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Contrasting Taphofacies in Ocean Island Settings: The Fossil Record of Mascarene Vertebrates

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Resum

Les Illes Mascarenyes, que comprenen Mauritius, La Réunion i Rodrigues, estan situades a l'Oceà Índic sud-occidental i són d'origen volcànic. Històricament, les illes estaven habitades per un nombre d'espècies endèmiques, el millor exemple de les quals és el dodó de Mauritius, *Raphus cucullatus*. Encara que hi ha referències sobre l'ecologia de Mauritius als diaris i quaderns de bitàcola dels vaixells, no fou fins el descobriment dels primers materials fòssils que es va poder percebre la composició faunística original. A Mauritius, als aiguamolls de Mare aux Songes, el 1865 varen ser descoberts nombrosos materials fòssils, mentre que es varen fer altres col·leccions a coves de valls poc fondes, particularment a la cadena muntanyenca de Le Pouce. A Rodrigues, les coves calcàries situades a la Plaine Corail han subministrat centenars de fòssils, principalment recol·lectats a les darreries del segle XIX. A La Réunion, les primeres restes fòssils varen ser descobertes el 1974, a talls dels penya-segats; s'ha trobat material subfòssil a aiguamolls i a localitats cavernícoles. Totes les restes fòssils són de l'Holocè. Alguns dels dipòsits fossilífers de les Mascarenyes presenten biaixos tafonòmics; en concret, els dipòsits dels aiguamolls són pobres en restes de petits vertebrats, com, per exemple, passerins. A Mauritius quasi no s'han trobat materials esquelètics a cap cova o tub volcànic, i els dipòsits de Mare aux Songes presenten biaixos elementals. A Rodrigues s'han conservat ocells marins, el solitari, *Pezophaps solitaria*, i la tortuga gegant, *Cylindraspis* sp., i relativament pocs ocells terrestres. Els sistemes cavernícoles i els tubs de lava són rars a Mauritius i La Réunion, i, a partir de les restes d'animals introduïts descobertes als tubs de lava de La Réunion, és clar que els elements esquelètics es degraden molt aviat. A més, als dipòsits d'aiguamolls s'han trobat centenars de restes de tortugues, mentre que, pel contrari, els ocells petits i de mida mitjana virtualment no s'hi troben.

Aquest treball descriu la situació tafonòmica de diferents localitats fossilíferes i fa comparacions, emprant el microscopi electrònic d'escandallatge, entre espècimens fòssils de cada dipòsit. Es presenta evidència de la geologia, topografia, estratigrafia i sedimentologia, i es discuteixen els paleoambients, vida mitjana, carronyeig, activitat antropogènica, biaixos de recol·lecció i probabilitat d'entrampament, en relació amb la preservació dels elements. Malgrat els materials de les Mascarenyes són holocènics, els problemes que comporten són complexes, i la interpretació de qualsevol registre fòssil aparentment recent s'ha d'emprendre amb molta cura.

Paraules clau: Mauritius, La Réunion, Rodrigues , localitats fossilíferes, tafonomia, biaixos en el registre fòssil.

Summary

The Mascarene Islands are situated in the southwest Indian Ocean and are volcanic in origin. Historically, the islands were inhabited by a number of endemic species, and although references were made about Mascarene ecology in ships' logs and journals, it was not until the discovery of the first fossil material that the diversity of the original fauna could be established. All of the fossil remains are Holocene. Some of the Mascarene fossil deposits exhibit marked taphonomic bias; in particular; the marsh and Réunion cave deposits are depauperate in small vertebrate remains, e.g. passerines, despite their presence being known from other evidence. On Rodrigues, comparatively few land birds other than solitaire *Pezophaps solitaria* and giant tortoise *Cylindraspis* sp. have been preserved. Cave systems and lava tunnels are rare on Mauritius and Réunion, and it is clear from the remains of introduced species found in such lava tunnels on Réunion that skeletal elements decay rapidly.

This paper describes the taphonomic setting of the various fossil sites and makes comparisons using SEM and light microscopy between fossil specimens from a range of deposits. Evidence from geology, topography, stratigraphy and sedimentology is presented and bioerosion, geochemistry, scavenging, collecting bias, entrapment and time-averaging are discussed in relation to element preservation. Although the Mascarene material is relatively young <5,000 years, the problems that can be encountered are complex; thus interpretation of any fossil record including recent ones must be approached with caution.

Keywords: Mauritius, Réunion, Rodrigues , fossil localities, taphonomy, bias in the fossil record.

Introduction

The Mascarene Islands comprise Réunion, Mauritius and Rodrigues and are situated in the southwestern Indian Ocean (Fig. 1). Although they share a volcanic origin (Courtillot, 1999), each is significantly different both geologically and biologically. Vertebrate endemism is high within the Mascarenes (Adler, 1994), epitomised by the family Raphidae, comprising the dodo, *Raphus cucullatus* and solitaire *Pezophaps solitaria*. Knowledge of the fossil record of Mauritius began with the discovery of a richly fossiliferous horizon in the Mare aux Songes marsh (Fig.2a) in 1865 (Clark, 1866; Owen, 1866). Most of the now extinct vertebrate species were discovered at this time although additional material was collected from the Mare aux Songes by Théodore Sauzier in 1889 (Newton & Gadow, 1893) and in the early 1900s by the amateur naturalist Etienne Thirioux (Carié, 1916) between 1897-1908. Thirioux collected important material in boulder fields and cliff undercuts at Le Pouce and various other unspecified localities on Mauritius. On Rodrigues, the first skeletal material was discovered, but not described, in the limestone caverns of the Plaine Corail (Fig.2c) in 1789 (Strickland & Melville, 1848; Newton & Newton, 1869). It was not until the 1860s, however, that a thorough survey of the caverns was undertaken (Slater, 1879a,b) and the fossil material described (Milne-Edwards, 1873; Günther & Newton, 1879). Remarkably, fossil localities were unknown on Réunion until 1974 (Kervazo, 1979; Cowles, 1987; 1994; Mourer-Chauviré *et al.*, 1999), when fossils were found in a large cavern on the northwest coast; subsequently new cave (Fig.2b) and marsh deposits have been discovered on Réunion (Mourer-Chauviré *et al.*, 1999).

Unlike many other oceanic islands, Mascarene ecology was comparatively pristine upon its discovery by western man, and although the fossil record is certainly incomplete, contemporary accounts derived from ships' logs and journals provide some indication of the original faunal diversity. Historical records are not necessarily accurate, but fossil remains can corroborate the existence of species mentioned in such accounts.

Each Mascarene Island has or had a comparable fossil depositional environment, i.e. marsh deposits and lava tunnels on Réunion and Mauritius, and cave infillings on all three islands. Here I compare the different fossiliferous deposits from each island and address some of the problems associated with the present Mascarene fossil record, particularly concerning a perceived lack of small vertebrates. The influences of sedimentology, taphonomic presence, topography, time-averaging, geochemistry and collecting bias are examined. Emphasis is placed on avian fossil remains, but data from mammals and reptiles is considered when available.

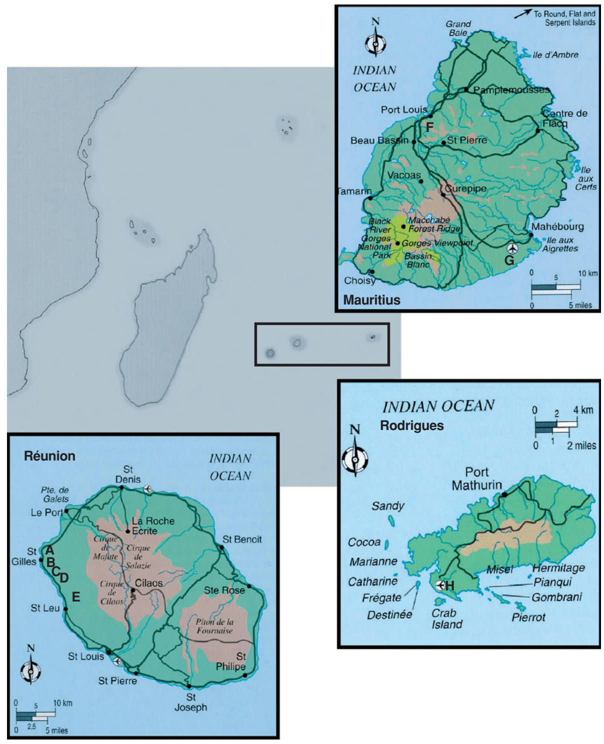


Fig. 1. Map of the Indian Ocean with Mascarenes (inset, middle left). On Mauritius, Réunion and Rodrigues, letters approximate fossil localities.

Fig. 1. *Mapa de l'Oceà Índic amb les Mascarenyes (al centre esquerra, emmarcades). A Mauritius, La Réunion i Rodrigues les lletres indiquen la localització aproximada de les localitats fossilíferes.*

Abreviations

The following abbreviations are used: BMNH, The Natural History Museum, London, England (formerly the British Museum (Natural History)); UMZC, University Museum of Zoology, Cambridge, England; MHNH, Muséum National d'Histoire Naturelle, Paris, France; UCB, Université Claude Bernard-Lyon 1, France; MI, Mauritius Institute.

Geological setting

The Mascarene Islands were created from the same hotspot that produced the vast Deccan Traps lava fields of India, leaving a trail of plateaux, island groups and seamounts across the southwestern Indian Ocean as the Indian plate drifted north (Courtillot, 1999). The hotspot is presently situated approximately 5 km southeast of Réunion (Duncan and Richards, 1991). Mauritius is thought to have developed between 7-9 My and comprises old lavas (> 7My) to young lavas (> 20 000 years); sand and coral deposits are comparatively recent (< 20 000 years) and the island is almost completely surrounded by actively growing reef formations (Montaggioni & Nativel, 1988; Saddul, 1995). Réunion is very much younger with the oldest lavas dated at 3 My (Rivals, 1989). It rises from a 4000m deep oceanic floor to a height of 7000m, but reef formation is extremely limited (Montaggioni & Nativel, 1988). Réunion is also volcanically active; the volcano *Piton de la Fournaise* continues to reshape the southwestern coast, whilst the other major volcano *Piton des Nieges,* although now dormant, catastrophically destroyed much of the island between 300,000 and 200,000 years ago (Mourer-Chauviré *et al.*, 1999). The geology of Rodrigues is less well understood and dating of the island stems from just one study (McDougall *et al.*, 1965). Although the island is presently considered the youngest Mascarene Island at 1.5 My, the faunal composition suggests it is the oldest. Rodrigues is dominated by a central ridge running W.S.W. parallel to its longer axis and is completely surrounded by a vast reef and lagoon extending beyond the shoreline. It reaches 6.5 km to the south, 3.2 km to the west and 6.5 km to the north; no reef is developed on the east side (North-Coombes, 1971; Saddul, 1995). The Mascarenes are basaltic islands and the basalts are transitional between tholeitic and alkalic; both rock suites contain olivine in proportions >5% (olivine basalt) plus plagioclase feldspars and pyroxenes (Saddul, 1995). Other basaltic rocks present throughout the Mascarenes include Oceanite, Ankaramite, Hawaiite, Mugearite and Trachyte (McDougall *et al.*, 1965; Saddul, 1995).

Pre-colonisation ecology of the Mascarene Islands

Despite the fact that no serious study of the island ecology was attempted until the 19th century, long after the initial ravages of human colonisation and rapid destruction of the forests (Cheke, 1987), some contemporary accounts describe Mascarene ecology in considerable detail for the time.

Early accounts from Mauritius describe dry, semi-open woodland dominated by palms around the leeward coastal plains, whilst dense climax forest dominated by ebony grew within the interior and on the windward side (Het Tweede Boeck, 1601). Wybrandt Warwicjk's account from 1598 (Het Tweede Boeck, 1601; see also Strickland & Melville, 1848; Barnwell & Tousaint, 1949), which is now known as the first description of Mauritius, notably stated:

"the island is uninhabited and very mountainous. The soil is extremely rocky but fertile as can be judged from the large number of trees, which are so close to each other that one can hardly walk in the forest. The trees are mostly black ebony. There are also a large number of palms, the palms and palmistes are edible"

Much of the original forest has been cleared, where it still remains, the same conditions still persist (Hume *pers. obs*). Records of the original fauna exist only for the coastal and lowland plains on the dry leeward side of the island and it is not unreasonable to postulate that the larger vertebrates, including the flightless species, may have been confined to this more open zone.

The majority of near pristine surviving forests within the Mascarenes are found on Réunion. This is largely a consequence of the topography as the island is extremely mountainous, with 61% of the land surface situated above 600 m (Blanchard, 2000). As on Mauritius, the vertebrate fauna was probably most abundant in the lowland region or leeward side (this was certainly the case for the endemic giant tortoise *Cylindraspis borbonica* (Mourer-Chauviré *et al.*, 1999)) and unfortunately easily accessible to man. Dry open woodland dominated by palms was present on the coasts and lowlands of Réunion upon its discovery (Charpentier de Cossigny, 1799; Rivals, 1952; Cadet, 1977) becoming climax wet forest a short distance into the interior (Cadet, 1977). A small remnant of dry forest survives on the south coast (less than two acres), which represents the only extant pristine forest of this type (Strasberg pers.comm).

Rodrigues lacks true mountains and can be best described as 'hilly.' Fire and agriculture have now removed almost all of the original forest, but two contemporary accounts describe the ecology in some detail (Leguat, 1708; Tafforet, 1726 [Dupon, 1969]). The rapid destruction of the forests can be ascertained from the account of Balfour (1879), the first botanist to record details about the flora of Rodrigues and who described the island as 'a dry and desolate place' as early as 1875! However, Francois Leguat (1708), marooned on Rodrigues for 2 years in 1691-2, described the forests as open woodland, dominated by palms and the Mascarene trees, Bois d'olive, *Cassine orientale*, and Fig, *Ficus* sp. Today, free-roaming goats and cattle heavily graze the island and have created open grassland with dense patches of introduced scrub (Cronk, 1995). The land is also divided into a mosaic of plots by small-scale farming. A few endemic plants survive amongst the exotics, most noticeably at the heads of the valleys and on the tops of the largest hills (Strahm, 1989). In June 2000, a Malais trap was set up to collect insects in the last remaining forested localities on Rodrigues. After analysis, the collections lacked endemics and comprised only pantropical or introduced species with low diversity (Noyes, pers. comm). This suggests that unlike Mauritius and Réunion, Rodrigues has suffered almost complete extinction in some aspects of the invertebrate faunas. The lack of refugia, e.g. mountain tops, montane forests etc, that have survived on Mauritius and Réunion, is almost certainly the main reason.

FOSSIL LOCALITIES

The Mare aux Songes (S20° 27', W57° 41), Mauritius (Fig. 1G)

The Mare aux Songes marsh is situated approximately 0.5 km south-east of the Plaisance airport on the south-eastern side of Mauritius and is less than 100 m above sea level. Despite suggestions to the contrary (e.g., Cowles, 1987), the marsh has not been completely destroyed by development of Plaisance airport. The deposit consists of peaty sediments overlying a rocky basaltic base with sediment depths ranging from 0.2-1 m and now covers an area of 106 m x 44 m compared with 4 or 5 acres when discovered by Clark (1866). The marsh is surrounded by gently undulating hills with a shallow outlet at the southern end. This outlet eventually reaches a lagoon 0.5 km to the southeast but fluvial energy is low and there is little evidence of erosion *en route*, e.g. undercut river banks, steep sided valleys etc. In the winter (dry season), the marsh is predominantly dry and only the southern end of the marsh remains damp and boggy. In the summer (wet season), the marsh can be immersed in 1m+ depth of water. Some intertidal invertebrates, which are still extant within the lagoon surrounding Mauritius, are present in the Mare aux Songes marsh sediments. This indicates that the marsh may have been subject to lagoonal influences in the past but the marsh must now be considered 'made-ground' and any conclusions concerning its evolution are difficult to ascertain. According to Clark (1866), the marshy deposits were deep, at least 3 springs were present and endemic trees were abundant. Today Sugar cane completely surrounds the vicinity with small stands of introduced trees situated along the edges of the marsh, thus, it is now difficult to discover new localities within the area without the aid of heavy duty digging machinery.

Le Pouce (exact coordinates undetermined), Mauritius (Fig.1F)

The mountainous regions of Le Pouce comprise sheer escarpments often incised by steep v-shaped valleys. Situated along the contact zone between escarpment and valley are a number of small undercuts, and vast boulder fields/scree cover the base of the escarpment and the valley sides. Some of the larger material within the scree also forms small caves or fissures. The area is now completely overgrown by exotic plants, particularly gauva (*Psidium cattleyanum*) and Acacia (*Leucaena leucocephala*) and collecting from old sites or discovering new sites on a casual basis has so far proved difficult. The Le Pouce valley has proved to be richly fossiliferous (see below) and the many holes and fissures proved to be excellent natural faunal traps and fossil depositional sites.

One of the greatest, yet much maligned, collectors of Mauritian fossil material was Louise Etienne Thirioux (1846-1917). He was a hairdresser by trade but diligently searched for fossil remains in his free time. Thirioux collected at a number of localities, e.g. Corde de Garde, but most of his material stems from Le Pouce and he often simply states '*Le Pouce valley*' on his collecting labels. Thirioux's fossil collection is by far the most important from Mauritius as it contains a high proportion of small <5 cm elements of vertebrate species that are almost unknown from the fossil record elsewhere in the Mascarenes (Table 1). The collection also includes the only associated dodo, *Raphus cucullatus* skeleton, an almost complete skeleton of the red rail, *Aphanapteryx bonasia* a unique skeleton of the Mauritian giant skink, *Leilopisma* (*Didosaurus*) *mauritiana*. After initially sending material to Alfred Newton in Cambridge and to the Paris Museum via Paul Carié (Carié, 1916), he deposited the remainder of his collection, including the dodo, skink and rail skeletons, in the Mauritius Institute at Port Louis, where they still reside.

Caverne de la Tortue (S21^{O} 04,' W55^{O} 16), Réunion (Fig.1E)

The Caverne de la Tortue is situated on the northwestern side of Réunion approximately 3.2 km from the coast and 250 m above sea level. The caves are not karstic, but a lava tunnel system developed within vesicular basaltic lava (Mourer-Chauviré *et al.,* 1999). The cavern system is complex, with many branches and narrow caves with shallow infilling sediments and extends for 200 metres (Brial, 1996). The main entrance is sheer and accessible only by rope ladder; a second entrance is accessible only by crawling. The first cavern forms a large chamber but quickly grades into narrow, shallow passages. Fallen blocks of basalt litter the main entrance but further in the floor is covered by very fine sediments, with thickness from 50 mm – 1.5 m approximately 2 m from the entrance. This sediment is continuous through the cave system. At 20 m from the main entrance, a small area approximately (4 x 4 m) has produced unusual formations of a 1-2mm layer of limestone developed around a central core of basalt. This peculiar formation represents the only known limestone deposit on Réunion (Brial, pers. comm). The cave atmosphere is extremely humid and some of the cave floor deposits show evidence of high-energy fluvial activity, most notably ripple marks on shallow compact sediments. This cave acted as a natural pit-fall trap for a number of endemic species, particularly tortoises and flightless birds (Mourer-Chauviré *et al.,* 1999); although the preservation of bone material is generally very poor.

Marais de L'Ermitage (S21 40', E55 16.5), Réunion (Fig.1D) (after Mourer-Chauviré *et al.,*1999 and pers.obs)

This marsh is found 0.7 km from the coast, between St-Gilles and St-Leu and is situated in a low-lying <50 m above sea level sedimentary basin. Unfortunately, recent road construction has now destroyed the locality (Mourer-Chauviré pers. comm). A 0.8 m layer of fossil-poor peaty sediment, overlies a breccia 0.3-0.4 m deep, comprising abundant vertebrate fossils, volcanic rocks, coral and shelly fragments. This layer in turn overlies a layer of marine sediments comprising coralline sands, coral and marine mollusc fragments. The area is waterlogged and rapidly infills with water once test pits have been dug. Many hundreds of bones of the endemic giant tortoise *Cylindraspis borbonica* have been recovered, but bird and bat bones are extremely rare (see Mourer-Chauviré *et al.,*1999).

Grotte des Premiers Français (1.5 km southeast of Saint Paul) (Fig.1A)**; Grotte "aux Sable" (1 km south of Saint Gilles)**(Fig.1B)**; Grotte de l'Autel (2 km south of Saint Gilles)**(Fig.1B)**, Réunion** (after Mourer-Chauviré *et al.,*1999) (Fig.1)

These cave localities have provided numerous bones of endemic birds and seabirds that excavate burrows to nest in, e.g., *Puffinus puffinus.* Only the sediments from Grotte "aux Sable" were sieved, although small <10 mm elements were obtained from the other localities. All of the sediments have now been removed.

The Plaine Corail (S19 44.5', W63 22 to S19 45', W63 24), Rodrigues (Fig.1H)

The Plaine Corail is an extensive area of limestone (calcarenite), representing the largest carbonate terrain

Data source	Species	Number of elements		Percent of juvenile elements recovered
		Adults	Juveniles	
MI; BMNH; UMZC; MNHN	Dodo *Raphus cucullatus*	~1710	3	0.17
MI; BMNH; UMZC; MNHN	Solitaire *Pezophaps solitaria*	~2000	0	0

Table 1. A comparison between the numbers of adult and juvenile dodo and solitaire (Raphidae) remains discovered in all of the Mascarene fossil yielding localities. As yet, no solitaire and only 3 juvenile dodo skeletal elements have been discovered.

Taula 1. *Comparació entre els nombres de restes d'adults i juvenils de dodó i solitari (Raphidae) descobertes a totes les localitats fossilíferes de les Mascarenyes. Fins ara, només s'han obtingut tres elements esquelètics juvenils de dodó i cap de solitari.*

within the Mascarene Archipelago (Montaggioni and Nativel, 1988; Saddul, 1995). It is located on the south-western corner of Rodrigues and encompasses an area 4 km x 3 km situated between 40-50 m above sea level. It has been suggested that the formation began ~5000 years ago when the wind direction favoured the build up of coral sand deposits on the south west coast (Saddul, 1995). Groundwater percolation and underground streams have continually eroded the carbonates, producing extensive and complex caverns and, where large-scale roof collapse has occurred, steep-sided canyons are now present. The limestone area has numerous small openings, creating natural pitfall traps on the surface and, as a result, accumulation of large numbers of vertebrate species has occurred. The surrounding area is very harsh and dry with little topsoil. Sediments within the caverns vary from a depth of 0.5 mm (along active underground streams) to 1.5 m (little or no fluvial action). The flora occurring on the Plaine Corail is sparsely distributed and often comprises stunted individuals. Sedimentation rates are low within the caverns and as a large number of fossil remains are unburied, the palaeoenvironment may not have differed significantly from that of today. No other fossil locality has been discovered on Rodrigues.

Fig. 2a. Mare aux Songe, Mauritius. View looking east.

Fig. 2a. *Mare aux Songes, Mauritius. Vista cap a l'est.*

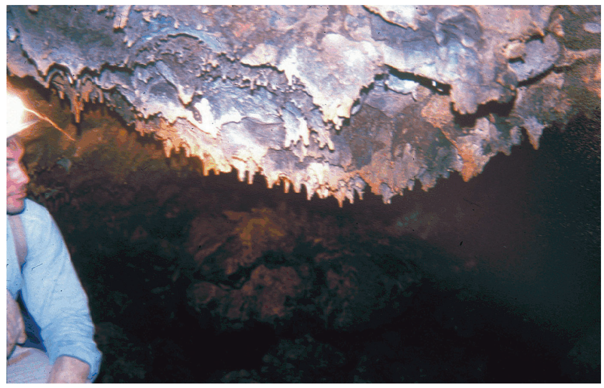


Fig. 2b. Caverne de la Tortue, Réunion. A view of the unique limestone deposit on the roof of the cave.

Fig. 2b. *Caverne de la Tortue, La Réunion. Vista de l'únic dipòsit càrstic al sòtil de la cova.*

Fig. 2c. A view from inside a cavern, Plaine Corail, Rodrigues. Note how minor roof collapse has acted as natural pitfall traps for the fauna.

Fig. 2c. *Vista de l'interior d'una cova, Plaine Corail, Rodrigues. Observar com un petit abissament ha actuat com a trampa natural per a la fauna.*

Taphonomy

Much of the fossil material collected from the Mascarenes has been obtained with little or no contextual data. Despite this, it is clear that there are highly contrasting preservational styles and faunal content between locations reflecting differing taphofacies.

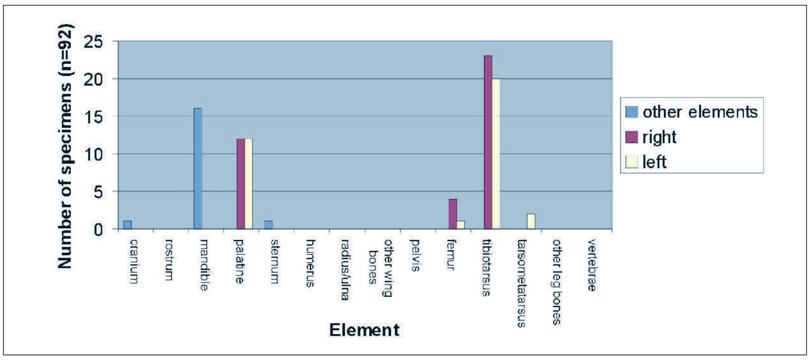
The Mauritian and Réunion marsh fossil deposits comprise almost entirely larger vertebrate fossils (Fig.4a and Fig.4c), with many of the bone samples exhibiting damage due to low energy fluvial activity and plant roots. Only the material collected from the caverns on Rodrigues, Thirioux's Mauritius cave and Réunion deposits contain an abundance of small (<5cm) delicate skeletal elements (Fig,4b, Fig. 4d, and Fig.4e). Furthermore, taphonomic bias has contributed to the preservation of certain elements. For example, of the endemic family Raphidae (dodo and solitaire), the remains of over 300 individual dodos were recovered from the Mare aux Songes (Clark, 1866), but only 5 crania, 7 or 8 rostra, 4 ulnae and radii and a single carpometatarsus (Fig.4a). The majority of fossil remains comprise tibiotarsi and tarsometatarsi, which suggests that dodos were wading into the marsh and becoming trapped. Presumably, the rest of the body was washed away or scavenged leaving an abundance of lower leg bones in the deposit. This is a scenario similar to the preservation of some moa remains collected from marsh deposits on New Zealand (Worthy, pers. comm). The lack of high energy fluvial damage to the fossils specimens also suggests that the material was deposited in situ or relatively close to the locality.

In terms of juvenile dodos, only one pair of tarsi (now lost) collected by Clark (1866) and a tarsus (now lost), collected and photographed by Thirioux in 1904 have been discovered. However, not a single juvenile solitaire element, out of many thousands of fossil adult bones collected, has yet been found (Table 2). This suggests either that Raphidae nested and reared young well away from the depositional area or that due to the fragility of juvenile elements, they are much less likely to have been preserved.

The broad-billed parrot *Lophopsittacus mauritianus* was described from a partial mandible by Owen (1866)

Fig. 3a. Remains of *Lophopsittacus mauritianus* collected from the Mare aux Songes, Mauritius. Note the comparatively numerous tibiotarsi, palatines and mandibles and the distinct paucity of other elements. Right and left bias of bone preservation is minimal.

Fig. 3a. Restes de Lophopsittacus mauritianus *recol·lectades a Mare aux Songes, Mauritius. Noteu els tibiotarses, pal·latins i mandíbules, relativament nombrosos, i la diferent escassesa d'altres elements. Els biaixos en la preservació dels ossos drets i esquerres són mínims.*



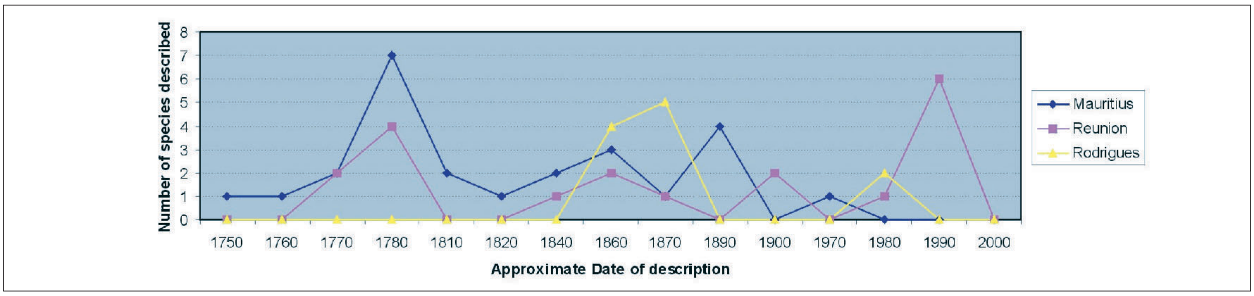


Fig. 3b. All of the Mascarene bird species described from physical (skins and fossil remains) and/or reliable historical evidence. Note the large number of passerine species from Mauritius and Réunion described between 1770-1780 (the heyday of French natural history), the 1860-1890 period (corresponding with the discovery of the Mare aux Songes, Mauritius and the caverns on Rodrigues), and the recent discoveries (e.g. Mourer-Chauviré *et al.*, 1999) on Reunion during the 1980-1990 period.

Fig. 3b. Totes les espècies d'ocells de les Mascarenyes descrites a partir d'evidències físiques (pells i restes fòssils) i/o històriques fiables. Noteu el gran nombre de passerins de Mauritius i La Reunión descrites entre 1770-1780 (l'apogeu de la història natural francesa), el període de 1860-1890 (que es correspon al descobriment de la Mare aux Songes, Mauritius i de les coves a Rodrigues), i els descobriments recents (e.g. Mourer-Chauviré et al., 1999) a La Reunion durant el període 1980-1990.

and postcranial material by Milne-Edwards (1873) and Newton & Gadow (1893); Thirioux also collected some elements from Le Pouce *c.* 1904. The number of elements recovered from the Mare aux Songes indicates that at least 23 individuals are represented. However, only 1 cranium, 1 tarsometatarsus, 1 sternum and whilst no rostra, pectoral elements and foot elements have been recovered, yet at least 16 mandibles, 24 palatines and 43 tibiotarsi exist (Fig.3a). The subtle differences in fluvial energy coupled with the morphology of the individual element are likely to be responsible. When experimenting with doves (Columbidae) and gulls (Laridae), Bickart (1984) showed that the skull is one of the first parts of a corpse to detach when placed in a fluvial environment. Air spaces are present in the cranium and the rostrum of most birds, therefore, in Mauritian parrots, dodos and other avifauna, this may have been sufficient to suspend these elements in the water for longer periods and thus increase dispersal. Changes in fluvial energy are very likely to have had a serious effect on the deposition of small vertebrates as well, but defining criteria is difficult to interpret (see Ericson, 1987).

Cave material appears to lack the preservation bias associated with marsh deposits, as a significant amount of associated material has already been collected (Table 2), and fossil material comprise much larger percentages of cranial and the smaller postcranial elements, e.g. carpometacarpus etc.

The Mascarenes were once inhabited by owls of the endemic genus *Mascarenotus* (Mourer-Chauviré *et al.*,1994). However, unlike the endemic but now extinct genus *Grallistrix* of the Hawaiian Islands, *Mascarenotus* appears to have not utilised caves for breeding or feeding as owl remains are extremely scarce in all deposits and no owl pellets have yet been recognised. Owl pellets have proved essential in determining the diversity of fossil passerines on the Hawaiian Islands (Olson & James, 1991; James & Olson, 1991), and it is apparent that passerines formed a major component of Hawaiian owl prey. Conversely, however, it appears that Mascarene owls preyed heavily on reptiles (no reptiles naturally occur on the Hawaiian Islands) and convergent morphologies of the Mascarene and Hawaiian genera, e.g. short wings (forest adaptation) and long strong tarsi and pelvis (bird and reptile hunting adaptations) are a result of similar ecological niches but different prey. Evidence suggesting that *Mascarenotus* was a forest specialist and bred only in tree holes/cavities can be further extrapolated from its rapid and comparatively recent extinction (Réunion unknown; Mauritius c. 1850; Rodrigues c.1780). The last reports of the owls coincides with intense and severe deforestation that took place during the period 1800-50 on Mauritius and from 1730-1780 on Rodrigues (see Cheke, 1987).

COLLECTING OR PRESERVATION BIAS OF SMALL VERTEBRATES

Volcanic islands are notorious for the poor preservation of skeletal elements, primarily due to chemical

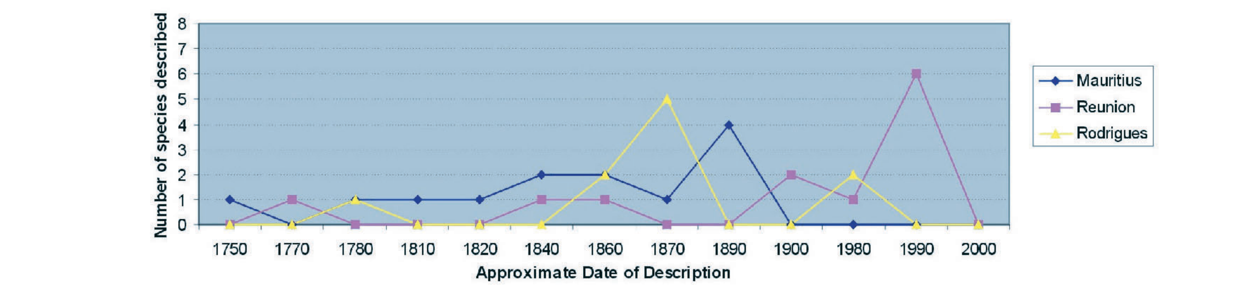
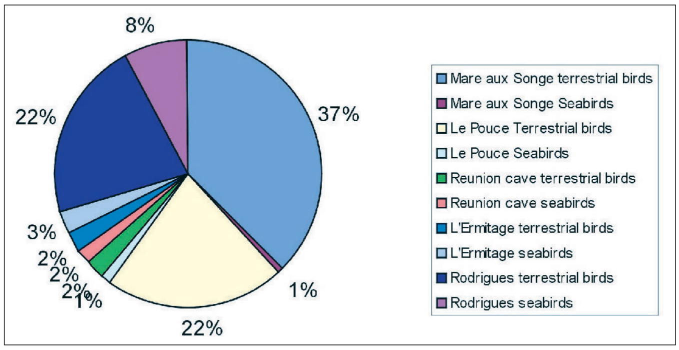


Fig. 3c. All of the Mascarene bird species described from physical (skins and fossil remains), minus all passerines described from skins. Note that comparatively few non-passerines were described before the 1860s, as it was not until the second half of the 19th century that the majority of non-passerine fossil remains were discovered. In contrast to Figure 3b, the only passerine described from the fossil record was the Rodrigues starling *Necropsar rodericanus* in 1879.

***Fig. 3c.** Totes les espècies d'ocells de les Mascarenyes descrites a partir d'evidències físiques (pells i restes fòssils), llevat dels passerins descrits a partir de pells. Noteu que es varen descriure relativament pocs passerins abans de la dècada dels 1860, i que no va ser fins la segona meitat del segle XIX que es va descobrir la major part de les restes fòssils d'ocells no passerins. En contrasta amb la Fig. 3b, l'únic passerí descrit a partir del registre fòssil va ser, el 1879, l'estornell de Rodrigues* Necropsar rodericanus.

Fig. 3d. Comparison between seabird and terrestrial bird fossil remains collected in cave and marsh localities on the Mascarene Islands. Seabirds constitute a large percentage of Mascarene avifauna, yet are under represented in the fossil record. A large amount of Mascarene seabird fossil material remains unsorted and/or little importance has been placed on it.

***Fig. 3d.** Comparació entre les restes d'ocells fòssils marins i terrestres recol·lectades a les localitats espeleològiques i als aiguamolls de les Illes Mascarenyes. Els ocells marins constitueixen un gran percentatge de l'avifauna de les Mascarenyes, encara que es troben sota-representats al registre fòssil. Una gran quantitat de el material fòssil d'ocells marins de les Mascarenyes be està sense catalogat o/i be se li ha donat poca importància.*



decomposition (Olson & James, 1982; Tennyson & Millener, 1994; Worthy & Holdaway, 1993) and for topograhical reasons, e.g. the steep, mountainous nature of the islands coupled with the absence of suitable sedimentary repositories encourages rapid run-off (Olson & James, 1982). It can be envisaged that a bias toward larger vertebrate bone on oceanic islands better surviving these mechanical and chemical agents as opposed to small vertebrate species may be prevalent. The techniques used to collect fossil material during the 19th century also suggest that fine sieving of the sediments was lacking (compare Figs.4a and 4c with Figs.4b and 4e), and that a bias towards the collecting of larger fossil vertebrate material is significant.

In the Mare aux Songe, only one and now lost, undescribed finch (Newton and Gadow, 1893) was collected; all the other vertebrates discovered were medium to large species, i.e. >10g. On Réunion, the marshy area of l'Ermitage has a high ratio of large bone >200 mm and only one passerine and few bat bones were discovered amongst the thousands of tortoise remains (Mourer-Chauvire *et al.*, 1999). The bias toward tortoise remains may well be explained in part by their ecology rather than preferential fossil preservation. Giant tortoises regularly wade into muddy pools (Grubb, 1971) and once there occasionally become trapped and die, therefore, increasing their representation in the fossil record. Like Réunion, Mauritius and Rodrigues once harboured large numbers of endemic tortoises and although they are not dealt with here in any detail, they constitute a major component of the known fossil remains (e.g., Clark, 1866; Arnold, 1979). Interestingly, the majority of the giant tortoise material collected from the Mare aux Songes represents bone >100mm, and smaller elements, e.g. digits, are comparatively rare.

The Plaine Corail fossil locality on Rodrigues, has fared somewhat better in terms of small vertebrate preservation. The only Mascarene passerine described from fossil material, the Rodrigues starling, *Necropsar rodericanus*, was described in 1879 (Günther & Newton, 1879) and Cowles (1987) collected two as yet undescribed passerines in 1974. Recent collections include the discovery of two *Nactus* geckos and two new geckos of unknown affinity (Arnold, 2000). Fine-mesh sieves were used to extract this extremely small, delicate material (Arnold *pers.comm*), which is in marked contrast to the 'hand-picking' techniques employed in the 1800s.

Bioerosion

Bioerosion can be classified as the abrasion of hard surfaces through the activity of organisms (Neumann, 1966) and according to Akpan (1990) divided into two groups depending on bioerosional activities. The first group, which includes all bacteria, lichen, plants, algae, fungi and insects, can result in partial or complete destruction of solid substrates leaving empty spaces in the material. The second group includes molluscs, which mechanically abrade substrates through the action of radulae.

Methods

Methodology comprises examination of the bone material using SEM, binocular microscopy and thin section petrography on a petrological microscope. These methods can reveal the extent of bone surface textures and aid in determining the state of bone preservation or decay. Due to the very young nature of the fossil material, all of the material examined exhibited minimal diagenetic changes at a scale resolvable at microscopic level. There may well have been changes at the molecular level, however, as the bone is no longer white. Unlike any of the other material used in this analysis, the hare *Lepus* sp., has a maximum age of c.1850, as this is the time when hares were first introduced onto Réunion (Cheke, 1987). However, in comparison with the other fossil bone material used, the hare material was extremely fragile and disintegrated with extreme ease when being examined.

Thin section analysis

Thin sections of 10? thickness were produced using standard petrological techniques. Sections were produced from the following localities; Mare aux Songes, Mauritius; Caverne Gastonia, Rodrigues; and Caverne de la Tortue, Réunion and including the skeletal elements listed in table 3.

Results

Dodo *Raphus cucullatus* (Fig.5a)

BMNHmau1 – proximal end of right humerus (see Table 3) with transverse section taken proximal to mid shaft.

The periosteal surface is exhibits no visible traces of damage. However, the endosteal layer exhibits minor bioerosion with possible penetration by bacteria or fungi of the lamellar cortical layer reaching 0.4 mm in depth. The Vascular canals are visible and remain intact with no erosional damage, particularly at the periosteal surface. The trabecular layer is intact in the specimen, but not visible in thin section. Osteocyte lucanae are visible and intact, particularly within the primary (lamellar) bone. Two large fractures in the upper lamellar cortical layer have been infilled with silt. Minor cracking has occurred throughout the specimen, probably as a result of the preparation technique. This is particularly noticeable when some shrinkage of the resin has occurred during curing and can cause cracking in delicate samples.

Solitaire *Pezophaps solitaria* (Fig.5b)

BMNHrod1 – left distal end of ulna (see Table 3) with transverse section taken proximal to distal end.

Despite the morphology being well preserved, the histology is poor due to early diagenetic changes. The periosteal surface is particularly well preserved in this solitaire and the bone is enveloped in a layer of laminated radial calcite 2 mm thick. The endosteal layer is also well preserved and has a thin layer of $CaCO_3$ covering the surface. The dark layers appear to represent silt sediment intrusions and clearly defined lamellae are present (arrowed), with each representing a possible mineralising event. The initial deposits surrounding the bone comprise lamellae of $CaCO_3$ separated with very fine sediment deposits. Between the outer lamellae, a large deposit of poorly sorted sediment, which includes mollusc fragments (upper right), is separated by a very narrow mineralising events, with calcite deposits accumulating between sediment input. Small Calcite deposits have also been deposited on the endosteal layer of the bone, otherwise the trabecular layer is not infilled. Vascular canals are visible and are unaffected by erosional agencies.

Hare *Lepus* sp. (Fig.5c)

BMNHre1. Proximal end of right femur (see Table 3) with transverse section taken distal to mid shaft.

This specimen exhibits extensive damage to the periosteal surface and lamellar cortical layer. The endosteal surface is less eroded, but the trabecular bone has almost completely disappeared. The specimen has been infilled with silt where structural damage has exposed the lamellar cortical layer. Small amounts of sediment have also adhered to the periosteal and endosteal surfaces. Vascular canals are visible but have been extensively enlarged by bioerosion or possible chemical agency in the upper lamellar cortical layer.

SEM

Small 2x2 mm samples of bone were cut from identifiable elements obtained from the following localities: Mare aux Songes and Le Pouce, Mauritius; Caverne Gastonia, Rodrigues; Caverne de la Tortue, Marais L'Ermitage, and Grotte aux Sable, Réunion. All samples were mounted on 20 mm stubs using conductive carbon compound.

Results

Dodo *Raphus cucullatus* (Fig.6a)

BMNHmau1 Proximal end of right humerus. Section taken from cranial surface distal to the proximal end (see Table 3).

On the natural surface at 100 µm magnification, the periosteal surface is generally undamaged with only the occasional indentation. Sediment has adhered to the surface, and some pitting is visible but restricted. At 10 µm magnification, the periosteal surface is also intact with little surface damage. The angular deposits lower left and right are sediment remains attached to the surface. Fracture damage (upper left) appears to be recent, as the edges are fresh, sharp and rough and at right angles to the periosteal surface.

Indet. bird (Fig.6f)

BMNHmau2. Section taken from the mid shaft, on the caudal surface of the tibiotarsus (see Table 3).

On the periosteal surface at 1 mm magnification, deep pitting is evident, which appears to be a result of possible bioerosion. This has expanded the vascular canals deep within the periosteal layer; otherwise the surface area appears intact. At 10 µm magnification, some damage to the periosteal surface has occurred but is erratically distributed. The damaged surface has exposed the lamellar cortical layer and almost reaches the endosteal surface within. These damaged areas comprise some sharp, rough edges at right angles to the periosteal surface and also rounded thinned edges with no sharp right angles, which indicates that their origins are both mechanical and bioerosional. The periosteal surface, when intact, is without pitting or indentation.

Solitaire *Pezophaps solitaria* (Fig.6b)

BMNHrod1. Distal end of tibiotarsus. Section taken from the caudal surface on the proximal end (see Table 3).

On the periosteal surface at 10 µm magnification, the periosteal surface is almost intact, but where mechanical damage occurs (middle center), the edges are rounded and thinned with no sharp edges indicating natural erosion. No pitting or indentation is visible, but a thin irregular coating of $CaCO_3$ has covered the periosteal surface. The surface is also irregularly covered with sediment particles. At 100 µm magnification, the periosteal surface is comparatively intact, with $CaCO_3$ and sediment particles adhered to the surface. There is no evidence of bioerosional activities.

Hare *Lepus* sp.(Fig.6c)

BMNHre1. Proximal end of right femur. Section taken from the mid-shaft on the dorsal surface (see Table 3).

Species	Associated material	Unassociated material (undamaged)	Unassociated material (damaged). Includes eroded proximal and distal ends of post cranial and cranial elements	Percentage of total fossil material per taxon collected from Mauritius fossil localities by Thirioux
Raphus cucullatus	1 complete/ 1 partial skeleton	1 carpus and metacarpals		10%
Aphanapteryx bonasia	1 complete skeleton, 1h, r, u	1 c; 2 h; 1 ra; 1 u; 16 ow; 2 p; 20 ol; 35 v	1 r; 1 m; 1 s; 6 h; 2 u; 4 ow; 2 p; 6 f; 6 t; 8 ta; 20 ol; 15 v	95.8%
Dryolimnas c. cuvieri		2 h		16%
Mascarenotus sauzieri	1 h, ra, u	2 h; 6 u; 2 ow; 3 f; 1 p; 3 t; 4 ta; 10 ol; 8 v	1 c; 3 r; 4 m; 4 h; 4 u; 2 ow; 1 f; 1 p; 5 t; 4 ta; 2 v	89%
Anas sp		1 ow		6%
Circus maillardi		1 s; 1 ta; 1 ol	1 h; 3 u; 3 ow; 1f; 1 t; 2 ta	70%
Lophopsittacus mauritianus		2 u; 1 ta	5 s; 1 ta	11.6%
Psittacula echo	1 h, ra, u, s	1 r; 8 h; 8 u; 10 ow; 8 f; 6 t; 7 ta; 10 ol; 10 v	5 m; 4 h; 2 u; 10 ow; 2 f; 6 t; 23 ta; 10 ol; 20 v	100%
Psittacula bensoni		3 h; 1 ow; 3 ta	1 r; 2 m; 2 h; 4 ow; 8 ta	100%
Streptopelia picturata?		1 h; 2 ow; 1 ta	1 p	100%
Alectroenas nitidissima		1 h		100%
Columba mayeri		8 h; 1 u; 2 f; 2 t		100%
Passerines		200+ including all elements	300+ including all elements	100%

Table 2. Material collected by Etienne Thirioux and deposited in the MI, MNHN, NHM, and UMZC. The importance of his collection can easily be appreciated, particularly concerning the smaller bird species. Key: c=cranium; r=rostrum, m=mandible, s=sternum, h=humerus; u=ulna; ra=radius; ow=other wing elements; p=pelvis; f=femur; t=tibiotarsus; ta=tarsometatarsus; ol=other leg elements; v=vertebra.

Taula 2. *Material recol·lectat per Etienne Thirioux i dipositat a les col·leccions MNHN, NHM, i UMZC. Es pot apreciar fàcilment la importància d'aquesta col·lecció, particularment pel que fa els ocells passerins petits. Clau: c=crani; r=rostre, m=mandíbula, s=esternó, h=húmer; u=ulna; ra=radi; ow=altres elements de les ales; p=pelvis; f=fèmur; t=tibiotarse; ta=tarsometatarse; ol=altres elements de les potes; v=vèrtebres.*

At 100 µm magnification, almost the entire periosteal surface exhibits surface damage. In particular, the numerous pits and furrows appear to be the result of invertebrate radulae. The lamellar cortical layer has been exposed and vascular canals have become visible through the periosteal surface. Also at 100 µm magnification, a number of comparatively large rod-shaped structures (middle center) appear to be invertebrate frass or possibly invertebrate egg cases. They are too large to represent bacteria. At 1 µm magnification, the vascular canals have been infiltrated with fungal mycelia creating severe destruction of the surface. The segmented hyphae can be seen on the surface and entering the pores. Some of the hyphae can be seen with secondary growth and very fine filaments attesting to fungal damage.

Indet. bird (Fig.6d)

BMNHre2. Section taken from the mid-shaft of the caudal surface of tibiotarsus (see Table 3).

At 1 µm magnification, the periosteal surface is generally intact, but complex fracturing has taken place in some areas forming hexagonal fracture zones and has exposed the lamellar cortical layer below. The edges of the damage are not sharp and at right angles to the periosteal surface and appear to represent non-mechanical destruction as compared to direct mechanical damage. Where the periosteal surface is undamaged, little pitting or indentation is visible. At 100 µm magnification, severe damage has occurred on large areas of the periosteal surface, resulting in exposure of the lamellar cortical layer. Some sediment has also infilled the damaged area. Where visible, the edges of the damaged areas are rounded and not at right angles to the periosteal surface suggesting that bioerosional or chemical degradation has taken place.

***Puffinus* sp.** (Fig. 6e)

BMNHre3. Proximal end of ulna. Section taken from the ventral surface of shaft, distal end (see Table 3).

At 100µm, the periosteal surface is intact and exhibits no pitting, cracking or large-scale damage. Some gentle indentation can be seen top right and this may be a result of chemical or bioerosional damage. The specimen is cracked with sharp edges at right angles to the periosteal surface from the proximal to the distal end, indicating that this may be a post-collection artifact. A deep groove running diagonally from left to right can be seen in the center, and appears to be the result of a tool mark or a knife mark, suggesting this particular specimen had been consumed by man.

Remarks

The SEM and microscopy data suggests that fossil material is subject to a number of destructive agencies that include mechanical, chemical and bioerosional means. Mechanical and bioerosional destruction to fossil bone is more prevalent in marsh deposit fossils, which are subject to periodic fluvial activity, greater exposure to weathering and increased scavenging. Rapid burial, although important to marsh material, is evidently not a prerequisite for good bone preservation within cave systems, since many of the cave fossil specimens were found on or near the surface and are in excellent condition. The cave localities seemingly prevent much of the scavenging agencies removing and disarticulating material but in certain conditions, possible chemical and certainly bioerosional agencies can rapidly destroy fossil material. Chemical agencies are much harder to ascertain and it is not within the scope of this paper to cover this aspect in any great detail.

Species and number	Locality colouration	Element	Locality
Raphus cucullatus NHMmau1	Characterised by a light tan, deep chocolate or almost black colouration exhibiting root marks where the background colour is light tan. Very rarely, <2% of the material is bleached white.	Proximal end of right humerus	Mare aux Songes, Mauritius
Indet bird NHMmau2	Characterised by a light tan, often with darker speckling.	Midshaft of ulna fragment	Le Pouce, Mauritius
Pezophaps solitaria NHMrod1	Characterised by a light cream to almost white colouration.	Left distal ulna	Caverne Gastonia, Plaine Corail, Rodrigues
Lepus sp. NHMre1	Characterised by dark cream, light tan to almost white.	Proximal end of right femur	Caverne de la Tortue, Réunion
Indet bird NHMre2	Characterised by a light tan, with some darker speckling	Midshaft of ulna fragment	Marais L'Ermitage, Réunion
Puffinus sp. NHMre3	Characterised by a light to dark tan with some visible root marks	Midshaft of ulna fragment	Grotte aux Sable, Réunion

Table 3. List of specimens used in diagnosis.

Taula 3. *Llista dels espècimens emprats a l'estudi.*

pH

All of the sediments collected from the Mascarenes are alkaline, a result of weathering from alkalinic basaltic rocks. This suggests that a low CO_3 content, coupled with high humidity of the Caverne de la Tortue may be the primary factor in rapid deterioration of bone in this locality. The neutral/alkaline composition of the marsh sediments on Réunion and Mauritius may act as a buffering agent to chemical degradation and protect the material from bioerosion. Unlike an acidic marsh environment, e.g. skin and nail but no bone preservation of the bog people (Shipman, 1981), only bone has survived in the marsh deposits of Mauritius and Réunion suggesting a more neutral/alkaline environment. Marsh environments usually have a low pH (Martin, 1999), therefore, the neutral-alkaline chemistry of the sediments (see Table 4) may be conducive to bone preservation. Although bioerosion is not significant on fossil material collected from marsh localities, minor damage due to fluvial agencies, however, is common to many of the elements and compared to cave deposits, rapid burial appears to be an important factor for preservation in the marsh deposits due to the abundance of scavengers (see below).

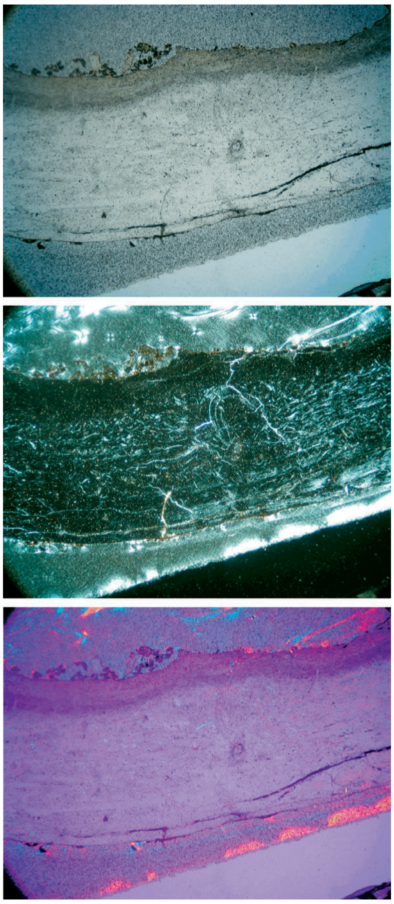


Fig. 5a. Thin section PPL (top); XPL (center); tint PPL (bottom). Dodo *Raphus cucullatus* BMNHmau1. Proximal end of right humerus with transverse section taken proximal to mid shaft. Scale bar = 1mm. In tint PPL, arrows indicate endosteal layer; bioerosion reaching the lamellar cortical layer; osteocyte lucanae; fractures within the upper lamellar cortical layer; periosteal layer. For full description see thin section results.

Fig. 5a. *Secció prima PPL (a dalt); XPL (centre); PPL tenyit (a sota). Dodó,* Raphus cucullatus, *BMNHmau1. Extrem proximal d'húmer dret amb secció transversa presa a la part proximal d'enmig de la canya. Escala = 1mm. A la secció PPL tenyida, les fletxes indiquen la capa endòstia; la bioerosió assoleix la capa cortical lamellar; osteocyte lucanae; fractures dintre la capa cortical lamellar superior; periosti. Per a una descripció completa, vegeu la secció de resultants de les seccions primes.*

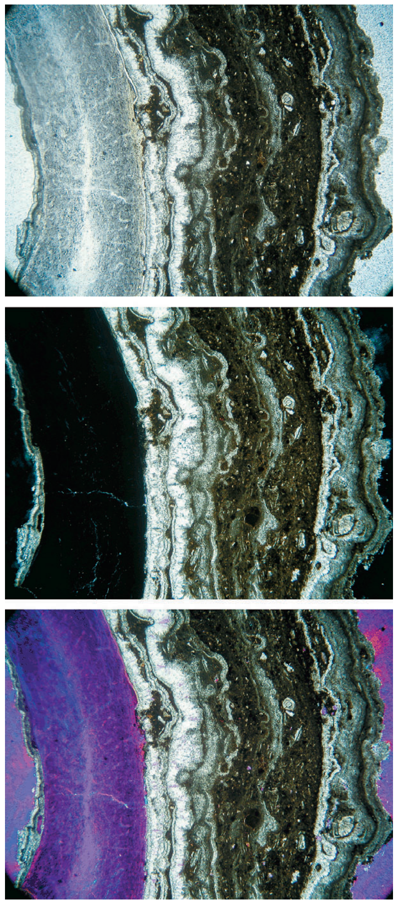


Fig. 5b. Thin section PPL (top); XPL (center); tint PPL (bottom). Solitaire *Pezophaps solitaria* BMNHrod1. Distal end of left ulna with transverse section taken proximal to distal end. Scale bar = 2mm. In tint PPL, arrows represent a different mineralising event. For full description see thin section results.

Fig. 5b. *Secció prima PPL (a dalt); XPL (centre); PPL tenyida (a sota). Solitari* Pezophaps solitaria *BMNHrod1. Part distal d'ulna esquerra amb secció transversa presa a la part proximal de l'extrem distal. Escala = 2mm. A la PPL tenyida, les fletxes representen un esdeveniment mineralitzador diferent. Per a una descripció completa, vegeu la secció de resultants de les seccions primes.*

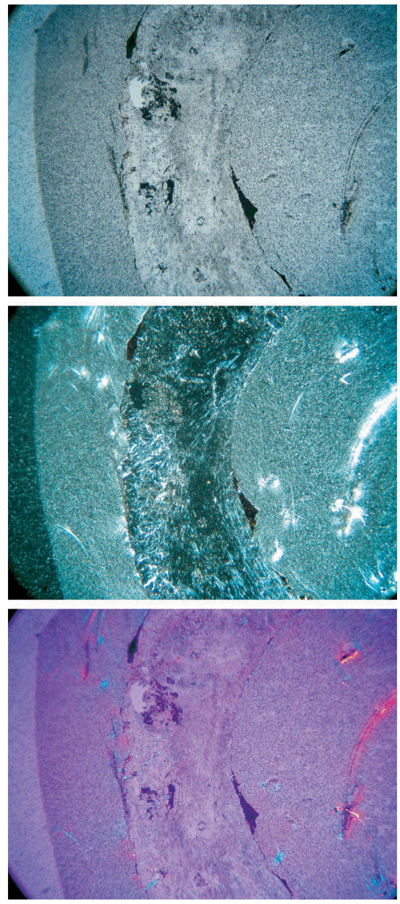


Fig. 5c. Thin section PPL (top); XPL (center); tint PPL (bottom). Hare *Lepus* sp. BMNHre1. Proximal end of right femur with transverse section taken distal to mid shaft. Scale bar = 1mm. In tint PPL, arrows indicate damage to the periosteal surface; upper lamellar cortical layer; sediment infill; endosteal layer; sediment adhesion to the endosteal layer. For full description see thin section results.

Fig. 5c. *Secció prima PPL (a dalt); XPL (centre); PPL tenyida (a sota). Llebre* Lepus *sp. BMNHre1. Extrem proximal de fèmur dret amb una secció transversa presa a la part distal de mig de la canya. Escala = 1mm. A la PPL tenyida, les fletxes indiquen danys a la superfície del periosti; capa cortical lamellar superior; reompliments de sediment; capa endòstia; adhesió de sedimenta la capa endòstia. Per a una descripció completa, veure els resultats de les seccions primes.*

Scavenging

Scavenging plays an extremely important role in any natural ecosystem. Carrion is broken down and minerals/nutrients become re-absorbed into several trophic levels via scavenger waste products, burial and dispersal (Shipman, 1981). On the pre-human Mascarenes, it is assumed that a number of species acted as scavengers on the islands, including terrestrial invertebrates, e.g. dipterid flies, molluscs, land crabs, and terrestrial vertebrates such as giant tortoises, scincid lizards and birds. With the extinction of many vertebrate species and a serious reduction in the numbers of invertebrate species after the arrival of man to the islands, scavenging by introduced rats, mice, pigs, cats, dogs, tenrecs, and monkeys presumably now play a significant part in the break down and removal of carrion.

Little attention has been given to the prodigious numbers of land crabs that formerly inhabited the Mascarenes, and in the coastal regions at least it can be envisaged that a scenario not too dissimilar to that on Christmas Island today once occurred there. In particular, Francois Leguat (1708) noted the vast numbers of crabs that were originally present on the mainland of Rodrigues:

"*The Land-Crabs were our next Enemy* [after rats]. *'Tis impossible to destroy them, there's being a prodigious quantity of them in the Grounds., and 'tis very difficult to get them out of their Holes. Their Burrows are very broad, and have several Entrances……, They tore up ourPlants in our Gardens day and Night, and if we shut up the Plants in a sort of Cage, in hopes of saving them ; if they were not far off, they wou'd dig under ground from their Burroughs to get to the plants, and tear them up under the cage.*"

He further describes the breeding season:

"*A little before and after the Full-Moons in July and August, these Crabs march by Millions, from all parts of the Island to the sea. We never met with one but what was laden with eggs : We might then have destroy'd great quantities of them with ease, for they go in Prodigious Troops, and being far from their Burroughs, have no place of Retreat. We'd sometimes kill'd three Thousand in one Evening with Sticks, yet we cou'd not perceive the next day, that their Number was anyway Diminish'd.*"

Large crabs, although somewhat scarce, can still be seen on some of the larger offshore islets of Rodrigues today (pers.obs) and their burrowing activities reflects the impact they would have had as major scavengers on the mainland.

Terrestrial crabs play a major part in excavating the ground and removing, disarticulating and burying all edible objects (Alexander, 1979). Most land crabs, i.e. crabs that predominantly or temporarily inhabit dry habitats, have been exterminated from Mauritius and Rodrigues, but in pre-human times there would have been a great diversity of species. On Rodrigues, the large carnivorous and scavenging species *Geograpsus grayi*, *Ocypoda cordimana*, and the hermit crab *Coenobita rugosa* were originally found in woods, and some distance from the shore (Miers, 1879). *Ocypoda* sp. is a scavenger but also an adept hunter of sea turtle eggs and hatchlings (Alexander, 1979) and, no doubt, preyed on terrestrial giant tortoise eggs and young as well. True carnivorous crabs, e.g. *Birgus*, *Geograptus*, and *Coenobita*, feed on other crabs, tortoise and turtle young and scavenge any dead carcasses they encounter (Alexander, 1979; Bourn & Coe, 1979). A very large species, the coconut crab, *Birgus latro,* has been hunted to extinction over most of its range including the Mascarene Islands (Cheke, 1987). On Aldabra, where it is still relatively common, it is a dominant nocturnal scavenger of large and small carcasses, particularly giant tortoises, *Aldabrachelys gigantea* (Bourn & Coe, 1979). According to Bourn and Coe, the coconut crab easily shears off large chunks of decaying flesh, dragging away limb bones and entrails. Up to 14 were observed together at one time on the carcasses of giant tortoises on Aldabra; an entire juvenile tortoise of 38.5 cm curved carapace length was also taken by the crabs. Assumedly, small vertebrate carcasses would, therefore, have needed to have been rapidly buried on the Mascarenes and to some depth in order not to have been removed and disarticulated by land crabs. Such are the scavenging depredations of land crabs, when present in large concentrations, they have been cited as the main reason why so few carrion-breeding flies occur on Aldabra (Alexander, 1979) and they can also seriously influence stratigraphical interpretation by inverting fossil remains due to burrowing (Worthy and Wragg, 2003). On Rodrigues, crab remains of *Geograpsus* and *Ocypoda* are extremely numerous within the caves of the Plaine Corail, which gives an indication of their former abundance and extent of their inland excursions. Unfortunately, little research has been undertaken concerning the techniques crabs use to dispatch carcasses and the resultant damage to bone. For example, claw marks and/or distinctive bone fractures caused by crab scavenging are unrecorded. The virtual extinction of land crabs on the Mascarenes and, as a consequence, the lack of recent crab-scavenged bone material, has made any comparative interpretations concerning the fossil material impossible.

Mass mortality or time averaging

On oceanic islands, many agencies can potentially cause mass mortalities. In the Mascarenes, these agencies include severe cyclones, drought and disease. Shipman (1981), although referring to mammals, suggested the following natural mortality factors: predation, disease, senility (old age), accident and starvation/dehydration, all of which could provide a continual supply of potential carcasses for deposition. However, faunal non-attritional mass mortalities are often difficult to detect in mixed and disarticulated fossil assemblages. Large numbers of disarticulated skeletal elements of a single species may provide evidence for mass mortality or conversely, a slow accumulation of specimens over many centuries. Austin & Arnold (2001) provided carbon isotope ratio dates ranging from 1700-400 BP for the giant tortoise *Cylindraspis* sp., collected from the Mare aux Songes, and 1000 BP for a specimen of *Cylindraspis* from l'Ermitage (Mourer-Chauviré *et al.*, 1999). These results indicate that the deposition of specimens has been going on for at least one millennium at both localities and thus a slow natural accumulation may well have taken place. These accumulations are, therefore, concluded to be a consequence of time-averaging.

Fig. 4a. Terrestrial birds and the fossil record: Mare aux Songes, Mauritius. All material collected from the Mare aux Songes. The data set is based on the collections held at the UMZC; BMNH; MI; MHNH; and UCB. The fossil elements of the dodo *Raphus cucullatus* constitute 75% of the total fossil elements, whilst passerines have not been preserved.

Fig. 4a. *Ocells terrestres i registre fòssil: Mare aux Songes, Mauritius. Tot el material recol·lectat a la Mare aux Songes. El conjunt de dades es basa a les col·leccions hostatjades als UMZC, BMNH, MI, MHNH i UCB. Els elements fòssils de dodó,* Raphus cucullatus, *constitueixen el 75% del total d'elements fòssils, mentre que els passerins no es troben ben representats.*

Fig. 4b. Terrestrial birds and the fossil record: Le Pouce, Mauritius. All material collected from caves on Le Pouce and adjacent areas. The data set is based on the collections held at the UMZC; BMNH; MI; MHNH; and UCB. The red rail *Aphanapteryx bonasia* represents 16% (constituting only 1.4% from the Mare aux Songes); echo Parakeet *Psittacula echo* 16% (no specimens have been recovered from the Mare aux Songes); and dodo *Raphus cucullatus* 11% of the total fossil elements represented. Passerines constitute 42% of the total fossil elements, which is in direct contrast with the marsh deposit of the Mare aux Songes.

Fig. 4b. *Ocells terrestres i registre fòssil: Le Pouce, Mauritius. Tot el material recol·lectat a coves de Le Pouce i àrees adjacents. El conjunt de dades es basa a les col·leccions hostatjades als UMZC, BMNH, MI, MHNH i UCB. El rascló roig* Aphanapteryx bonasia *representa el 16% (fa només l',.4% a Mare aux Songes);* Psittacula echo *16% (no s'han recuperat exemplars a Mare aux Songes), i el dodó* Raphus cucullatus, *l'11% del total d'elements fòssils representats. Els Passerines fan el 42% del total d'elements fòssils, cosa que contrasta molt amb el dipòsit de l'aiguamoll de Mare aux Songes.*

Fig. 4c. Terrestrial birds and the fossil record: Marais de l'Ermitage, Réunion. Data from Mourer-Chauviré *et al* (1999). Understandably, water and marsh birds, e.g. flamingo *Phoenicopterus ruber*; solitaire (ibis) *Threskiornis solitarius*; night heron *Nycticorax duboisi* and the anseriformes genera *Anas*; *Aythya*; and *Alopochen* comprise 87% of the total fossil elements discovered. This marsh locality is situated 0.7km from the coast in a low lying sedimentary basin.

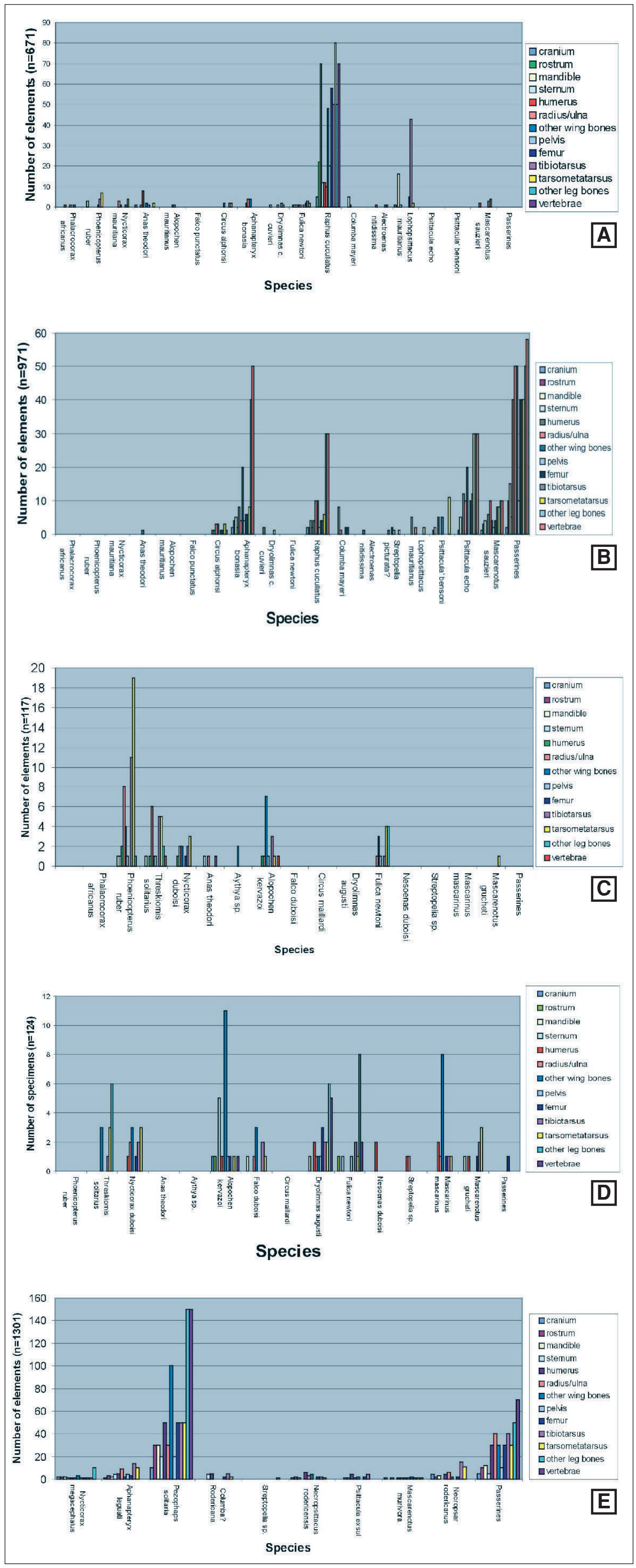
Fig. 4c. *Ocells terrestres i registre fòssil: Marais de l'Ermitage, Réunion. Dades de Mourer-Chauviré et al (1999). Comprensiblement, els ocells aquàtics i limícoles, com, per exemple, el flamenc* Phoenicopterus ruber, *el solitari (un ibis)* Threskiornis solitarius, *l'orval* Nycticorax duboisi *i les Anseriformes dels gèneres* Anas, Aythya *i* Alopochen *comprenen el 87% del total dels elements fòssils obtinguts. Aquest aiguamoll està situat a 0,7 km de la costa en una conca sedimentària baixa.*

Fig. 4d. Terrestrial birds and the fossil record: Grotte des Premiers Francais; Grotte de l'Autel; Caverne de la Tortue, Réunion. Data from Mourer-Chauviré *et al* (1999). The lack of passerine material within these three cave systems suggests that they have not being preserved in the deposits. Mourer-Chauviré *et al* (1999) mention the absence of passerines from all of the Réunion fossil localities, despite fine-sieving much of the sediments.

Fig. 4d. *Ocells terrestres i registre fòssil: Grotte des Premiers Francais; Grotte de l'Autel; Caverne de la Tortue, Réunion. Dades de Mourer-Chauviré et al. (1999). La manca de materials de passerins a aquests tres sistemes cavernícoles suggereix que no es conserven be a aquests depòsits. Mourer-Chauviré et al. (1999) esmenta l'absència de passerins a tots els depòsits de la Réunion, malgrat que molts dels sediments es varen porgar amb cedasos de malla fina.*

Fig. 4e. Terrestrial birds and the fossil record: Plaine Corail, Rodrigues. The data set is based on the collections held at the UMZC; BMNH; MI; MHNH; and UCB. Due to the large number of specimens of the solitaire *Pezophaps solitaria*, only unnassociated material was counted and constitutes 56% of the total fossil elements. Many complete associated skeletons have also been discovered. Passerines are also well represented comprising 28% of the total. Conversely, owls (0.7% of the total) and parrots (2.8% of the total) are extremely rare.

Fig. 4e. *Ocells terrestres i registre fòssil: Plaine Corail, Rodrigues. El conjunt de dades es basa a les col·leccions hostatjades als UMZC, BMNH, MI, MHNH i UCB. Degut al gran nombre d'especímens de solitari,* Pezophaps solitaria, *només es va contabilitzar el material no associat, que constitueix el 56% del total d'elements fòssils. També s'han descobert molts d'esquelets associats complets. Els Passerines també es troben ben representats, comprenent el 28% del total. Contràriament, les òlibes i mussols (0.7% del total) i els lloros (2.8% of the total) són extremadament rars.*



In addition, it has been suggested that the large accumulation of articulated and associated remains of the solitaire, *Pezophaps solitaria*, in the caverns of the Plaine Corail was due to the last survivors taking refuge from severe cyclonic events or the forest burning by tortoise hunters (Slater, 1879a; Cowles, 1987). As no carbon dating of the material has been attempted, it is premature to suggest that a mass mortality has occurred and again it is more likely to represent a slow, periodic build up of individuals.

THE LACK OF SMALL VERTEBRATE REMAINS, E.G. PASSERINES

Certain Mascarene Island fossil localities including the Mare aux Songes are depauperate in small vertebrate remains, i.e. species weighing <10g or elements <5cm. However, many hundreds of small elements have been collected in cave localities where sieving has taken place (Figs. 4a and 4e). Passerines are known from historical accounts and occasionally approached plague proportions, e.g. the endemic Fody *Foudia* sp., on Réunion (Dubois, 1674). Therefore, certain conditions must exclude small vertebrate remains such as those of passerines from the fossil record of the marsh and Réunion cave localities. The possible reasons for the absence of small vertebrate taxa in the fossil record may be due to:

a) Small taxa evolved/arrived after formation of the fossil locality – unlikely due to the young age of the fossil localities
b) Collection failure – particularly relevant when sediments not sieved
c) Taxa absent due to taphonomic processes – small, lightweight carcasses more likely to be washed away and/or completely removed by scavengers from marsh deposit; bioerosional and chemical degradation within cave deposits
d) Taxa absent due to restricted distribution – unknown as there is extremely limited knowledge about former distribution of passerines on the Mascarenes. Presumably, volant passerines could have inhabited all of the available land space but some species, e.g. Réunion cuckoo-shrike *Coracina newtoni* are extremely restricted in range (Probst 1997), and appear to have always been so
e) Taxa extant but absent in area due to localised extinction or unsuitability of habitat – unknown as there is extremely limited knowledge about former distribution of passerines on the Mascarenes

Assessing fossil diversity can be confused by variation in the durability of skeletal remains present. Some bone may be unidentified in an assemblage because processes such as fluvial activity, predation and scavenging, bioerosion and dissolution may all render small or delicate bones unrecognisable or remove them completely from the fossil record. There is a bias towards the preservation of large bone (>10cm) compared to small bone in the marshy deposits, but not elsewhere, e.g. the cave deposits on Mauritius and Rodrigues. After sieving, Sauzier collected proportionally very few small fossil elements of larger vertebrate species from the Mare aux Songes (Newton & Gadow, 1893)(Fig.4a), and intense sieving in the marsh of L'Ermitage, Réunion, produced very few small vertebrate fossil elements (Mourer-Chauviré *et al.*, 1999) (Fig.4c). Lava tunnel deposits are subject to intense bioerosional and chemical activities, which can completely destroy fossil remains in a comparatively short time, e.g. the hare *Lepus* sp., a species introduced no earlier than c. 1850 (Cheke, 1987). Human bias can also skew faunal composition based on the fossil record. It is much more difficult to identify small, often homogenous skeletal material than larger vertebrate remains and thus the smaller elements are often ignored even when collections are available. Further difficulties arise from historical accounts and the passerine fossil record. Passerines were barely mentioned in the early literature unless they were of an edible size, e.g. *Hypsipetes* bulbuls (Cheke, 1987), and only one of the larger passerine species has been described from the fossil record (Figs.3b and Fig.3c); all other passerines were described from skin specimens held in collections. Determining the diversity of small birds from the historical record is thus problematical.

CONCLUSION

Is the fossil record of the Macarenes representative of the prehuman biota? It is crucial that mode of formation of the fossil assembly is recognised and also that the nature of any taphonomic biases that have affected a particular fossil assemblage be determined. Fossil localities can contain distorted proportions of taxa or skeletal elements. They are assumed to be strongly biased assemblages and therefore are unrepresentative of the original diversity that was available to be fossilised at the time of formation. Furthermore, unscientific collecting and description of specimens can result in further bias (Figs.3b and 3c). For example, seabirds form only a small proportion of museum fossil remains from the Mascarenes (Fig.3d), yet comprise (or comprised) a large component of the ecology (Cheke 1987). This bias has important implications for their use in palaeodiversity estimates and palaeoecological reconstruction. Unfortunately, for most fossil assemblages the true diversity of preservable taxa that were available for inclusion can never be known.

Mascarene fossil assemblages are the result of a complex interaction of biological, chemical and sedimentologi-

Locality	pH value	Sediment status
Mare aux Songe, Mauritius	6.9	Neutral-Alkaline
Marais l'Ermitage, Réunion	7.4	Alkaline
Caverne de la Tortue, Réunion	8.0	Alkaline
Plaine Corail, Rodrigues	7.4	Alkaline
Standard	6.5	Neutral-Alkaline

Table 4. pH results of samples taken from selected Mascarene fossil localities. The poorest preservation of fossil material and the highest alkalinity was found in the Caverne de la Tortue, Réunion.

Taula 4. *Resultats de pH de les mostres preses a diferents localitats fossilíferes mascarenyes seleccionades. La pitjor preservació i la major alcalinitat es va trobar a la Caverne de la Tortue, Réunion.*

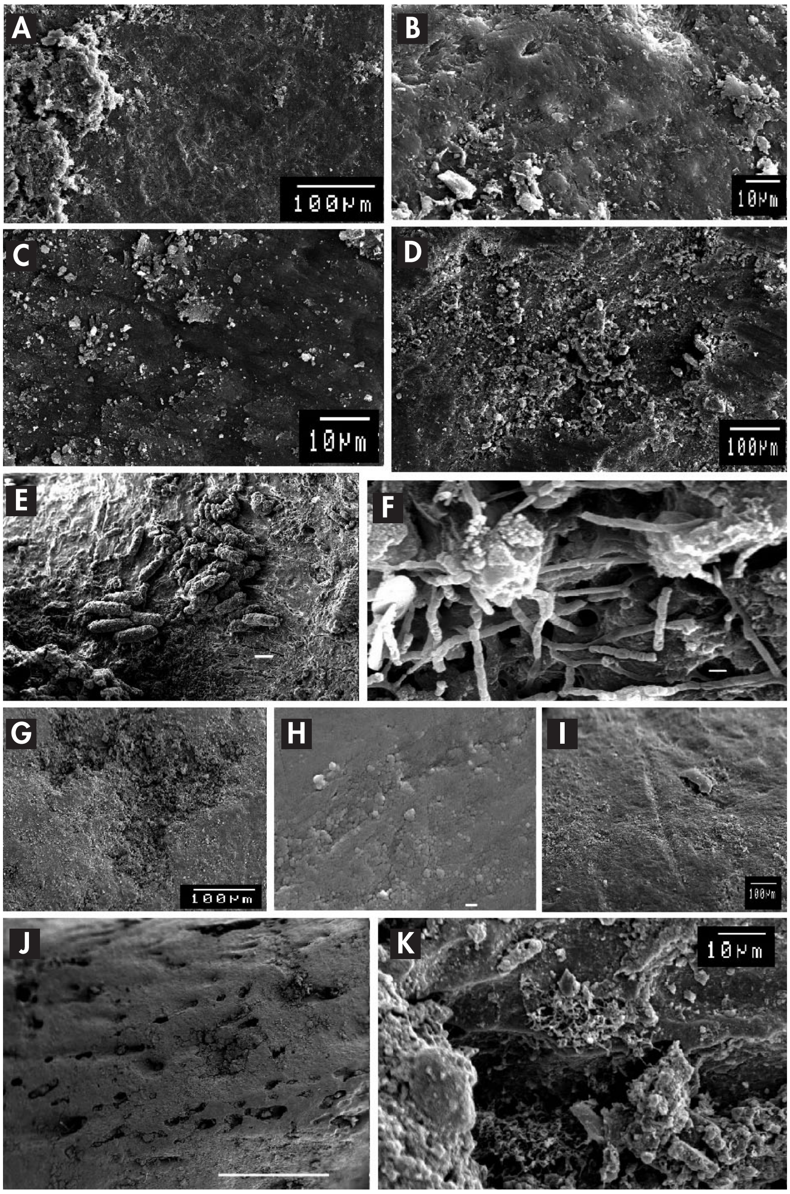


Fig. 6. SEM. **Dodo *Raphus cucullatus* BMNHmau1**. Proximal end of right humerus with transverse section taken proximal to mid shaft. Scale = 100µm (A) and 10µm (B). **Solitaire *Pezophaps solitaria* BMNHrod1**. Distal end of left ulna with transverse section taken proximal to distal end. Scale = 10µm (C) and 100µm (D). **Hare *Lepus* sp. BMNHre1**. Proximal end of right femur with transverse section taken distal to mid shaft. Scale bar =100µm (E), 1µm (F) and 100µm (G). **Indet bird BMNHre2**. Section taken from the mid-shaft of the caudal surface of tibiotarsus. Scale bar = 1µm (H). ***Puffinus* sp. BMNHre3.** Proximal end of ulna with section taken from the ventral surface of shaft, distal end. Scale bar = 100µm (I). **Indet. bird BMNHmau2**. Section taken from the mid shaft, on the caudal surface of the tibiotarsus. Scale bars = 1µm (J) and 10µm (K).

Fig. 6. *SEM.* ***Dodó,*** **Raphus cucullatus,** ***BMNHmau1****. Extrem distal d'húmer dret amb una secció transversa presa a la part proximal de la canya central. Escales = 100µm (A) i 10µm (B).* ***Solitari,*** **Pezophaps solitaria,** ***BMNHrod1****. Extrem distal d'ulna esquerra amb una secció transversa presa a la part proximal de l'extrem distal. Escales = 10µm (C) i 100µm (D).* ***Llebre*** **Lepus** ***sp. BMNHre1****. Extrem proximal d'húmer dret amb secció transversa presa a la part distal de la canya central. Escales = 100µm (E), 1µm (F) i 100µm (G).* ***Indet ocell BMNHre2****. Secció presa a la meitat de la canya de la superfície caudal del tibiotars. Escala = 1µm (H).* **Puffinus** ***sp. BMNHre3****. Extrem proximal d'ulna amb una secció presa a la superfície ventral de la canya, a l'extrem distal. Escala = 100µm (I).* ***Ocell indeterminat, BMNHmau2****. Secció presa a la meitat de la canya, a la superfície caudal del tibiotars. Escala = 1µm (J) i 10µm la (K).*

cal processes. Hydrological processes are also important but all of these processes do not explain all depositional criteria. There is a fundamental lack of knowledge concerning other taphonomic processes operating during the formation and deposition of fossil material from marsh and cave environments. As with many palaeontological studies, interpretation of data is often difficult to resolve and many factors have to be taken into consideration when attempting to reconstruct palaeoenvironments, particularly on dynamic oceanic islands.

Sadly, further data from the Masacarenes may not be obtainable in the foreseeable future. It is ironic that recent high profile ecological research and conservation on a group of islands, which famously contain so many endangered species, has failed to notice that the most endangered areas today are the fossil localities themselves. On Mauritius, the collecting areas of Thirioux are now impenetrable and completely overgrown with dense exotic scrub. The Mare aux Songes has witnessed a hundred years of neglect and is presently scheduled to become part of a golf course. The largest and almost unique limestone locality at Bel Ombre has also been extensively quarried. On Réunion, the Kervazo cave site has now been removed for construction purposes and in early 2003, a road was built right through l'Ermitage marsh completely destroying the locality (Mourer-Chauviré pers. comm). On Rodrigues, a recent extension of the airport threatens some very important caverns on the Plaine Corail and roof collapse has already occurred (pers. obs). It is, therefore, imperative that as much information is obtained from seemingly well-known or new fossil localities while the opportunities still exist.

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