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The fossil record

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Chapter 1 has outlined the extent to which many endemic Mascarene Island birds have become extinct, probably during the last 300 years since man arrived on the islands. Thirty extinct species are recognised today (Cowles in press), but of these only five are known from skins preserved in museums and institutions throughout the world. Four of these species, the Mauritian Blue Pigeon *Alectroenas nitidissima*, the Mascarene Parrot from Réunion *Mascarinus mascarinus*, the Rodrigues Parakeet *Psittacula exsul* and the contentious Leguat's Starling *Necropsar* (*Orphanopsar*) *leguati* of unknown locality, are represented by a total of only eight skins. The Réunion Crested Starling *Fregilupus varius* was better represented by 24–25 skins, all documented by Hachisuka (1953), although fewer survive today (Chapter 1). The remaining 25 extinct species are known only from fossil bones discovered in caverns and deposits on the three islands. In number these range to well over 200 elements for the better known Solitaire of Rodrigues *Pezophaps solitaria* and perhaps the Mauritius Dodo *Raphus cucullatus*, but the remaining species are unfortunately known from very few bones or bone fragments.

Identifications based on the osteological evidence are in some instances substantiated by field descriptions and illustrations in journals of seventeenth-century voyagers to the islands. The visitors who added notably to early ornithological history were Leguat (1708), on Rodrigues in 1691, Dubois (1674), on Réunion 1671–2, and Van Neck, on Mauritius 1598 or 1599 (see Strickland 1848). The other voyagers were listed by Hachisuka (1953) and Cheke (Chapter 1). These brief accounts of the flora and fauna of the islands were compiled by people with little ornithological knowledge, but they do provide a most valuable and historical record of the lost avifauna of the islands.

The major descriptive osteological studies based on fossil bones were completed between the years 1848 and 1893, notably by Strickland & Melville (1848), Milne-Edwards (1867*a*, *b*, 1868, 1873), Owen (1866), A. & E. Newton (1870), Günther & E. Newton (1879) and E. Newton & Gadow (1893).

Recent research

At the invitation of the British Ornithologists' Union, I visited the Mascarene Islands in 1974 as part of the BOU research programme approved by the Government of Mauritius. Between September and December the islands of Mauritius, Rodrigues and Réunion were studied, the last after consultation with the French authorities. The sites of previous subfossil finds were investigated and several new areas explored in the attempt to obtain further bone material and thus increase our knowledge of the extinct avifauna of the islands.

In consequence of the fieldwork, a complete review of the Mascarene subfossil bird material has been made. This, together with additional material discovered in museums, and on the islands in 1974, has resulted in the re-identification of some older type material, and the description of seven new species of extinct birds. Included in the review are the previously unstudied collections of E. Thirioux from Mauritius about 1900, and the important collections of B. Kervazo made on Réunion in 1974.

The present chapter is based on the above data. The full review (Cowles in press) gives names and descriptions of the new species (referred to here as 'sp. nov.').

The following abbreviations are used:

BMNH(P), British Museum (Natural History) Department of Palaeontology;

BMNH(O) British Museum (Natural History) Sub-department of Ornithology;

UMZC, University Museum of Zoology, Cambridge;

MNHM, Muséum Nationale d'Histoire Naturelle, Paris.

History of sites and collectors

Mauritius

The Dodo, the most famous of the Mauritius endemics, is thought to have become extinct by about 1693 (although Cheke puts this at 1665: see Chapter 1). Strickland (1844) suggested that naturalists residing in the Mascarene Islands should search diligently in the alluvial soil and cave floors for evidence of the extinct avifauna. Twenty-one years later George Clark (1866), a school-teacher resident on Mauritius, discovered that a marshy area near the south-east coast of Mauritius called the Mare aux Songes contained bones of the Dodo and other animals. In September 1865 workmen digging peat for enriching the soil on the Plaisance Estate uncovered bones and a carapace of an extinct tortoise. The landowner allowed Clark to remove any bones that he might find in the marsh, and workmen were sent into deep water to feel with their feet for bones; this technique met with success and soon a few Dodo bones started to emerge. Clark then cleared some floating vegetation from the deepest part of the marsh, and trapped in the underlying mud he found large quantities of bones belonging to the Dodo and other birds. The material was sent to Richard Owen and Alfred Newton in England and Alphonse Milne-Edwards in Paris, for examination and identification.

In 1889, 24 years after Clark's great discovery, the Government of Mauritius appointed a Commission to enquire into the 'Souvenirs Historiques' of the island. Under the direction of Théodore Sauzier digging was resumed in the marsh. Many more bones were excavated, representing various extinct species which E. Newton & Gadow (1893) examined and described.

At the end of the nineteenth century the collector E. Thirioux made excursions to the mountain Le Pouce and ranges close to the capital of Port Louis and obtained many bones from various unnamed caves. There is in the Mauritius Institute a very fine and almost complete mounted skeleton of the extinct rail *Aphanapteryx bonasia* attributed to his collecting. The remainder of the Thirioux collection is in the UMZC.

It is extraordinary that nearly all the fossil evidence relating to the extinct avifauna of Mauritius has been obtained from the two sites, Mare aux Songes and Le Pouce. With the exception of one Dodo bone no new avian material of any extinct species has been found on Mauritius in the last 80 years.

Réunion

There seems to be no previous published record of fossil bird bones having been found on Réunion. Berlioz (1946) and Barré & Barau (1982) have given details of the early visitors to the islands and discussed the birds seen and listed by them. Dubois (1674) mentioned many of the birds, now extinct, and much of his journal is now confirmed by the new fossil evidence found in 1974. I spent 10 days on the island in November of that year, investigating caves on the north-west coast, near the town of St.-Paul. It is known that the caves were inhabited in the seventeenth century by the first French settlers to reach the island, and in investigating these rock shelters it was hoped that bird bones would be found, perhaps in kitchen middens, which would reflect the early endemic avifauna. In April 1974, B. Kervazo had conducted excavations in two of the caves (Bour 1979), and through the kindness of Dr Dorst, Director of the Muséum National d'Históire Naturelle, Paris, permission was granted for the examination and identification of the resulting material. The Kervazo collection has added much to our knowledge of the extinct avifauna of Réunion.

During November 1974 a visit was also made to a subterranean tunnel near the village of la Saline, West Réunion. The Caverne Vergoz, so named after M. Armand Vergoz who was first to discover bones in the cavern entrance, is situated on a seaward-facing slope called Bois de Nèfles. The tunnel, probably an old lava tube, descends quite steeply at an angle towards the sea. The interior is wet and receives the drainage from the soil above. Small stalactites hang from the roof. In the damp mud of the floor, bones were found of the extant Audubon's Shearwater *Puffinus lherminieri* and Wedge-tailed Shearwater *P. pacificus*, which still breed on Réunion. With these bones were found those of the giant tortoise *Geochelone* sp. which became extinct on Réunion in the nineteenth century (Arnold 1980, Bour 1981; Chapter 1). Tortoise bones were also found in the coastal caves near St.-Paul, together with those of a large extinct skink *Leiolopisma telfairii* not previously known from Réunion (Arnold 1980). It seems possible that the petrel bones are contemporary with the extinct reptile remains.

A 1-day excursion was made to an inland area called Plaine des Cafres, a large area of flat heathland about 1676 m above sea level. It was here that th

flightless rail-like bird the *oiseau bleu* was said to have lived. The bird is known only from descriptions in the early literature of the island (Olson 1977; Chapter 1), but has been given the scientific name *Porphyrio caerulescens* (Sélys-Longchamps 1848). In the part of the plain which was visited there were no visible caves to explore and it was decided that a very careful study of the area would be necessary before any excavating is undertaken.

Rodrigues

François Leguat (1708), who landed on the uninhabited island in 1691, gave the earliest known account of the flora and fauna. He found the island fertile, with good vegetation and fresh-water streams. Rodrigues was rather different when visited in November 1974. There had been no rain for almost a year, the country was parched, the vegetation sparse, and water was in very short supply. Leguat described the birds of the island including the flightless Solitaire which, together with parrots, other birds and giant tortoises, his exiled Huguenot party captured for food. Leguat and his companions left the island after 2 years. Thirty-two years later, in 1725, Tafforet, a naval officer on board the sailing ship *La Ressource*, was marooned on Rodrigues with a survey party of four men for 9 months (North-Coombes 1971). An anonymous account of the now extinct avifauna described in the manuscript 'Relation de l'île Rodrigue' written about 1726, has been attributed to Tafforet by Dupon (1969). Some time after 1750 settlers came to the island; cats and other domestic animals were introduced, tortoises were exported from the island for food, and many of the endemic animals soon became extinct.

About 1789 (or 1786: see Chapter 1) bones heavily encrusted with a mineral deposit were discovered inside a cave situated on the Plaine Corail apparently by Mr Labistour, a resident of the island, and sent to the anatomist Cuvier in Paris (Strickland & Melville 1848). In 1832 Telfair (1833) announced that Colonel Dawkins, Secretary to the Governor of Mauritius, had visited the caves in which the bones had previously been found and had succeeded in finding more. At about the same time Mr Eudes, a resident of the island, was also successful in excavating bones "of a large bird which no longer exists on the island". The bones were presented to the Zoological Society of London and the Andersonian Museum, Glasgow (Strickland & Melville 1848). In 1845 Captain Kelly of HMS *Conway* made an unsuccessful search for the exact locality of the excavation. The bones presented to Paris and Glasgow were examined and Strickland rightly concluded that they all belonged to the same species, the extinct Solitaire (*Pezophaps solitaria*) which Leguat had described.

Edward Newton (1865*a*) visited Rodrigues in 1864 in order to investigate the caves. In one of them he found remains of a giant tortoise and two bird bones. One of the bird bones, a tarsometatarsus, fitted the illustration of the Solitaire bones shown in Strickland & Melville's book. A third Solitaire bone was given to Newton by a Captain Barclay. Newton's hurried visit to Rodrigues was fortunately supplemented by the work of George Jenner, the magistrate of the island, who succeeded in uncovering bones which represented 16 individuals in the caves of Plaine Corail. The bones were despatched to Alfred Newton while Jenner continued to direct the digging inside the caves. In 1866 Newton sent four Indian labourers from Mauritius to work at the excavations under the supervision of police sergeant Morris. Nearly 2000 bones and fragments were excavated by this party and the results published by the Newton brothers in 1869, and Günther & E. Newton (in 1879).

H. Slater, one of the naturalists accompanying the Transit of Venus Expedition, visited Rodrigues in 1874 with special instructions to investigate the caves. With the assistance of nine men to dig, and a cook, he set out for the caves on the Plaine Corail in small boats from Port Mathurin on the north coast, the country being so rough that he would not have been able to carry his equipment overland without great expense (Slater 1879*a*). (In 1974, exactly 100 years after Slater's visit, the journey was made quickly by Land Rover from Port Mathurin to the caves with little trouble over fairly good roads.) Slater carried out his tasks in the caves thoroughly, although he remarked that he was surprised to find how much excavation had already been done: "Out of the first 13 caves, I found 12 to bear the unmistakeable signs of previous research". A report on Slater's important collection, combined with that of Jenner, was published by Günther & E. Newton (1879) and E. Newton & Clark (1879), adding greatly to the knowledge of the extinct avifauna of Rodrigues. In addition to the Solitaire, bones of other extinct birds had been collected, including an owl, pigeon, parrot, rail, heron and starling. A year after Slater's visit, more

›ones, including two almost complete Solitaire skele-ons, were found in a cave by J. Caldwell, ably assisted ›y Sergeant Morris (Caldwell 1875).

The caves

Cheke (1974*a*) discussed cave nomenclature; here I use current local names. The caves are situated in the south-west of the island in the region named Plaine Corail, a flattish area sloping gently towards the sea. It is here that the island's small airfield is situated. Plaine Corail is composed mainly of calcarenite limestone (McDougall, Upton & Wadsworth 1965) with very little soil and a thin covering of sparse low vegetation. In places the surface limestone has been eroded into small pinnacles. With one exception (Caverne Tamarin) the caves visited lie beneath the surface of the limestone plain and might be described as 'pot-holes', as access is possible only by descent. Caverne Tamarin is situated on the northern edge of the limestone escarpment and can be entered from ground level. Below the surface of the flat plain is a labyrinth of tunnels and subterranean passageways which have been cut out of the limestone probably by the action of water. In 1974 water was found in two caves despite the island's drought. Balfour (1879*a*) suggested that the island was once at a lower level than at present, as he found evidence of raised beaches, so perhaps some caves were formed by sea action. The floor of most caves had a deposit of reddish soil brought down from the higher ground by the heavy seasonal rains, and ripple marks on this soil showed that at times water still flows through some of the tunnels. The cave entrances, with the exception of Caverne Tamarin, have been formed by the collapse of part of the tunnel roofs, and may be of any size from a small hole a metre or so wide, to a deep valley open to the sky with the original tunnel continuing as caves at either end. One of these valleys is perhaps 30 m deep and about 400 m in length and affords such good protection from wind and sun that quite large trees have grown in it; because the valleys are below the level of the plain they are not visible until one stands at the edge. Probably because of the difficulty of providing sufficient light further inside the caves, most of the digging by previous excavators took place just inside the cave entrances where the daylight penetrated, and in Caverne Tamarin there are still signs of the work which was carried out some years ago. Slater found the red cave soil soft and easy to dig, but the soil in Caverne Tamarin has since been consolidated by the feet of cattle which are penned up in the cave during cyclones. In Grande Caverne, one of the larger caves, the soil of the main tunnel has been trampled hard by the feet of tourists who are at times taken through by guides. This cave is spectacular, with large stalagmites and stalactites, the roof being about 12 m high in places, but it was in the low-roofed side-tunnels that the new bone material was collected.

Caverne Tamarin was also explored, together with many smaller caves, where the roofs are so low that progress could be made only by crawling on hands and knees. The interiors of the caves are completely dark, and light for exploration was provided by a battery torch fitted on a head-band and by a hand-held battery lantern. Light for excavating was supplied by a small portable lamp which gave 75 watts of illumination for 5 hours. For digging a folding shovel and a small trowel were used.

Systematic list of Mascarene subfossil material

Procellariidae

Pterodroma sp. nov., Rodrigues. An extinct new species of large petrel is represented by bones obtained in the caves of Rodrigues. It may perhaps be the petrel referred to by Tafforet (*c.* 1726), which was said to nest in holes in the ground on the higher parts of the mountains.

Pterodroma aterrima, Rodrigues. The Mascarene Petrel *P. aterrima* is today confined to Réunion, but an upper jaw was correctly identified by Bourne (1968) from a nineteenth-century collection of bones from Rodrigues in the BMNH(P).

Podicipedidae

Podiceps gadowi, see *Numenius phaeopus* (p. 96).

Phaethontidae

Phaethon lepturus, Rodrigues. At least 25 skulls and many other bones of the White-tailed Tropic-bird have been found by the eighteenth-century and 1974 expeditions to Rodrigues. The species is common on Mauritius and occurs on Réunion; on Rodrigues it is now rare (Staub 1973, Cheke 1974*a*). From the subfossil evidence it would appear that *P. lepturus* was common, most probably breeding, on the main island of Rodrigues at some time in the past.

Phalacrocoracidae

Phalacrocorax africanus, Mauritius. The bones described as a darter *Anhinga (Plotus) nana* by E. Newton & Gadow (1893) were re-identified by Olson (1975) as the extant cormorant *Phalacrocorax africanus*. This is the first evidence of the Long-tailed Cormorant occurring in the Mascarene Islands.

Anhinga (Plotus) nana, see *Phalacrocorax africanus*

Sulidae

Sula abbotti, Mauritius. A humerus and ulna excavated in the Mare aux Songes ("Gannet": E. Newton & Gadow 1893), were said by Bourne (1976) to resemble the bones of the extant Abbott's Booby *S. abbotti*. The species had not previously been positively identified from the islands.

Ardeidae

Nycticorax mauritianus, Mauritius. Seven fossil bones from a heron, found in the Mare aux Songes, were described as *Butorides mauritianus* by E. Newton & Gadow (1893). Of these bones only two are available for study today: the coracoid and a tarsometatarsus. The radius has been shown not to belong to the Ardeidae. Examination of the bones suggests a closer relationship to the night-herons *Nycticorax* than to the genus *Butorides* (*Ardeola*). Measurements taken from the extant species *N. nycticorax* confirm that the tarsometatarsus of *N. mauritianus* is more robust and longer, not shorter as might be suggested by the term "short footed heron" applied by E. Newton & Gadow and perhaps misinterpreted later by Hachisuka (1953) as being a very small bird. The tarsometatarsus of *N. mauritianus* is short only in comparison with species of genus *Ardea*, to which Rothschild (1907*b*) referred it.

Nycticorax megacephalus, Rodrigues. This was originally described by Milne-Edwards (1873) from several bones, including a complete sternum and skull, as *Ardea megacephala*. The recent discovery of a previously unknown cranium in the BMNH(P) confirms the opinion of Günther & E. Newton (1879) that the bones represent an extinct night-heron in the genus *Nycticorax*, and not *Ardea*.

Doubt must also be cast on the supposed total flightlessness of the bird (Hachisuka 1953). Milne-Edwards (1873) and Günther & E. Newton (1879) suggested the bird had reduced powers of flight and indeed it was stated by an early voyager to Rodrigues that the bird flew only a little, and ran away when chased (Tafforet *c.* 1726). In their table of measurements Günther and E. Newton unknowingly used a skeleton of the large South American race *N. n. obscurus*. Comparison with this skeleton gave the impression that the wings of *N. megacephalus* were unusually small, but they are not small by comparison with *N. n. nycticorax*. The femur, tibiotarsus and tarsometatarsus of *N. megacephalus* are broader, longer and more robust than those of *N. n. nycticorax* and, like other species endemic to oceanic islands, the legs of *N. megacephalus* have become stronger as the need to fly decreased.

Nycticorax sp. nov., Réunion. The first osteological evidence to show that a species of *Nycticorax* also occurred on Réunion was obtained from the caves near St.-Paul in 1974. The incomplete tibiotarsus suggests that the extinct Réunion night-heron was probably longer in the leg than either *N. mauritianus* or *N. megacephalus*.

The historical record contains several references to 'bitterns' on all three islands, although there is no evidence that *Ixobrychus* or *Botaurus* has ever been found there. On Mauritius in 1696 Leguat stated "You shall see great flights of bitterns" (Oliver 1891). On Rodrigues Tafforet (*c.* 1726) wrote "There are plenty of bitterns . . . They are the size of an egret". Leguat also wrote of Rodrigues during 1691–3, "We had bitterns as big as fat capons" (Oliver 1891). On Réunion during 1671–2 Dubois (1674) described "Bitterns or Great Egrettes . . . they have grey plumage, each feather tipped with white . . . and the feet green". Berlioz (1946) thought Dubois' description reminiscent of a *Nycticorax* in immature plumage and it seems quite possible that all references to 'bitterns' were really night-herons. In stance and in immature plumage a night-heron appears very much like a bittern. The historical and osteological evidence confirms that an endemic species of *Nycticorax* occurred in each of the three Mascarene Islands, at least until the late seventeenth century.

Ciconiidae

Ciconia sp. nov., Réunion. A distal part of a tarsometatarsus found in the caves near St.-Paul in 1974 is the first positive evidence that a stork once inhabited the Mascarene Islands. This recent dis-

covery may explain the identity of the bird recorded by Dubois who wrote (translated by Oliver 1897) "There are great birds of the height of a man because of their legs and neck which are very long. They have a body as large as the geese and plumage white and black at the point of the wings". Dubois referred to these birds as *"flamands"* and they may indeed have been flamingos *Phoenicopterus* sp., or perhaps the hypothetical giant bird of Mauritius *Leguatia gigantea* (see Chapter 1). The bone from Réunion is certainly that of a stork *Ciconia*, and Dubois' description could also fit a bird of this genus.

Anatidae

Sheldgoose sp. nov., Réunion. An upper jaw, sterna and other bones have been found in the cave near St.-Paul and represent a new extinct genus of short-billed Sheldgoose. Geese were said to be common on the fresh water near St.-Paul (Chapter 1) and Dubois (1674) described them as follows: "Wild Geese, a little smaller than the geese of Europe, they have the plumage the same and the beak and feet red". There are no wild species of geese living on Réunion today.

Alopochen mauritianus, Mauritius. This was described from a carpometacarpus by E. Newton & Gadow (1893) as *Sarcidiornis mauritianus*. However, Andrews (1897) showed that it was related not to the Comb Ducks *Sarcidiornis* but to the goose *Alopochen*. A second carpometacarpus from the Mare aux Songes recently discovered in the BMNH(P) confirms Andrews' conclusion.

Fossil bones of a duck *Aldabranas cabri*, described by Harrison & Walker (1978) from a femur and incomplete humerus collected on Aldabra Is., are said to resemble some of the characters found in the Sheldgoose *Alopochen*, but a direct relationship was not inferred.

Anas theodori, Mauritius. E. Newton & Gadow (1893) described the bones of a duck found in the Mare aux Songes and named it in honour of Théodore Sauzier. The incomplete sternum, coracoid, humeri and tibiotarsi are now supplemented by a previously uninvestigated cranium from the Thirioux collection. A recent study of the cranium confirms a dissimilarity to any other extant duck species already recorded from Mauritius. It has been concluded that it is the first known cranium of *Anas theodori* and differs significantly from those of other species.

Accipitridae

Accipiter alphonsi, see *Circus alphonsi* below.

Circus alphonsi, Mauritius. Milne-Edwards (1873) described two tibiotarsi from the Mare aux Songes as belonging to the genus *Astur* (= *Accipiter*). E. Newton & Gadow (1893), while describing further material obtained from the site, applied the name *A. alphonsi* to them although it appears from the rather contradictory text that they could find no difference between the excavated bones and those of *Accipiter melanoleucus*. However, recent comparisons made between the bones from Mauritius and those of the genera *Accipiter* and *Circus* show a quite obvious likeness to *Circus* rather than *Accipiter*. The tarsometatarsus, tibiotarsus and carpometacarpus are similar to bones of the extant Réunion Marsh Harrier *C. maillardi*, but until skeletal material of the latter is available the specific name of the harrier of Mauritius must remain in some doubt.

Falconidae

Falco sp. nov., Réunion. Bones from an extinct kestrel have been obtained from the caves near St.-Paul, and the bird called 'Merlin' of Réunion can now be identified. Dubois (1674, English translation by Oliver 1897) mentioned three different birds of prey on Réunion, of which only the Réunion Marsh Harrier or *papangue Circus maillardi* remains resident on the island. The identity of the *pieds jaunes* is explained by Verreaux (1863) who noted that the Réunion Marsh Harrier, when in immature plumage, is called by this name by the islanders. There seems little doubt that *papangues* and *pieds jaunes* were names given to the same bird and are still used (Barré and Barau 1982), though Cheke (1982*b* and Chapter 1) suggests *pieds jaunes* refers to the Sooty Falcon *Falco concolor*.

The third bird of prey referred to by Dubois can now also be identified, because confirmatory bone material has been found. Continuing his account of the birds of prey, Dubois wrote: "The third kind are Merlins [*emerillons*], which although small, still do not fail to carry off chickens and eat them". The word 'chickens' here means the young chicks of birds, not domestic fowl. (The original word is "poulet", normally used for domestic fowl, rather than "poussin" (baby bird) (ed.)). The Eurasian Merlin *Falco columbarius* is similar in size to a kestrel, of which several species are found on Indian Ocean islands (Chapter 5). It is not surprising that Réunion too should have

supported an endemic kestrel, which was common enough in Dubois' time for him to comment on its habits. Since the seventeenth century it has become extinct, as have many of the other birds he listed.

Rallidae

Aphanapteryx bonasia, Mauritius. A large flightless rail with a long bill called *poule rouge* (red hen) has been known from the historical record since Cauche wrote of it in 1638 (published 1651). A painting by Hoefnagel made about 1610 and discovered by Frauenfeld (1868) depicts the rail with a decurved bill, long legs and reddish-brown plumage. The former existence of the bird was confirmed by Milne-Edwards (1868), who identified bones obtained from the Mare aux Songes, and used the name *Aphanapteryx broeckei* (Schlegel) for the rail. E. Newton & Gadow (1893) studied further bones from the site, and a cranium was described by Piveteau (1945). Hachisuka (1953) discussed the historical, pictorial and osteological evidence, and Olson (1977) produced a very comprehensive review of the species, giving the reasons for reverting to the name *A. bonasia*. It is thought that the bird became extinct around 1700 (Chapter 1).

Aphanapteryx leguati, Rodrigues. François Leguat (1708) saw this species alive on Rodrigues in 1691. He recorded the plumage as being bright grey, unlike *bonasia* of Mauritius which was reddish. The rail could not fly and was known to Leguat as a *Gellinote* (Woodhen). Tafforet (*c.* 1726) provided an additional record of the field characters and noted that the plumage was flecked white and grey, feet and bill red, and that it was similar in some ways to that of a Curlew; he also confirmed that it was unable to fly. Milne-Edwards (1874) provided confirmation of the sight records, when he recognised that the bones from the caves on Rodrigues belonged to a large rail which he named *Erythromachus leguati*. Günther & E. Newton (1879) examined additional material from the caves on Plaine Corail, and concluded that *leguati* should be placed in the genus *Aphanapteryx*. Olson (1977) thoroughly reviewed all the data relating to the species, which is now extinct. Further material was collected in 1974.

Dryolimnas cuvieri, Mauritius. Bones from the Mare aux Songes, now in the UMZC, were identified as "Water-hen" by E. Newton & Gadow (1893, p. 282) and marked *Gallinula chloropus pyrrhorrhoa*, the Madagascar Moorhen, which is a common resident on Mauritius (Rountree *et al.* 1952) and also occurs on Réunion (Chapter 6). The bones are not, however, those of *Gallinula* but are *Dryolimnas cuvieri*, the White-throated Rail, a bird which no longer exists on Mauritius but still inhabits Madagascar and Aldabra and has been extirpated from Assumption Is. (Benson 1967). The only other evidence of *Dryolimnas cuvieri* occurring on Mauritius is the holotype study skin in the MNHM, collected in January 1809 from the Plain of St.-Martin in the west of the island.

It is possible that the bird illustrated in the journal of Thomas Herbert (1634), which has caused so much discussion amongst various authors over the years, and has been known as 'Herbert's Hen' (*Didus herberti*: Schlegel 1854), may be *Dryolimnas cuvieri*.

Fulica newtonii. Mauritius, Réunion. The first known osteological remains of a Coot in Réunion were recovered in 1974 from a cave near St.-Paul. *Poules d'eau* (water-hens) were recorded by Dubois (1674) as being present on Réunion in the early 1670s, but actual evidence of the coot's existence has, until now, been found only on Mauritius (Milne-Edwards 1867*a*). A comparative study of the bones has shown that the long- and strong-legged coot of Réunion is identical in anatomical details to *F. newtonii* of Mauritius, which may have become rare on that island by 1693 (Leguat 1708). The populations of the two islands form a monotypic extinct species. Olson (1977) suggested *F. newtonii* was probably derived from the extant *F. atra*.

Charadriidae

Numenius phaeopus, Mauritius. The single ulna said to be from the wing of an extinct grebe *Podicepes* [*sic*] sp. by E. Newton & Gadow (1893) (*Podiceps gadowi* of Hachisuka 1953), is in fact the ulna of a Whimbrel, which is a common migrant to the islands (Rountree *et al.* 1952).

Raphidae

Raphus cucullatus, Mauritius. Only the head and foot of the Dodo had been studied prior to the discovery by Clark (1866) that quantities of bones were deposited in the Mare aux Songes. Since 1866 the osteology of the bird has been the subject of much research. Hachisuka (1953) documented the data, extending the bibliography of Strickland & Melville (1848) up to 1941. Several museums and institutions

throughout the world contain composite Dodo skeletons, constructed from the many bones found in the Mare aux Songes. It is generally accepted on osteological characters that the affinities of the Dodo lie close to the pigeons in the family Columbidae.

Pezophaps solitaria, Rodrigues. Since the discovery of the first Solitaire bones in the Rodrigues caves in about 1786, it has been stated that over 2000 bones and fragments have been collected, mostly in the years 1864 to 1875. E. Newton & Clark (1879) remarked: "We are not aware that the osteology of any vertebrate, other than man, has been studied with the same wealth of material as that of the Solitaire". There is very little fresh information at present that can be added to the early osteological studies (A. & E. Newton 1870, E. Newton & Clark 1879). The bone evidence confirmed the written account and drawings made by Leguat, who stated that there was a large flightless endemic bird which was good to eat and extremely fat, weighing as much as 45 pounds (20 kg), and described its habits and behaviour in some detail. It is still a matter of conjecture how so many Solitaires found their way into the Plaine Corail caves. Caldwell (1875) found two almost complete skeletons and suggested that the birds had sought shelter in the caves during a "hurricane" and died. The caves which Caldwell explored showed no signs of the action of water as did some of the caves which were visited in 1974. E. Newton thought that pigs might have destroyed the population; another theory (supported by North-Coombes 1971) is that a devastating fire may have driven the birds into the caves where they died.

Caldwell found gizzard stones *in situ* beneath the sternum and ribs of nearly complete Solitaire skeletons, confirming Leguat's statement that large stones, which he used for sharpening knives, could be found in the Solitaire's gizzard. Caldwell mentioned that the stones he found were basalt (dolerite: E. Newton & Clark 1879), a rock not seen by Caldwell within 2 miles (3 km) of the limestone plain. Temple (1977*b*) has suggested that the gizzard stones of the Mauritius Dodo *Raphus cucullatus* helped to remove the hard outer covering of large seeds, a process he believed was necessary to ensure the successful germination of the now nearly extinct tree *Calvaria major* on Mauritius. Wiehé (1949) mentioned that *Calvaria galeata* was probably a dominant tree in the original Rodrigues forest formation, but is now rare. Possibly trituration in the gizzard of the Solitaire helped the seeds of some Rodrigues plants to germinate (but see Chapter 1 where Cheke argues against Temple's hypothesis).

The relationship between the Solitaire and the Dodo was discussed by Strickland & Melville (1848), and by Storer (1970), who argued that the two birds were derived independently from flying ancestors and should be placed in separate monotypic families, Pezophapidae and Raphidae. There is no osteological evidence supporting the suggestion that a Solitaire-like or a Dodo-like bird once existed on Réunion (Hachisuka 1937, 1953), although the bones may only await discovery.

A comprehensive bibliography of the family is given by Strickland & Melville (1848) and Hachisuka (1953).

Columbidae

Alectroenas rodericana, Rodrigues. Milne-Edwards (1874) identified a sternum and other bones from the caves on Rodrigues as a pigeon *Columba rodericana*. The sternum is, as Milne-Edwards pointed out, quite unlike that of any living genus known today; it may warrant separate generic status in the family Columbidae. Additional material collected in 1974 helps little to settle the affinities of the species. However, at present it is placed in *Alectroenas*, together with the extinct pigeon of Mauritius *A. nitidissima*, which is known only from three skins.

Leguat (1708) apparently saw *A. rodericana* on Rodrigues. It was somewhat smaller than "ours", he writes (presumably comparing it with *Columba livia*), grey in colour and very tame.

Psittacidae

Lophopsittacus mauritianus, Mauritius. There seems little doubt that flocks of parrots were present on Mauritius in the early seventeenth century. The eventual extermination of all endemic species, with the exception of the rare resident *Psittacula echo*, was probably caused or at least helped by the sailors and early visitors, who killed the parrots for food. A woodcut in the journal by Willem van West-Zanen (reproduced in Hachisuka 1953) depicts men catching large parrots in Mauritius about the year 1602.

Owen (1866) recognised and described a massive lower mandible and a tarsometatarsus as belonging to a large macaw-sized parrot. E. Newton & Gadow (1893) examined further material obtained by Sauzier

from the Mare aux Songes, adding details of the femur, tibiotarsus and incomplete sternum to the record. The first known cranium of this extinct parrot has now been discovered in the collection of the BMNH(O).

Lophopsittacus bensoni, Mauritius. A second, and smaller species of *Lophopsittacus* was named by Holyoak (1973) from a lower mandible, palatine and tarsometatarsi collected by Thirioux in the caves near Port Louis. Mr Norman, late of the UMZC, has pointed out (pers. comm.) that the photographs of the holotype lower jaw, said to be (*a*) dorsal view and (*b*) ventral view, are in fact two quite separate specimens. Also, although marked 8/10 magnification, they are almost natural size. It is not at all certain that *bensoni* should have been placed in the genus *Lophopsittacus*.

Necropsittacus rodericanus, Rodrigues. Leguat (1708) and Tafforet (*c.* 1726) both provided details of the plumage and feeding habits (recounted in Hachisuka 1953 and Staub 1973*b*) of two Rodrigues parrots then common, but which no longer exist. From these field descriptions one species, the Rodrigues Parakeet *Psittacula exsul*, can easily be recognized as it is fortunately represented by two study skins. The other parrot, said to be larger than *P. exsul* and to have all green plumage, a long tail, large head and bill, is generally accepted to be *Necropsittacus rodericanus*, the fossil species named by Milne-Edwards (1867*b*) from an upper jaw discovered in the caves of Plaine Corail by Jenner. Günther and E. Newton (1879) illustrated a cranium and other bones of *N. rodericanus* from the collection of Jenner and Slater. This additional material helped maintain the theory of Milne-Edwards that the affinities of the parrot lie close to the genus *Psittacula*. The peculiarities of the cranium, however, keep *rodericanus* in the separate genus *Necropsittacus* as proposed by Milne-Edwards (1873). No further material of the parrot has since been collected but a comparative study of the recently found cranium of *Lophopsittacus mauritianus* and *N. rodericanus* shows that there is probably no very close relationship between the two island species of large-headed parrots from Mauritius and Rodrigues.

Psittacula exsul, Rodrigues. Parrots were apparently common on Rodrigues in the late seventeenth century. Two species were seen by Leguat in 1691, one of which, *Psittacula exsul*, was said to be in "abundance". Both Jenner and Slater collected bones of *P. exsul* in the caves (Günther & E. Newton 1879), and a proximal end of a tibiotarsus collected in 1974 from the same area agrees well with the material in the BMNH(P). Two study skins of *P. exsul* are preserved, from which A. Newton (1872) first described the species, which was last seen in 1875 (Chapter 1).

Strigiformes

'Tyto' sauzieri, Mauritius, Réunion. New fossil evidence confirms that owls once inhabited all three islands of the Mascarene group. Bones collected in 1974 on Réunion are the first indication that a nocturnal bird of prey existed on this island. Previously, as Berlioz (1946) pointed out, no member of the Order Strigiformes had been recorded from Réunion (except for the rather prophetic misprint in a table of island species in Greenway 1967). Réunion owls were not mentioned by Dubois (1674), so the bird was either extinct before his visit in 1671–2, or was overlooked.

Comparison of the Réunion bones with those of *sauzieri*, named by E. Newton & Gadow (1893), shows them to be very similar, and there seems to be no definite osteological character on which to separate the two populations. E. Newton & Gadow placed *sauzieri* in the genus *Strix*, which is now *Tyto* (the barn owls) and not *Strix* as applied to the wood owls of today. Re-examination of the Mauritius material, however, shows clearly that *sauzieri* is not related to *Tyto*. Some osteological characters of the pelvis are not found in other extant genera and a new genus may have to be erected for the Mascarene owls.

'Tyto' newtoni, Mauritius. This was named by Rothschild (1907*b*), from two tarsometatarsi, smaller than those of *sauzieri*, but probably synonymous with *sauzieri*.

'Tyto', 'Ninox' murivora, Rodrigues. In 1874 Milne-Edwards described as *Strix* (*Athene*) *murivora* an extinct species of owl from bones discovered in the caves of Rodrigues. Since that time, all subsequent authors have continued with the mistaken supposition that the Rodrigues owl *murivora* was a member of the genus *Athene* (or *Carine*: Günther & E. Newton 1879). Milne-Edwards used comparative osteological material named *Athene superiliaris* and *A. polleni*, but shortly after his publication, both species (now con-

sidered conspecific) were placed in the genus *Ninox*, where they have remained ever since. Overlooked too has been the greater emphasis placed by Milne-Edwards upon *Strix* (now Tyto) in his original description, and '*Strix murivora*' in the caption to his plate 11.

The remains of *murivora* show that the owl is not related to *Tyto* or to the present-day *Athene*. The pelves of *murivora* and *sauzieri* share the same unusual osteological characters not found in any other extant genera, and strongly suggest a close relationship between the two extinct species. The owl *sauzieri* of Mauritius and Réunion has longer and slimmer legs than those of the Rodrigues Owl *murivora*, and therefore the separate species are retained.

Timaliinae

Babbler, sp. nov., about thrush size, Rodrigues. An incomplete sternum collected from Rodrigues in 1974 is from a bird in the Order Passeriformes, about the size of a small thrush. The unique characters of the sternum, which differ greatly from those of other genera examined, have prompted the bird's assignment to a new genus, and represent a new species of extinct Mascarene Island passerine. The genus has provisionally been placed in the subfamily Timaliinae.

Pycnonotidae

Hypsipetes sp. nov., Rodrigues. Bones representing a new species of extinct bulbul have been identified from material collected in 1974.

Sturnidae

Necropsar rodericanus, Rodrigues. H. Slater was a member of the 1874 Transit of Venus Expedition and while on Rodrigues was first to discover and recognise bones of an extinct starling. Günther & E. Newton (1879) described, illustrated and named the material *Necropsar rodericanus*. Further material was collected in 1974 and examination of the remains confirms that they are from a bird in the family Sturnidae. It is possibly related to the extinct Crested Starling of Réunion *Fregilupus varius*, known from several skins and dissected specimens. Berger (1957) after studying the anatomy of *F. varius* concluded that it was not a starling and suggested a possible relationship to the family Prionopidae. *Necropsar rodericanus*, however, is closer osteologically to Sturnidae.

Discussion

The present evidence indicates that at least 30 endemic species of birds have been lost to the Mascarene Islands in the short period since records of the avifauna were first compiled, just over 300 years ago. Many different factors probably combined to cause the extinction of the birds; these are discussed in detail by Cheke (Chapter 1). Here I discuss possible reasons for the accumulation of bones in the few sites from which they are known.

It has been suggested by some authors that a severe fire once swept Rodrigues, causing the flightless Solitaires to seek shelter in the caves where some complete skeletons were later found. E. Newton (1865*a*), however, could find no evidence to support the fire theory. Prolonged drought, especially on Rodrigues where water is scarce in the dry season, must have resulted in a reduction of the bird populations, sometimes perhaps to dangerously low levels from which they never recovered. Birds unable to fly into the mountain range, where some springs continued to flow, may have entered the caves of Plaine Corail in a search for water, and died there. In the dry season of 1974 small streams and pools of water certainly did exist inside some caves. At other times of the year heavy rain in the wet season and high winds associated with the cyclonic period must also cause the death of some birds. Large flightless birds such as the rail *Aphanapteryx* and the Dodo would perhaps be most susceptible to waterlogging of plumage and death by hypothermia. There has been such a diversity of species recovered from the marsh, it would seem that a natural catastrophe such as severe weather was responsible for the bone deposits, although tortoises may have become trapped in the mud while at the edge of the marsh. Bones accumulated in the marsh because it received the surface water draining from the surrounding high country, and heavy rain may have carried down bones or carcasses, together with the alluvium seen by Clark (1866) which remained trapped in the marsh as the water drained out to sea. On Rodrigues, it is also possible that bones were deposited when birds fell into the underground tunnel system beneath Plaine Corail. Indeed, deep inside one cave in 1974 I saw the carcass of a goat which seemed to have fallen in through a hole when the tunnel roof collapsed.

On Réunion the bones found in the coastal caves may have been the result of early human occupation.

Bour (1979) suggested that a cyclone may have taken the birds to the vicinity. Petrel and shearwater bones were probably contained in burrows in the ground above the caves and as the cave roofs collapsed the soil containing the bones then fell to the floor. Many of the species found at St.-Paul were associated with water and some old maps show a lagoon close to the caves which would have attracted coots, herons and geese. These would have been easily captured by early settlers or mariners and St.-Paul is known to have been a port for sailing ships where fresh stores were taken aboard.

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