

WAS THE FLYING-FOX *PTEROPUS COMORENSIS* ON MAFIA ISLAND (TANZANIA) INTRODUCED BY HUMANS?

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ABSTRACT

While there is no firm evidence either way, the fact of long cultural contact and that birds and lizards have been introduced by Comorians to Mafia and other East African islands, suggests that the flying-fox *Pteropus comorensis* is more likely to have been introduced to Mafia Island by humans than to have arrived there by itself as generally assumed.

Keywords: Comoros, Zanzibar, Unguja, fruit-bat, *Pteropus comorensis*, trans-oceanic

INTRODUCTION

Mafia (519 km²) and Pemba (980 km²), two medium-sized islands close to the coast of Tanzania (figure 1), each support a species of large fruit bat known as flying-foxes *Pteropus* spp. They are representatives of an otherwise Indo-Australasian and Oceanic genus that is widespread across Indian Ocean islands, but does not occur on the East African mainland (Mickleburgh *et al.*, 1992), or indeed on the island of Zanzibar (Unguja) that lies between Pemba and Mafia. Pemba, separated by 40 km from the mainland by a deep channel (Moreau & Pakenham, 1940; Kingdon, 1990), may have been an island since the Miocene. It has an endemic bat *P. voeltzkowi* Matschie, 1909, dating from the earliest (probably Pliocene) natural transoceanic colonisation of the Indian Ocean and related to the rare relict Comorian species *P. livingstonii* Dobson, 1866 (O'Brien *et al.*, 2009). Pemba also has another endemic whose origin is the Malagasy biogeographical sub-region: the day-gecko *Phelsuma parkeri* Loveridge, 1941 (Rocha *et al.*, 2007¹). By contrast, like Unguja, Mafia is on the African continental shelf and only separated from the mainland at the beginning of the Holocene, as indicated by Indian Ocean sea-level records (Camoin *et al.*, 2004, and refs. therein, *contra* Pakenham, 1984). It is only 19 km offshore, and its flying-fox *P. comorensis* Nicoll, 1908, is the same as the common taxon on all four Comoro islands (Hill, 1971; Bergmans, 1988–97; Kock & Stanley, 2009). Mafia has no other putatively native fauna of non-mainland origin. This raises the question of whether the Mafia flying-foxes could have been introduced by human agency, as I suggested informally at a bat conference in Mauritius in 2008 (Jenkins

¹ Pakenham (1979) claimed the endemic owl *Scops pembaensis* (Pakenham, 1937) and the gecko *Ebenavia inunguis* Boettger, 1878 as further Malagasy connections, but DNA analysis shows the former is African (Fuchs *et al.*, 2008), and the latter is considered "a dubious and unconfirmed record" by Glaw & Vences, (2007).

& Tatayah 2009). Kock & Stanley (2009) drew further attention to this possibility in a recent survey of the mammal fauna; however they did not investigate the historical and cultural context, which is the purpose of this note.

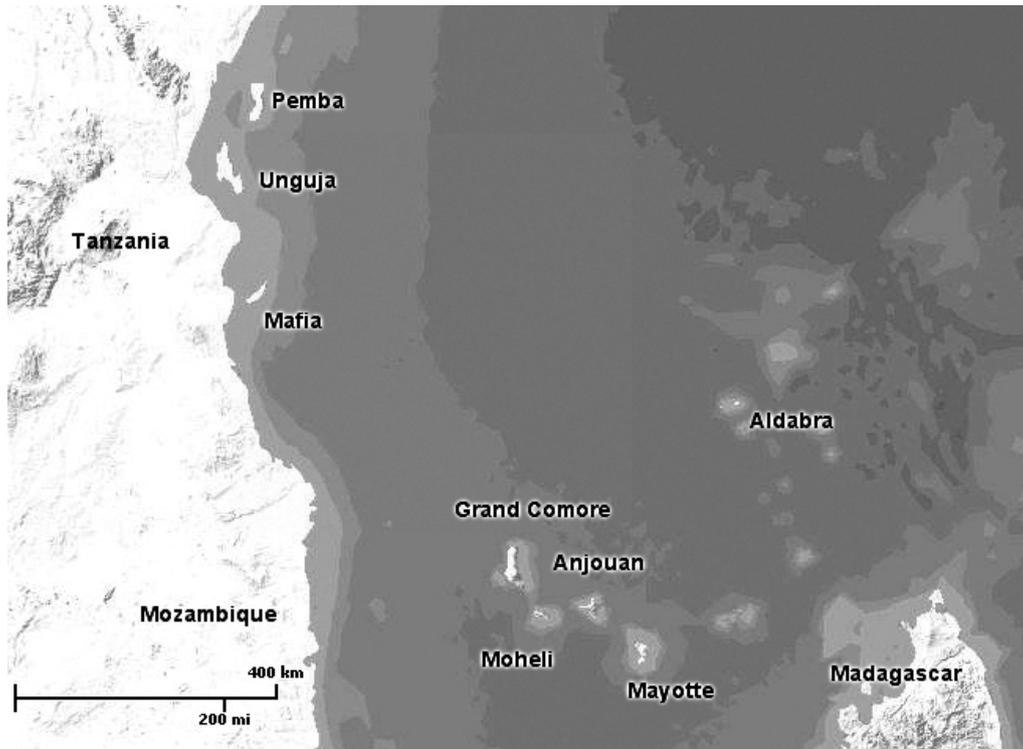


Figure 1. The East African islands of Mafia, Unguja (Zanzibar) and Pemba in relation to the Comoros and Madagascar.

Since Hill's revision (1971), the common Comorian flying-fox has generally been treated as a race of the Seychelles species *Pteropus seychellensis* Milne-Edwards, 1887, but O'Brien *et al.*'s (2009) DNA study showed that '*seychellensis*' in the broad sense is paraphyletic, and that *comorensis* is sister to *seychellensis* + *niger* (Kerr, 1792) (Mauritius). All three are very closely related to *aldabrensis* True, 1893 (Aldabra), *rufus* E. Geoffroy, 1803 (Madagascar) and *giganteus* (Brünnich, 1782) (India). This led O'Brien *et al.* (2009) to consider lumping them all into one polytypic species. Morphologically however they are all distinct (Andersen 1912, Bergmans 1988–97). Bergmans noted that the few specimens from Mafia in the London Natural History Museum are greyer on the back than Comorian specimens and concluded that "the position of the Mafia population within the species needs further analysis". In a genus with notoriously variable pelage this could simply be a founder effect from a recent colonisation or, alternatively, an indication of change over a longer time-scale. O'Brien *et al.*, (2009) unfortunately did not include any Mafia bats in their DNA sampling, and Kock & Stanley (2009), despite having further specimens, felt unable to add anything to this question.

For reasons of clarity, in the rest of this paper 'Unguja' is used to refer to the island formerly called Zanzibar, and 'Zanzibar' to the political entity in its various historical guises, except when directly quoting earlier writings.

HISTORICAL AND CULTURAL EVIDENCE

Late discovery of bats

Compared with Unguja and Pemba, Mafia has been rather neglected by biological investigators. The presence of the flying-fox (and indeed any bat) was not noted until the 1930s, the first published references being those of Moreau (1939²) and Moreau & Pakenham (1940). This is despite being under German rule from 1890–1915 (King, 1917; Piggott, 1941) when collectors and explorers from that country investigated the new colonial territories. Even the flying-fox on Pemba was overlooked until collected by Voeltzkow in 1903 (Andersen, 1912). Werth (1915), purporting to survey the gamut of wildlife in German East Africa, referred only to the Afrotropical genera *Epomophorus* and *Xantharpyia* (= *Eidolon*) when discussing 'Fliegende Hunde'. Articles on Mafia itself (Baumann, 1896; King, 1917), although discussing the conspicuous fauna, mentioned no bats. Voeltzkow himself "spent some weeks" on Mafia in 1903 but neither reported nor collected any bats (Voeltzkow, 1904, 1923; Moreau, 1940). As Kock & Stanley (2009) point out, large fruit-bats are generally noisy, conspicuous, menace fruit trees, and, I would add, are usually active before dark, so these omissions are odd, particularly from the explorer-naturalist Voeltzkow. The other two fruit-bats present on Mafia, the Egyptian fruit-bat *Rousettus egyptiacus*³ (E.Geoffroy, 1810) and Wahlberg's epauletted fruit-bat *Epomophorus wahlbergi* (Sundevall, 1846), are much smaller, more nocturnal and (*Rousettus* only) cave-dwelling. Hence they are more easily over-looked, and indeed were not recorded until much later still: *Rousettus* in 1959 (Kock & Stanley, 2009), *Epomophorus* in the 1990s (Dickinson in Clark, 1994: 34, footnote), identified to species by Cockle *et al.* (1998), confirmed by Kock & Stanley (2009). The larger *Eidolon helvum* (Kerr, 1792) appears to be only an infrequent visitor (*ibid.*). According to Annalisa Christie (*in litt.* 25 January, 2011), no bones corresponding to *Pteropus* have been reported from archaeological sites on Mafia, nor has she found any in the 14th–17th C middens she has investigated. This may however simply indicate that the animals were not eaten.

Comorian contact and settlement on East African islands

Although much better documented for Unguja (Saleh, 1941) than for Mafia, there has been interaction and commerce between east African islands, coastal towns and the Comoro Islands for many centuries, and communities of Comorians have been settled in these areas since the 15th century at least—some originating as slaves, others as traders or exiles (Werth, 1915; Rispal, 2005). Baumann (1896) specifically mentioned that in Mafia "a small colony of Comorians (Angasija) lives in Baleni"; 'Angasija' (now spelt Ngazidja) is the Comorian name for Grande Comore.

² The London Natural History Museum has a specimen deposited by Reg Moreau in 1938 (BMNH 1938.10.24.1; see Bergmans, 1988–97). This bat was not, as implied by Bergmans's specimen list, collected by Moreau himself, but by an unnamed 'collector from Amani' (Moreau, 1939).

³ Spelling follows Bergmans (1988–97) who, following nomenclatural rules, reverted to E.Geoffroy's original orthography rather than the later 'corrected' form '*aegyptiacus*'.

Subject to Kilwa in the 15th century (Saleh, 1941; Rispal, 2005), then ruled by Portuguese who imported Comorian slaves (Newitt 1983), Mafia later formed with Unguja and Pemba part of the Sultanates of Oman and Zanzibar, and shared their history until Britain and Germany established protectorates in 1890 (Piggott 1941). Unguja, at least, had Comorian communities before the Omanis took over in 1828 (Saleh 1941). There were some 2000 there in the mid-1850s (Burton 1872), and Comorian trading dhows were active throughout the area for centuries (Vienne, 1900; Newitt, 1983; Guébourg, 1994).

There was repeated Zanzibari influence in the Comores in the 19th century (Gevrey, 1870; Vienne, 1900; Allibert, 1984; Verin, 1994; Rispal, 2005). People from Grande Comore fled to East Africa and Zanzibar following a destructive eruption of the Karthala volcano in 1858 (Saleh 1941), and John Kirk (in Sclater, 1864) noted that “as servants” people from Grande Comore “are much esteemed at Zanzibar”. As late as 1900 Zanzibar was still the principal trading partner of the Comoro islands (Vienne, 1900), by then a French protectorate.

Birds and lizards introduced by Comorians to Mafia, Unguja and Pemba.

At least two bird species are known to have been (temporarily) introduced to the Tanzanian islands from or via the Comoros, the endemic red-headed fody *Foudia eminentissima* Bonaparte, 1850 (to Unguja) and the grey-headed lovebird *Agapornis canus* (Gmelin, 1788) (to Unguja and Mafia). Although the introduction details are unknown in both cases, and the populations did not persist (Pakenham, 1979), they are assumed (Moreau & Pakenham, 1940) to have been introduced by Comorians who (in 1940) “still form an element among the immigrants to the islands”, presumably keeping these birds as personal pets or as tradable cage-birds. The fody was recorded from Unguja as early as 1841 (Benson, 1960), and the lovebird was in Mafia by 1870 (Moreau, 1940), *i.e.* in both cases before British & German colonial involvement. Vaughan (1929–30) reported the lovebird in Unguja as “introduced from Madagascar many years ago”.

Vaughan (*contra* Moreau's later view, but supported by Benson, 1960) possibly cited Madagascar as the source because the bird is best known from there. However there were Malagasy settlers in Unguja in the 1850s (Burton 1872), though earlier (until *ca.*1820) they were raiders rather than settlers along the African coast and its islands (*e.g.* Piggott, 1941), and unlikely then to have brought pet birds! In fact the bird's appearance on Mafia pre-dates the first reported occurrence in the Comoros (Anjouan in late 1870s, Mayotte in the 1880s, Benson, 1960; Louette *et al.*, 2004), so this popular cage-bird was clearly being actively distributed around the area, presumably by trading vessels.

Benson (1960), reviewing the 1841 fody specimen following earlier doubts as to its real provenance, was also doubtful (as was Pakenham, 1979), but identified the skin (in Paris) as the Mohéli race *F. e. eminentissima*, collected by Louis Rousseau. Rousseau travelled the western Indian Ocean on the French corvettes *Prévoyante* and *Dordogne* in 1839–41 (Jaussaud & Brygoo, 2004). The *Prévoyante* visited Mayotte in 1840 and 1841 (Gevrey, 1870) and the *Dordogne* visited Mayotte and 'Zanzibar' (*i.e.* Unguja) at least in 1840 (Rispal, 2005) as part of French politicking over Mayotte and Nosy Bé. However, there is no evidence that either ship touched at Mohéli (Guillain, 1845; Karimbhay, 2011), hence there is no reason to reject the fody record from Unguja, particularly as von der Decken also collected it there in the 1860s (Moreau, 1940). Benson's (1960) identification does however pinpoint Mohéli as the geographical source of the introduction.

Populations of the gecko *Phelsuma dubia* (Boettger, 1881) on Pemba, Unguja and the Tanzanian coast also appear from DNA to have been introduced from the Comoros (Rocha *et al.*, 2007) at unknown dates.

Fruit-bat trapping, keeping and consumption

Although there is no evidence of Comorians keeping flying-foxes as pets as is sometimes done in the Seychelles (pers. obs. 1970s; Racey, 1979), they are eaten by some sectors of society (Thorpe, 1988 *in* Mickleburgh *et al.*, 1992; Louette *et al.*, 2004), and could have been carried alive to new areas as traditional food items. John Kirk (in Sclater, 1864) enjoyed eating a flying-fox in Mohéli in *ca.*1860, which suggests it was then accepted practice. Jeremy Dahl, however, found no evidence of bat-eating in Grande Comore in 1975 and 1977 (Cheke & Dahl, 1981: 226). In the Seychelles and Madagascar they are often kept alive after capture pending being eaten (Racey, 1979; Racey *et al.*, 2010), and Comorians may do (or have done) the same. Although bats are generally considered ‘forbidden’ as food (*haram*) to Muslims, the Pemba flying-fox (although protected) is still eaten in Muslim Pemba (Walsh, 1995, 2007; Mickleburgh *et al.*, 2009), though less so than formerly (Robinson *et al.*, 2009). Such consumption may be a practice introduced long ago by Austronesian (proto-Malagasy) settlers/invaders. Similar methods, notably entanglement in thorns and burrs set in fruiting trees, are used to live-trap flying-foxes on Pemba (Walsh, 1995) and Madagascar (Racey *et al.*, 2010), suggesting a cultural connection. The Comoros are, like Pemba, an almost purely Muslim society with ancient links to Madagascar, where fruit-bats are widely eaten (Mickleburgh *et al.*, 2009; Racey *et al.*, 2010). A "large species of bat" (presumably *Eidolon*) was said to be "pronounced delicious by curious gourmands" in Unguja in the 1850s (Burton 1872), but the author did not say who it was that ate it, possibly expatriate Malagasy or Europeans.

The anomalous Vienna specimen

While in Mafia itself the bats went unnoticed (or perhaps were not present) until the 1930s, there is one much older specimen of *P. comorensis* that has been assigned to Mafia (Bergmans, 1988–97; Kock & Stanley, 2009), apparently purely by association and inference. It is a skin and skull in the Vienna natural history museum presented by Mauritius-based Bohemian botanist Wencelas Bojer in 1827, long wrongly labelled as *P. chrysoproctus* (Temminck, 1837). This specimen was identified as *comorensis* by Kurt Bauer in the 1970s (re-checked in 1978: Bauer, *in litt.* July 1st, 1978), and confirmed as such by Bergmans (1988–97). Bojer, however, never visited Mafia, but did travel to Unguja and Pemba on an expedition in 1824, collecting mainly plants, but also some animals (Vaughan, 1958; Dorr, 1997). Although the specimen itself has lost its original label, the accession records, investigated on my behalf by Bauer in 1978, clearly state that it was acquired on Unguja⁴. This raises the possibility that *P. comorensis* was present at that time on Unguja (though there are no other such indications). At the very least this indicates that flying-foxes were being brought there from the Comoros (or possibly Mafia). Bojer did not visit the Comoros himself until over a decade later (1835; Vaughan, 1958), so could not have acquired it there. This specimen, while of great interest, cannot reliably be used as evidence of the presence of flying-foxes on Mafia in the early 19th century.

In the Winterton Collection of East African Photographs held at the Melville J. Herskovits Library of African Studies at Northwestern University in Evanston Illinois, there is a photo, taken *ca.*1900, entitled "Zanzibari man with bat" showing an African in white Muslim dress holding a large fruit bat (online at <http://hdl.handle.net/2166.DL/inu-wint-72-3-11-3>). At first

⁴ “By chance, looking at the acquisitions of birds of the same year, I found an appendix with the following entry: ‘und 1 *Pteropus* - Ins. Zanzibar’ ” - Kurt Bauer *in litt.* 9 May 1978). Bojer’s collections include no plant or animal specimens from Mafia (Bauer *in litt.* 1 July 1978; Dorr, 1997).

glance this might have been a *Pteropus*, but careful examination and measurement of the photo shows it to be an exceptionally large example of *Eidolon helvum*, no doubt the reason the photo was taken. Exact date and locality are not recorded (David Easterbrook *in litt.*, 17 February, 2011).

THE POSSIBILITY OF NATURAL COLONISATION

Although the indications are that flying-foxes were introduced to Mafia, it is certainly also possible that they arrived naturally, as assumed by earlier writers (*e.g.* Moreau & Pakenham, 1940; Hill, 1971; Bergmans, 1988–97; Kingdon, 1990; Mickleburgh *et al.*, 1992). During late Tertiary and Pleistocene they spread and diversified across widely dispersed islands in the Pacific and Indian Oceans (Mickleburgh *et al.*, 1992; O'Brien *et al.*, 2009), but there are few contemporary observations of trans-oceanic movement. The most remarkable is of a single living *Pteropus scapulatus* Peters, 1862 which reached New Zealand from Australia (*ca.* 3200 km) in 1929 (Daniel, 1975). *P. vampyrus* (Linnaeus 1758) regularly crosses 70+ km of Malacca Strait between Malaya and Sumatra (Epstein *et al.*, 2009), and *P. rufus* the 50 km from Ile Sainte-Marie to mainland Madagascar (Racey *et al.*, 2010). Recently, in the Indian Ocean, Réunion was recolonised naturally from Mauritius by a group of *P. niger* in *ca.* 2001, probably supplemented in 2007, across 164 km of open sea (Jenkins *et al.*, 2008; Roué & Probst, 2010); the original *P. niger* population had been exterminated in Réunion by 1800 (Cheke & Hume, 2008). The opposite coasts of these last three crossings are all potentially visible from the departure side, particularly if the bats first soar to a good altitude before flying across, as suggested long ago (Lanux, 1772) for the Mauritius–Réunion traverse. The recent Mauritius to Réunion movement appears to have been facilitated in part by a cyclone in February 2007, but cyclones, which sweep east to west across the tropical southern Indian Ocean rarely reach the African mainland. A severe cyclone hit Zanzibar in 1872, which also devastated Bagamayo on the Tanzanian coast (Hollingsworth, 1929; Moreau & Pakenham, 1940); the mainland was visited by weakened storms at Lindi in 1952 (Darwall & Guard, 2000), and Dar-es-Salaam (Cyclone ‘Bondo’) in 2006 (Xinhua News Agency, via <http://www.highbeam.com/doc/1P2-16099676.html>, accessed 20 February 2011), but none are known for Mafia⁵.

The minimum distance from the Comoros to Mafia is around 550 km, much longer than the regular crossings mentioned above. Although the prevailing winds (SE Trades; Moreau & Pakenham, 1940; Kingdon, 1990) are fairly favourable, the chances of a gravid female or viable group arriving must nevertheless be very low, lower than the likelihood of introduction by human agency, at least since humans occupied the various islands and travelled between them. That the Comoros may have been settled by East Africans as early as the 5th century BCE, though the 8th century CE is more generally accepted (Cheke, 2010), but how much return traffic towards Africa there was in the early days remains unknown.

⁵ It is claimed online by Peter Byrne (<http://nabataea.net/mafia.html>) that “in 1872 the remarkable town of Kisimani Mafia was lost in a cyclone”, but since all other sources refer to this cyclone crossing Unguja not Mafia, and other Mafia histories (Baumann, 1896; King, 1917; Piggott 1941) mention no such loss, this reference appears to be in error.

DISCUSSION & CONCLUSIONS

The specimen of a Comorian flying-fox from Unguja, the late discovery of the Mafia population, the absence of *Pteropus* bones in middens, and the sometime presence in Mafia, Unguja and Pemba of birds and lizards introduced from or via the Comoros by Comorians, are all indicative of a possibly recent human introduction of the flying-fox population on Mafia. Absence of earlier records is not itself evidence of absence, and against the implied 19th century introduction, there is apparently no tradition of any bat being imported (no such tale was volunteered by Kathryn Clark's informants in 1994), nor has the bat a Comorian name. However, as Clark (1994) has pointed out, the locals on Mafia do not, now at least, fully distinguish between *P. comorensis* and other fruit-bats (*Epomophorus wahlbergi*, *Rousettus egyptiacus*), the latter being widely considered as young individuals of the former. Similarly *Pteropus* and *Eidolon* are also barely distinguished on Pemba, although both are eaten (Walsh, 1995), and hence seen at close range. The name used on Mafia for all fruit-bats, *popo kubwa* (Swahili; = 'large bat'; Walsh, 2007, online appendix), would presumably have been in use for *Rousettus* and *Epomophorus* before the putative arrival of the similar though much larger Comorian bat. In the Comoros flying-foxes are known as *ndema/ndrema* (Comorian) and variants (Cheke & Dahl, 1981; Louette *et al.*, 2004; Walsh, 2007; spelling varies). Likewise the bats on Mafia are not currently eaten by locals, only by occasional visitors from Pemba (Clark, 1994; Walsh, 1995), although Kock & Stanley (2009) suggested there might be some low-key local consumption. If the bats were introduced by Comorians, this could also have been much longer ago, any folk-memory of this act has having long since faded. Although cultural and trading contact from the 12th century onwards is well-established (see above and Spear, 2000), active population (and thus associated animal) movement between the Comoros and East Africa prior to European arrival in the area lacks adequate documentation (Walsh 2007).

Given the evident plasticity of the genus (O'Brien *et al.*, 2009), any pre-Holocene natural colonisation should have produced discernible morphological characteristics. However, given that historical evidence is unlikely to be forthcoming, and archaeology has not so far generated any bat bones (Annalisa Christie, *in litt.* 25 January, 2011), DNA analysis would provide a route forward. However, even an analysis for a recent bottleneck from a small founding group in the Mafia population would not distinguish between natural invasion and human-mediated introduction, though it might give some indication of how long ago the event occurred. Nonetheless, given Bergmans's (1988–97) comments on pelage (above), such an investigation would be most worthwhile. Archaeology on Mafia (and Unguja?) may yet provide useful clues, and information on former bat presence, consumption and/or transportation may turn up in historical documents—the mystery will only be solved through using all possible investigatory avenues.

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REFERENCES

- Allibert, C. (1984). *Mayotte: Plaque Tournant et Microcosme de l'Océan Indien Occidental. Son Histoire avant 1841*. Editions Anthropos, Paris.
- Andersen, K. (1912). *Catalogue of the Chiroptera in the Collection of the British Museum. Vol. 1. Megachiroptera*. Second Edition. Trustees of the British Museum, London.
- Baumann, O. (1896). *Der Sansibar Archipel. Erstes Heft. Die Insel Mafia und ihre Kleineren Nachbarinseln*. Duncker & Humblot, Leipzig. [English translation by "a former clerk in the Kilindoni Boma" in G.S.P. Freeman-Grenville (ed.) (1957). Mafia Island by Dr Baumann. *Tanganyika Notes & Records* **46**: 1–28].
- Benson, C.W. (1960). The birds of the Comoro Islands: results of the British Ornithologists' Union Centenary Expedition 1958. *Ibis* **103b**: 5–106.
- Bergmans, W. (1988–97). Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). *Beaufortia* **38**(5): 75–146, **39**(4): 89–153, **40**(7): 111–177 [includes *Pteropus* & *Eidolon*], **44**(4): 79–126 [includes *Roussettus*] & **47**(2): 11–90 [discussion/conclusions].
- Burton, R.F. (1872). *Zanzibar: City, Island and Coast*. Tinsley Brothers, London. 2 vols.
- Camoin, G.F., L.F. Montaggioni & C.J.R. Braithwaite (2004). Late glacial to post glacial sea-levels in the western Indian Ocean. *Marine Geology* **206**: 119–146.
- Cheke, A.S. & J.D. Dahl (1981). The status of bats on western Indian Ocean islands, with special reference to *Pteropus*. *Mammalia* **45**: 205–238.
- Cheke, A.[S.] & J.[P.] Hume (2008). *Lost Land of the Dodo. An Ecological History of Mauritius, Réunion and Rodrigues*. A&C Black, London & Yale University Press, New Haven, Connecticut.
- Cheke, A.[S.] (2010). The timing of arrival of humans and their commensal animals on Western Indian Ocean oceanic islands. *Phelsuma* **18**: 38–69.
- Clark, K.M. (1994). People and bats: Conservation of the Comoros Lesser Fruit Bat on Mafia island, Tanzania. Unpublished M.Phil. thesis, Dept. of Geography, Cambridge University. 67pp.
- Cockle, A., D. Kock, L. Stublefield, K.M. Howell & N.D. Burgess (1998). Bat assemblages in Tanzanian coastal forests. *Mammalia* **62**: 53–68.
- Daniel, M.J. (1975). First record of an Australian fruit bat (Megachiroptera: Pteropodidae) reaching New Zealand. *New Zealand Journal of Zoology* **2**: 227–231.
- Darwall, W.R.T. & M. Guard (2000). Southern Tanzania. In T.R. McClanahan, C.R.C. Sheppard & D.O. Obura (eds.), *Coral reefs of the Indian Ocean*. Oxford University Press, New York. Chapter 5, pp. 131–166.
- Dorr, L.J. (1997). *Plant Collectors in Madagascar and the Comoro Islands*. Royal Botanic Gardens, Kew.
- Epstein J.H., K.J. Olival, J.R.C. Pulliam, C. Smith, J. Westrum, T. Hughes, A.P. Dobson, A. Zubaid, S.A. Rahman, M.M. Basir, H.E. Field & P. Daszak (2009). *Pteropus vampyrus*, a hunted migratory species with a multinational home-range and a need for regional management. *Journal of Applied Ecology* **46**: 991–1002.
- Fuchs, J., J-M. Pons, S.M. Goodman, V. Bretagnolle, M. Melo, R.C.K. Bowie, D. Currie, R. Safford, M.Z. Virani, S. Thomsett, A. Hija, C. Cruaud & E. Pasquet (2008). Tracing the colonization history of the Indian Ocean scops-owls (Strigiformes: *Otus*) with further

- insight into the spatio-temporal origin of the Malagasy avifauna. *BMC Evolutionary Biology* **8**: 197–211.
- Gevrey, A. (1870). *Essai sur les Comores*. Pondicherry. [reprinted 1997, Editions du Baobab, Mayotte]
- Glaw, F. & M. Vences (2007). *A Field Guide to the Amphibians and Reptiles of Madagascar*. Third edition. Vences & Glaw Verlag, Köln.
- Guébourg, J.-L. (1994). *La Grande Comore. Des Sultans aux Mercenaires*. L'Harmattan, Paris.
- Guillain, [C]. (1845). Documents sur l'Histoire, la Géographie et la Commerce de la Partie Occidentale de Madagascar, Extrait des Annales Maritimes et Coloniales. Paris, Imprimerie Royale.
- Hill, J.E. (1971). The bats of Aldabra Atoll, western Indian Ocean. *Philosophical Transactions of the Royal Society of London B* **260**: 573–576.
- Hollingsworth, L.W. (1929). *A Short History of the East Coast of Africa*. Macmillan, London.
- Jaussaud, P. & E.-R. Brygoo (2004). *Du Jardin au Muséum en 516 Biographies*. Paris, Muséum Nationale d'Histoire Naturelle.
- Jenkins, R.K.B., V. Tatayah & P.A. Racey (2008). *Pteropus niger*. In: IUCN 2010. *IUCN Red List of Threatened Species. Version 2010.4*. <www.iucnredlist.org>. [<http://www.iucnredlist.org/apps/redlist/details/18743/0>, accessed 18 December 2010].
- Jenkins, R.K.B. & V. Tatayah (2009). Flying foxes (Pteropodidae: *Pteropus*) in the Western Indian Ocean: A new regional initiative. *African Bat Conservation News* **21**: 2–3.
- Karimbhay, T. [writing as 'Kartami'] (2011). http://www.lepost.fr/article/2011/04/14/2465802_ile-de-la-reunion-ile-de-nosy-be-et-ile-mayotte-trois-destinees-coloniales-francaises-trois-trajectoires-differentes-dans-l-histoire-maritime-de-l-ocean-indien.html [accessed 13 June 2011].
- King, N. (1917). Mafia. *Geographical Journal* **50**: 117–125.
- Kingdon, J. (1990). *Island Africa - the Evolution of Africa's Rare Animals and Plants*. Collins, London.
- Kock, D. & W.T. Stanley (2009). Mammals of Mafia Island, Tanzania. *Mammalia* **73**: 339–352.
- Lanux, J.-B.F. de (1772). [letter on *roussettes* and *rougettes*] In G.L.LeClerc, Comte de Buffon (1776). *Histoire Naturelle Générale et Particulière, Servant de Suite à l'Histoire des Animaux Quadrupèdes*. Supplément, vol.3, Pp.253–262. Imprimerie Royale, Paris: [reprinted 1979 in *Info-Nature, Isle Réunion* **17**: 35–41]
- Louette, M., D. Meirte & R. Jocqué (eds.) (2004). *La Faune Terrestre de l'Archipel des Comores. Studies in Afrotropical Zoology* **293**: 1–456.
- Mickleburgh, S.P., A.M. Hutson & P.R. Racey (1992). *Old World Fruit Bats. An Action Plan for their Conservation*. I.U.C.N, Gland, Switzerland.
- Mickleburgh, S.P., K. Waylen & P.R. Racey (2009). Bats as bushmeat. *Oryx* **43**: 217–234.
- Moreau, R.E. (1939). A note on the fauna of Mafia. *Tanganyika Notes & Records* **7**: 115.
- Moreau, R.E. (1940). Contribution to the ornithology of the East African islands. *Ibis* (14) **4**: 48–91.
- Moreau, R.E. & R.H.[W.] Pakenham (1940). The land vertebrates of Pemba, Zanzibar and Mafia: a zoogeographical study. *Proceedings of the Zoological Society of London (A)* **110**: 97–128.
- Newitt, M. (1983). The Comoro Islands in Indian Ocean trade before the 19th century. *Cahiers d'Études Africaines* **23**(1/2): 139–165.

- O'Brien, J., C. Mariani, L. Olson, A.L. Russell, L. Say, A.D. Yoder & T.J. Hayden (2009). Multiple colonisations of the western Indian Ocean by *Pteropus* fruit bats (Megachiroptera: Pteropodidae): the furthest islands were colonised first. *Molecular Phylogenetics & Evolution* **51**: 294–303.
- Pakenham, R.H.W. (1979). *The birds of Zanzibar and Pemba: an Annotated Checklist*. British Ornithologists' Union, London.
- Pakenham, R.H.W. (1984). *The Mammals of Zanzibar and Pemba Islands*. Published by the author, Harpenden, UK.
- Piggott, D.W.I. (1941). History of Mafia. *Tanganyika Notes & Records* **11**: 35–40.
- Racey, P.[A.] (1979). Two bats in the Seychelles. *Oryx* **15**: 148–152.
- Racey, P.A., S.M. Goodman & R.G.B. Jenkins (2010). The ecology and conservation of Malagasy bats. In T.H. Fleming & P.A. Racey (eds.) *Island bats. Evolution, Ecology and Conservation*. University of Chicago Press, Chicago. Pp. 369–404.
- Rispal, J-F. (2005). Zanzibar et la politique française dans l'Océan Indien (1776–1904). *Rahia* **15**: 1–95.
- Rocha, S., D. Posada, M.A. Carretero & D.J. Harris (2007). Phylogenetic affinities of Comoroan and East African day geckos (genus *Phelsuma*): multiple natural colonisations, introductions and island radiations. *Molecular Phylogenetics & Evolution* **43**: 685–692.
- Robinson, J.E., D.J. Bell, F.M. Saleh, A.A. Suleiman & I. Barr (2009). Recovery of the Vulnerable Pemba flying fox *Pteropus voeltzkowii*: population and conservation status. *Oryx* **44**: 416–423.
- Roué, S. & J-M. Probst (2010). Nouvelles observations de roussette noire (*Pteropus niger*) sur l'île de la Réunion. *Symbioses* NS **25**: 1–3.
- Saleh, I. (1941). The Comoro Islands. Notes of a lecture delivered at the Zanzibar Museum. *Tanganyika Notes & Records* **12**: 51–60.
- Sclater, P.L. (1864). On the birds of the Comoro Islands. *Ibis* **6**: 292–301.
- Spear, T. (2000). Early Swahili history reconsidered. *International Journal of African Historical Studies* **33**(2): 257–290.
- Thorpe, I. (1988). University of East Anglia Comoro Islands Expedition 1988, Final Report. Unpublished.
- Vaughan, J.H. (1929–30). The birds of Zanzibar and Pemba. *Ibis* (12)**5**: 577–608, (12)**6**: 1–48.
- Vaughan, R.E. (1958). Wencelaus Bojer 1795–1856. *Proceedings of the Royal Society of Arts & Sciences, Mauritius* **2**: 73–98.
- Verin, P. (1994). *Les Comores*. Editions Karthala, Paris.
- Vienne, E. (1900). *Notice sur Mayotte et les Comores*. Exposition Internationale de 1900, Paris.
- Voeltzkow, A. (1904). Bericht über eine Reise nach Ost-Afrika zur Untersuchung der Bildung und des Aufbaues der Riffe und Inseln des westlichen Indischen Ozeans. III: Mafia und Sansibar. *Zeitschrift der Gesellschaft für Erdkunde zu Berlin* **39**: 274–278.
- Voeltzkow, A. (1923). *Reise in Ostafrika in den Jahren 1903–1905. Wissenschaftliche Ergebnisse*, Band 1, Abt. 1. *Reisebericht. Witu-Inseln und Zanzibar-Archipel*. E. Schweizerbart'sche Verlagsbuchhandlung (Erwin Nägele), Stuttgart.
- Walsh, M.T. (1995). Eating bats on Pemba Island: a local innovation or cultural borrowing? *Mvita: Newsletter of the Regional Centre Study for the Archaeology of Eastern & Southern Africa* **6**:15–18.
- Walsh, M.T. (2007). Island subsistence: hunting, trapping and the translocation of wildlife in the western Indian Ocean. *Azania* **42**: 83–113 + online appendix.
- Werth, E. (1915). *Das Deutsch-ostafrikanische Küstenland und die Vorgelagerten Inseln*. Dietrich Reimer, Berlin. 2 vols.