*Zoological Journal of the Linnean Society*, 2019, **186**, 666–672. With 7 figures.

# Repeated evolution of flightlessness in *Dryolimnas* rails (Aves: Rallidae) after extinction and recolonization on Aldabra

JULIAN P. HUME[1,*] and DAVID MARTILL[2]

[1]*Bird Group, Department of Life Sciences, Natural History Museum, Akeman St, Tring, Herts HP23 6AP, UK*
[2]*School of Earth and Environmental Sciences, University of Portsmouth, Portsmouth PO1 3QL, UK*

*Received 9 November 2018; revised 4 February 2019; accepted for publication 9 February 2019*

The Aldabra rail, *Dryolimnas cuvieri* subsp. *aldabranus*, endemic to the Aldabra Atoll, Seychelles, is the last surviving flightless bird in the Indian Ocean. Aldabra has undergone at least one major, total inundation event during an Upper Pleistocene (Tarantian age) sea-level high-stand, resulting in the loss of all terrestrial fauna. A flightless *Dryolimnas* has been identified from two temporally separated Aldabran fossil localities, deposited before and after the inundation event, providing irrefutable evidence that a member of Rallidae colonized the atoll, most likely from Madagascar, and became flightless independently on each occasion. Fossil evidence presented here is unique for Rallidae and epitomizes the ability of birds from this clade to successfully colonize isolated islands and evolve flightlessness on multiple occasions.

KEYWORDS: Aldabra Atoll – fossil – flightless – extinction – sea-level rise – recolonization.

## INTRODUCTION

The white-throated rail, *Dryolimnas cuvieri* (Pucheran, 1845), is indigenous to islands in the south-western Indian Ocean and occurs widely throughout the region (Fig. 1) where it is known to include three subspecies. Volant *D. c.* subsp. *cuvieri* is found today on Madagascar and Mayotte (Safford & Hawkins, 2013), with a totally flightless derivative on Aldabra, *D. c.* subsp. *aldabranus* (Günther, 1879), the last surviving flightless rail in the Indian Ocean (Stoddart & Wright, 1967), and a poorly volant/flightless subspecies, *D. c.* subsp. *abbotti* (Ridgway, 1894) formerly on Assumption (Nicoll, 1908), which became extinct between 1907 and 1937 (Safford & Hawkins, 2013; Hume, 2017). Possibly distinct, but now extinct, rail populations reputedly occurred on Ile aux Cèdres (Aldabra), Cosmoledo Atoll and Astove Island (Collar, 1993) (Figs 1, 2), but no specimens were collected to confirm their status. However, a distinct *Dryolimnas* population on the tiny islet of Ile aux Cèdres in the Aldabra lagoon appears unlikely. In addition, two *Dryolimnas* species once inhabited the Mascarenes: the large, flightless Réunion rail, *D. augusti* Mourer-Chauviré *et al.*, 1999, which survived until at least the end of the 17th century (Mourer-Chauviré *et al.*, 1999), and a probably flightless, undescribed *Dryolimnas* from Mauritius that was last recorded in 1638 (Hume, 2013, 2017).

The discovery of fossil remains of a flightless *Dryolimnas* (two humeri) at Bassin Cabri on Ile Picard confirms the presence of the bird on Aldabra during the Middle Pleistocene (Chibanian age) to the Upper Pleistocene (Tarantian age; Hume *et al.*, 2018) (Fig. 2). The absolute maximum age of the Aldabra Atoll is unknown, but inferences made from sea-level high-stands dating back 400 000 years before present (YBP) show that the Aldabra platform was subject to at least one total inundation event around 340 000 YBP, with possibly two others at 240 000 and 200 000 YBP, respectively (Braithwaite *et al.*, 1973; Braithwaite, 1984) (Fig. 3). An undated limestone depositional sequence (Picard Calcarenites) exposed on present-day Ile Picard must be in excess of 136 000 YBP, as the younger, overlying and island-wide Aldabra Limestone has been dated from Ile Picard deposits between 136 000 (Middle Pleistocene) and 118 000 (Upper Pleistocene) YBP ± 9000 (~127 000+) (Thomson

*Correspondening author. E-mail: j.hume@nhm.ac.uk

 

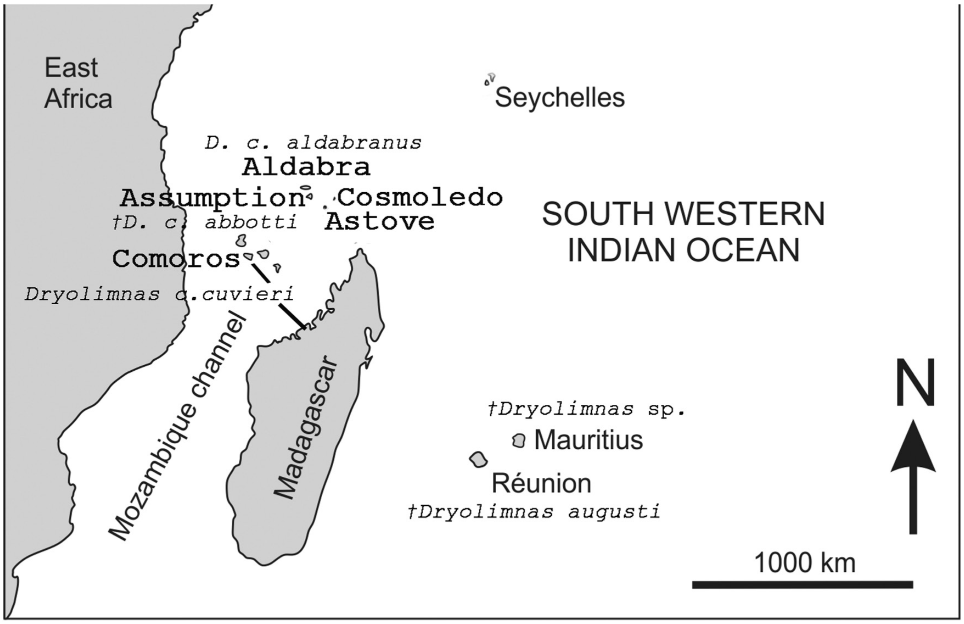


**Figure 1.** Outline map of the south-western Indian Ocean showing the distribution of *Dryolimnas*: *Dryolimnas c. cuvieri*; *D. c. aldabranus*; †*D. c. abbotti*; †*D. augusti*; †*D.* sp. † = extinct.

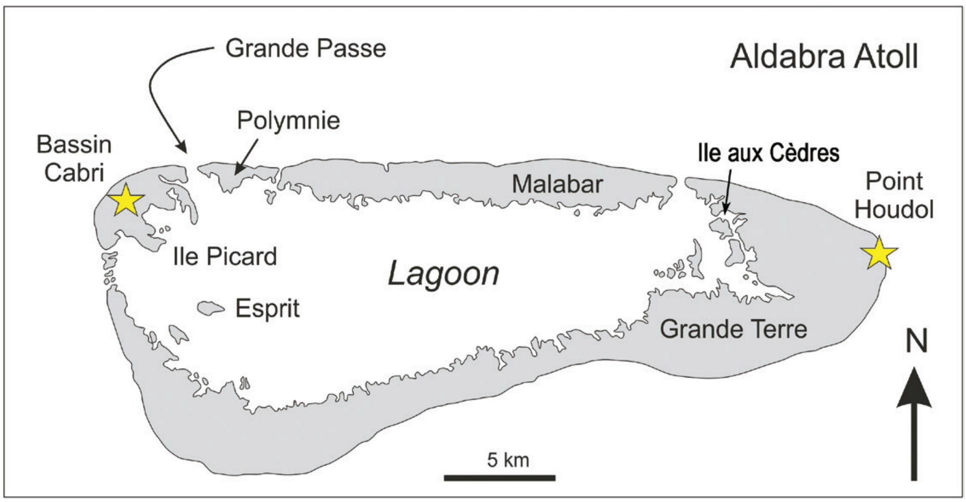


**Figure 2.** Outline map of Aldabra Atoll indicating the fossil localities discussed in the text. Adapted from Hume *et al.* (2018).

& Walton, 1972; Braithwaite *et al.*, 1973) (Fig. 3), which represents the most recent complete inundation event. The Bassin Cabri cavity-fill fossil material accumulated during this period (for a detailed depositional history see: Braithwaite *et al.*, 1973). After the deposition of the Aldabra Limestone, and with falling sea levels, terrestrial soils were created. A reptile-rich fossil deposit formed at Point Hodoul (inferred date ~100 000 YBP; Taylor *et al.*, 1979), which included a distal tarsometatarsus of a *Dryolimnas* rail (Harrison & Walker, 1978).

## MATERIAL AND METHODS

### Specimens

Two humeri held at the Smithsonian Institution National Museum of Natural History (USNM) and a distal tarsometatarsus held at the Natural History Museum, London (NHMUK) of Pleistocene *Dryolimnas cuvieri* were compared with modern specimens held at the Natural History Museum, Tring (NHMUK) of *D. c. cuvieri*, *D. c. aldabranus* and a unique skeleton

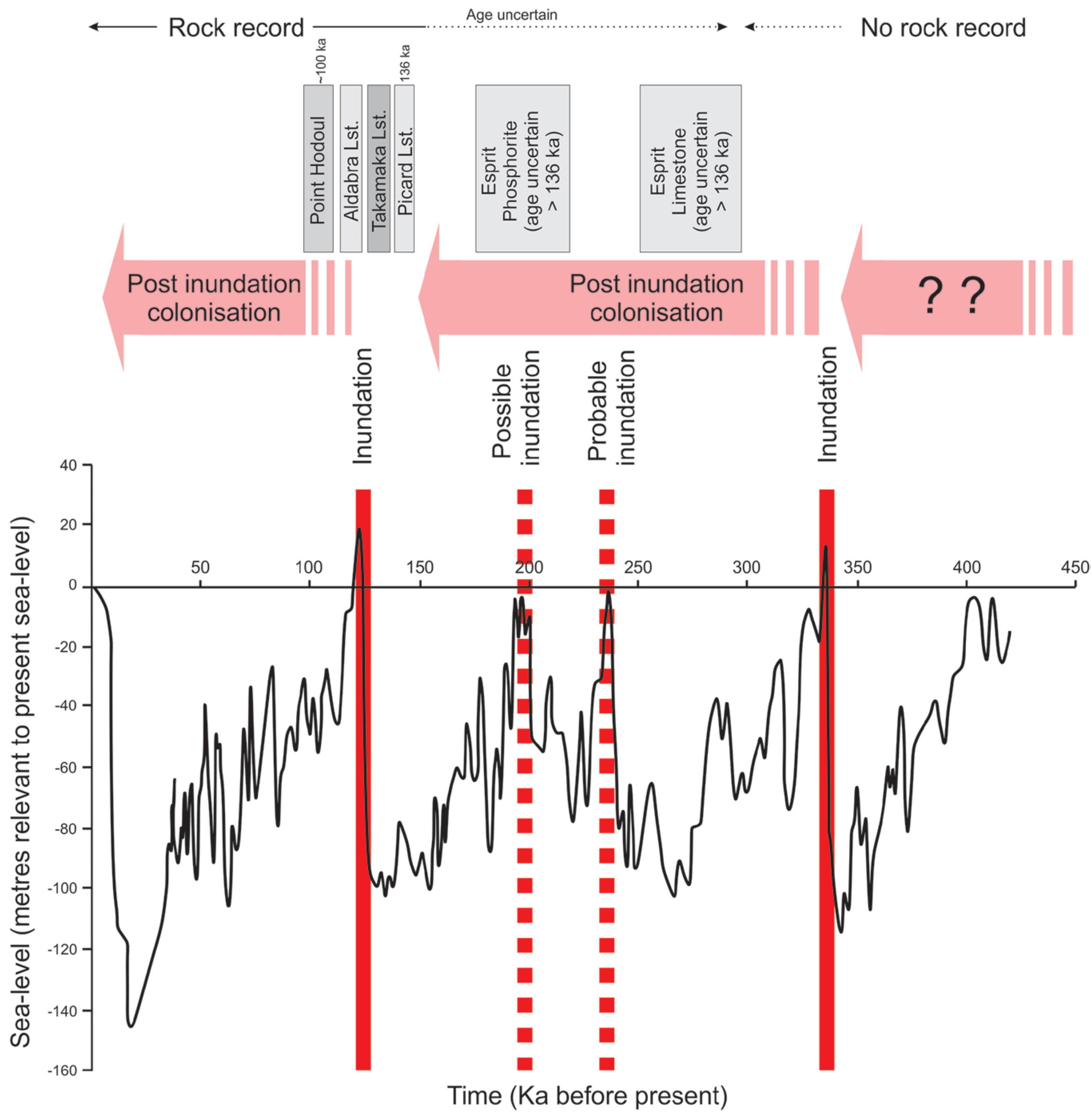


**Figure 3.** Figure showing the sea-level curve and possible inundation events that affected the Aldabra platform in the last 400 000+ YBP. The 118 000 and 136 000 YBP ± 9000 (~127 000+) sea-level high-stand separates the Ile Picard and Point Hodoul fossil localities. Adapted from Perry & Hsu (2000) and Andreas *et al*. (2012).

of the extinct, *D. c. abbotti* (Supporting Information, Tables S1, S2).

### Morphometric analysis

Measurements were taken using a dial calliper and rounded to the nearest 0.1mm. Only humeri and distal tarsometatarsi were available, so measurements of total length, proximal width, proximal depth, shaft width, shaft depth, distal width and distal depth of humerus (Supporting Information, Table S1) and distal width, distal depth and greatest depths taken proximal to trochlea. Metatarsi II were used for tarsometatarsus (Supporting Information, Table S2). Anatomical terminology follows Baumal & Witmer (1993).

## RESULTS

### Morphology

The rail humeri from Bassin Cabri are almost undifferentiated from modern *D. c. aldabranus*, other than being more robust proximally, with the crista bicipitalis more expanded, the shaft more


**Figure 4.** A comparison of humeri (left side) of *Dryolimnas* used in this study. From left to right: *D. cuvieri aldabranus* NHMUK S/1989.38.7 ♂; *D. cuvieri* (Upper Pleistocene) USNM UJP79 unsexed; *D. c. abbotti* NHMUK 1910.4.8.1 unsexed; *D. c. cuvieri* NHMUK 1897.5.10.47 unsexed. Scale bar = 10mm. From Hume *et al.* (2018).


**Figure 5.** A comparison of tarsometatarsi (right side) of *Dryolimnas* used in this study. From left to right: *D. cuvieri* (Upper Pleistocene) NHMUK A4380 unsexed; *D. cuvieri aldabranus* NHMUK S/1989.38.7 ♂; *D. c. abbotti* NHMUK 1910.4.8.1 unsexed; *D. c. cuvieri* NHMUK 1897.5.10.47 unsexed. Scale bar = 10mm.

robust and straighter, and the epicondylus dorsalis less pronounced. Like *D. c. aldabranus*, it also differs considerably in size from *D. c. cuvieri* and *D. c. abbotti* (Fig. 4; Supporting Information, Tables S1, S3). In the few morphometrics available from the tarsometatarsus, the Point Hodoul specimen shows a very similar morphology to *D. c. aldabranus* and *D. c. abbotti* compared with nominate, with the foramen vasculare distale more deeply situated and further distad, the incisura intertrochlearis more open and trochlea. metatarsi II larger and directed further mediad (Fig. 5; Supporting Information, Tables S2, S4); characters indicative of flightlessness (Olson, 1977). The more robust distal end of the tarsometatarsus in the Pleistocene specimen, together with the depth of the shaft proximal to the trochlea also greater than in nominate, suggests that *Dryolimnas* had become more terrestrial and flightless.

## DISCUSSION

The complete inundation of the Aldabra Atoll during deposition of the Aldabra Limestone resulted in the extinction of the endemic Aldabra petrel *Pterodroma kurodai* Harrison & Walker, 1978, Aldabra duck *Aldabranus cabri* Harrison & Walker, 1978 and loss of other bird taxa, including the flightless *Dryolimnas* rail (Harrison & Walker, 1978; Taylor *et al.*, 1979). A number of reptiles also disappeared, including an endemic horned crocodile *Aldabrachampsus dilophus* Brochu, 2006, the giant tortoise *Aldabrachelys* cf. *gigantea* Loveridge & Williams, 1957, an *Oplurus* iguana and terrestrial skinks (Arnold, 1979). At the younger Point Hodoul fossil deposit, the occurrence of giant tortoise, iguana, skinks and *Dryolimnas* show that the atoll was seemingly rapidly recolonized on re-emergence, at least from 100 000 YBP (Taylor *et al.*, 1979).

The presence of *Dryolimnas* at both deposits requires explanation. The Bassin Cabri humeri indicate the rail was already flightless at ~127 000+ YBP during the Middle Pleistocene (Fig. 6); therefore, it must have disappeared, along with the other terrestrial fauna, when the atoll was completely submerged (Thomson & Walton, 1972; Taylor *et al.*, 1979). Furthermore, characters of the tarsometatarsus in the Pleistocene specimen suggest that it had evolved a degree of flightlessness at least comparable with *D. c. abbotti* (Harrison & Walker, 1978), being shorter and more robust than the nominate and *D. c. aldabranus* (Fig. 7). This, and its presence on Aldabra today, provides irrefutable evidence that *Dryolimnas* subsequently recolonized Aldabra after inundation and became flightless for a second time. This scenario may seem surprising, but rails are known to be persistent colonizers of isolated islands and can evolve flightlessness rapidly if suitable conditions exist (Olson, 1977). Therefore, it is likely that the dispersal of nominate *Dryolimnas*

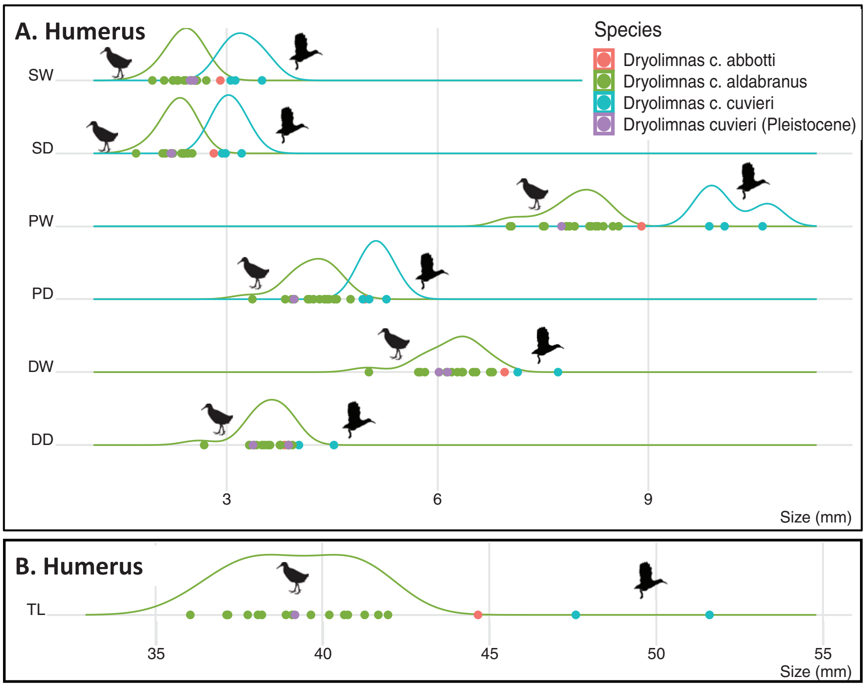


**Figure 6.** Density plots of measurements (mm) of the humerus of Dryolimnas, showing that Pleistocene Dryolimnas cuvieri nestles in with the flightless species. Abbreviations: TL, total length; PW, proximal width; PD, proximal depth; SW, shaft width; SD, shaft depth; DW, distal width; DD, distal depth; (n), number of specimens; (m), mean; SD, Standard Deviation.

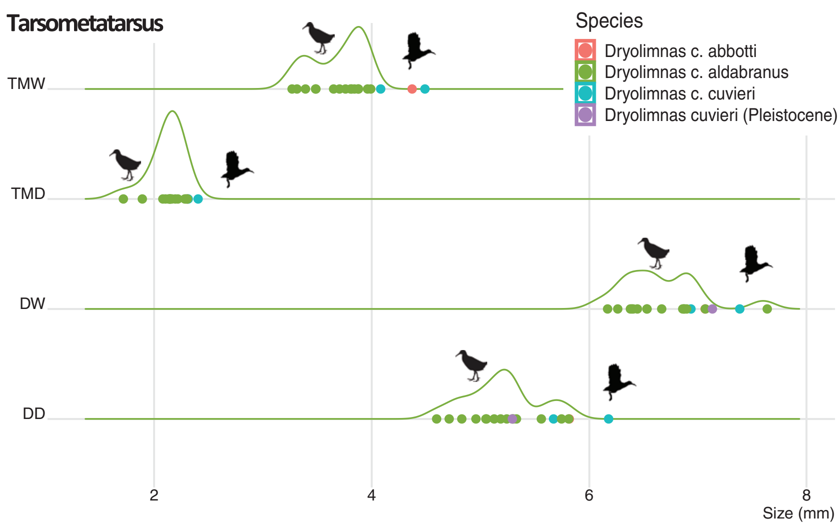


**Figure 7.** Density plots of measurements (mm) of the tarsometatarsus of Dryolimnas, showing that Pleistocene Dryolimnas cuvieri approximates flightless species. Abbreviations: DW, distal width; DD, distal depth; TMD, greatest depth taken proximal to trochlea. metatarsi II; (n), number of specimens; (m), mean; SD, Standard Deviation.

from Madagascar to remote Aldabra occurred on multiple occasions, as did giant tortoises (Taylor *et al.*, 1979). The Point Hodoul fossil record shows that the giant tortoise, iguana, a number of lizard taxa and *Dryolimnas* successfully recolonized the atoll (Hume *et al.* 2018), but the iguana and most other lizards subsequently perished. Based on the geological record (Braithwaite *et al.*, 1973), this extinction event appears to be unrelated to inundation and may have been the result of introduced black rats *Rattus rattus* (Linneaus, 1758), which were present on Aldabra in 1890 (Cheke, 2010) but no doubt arrived much earlier.

Only relatively few taxa from the Middle to Upper Pleistocene fossil deposits on Aldabra survived into the Holocene. Of those that did, apart from breeding sea birds, the most notable are adept open-water travellers, including giant tortoises (by floating) (Gerlach *et al.*, 2006) and *Dryolimnas* rails (periodic, long-distance flight dispersal) (Wanless & Hockey, 2008). Evidence of multiple avian colonization events with recurring flightlessness are extremely rare in the fossil record (e.g. Olson & James, 1991; Fulton *et al.*, 2012), especially on smaller oceanic islands where long-term preservation of fossiliferous material is generally poor. We know of no other example in Rallidae, or of birds in general, that demonstrates this phenomenon so evidently. Only on Aldabra, which has the oldest palaeontological record of any oceanic island in the Indian Ocean region (Thomson & Walton, 1972), is fossil evidence available that demonstrates the effects of changing sea levels on extinction and recolonization events. Conditions were such on Aldabra, the most important being the absence of terrestrial predators and competing mammals, that a *Dryolimnas* rail was able to evolve flightlessness independently on each occasion.

## ACKNOWLEDGEMENTS

We thank Robert Prŷs-Jones, Julia Heinen, Anthony Cheke and an anonymous reviewer for comments that helped improve this paper, and we especially thank Julia Heinen for providing the excellent statistical figures. We thank Storrs Olson, Helen James, Jennifer Strotman and Mark Florence (USNM) for the long-term loan of the John Becker Aldabra material. We thank Sandra Chapman and Lorna Steel (NHMUK) for access to material in their care; Harry Taylor (NHMUK) for photography and Richard Hing (University of Portsmouth) for some fossil preparation. We especially thank the Percy Sladen Centenary Fund whose financial support made this research possible.

## REFERENCES

**Andreas P**, **Reijmer JJG**, **Fürstenau J**, **Kinkel H**, **Betzler C. 2012.** Relationship between Late Pleistocene sea-level variations, carbonate platform morphology and aragonite production (Maldives, Indian Ocean). *Sedimentology* **59:** 1640–1658.

**Arnold EN. 1979.** Fossil reptiles from Aldabra Atoll, Indian Ocean. *Bulletin of the British Museum (Natural History), Zoology* **29:** 85–116.

**Baumel JJ**, **Witmer LM. 1993.** Osteologia. In: Baumel JJ, King AS, Breazile JE, Evans HE, Vanden Berge JC, eds. *Handbook of avian anatomy: nomina anatomica avium*, *2nd edn*. Cambridge: Publications of the Nuttall Ornithological Club, 45–132.

**Braithwaite CJR. 1984.** Geology of the Seychelles. In: Stoddart DR, ed. *Biogeography and ecology of the Seychelles Islands*. The Hague: Dr W. Junk Publishers, 17–38.

**Braithwaite CJR**, **Taylor JD**, **Kennedy WJ. 1973.** The evolution of an atoll: the depositional and erosional history of Aldabra. *Philosophical Transactions of the Royal Society of London B* **266:** 307–340.

**Brochu CA. 2006.** A new miniature horned crocodile from the Quaternary of Aldabra Atoll, western Indian Ocean. *Copeia* **2:** 149–158.

**Cheke A. 2010.** The timing of arrival of humans and their commensal animals on Western Indian Ocean oceanic Islands. *Phelsuma* **18:** 38–69.

**Collar NJ. 1993.** The conservation status in 1982 of the Aldabran white-throated rail *Dryolimnas cuvieri aldabranus*. *Bird Conservation International* **3:** 299–305.

**Fulton TL**, **Letts B**, **Shapiro B. 2012.** Multiple losses of flight and recent speciation in steamer ducks. *Proceedings of the Royal Society B, Biological Sciences* **279:** 2339–2346.

**Gerlach J**, **Muir C**, **Richmond MD. 2006.** The first substantiated case of trans-oceanic tortoise dispersal. *Journal of Natural History* **40:** 2403–2408.

**Günther A. 1879.** On the occurrence of a land-rail (*Rallus*) in the Island of Aldabra. *Annals and Magazine of Natural History* **3:** 164–168.

**Harrison CJO**, **Walker CA. 1978.** Pleistocene bird remains from Aldabra Atoll, Indian Ocean. *Journal of Natural History* **12:** 7–14.

**Hume JP. 2013.** A synopsis of the pre-human avifauna of the Mascarene Islands. In: Göhlich UB, Kroh A, eds. *Proceedings of the 8th international meeting of the Society of avian paleontology and evolution*. Vienna: Natural History Museum, 195–237.

**Hume JP. 2017.** *Extinct birds*, *2nd edn*. London: Christopher Helm.

**Hume JP**, **Martill D**, **Hing R. 2018.** A palaeontological review of Aldabra Atoll, Aldabra Group, Seychelles. *PlosOne*. doi: 10.1371/journal.pone.0192675.

**Perry CA**, **Hsu KJ. 2000.** Geophysical, archaeological, and historical evidence support a solar-output model for climate change. *PNAS* **97:** 12433–12438.

**Loveridge A**, **Williams EE. 1957.** Revision of the African tortoises and turtles of the suborder Cryptodira. *Bulletin of the Museum of Comparative Zoology, Harvard* **115:** 161–557.

**Mourer-Chauviré C**, **Bour R**, **Ribes S**, **Moutou F. 1999.** The avifauna of Réunion Island (Mascarene Islands) at the time of the arrival of the first Europeans. *Smithsonian Contributions to Paleobiology* **89:** 1–38.

**Nicoll MJ. 1908.** *Three voyages of a naturalist*. London: Witherby and Co.

**Olson SL. 1977.** A synopsis of the fossil Rallidae. In: Ripley SD, ed. *Rails of the world. A monograph of the family Rallidae*. Boston: David R. Godine, 338–378.

**Olson SL**, **James HF. 1991.** Descriptions of 32 new species of birds from the Hawaiian Islands: part 1, non-Passeriformes. *Ornithological Monographs* **45:** 1–88.

**Pucheran MLD. 1845.** Notes sur quelques espèces Madécasses de l'ordre des Échassiers. *Revue Zoologique par la Société Cuvierienne* **1845:** 277–280.

**Ridgway R. 1894.** Descriptions of some new birds from Aldabra, Assumption, and Gloriosa Islands, collected by Dr W. L. Abbott. *Proceedings of the United States National Museum* **17:** 371–373.

**Safford R**, **Hawkins F. 2013.** *Birds of Africa, vol. VIII: the Malagasy region*. London: Christopher Helm.

**Stoddart DR**, **Wright CA. 1967.** Geography and ecology of Aldabra Atoll. *Atoll Research Bulletin* **118:** 11–52.

**Taylor JD**, **Braithwaite CJR**, **Peake JF**, **Arnold EN. 1979.** Terrestrial faunas and habitats of Aldabra during the Late Pleistocene. *Philosophical Transactions of the Royal Society of London B* **286:** 47–66.

**Thomson J**, **Walton A. 1972.** Redetermination of chronology of Aldabra Atoll by $^{230}$Th/$^{234}$U dating. *Nature* **240:** 145–146.

**Wanless RM**, **Hockey PAR. 2008.** Natural behaviour of the Aldabra Rail (*Dryolimnas* [*cuvieri*] *aldabranus*). *Wilson Journal of Ornithology* **120:** 50–61.

## SUPPORTING INFORMATION

Supporting information may be found in the online version of this article at the publisher's web-site.

**Table S1.** Summary statistics for measurements (mm) of the humerus of *Dryolimnas*.
**Table S2.** Summary statistics for measurements (mm) of the tarsometatarsus of *Dryolimnas*.
**Table S3.** Raw measurements (mm) of the humerus of *Dryolimnas*.
**Table S4.** Raw measurements (mm) of the tarsometatarsus of *Dryolimnas*.