1783. *Planches Enluminées,* p.13, pl. 215 (based on a painting by Martinet).
Psittacus eques Boddaert, 1783. *Planches Enluminées*, p.13 (Based on Daubenton's figure.).
Psittacus alexandri var. Δ; Gmelin, 1788: 321.
Psittacus semirostris; Herman, 1804: 125.
Psittacus bitorquatus; Kuhl, 1820: 92.
Rose-ringed Parakeet var.B, Latham, 1822: 161.
Psittacus bicollaris; Viellot, 1823: 1385.
Palaeornis bitorquatus; Vigors, 1825: 51; Souancé, 1856: 185.
Palaeornis cubicularis; (part) Wagler, 1832:.507.
Palaeornis torquatus; (part) Gray, 1846: 409.
Palaeornis borbonicus; Bonaparte, 1854: 152, n.140.
Palaeornis eques; Gray, 1859: 20; Salvadori, 1891: 442; Oustalet, 1896: 28; Rothschild, 1907: 67.
Psittacula eques; Peters, 1937: 243.

FIGURE 8a. *Psittacula eques* (Barraband in Levaillant, 1805); **8b.** *P. eques* (Martinet in Buffon, 1779).

Holotype: Boddaert's name *eques* was based on a painting described as *Perruche à double collier de I'Isle de Bourbon* in Daubenton's (1783) work on Buffon's *Planches Enluminées,* p.13, pl.215.

Measurements: None available.

Type locality: Réunion Island, Mascarenes

Distribution: Réunion Island, Mascarenes

Etymology: From Latin e*ques* referring to the military colours of a French cavalryman.

Referred material: None.

Diagnosis: Presumably as for *Psittacula echo*.

Description and comparison: Presumably as for *Psittacula echo*.

Remarks: The Réunion ring-necked parakeet is known from illustrations only but it is not known whether the subjects of the illustrations were based on living individuals or stuffed specimens. The type illustration is a poor rendition (Fig. 25b) by Martinet in Buffon (1779: pl. 215). According to Jones (1987), a skin (Fig. 20) held at the Royal Museum, Edinburgh, may be the specimen used for Martinet's illustration, but recent work concerning the provenance of this specimen raises doubts about its origin (A. Cheke pers. comm. 19.10.2004). A far superior illustration (Fig 23a), hitherto not cited by ornithologists, was done by Barraband (Levaillant 1805). From this illustration, there are few, if any, distinct plumage differences between the Réunion and Mauritius populations, which may have been conspecific. If this can be shown to be the case, either by fossils or skin specimens, the name *P. eques* has many years priority over *P. echo*. It has been suggested that at least three specimens reached Paris during the latter half of the 18th century (Cheke 1987), the first described by Brisson (1760), followed by Buffon (1779), Mauduyt (1784) and Levaillant (1805), but there is no evidence from the descriptions or the plates that certain ones were based on the same or different specimens. Brisson (1760) describes the Réunion ring-necked parakeet (termed "double-collared parakeet") as follows:

> Its length is thirteen inches, in a fixed line from the extremity of the beak to the end of the tail : it is a little larger than a turtle-dove : the head, the neck, the back, the rump, the coverts on top of the tail, the scapulars and the breast are of a bright green : at the base of the head and at the back is a narrow band the colour of rose, which extends each side around the neck, becoming much wider toward the throat and forming a sort of collar, at the top edge the green is mingled with a little blue ; under the throat is another band or half-collar with the two extremities joining the rose-coloured collar ; the belly, the sides, the legs are of a green drawn on a yellow ; the wings are green and the large feathers are ashen underneath : the tail is lined yellowish ashen ; it is uniformly green on top ; the beak is blackish at its tip, of a bright red at its upper part and a duller red at its lower part; the feet are of a dark ashen, the claws blackish [my translation].

Buffon (1779) describes the bird in less detail:

> Two small rings, one rose-coloured and the other blue, entirely encircle the neck of this parakeet, which is of the size of a turtle dove; the rest of the plumage is green, which is darker on the back, yellowing under the body; and in several parts with a dusky streak on the middle of each feather; below the tail and laid out on each quill is a yellowish fringe bordering the brown-grey; the superior half of the beak is a fine red; the inferior is brown; it is probable that this parakeet, coming from the island of Bourbon, is also found on the corresponding continent, either Africa or India [my translation].

Considering the available habitat on Réunion and the fact that *P. echo* survived on Mauritius, it is surprising that this parakeet died out very early in Réunion's post-human history. Wild ring-necks were mentioned in 1671-2 by Dubois (1674), in 1703 by Borghesi (Lougnon, 1992), in 1704 by Feuilley (1705), and in 1732 by Cossigny (Cheke, 1987; Lougnon, 1992). The birds must have still been fairly common during the early years of the 18th century as Borghesi, in 1703, stated that:

> Still in this Isle, I have observed numerous sorts of perroquets, of large or of small size : some green, the others grey, and others mottled of different colours [my translation]

Cossigny's account in 1732 is the last time that green or grey parrots were mentioned (see also Réunion Grey parrot).

FIGURE 9. An enigmatic skin of *Psittacula* RMS missing its tail, supposedly representing *Psittacula eques* held at RMS. This specimen is labelled 'Plate 39' from Buffon's planche elumineé (1779), the same plate number of *Psittacula eques* (see Systematic Palaeontology), from which the species was described. This may be the one and same specimen (see Jones 1987), or that the label refers to a Mauritius specimen, as these two populations were considered conspecific.

Rodrigues parakeet *Psittacula exsul* (Newton, 1872)

Perroquets verds et bleus, Leguat, 1708: 107.
La seconde espéce [of parrot], text attributed to Tafforet, 1726: 25.
Perruche, Pingré, 1761., in Alby, J., & Serviable, M (eds.) 1993: 45,51.
Palaeornis exsul Newton, 1872: 31; Salvadori, 1891: 459; Oustalet, 1896: 14; Rothschild, 1907a: 65.
Psittacula exsul; Peters, 1937: 244.

Holotype: Preserved skin UMZC 18/Psi/67/h/I female, Rodrigues, 1871 collected by police magistrate George Jenner and originally preserved in spirit.

Measurements: See Appendix 3, tables 1–11..

Type locality: Rodrigues Island, Mascarenes.

Distribution: Rodrigues Island, Mascarenes.

Etymology: From Latin *exsul* meaning an exile, a banished person.

Paratype: Preserved skin (originally in alcohol) UMZC 18/Psi/67/h/2 male, Rodrigues, 1874 (Fig. 21).

Referred material: Mandible (removed from holotype) UMZC 564; sternum (removed from holotype)

UMZC 564(p). Subfossil material collected by George Jenner, Graham Cowles and the author from the Plaine Corail caverns, Rodrigues: palatine FLMR (L); sternum UMZC 997; pelvis BMNH Rod1(p); furcula UMZC 997; coracoid UMZC 997(R); UMZC 997(L); BMNH A1463(L); BMNH A1463(Ld); scapula UMZC 997(R); UMZC 997(L); humerus BMNH A1463(L); BMNH A1463(R); FLMR R166 (L); ulna BMNH Rod1(R); FLMR R206 (R); femur BMNH A1463(L); BMNH A1463(L); tibiotarsus BMNH A1463(R); BMNH A1463(R); (u/cR).

FIGURE 10. *Psittacula exsul* holotype UMZC18/Psi/67/h/I ♀ (above); UMZC18/Psi/67/h/2 ♂ (below).

Diagnosis: Differs from all other Mascarene *Psittacula* parrots by the following suite of characters mandible: when viewed in dorsal aspect, the internal margin of symphysis oval, not square-shaped. Humerus: proximal end proportionally less expanded than in *Psittacula bensoni* or *P. echo*. Coracoid: processus procoracoideus reduced with a shallow cotyla scapularis; a small raised ridge distal to angulus medialis forms a square-shaped lateral edge; proximal to facies articularis clavicularis, a foramen pneumaticum present but not markedly excavated or pneumaticized. Femur: distinct impressiones obturatoriae with deep excavation distal to the trochanter. The Rodrigues parakeet exhibits osteological characters that suggest a close relationship with other Mascarene species of *Psittacula*, which is particularly evident in the comparatively reduced sternum with an anterodorsal projection of the spina externa and the pelvic elements proportionally robust.

Description and comparison: See Appendix 2d.

Remarks: It has been suggested that *Psittacula eupatria* may be the founding species for all species of *Psittacula* that occur on islands in the Indian Ocean. These species tend to lose characters of *P. eupatria*, including reduction in size, as one progresses southward (Smith 1975; Jones 1987). The present day distribution of *P. eupatria* includes India and parts of Southeast Asia (Fig. 18) and southward colonisation appears to have given rise to the parrots of the islands of the Indian Ocean (see Discussion). Skeletal morphology further supports a close relationship between *P. exsul* and *P. eupatria*, but the derived nature of *P. exsul* suggests that it has long been on Rodrigues.

Leguat (1708) briefly described parakeets during his stay on Rodrigues and commented on their partiality to the nuts of Bois d'olive *Cassine orientale*. He took a living bird that had been taught to speak French and Flemish with him to Mauritius (see below). Leguat's account of the Rodrigues parakeet also opened a historical conundrum that has not been satisfactorily resolved (Grant 1801; Newton 1872; Newton & Newton 1876):

> There are abundance of green and blew Parrets, they are of a midling and equal bigness; when they are young, their Flesh is as good as young Pigeons [Leguat 1708: 77].

Leguat's account suggests either that there were green parrots and blue parrots of the same size (possibly referring to *Necropsittacus rodericanus* and *Psittacula exsul*), or that he was describing colour variations of *Psittacula exsul*. The two surviving skins are blue (Fig.21), but in the original description by Newton (1872), which may partly explain the contradictory statements (see also the account of the Mascarene parrot, below), he states that the 'head, nape, shoulders, upper wing-coverts and retrices above dull greyish-glaucous, the blue tinge in which predominates when the bird is seen against the light, and the green when seen in contrary aspect.' Furthermore, a live specimen was received by the naturalist Philibert Commersen on Mauritius during the 1770s, where it was described as long-tailed, greyish-blue parrot with a black collar (Oustalet 1897: 11). This individual was illustrated by Jossigny on at least 2 occasions, the only time this species was depicted in life (Hume & Prys-Jones 2005), and here published for the first time (Fig. 27). Frustratingly for science, a more detailed account by Tafforet in 1726 [Dupon 1973]) describes a predominantly green *P. exsul* but fails to mention a blue one:

> The parrots are of three kinds, and in quantity……The second species [=♂P. exsul] is slightly smaller and more beautiful, because they have their plumage green like the preceding [*Necropsittacus*], a little more blue, and above the wings a little red as well as their beak. The third species [=♀P. exsul] is small and altogether green, and the beak black [translation from Cheke & Hume in prep.].

Despite the lack of detail, Tafforet's account is extremely important because he describes the green bird as having a red shoulder patch. The astronomer Abbé Pingré, who visited Rodrigues in 1761 to monitor the Transit of Venus, discussed the fauna in some detail, including parrots. He may have been referring to this character as well:

> the perruches I saw at Rodrigues were entirely green, without any [word illegible] of red or other colour [Cheke 1987: 47].

The red shoulder is found only in *Psittacula eupatria* but not in *P. krameri*. In selective breeding by aviculturists, green to blue colour alteration is the most frequent change in psittacines (Nemésio 2001) and easily produced in *Psittacula* (Fig.18). Furthermore, the suppression of yellow (which produces the blue colouration) also results in the suppression of red (Jones 1987; Nemésio 2001), so a blue bird might lack red shoulder patches. As the two skins were originally preserved in alcohol, the blue colouration may have been an artifact of spirit storage with the original green changing to blue, but examination of specimens preserved in alcohol averaging 75 years old (*Psittacula cyanocephala* BMNH1933.3.5.1; *P. calthrapae* BMNH1929.7.1.1 and *P. alexandri fasciata* BMNH1924.4.7.11) show negligible changes in colour. The greens, which have a carotenoid component, are dull and browner whereas the blues, based on melanin, are unchanged.

The Rodrigues parakeet survived until comparatively recently but the species was in decline from the1760s. Leguat reported it as abundant during his stay in 1691-2, and amused himself with captive birds, primarily because they were too easy to kill:

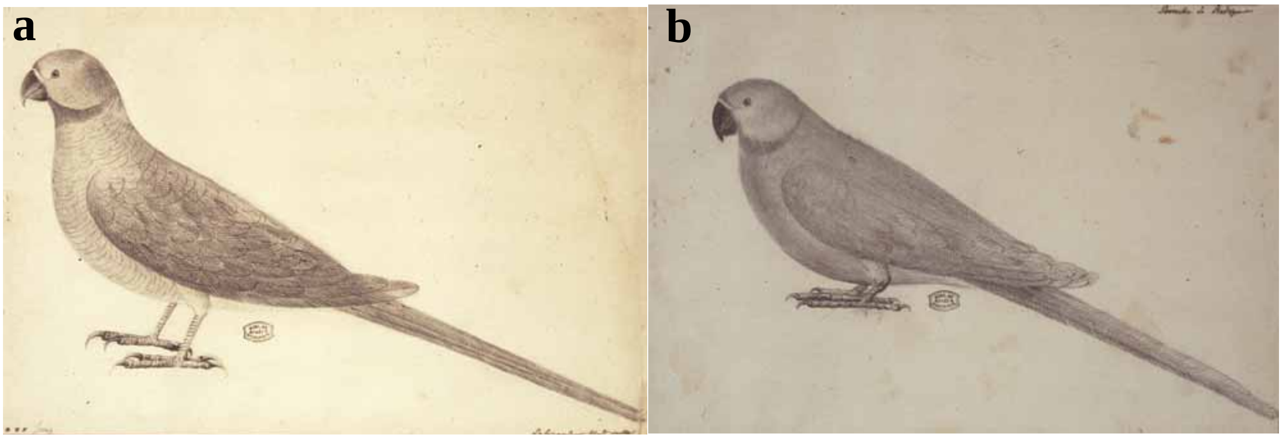

FIGURE 11. *Psittacula exsul* (Jossigny in Oustalet, 1897). These illustrations by Jossigny c.1770 are the only known depictions of a live bird (Hume & Prys-Jones 2005).

> Hunting and Fishing were so easie to us, that it took away from the Pleasure. We often delighted our-selves in teaching the Parrots to speak, there being vast numbers of them. We carried one to Maurice Isle, which talk'd French and Flemish [Leguat 1708: 95].

It was still common during Tafforet's stay in 1726 (Dupon 1973), but had become rare by the time of Pin gré's visit in 1761 (see also *Necropsittacus* below; Alby & Serviable 1993). Like *Necropsittacus*, however, it still occurred on the southern islets:

> On the 19th [June 1761] at Isle Mombrani [=Gombrani], the multitude of grey terns on our side [of the boat] served exactly as a parasol; they fly about our heads, in the manner more or less to ease the heat of the sun. In an additional premium to this there were tropic birds and their eggs. There are also some frigates, some tratras [Red-footed Booby *Sula sula*], some perruches [*Psittacula exsul*] [my translation].

FIGURE 12. Grey and fawn-colour morphs of *Psittacula eupatria*. The grey is easiest colour to produce though artificial selection in captivity. Photograph courtesy of Lorna Steel.

After the visit of Pingré, Rodrigues suffered severe deforestation and increased land use for free-roaming livestock (North-Coombes 1971). Government surveyor Thomas Corby was sent to survey Rodrigues in 1843, to ascertain the suitability of the land to support cattle (North-Coombes 1971: 85). Corby remarked that the western side of the island, although severely deforested, still contained the best stands of palms and vacoas (*Pandanus* sp.). He also mentioned the presence of many wild bullocks, pigs, great flights of guinea fowl and green parrots, indicating that *P. exsul* must still have been fairly numerous. The first specimen was received by Alfred Newton in 1871 (Newton 1872), but by this time, the parakeets had become pitifully scarce. The biologist Henry H. Slater stayed on Rodrigues for 3 months during the 1874 Transit of Venus expedition and saw only one parakeet on 30 September in forests on the southwestern side of the island (Slater 1879a). The assistant colonial secretary William James Caldwell, arriving on 12 May 1875, saw several during his stay of 3 months but failed to obtain a specimen (Caldwell 1875). He did, however, receive a male of the species from ships' pilot and local resident William Vandorous on 14 August 1875 (Newton & Newton 1876). Alfred Newton received this individual at Cambridge, England, and this was the last time the species was recorded. A devastating series of cyclones struck the following year (North-Coombes 1971), perhaps wiping out the last few survivors (Cheke 1987). Contrary to Greenway's (1967) suggestion that *P. exsul* might survive on offshore islets, the Rodrigues islets are probably too small to support viable populations of birds.

Seychelles parakeet *Psittacula wardi* (Newton, 1867).

Cateau vert, Newton, 1867: 348.
Palaeornis wardi Newton, 1867: 335.
Psittacula wardi; Peters, 1937.242.

Measurements: See Appendix 3.

Type locality: Mahé, Seychelles.

Distribution: Mahé, Silhouette and possibly Praslin, Seychelles.

Etymology: Named after Swinburne Ward (1830–1897), British Civil Commissioner to the Seychelles, 1862–1868.

Syntypes: UMZC18/Psi/67/g/1-3. 2 females, 1 male collected on Mahé by Swinburne Ward.

Diagnosis: Although of limited use, some morphometric comparisons have been made using an x-radiograph of a female *P. wardi* BMNH1890.10.10.5 (Fig.13D). This specimen is larger than female *P. eupatria* in the cranium, rostrum, mandible, ulna, and tibiotarsus but smaller in tarsometatarsal and carpometacarpal length; male *P. eupatria* are larger in all elements.

Description and comparison: Skeletal specimens are unavailable. In the skin (Fig.13C), *P. wardi* is smaller and shorter-winged, with the bill (rhampthotheca) slightly less robust than its mainland congener *P. eupatria*. Males of *P. wardi* differs from those of *P. eupatria* by the lack of a rosy collar, the cheeks and hindneck are suffused with blue rather than blue-grey, the black band encircling cheeks is finer, extending to the hind neck, and the undersides are more yellowish. The wings and tail are shorter and broader. Newton (1867: 346) describes this species as similar to *P. alexandri* [=*P.eupatria*], but with stouter bill, purple red shoulder patches, and the hind neck without a red band. Several authors (e.g., Greenway 1967) have reduced *P. wardi* to a subspecies of *P. eupatria*. Although Groombridge *et al.* 2004) did not include *P. wardi* or *P. exsul* in their study, the distinctive characters just mentioned surely warrant specific status for the Seychelles bird.

Remarks: The Seychelles Parakeet is known only from 10 specimens. It died out in the early years of the 20th Century, persecuted for supposed damage to maize crops (Newton 1867; Newton & Newton 1876; Greenway 1967; Forshaw 1989). E. Newton (1867) gave a brief description of the bird during a visit to Silhouette:

> The cocoa-nuts are now planted more than halfway up the mountain, and it is probable that in ten years none of the native forests will remain……; and here we saw the :"Cateau vert' [=Psittacula

wardi] at the edge of the forest, in a place some 600 or 700 feet high, where was a patch of maize; but they had been so often fired at that they would not come within shot [Newton 1867: 357].

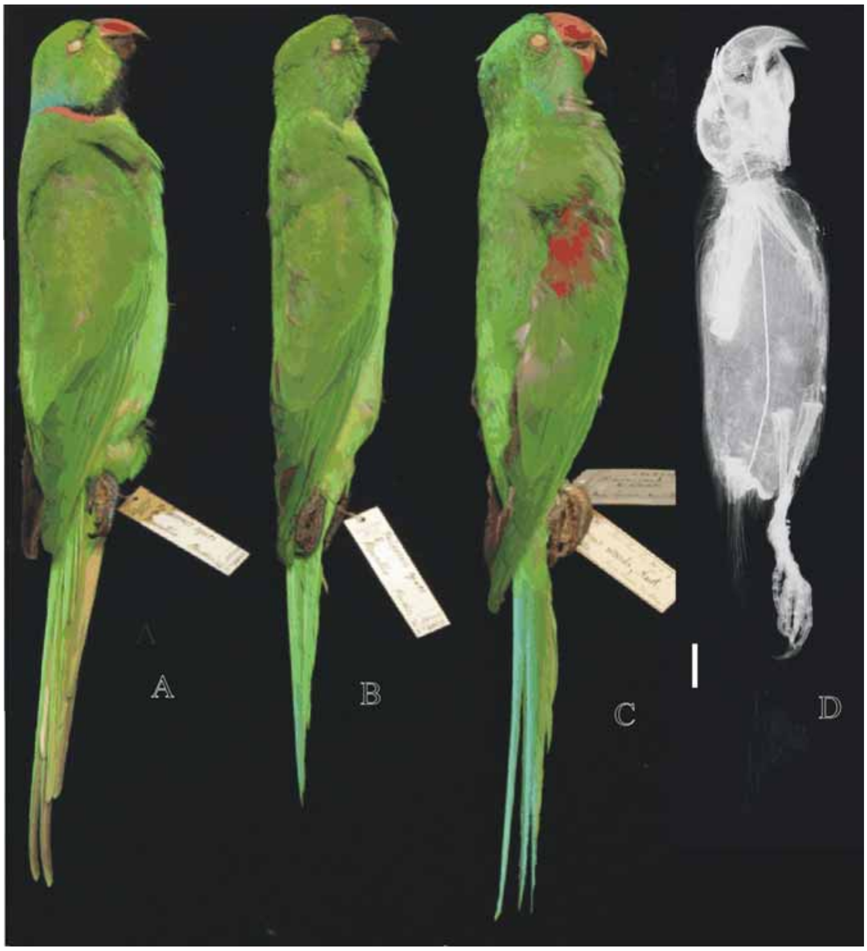

FIGURE 13. Skins of *Psittacula echo* **A,** BMNH 1859.11.22.42♂; **B,** BMNH 1890.10.10.8♀; and *Psittacula wardi*. **C,** BMNH80.6.3.1 ♀ and **D,** BMNH1890.10.10.5 ♀ x-radiograph. Although the x-radiograph is of limited use, it illustrates the big-headiness of *P. wardi* with comparatively reduced but robust wing and leg elements. Scale bar = 10mm.

Newton personally never saw the green parakeet on Mahé, but while there was informed that:

> The "Cateau vert," from the constant persecution against it brought on by its unfortunate partiality for ripe maize, was said to be nearly exterminated [Newton 1867: 348].

The Civil Commissioner, Swinburne Ward had, however, procured three skins of the bird from Mahé. Newton (1867) described the species from these specimens naming it to commemorate the donor. Newton also gathered hearsay evidence that the species had also once occurred on Praslin (Newton & Newton 1876; Diamond 1984). Rothschild (1907a) gave the last word on the continued persistence of the Cateau vert stating that:

> On the Seychelles another Ringed Parakeet, *Palaeornis wardi*, is practically gone, for whereas a few years ago it was fairly common on Mahé, it is now confined to the small island of Silhouette, near Mahé, and is even there almost extinct [Rothschild 1907a: 203].

The granitic Seychelles are an ancient part of the Gondwanaland continental landmass of which only the mountain tops now remain above sea level (Plummer & Belle 1995). Although it is now difficult to determine how much faunal turnover may have occurred since human colonization, much of the Seychelles avifauna is little differentiated from the mainland at the generic level (Prys-Jones & Diamond 1984), and can be considered comparatively recent. It is not known if *P. wardi* has any relationships with other Indian Ocean *Psittacula* as no fossil or skeletal remains are available and no DNA analysis has yet been undertaken.

Genus *Necropsittacus* Milne-Edwards, 1874: 18.

Necropsittacus; Milne-Edwards, 1874 [1873]: 18, pl.15, fig. a–b. Type by original designation: *Psittacus Rodricanus* A. Milne-Edwards.

Etymology: From Greek *necros*, meaning dead, and *psittakos* parrot, in reference to this species being extinct.

Diagnosis: A monotypic genus of large, big-headed parrot with a long tail and lacking the distinctive crest of *Lophopsittacus*. The genus is distinguished from all other Mascarene parrots by the following suite of characters. Cranium: dorsoventrally flattened with lateral edge of the craniorostral hinge sharply right-angled; processus postorbitalis short; crista nuchalis transversus forms a prominent ridged semi-circle; parietals gently slope toward occipital region, which is steeply angled and has a deeply excavated fossa temporalis. Rostrum: narial openings oriented on a different plane, i.e. upward as opposed to forward. Mandible: when viewed in dorsal aspect, the internal margin of symphysis broad and square-shaped. Coracoid: processus procoracoideus reduced with a shallow cotyla scapularis; distal to the angulus medialis, a raised ridge forms a small square-shaped lateral edge; proximal to the facies articularis clavicularis, a deeply excavated, pneumaticised circular pit present. Femur: comparatively indistinct impressiones obturatoriae with a shallow excavation distal to the trochanter; sulcus patellaris narrow and deeply excavated; fovea ligamenti capitis forms a shallow rounded depression; sulcus distal to fossa poplitea deeply excavated. Tibiotarsus: reduced pons supratendineus with no enclosing of the canalis extensorius. Tarsometatarsus: reduced fossa metatarsi I.

Rodrigues parrot *Necropsittacus rodericanus* (Milne-Edwards, 1867)

Les plus gros [perroquet] sont plus gros qu'in pigeon, text attributed to Tafforet, 1726: 25.
Perroquet, Pingré, 1761., in Alby, J., & Serviable, M (eds.) 1993: 45.
Psittacus rodericanus Milne-Edwards, 1867: 151, pl.7, figs. 1–2.
Necropsittacus rodericanus; Milne-Edwards, 1874 [1873]: 18, pl.15, fig. a–b.

Holotype: Anterior portion of rostrum designated by Milne-Edwards (1867: 151, pl. 7, figs. 1–2), whereabouts now uncertain. A specimen catalogued as UMZC 575 matches Milne-Edwards' description and drawing of the holotype. It was sent by Milne-Edwards to Alfred Newton, Cambridge, some time after 1880 and is still in the collection. This specimen might be the missing holotype but confirming data are lacking.

Measurements: See Appendix 3, tables 1–11.

Type locality: Rodrigues Island, Mascarenes

Distribution: Rodrigues Island, Mascarenes

Etymology: *rodericanus*, of Rodrigues, the island having been named in honour of the Portuguese navigator Diego Rodriguez, who discovered it in 1528.

Referred material: Subfossil elements collected from the Plaine Corail, Rodrigues: cranium UMZC 562; rostrum UMZC 562; mandible UMZC 562; UMZC 575; BMNH A1455(d); humerus BMNH A1455(R); BMNH A1455(R); BMNH A1455(R); BMNH A1455(L); BMNH A1455(L); BMNH A1455(L); FLMR R205 (L); coracoid BMNH A1455(R); BMNH A1455(L); u/c (L); ulna BMNH A1455(R); BMNH A1455(L); (Rp); (Lp); FLMR R205 (R); carpometacarpus (Ld); (Rd); femur UMZC A1455(R); UMZC A1455(Lp); (Ld); FLMR R141(Lp); FLMR R34(Rd); tibiotarsus UMZC A1455(R); UMZC A1455(L); FLMR R205 (Rp); FLMR R205 (Ld) tarsometatarsus BMNH A1455(L). At least 4 individuals are represented, including one partial associated skeleton.

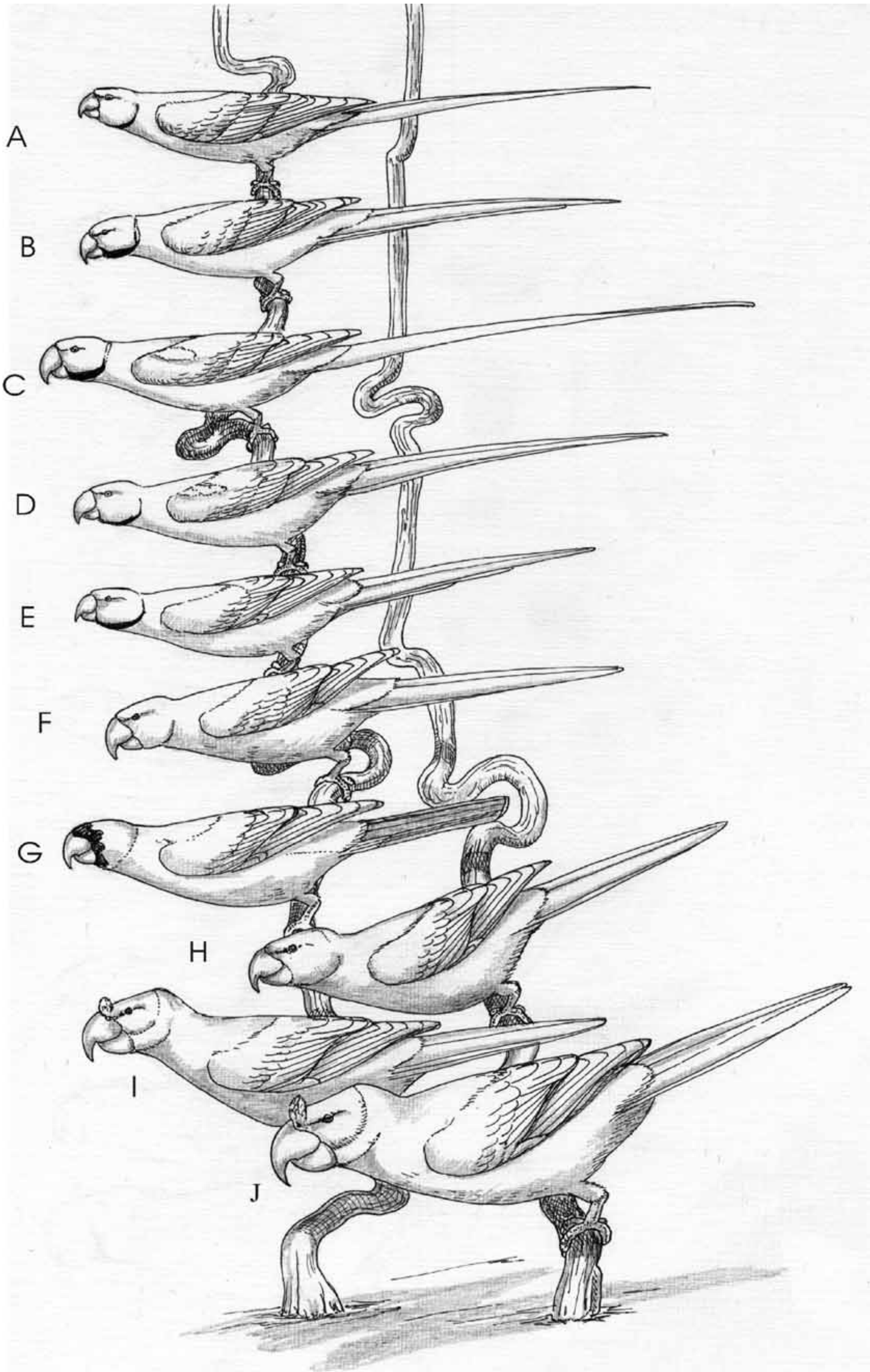

FIGURE 14. Author's scaled drawing of the Mascarene parrots, based on skins and skeletal evidence, in comparison with species of *Psittacula*. **A,** *Psittacula krameri*; **B,** *Psittacula echo*; **C,** *Psittacula eupatria*; **D,** *Psittacula wardi*; **E,** *Psittacula exsul*; **F,** *Psittacula bensoni* new comb.; **G,** *Mascarinus mascarinus*; **H,** *Necropsittacus rodericanus*; **I,** *Lophopsittacus mauritianus* (Type B = female); **J,** *Lophopsittacus mauritianus* (Type A = male).

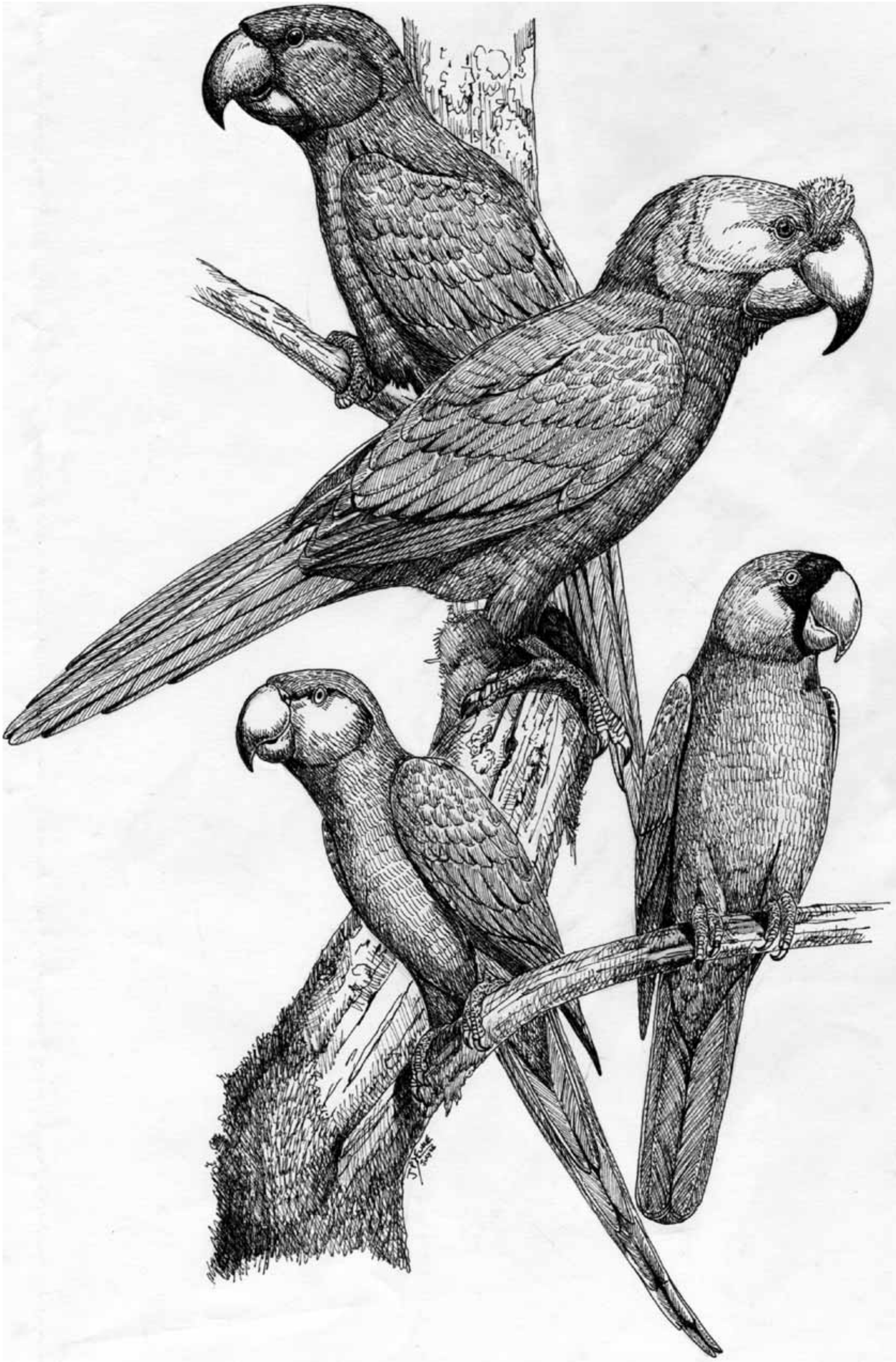

FIGURE 15. Author's scaled drawing illustrating the morphologies of the larger endemic Mascarene parrots. **A,** *Necropsittacus rodericanus* (extremely large head and jaws, comparatively small body with long tail); **B,** *Lophopsittacus mauritianus* (frontal crest, extremely large head and jaws, comparatively small body with long graduated tail, the two central tail feathers longer than the rest); **C,** *Psittacula bensoni*, new comb. (typical *Psittacula* morphology, most similar to *Psittacula eupatria*); **D,** *Mascarinus mascarinus* (comparatively large head and jaws, stocky body with a moderately long, broad and rounded, not graduated tail).

Diagnosis: As for the genus.

Description and comparison: See Appendix 2e.

Remarks: *Necropsittacus* was smaller than female *Lophopsittacus* (e.g. 32% in the tibiotarsus), but had pectoral elements of equivalent size and had proportionally the largest head and jaws of any of the Mascarene parrots (see also Newton & Gadow 1893). The pectoral and pelvic elements are comparable in size to the New Zealand Kaka *Nestor meridionalis*, so in life it may have looked somewhat similar to *Tanygnathus megalorhynchus*, but with an even larger head and longer tail (Figs. 14 & 15). For lack of sufficient fossil material, it is not at all certain if this species exhibited the distinctive sexual dimorphism seen in *Lophopsittacus*, and there are also no cranial characteristics to suggest that it may have had a *Lophopsittacus*-type crest. Characters of the postcranial skeleton indicate a distant relationship with *Lophopsittacus* and there are also some similarities to *Psittacula* and *Tanygnathus*.

In 1725, Tafforet in 1726 (Dupon 1973) gave the only detailed description of the Rodrigues parrot in life:

The largest [=*Necropsittacus*] are larger than a pigeon, and have a tail very long, the head large as well as the beak. They mostly come on the islets which are to the south of the island, where they eat a small black seed, which produces a small shrub whose leaves have the smell of the orange tree, and come to the mainland to drink water…..they have their plumage green [translation from Cheke & Hume in prep.].

Tafforet also mentions a species of tree on which the parrots (presumably *Psittacula exsul* as well) fed:

> The "Bois de buis" [=*Fernelia buxufolia*] is common there [Rodrigues] and very small. The perroquets eat the seeds [my translation].

Today this shrub is endangered and restricted to a few localities (Strahm 1989). It was considered common during Tafforet's visit and grew at any altitude on Rodrigues including the islets. Even as early as 1725, the parrots were frequenting or nesting on these numerous islets within the Rodrigues lagoon as did the now-extinct Rodrigues starling *Necropsar rodericensis* and Rodrigues pigeon "*Columba*" *rodericanus*. This was also reported by Leguat (1708) and was attributed to the huge rat population inhabiting the mainland. Unfortunately, all of the islets gradually became rat-infested and it can be assumed that *Necropsittacus* and other endemic birds of Rodrigues disappeared shortly after. In 1761, Pingré regretted most the increasing scarcity of the parrots – because they were so good to eat:

> The perruche [=Psittacula exsul] seemed to me much more delicate [in flavour, compared to the flying-fox]. I would not have missed any game from France if this one had been commoner in Rodrigues; but it begins to become rare. There are even fewer perroquets [=Necropsittacus rodericanus], although there were once a big enough quantity according to François Leguat; indeed a little islet south of Rodrigues still retains the name Isle of Parrots [Isle Pierrot] [translation from Cheke and Hume in prep].

This suggests that both Rodrigues parrots had become rare by 1761, the larger *Necropsittacus* particularly so. Pingré noted the large number of fires that were lit to clear the vegetation by tortoise hunters, so deforestation as well as direct hunting had probably seriously reduced parrot populations by this time. Pingré's account is the last mention of *Necropsittacus* in life and presumably it died out shortly thereafter.

Réunion red and green parakeet, genus indeterminate

Perroquets verts de méme grosseur, ayant la teste, le dessus des aisles, & la queue couleur de feu, Dubois 1674: 173.
Necropsittacus ? *borbonicus* Rothschild 1907b: 62.

Holotype: none, based entirely on the description of Dubois (1674).

Measurements: None available.

Type locality: Réunion Island.

Distribution: Réunion Island.

Etymology: from Bourbon, the original name of Réunion Island.

Diagnosis: None available.

Description & comparison: Described as the same size as *Psittacula eques*.

Remarks: The most enigmatic species of Réunion parrot is the bird described by Dubois (1674:173) in 1671–2 as:

> Green parrots of the same size [presumably as *P. eques*] with head, upper parts of the wings, and tail the colour of fire [my translation].

A fourth species of parrot mentioned by Lespinay in 1671 (Barré *et al.* 1996: 38) might refer to this species as well, but he gave no description. Rothschild (1907a: 197)) named this red and green species as *Necropsittacus* (?) *borbonicus* assuming that it was related to *N. rodericanus* of Rodrigues, probably because he mistakenly incorporated Dubois' account into his description of the appearance of the Rodrigues parrot *Necropsittacus rodericanus*:

> On Rodriguez were two Parrots; one, *Necropsittacus rodericanus*, a very large parrot allied to *Palaeornis* [=*Psittacula*], *but with head, tail, and wings red* [my italics]. Of this we have bones as well as Dubois' and Leguat's descriptions; the second species was grey, probably a Vaza (*Coracopsis*)[=*Psittacula exsul*] [Rothschild 1907a:197].

Dubois never visited Rodrigues or Mauritius and the Rodrigues parrot was almost certainly all green. Then Rothschild completely confounded himself by attributing Dubois' description of a Réunion parrot to a third species:

> On Mauritius there were two [species of parrot], one of which we only know from Dubois' description to have been green, with a *red head and tail* [my italics], which I will call *Necropsittacus francicus,* nom. nov (Rothschild 1907a: 197).

This name has no basis other than the muddled imagination of Lord Rothschild. Hachisuka (1953) recognised *Necropsittacus*? *borbonicus*, and included an elaborate artistic reconstruction combining the colour pattern described by Dubois with a *Necropsittacus*-like body plan.

If Dubois' description was a parrot endemic to Réunion, this may have been a derivative of *Psittacula* '*eupatria*' as it corresponds well with the colouration of *P. eupatria* except for the red tail. Red feathering on the head, scapulars, and tail are typical psittaculine signal areas (Smith 1975).

Genus *Mascarinus* Lesson, 1831: 188.

Mascarinus madagascariensis Lesson, livre 3, 1831: 188. Type by tautonomy: *Mascarinus madagascariensis* Lesson (1831: 189), based on "*Psittacus mascarinus*, Gm; Levaill., Perroq., pl. 139" (Lesson, 1831: 189).

Etymology: From the French name for the parrot *Le Mascarin* referring to the Mascarene Islands, which were named after the Portuguese navigator Pedro Mascarenhas, who discovered them in 1505.

Diagnosis: An aberrant monotypic genus, with large bill and a moderately long and broadly rounded tail. Cranium moderately dorso-ventrally flattened; in rostrum, diameter of nares greater than width of the internarial septum; indistinct notch on the ventral surface; in mandible, fenestra mandibulae absent; proximal edge of symphysis broadly oval; angulus mandibulae flattened not angled and symphysis sharply angled, projecting ventrally (description based on drawings in Milne-Edwards (1866, 1867) (Fig.24b), who had the skull and jaws removed from the Paris skin).

FIGURE 16. *Mascarinus mascarinus* MNHN 211 u/s. Note the damaged tail destroyed by sulphuric acid.

Mascarene parrot *Mascarinus mascarinus* (Linnaeus, 1771)

Perroquets un peu plus gros que pigeons, ayant le plumage de couleur de petit gris, un chaperon noir sur la teste, le becq fort gros, & couleur de feu, Dubois, 1674: 172.

Les uns sont de la grosseur d'une poulle, de couleur grise, le bec rouge, Feuilley, 1705: 129., in Mission à I'lle Bourbon du Sieur Feuilley en 1704. Recueil trimestriel de documents et travaux inédits pour servir á l'histoire des Mascareignes françaises. [Original not seen.].

Psittacus Mascarinus Brisson 1760: 315 (nonbinomial).

Psittacus mascarinus, Linnaeus, 1771: 524; Hahn, 1834: 54, pl.39 (probably based on the type specimen held in the MNHN, Paris).

Mascarin, Daubenton, 1779: pl. 35; Buffon, 1779: 120, pl.v; Mauduyt, 1784: 194.

Mascarine Parrot, Latham, 1781: 265, n.72.

Perroquet Mascarin, Levaillant, 1805: II, 171, pl. 189, "Madagascar," errore.

Mascarinus madagascariensis Lesson, 1831: 189, "Madagascar," ex Levaillant.

Coracopsis mascarina; Wagler, 1832.: 679; Pelzeln, 1863: 934; Gray, 1846:.407, n,i.

Mascarinus obscurus (non *Psittacus obscurus* Linnaeus)*;* Bonaparte, 1854: 154. (Linnaeus, *Psittacus obscurus*, 1758, X, 97, ex Hasselquist M.S – identified with Psittacus mascarinus in error. See Appendix 1).

Vaza mascarina; Schlegel, 1864: 71.

Psittacus madagascariensis; Finsch, 1868: 306 (Finsch was unfamiliar with the history of this parrot and still thought it origins were in Madagascar); Finsch, *ibid* (footnote); Pelzeln, 1873: .32.

Coracopsis obscura; Gray, 1870: pl.159, n. 8262.

Coracopsis mascarinus; Newton & Newton, 1876: 289.

Mascarinus mascarinus; Salvadori, 1891: 421, Réunion.
Mascarinus duboisi Forbes; 1879: 304, 306, fig.306; Milne-Edwards & Oustalet; 1893: 191, pl. 1.

Holotype: skin (unsexed) MNHN 211 (Fig. 16). This may be the same specimen that was described by Brisson (1760). See below and Forbes (1879).

Measurements: See Appendix 3, tables 1–11.

Type locality: Réunion Island, Mascarenes

Distribution: Réunion Island and possibly Mauritius (see below)

Etymology: As for the genus.

Referred material: Skin (unsexed) NMW 50.688. For fossil material see Mourer-Chauviré *et al* (1999).

The Mascarene parrot *Mascarinus mascarinus* is known from two ancient skins, the type in Paris (Milne-Edwards and Oustalet 1893) and a partially albinistic specimen in NMW (Greenway 1967). The presence of white feathers in this specimen is almost certainly a result of a long period in captivity (Schifter 1994). This specimen, listed as '*5828 Parrot, a curious variety, America*,' was obtained at the sale of the Leverian Museum, London in 1806 (Pelzeln 1873; Sassi 1940; Schifter 1994).

Diagnosis: As for the genus.

Description and comparison: See Appendix 2f.

Remarks: Facts concerning the natural colouration and date of extinction of the Mascarene parrot have long been documented (Hahn 1834; Newton & Newton 1876; Milne-Edwards & Oustalet 1893; Rothschild 1907b; Hachisuka 1953; Forshaw 1989; Day 1981; Fuller 1987, 2001), all based on the account of Hahn (1834). Hahn supposedly saw the last of the species, an aged specimen living in the King of Bavaria's menagerie in 1834, although other evidence suggests that this may not have been the case (Hume 2004; Hume & Prys-Jones 2005). Hahn's (1834: 54**)** account reads:

> bill red; base of bill black; head and throat bluish-grey; remainder of body brownish-red, lower parts paler; tail white at base, remaining half brownish-red; feet blackish. ORIGIN: Madagascar. WHERE FOUND: Unknown. FOOD: Fruits. BREEDING: Unknown. CHARACTERS: It is not very lively and its call is harsh. There is a living example in the menagerie of King Maximilian of Bavaria at Munich on which the illustration is based [my translation].

Although Hahn supposedly based his illustration of the *Mascarinus* in his book, *Ornithologischer Atlas: Papageien* (Fig. 17b) on this living example, it is almost a direct copy of Martinet's plate (Fig. 17a) in Buffon (1779: pl. 35) executed some 50 to 60 years before. After the death of the king on 13 October 1825, the menagerie was auctioned off on 25–28 August 1826, and an inventory lists all species in precise detail (Anonymous 1826). No Mascarene parrot is on the list. Furthermore, such a rare parrot would surely have been mounted after death, but no such specimen was preserved. Without giving reasons, Newton & Newton (1876, p. 287) suspected Hahn's veracity on the subject, but one important fact is overlooked: Hahn's account of a live bird says nothing about the date of his observation. The book was published in 1834 and, in Hahn's defense, it is possible for him to have made an observation well before that date, as the collection of data and final publication may have taken many years. Hahn died the following year in 1835 (Schifter 1994).

Nonetheless, inconsistencies in Hahn's description (i.e. date and provenance of observation and plagiarized image of *Mascarinus*), cast doubt on his statement. Although not conclusive, it is very doubtful that Hahn saw a living Mascarene parrot as late as 1834, if at all, and he may have derived his description and illustration from other sources, even hearsay evidence.

The 1834 date of extinction is, therefore, unfounded and the species had almost certainly died out long before then. The Mascarene parrot was last mentioned alive on Réunion in the 1770s (Cheke 1987) and captive birds were alive in Paris during the 1780s and described by Mauduyt (1784):

The Mascarin is found at Ile Bourbon [=Réunion]; I have seen several alive in Paris, they were rather gentle birds; they had in their favour only that the red beak contrasted agreeably with the dark background of their plumage; they had not learnt to talk (translation from Cheke and Hume in prep.)

FIGURE 17a. *Mascarinus mascarinus* (Martinet's illustration in Buffon, 1779); **17b.** *M. mascarinus* (Hahn, 1834).

No records indicate that they survived longer, which suggests that *Mascarinus* probably became extinct before 1800.

It has been suggested that *Mascarinus* may have also once inhabited Mauritius (e.g. Hachisuka 1953; Greenway 1967), based on the account of Peter Mundy (1608–67 [1914]), quoting his observation of '*russet* parrots'. Réunion and Mauritius share a number of genera, including parrots, so a possibility exists that *Mascarinus* occurred on both islands, which can only be resolved by the discovery of fossil material on Mauritius.

The accounts of Dubois (1674), Feuilley (1704 [1939]) and Borghesi in 1703 (Lougnon 1992) include descriptions of live *Mascarinus* on Réunion. At least 3 specimens also reached France alive (Brisson 1760; Mauduyt 1784; Levaillant 1805; Finsch 1867; Milne-Edwards & Oustalet 1893) and two of these live birds were described, the first and most detailed by Brisson (1760) and a second by Mauduyt (1784) (see above). A third specimen belonged to the Cabinet Aubry (Newton & Newton 1876; Milne-Edwards & Oustalet 1893), eventually becoming part of the Cabinet du Roi (Cheke 1987). Buffon (1779: pl 35); Martinet (1787); Levaillant (1805) and Hahn (1834) followed by Rothschild (1907b), Hachisuka (1958) and Forshaw (1989), describe or depict a brown bird with bluish-lilac head – a colouration that has become the orthodox image today. Dubois (1674), however, described *Mascarinus* as *Petit-gris*, which is the colour of the dark phase of the Eurasian red Squirrel (*Sciurus vulgaris*) (Mourer-Chauviré *et al.* 1999), a variable dark blackish grey/brown (pers. obs.). Feuilley (1705 [1939]) in 1704 mentions *Mascarinus* and other parrots on Réunion (see Réunion Grey parrot), and Brisson (1760:315) described a captive *Mascarinus* as follows:

> Upperparts of head and neck clear (ash) grey. Back, rump, underparts of neck, breast, belly, sides, legs, scapular feathers, uppercoverts of tail very-dark (ash) grey. Wing feathers of the same colour. The tail is composed of 12 feathers: the two median ones are also very-dark (ash) grey. All the lateral ones are of the same colour, except that they have a little white at their base.
> The eyes are surrounded by a naked skin, bright red. Pupil black, iris red. The base of the superior half of the beak is also surrounded by a red naked skin in which the nostrils are placed. Beak similarly red.
> Legs pale flesh. Claws grey-brown. I am unaware from which country it is found. I have seen it living in Paris [my translation]. As above

The overall grey colouration is in direct contrast with more modern interpretations**.** Buffon (1779:120) also described *Mascarinus*, based on a mounted specimen:

> Its bill is red; a grey hood covers the back of the head and neck; the rest of the body is brown; the quills of the tail, which are brown for two-thirds of their length, are white at their origin [my translation].

Finsch (1867) also described the Vienna specimen as brownish grey. The contradictory colour descriptions I believe are an artifact of aging in museum specimens in which blacks and greys can change to brown, a process hastened if specimens are not kept out of light (see Brothwell 1987). For example, *Spiza townsendi*, a unique specimen collected by Audubon in the 1830s was originally grey but is now brown (see Fuller 2001). Furthermore, Dubois (1674) and Brisson (1760) described wild and captive birds as dark grey. Another probable erroneous depiction is the bluish-lilac head. No such colour is mentioned in any of the early accounts of live birds in which the head is described as grey (e.g. Brisson 1760). Levaillant (1805) followed by Salvadori (1891), gave the following description of a stuffed individual:

> ….the rest of the head and the neck is an ashen grey, lightly purplish [or mauvish]; upper back , mantle, wings and all coverts are dull brown, greyish in certain aspect [or appearance] [my translation].

The light purplish head and the greyish colouration are obviously subtle colours, perhaps evident only in certain angles of light. The overall dark colouration can swamp these colours when seen from any distance and this may well account for the confusion. The origin of the purplish and brown bird stems from a painting, the first coloured illustration of *Mascarinus*, by Martinet (in Buffon 1779: pl.35) (Fig.17a). Martinet was employed to illustrate Buffon's work, and would not have been responsible for all final reproductions**.** He was head of a workshop employing over 80 artists and workers and was subject to a strict timetable for completing Buffon's and other works (Jackson 1999). Furthermore, the original plates were hand-coloured, a standard practice during the 18th and early 19th centuries (Dance 1978) that led to considerable variation. Martinet's depiction is almost certainly the same stuffed bird described by Buffon, and examination of several copies of his plates of *Mascarinus* showed marked discrepancies in colouration between them (Table 2). Despite the best efforts of the artists, depicting subtle colours using water-based paints is extremely difficult and in the renditions of *Mascarinus* the purples and browns appear much too strong. It is not surprising, therefore, that so many inconsistencies exist.

TABLE 2. Variations in the plates of *Mascarinus* by Martinet in Buffon (1779 *planches enluminées* edition.

Location	Head colouration	Body and wings	Tail
Rothschild Library, Tring 14/G	Bluish-grey	Chocolate brown, wings blackish brown	Light grey
Rothschild Library, Tring 16/A	Grey-blue	Chestnut brown washed with rufous, paler below. Wings dark chocolate	Mid grey
Errol Fuller collection	Grey-blue	Greyish chocolate, paler below. Wings blackish brown	Dark grey - brown
Bodleian Library, Oxford	Dove-grey	Medium brown, paler grey-brown below. Wings dark blackish brown	Light grey
Muséum d'Histoire Naturelle, Réunion	Bluish-grey	Chocolate brown. Wings blackish	Blackish grey-brown

Martinet's plate also has one feature that links it to the majority of the subsequent illustrations of *Mascarinus*: the absence of two dark central tail feathers without white bases as described by Brisson (1760). In Martinet's illustration, the central tail feathers are shown with a white base which suggests that the specimen (almost certainly the Paris bird) lacked these feathers. This might have arisen from the fact that the Paris specimen was severely damaged during an attempt to fumigate the cases in the 1790s by burning sulphur (Milne-Edwards & Oustalet 1893), which combined with water to produce sulphuric acid, and almost all of the tail and distal wing areas were destroyed (Fig. 16). Unfortunately the Vienna specimen, which has an undamaged tail, cannot be used as a comparison because the tail is almost entirely albinistic (Hume pers.obs.). Martinet (locs.cit.), Martinet (1787), Hahn (1834), Keulemans (in Milne-Edwards & Oustalet, 1893), Keulemans (in Rothschild, 1907b) have all included this feature in their works. This implies that Martinet's illustration, which was an unreliable source to begin with, provided the basis for all of these renditions of *Mascarinus*.

Further confusion appears in the account of Forbes (1879), who described *Mascarinus* as having nostrils entirely covered with feathers. This may not have originally been the case. Brisson (1760) and Wagler (1832[1835]) clearly stated that the nostrils are exposed and surrounded by red skin. Forbes examined the specimen after Milne-Edwards had removed the skull and presumably when the rampthotheca was reattached to the skin, the nostrils were obliterated. The removal of the skull and jaws also explains the unnatural shape of the head (Fig. 16) in this specimen.

Based on the distinctive large red bill, Garrod (1874), Forbes (1879) and Oustalet (1897) suggested a close relationship among *Mascarinus*, *Tanygnathus* and *Psittacula*. A red bill is a diagnostic feature of the tribe Psittaculini (Forshaw 1989, Collar 1997, Juniper and Parr 1998). Although *Mascarinus* possessed a bright red bill, it exhibited atypical plumage patterns, including a moderately long tail with white bases to the dorsal surface of the outer tail feathers, and a thick, black, velvety facemask (Fig. 17a & 17b). Black facial feathering occurs widely within the Psittaculini, however, and may range from moderate, e.g. *Tanygnathus gramineus*, to extensive, e.g. *Psittacula derbianus* and *P. caniceps*.

An enigmatic specimen, mentioned here for completeness, was housed in the Cabinet du Roi. It was noted by Buffon (1779: 132) in his description of *Mascarinus*:

> We have an individual in the King's Cabinet of the same size and of the same colour [as *Mascarinus*], except that it has not got a black mask, nor the white on the tail, and that all its body is equally brown; the beak is also smaller, and it that respect, it resembles a vaza [*Coracopsis*], of which it would appear to be a variety, if it does not form an intermediate species between that bird and the Mascarine. To the same species or variety, we would refer the *brown parrot* of Brisson [my translation].

Although it is now impossible to determine what species is being discussed here, it is clearly not a misidentified vaza *Coracopsis vasa* or *Mascarinus*. Of the 2 species of *Coracopsis*, the larger, *C. vasa*, is 50 cm in total length, much larger than *Mascarinus*, whereas *C. nigra*, at 35 cm, is roughly equal in size. Thus this specimen may have been *C. nigra* or an aged specimen of the now long extinct Réunion Grey parrot *Psittacula* cf. *bensoni* and, as with *Mascarinus*, the greys had changed to browns. Unfortunately, the whereabouts of this specimen are now unknown.

Discussion

Extinction

Parrots have suffered considerably at the hands of man. Their bright colours and raucous nature invite detection and coupled with an apparent tameness, island parrots have been particularly vulnerable. Although referring to Mauritian birds in general, an account written in 1662 by assistant minister Simon van den Kerkloven (1663) epitomises the vulnerability of the avifauna:

> But what appeared strange to me of a certain (sort of) fowls (or birds) which often feed in great numbers in the trees, and which were daily asundered by our people, who killed (or struck them dead) with sticks, although it was never observed that a single one flew away; for it (as) one received the blow, the others (quickly) looked after him and even if twenty were wounded, the rest remained (in their place) after the blows [translation in correspondence between Bouton and Strickland, 31st March 1848].

On the Mascarenes, 8 out of 9 parrot species are now extinct due to a combination of three factors; direct hunting by humans, the introduction of exotic animals, and deforestation. On Réunion, the enigmatic red and green parrot disappeared between 1672 and 1704, possibly as a direct result of the Black Rat *Rattus rattus* having become established on the island about 1675. However, both *Psittacula eques* and *Psittacula* cf. *bensoni* survived until at least the 1730s, but became extinct after an escalation of hunting and deforestation between 1730–50. Remarkably *Mascarinus* survived until at least the 1780s with captive birds in Paris outliving the wild population by a decade. On Mauritius, *Lophopsittacus mauritianus* disappeared by the 1680s at a time when large-scale harvesting of endemic palms was taking place (Barnwell 1948:48). These parrots may have been palm specialists. Despite parrots of various species being reported as numerous by Leguat during 1693–4 (Leguat 1708), *Psittacula bensoni* disappeared sometime after the 1730s when forest cleareance, particularly in the lowlands, was being made for agriculture (see Cheke 1987). On Rodrigues *Necropsittacus rodericanus* became extinct between 1726 and 1770 as a result of forest clearance, rat predation and hunting, while *Psittacula exsul* finally succumbed to almost complete deforestation of Rodrigues by the 1870s. Only on Mauritius, and then only on one mountain range in the southwest, did the sole surviving but critically endangered Mascarene parrot *Psittacula echo* persist.

Biogeography

It is evident that many Mascarene birds, but not all (e.g. *Streptopelia*/*Nesoenas* doves, Johnson *et al.* 2001), are derived from southeast Asia, including the Dodo *Raphus cucullatus*, Solitaire *Pezophaps solitaria*, blue pigeons (*Alectroenas* sp., Shapiro *et al.* 2002), and starlings (Sturnidae, Hume *et al.* in prep.), and this appears to be the case with parrots as well. For parrots to reach isolated archipelagos such as the Mascarenes, it is probable that sea level changes provided opportunities for island-hopping. During periods of lower sea levels that occurred during the Pleistocene, some low stands continued for tens of thousands of years and were up to 145 m lower than present (Haq *et al.* 1987; Rohling *et al.* 1998). Indian Ocean islands situated on plateaux would therefore have been much greater in land area. This would not only have provided long-term stepping stones for species dispersal but also narrowed the distances for over-water crossing. It is now impossible to determine with any certainty which route parrots took in order to reach the Mascarenes, but the present distribution of Psittaculini provides a number of options. The dispersal events may have occurred via India or south-east Asia. An Indian route concurs with present day Indian Ocean geomorphology (Fig. 18), where islands and island groups such as the Maldives, Chagos Archipelago, and St Brandon are situated along or adjacent to the Central Indian Ridge. The ridge forms a north-south corridor of comparatively shallow water terminating with the Seychelles in the north and the Mascarenes in the south, providing opportunities to reach the Mascarenes over a considerable period of time. Parrots evidently colonised the Mascarenes in pulses, as the parrots have not radiated in situ, a scenario similar to dispersal of *Aplonis* starlings in the Pacific (Hume 2000). Ultimately, however, the Mascarenes and Seychelles became dead ends for parrot colonisations across the Indian Ocean because parrots never advanced any further west.

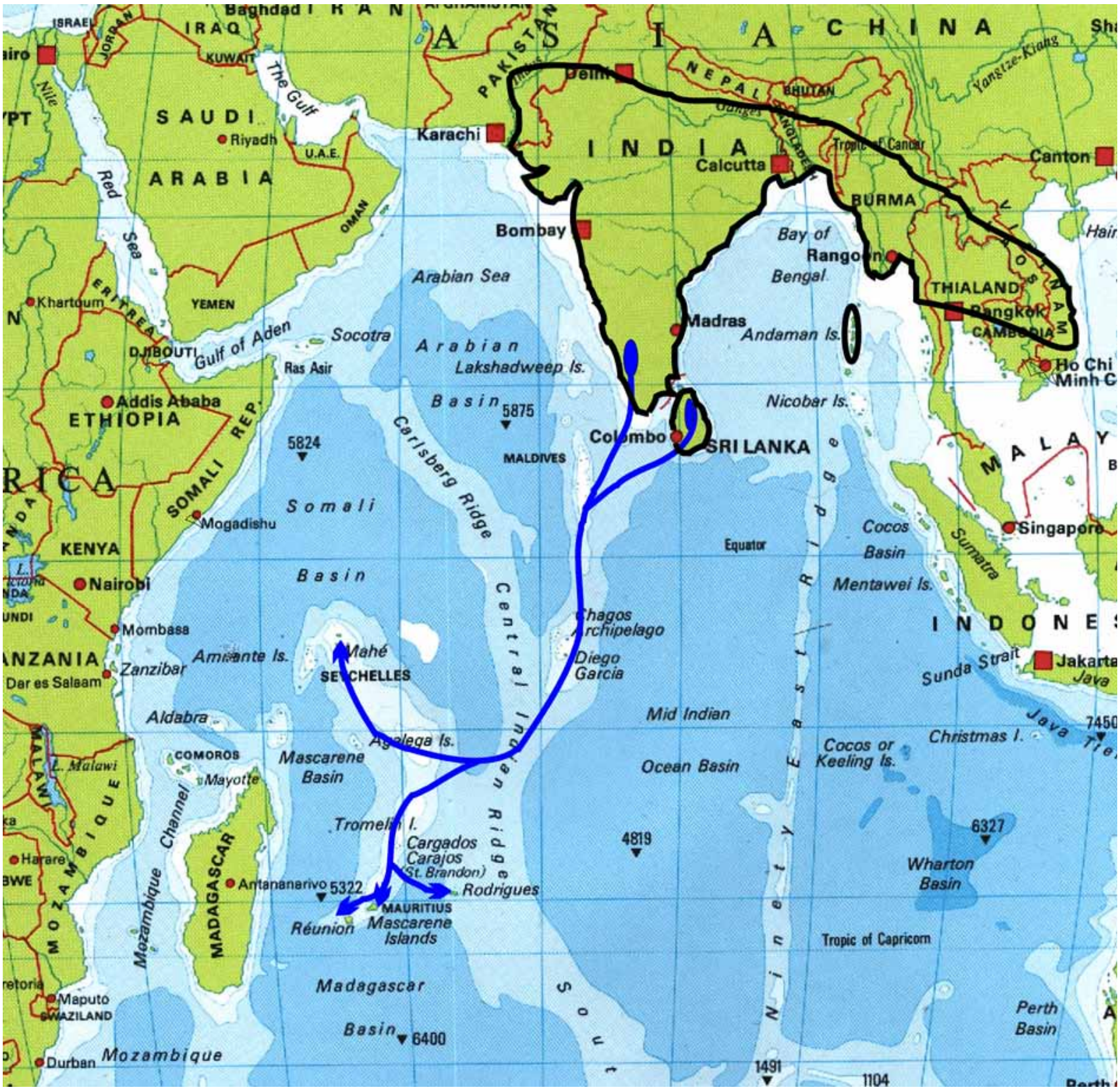

FIGURE 18. Map of the Indian Ocean and a possible route used by parrots (blue) in order to reach the Mascarene Islands. A number of islands, seamounts and atolls are situated along the Indian Ocean ridge, which may have provided a series of island stepping stones. Black outline illustrates the present range of *Psittacula eupatria* (based on Forshaw 1989: 355), a possible founding species for all Mascarene species of *Psittacula*.

Affinities

The order Psittaciformes is a remarkably homogeneous group in structural terms (Forshaw 1989, Collar 1997, Juniper & Parr 1998). Parrots are characterised by a generally disproportionately large hooked bill and a zygodactyl foot with a reversible fourth toe. Defining osteological characteristics at the specific and generic level from the fossil record is problematic, as differences are often of degree only. Despite its inadequacies, the fossil record indicates that all Mascarene parrots to a greater and lesser degree evolved disproportionately large heads and jaws, comparatively reduced pectoral elements, particularly in the sternum, and robust pelvic elements (Fig. 19). A comparative reconstruction (Figs. 14 & 15) of the Mascarene parrots and *Psittacula eupatria* and *P. krameri* shows the size and morphological evolution that has taken place in the endemic genera *Lophopsittacus*, *Necropsittacus*, *Mascarinus* and the species *Psittacula bensoni*. The affinities of the endemic parrot genera are now difficult to determine, but as *Psittacula* has managed to colonise a number of isolated Indian Ocean islands (Groombridge *et al*. 2004), it is not unreasonable to postulate that members of the tribe Psittaculini gave rise to all Mascarene parrots. A number of authorities have already postulated a close relationship between *Lophopsittacus*, *Necropsittacus*, and *Psittacula* (Milne-Edwards 1873, Berlioz 1946, Holyoak 1973a), but did not provide supporting evidence. Morphological evidence presented in this paper suggests that the endemic Mascarene genera *Lophopsittacus*, *Necropsittacus* and *Mascarinus* are clearly nested within the Psittaculini, and that the Mascarene and Seychelles forms of *Psittacula* have a probable ancestor closely related to *Psittacula eupatria*.

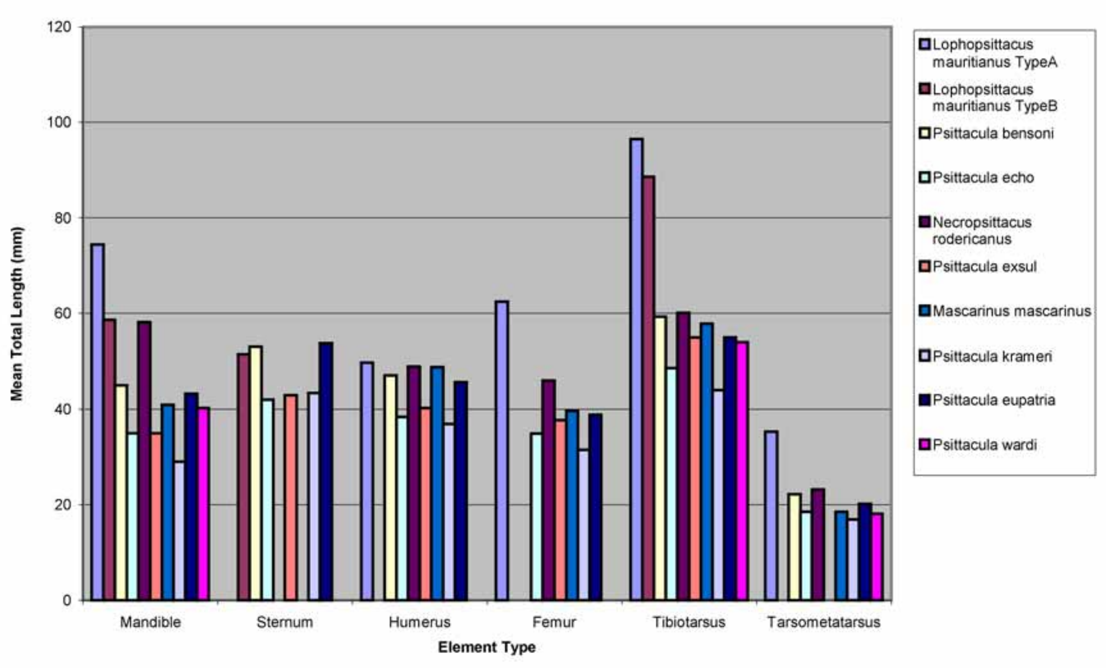

FIGURE 19. Comparison of selected skeletal elements of Mascarene parrots with species of *Psittacula eupatria*. Note the trend of relatively large mandibles and leg elements with reduced pectoral elements in Mascarene parrots compared with *Psittacula*, with *Necropsittacus* having the largest jaws in comparative terms of any of the Mascarene parrots (see Newton and Gadow (1893).

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Appendices

Appendix 1.

Psittacus obscurus Linnaeus, 1758: 97, ex Hasselquist M.S

Although Linnaeus identified *Psittacus obscurus* with the Mascarine parrot (Linnaeus, 1766: 140), it cannot be the same as *Psittacus mascarinus* as the description disagrees entirely. The bird was described from a specimen probably seen alive by Hasselquist, with uncertain locality. The identification of Linnaeus' *P. obscurus* is difficult to determine. It agrees with the Grey Parrot *Psittacus erithacus* to some degree but it is described as crown variegated black and grey, blackish neck and wings, grey barred with whitish grey below and has a longer ash grey tail. *Psittacus obscurus* is stated as being the size of a Jackdaw *Corvus monedula* (34 cm in total length). *Mascarinus*, at 35 cm in total length, has a long tail but differs in colouration, while the Grey Parrot *Psittacus erithacus* (33 cm total length) has a short scarlet tail. The following is a direct translation from the original latin:

18. PSITTACUS (obscurus) niger...

The obscure PARROT - black with crown variegated ash-grey & blackish, ash-grey tail.

HEAD oblong, with flattened sides, depressed at the back, in relation to the body pretty large.

Beak wide all along, thick, very blunt, three times shorter than the head. Upper mandible slightly convex, lower down a bit broader, a bit sharper towards the back, able to move. At the base of the upper mandible between the nostrils a furrow [=groove] is noticeable, as though the bone was ridged. From this the groove proceeds lengthwise to the tip. Tip of the upper mandible hooked, extending beyond the lower mandible by a quarter of its own length. At the very tip it has a very shallow little groove. A small lobe on each side at the base where the upper closes on the lower mandible into which it sits [?=fits]. Lower mandible thicker than the upper, more convex, shorter by the tip of the upper; at its base lower than the throat, further back on the same level. Tip blunt, with hardly any edge, with a little half moon hollow at the tip's base. Nostrils close above the beak, completely round, the size of a fowl's quill [? in cross-section].

Eyes closer to the crown than to the throat, likewise to the nostrils than the back of the head. Iris yellow, pupil black. The area around the eyes right from the end of the upper mandible to the beginning of the crown, sideways, and from the nostrils almost to the base of the crown, lengthwise, bare, wrinkled, surrounded by scarcely visible hairs.

Ears have an oblong opening, transverse, the same distance from the eyes as the eyes are from the nostrils, much closer to the base than the crown of the head, covered with a retractile membrane [?] & tiny feathers.

REMIGES [flight feathers] about 20: 1,2 longer than the others, 3,4,5, a little shorter, of equal length, 6,7,8 decreasing in size by degree; the rest shorter and of equal length.

TAIL wedge-shaped. Retrices [tail feathers] about 10, the laterals shorter, with longer intermediaries.

FEET: legs very downy as far as the tarsal joint; toes 4, 2 in front & 2 behind. Of the front ones the inside one is shorter than the outer by three knuckles; of the hinder ones, the inner is half as long as the outer. All the toes are scaly, with wrinkled scales, the two lowest joints being rough. The rest of the foot is tuberculate, with slightly raised minor rounded humps.

Tongue thick, extremely blunt & almost semicircular, emarginate at its sides, the margin being turned upwards, from which emerges a tiny groove.

Claws hooked, slightly blunt.

COLOUR: beak black. Area around the eyes white. Crown variegated ash-grey & blackish. Neck & wings black above. Abdomen & legs grey, barred with whitish grey. Tubercles on the feet black. Claws black. Tail all ash-grey.

SIZE of jackdaw [translation by D. Ashcroft and amended by A. Cheke].

Appendix 2. Osteological descriptions and comparisons

2a. *Lophopsittacus mauritianus*

Cranium (Fig. 2B; Appendix 3, Table 1): Unlike other Mascarene parrot genera, in lateral aspect, cranium dorso-ventrally flattened, parietals gently slope towards the sharply angled occipital region, with deeply excavated fossa temporalis. In ventral aspect, posterior to tuba auditivia communis, two triangular processes project ventro-anteriorly and fonticuli orbitocraniales form deep pits and are not connected to the cranial cavity by large openings. These structures are particularly diagnostic in *Lophopsittacus*. They are pronounced and long in *Lophopsittacus*, short in *Necropsittacus*, *Nestor*, *Strigops*, *Calyptorhynchus*, *Tanygnathus*, *Psittacula*, *Psittacus*, and absent in all other genera studied. In dorsal aspect, craniolfrontal hinge medially concave in *Lophopsittacus*, *Necropsittacus*, *Psittacula*, *Tanygnathus*, craniomedially depressed in *Calyptorhynchus*, *Nestor*, *Strigops*, *Anodorhynchus*, *Probosciger*, *Coracopsis*, *Psittrichas*, *Pezoporus* and *Cyanoramphus* or rounded in *Eclectus* and *Psittacus*. Unlike *Lophopsittacus*, in *Probosciger* and *Calyptorhynchus*, lateral corners of frontal hook-shaped. In *Lophopsittacus*, distinct ridges occur on rostral surface of the frontal, present but indistinct in *Necropsittacus*, *Psittacula eupatria*, and *Tanygnathus*, absent in all other genera studied.

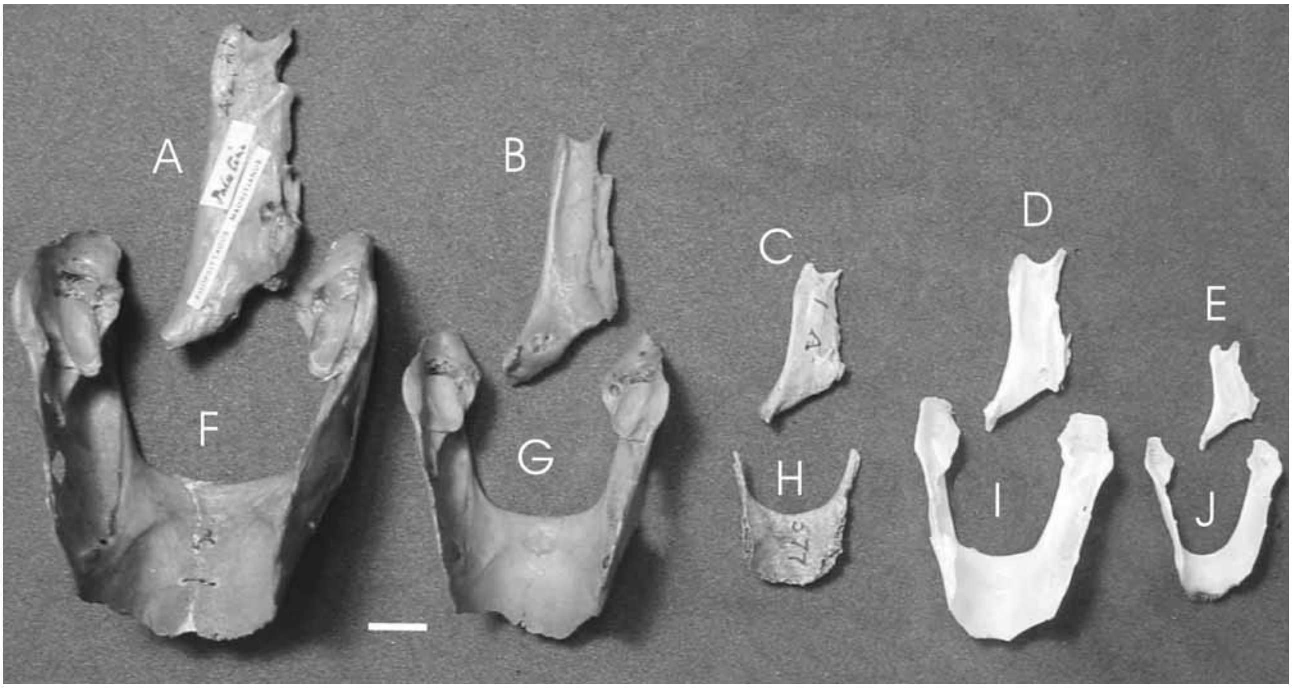

FIGURE 20. Cranial elements of Mauritian parrots compared with species of *Psittacula*: (above) palatines, left side in lateral aspect ;(below) mandibles, dorsal aspect. **A,** UMZCA24AA and F, UMZCA24AA, *Lophopsittacus mauritianus* (type A, ♂); **B,** BMNHA3300 and G, BMNH3296, *Lophopsittacus mauritianus* (type B, ♀); **C,** UMZC577 and H, UMZC577, *Psittacula bensoni*, new comb.; **D,** and I, BMNHS/1999.11.5, *Psittacula eupatria* ♂; **E,** and J, BMNHS/1975.103.62, *Psittacula krameri borealis* ♂. Scale bar = 10mm.

Mandible (Fig. 20F (type A) & Fig. 3G (type B); Appendix 3, Table 3): In dorsal aspect, the most distinctive character is the large articulation (crista intercotylaris) with the quadrate. It is oval-shaped with a pronounced rim and distal lip in *Lophopsittacus*, *Necropsittacus*, *Probosciger*, *Eclectus*, and *Coracopsis*, without a pronounced distal lip, but open proximally in *Anodorhynchus*, *Psittrichas*, *Calyptorhynchus*, and *Cyanoramphus*; weak in *Psittacus* and obsolete in *Strigops*. A shallow pneumatic fossa present in all genera studied except *Anodorhynchus*, *Calyptorhynchus*, *Probosciger* and *Strigops*, in which the pneumatic fossa is deep, or distinctly incised in *Lophopsittacus*, *Tanygnathus*, and *Psittacula*; absent in *Necropsittacus*. Crista transversus fossae deep and strongly pneumatised in *Lophopsittacus*, *Necropsittacus*, *Anodorhynchus*, *Psittrichas*, *Cyanoramphus*, shallow and not markedly pneumatised in *Nestor*, *Calyptorhynchus*, and *Psittacus*. When viewed in dorsal aspect, posterior edge of symphysis square-shaped in *Lophopsittacus*, *Necropsittacus*, *Anodorhynchus*, and *Psittacula bensoni*, broadly oval in *Mascarinus*, *Psittacula exsul*, *P. krameri*, *Eclectus*, *Strigops*, *Pezoporus*, *Psittacus*, and *Cyanoramphus novaezelandiae*, or narrow in *Nestor* and *Psittrichas*. Width of proximal edge of the symphysis is over half the total width taken between the angulus mandibulae in *Lophopsittacus*, *Eclectus*, *Necropsittacus*, *Mascarinus*, *Tanygnathus*, *Psittacula*, and *Cyanoramphus*, indicating that these species have comparatively broad jaws. In lateral aspect, angulus mandibulae pronounced forming an angular projection above the Os dentale and symphysis sharply angled in *Lophopsittacus*, *Anodorhynchus*, *Calyptorhynchus*, and *Necropsittacus* with a flattened ventral surface. Symphysis projects ventrally in other parrots. Single fenestra mandibulae present in some specimens of *Lophopsittacus*, but variable, sometimes absent. One in *Calyptorhynchus*, *Eclectus*, *Coracopsis*, *Probosciger*, *Psittacula*, and *Strigops*, two in *Necropsittacus*, *Nestor*, *Psittrichas*, *Tanygnathus*, and *Psittacus*. Obsolete in all other taxa. Female *Lophopsittacus* mandible is morphologically similar, but averages 21% less in total length and is less robust than in the male.

Palatine (Figures 20A (type A), 20B (type B), 6B and 6C; Appendix 3, Table 2): Palatine extremely robust, particularly at articulation with the rostrum maxillare. In lateral aspect, a distinct furrow runs antero-posteriorly along upper lateral surface, terminating on the pars lateralis in *Lophopsittacus*, *Coracopsis*, *Eclectus*, *Psittacula*, *Tanygnathus*, and *Cyanoramphus*, occurs in the mid-section only in *Probosciger*, *Calyptorhynchus*, *Psittacus*, and *Eclectus*, visible but reduced in *Strigops*, or absent in *Anodorhynchus* and *Psittrichas*. Pars lateralis forms a long expanded blade-like caudal end in all genera studied except *Strigops*, *Nestor*, and *Psittrichas*, where it is short, slender and distally less expanded. Size is the main difference between the sexes of *L. mauritianus*, the male being approximately 19% larger in total length; female palatine also less robust and the caudal end terminates more sharply.

Sternum (Fig. 29A; Appendix 3, Table 4): Sternum lacking the entire posterior end including part of the processus costales, however, at least four costals are present. Carina sterni is missing the apex carinae and much of the medial edge. Unlike other Mascarene parrot genera (*Necropsittacus* unknown), sternum of *Lophopsittacus* has a reduced carina sterni and pronounced flattening of the facies muscularis sterni surface. In *Nestor*, *Anodorhynchus*, *Probosciger*, *Calyptorhynchus*, *Psittacus*, *Cyanoramphus*, and *Geopsittacus*, spina externa distinctly indented and the anterior end distinctly bifurcated. The division forms wing-like processes in *Strigops* and *Calyptorhynchus*. In *Lophopsittacus*, *Psittacula*, and *Tanygnathus* the anterior end of the spina externa forms a single projection with indistinct bifurcation but deeply bifurcated in *Coracopsis*. Only the Mascarene genera and species *Lophopsittacus*, *Psittacula bensoni*, *P. exsul* and *P. echo* exhibit anterior not dorsal projection of the spina externa. Apex carinae projects ventrally and the pila carinae projects ventrally in all genera studied except *Lophopsittacus*, *Cyanoramphus*, and *Geopsittacus*, where they project anteriorly. The carinae sterni greater in depth than distance between the processus costalis and sulcus medianus sterni in all species examined except *Lophopsittacus*, where subequal, equal or slightly greater in *Cyanoramphus*, obsolete in *Strigops*. In dorsal aspect, foramen pneumaticum posterior to spina interna extends over the entire length of sulcus medianus sterni in *Lophopsittacus*, *Probosciger*, *Geopsittacus*, *Coracopsis*, *Psittacula*, and *Tanygnathus*. In *Lophopsittacus*, *Psittrichas*, and *Cyanoramphus*, tuberculum labri externi projects posteriorly. In *Cyanoramphus*, some flattening of the facies muscularis sterni occurs, apex carina insignificant and similarly to *Lophopsittacus*, entire carina sterni projects anteriorly. In ventral aspect, sulcus articularis coracoideus distinctly unequal in *Lophopsittacus* and *Psittacula exsul*, without meeting at the midline.

Furcula (Fig. 28D): Furcula gently rounded, narrow distally with no visible clavicle synosis in *Lophopsittacus*, synosis not visible and furcula pointed more angular in *Psittacula*, *Tanygnathus*, *Psittacus*, *Nestor meridionalis*, and *Anodorhynchus* (processus acromialis extending anteriorly in *Coracopsis*). Synosis present and distally expanded in *Calyptorhynchus* (rounded in *Nestor notabilis* and *Probosciger*), almost obsolete in *Geopsittacus*, *Psephotus*, and *Cyanoramphus* and claviculae are not fused to form a furcula in *Strigops*.

Coracoid (Fig. 27F; Appendix 3, Table 5): One specimen missing facies articularis clavicularis and the lateral edge of the processus lateralis. On the humeral end, cotyla scapularis shallow in *P. bensoni*, *Necropsittacus*, *Psittacula*, *Coracopsis*, *Psittrichas*, *Psittacus*, *Probosciger*, *Tanygnathus*, *Mascarinus*, deeply excavated in *Calyptorhynchus*, *Strigops*, *Nestor* and *Anodorhynchus*. Processus procoracoideus short and not extending past processus acrocoracoideus in all genera studied, but shorter in *Necropsittacus* or elongate extending past processus acrocoracoideus in *Strigops*.

Humerus (Fig. 23A; Appendix 3, Table 6): The extremely limited number of unassociated fossil humeri available from Mauritius, excluding *Psittacula echo*, are of a similar size and of comparatively similar morphology, which makes assigning specimens to *Lophopsittacus* difficult. All specimens designated *Lophopsittacus* are damaged and lack the crista deltopectoralis. Humerus slightly longer than *Psittacula bensoni*, equal in size to *Necropsittacus*, but differing from either by a proportionally smaller caput humeri and less pronounced tuberculum ventrale, which is deflected more dorsoanteriorly. Shaft more curved than *Necropsittacus* and distal end more laterally compressed. Differs from *Psittacula bensoni* by a less expanded distal end, fossa pneumotricipitalis circular, less elongate, lateral edge of crista bicipitalis more angular distally as it merges with the shaft, tuberculum supracondylare ventrale less pronounced, and shaft more robust and medially curved. Easily distinguishable from that in *P. echo* by much larger size. Compared to *Coracopsis*, the distal end less laterally compressed, the fossa olecrani narrower and the sulcus scapulotricipitalis more excavated.

Ulna (Fig. 24A; Appendix 3, Table 7): The ulna is remarkably uniform in psittaciforms. Ulnae assigned to *Lophop-*

sittacus are approximately the size of that in *Tanygnathus* and here are referred to a female, but more expanded at proximal and distal ends than this species. *Crista intercondylaris* weakly developed in *Lophopsittacus*, *Necropsittacus*, *Psittacula*, *Coracopsis*, *Eclectus*, and *Tanygnathus*, well developed in *Calyptorhynchus*, *Anodorhynchus*, and *Probosciger*, with a small depression proximal to the cotyla dorsalis in *Nestor*; *olecranon* short and blunt in *Strigops*. Ulna approximately 25% longer than the humerus in all genera studied including *Lophopsittacus* except *Cyanoramphus*, *Strigops* and *Nestor*, where it is approximately 10% longer in the former or equal/slightly longer in size in the latter two species.

Carpometacarpus (Appendix 3, Table 8). Although longer in total length than *Psittacula bensoni* and *P. echo*, overall comparatively gracile, particularly at the proximal end, distal end and Os metacarpale minus.

Femur (Fig. 21A; Appendix 3, Table 9): In caudal aspect, impressiones obturator forms a distinct ridge distal to the trochanter in *Lophopsittacus*, *Coracopsis*, *Psittacus*, *Tanygnathus*, *Eclectus*, *Psittacula eupatria*, *P. krameri*, *Cyanoramphus novaezelandiae*, and *C. unicolor*, indistinct in *Necropsittacus*, *Anodorhynchus*, *Nestor*, *Strigops*, *Calyptorhynchus* or obsolete in *Calyptorhynchus* and *Psittrichas*. Sulcus proximal to the medial and lateral condyles deeply excavated, not shallow in *Lophopsittacus*, *Strigops*, *Nestor*, and *Coracopsis*. In cranial aspect, sulcus patellaris narrow and u-shaped in all genera except in *Lophopsittacus*, *Strigops*, and *Nestor*, in which it is broader and shallower.

Tibiotarsus (Fig. 21A (type A), Fig. 21B (type B); Appendix 3, Table 10): In cranial aspect, pons supratendineus incomplete, i.e. not enclosing canalis extensorius in *Probosciger*, *Tanygnathus*, *Lophopsittacus*, *Necropsittacus*, *Psittrichas*, *Psittacula exsul*, and *P. eupatria*, otherwise entire enclosing canalis extensorius. Condylus lateralis subequal to condylus medialis in *Lophopsittacus*, *Anodorhynchus*, *Calyptorhynchus*, *Probosciger*, but almost equal in *Strigops* and *Cyanoramphus*. Incisura intercondylaris deeply excavated forming a u-shaped depression in all parrots including *Lophopsittacus*, but flat and not excavated in *Strigops*. In total length, tibiotarsus of *Lophopsittacus* exceeds that of *Anodorhynchus* in some specimens; only *Strigops* is greater in size. The female element is smaller, averaging 8% less in total length and is less robust.

Tarsometatarsus (Fig. 21A; Appendix 3, Table 11): Specimen damaged on the proximal extremity of trochlea. metatarsi II, the distolateral extremity of trochlea. metatarsi III and loss of the crista intermediae hypotarsi on the proximal end. Unlike *Lophopsittacus* and in other parrot genera, in the proportionally long tarsi of *Nestor meridionalis*, *N. notabilis*, and *Strigops*, plantar extension of trochlea. metatarsi IV has a marked and deep furrow on the ventral surface. In dorsal aspect, a distinct *impressiones retinaculi extensorii* forms a deep open furrow distal to the cotyla medialis in *Lophopsittacus*, and *Eclectus*, enclosed by a narrow bridge in *Nestor*, or divided by a ridge in *Tanygnathus*, *Coracopsis*, *Psittacus*, *Calyptorhynchus*; shallow in *Anodorhynchus*, *Probosciger*, *Psittacula*, and *Necropsittacus*.

2b. *Psittacula bensoni*

Description and comparison. Rostrum (Fig.31B; Appendix 3, Table 2). Anterior end missing and only the medial margins of the nares visible, but internarial septum complete. Anterior portions of tomia intact and distocranial curvature complete from proximal edge of nares to anterior tip of tomium. Ventral surface intact. Internarial septum medium-sized, and diameter of nares probably greater than width of internarial septum (as seen in *Psittacula* and *Necropsittacus*). Lateral section of nares missing but is orientated in same plane as in *Psittacula*. Rostrum of *P. bensoni* approximately 29% larger than in *P. echo*, but slightly smaller and more gracile than in *P. eupatria*, the species it most closely resembles.

Mandible (Fig.14H; Appendix 3, Table 3). Only the posterior end of the symphysis in the holotype is preserved and all anterior and lateral edges are lost. When viewed in dorsal aspect, posterior margin of symphysis similar to *Psittacula eupatria* in size and characteristics including a medially situated pneumatic foramen. Angle of rami in *P. bensoni* deflects wider laterally than in *P. eupatria* and is approximately 6% greater in width indicating that *P. bensoni* had a proportionally broader mandible than that species.

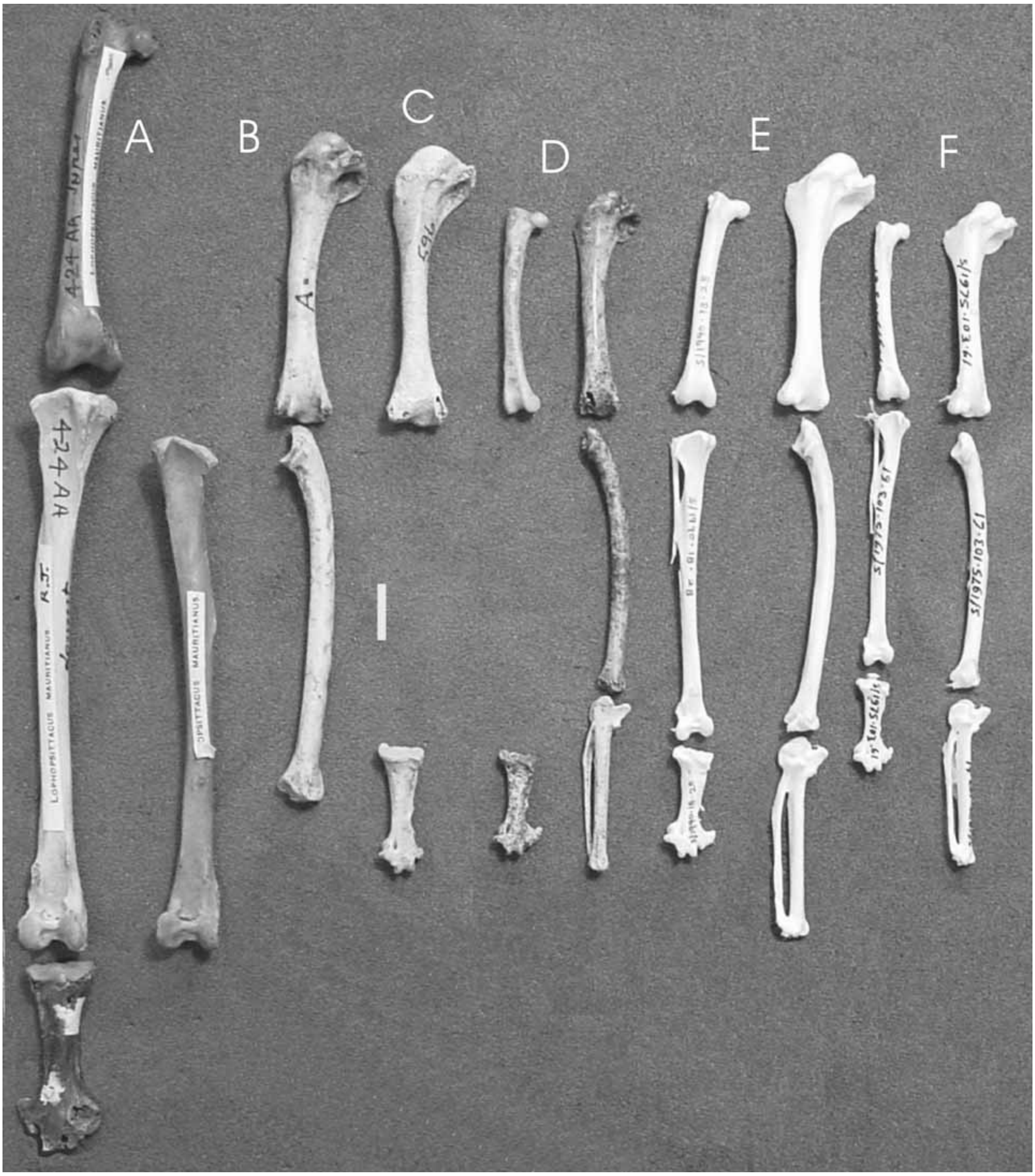

FIGURE 21. Comparison of wing and leg elements of Mauritian parrots with species of *Psittacula.* **A,** *Lophopsittacus mauritianus* (type A) UMZC424AA right femur, right tibiotarsus, left tarsometatarsus, left humerus, left ulna; *Lophopsittacus mauritianus* (type B) BMNHA3300 left tibiotarsus; **B,** *Psittacula bensoni,* new comb.UMZC596 left humerus, UMZC577 right tarsometatarsus; **C,** *Psittacula echo* UMZC600 right femur, right tarsometatarsus, left humerus, left ulna, left carpometacarpus; **D,** *Psittacula eupatria* BMNHS/1990.18.28 ♂, right femur, right tibiotarsus, right tarsometatarsus, left humerus, left ulna, left carpometacarpus; **E,** *Psittacula krameri borealis* BMNHS/1975.103.62 ♂ right femur, right tibiotarsus, right tarsometatarsus, left humerus, left ulna, left carpometacarpus. Scale bar = 10mm.

Palatine (Fig. 14C; Appendix 3, Table 2). *P. bensoni* is intermediate in size between *Psittacula krameri* and *P. eupatria*, but otherwise similar. The palatine of *P. echo* is unavailable for comparison.

Sternum (Appendix 3, Table 4). Only the termini caudalis and left margo lateralis with costals intact preserved; pila coracoidea and processus craniolateralis missing and carina sterni lacking all of the posterior margin. In lateral aspect, spina externa comparatively broad and similar to *Psittacula eupatria*. Differs from *Lophopsittacus* in lesser overall width, spina externa directed less anteriorly, pila carinae more ventrally directed and the facies muscularis sterni less flattened. Overall larger than *Psittacula echo*, the incisura costalis particularly so, with the 5th deeply excavated and the sulcus medianus sterni less pneumatised.

Coracoid (Fig. 27C; Appendix 3, Table 5). Intermediate in size between *Lophopsittacus* and *P. echo*, in dorsal view, angulus medialis appears square-shaped with a prominent distally raised ridge. Processus procoracoideus directed more distally than in *P. echo*. A small depression instead of a furrow located distal to processus procoracoideus. Similar in morphology to *Psittacula eupatria* except more robust, particularly in shaft, and processus procoracoideus projects further medially.

Humerus (Fig. 23B; Appendix 3, Table 6). See also *Lophopsittacus*. Differs from all other Mauritian parrots mainly by size, being much larger than in *Psittacula echo*, and by morphology and slightly smaller size compared to that in female *Lophopsittacus*. Differs from *P. eupatria* in being larger and more robust, shaft straighter, condylus dorsalis more elongate, distal end mediolaterally more expanded and fossa olecrani less excavated.

Ulna (Appendix 3, Table 7). Much larger than *Psittacula echo*, slightly shorter in total length than *P. eupatria* but more robust, particularly on the proximal end.

Carpometacarpus (Appendix 3, Table 8). Smaller than *Psittacula eupatria*, similar in total length and morphology as *P. echo*, but more robust proximally than both species.

Tibiotarsus (Appendix 3, Table 10). Much larger than *Psittacula echo* and larger and more robust than *Psittacula eupatria*, but otherwise morphologically similar.

Tarsometatarsus (Fig. 21B; Appendix 3, Table 11). All tarsometatarsi material referable to *P. bensoni* are damaged. Easily distinguished from any other Mauritian parrot species by size, being 16% larger than *P. echo*, but 37% smaller than *Lophopsittacus* in total length (see measurements). *P. bensoni* larger and more robust than *P. eupatria* and equal in length to *Necropsittacus*, but more gracile in all dimensions compared to the latter. On the proximal end, a single prominent crista intermediae hypotarsi enclosed forming two canals as in other *Psittacula*, but in *P. bensoni*, proportionally shallower. In dorsal aspect, the impressiones retinaculi extensorii forms a distinct groove distal to cotyla medialis in *P. bensoni* and *P. echo*, but shallow in other *Psittacula*. In plantar aspect, two foramina vascularia proximalia occur in *P. bensoni*, one in *Lophopsittacus*, *P. echo*, and *P. eupatria*, and indistinct in *P. krameri* and *Necropsittacus*; fossa metatarsi I distinct and deeply indents medially on side of shaft.

2c. *Psittacula echo*

Sternum (Fig. 29C; Appendix 3, Table 4). In lateral aspect, spina externa reduced compared to *P. bensoni*, pila carinae directed more ventrally and facies muscularis sterni less flattened. Spina externa forms a prominent single projection and anterior end weakly bifurcated. In ventral aspect, differs from *Lophopsittacus* in smaller width and narrow spina externa, from *P. bensoni* by lateral lineae musculares being less prominent. Compared with *P. krameri*, length shorter but width greater, spina externa more anteriorly deflected, carina sterni more reduced and apex carinae directed ventro-posteriorly; fenestra medialis much larger in *P. krameri*.

Coracoid (Fig. 27A; Appendix 3, Table 5). Distinguishable from *P. bensoni* by a raised ridge distal to angulus medialis less prominent, so lateral edge appears more pointed. Differs from *P. krameri* in being more robust, particularly in shaft and processus procoracoideus more medially projected.

Humerus (Fig. 23C; Appendix 3, Table 6). Generally more robust than in *P. krameri*, particularly in shaft. On the cranial surface, condylus dorsalis deflected proximomedially compared to that in *P. bensoni*, *P. krameri* and *P. eupatria*. On the proximal end, sulcus transversus more excavated. Distal end more laterally expanded, fossa olecrani wider and condylus ventralis more proximodistally compressed than *P. krameri* and in cranial aspect, tuberculum ventrale more prominent. In *P. exsul*, longer but more gracile.

Ulna (Fig. 21C; Appendix 3, Table 7). Differs from *P. krameri* in larger size and being much more robust, particularly in shaft. Smaller than in *P. eupatria*, tuberculum ligamentis collateralis ventralis less distinct and impressio brachialis less excavated.

Carpometacarpus (Fig. 21C: Appendix 3, Table 8). Equal to or slightly larger and more robust than in *P. krameri*, but otherwise similar. Processus pisiformis intermediate in size between *P. krameri* and *P. eupatria*, but projects less dorsally and connected to os metacarpale minus by a ridge, which is absent in *P. eupatria*.

Femur (Fig. 4C; Appendix 3, Table 9). A distinct ridge formed by the impressiones obturatoriae is characteristic of *P. echo*, *P. exsul*, *P. krameri* and *P. eupatria*. Larger and more robust than *P. krameri*, sulcus proximal to condyles more excavated, but smaller and less robust than *P. exsul* and *P. eupatria*; shaft of *P. eupatria* straighter.

Tarsometatarsus (Fig. 21C; Appendix 3, Table 11). Compared to *P. krameri*, comparatively robust, with stout shaft and robust distal end. In size, approximately 16% smaller than *P. bensoni* (see measurements) with a less defined but still distinct grooved impressiones retinaculi extensorii distal to cotyla medialis, which extends to midway point of shaft. In plantar aspect, one foramina vascularia proximalia present, indistinct in *P. krameri*. Apart from size, *P. echo* is morphologically more similar to *P. eupatria* than *P. krameri*, the species from which it is supposedly derived (e.g., Groombridge *et al.* 2004).

2d. *Psittacula exsul*

Mandible (Fig.30B; Appendix 3, Table 3). Posterior end missing with only the posterior part of one crista intercotylaris preserved. In lateral view, a single small fenestra mandibulae appears to be present, but has eroded into a larger opening. Larger and more robust than *Psittacula krameri*, posterior margin of symphysis laterally sharper angled and similar to a small *Psittacula eupatria*. In lateral aspect, angulus mandibulae more pronounced and triangular-shaped compared to *P. eupatria* and *P. krameri*.

Palatine (Appendix 3, Table 2). Palatine missing anterior end and ventral edge. Much more robust than *P.krameri borealis*, especially at the posterior end and intermediate in size between this species and *P. eupatria*.

Sternum (Fig.29B; Appendix 3, Table 4). In lateral aspect, the spina externa comparatively broad and similar in morphology to *P. eupatria*. Similarly to *P. echo,* sternum total length and carina sterni proportionally reduced, pila carinae directed ventro-anteriorly, not posteriorly. Spina externa more robust than *P. echo* but directed in the same plane. In ventral aspect, width greater than *P. echo* and *P. krameri* and the anterior end more expanded. Fenestra medialis equal in size to *P. krameri*.

Coracoid (Fig. 27B; Appendix 3, Table 5). Differs from *Psittacula eupatria* in its much smaller size, otherwise similar in size to *Psittacula echo* and *P. krameri* but processus procoracoideus shorter; scapula end mediolaterally reduced and sternal end proximodistally more expanded.

Humerus and Ulna (Fig. 23E and Fig. 22B; Appendix 3, Tables 6 and 7). Humerus Intermediate in size between *Psittacula eupatria* and *P. krameri*. When compared to *P. krameri*, proximal end less expanded and proportionally reduced, otherwise more robust. Compared to *P. eupatria*, tuberculum ventrale more prominent; shaft more curved; and fossa m. brachialis more excavated. Size variation in the specimens probably due to sexual dimorphism. Ulna Smaller than *Necropsittacus*, and intermediate in size between *Psittacula eupatria* and *P. krameri*, but comparatively much less robust. Tuberculum ligamentis collateralis ventralis laterally extended forming a ridge, which terminates further distally and shaft comparatively gracile compared with *P. krameri* and *P. eupatria*; more curved than the latter.

Femur (Fig. 22B; Appendix 3, Table 9). A ridge formed by impressiones obturatoriae particularly distinct in *P. exsul* and deeply excavated distal to trochanter. Equivalent in length to *P. eupatria*, but much less robust, shaft more curved, proximal neck of shaft narrower and proximal end medially deflected. Much larger and robust than *P. krameri*; shaft straighter in *P. krameri*.

Tibiotarsus (Fig. 22B; Appendix 3, Table 10) Most similar to *Psittacula eupatria*, but overall dimensions generally more gracile. Differs from *P. eupatria* in having a ridge lining sulcus extensorius less well defined distal from the condylus lateralis and extending further distally from the condylus medialis; crista cnemialis lateralis less hooked; and proximal/ distal ends less expanded.

2e. *Necropsittacus rodericanus*

Cranium (Fig. 2C; Appendix 3, Table 1) Cranium wide and dorso-ventrally flattened. Right lateral side is damaged, but complete on left with an extremely robust processus postorbitalis. In dorsal aspect, posterior margin of craniofrontal hinge slightly concave, and rounded/right-angled at extremities. Processus postorbitalis short in *Necropsittacus*, *Psittrichas, Pezoporus, Cyanoramphus, Psittacus,* long in *Nestor, Anodorhynchus, Eclectus, Coracopsis, Tanygnathus, Psittacula* but not fused to the lacrimal forming an open orbit. Fused enclosing the orbit in *Strigops*, *Calyptorhynchus*, and *Probosciger.* Differs from *Lophopsittacus* in smaller size, ventral surface less distinct, fossa temporalis more excavated, in dorsal aspect, lateral extremities of nasofrontal hinge more rounded, less sharp and proportionately more dorso-ventrally flattened with a less distinctive condylus occipitalis; absence of characteristic grooves on the frontal region. Similar in size to *Tanygnathus* and morphologically similar to this species and *Psittacula eupatria* except processus postorbitalis more robust, and cranium more dorso-ventrally flattened. In *Necropsittacus,* crista nuchalis transversus forms a prominent ridged semi-circle divided by two deep indentations, in *Tanygnathus* semi-circle entire without indentations, or semi-circle with two shallow excavations in *P. eupatria*.

Rostrum (Fig. 31A; Appendix 3, Table 2). Internarial septum medium-sized in width, and diameter of nares greater than width of the septum. In lateral aspect and similarly to *Psittacula*, the tomium is distinctly notched, with a concavity that abruptly indents cranial border, creating a single tooth. For the size of element, *Necropsittacus* has proportionally larger nares than species of equivalent size, e.g., *Tanygnathus*, and orientated in a different plane. In *Necropsittacus* and *P. eupatria*, outline of nasofrontal hinge slightly convex over entire length with no indentation at midpoint. Unlike *Psittacula*, notch on the proximoventral surface indistinct.

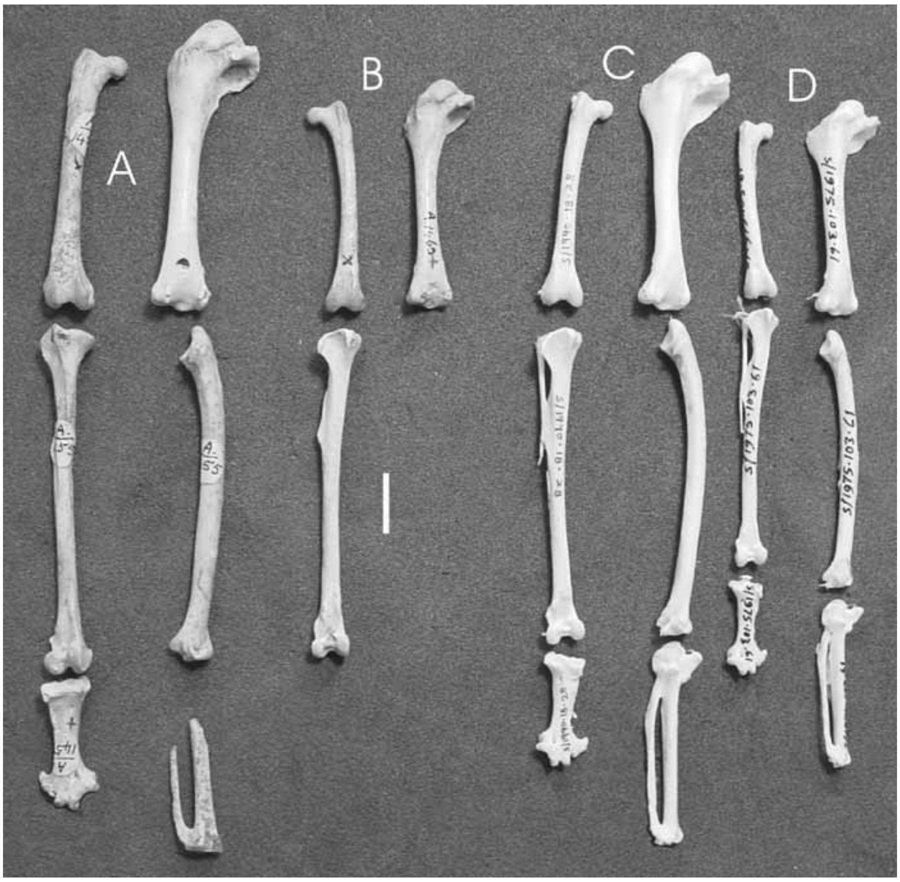

FIGURE 22. Comparison of wing and leg elements of Rodrigues parrots with species of *Psittacula*. **A,** *Necropsittacus rodericanus* UMZCA1455 right femur, right tibiotarsus, left tarsometatarsus, left humerus, left ulna, partial left carpometacarpus; **B,** *Psittacula exsul* UMZCA1463 left femur, right tibiotarsus, left humerus; **C,** *Psittacula eupatria* BMNHS/1990.18.28 ♂, right femur, right tibiotarsus, right tarsometatarsus, left humerus, left ulna, left carpometacarpus; **D,** *Psittacula krameri borealis* BMNHS/1975.103.62 ♂ right femur, right tibiotarsus, right tarsometatarsus, left humerus, left ulna, left carpometacarpus. Scale bar = 10mm.

Mandible (Fig. 30E; Appendix 3, Table 3). In dorsal view, attachment area for rhamphotheca obsolete, no pneumatic fossa present and *crista transversa fossae* deeply pneumatised. In medial aspect, indistinct incisions occur on internal lateral surface. Mandible of *Necropsittacus* most similar to *Tanygnathus* and *P. eupatria*, having similar morphological characteristics, but overall broader and heavier.

Coracoid (Fig. 27D; Appendix 3, Table 5). Differs from *Lophopsittacus* and *P. bensoni* by lack of a depression distal to processus procoracoideus, scapula end more mediolaterally reduced and in medial aspect, processus procoracoideus smaller. Similar in size to *P. eupatria* but shaft more robust, scapula end more mediolaterally compressed and foramen pneumaticum proximal to processus acrocoracoideus more pronounced.

Humerus and Ulna (Fig. 23D and Fig. 24B; Appendix 3, Tables 6 and 7). Humerus similar to *Psittacula eupatria* except that in *Necropsittacus*, size overall larger, tuberculum ventrale deflected medially, fossa olecrani more expanded, shaft straighter and processus flexorius more pronounced. Ulna slightly longer than *Psittacula eupatria* but more robust. On the proximal end, olecranon prominent and comparatively sharp. Tuberculum ligamentis collateralis ventralis lateral extended forming a ridge but less triangular in shape and impressio brachialis deeply excavated compared to *P. eupatria*. The two available ulnae appear to be associated.

Carpometacarpus (Fig. 22A; Appendix 3, Table 8). In dorsal aspect, sulcus interossi closed and sulcus tendineus forms a deep furrow; os metacarpale minus bow-shaped. In size, larger than *P. eupatria* and equivalent to *Tanygnathus*, but morphologically very similar to these species.

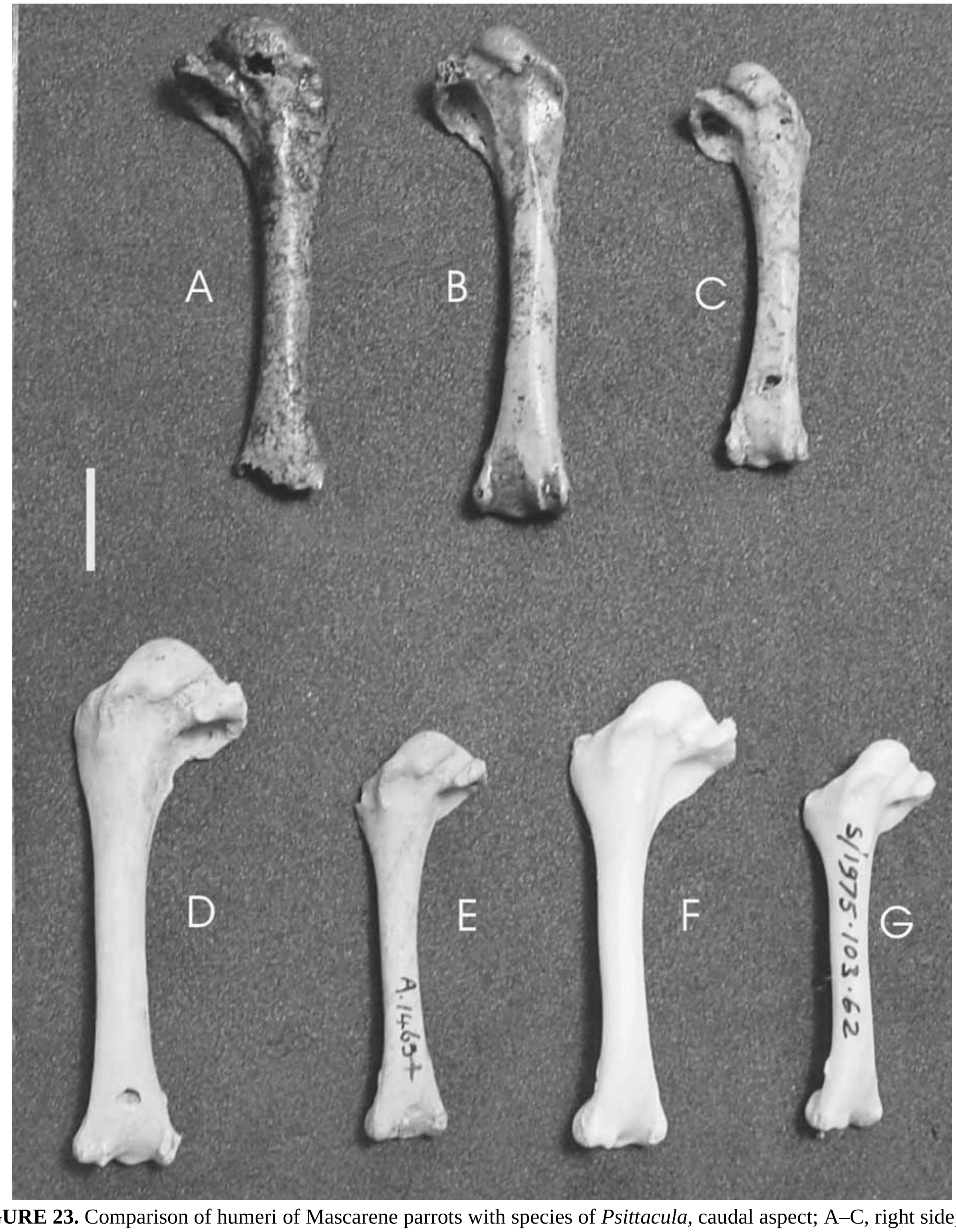

FIGURE 23. Comparison of humeri of Mascarene parrots with species of *Psittacula*, caudal aspect; A–C, right side, D–G, left side. **A,** UMZC596 *Lophopsittacus mauritianus*; **B,** UMZC596 *Psittacula bensoni*, new comb.; **C,** UMZC600 *Psittacula echo*; **D,** UMZCA1455 *Necropsittacus rodericanus*; **E,** UMZCA1463 *Psittacula exsul*; **F,** BMNHS/1999.11.5 *Psittacula eupatria* ♂; **G,** BMNHS/1975.103.62 *Psittacula krameri borealis* ♂. Scale bar = 10mm.

FIGURE 24. Comparison of left ulnae of Mascarene parrots with *Psittacula eupatria*, dorsal aspect. **A,** UMZC600 *Lophopsittacus mauritianus*; **B,** UMZC1455 *Necropsittacus rodericanus*; **C,** BMNHS/1999.11.5 *Psittacula eupatria* ♂. Scale bar = 10mm.

FIGURE 25. X-radiograph of the Vienna specimen of *M. mascarinus*. Unlike the Paris specimen, the skull has not been removed. Courtesy of Cécile Mourer-Chauviré.

Femur (Fig. 22A; Appendix 3, Table 9) In *Necropsittacus* and *Psittacula eupatria*, impressiones obturator forms a ridge, with a shallow medial excavation distal to trochanter, which is deeply excavated in *P. exsul*, *P. echo* and *P. krameri*. Shaft straighter in *Necropsittacus* and *P. eupatria* compared to other *Psittacula*. In cranial aspect, sulcus patellaris narrow in *Necropsittacus*, and *Psittacula*.

Tibiotarsus (Fig. 22A; Appendix 3, Table 10) Larger and more robust than *Psittacula eupatria* and *P. exsul*, sulcus extensorius wider and less clearly defined. Pons supratendineus reduced compared to *Psittacula,* with no partial enclosing of the canalis extensorius.

Tarsometatarsus (Fig. 22A; Appendix 3, Table 11) Compared to other parrot genera, in dorsal aspect, impressiones Retinaculi extensorii distal to cotyla medialis indistinct in *Necropsittacus*. In plantar aspect, one foramina vascularia proximalia present, and fossa metatarsi I reduced in *Necropsittacus* compared to all other genera studied. As exhibited in *Lophopsittacus* and *Psittacula*, trochlea. metatarsi IV less hooked and medially projected. Proximal to foramen vasculare distale, plantar extension of trochlea. metatarsi III is not separated from Trochlea. metatarsi IV by a deep furrow as seen in *Coracopsis* and *Eclectus*.

2f. *Mascarinus mascarinus*

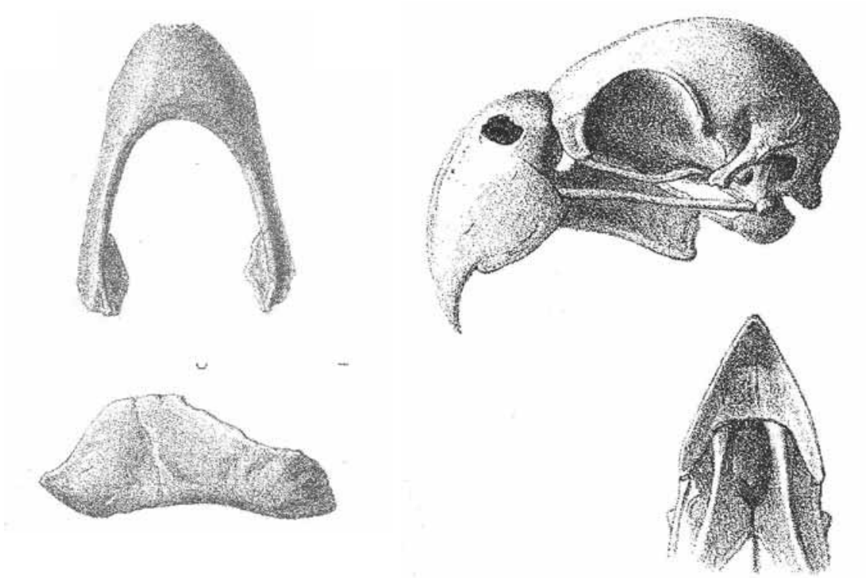

FIGURE 26. *Mascarinus mascarinus*. (right)Skull and rostrum in lateral aspect and rostrum in ventral aspect removed from the skin and illustrated in Milne-Edwards (1866); (left) Mandible in lateral and dorsal aspect taken from Milne-Edwards (1867).

The post-cranial elements are discussed by Mourer-Chauviré *et al* (1999). Cranium (Fig. 26). Milne-Edwards (1866, 1867) removed and illustrated the cranial elements from the Paris specimen of *Mascarinus* and this is confirmed by x-radiographs of the specimen (Mourer-Chauviré pers.comm), but unfortunately their present whereabouts is unknown. X-radiographs of the Vienna specimen (Fig. 25) indicate that the cranium is unlike the other endemic Mascarene genera, *Lophopsittacus* and *Necropsittacus*, or the Madagascan *Coracopsis*, and is most similar to *Psittacula*. In lateral aspect, moderately dorso-ventrally flattened, parietals rounded and gently slope towards a sharply angled occipital region. Fossa temporalis shallow. Similarly to *Eclectus*, *Tanygnathus*, and *Psittacula*, processus postorbitalis long but not fused to lacrimal and forms an open orbit. Cranialfrontal hinge appears medially concave. In rostrum, and similarly to *Psittacula*, tomium distinctly notched in lateral aspect, with a concavity that abruptly indents the cranial border, creating a single tooth. Distocranial curvature rounded to anterior tip of tomium; diameter of the nares greater than width and orientates in the same plane as *Psittacula*, i.e. forward (see Boles, 1993). In ventral view, notch on proximoventral surface indistinct. In mandible, posterior margin of symphysis broadly oval and comparable to *Psittacula exsul*, and width of proximal margin of symphysis is just over half the total width taken between the angulus mandibulae inferring that *Mascarinus* had proportionally broad jaws.

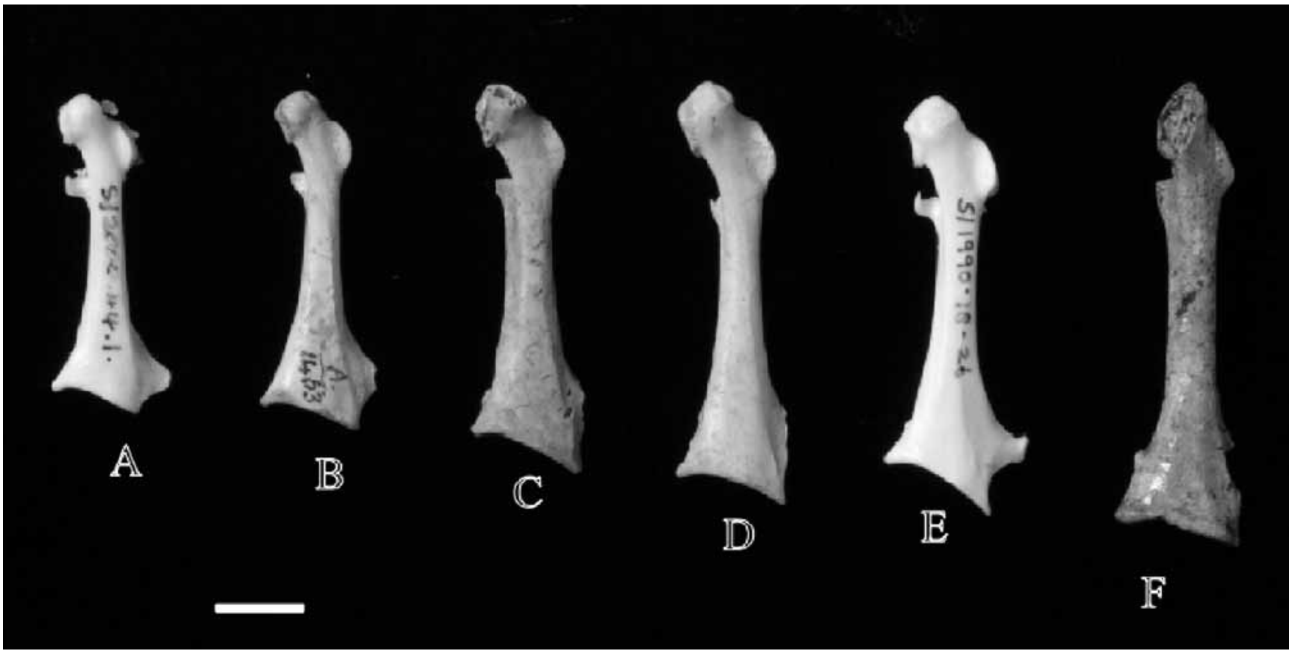

FIGURE 27. Left coracoids of Mascarene parrots, ventral aspect, compared with *Psittacula eupatria*. **A,** BMNHS/2000.44.1 *Psittacula echo* ♀; **B,** UMZCA1463 *Psittacula exsul*; **C,** UMZC596 *Psittacula bensoni,* new comb.; **D,** UMZC1455 *Necropsittacus rodericanus*; **E,** BMNHS/1990.18.26 *Psittacula eupatria* ♂; **F,** UMZC599 *Lophopsittacus mauritianus*. Scale bar = 10mm.

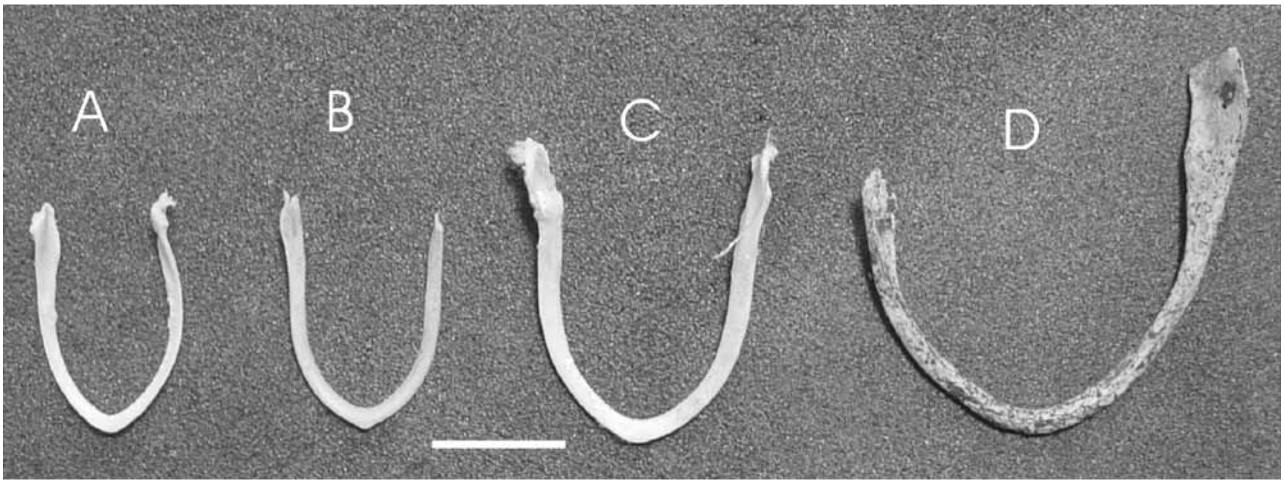

FIGURE 28. Comparison of furculae of Mascarene parrots with species of *Psittacula*. **A,** BMNHS/1975.103.62 *Psittacula krameri borealis* ♂; **B,** UMZC997 *Psittacula exsul*; **C,** BMNHS/1999.11.5 *Psittacula eupatria* ♂; **D,** UMZC599 *Lophopsittacus mauritianus* u/s. Scale bar = 10mm.

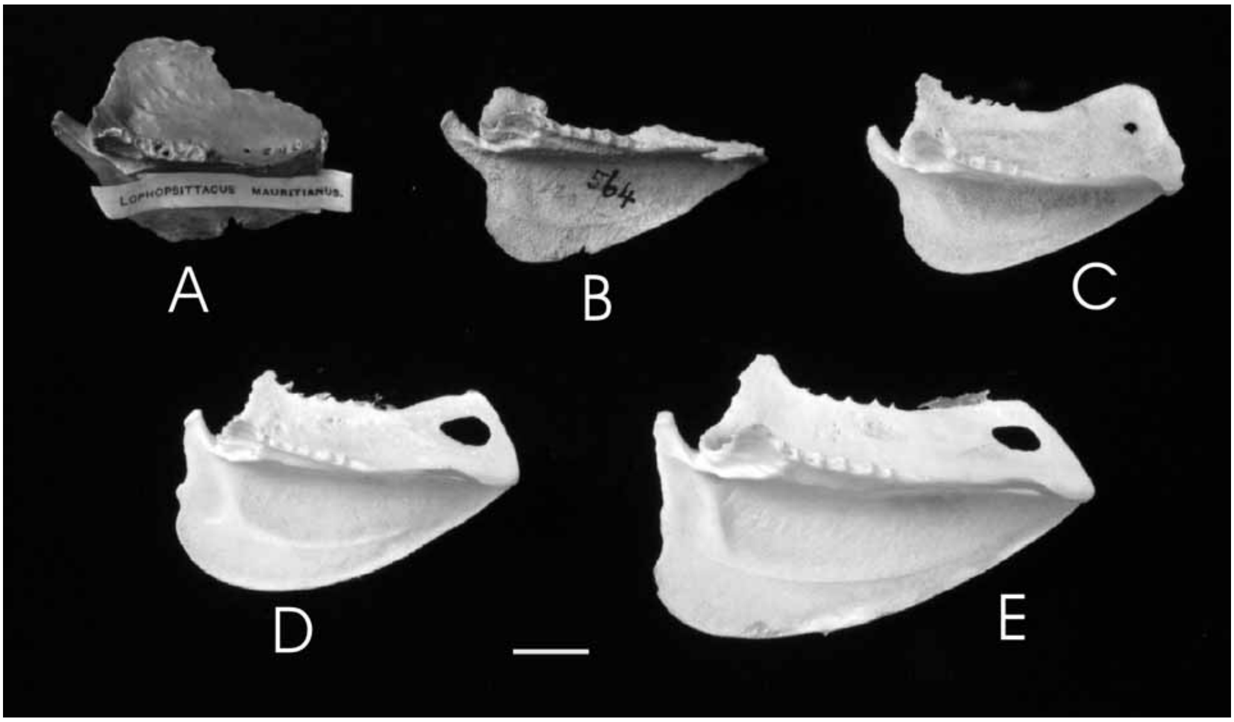

FIGURE 29. Lateral view of sterna of Mascarene parrots compared with species of *Psittacula*. **A,** UMZC424.AA *Lophopsittacus mauritianus*; **B,** UMZC564 *Psittacula exsul*; **C,** BMNHS/2000.44.1 *Psittacula echo*; **D,** BMNHS/1975.103.62 *Psittacula krameri borealis* ♂; **E,** BMNHS1999.11.5 *Psittacula eupatria* ♂. Scale bar = 10mm.

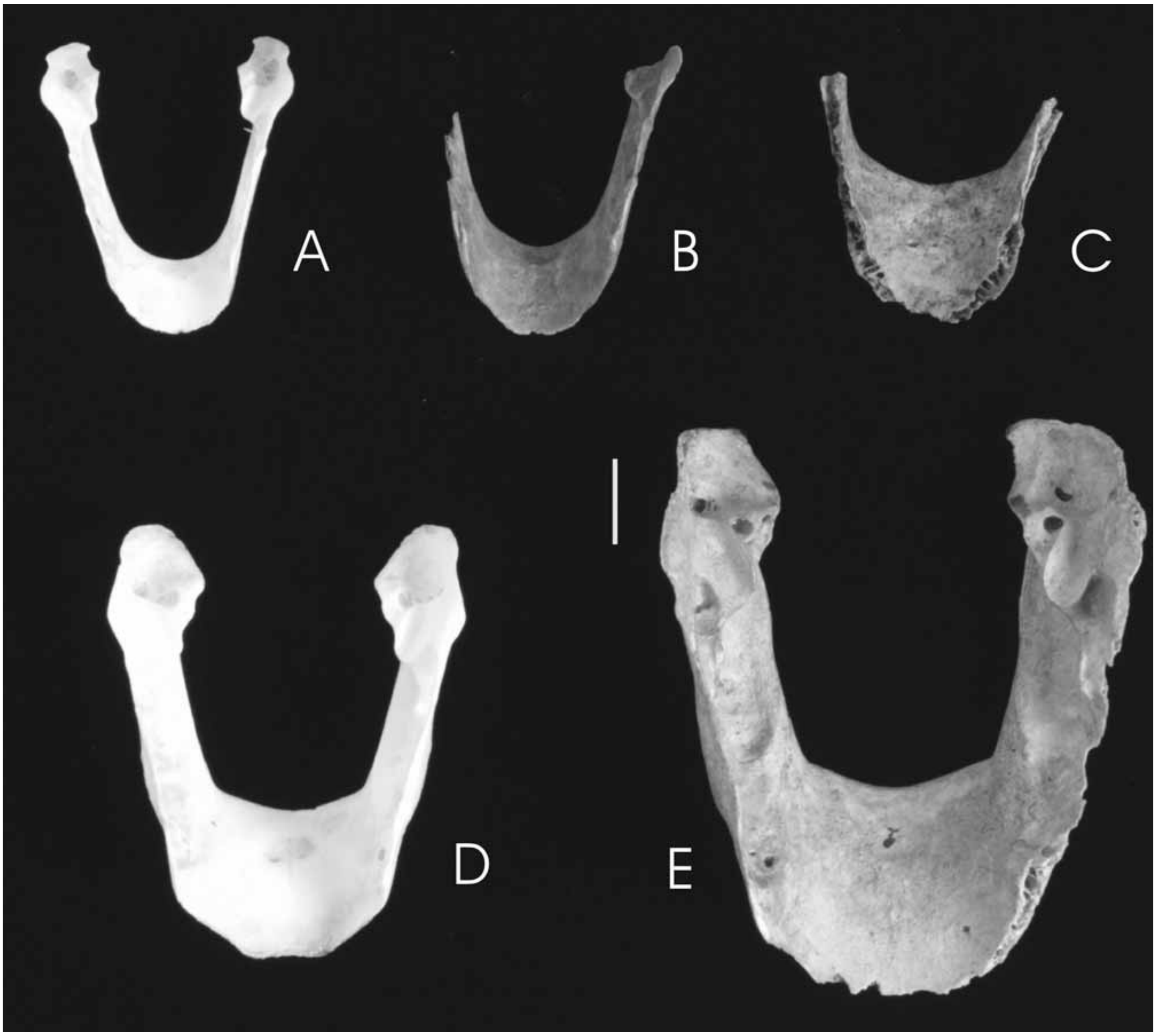

FIGURE 30. Mandibles of Mascarene parrots, dorsal view, compared with species of *Psittacula*. **A,** BMNHS/ 1975.103.62 *Psittacula krameri borealis* ♂; **B,** UMZC564 *Psittacula exsul*; **C,** UMZC577 (type) *Psittacula bensoni*, new comb.; **D,** BMNHS/1990. 18.26 *Psittacula eupatria* ♂; **E,** UMZC562 *Necropsittacus rodericanus*. Scale bar = 10mm.

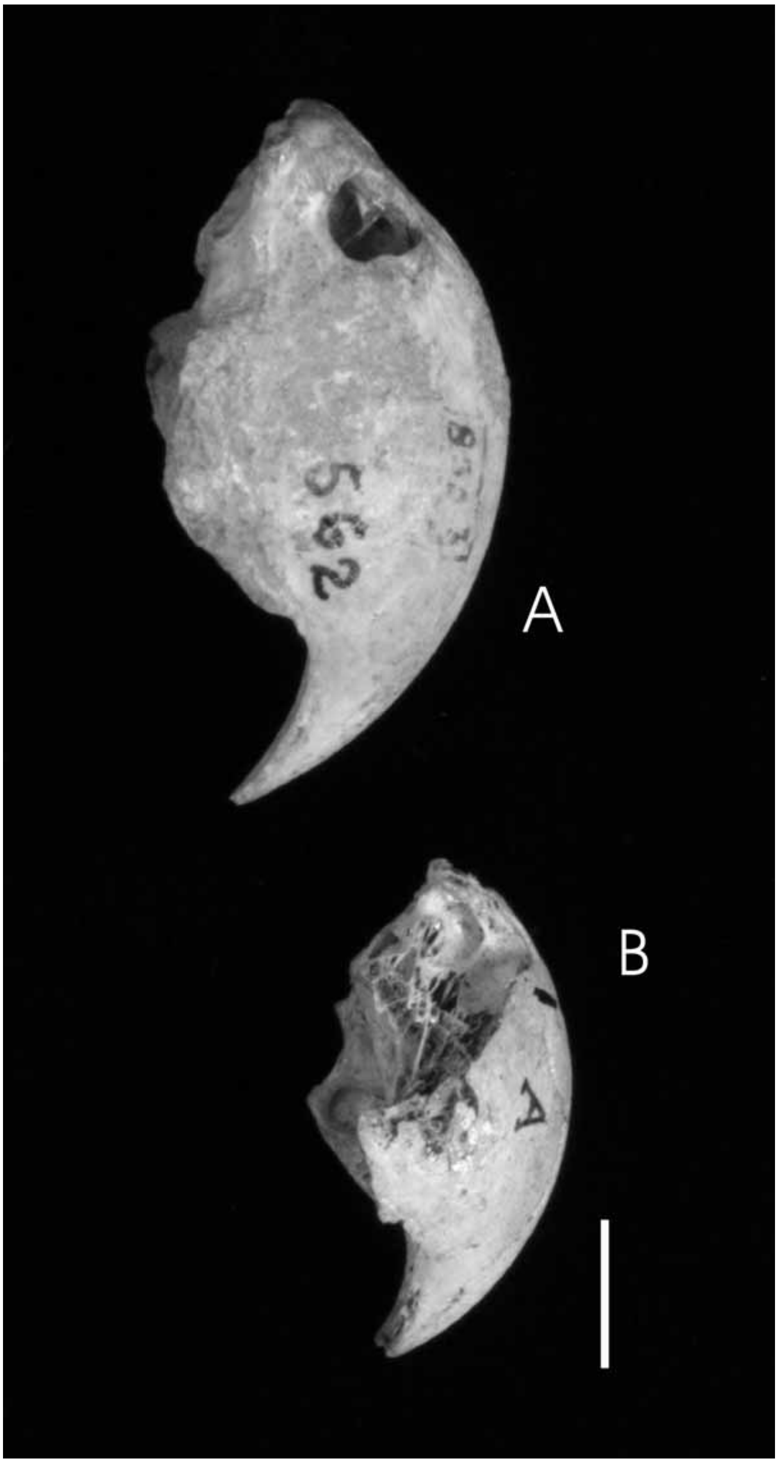

FIGURE 31. Rostra of Mascarene parrots, lateral view. **A,** UMZC562 *Necropsittacus rodericanus*; **B,** UMZC577 *Psittacula bensoni*, new comb. Scale bar = 10mm.

Appendix 3. Measurements

TABLE 1. Measurements (mm) of Mascarene parrots compared with other parrots: cranium. For abbreviations see methods

Species	LP Mean (n)	LP Range	GB Mean (n)	GB Range	DW Mean (n)	DW Range	GH Mean (n)	GH Range
Lophopsittacus mauritianus (m)	68.5 (1)	68.5	~45.9 (1)	~45.9	31.7	31.7	32.9	32.9
Necropsittacus rodericanus	52.8 (1)	52.8	37.7 (1)	37.7	~26.0 (1)	~26.0	24.2 (1)	24.2
Psittacula echo	28.4 (1)	28.4	23.1 (1)	23.1	13.0 (1)	13.0	21.1 (1)	21.1
Psittacula wardi	39.4 (1)	39.4	–	–	–	–	–	–
Psittacula krameri krameri (m)	29.0 (4)	28.2–30.5	25.0 (4)	24.5–25.5	15.3 (4)	14.8–16.3	20.55 (4)	20.3–21.0
Psittacula krameri krameri (f)	29.1 (2)	28.5–29.8	24.5 (2)	24.0–25.0	14.5 (2)	13.9–15.1	20.1 (2)	19.6–20.6
Psittacula krameri krameri (u/s)	30.4 (1)	30.4	24.7 (1)	24.7	14.8 (1)	14.8	20.7 (1)	20.7
Psittacula krameri borealis (m)	30.3 (2)	30.0–30.6	24.7 (2)	24.6–24.9	14.7 (2)	14.7–14.8	20.95 (2)	20.8–21.1
Psittacula krameri borealis (f)	27.6 (1)	27.6	25.1 (1)	25.1	14.0 (1)	14.0	20.6 (1)	20.6
Psittacula krameri manillensis (f)	30.4 (1)	30.4	24.6 (1)	24.6	15.6 (1)	15.6	22.0 (1)	22.0
Psittacula krameri manillensis (u/s)	29.6 (2)	29.4–29.9	25.1 (2)	25.0–25.2	14.9 (2)	14.8–15.1	19.6 (2)	19.3–19.9
Psittacula eupatria eupatria (m)	41.1 (5)	39.9–42.3	31.5 (5)	31.0–32.5	20.4 (5)	20.1–21.4	22.7 (5)	21.8–23.8
Psittacula eupatria eupatria (f)	38.2 (5)	37.1–39.7	30.4 (5)	29.5–31.9	19.0 (5)	18.3–20.1	22.6 (5)	22.1–23.1
Psittacula eupatria eupatria (u/s)	38.9 (3)	38.5–39.6	30.1 (3)	30.0–30.3	19.5 (3)	18.9–20.7	21.9 (3)	21.7–22.0
Coracopsis nigra	36.2 (2)	36.0–36.4	27.0 (2)	26.9–27.2	14.3 (2)	14.3–14.4	24.3 (2)	22.7–25.9
Coracopsis vasa	47.7 (2)	44.1–51.3	37.6 (2)	36.2–39.0	21.2 (2)	21.2–22.6	27.6 (2)	27.4–27.8
Psittacus erithacus	44.8 (2)	43.5–46.1	35.6 (2)	35.5–35.8	20.6 (2)	19.4–21.8	28.5 (2)	28.0–29.1
Tanygnathus megalorhynchus	46.7 (2)	43.0–50.5	37.3 (2)	36.0–38.7	24.7 (2)	22.8–26.7	26.1 (2)	24.8–27.5
Eclectus roratus	38.1 (2)	37.9–38.3	35.1 (2)	34.8–35.5	20.8 (2)	19.8–21.9	26.4 (2)	25.5–27.4
Strigops habroptilus	50.6 (4)	49.0–52.2	38.1 (4)	35.4–39.9	22.3 (4)	20.7–23.7	33.6 (4)	32.6–34.9
Nestor meridionalis	48.5 (2)	47.0–50.1	33.9 (2)	32.2–35.7	19.2 (2)	18.6–19.8	29.1 (2)	28.3–29.9
Nestor notabilis	51.8 (2)	48.3–55.3	36.2 (2)	34.8–37.7	21.3 (2)	20.5–22.1	32.9 (2)	32.3–33.5
Cyanoramphus novaezelandiae	24.2 (2)	23.7–24.8	17.9 (2)	17.5–18.4	8.7 (2)	8.5–8.9	16.1 (2)	15.5–16.7
Cyanoramphus unicolor	27.5 (1)	27.5	25.0 (1)	25.0	12.7 (1)	12.7	19.1 (1)	19.1
Calyptorhynchus magnificus magnificus	57.8 (2)	51.1–64.6	45.0 (2)	42.7–47.4	32.3 (2)	30.1–34.5	32.0 (2)	31.7–32.3
Probosciger aterrimus	71.3 (2)	67.4–75.2	51.8 (2)	51.6–52.1	30.0 (2)	27.5–32.6	35.8(2)	34.7–37.0
Psittrichas fulgidus	45.4 (2)	42.0–48.9	31.0 (2)	27.7–34.4	19.6 (2)	17.7–21.6	27.0 (2)	25.8–28.2
Anodorhynchus hyacinthinus (m)	80.3 (1)	80.3	55.4 (1)	55.4	33.0 (1)	33.0	38.8 (1)	38.8

TABLE 2. Measurements (mm) of Mascarene parrots compared with other parrots: rostrum and palatine For abbreviations see methods

Species	Ros TL Mean (n)	Ros TL Range	Ros NFW Mean (n)	Ros NFW Range	Ros SW Mean (n)	Ros SW Range	Pal PL Mean (n)	Pal PL Range	Pal PD Mean (n)	Pal PD Range
Lophopsittacus mauritianus (m)	–	–	–	–	–	–	44.3 (12)	40.9–49.6	18.5 (20)	17.0–20.7
Lophopsittacus mauritianus (f)	–	–	–	–	–	–	35.5 (4)	35.3–36.0	15.5 (4)	15.2–15.9
Necropsittacus rodericanus	44.8 (1)	44.8	24.3 (1)	24.3	6.0 (1)	6.0	–	–	–	–
Psittacula bensoni new comb.	32.5 (1)	32.5	14.9 (1)	14.9	4.7 (1)	4.7	21.3 (1)	21.3	11.6 (1)	11.6
Psittacula echo	22.9 (1)	22.9	13.1 (1)	13.1	2.0 (1)	2.0	–	–	–	–
Psittacula exsul	–	–	–	–	–	–	~23.0(1)	~23.0	–	–
Psittacula wardi	34.4 (1)	34.4	–	–	–	–	22.8 (1)	22.8	–	–
Psittacula krameri krameri (m)	24.7 (4)	23.8–25.7	14.9 (4)	13.9–15.8	3.0 (4)	2.9–3.4	14.5 (4)	13.9–15.4	7.5 (4)	7.2–8.1
Psittacula krameri krameri (f)	23.4 (2)	23.4–23.5	14.5 (2)	14.0–15.0	3.0 (2)	2.9–3.1	13.4 (2)	13.2–13.7	7.9 (2)	7.9–8.0
Psittacula krameri krameri (u/s)	23.2 (1)	23.2	15.0 (1)	15.0	2.9 (1)	2.9	14.7 (1)	14.7	7.5 (1)	7.5
Psittacula krameri borealis (m)	23.5 (2)	22.4–24.6	14.7 (2)	14.7–14.8	3.1 (2)	2.7–3.5	14.5 (2)	14.3–14.8	6.6 (2)	6.0–7.2
Psittacula krameri borealis (f)	23.7 (1)	23.7	14.2 (1)	14.2	2.5 (1)	2.5	13.6 (1)	13.6	6.4 (1)	6.4
Psittacula krameri manillensis (f)	23.5 (1)	23.5	14.4 (1)	14.4	2.9 (1)	2.9	13.4 (1)	13.4	7.1 (1)	7.1
Psittacula krameri manillensis (u/s)	22.0 (2)	22.4–23.7	14.3 (2)	14.3	2.8 (2)	2.8	13.4 (2)	13.3–13.6	6.5 (2)	6.3–6.7
Psittacula eupatria eupatria (m)	37.2 (5)	36.8–37.7	20.4 (5)	20.0–21.5	5.8 (5)	5.4–6.4	25.6 (5)	23.8–27.2	11.0 (5)	10.0–11.7
Psittacula eupatria eupatria (f)	33.7 (5)	31.6–36.6	18.9 (5)	18.3–19.7	4.9 (5)	4.4–6.0	23.0 (5)	22.5–23.5	9.9 (5)	9.9–10.8
Psittacula eupatria eupatria (u/s)	33.9 (3)	33.8–34.2	19.3 (3)	18.8–19.7	4.9 (3)	4.0–5.4	22.7 (3)	22.2–23.0	9.9 (3)	9.9–10.0
Coracopsis nigra	25.6 (2)	25.1–26.1	12.7 (2)	12.4–13.1	2.2 (2)	1.9–2.6	13.8 (2)	13.6–14.0	9.6 (2)	9.0–10.3
Coracopsis vasa	39.3 (2)	36.7–41.9	18.8 (2)	17.2–20.5	3.7 (2)	3.5–4.0	23.3 (2)	22.6–24.0	13.8 (2)	12.7–15.0
Psittacus erithacus	37.0 (2)	37.0	20.1 (2)	19.1–21.1	5.1 (2)	4.9–5.4	22.5 (2)	22.5–22.6	11.2 (2)	11.0–11.4
Tanygnathus megalorhynchus	45.6 (2)	42.0–49.3	24.4 (2)	22.0–26.9	8.3 (2)	7.4–9.3	28.6 (2)	25.0–32.2	13.4 (2)	12.2–14.7
Eclectus roratus	38.7 (2)	36.6–40.8	19.5 (2)	17.9–21.2	6.8 (2)	6.7–7.0	22.9 (2)	22.6–23.2	11.6 (2)	11.0–11.4
Strigops habroptilus	44.6 (4)	40.0–48.6	22.1 (4)	20.9–23.7	3.4 (2)	3.2–3.6	23.4 (4)	22.5–23.9	14.3 (4)	12.7–15.5
Nestor meridionalis	51.3 (1)	51.3	21.8 (1)	21.8	4.4 (2)	3.8–4.1	27.1 (2)	23.7–30.6	12.4 (2)	12.0–12.8
Nestor notabilis	47.8 (2)	44.2–51.5	29.2 (2)	26.8–31.7	3.7 (2)	3.4–4.0	24.4 (2)	22.9–25.9	11.6 (2)	10.6–12.7
Cyanoramphus novaezelandiae	14.8 (2)	14.0–15.6	8.6 (2)	8.5–8.8	1.0 (2)	1.0–1.1	10.5 (2)	10.3–10.7	4.7 (2)	4.6–4.9
Cyanoramphus unicolor	21.5 (1)	21.5	12.8 (1)	12.8	1.9 (1)	1.9	14.5 (1)	14.5	6.8 (1)	6.8
Calyptorhynchus magnificus magnificus	38.9 (2)	38.7–39.2	32.0 (2)	30.5–32.8	20.4 (2)	18.4–22.4	35.1 (2)	34.0–36.2	14.5 (2)	14.0–15.0
Probosciger aterrimus	80.0 (2)	76.2–83.9	31.1 (2)	30.5–32.8	15.7 (2)	15.3–16.2	50.5 (2)	46.7–54.3	21.5 (2)	19.5–23.6
Psittrichas fulgidus	39.3 (2)	33.6–45.0	19.6 (2)	17.7–21.5	3.8 (2)	2.6–~5.0	16.3 (1)	16.3	7.5 (1)	7.5
Anodorhynchus hyacinthinus	83.5 (1)	83.5	35.8 (1)	35.8	11.6 (1)	11.6	55.7 (1)	55.7	19.6 (1)	19.6

TABLE 3. Measurements (mm) of Mascarene parrots compared with other parrots: mandible. For abbreviations see methods

Species	GL Mean (n)	GL Range	LS Mean (n)	LS Range	WS Mean (n)	WS Range	GW Mean (n)	GW Range	GD Mean (n)	GD Range
Lophopsittacus mauritianus (m)	74.4 (4)	70.0–78.4	28.5 (8)	25.9–30.8	27.5 (5)	24.9–30.5	60.35 (2)	55.3–65.4	34.2 (4)	31.8–35.8
Lophopsittacus mauritianus (f)	58.6 (2)	57.5–59.7	22.3 (3)	22.2–22.5	19.5 (4)	18.8–21.3	45.7 (1)	45.7	25.1 (2)	24.5–25.7
Necropsittacus rodericanus	58.1 (1)	58.1	22.7 (1)	22.7	18.5 (1)	18.5	46.7 (1)	46.7	22.0 (1)	22.0
Psittacula bensoni new comb.	–	–	14.2 (2)	14.2	14.9 (1)	14.9	–	–	–	–
Psittacula echo	30 (1)	30	–	–	–	–	–	–	–	–
Psittacula wardi	40.3 (1)	40.3	–	–	–	–	30.2 (1)	30.2	15.6 (1)	15.6
Psittacula exsul	35.0 (1)	35.0 (1)	9.0 (1)	9.0	11.7 (1)	11.7	–	–	15.4 (1)	15.4
Psittacula krameri krameri (m)	29.0 (4)	26.7–30.0	7.4 (4)	6.8–8.7	8.6 (4)	8.2–9.4	24.3 (4)	23.7–24.7	10.8 (4)	10.7–11.1
Psittacula krameri krameri (f)	30.0 (2)	29.8–30.2	7.6 (2)	7.4–7.9	9.6 (2)	9.2–10.0	24.8 (2)	24.7–24.9	10.8 (2)	10.5–11.1
Psittacula krameri krameri (u/s)	30.4 (1)	30.4	7.0 (1)	7.0	9.2 (1)	9.2	23.6 (1)	23.6	11.3 (1)	11.3
Psittacula krameri borealis (m)	30.3 (2)	30.3	7.5 (2)	7.3–7.7	9.4 (2)	9.4–9.5	24.3 (2)	24.0–24.7	10.8 (2)	10.7–11.0
Psittacula krameri borealis (f)	29.1 (1)	29.1	6.9 (1)	6.9	8.6 (1)	8.6	24.8 (1)	24.8	11.4 (1)	11.4
Psittacula krameri manillensis (f)	31.2 (1)	31.2	7.0 (1)	7.0	8.4 (1)	8.4	24.5 (1)	24.5	11.3 (1)	11.3
Psittacula krameri manillensis (u/s)	28.6 (2)	28.2–29.1	7.2 (2)	6.8–7.6	9.6 (2)	9.6–9.7	24.2 (2)	23.8–24.6	10.4 (2)	10.2–10.7
Psittacula eupatria eupatria (m)	43.3 (5)	42.0–46.7	15.4 (5)	15.1–16.0	14.0 (5)	13.2–15.1	34.7 (5)	33.7–35.5	18.3 (5)	17.9–18.9
Psittacula eupatria eupatria (f)	39.2 (5)	38.1–41.0	13.8 (5)	13.0–14.8	13.6 (5)	12.8–14.7	32.3 (5)	31.3–33.6	17.4 (5)	16.6–17.8
Psittacula eupatria eupatria (u/s)	38.6 (3)	37.7–39.3	13.3 (3)	12.7–14.3	13.1 (3)	12.7–13.7	32.5 (3)	33.1–32.6	17.5 (3)	17.1–17.8
Coracopsis nigra	36.7 (2)	35.9–37.5	6.7 (2)	6.4–7.0	9.9 (2)	9.8–10.1	26.2 (2)	24.9–27.5	12.3 (2)	11.9–12.8
Coracopsis vasa	53.4 (2)	50.1–56.8	11.5 (2)	11.3–11.8	13.6 (2)	11.9–15.3	37.2 (2)	35.4–39.1	16.3 (2)	15.5–17.2
Psittacus erithacus	50.2 (2)	49.4–51.0	13.9 (2)	13.4–14.5	13.0 (2)	13.0	37.5 (2)	37.3–37.7	16.7 (2)	16.7–16.8
Tanygnathus megalorhynchus	51.7 (2)	47.5–56.0	18.2 (2)	15.5–20.9	15.7 (2)	14.5–17.0	40.4 (2)	37.6–43.3	23.9 (2)	21.6–26.2
Eclectus roratus	44.1 (2)	43.1–45.2	11.7 (2)	10.8–12.6	13.0 (2)	12.7–13.3	34.6 (2)	34.5–34.8	20.4 (2)	18.8–20.0
Strigops habroptilus	60.0 (4)	53.4–63.4	14.1 (4)	11.0–16.0	16.4 (4)	15.0–18.0	46.1 (4)	42.8–48.3	19.5 (4)	18.1–20.3
Nestor meridionalis	60.1 (2)	53.0–67.3	21.3 (2)	17.6–25.0	14.9 (2)	13.7–16.1	33.8 (2)	30.7–37.0	15.5 (2)	14.3–16.8
Nestor notabilis	64.9 (2)	61.3–68.6	17.6 (2)	16.2–19.1	14.3 (2)	14.3	35.8 (2)	33.5–38.2	16.3 (2)	14.4–18.2
Cyanoramphus novaezelandiae	22.3 (2)	22.3–22.4	5.0 (2)	4.8–5.3	6.7 (2)	6.6–6.9	16.8 (2)	15.8–17.8	7.4 (2)	7.4–7.5
Cyanoramphus unicolor	29.6 (1)	29.6	7.0 (1)	7.0	9.9 (1)	9.9	23.0 (1)	23.0	10.8 (1)	10.8
Calyptorhynchus magnificus magnificus	58.4 (2)	54.5–62.4	20.4 (2)	18.7–22.1	17.0 (2)	15.5–18.6	46.3 (2)	43.5–49.1	30.7 (2)	28.6–32.9
Probosciger aterrimus	67.3 (2)	66.9–67.8	30.6 (2)	30.2–31.1	22.9 (2)	22.5–23.4	56.8 (2)	55.6–58.0	37.2 (2)	34.6–39.8
Psittrichas fulgidus	57.5 (2)	53.4–61.6	9.2 (2)	9.2–9.3	7.0 (2)	6.0–8.1	30.5 (2)	29.0–32.1	18.7 (2)	15.9–21.5
Anodorhynchus hyacinthinus	81.0 (1)	81.0	34.5 (1)	34.5	23.9 (1)	23.9	67.0 (1)	67.0	41.5 (1)	41.5

TABLE 4. Measurements (mm) of Mascarene parrots compared with other parrots: sternum. For abbreviations see methods

Species	LM Mean (n)	LM Range	LC Mean (n)	LC Range	DL Mean (n)	DL Range	2nd IC Mean (n)	2nd IC Range	LK Mean (n)	LK Range
Lophopsittacus mauritianus (m)	~51.5 (1)	~51.5	-	-	-	-	~31.2 (1)	~31.2	~18.0 (1)	~18.0
Psittacula echo	42.0 (1)	42.0	37.6 (1)	37.6	37.3 (1)	37.3	19.1 (1)	19.1	19.1 (1)	19.1
Psittacula exsul	42.9 (2)	42.2–43.7	38.9 (2)	38.9	37.4 (2)	36.2–38.7	20.5 (2)	~20.2–20.9	18.2 (2)	18.2–18.3
Psittacula krameri krameri (m)	43.4 (4)	42.2–45.7	44.3 (4)	43.5–46.4	38.5 (4)	37.2–40.8	16.6 (4)	16.5–16.8	18.5 (4)	18.2–19.6
Psittacula krameri krameri (f)	42.9 (2)	41.5–44.4	44.0 (2)	42.4–44.4	39.4 (2)	37.3–41.5	17.1 (2)	16.3–17.9	18.4 (2)	17.5–19.4
Psittacula krameri krameri (u/s)	44.5 (1)	44.5	44.4 (1)	44.4	39.3 (1)	39.3	18.0 (1)	18.0	19.4 (1)	19.4
Psittacula krameri borealis (m)	44.9 (2)	43.0–46.9	46.7 (2)	45.7–47.8	40.7 (2)	39.4–42.1	17.2 (2)	16.9–17.6	19.7 (2)	19.0–20.4
Psittacula krameri borealis (f)	43.4 (1)	43.4	43.6 (1)	43.6	38.0 (1)	38.0	17.0 (1)	17.0	16.6 (1)	16.6
Psittacula krameri manillensis (f)	45.4 (1)	45.4	46.0 (1)	46.0	40.7 (1)	40.7	17.8 (1)	17.8	19.4 (1)	19.4
Psittacula krameri manillensis (u/s)	43.6 (2)	42.8–44.5	44.1 (2)	43.5–44.7	38.6 (2)	38.0–39.4	16.4 (2)	15.8–17.1	17.7 (2)	17.3–18.1
Psittacula eupatria eupatria (m)	53.7 (5)	52.3–54.8	54.4 (5)	53.4–56.9	47.5 (5)	46.2–48.5	21.0 (5)	20.0–22.2	21.6 (5)	20.7–22.9
Psittacula eupatria eupatria (f)	50.6 (5)	49.9–52.3	51.8 (5)	49.6–54.8	44.9 (5)	44.3–45.7	19.6 (5)	19.4–19.8	20.3 (5)	18.7–22.3
Psittacula eupatria eupatria (u/s)	51.0 (3)	50.7–51.3	52.1 (3)	51.7–52.9	45.7 (3)	45.4–46.1	20.7 (3)	20.4–21.2	20.6 (3)	20.1–21.4
Coracopsis nigra	54.9 (2)	54.3–55.5	54.9 (2)	54.7–55.1	47.5 (2)	47.4–47.7	21.4 (2)	20.9–21.9	21.9 (2)	20.6–23.3
Coracopsis vasa	72.1 (3)	65.9–77.3	73.8 (3)	67.0–81.9	63.1 (3)	57.0–67.6	28.4 (3)	26.7–29.5	29.9 (3)	26.7–33.6
Psittacus erithacus	69.2 (2)	68.7–69.8	69.4 (2)	68.7–70.1	61.6 (2)	60.7–62.5	28.3 (2)	26.9–29.8	26.0 (2)	24.2–27.8
Tanygnathus megalorhynchus	58.1 (2)	57.0–59.3	57.6 (2)	56.3–59.0	51.7 (2)	51.4–52.1	24.2 (2)	23.1–25.3	21.6 (2)	20.0–23.3
Eclectus roratus	59.6 (2)	57.7–61.5	58.1 (2)	56.5–59.7	52.4 (2)	50.8–54.0	26.3 (2)	25.6–27.1	20.8 (2)	20.5–21.2
Strigops habroptilus	71.5 (4)	62.2–76.6	n/a	n/a	64.0 (4)	55.2–68.9	38.6 (4)	33.6–41.5	5.4 (4)	4.4–5.9
Nestor meridionalis	62.5 (2)	58.8–66.2	58.2 (2)	54.8–61.7	54.1 (2)	51.9–56.4	24.8 (2)	23.2–26.5	24.3 (2)	22.6–26.1
Nestor notabilis	75.6 (2)	71.7–79.5	69.9 (2)	67.4–72.5	65.2 (2)	62.8–67.7	31.5 (2)	30.6–32.5	28.0 (2)	26.8–29.2
Cyanoramphus novaezelandiae	31.5 (2)	31.0–32.0	25.7 (2)	24.6–26.9	27.5 (2)	27.2–27.8	12.9 (2)	12.6–13.2	12.1 (2)	11.8–12.5
Cyanoramphus unicolor	39.3 (1)	39.3	31.0 (1)	31.0	33.9 (1)	33.9	17.2 (1)	17.2	13.7 (1)	13.7
Geopsittacus occidentalis	44.6 (1)	44.6	44.4 (1)	44.4	39.5 (1)	39.5	14.3 (1)	14.3	18.4 (1)	18.4
Calyptorhynchus magnificus magnificus	71.0 (2)	68.7–73.4	71.0 (2)	68.3–73.7	63.4 (2)	61.1–65.7	30.9 (2)	30.1–31.8	32.1 (2)	30.7–33.6
Probosciger aterrimus	74.5 (2)	73.8–75.3	75.0 (2)	73.5–77.0	65.3 (2)	65.2–65.4	29.2 (2)	28.0–30.5	26.9 (2)	25.8–28.0
Psittrichas fulgidus	–	–	–	–	–	–	30.7 (1)	30.7	–	–
Anodorhynchus hyacinthinus	99.9 (1)	99.9	103.8 (1)	103.8	87.0 (1)	87.0	42.3 (1)	42.3	34.3 (1)	34.3

TABLE 5. Measurements (mm) of Mascarene parrots compared with other parrots: coracoid. For abbreviations see methods

Species	TL Mean (n)	TL Range	WSE Mean (n)	WSE Range	SW Mean (n)	SW Range
Lophopsittacus mauritianus	35.0 (6)	33.9–39.1	10.4 (6)	10.2–10.6	3.8 (10)	3.4–4.0
Psittacula bensoni new comb.	32.0 (7)	31.4–33.0	9.2 (4)	8.0–11.3	3.3 (8)	2.7–3.9
Psittacula echo	27.0 (15)	25.1–27.8	8.5 (13)	7.2–9.8	2.9 (17)	2.5–3.3
Necropsittacus rodericanus (u/s)	35.2 (2)	35.0–35.4	12.7 (1)	12.7	3.5 (2)	3.4–3.7
Psittacula exsul	28.5 (3)	28.1–29.0	10.2 (2)	9.8–10.7	2.9 (4)	2.9–3.0
Psittacula krameri krameri (m)	26.3 (4)	25.7–26.9	9.1 (4)	8.8–9.5	2.7 (4)	2.6–2.8
Psittacula krameri krameri (f)	26.6 (2)	26.1–27.2	9.0 (2)	8.4–9.6	2.8 (2)	2.7–2.9
Psittacula krameri krameri (u/s)	27.6 (1)	27.6	8.7 (1)	8.7	2.8 (1)	2.8
Psittacula krameri borealis (m)	27.2 (2)	27.0–27.5	9.4 (2)	9.3–9.6	3.1 (2)	3.0–3.2
Psittacula krameri borealis (f)	28.0 (1)	28.0	9.3 (1)	9.3	3.0 (1)	3.0
Psittacula krameri manillensis (f)	27.3 (1)	27.3	9.3 (1)	9.3	3.0 (1)	3.0
Psittacula krameri manillensis (u/s)	25.7 (2)	24.9–26.5	9.1 (2)	9.0–9.3	3.0 (1)	3.0–3.1
Psittacula eupatria eupatria (m)	33.2 (5)	32.0–34.5	11.5 (5)	10.8–11.9	3.3 (5)	3.1–3.6
Psittacula eupatria eupatria (f)	31.9 (5)	31.1–32.8	11.1 (5)	11.0–11.6	3.3 (5)	3.0–3.6
Psittacula eupatria eupatria (u/s)	31.9 (3)	31.5–32.4	11.5 (3)	11.3–11.7	3.3 (3)	3.1–3.6
Coracopsis nigra	33.1 (2)	33.1	11.6 (2)	11.5–11.7	3.3 (2)	3.2–3.4
Coracopsis vasa	44.0 (2)	40.3–47.7	15.6 (2)	14.2–17.0	4.5 (2)	4.0–5.0
Psittacus erithacus	44.4 (2)	44.0–44.8	15.2 (2)	14.3–16.1	4.5 (2)	4.3–4.8
Tanygnathus megalorhynchus	38.9 (2)	37.3–40.6	13.4 (2)	13.0–13.8	4.3 (2)	4.2–4.4
Eclectus roratus	40.7 (2)	39.9–41.5	14.1 (2)	14.0–14.3	4.5 (2)	4.3–4.7
Strigops habroptilus	43.6 (4)	40.3–46.5	15.9 (4)	13.1–18.8	5.3 (4)	4.6–6.5
Nestor meridionalis	40.5 (2)	37.5–43.5	11.6 (2)	11.5–11.8	4.0 (2)	4.0–4.1
Nestor notabilis	50.7 (2)	48.4–53.0	15.4 (2)	14.2–16.6	5.3 (2)	5.0–5.7
Cyanoramphus novaezelandiae	22.0 (3)	20.0–25.5	7.4 (3)	6.6–9.0	2.0 (3)	1.9–2.3
Cyanoramphus unicolor	26.3 (1)	26.3	8.7 (1)	8.7	2.8 (1)	2.8
Psephotus pulcherrimus	20.9 (1)	20.9	7.2 (1)	7.2	2.0 (1)	2.0
Geopsittacus occidentalis	25.0 (1)	25.0	8.7 (1)	8.7	2.8 (1)	2.8
Calyptorhynchus magnificus magnificus	47.0 (2)	43.8–50.2	17.2 (2)	16.4–18.0	5.2 (2)	5.0–5.4
Probosciger aterrimus	48.7 (2)	47.6–49.8	15.4 (2)	14.8–16.0	4.4 (2)	4.4–4.5
Psittrichas fulgidus	46.4 (1)	46.4	14.8 (2)	14.8	4.6 (2)	4.6
Anodorhynchus hyacinthinus	63.9 (1)	63.9	21.9 (1)	21.9	7.0 (1)	7.0

TABLE 6. Measurements (mm) of Mascarene parrots compared with other parrots: Humerus. For abbreviations see methods

Species	TL Mean (n)	TL Range	PW Mean (n)	PW Range	PD Mean (n)	PD Range	SW Mean (n)	SW Range	SD Mean (n)	SD Range	DW Mean (n)	DW Range	DD Mean (n)	DD Range
Lophopsittacus mauritianus	50.8 (3)	50.4–51.4	12.4 (5)	12.5–12.6	7.8 (4)	7.3–8.6	4.8 (4)	4.7–4.9	4.2 (4)	4.1–4.3	10.6 (3)	10.1–11.3	6.9 (3)	6.3–7.5
Psittacula bensoni new comb.	48.3 (3)	47.0–49.3	12.4 (4)	12.1–12.9	6.8 (4)	6.2–7.5	4.4 (4)	4.2–4.6	4.0 (4)	3.9–4.2	9.8 (2)	9.4–10.2	6.3 (3)	6.0–6.9
Psittacula echo	37.0 (16)	36.8–41.7	9.3 (17)	9.0.9.9	5.0 (18)	4.5–5.9	3.7 (18)	3.5–4.1	3.0 (18)	2.8–3.4	7.6 (15)	7.1–7.9	4.7 (13)	4.2–5.0
Necropsittacus rodericanus	49.0 (8)	47.5–50.6	12.9 (7)	12.4–13.7	7.5 (6)	7.5–7.8	4.7 (8)	4.5–5.0	4.1 (7)	3.8–4.3	10.1 (5)	9.7–10–3	6.6 (6)	6.2–6.9
Psittacula exsul	40.3 (4)	39.3–41.4	9.5 (6)	9.2–9.9	5.7 (4)	5.5–5.9	3.5 (6)	3.4–3.7	3.0 (4)	2.9–3.1	7.8 (4)	7.6–8.1	5.0 (2)	4.8–5.2
Mascarinus mascarinus	48.8 (1)	48.8	13.0 (1)	13.0 (1)	–	–	4.7 (1)	4.7	–	–	9.3 (1)	9.3	–	–
Psittacula krameri krameri (m)	36.9 (4)	36.3–37.5	9.3 (4)	8.6–10.0	5.5 (4)	5.4–5.7	3.5 (4)	3.5–3.6	2.8 (4)	2.8–2.9	7.2 (4)	6.9–7.4	4.8 (4)	4.7–4.9
Psittacula krameri krameri (f)	35.8 (2)	34.7–36.9	9.2 (2)	8.5–9.9	5.3 (2)	5.1–5.6	3.5 (2)	3.3–3.8	3.0 (2)	2.8–3.2	7.0 (2)	6.6–7.5	4.6 (2)	4.5–4.8
Psittacula krameri krameri (u/s)	38.1 (1)	38.1	9.1 (1)	9.1	5.3 (1)	5.3	3.6 (1)	3.6	3.1 (1)	3.1	7.2 (1)	7.2	4.6 (1)	4.6
Psittacula krameri borealis (m)	38.3 (2)	38.3–38.4	9.7 (2)	9.6–9.9	5.6 (2)	5.6–5.7	3.6 (2)	3.5–3.7	2.9 (2)	2.8–3.0	7.5 (2)	7.5	5.0 (2)	5.0
Psittacula krameri borealis (f)	37.3 (1)	37.3	9.4 (1)	9.4	5.2 (1)	5.2	3.4 (1)	3.4	3.1 (1)	3.1	7.2 (1)	7.2	4.9 (1)	4.9
Psittacula krameri manillensis (f)	37.3 (1)	37.3	9.4 (1)	9.4	5.4 (1)	5.4	3.6 (1)	3.6	2.8 (1)	2.8	7.3 (1)	7.3	4.6 (1)	4.6
Psittacula krameri manillensis (u/s)	35.9 (2)	35.9–36.0	9.0 (2)	8.9–9.1	5.2 (2)	5.1–5.4	3.6 (2)	3.6–3.7	2.8 (2)	2.8	7.1 (2)	7.0–7.2	4.7 (2)	4.6–4.8
Psittacula eupatria eupatria (m)	45.7 (5)	45.4–46.0	11.8 (5)	11.3–12.3	6.5 (5)	6.2–6.9	4.3 (5)	4.2–4.5	3.6 (5)	3.5–3.9	9.0 (5)	8.8–9.4	5.9 (5)	5.8–6.1
Psittacula eupatria eupatria (f)	44.0 (5)	43.0–44.8	11.1 (5)	10.7–11.7	6.6 (5)	6.1–6.9	4.1 (5)	4.0–4.4	3.5 (5)	3.3–3.6	8.6 (5)	8.5–9.1	5.8 (5)	5.5–6.1
Psittacula eupatria eupatria (u/s)	43.7 (3)	43.3–44.1	11.3 (3)	10.9–11.6	6.6 (3)	6.6	4.2 (3)	4.1–4.3	3.6 (3)	3.5–3.7	8.5 (3)	8.2–8.9	5.6 (3)	5.5–5.7
Coracopsis nigra	51.8 (2)	51.2–52.4	12.7 (2)	12.3–13.1	8.0 (2)	7.5–8.5	5.0 (2)	4.9–5.1	4.3 (2)	4.2–4.4	10.9 (2)	10.7–11.2	6.4 (2)	6.2–6.6
Coracopsis vasa	68.9 (2)	65.2–72.7	18.8 (2)	17.4–20.3	11.4 (2)	10.7–12.2	6.6 (2)	5.9–7.4	5.5 (2)	5.0–6.0	14.8 (2)	13.7–15.9	8.6 (2)	8.1–9.2
Psittacus erithacus	60.4 (2)	60.2–60.6	15.9 (2)	15.7–16.2	9.0 (2)	9.0	5.5 (2)	5.5–5.6	4.8 (2)	4.8–4.9	12.9 (2)	12.8–13.1	7.9 (2)	7.8–7.9
Tanygnathus megalorhynchus	55.4 (2)	54.0–56.8	13.6 (2)	13.1–14.2	8.0 (2)	7.5–8.5	5.2 (2)	5.1–5.3	4.3 (2)	4.0–4.6	10.9 (2)	10.7–11.2	6.9 (2)	6.5–7.3
Eclectus roratus	63.9 (2)	62.1–65.8	15.6 (2)	15.5–15.8	9.3 (2)	9.2–9.4	6.0 (2)	5.8–6.3	4.9 (2)	4.9–5.0	12.6 (2)	12.4–12.8	7.6 (2)	7.6–7.7
Strigops habroptilus	74.9 (4)	70.4–78.0	16.6 (4)	15.1–17.4	9.9 (4)	9.2–11.0	6.9 (4)	5.9–7.3	6.0 (4)	5.5–6.4	13.9 (4)	12.6–15.0	8.2 (4)	7.4–8.9
Nestor meridionalis	62.4 (2)	59.7–65.1	16.4 (2)	16.0–16.9	9.2 (2)	9.0–9.4	5.5 (2)	5.4–5.7	5.1 (2)	5.0–5.2	12.5 (2)	12.0–13.1	7.6 (2)	7.2–8.0
Nestor notabilis	77.9 (2)	74.0–81.9	20.4 (2)	20.0–20.9	12.0 (2)	10.5–13.5	7.4 (2)	7.1–7.7	6.4 (2)	5.9–6.9	16.0 (2)	15.0–17.1	9.6 (2)	9.0–10.3
Cyanoramphus novaezelandiae	25.2 (2)	25.2	6.5 (2)	6.5–6.6	4.1 (2)	4.0–4.3	2.5 (2)	2.5	2.0 (2)	2.0	5.5 (2)	5.5–5.6	3.3 (2)	3.2–3.5
Cyanoramphus unicolor	33.1 (1)	33.1	9.0 (1)	9.0	4.8 (1)	4.8	3.0 (1)	3.0	2.7 (1)	2.7	7.1 (1)	7.1	4.3 (1)	4.3
Calyptorhynchus m magnificus	79.4 (2)	72.8–86.1	20.7 (2)	19.9–21.5	11.6 (2)	11.0–12.2	7.0 (2)	6.9–7.1	5.5 (2)	5.3–5.8	15.6 (2)	14.6–16.7	9.1 (2)	8.8–9.4
Probosciger aterrimus	81.3 (2)	80.7–82.0	20.0 (2)	20.0	11.2 (2)	11.0–11.5	7.0 (2)	6.8–7.3	6.0 (2)	5.8–6.2	17.2 (2)	17.0–17.4	8.8 (2)	8.8–8.9
Psittrichas fulgidus	70.0 (1)	70.0	19.6 (1)	19.6	10.9 (1)	10.9	6.5 (1)	6.5	5.9 (1)	5.9	14.2 (1)	14.2	8.9 (1)	8.9
Anodorhynchus hyacinthinus	88.8 (1)	88.8	24.5 (1)	24.5	15.8 (1)	15.8	8.6 (1)	8.6	7.4 (1)	7.4	18.9 (1)	18.9	12.0 (1)	12.0

TABLE 7. Measurements (mm) of Mascarene parrots compared with other parrots: ulna. For abbreviations see methods

Species	TL Mean (n)	TL Range	PW Mean (n)	PW Range	SW Mean (n)	SW Range	DW Mean (n)	DW Range
Lophopsittacus mauritianus (m)	65.8 (2)	65.8–65.9	8.8 (2)	8.4–9.4	4.3 (2)	4.2–4.4	8.3 (2)	8.2–8.4
Lophopsittacus mauritianus (f)	61.45(2)	60.0–62.9	7.6 (2)	6.9–8.3	3.7(2)	3.7	6.7(1)	6.7
Psittacula bensoni new comb.	52.4 (2)	52.1–52.7	7.4(2)	7.0–7.8	3.6 (5)	3.1–4.0	6.5(3)	6.5–6.7
Psittacula wardi	54.0 (1)	54.0	–	–	2.9 (1)	2.9	5.5 (1)	5.5
Psittacula echo	45.5 (2)	43.4–47.7	5.7 (3)	5.0–6.3	2.9 (3)	2.7–3.1	5.3 (3)	4.9–5.9
Necropsittacus rodericanus	57.7 (4)	56.8–58.9	7.4 (4)	7.0–7.6	3.5 (4)	3.5–3.6	7.4 (3)	7.2–7.6
Psittacula exsul	50.0 (3)	49.0–51.0	6.3 (3)	5.8–6.6	2.9 (3)	2.8–3.1	6.0 (3)	5.8–6.1
Psittacula krameri krameri (m)	43.7 (4)	43.2–44.5	5.7 (4)	5.5–6.0	2.6 (4)	2.6–2.7	5.2 (4)	5.1–5.4
Psittacula krameri krameri (f)	41.8 (2)	40.1–43.5	5.6 (2)	5.3–5.9	2.9 (2)	2.9–3.0	5.1 (1)	5.0–5.3
Psittacula krameri krameri (u/s)	44.8 (1)	44.8	5.5 (1)	5.5	2.8 (1)	2.8	5.0 (1)	5.0
Psittacula krameri borealis (m)	46.2 (2)	45.3–47.1	5.8 (2)	5.8	2.8 (2)	2.8	5.6 (2)	5.6–5.7
Psittacula krameri borealis (f)	45.0 (1)	45.0	5.5 (1)	5.5	2.6 (1)	2.6	5.3 (1)	5.3
Psittacula krameri manillensis (f)	42.2 (1)	42.2	5.3 (1)	5.3	2.7 (1)	2.7	5.3 (1)	5.3
Psittacula krameri manillensis (u/s)	43.3 (2)	42.7–44.0	5.4 (2)	4.9–5.9	2.9 (2)	2.8–3.0	5.4 (2)	5.3–5.5
Psittacula eupatria eupatria (m)	54.7 (5)	53.9–55.5	6.5 (5)	6.2–6.8	3.4 (5)	3.2–3.5	6.6 (5)	6.3–6.9
Psittacula eupatria eupatria (f)	52.4 (5)	51.3–53.2	6.4 (5)	5.9–6.8	3.1 (5)	3.0–3.2	6.4 (5)	6.3–6.8
Psittacula eupatria eupatria (u/s)	52.0 (3)	51.5–52.3	6.1 (3)	6.0–6.3	3.3 (3)	3.1–3.4	6.3 (3)	6.1–6.6
Coracopsis nigra	60.9 (2)	60.4–61.5	8.7 (2)	8.3–9.1	3.8 (2)	3.8–3.9	7.1 (2)	6.9–7.4
Coracopsis vasa	83.0 (2)	77.9–88.2	10.9 (2)	10.4–11.5	4.9 (2)	4.7–5.2	9.7 (2)	8.8–10.6
Psittacus erithacus	74.6 (2)	74.4–74.9	8.5 (2)	8.3–8.8	4.2 (2)	4.2	7.6 (2)	7.0–8.3
Tanygnathus megalorhynchus	68.8 (2)	66.0–71.6	7.9 (2)	7.7–8.1	4.0 (2)	3.8–4.2	7.3 (2)	7.0–7.6
Eclectus roratus	72.2 (2)	66.0–78.5	9.1 (2)	8.8–9.5	4.5 (2)	4.5–4.6	7.8 (2)	7.5–8.2
Strigops habroptilus	73.7 (3)	69.4–77.2	11.4 (3)	10.2–12.4	5.2 (3)	4.8–5.7	8.5 (3)	7.6–9.3
Nestor meridionalis	68.9 (2)	65.1–72.8	9.8 (2)	9.5–10.2	4.9 (2)	4.7–5.1	7.8 (2)	7.2–8.5
Nestor notabilis	85.2 (2)	80.7–89.7	12.3 (2)	11.7–13.0	5.6 (2)	5.1–6.2	10.4 (2)	10.0–10.9
Cyanoramphus novaezelandiae	27.7 (2)	27.4–28.1	4.2 (2)	4.2–4.3	1.9 (2)	1.9–2.0	3.5 (2)	3.2–3.8
Cyanoramphus unicolor	36.0 (1)	36.0	4.9 (1)	4.9	2.5 (1)	2.5	3.8 (1)	3.8
Calyptorhynchus magnificus magnificus	92.2 (2)	88.7–~95.7	11.7 (2)	11.5–12.0	5.4 (2)	5.4–5.5	10.3 (2)	10.0–10.7
Probosciger aterrimus	102.6 (2)	101.2–104.0	11.9 (2)	11.7–12.1	5.5 (2)	5.5–5.6	10.6 (2)	10.5–10.8
Psittrichas fulgidus	82.6 (1)	82.6	9.2 (1)	9.2	5.1 (1)	5.1	8.3 (1)	8.3
Anodorhynchus hyacinthinus	119.6 (1)	119.6	13.8 (1)	13.8	6.8 (1)	6.8	13.5 (1)	13.5

TABLE 8. Measurements (mm) of Mascarene parrots compared with other parrots: carpometacarpus. For abbreviations see methods

Species	TL Mean (n)	TL Range	PW Mean (n)	PW Range	DW Mean (n)	DW Range
Lophopsittacus mauritianus	40.4 (4)	36.7–46.7	9.4 (5)	8.2–10.7	3.9 (4)	3.1–4.4
Psittacula bensoni new comb.	31.2 (1)	31.2	9.3 (1)	9.3	3.5 (1)	3.5
Psittacula echo	30.7 (4)	30.0–31.3	6.8 (3)	6.6–7.2	3.2 (4)	3.1–3.4
Psittacula wardi	33.6 (1)	33.6	–	–	–	–
Necropsittacus rodericanus	–	–	–	–	3.3 (2)	3.3–3.4
Psittacula krameri krameri (m)	29.1 (4)	28.3–30.1	7.0 (2)	6.8–7.2	3.2 (4)	3.1–3.3
Psittacula krameri krameri (f)	27.7 (2)	26.6–28.8	6.9 (2)	6.6–7.2	3.1 (2)	3.1
Psittacula krameri krameri (u/s)	29.9 (1)	29.9	7.0 (1)	7.0	3.3 (1)	3.3
Psittacula krameri borealis (m)	30.1 (2)	29.8–30.4	6.9 (2)	6.8–7.1	3.5 (2)	3.5–3.6
Psittacula krameri borealis (f)	28.8 (1)	28.8	7.1 (1)	7.1	3.3 (1)	3.3
Psittacula krameri manillensis (f)	28.0 (1)	28.0	7.3 (1)	7.3	3.1 (1)	3.1
Psittacula krameri manillensis (u/s)	28.4 (2)	27.9–28.4	6.9 (2)	6.8–7.0	3.0 (2)	3.0
Psittacula eupatria eupatria (m)	36.3 (5)	35.5–37.2	8.5 (5)	8.2–8.8	3.8 (5)	3.6–4.0
Psittacula eupatria eupatria (f)	35.2 (5)	34.2–35.8	8.1 (5)	7.9–8.5	3.7 (5)	3.6–3.9
Psittacula eupatria eupatria (u/s)	35.1 (3)	35.0–35.2	8.1 (3)	8.1–8.2	3.6 (3)	3.6

TABLE 9. Measurements (mm) of Mascarene parrots compared with other parrots: Femur. For abbreviations see methods

Species	TL Mean (n)	TL Range	PW Mean (n)	PW Range	SW Mean (n)	SW Range	SD Mean (n)	SD Range	DW Mean (n)	DW Range
Lophopsittacus mauritianus	62.4 (3)	59.2–64.5	13.6 (5)	13.1–14.2	5.2 (5)	4.9–5.7	4.9 (4)	4.5–5.5	13.6 (3)	12.9–14.3
Psittacula echo	34.9 (2)	33.9–36.0	6.8 (6)	6.3–7.2	2.6 (6)	2.5–2.9	2.6 (6)	2.5–2.8	6.2 (6)	5.9–6.5
Necropsittacus rodericanus	47.1 (2)	46.0–48.3	9.5 (4)	9.2–10.0	3.9 (4)	3.7–4.3	3.9 (4)	3.8–4.3	9.0 (5)	8.9–9.1
Psittacula exsul	37.7 (2)	37.2–38.3	7.1 (2)	7.1–7.2	2.9 (2)	2.8–3.0	2.8 (2)	2.7–3.0	7.0 (2)	6.9–7.1
Psittacula krameri krameri (m)	31.5 (4)	31.0–32.3	6.0 (4)	5.9–6.5	2.4 (4)	2.3–2.6	2.4 (4)	2.3–2.5	5.7 (4)	5.6–5.9
Psittacula krameri krameri (f)	31.0 (2)	31.0–32.0	5.8 (2)	5.5–6.2	2.4 (2)	2.3–2.5	2.4 (2)	2.3–2.6	5.8 (2)	5.6–6.0
Psittacula krameri krameri (u/s)	31.9 (1)	31.9	5.9 (1)	5.9	2.5 (1)	2.5	2.5 (1)	2.5	5.6 (1)	5.6
Psittacula krameri borealis (m)	32.5 (2)	32.2–32.9	5.9 (2)	5.8–6.0	2.4 (2)	2.4–2.5	2.6 (2)	2.5–2.7	5.7 (2)	5.7
Psittacula krameri borealis (f)	32.8 (1)	32.8	5.9 (1)	5.9	2.3 (1)	2.3	2.3 (1)	2.3	5.8 (1)	5.8
Psittacula krameri manillensis (f)	31.3 (1)	31.3	6.3 (1)	6.3	2.3 (1)	2.3	2.2 (1)	2.2	6.4 (1)	6.4
Psittacula krameri manillensis (u/s)	30.3 (2)	29.7–31.3	5.6 (2)	5.6	2.3 (1)	2.3–2.4	2.3 (2)	2.2–2.5	5.7 (2)	5.6–5.8
Psittacula eupatria eupatria (m)	38.9 (5)	37.8–40.2	7.5 (5)	7.2–7.7	3.1 (5)	3.0–3.4	3.1 (5)	2.9–3.4	7.2 (5)	7.0–7.5
Psittacula eupatria eupatria (f)	37.2 (5)	36.6–37.8	7.4 (5)	7.2–7.7	2.9 (5)	2.8–3.2	2.9 (5)	2.9–3.0	7.1 (5)	6.8–7.5
Psittacula eupatria eupatria (u/s)	37.4 (3)	37.4–37.6	7.6 (3)	7.3–8.0	3.0 (3)	3.0–3.1	3.0 (3)	2.9–3.1	7.0 (3)	6.8–7.2
Coracopsis nigra	38.8 (2)	38.7–38.9	8.4 (2)	7.9–9.0	3.3 (2)	3.3	3.2 (2)	3.2	7.8 (2)	7.7–8.0
Coracopsis vasa	50.8 (2)	47.0–54.7	11.1 (2)	10.5–11.8	4.6 (2)	4.2–5.0	4.2 (2)	3.8–4.6	11.3 (2)	10.8–11.9
Psittacus erithacus	49.6 (2)	49.6	10.7 (2)	10.5–11.0	4.2 (2)	4.2	4.1 (2)	4.1–4.2	9.8 (2)	9.7–10.0
Tanygnathus megalorhynchus	46.5 (2)	45.4–47.7	8.9 (2)	8.8–9.0	3.9 (2)	3.9	3.8 (2)	3.7–3.9	8.9 (2)	8.8–9.0
Eclectus roratus	47.5 (2)	46.5–48.5	9.7 (2)	9.6–9.8	3.8 (2)	3.8–3.9	4.2 (2)	4.2	9.7 (2)	9.7–9.8
Strigops habroptilus	80.6 (4)	75.2–84.5	17.4 (4)	14.9–19.5	7.5 (4)	6.5–8.3	7.2 (4)	6.6–7.9	18.1 (4)	16.1–19.7
Nestor meridionalis	52.3 (2)	50.6–54.0	11.4 (2)	11.0–11.9	5.1 (2)	5.0–5.2	4.6 (2)	4.6–4.7	11.7 (2)	11.2–12.3
Nestor notabilis	65.7 (2)	60.3–71.1	14.2 (2)	13.0–15.5	6.4 (2)	5.9–7.0	5.8 (2)	5.6–6.1	14.4 (2)	13.2–15.7
Cyanoramphus novaezelandiae	26.9 (3)	23.7–32.5	5.1 (3)	4.5–6.2	2.0 (3)	1.8–2.5	1.9 (3)	1.8–2.3	5.4 (3)	4.7–6.6
Cyanoramphus unicolor	34.5 (1)	34.5	6.6 (1)	6.6	2.5 (1)	2.5	2.4 (1)	2.4	6.9 (1)	6.9
Calyptorhynchus magnificus magnificus	52.1 (2)	48.6–55.6	12.2 (2)	11.4–13.0	4.6 (2)	4.3–5.0	4.5 (2)	4.2–4.8	12.0 (2)	11.5–12.5
Probosciger aterrimus	59.1 (2)	58.5–59.7	13.0 (2)	12.8–13.2	4.8 (2)	4.8–4.9	5.0 (2)	5.0–5.1	12.7 (2)	12.3–13.2
Psittrichas fulgidus	53.9 (1)	53.9	11.4 (1)	11.4	5.2 (1)	5.2	4.9 (1)	4.9	10.7 (1)	10.7
Anodorhynchus hyacinthinus	69.9 (1)	69.9	15.3 (1)	15.3	6.6 (1)	6.6	6.7 (1)	6.7	15.2 (1)	15.2

TABLE 10. Measurements (mm) of Mascarene parrots compared with other parrots: Tibiotarsus. For abbreviations see methods

Species	TL Mean (n)	TL Range	PW Mean (n)	PW Range	PD Mean (n)	PD Range	SW Mean (n)	SW Range	SD Mean (n)	SD Range	DW Mean (n)	DW Range
Lophopsittacus mauritianus (m)	96.5 (14)	94.1–100.9	15.9 (8)	15.3–16.5	12.1 (16)	12.6–14.7	5.4 (30)	5.0–5.9	4.8 (32)	4.4–5.4	12.6 (24)	11.7–13.9
Lophopsittacus mauritianus (f)	88.6 (7)	86.5–90.7	14.4 (7)	13.4–16.5	12.5 (6)	11.8–13.4	4.9 (16)	4.7–5.3	4.4 (16)	4.1–4.7	11.1 (8)	10.9–11.4
Psittacula bensoni new comb.	59.3 (1)	59.3	7.1 (1)	7.1	8.4 (1)	8.4	3.2 (4)	2.9–3.8	2.9 (4)	2.7–3.3	7.3 (4)	6.6–8.0
Psittacula echo	49.6 (4)	48.6–51.0	5.5 (4)	5.3–5.6	6.1 (2)	6.0–6.2	2.4 (7)	2.3–2.6	2.4 (7)	2.2–2.8	5.9 (8)	5.5–6.4
Psittacula wardi	53.9 (1)	53.9	8.6 (1)	8.6	7.0 (1)	7.0	2.5 (1)	2.5	2.7 (1)	2.7	6.9 (1)	6.9
Necropsittacus rodericanus	60.1 (2)	60.1–60.2	9.6 (2)	9.3–9.9	8.2 (4)	7.9–8.5	3.6 (6)	3.4–3.8	3.2 (6)	3.1–3.4	7.8 (4)	7.6–8.1
Psittacula exsul	54.9 (2)	53.6–56.3	8.0 (4)	7.4–8.7	6.9 (4)	6.7–7.1	2.8 (3)	2.6–3.0	2.6 (3)	2.6–2.7	6.5 (2)	6.2–6.9
Psittacula krameri krameri (m)	44.0 (4)	43.0–44.8	5.4 (4)	4.9–5.8	5.6 (4)	5.3–6.0	2.2 (4)	2.1–2.3	2.1 (4)	2.0–2.3	5.3 (4)	5.1–5.5
Psittacula krameri krameri (f)	43.3 (2)	42.1–44.6	5.4 (2)	5.4	5.4 (2)	5.1–5.7	2.2 (2)	2.1–2.4	2.3 (2)	2.2–2.5	5.3 (2)	5.0–5.6
Psittacula krameri krameri (u/s)	45.7 (1)	45.7	4.8 (1)	4.8	5.8 (1)	5.8	2.2 (1)	2.2	2.2 (1)	2.2	4.9 (1)	4.9
Psittacula krameri borealis (m)	45.9 (2)	45.6–46.2	5.3 (2)	4.9–5.8	5.5 (2)	5.4–5.6	2.3 (2)	2.3–2.4	2.1 (2)	2.1–2.2	5.2 (2)	5.0–5.4
Psittacula krameri borealis (f)	45.1 (1)	45.1	6.5 (1)	6.5	5.5 (1)	5.5	2.1 (1)	2.1	2.0 (1)	2.0	5.8 (1)	5.8
Psittacula krameri manillensis (f)	43.0 (1)	43.0	5.4 (1)	5.4	5.6 (1)	5.6	2.4 (1)	2.4	2.3 (1)	2.3	4.8 (1)	4.8
Psittacula krameri manillensis (u/s)	45.3 (2)	44.4–46.3	6.3 (2)	6.1–6.6	6.1 (2)	5.8–6.5	2.1 (2)	2.1–2.2	2.1 (2)	2.1–2.2	4.7 (2)	4.6–4.8
Psittacula eupatria eupatria (m)	54.9 (5)	53.9–56.0	8.9 (5)	8.4–9.3	7.5 (5)	7.1–8.3	2.7 (5)	2.6–3.0	2.9 (5)	2.8–3.2	6.7 (5)	6.6–6.8
Psittacula eupatria eupatria (f)	51.8 (5)	50.7–52.7	8.2 (5)	8.0–8.4	7.0 (5)	6.9–7.2	2.7 (5)	2.5–2.9	2.8 (5)	2.8–2.9	6.3 (5)	6.2–6.7
Psittacula eupatria eupatria (u/s)	52.4 (3)	52.1–52.9	8.2 (3)	8.0–8.5	6.8 (3)	6.6–7.0	2.7 (3)	2.6–2.8	2.9 (3)	2.8–3.2	6.5 (3)	6.3–6.7
Coracopsis nigra	58.3 (2)	57.2–59.4	7.6 (2)	6.9–8.4	7.6 (2)	7.2–8.1	2.9 (2)	2.6–3.2	3.0 (2)	2.8–3.3	7.1 (2)	6.8–7.5
Coracopsis vasa	75.0 (2)	68.2–81.9	9.8 (2)	9.2–10.4	10.3 (2)	9.5–11.1	3.7 (2)	3.4–4.1	4.1 (2)	4.0–4.2	9.3 (2)	9.1–9.5
Psittacus erithacus	68.0 (2)	67.7–68.3	9.1 (2)	8.8–9.4	10.2 (2)	10.2–10.3	3.9 (2)	3.8–4.0	3.7 (2)	3.6–3.8	9.2 (2)	8.8–9.6
Agapornis cana	26.2 (1)	26.2	3.5 (1)	3.5	3.1 (1)	3.1	1.3 (1)	1.3	1.3 (1)	1.3	3.0 (1)	3.0
Tanygnathus megalorhynchus	63.0 (2)	61.3–64.8	8.9 (2)	7.8–10.1	8.9 (2)	8.7–9.1	3.4 (2)	3.3–3.6	3.2 (2)	3.1–3.3	8.1 (2)	7.9–8.4
Eclectus roratus	63.9 (2)	62.8–65.0	7.7 (2)	7.6–7.9	8.8 (2)	8.6–9.0	3.6 (2)	3.6–3.7	3.2 (2)	3.1–3.3	8.2 (2)	7.8–8.6
Strigops habroptilus	116.5 (4)	108.1–121.3	15.1 (4)	13.8–16.1	18.4 (4)	16.1–20.0	6.4 (4)	5.7–7.3	6.3 (4)	5.6–6.8	14.8 (4)	13.1–15.7
Nestor meridionalis	84.9 (2)	82.8–87.0	11.1 (2)	10.5–11.8	11.1 (2)	11.0–11.2	4.3 (2)	4.3–4.4	4.2 (2)	3.8–4.6	9.4 (2)	9.2–9.7
Nestor notabilis	101.0 (2)	96.3–105.7	14.3 (2)	13.6–15.0	13.3 (2)	12.8–13.9	5.4 (2)	5.4–5.5	4.9 (2)	4.7–5.1	11.7 (2)	11.0–12.5
Cyanoramphus novaezelandiae	38.5 (2)	38.2–38.9	5.1 (2)	4.9–5.3	4.4 (2)	4.3–4.6	1.7 (2)	1.6–1.8	1.6 (2)	1.6	3.8 (2)	3.8–3.9
Cyanoramphus unicolor	51.9 (1)	51.9	6.9 (1)	6.9	6.5 (1)	6.5	2.3 (1)	2.3	2.4 (1)	2.4	5.4 (1)	5.4
Calyptorhynchus m. magnificus	74.3 (2)	68.5–80.2	9.8 (2)	9.4–10.3	12.1 (2)	11.4–12.8	4.0 (2)	4.0–4.1	3.7 (2)	3.6–3.9	9.6 (2)	9.0–10.2
Probosciger aterrimus	88.5 (2)	88.5–88.6	10.9 (2)	10.5–11.3	12.3 (2)	11.9–12.8	4.4 (2)	4.4–4.5	4.1 (2)	4.0–4.3	10.7 (2)	10.5–10.9
Psittrichas fulgidus	70.0 (1)	70.0	10.2 (1)	10.2	11.1 (1)	11.1	4.7 (1)	4.7	3.6 (1)	3.6	10.2 (1)	10.2
Anodorhynchus hyacinthinus	95.4 (1)	95.4	12.9 (1)	12.9	13.6 (1)	13.6	5.8 (1)	5.8	5.0 (1)	5.0	12.5 (1)	12.5

TABLE 11. Measurements (mm) of Mascarene parrots compared with other parrots: Tarsometatarsus. For abbreviations see methods

Species	TL Mean (n)	TL Range	LIT Mean (n)	LIT Range	PW Mean (n)	PW Range	SW Mean (n)	SW Range	SD Mean (n)	SD Range	DW Mean (n)	DW Range
Lophopsittacus mauritianus (m)	35.3 (5)	33.0–~36.3	25.1 (3)	23.2–26.2	11.9 (5)	9.6–13.2	6.6 (7)	6.1–7.4	3.2 (2)	3.6–4.4	16.5 (3)	16.2–17.0
Lophopsittacus mauritianus (f)	~31.0 (1)	~31.0	–	–	~11.7	~11.7	5.4 (1)	5.4	3.5 (1)	3.5	–	–
Psittacula bensoni new comb.	22.2 (14)	21.2–23.2	16.8 (7)	16.5–17.5	7.8 (11)	7.2–8.3	3.6 (18)	3.3–4.1	2.1 (14)	1.8–2.5	9.0 (11)	8.0–10.0
Psittacula echo	18.5 (22)	17.5–19.5	13.9 (11)	12.5–14.9	6.5 (25)	5.9–7.0	3.2 (27)	2.8–3.8	1.8 (19)	1.7–2.0	8.2 (25)	7.1–9.1
Psittacula wardi	18.1 (1)	18.1	–	–	7.2 (1)	7.2	3.3 (1)	3.3	–	–	8.5 (1)	8.5
Necropsittacus rodericanus	23.2 (1)	23.2	16.7 (1)	16.7	8.5 (1)	8.5	4.1 (1)	4.1	2.4 (1)	2.4	11.5 (1)	11.5
Psittacula krameri krameri (m)	16.9 (4)	16.7–17.3	12.3 (4)	11.7–12.9	5.9 (4)	5.7–6.2	2.7 (4)	2.7–2.8	1.8 (4)	1.7–1.9	8.1 (4)	8.0–8.4
Psittacula krameri krameri (f)	16.8 (2)	16.6–17.1	12.2 (2)	11.4–13.0	5.8 (2)	5.6–6.1	2.7 (2)	2.5–2.9	1.7 (2)	1.6–1.9	7.6 (2)	7.4–7.9
Psittacula krameri krameri (u/s)	17.0 (1)	17.0	12.7 (1)	12.7	5.7 (1)	5.7	2.6 (1)	2.6	1.7 (1)	1.7	7.7 (1)	7.7
Psittacula krameri borealis (m)	17.6 (2)	17.6–17.7	12.7 (2)	12.6–12.8	5.6 (2)	5.6–5.7	2.7 (2)	2.7–2.8	1.9 (2)	1.9–2.0	8.1 (2)	8.1–8.2
Psittacula krameri borealis (f)	17.3 (1)	17.3	12.8 (1)	12.8	5.7 (1)	5.7	2.9 (1)	2.9	1.8 (1)	1.8	8.3 (1)	8.3
Psittacula krameri manillensis (f)	17.1 (1)	17.1	12.4 (1)	12.4	5.8 (1)	5.8	2.9 (1)	2.9	1.9 (1)	1.9	8.1 (1)	8.1
Psittacula krameri manillensis (u/s)	16.9 (2)	16.2–17.6	12.4 (2)	12.3–12.5	5.4 (2)	5.3–5.5	2.8 (2)	2.8–2.9	1.9 (2)	1.9–2.0	8.0 (2)	8.0–8.1
Psittacula eupatria eupatria (m)	20.2 (5)	19.4–20.7	14.5 (5)	14.4–14.8	7.2 (5)	7.0–7.3	3.6 (5)	3.4–3.7	2.2 (5)	2.0–2.4	9.9 (5)	9.3–10.3
Psittacula eupatria eupatria (f)	19.4 (5)	19.2–20.0	13.5 (5)	13.3–13.8	6.9 (5)	6.5–7.5	3.2 (5)	3.0–3.5	2.1 (5)	2.0–2.4	9.1 (5)	8.9–9.6
Psittacula eupatria eupatria (u/s)	19.4 (3)	19.3–19.5	13.8 (3)	13.5–14.2	6.9 (3)	6.8–7.2	3.3 (3)	3.3–3.4	2.1 (3)	2.0–2.2	9.4 (3)	9.3–9.6
Coracopsis nigra	21.9 (2)	21.8–22.0	15.6 (2)	15.6–15.7	7.4 (2)	7.2–7.6	3.3 (2)	3.1–3.6	2.3 (2)	2.3	9.4 (2)	9.0–9.9
Coracopsis vasa	29.2 (2)	28.4–30.1	21.0 (2)	20.7–21.3	10.4 (2)	9.5–11.3	4.2 (2)	3.9–4.6	3.0 (2)	2.8–3.2	12.1 (2)	12.0–12.2
Psittacus erithacus	25.4 (2)	24.8–26.0	19.1 (2)	18.0–20.2	10.0 (2)	9.9–10.2	4.8 (2)	4.5–5.1	2.7 (2)	2.7	12.7 (2)	12.6–12.8
Tanygnathus megalorhynchus	23.6 (2)	23.2–24.1	17.4 (2)	16.8–18.0	9.2 (2)	8.6–9.8	4.5 (2)	4.4–4.6	2.7 (2)	2.5–3.0	11.1 (2)	11.0–11.3
Eclectus roratus	23.5 (2)	22.7–24.4	18.2 (2)	17.5–19.0	8.8 (2)	8.1–9.6	3.8 (2)	3.8–3.9	2.3 (2)	2.3–2.4	11.8 (2)	11.8–11.9
Strigops habroptilus	49.2 (4)	46.4–52.0	39.3 (4)	37.3–41.3	15.5 (4)	14.5–16.7	6.6 (4)	5.5–7.6	4.7 (4)	4.2–5.3	17.7 (4)	17.7
Nestor meridionalis	36.3 (2)	35.8–36.9	27.9 (2)	27.9–28.0	10.5 (2)	10.2–10.8	4.3 (2)	4.0–4.7	3.4 (2)	2.9–3.9	12.7 (2)	11.8–13.6
Nestor notabilis	44.5 (2)	41.5–47.5	37.1 (1)	37.1	12.1 (2)	11.4–12.9	5.0 (2)	4.7–5.4	4.1 (2)	3.9–4.3	16.1 (1)	16.1
Cyanoramphus novaezelandiae	18.3 (2)	18.2–18.5	15.9 (2)	15.9	4.3 (2)	4.3–4.4	1.7 (2)	1.7	1.3 (2)	1.3	4.9 (2)	4.9
Cyanoramphus unicolor	25.1 (1)	25.1	21.8 (1)	21.8	5.8 (1)	5.8	2.2 (1)	2.2	1.9 (1)	1.9	6.7 (1)	6.7
Calyptorhynchus m. magnificus	24.7 (2)	23.1–26.3	17.2 (2)	16.2–18.2	11.4 (2)	10.7–12.2	5.7 (2)	5.6–5.9	2.9 (2)	2.7–3.1	14.1 (2)	13.0–15.3
Probosciger aterrimus	27.7 (2)	27.2–28.3	19.0 (2)	18.6–19.4	11.7 (2)	11.6–11.9	5.1 (2)	5.0–5.3	3.2 (2)	3.2–3.3	14.0 (2)	13.6–14.4
Psittrichas fulgidus	27.7 (1)	27.7	20.3 (1)	20.3	11.5 (1)	11.5	5.8 (1)	5.8	3.3 (1)	3.3	13.9 (1)	13.9
Anodorhynchus hyacinthinus	38.5 (1)	38.5	28.2 (1)	28.2	13.8 (1)	13.8	6.3 (1)	6.3	3.7 (1)	3.7	16.2 (1)	16.2