

Research



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Palaeontology

Ancient DNA from the extinct Haitian cave-rail (*Nesotrochis steganinos*) suggests a biogeographic connection between the Caribbean and Old World

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Worldwide decline in biodiversity during the Holocene has impeded a comprehensive understanding of pre-human biodiversity and biogeography. This is especially true on islands, because many recently extinct island taxa were morphologically unique, complicating assessment of their evolutionary relationships using morphology alone. The Caribbean remains an avian hotspot but was more diverse before human arrival in the Holocene. Among the recently extinct lineages is the enigmatic genus *Nesotrochis*, comprising three flightless species. Based on morphology, *Nesotrochis* has been considered an aberrant rail (Rallidae) or related to flufftails (Sarothruridae). We recovered a nearly complete mitochondrial genome of *Nesotrochis steganinos* from fossils, discovering that it is not a rallid but instead is sister to Sarothruridae, volant birds now restricted to Africa and New Guinea, and the recently extinct, flightless Aptornithidae of New Zealand. This result suggests a widespread or highly dispersive most recent common ancestor of the group. Prior to human settlement, the Caribbean avifauna had a far more cosmopolitan origin than is evident from extant species.

1. Introduction

Islands have been recognized as places to study evolution, ecology and biogeography [1,2]. The natural biota of all islands, no matter how remote, has been altered by humans, leaving a residual modern diversity that is different from its pre-human condition [3]. Most island diversity has been lost relatively recently because the mass extinction events that began on continents during the late Pleistocene did not affect islands until human colonization in the Holocene (e.g. [4]). Because of this delay, islands acted as refugia of diversity in the recent past [4,5]. Still, we have a limited understanding of the phylogenetic affinities of species lost after human contact, thereby limiting what we know about the evolutionary and biogeographic mechanisms underpinning these communities.

The unique morphology of many island birds has been driven by niche availability and the lack of mammalian predators, making them susceptible to predation by humans and other invasive predators [6,7]. Doves, rails, passerines and certain seabirds had the highest overall numbers of insular avian extinctions [8,9], although losses occurred across all groups of island birds, involving entire subfamilies (Raphinae—dodo and solitaire), families (Aptornithidae—adzebills) and even orders (Aepyornithiformes—elephant

birds; Dinornithiformes—moas). The extreme morphological diversity that was lost, exemplified by large herbivores (elephant birds) or predators (adzebills), complicates the recovery of their evolutionary relationships with living taxa. Recently, ancient DNA (aDNA) has illuminated the phylogenetic placement of previously enigmatic extinct island birds. For example, aDNA has revealed that elephant birds are sister to Apterygiformes [10], and adzebills (Aptornithidae) are sister to flufftails (Sarthruridae; [11]) from sub-Saharan Africa and New Guinea. These results provide context for lost biogeographic connections, long-distance dispersal events, and the evolution of gigantism and flightlessness [12,13].

Nesotrochis is an extinct genus with three flightless species once found in the Greater Antilles. *Nesotrochis debooyi* was described from bones in archaeological middens in the Virgin Islands, suggesting it survived until European arrival [14]; later it was discovered in Puerto Rico [15,16]. *Nesotrochis* was believed to be related to the rallid genus *Aramides*, with a South American origin [15]. Later, Wetmore considered *Nesotrochis* related to gallinules (*Gallinula*, Rallidae; [17]), which Olson [16] supported. *Nesotrochis picipicensis* on Cuba was described first as a coot, *Fulica picipicensis* (Rallidae; [18]), but then placed in *Nesotrochis* from osteological characters by Olson [16], who also described *Nesotrochis steganinos* from Hispaniola. However, morphological and ecological convergence is commonplace across rails (Rallidae) and the closely related flufftails (Sarthruridae) [19,20]. Recent work suggests that *Nesotrochis* shares diagnostic hypotarsus characters with flufftails (Sarthruridae) and related taxa (Heliornithidae) that differ from Rallidae, indicating that *Nesotrochis* may not be a member of the Rallidae [21].

The affinities of *Nesotrochis* based on skeletal morphology have been conjectural since its description. Here, we use aDNA from *N. steganinos* to evaluate the osteology-based hypothesis that *Nesotrochis* is closely related to *Gallinula* (Rallidae) or to other closely related families, and discuss the systematic and biogeographic implications of our findings.

2. Methods

A *Nesotrochis steganinos* pedal phalanx (Florida Museum, University of Florida (UF) 431763; Haiti: Trouing Marassa; 20 July 1983, 10X.31Y.26Z subunit A; GenBank accession no. MW145005.1) was used for DNA extraction and sequencing. DNA extraction, library preparation, target capture enrichment and post-sequencing data cleaning followed the methods in Oswald *et al.* ([22,23]; full details are also provided in the electronic supplementary material). An associated phalanx of UF 431763 (same catalogue number) was radiocarbon dated (Beta Analytic Testing Laboratory ID: Beta-502522) at 6430 ± 30 BP (conventional radiocarbon age) and calendrically calibrated (using INTCAL13) to 7424 to 7289 cal BP (early Holocene). Radiocarbon pretreatment was a collagen extraction with alkali and ultrafiltration. For target capture enrichment, we used a mitochondrial DNA bait set designed by Arbor Biosciences (Ann Arbor, MI) based on the rallid *Porphyrio melanotus* (NC025508.1; a hypothetical close relative of *Nesotrochis* based on osteology; see electronic supplementary material, table S1 for sample and taxonomic information).

In Geneious (v. 11.1.4; <https://www.geneious.com>), the Map to Reference feature set to default settings (Medium-Low Sensitivity; five iterations) was used to map the cleaned, unpaired reads to *P. melanotus*. An initial BLAST [24] search of the recovered cytochrome b gene indicated that *Nesotrochis* was not closely related to *P. melanotus* so we repeated the Map to

Reference approach using other Gruiformes as references including *Aptornis otidiformis* (MK434262.1; Aptornithidae), *Sarthrura ayresi* (NC034316.1; Sarthruridae) and *Canirallus oculus* (MK434261.1; Rallidae). mapDamage [25] was used to determine if the base patterns in our reads were consistent with those found in a DNA, using paired reads mapped to the *P. melanotus* mitochondrial genome as a reference.

The majority consensus sequences for each of the four references were aligned to discern possible discrepancies between the reference used and the resultant base calls. Sites where more than two of the consensus sequences had an ambiguous base call (e.g. M or Y, not including the D loop) were reviewed by eye in the read pile-ups to evaluate the number of reads that supported the ambiguity and whether it was a possible site of deamination or degradation, i.e. at the end of the read, where degradation is more prevalent in ancient data. The greatest area of disagreement across different references was located in the D loop, which we subsequently removed from the *N. steganinos* data before further analyses.

Following the eBird/Clements checklist [26], we downloaded all available Gruiformes mitochondrial genome data from GenBank. The Gruiformes comprise 192 currently recognized extant or very recently extinct species. Whole or nearly complete mitochondrial genome sequences were available for 21% of gruiform species. Rallids represented 89% of the missing species. All recognized extant families were represented by at least one species in our dataset. The mitochondrial genome of *Rallula forbesi* (Rallina per [26]) was obtained by mapping the raw read data from Garcia-R *et al.* [27] to the mitochondrial genome of *C. oculus* in Geneious (v. 11.1.4) using the Medium-Low Sensitivity default settings. Along with extant species, we included partial mitochondrial genomes of the extinct New Zealand adzebills: *A. otidiformis* and *Aptornis defossor* (Aptornithidae; [11]). To increase our sampling of Sarthruridae, we also included three mitochondrial gene regions (ATP6, tRNA-Gly ND3 and CytB) of *Mentocrex kioloide* and *Mentocrex beankaensis*. *Tringa semipalmata* and *Tringa ochropus* (Scolopacidae) were used as the outgroup. GenBank accession numbers are given in electronic supplementary material, table S1.

Mitochondrial sequences were aligned using the Geneious multiple sequence alignment algorithms. Because of the phylogenetic diversity in our dataset, the D loop region remaining in the other taxa aligned poorly and was removed (dataset 1; 15 954 bp). Gblocks [28] was used to remove poorly aligning regions (dataset 2; 14 514 bp). With each dataset, we performed a maximum-likelihood analysis in RAXML (8.2.11; [29]) with three partitions: (i) protein-coding sequences (CDS), (ii) rRNA and tRNA sequences, and (iii) non-coding sequences. We assessed topological support with 1000 bootstrap replicates. Dataset 1 recovered low support for *Nesotrochis* and putative sister taxa, so we visualized alternative topologies by calculating the Robinson-Foulds distance matrix [30] using the package phytools [31] in R v. 3.6.1 [32]. We used classical multidimensional scaling to reduce this matrix to a single axis representing tree similarity. We coloured each tree according to topological similarity based on this metric (similarity index).

3. Results

Using *Aptornis otidiformis*, *Sarthrura ayresi*, *Canirallus oculus* (MK434261.1) and *Porphyrio melanotus* as references, we recovered 329 330, 330 367, 325 644 and 336 218 on-target reads, respectively, of *Nesotrochis steganinos*. Average read length ranged from 93.5 to 93.9 bp with a coverage mean of 1892–1903 reads across the four references. mapDamage fragment misincorporation plots indicate the expected C→T and A→G substitutions characteristic of a DNA (electronic

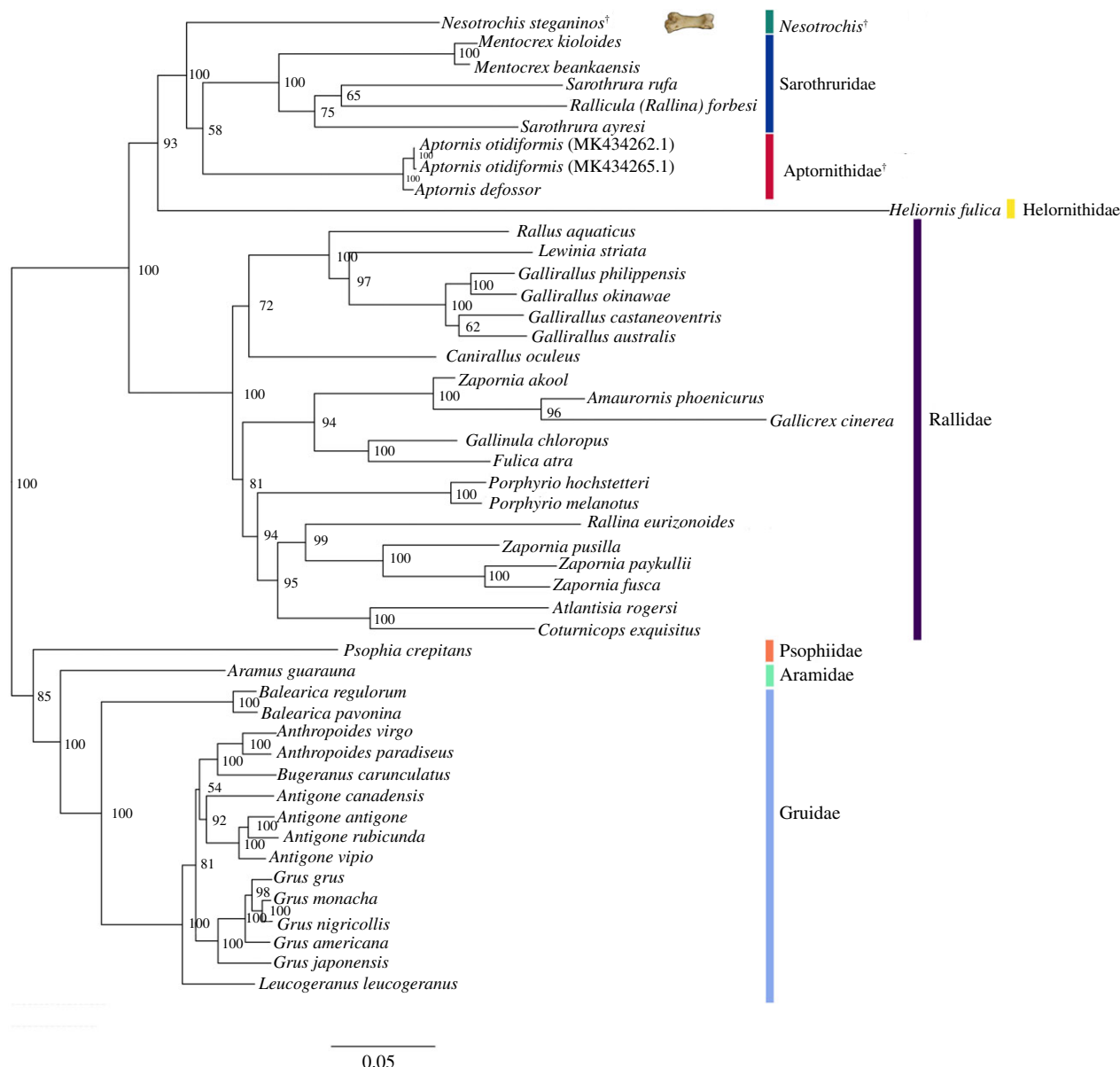


Figure 1. RAxML phylogeny of the Gruiformes based on the Gblocks dataset (dataset 2). The bootstrap support for the sister relationship of *Nesotrochis steganinos* to Sarothruridae + Aptornithidae is 100% yet the phylogenetic relationships within this clade are not resolved. See electronic supplementary material, figures S1 and S2 for the alternative topology, where *N. steganinos* is sister to Sarothruridae (based on dataset 1). The *N. steganinos* pedal phalanx from which aDNA was extracted is shown next to the tip name.

supplementary material, figure S1). The only missing data, regardless of the reference used, were within the D loop as expected based on high divergence within and across taxa.

Our mitochondrial phylogeny, based on both datasets, recovered the same topology of extant gruiform families as Prum *et al.* [33] using targeted genome sequencing. Relationships within Gruidae differ between datasets 1 and 2. The dataset 1 RAxML phylogeny is the same as that of Krajewski *et al.* [34]. The Rallidae topology does not differ between datasets. Both RAxML phylogenies indicate that *N. steganinos* does not fall within the Rallidae and instead is in the clade composed of Sarothruridae and the extinct Aptornithidae (represented by *A. otidiformis* and *Aptornis defossor*). The relationships among *Nesotrochis*, Sarothruridae and Aptornithidae are not resolved. Dataset 1 suggests *Nesotrochis* is sister to Sarothruridae, albeit with only marginal support (52%; electronic supplementary material, figure S2), and this clade is sister to Aptornithidae. The alternative topology (48% of bootstrap replicates) of dataset 1 recovered *Nesotrochis*

as sister to Aptornithidae + Sarothruridae (electronic supplementary material, figure S3). Dataset 2 resulted in 100% topological support of a clade comprising *Nesotrochis*, Aptornithidae and Sarothruridae and 58% topological support for *Nesotrochis* as sister to Aptornithidae and Sarothruridae (figure 1).

4. Discussion

The Cenozoic fossil record of Gruiformes is relatively species-rich, but the repeated convergent evolution of rail-like body plans, along with convergence due to flightlessness, hinders the phylogenetic placement of extinct species. Our aDNA results support *Nesotrochis* as sister to the clade Sarothruridae + the extinct Aptornithidae, or just to the Sarothruridae, both of which inhabit(ed) the Old World (figure 2). They are part of a larger clade that also includes the Heliornithidae. *Nesotrochis* is the only DNA-based example of a Caribbean avian genus that

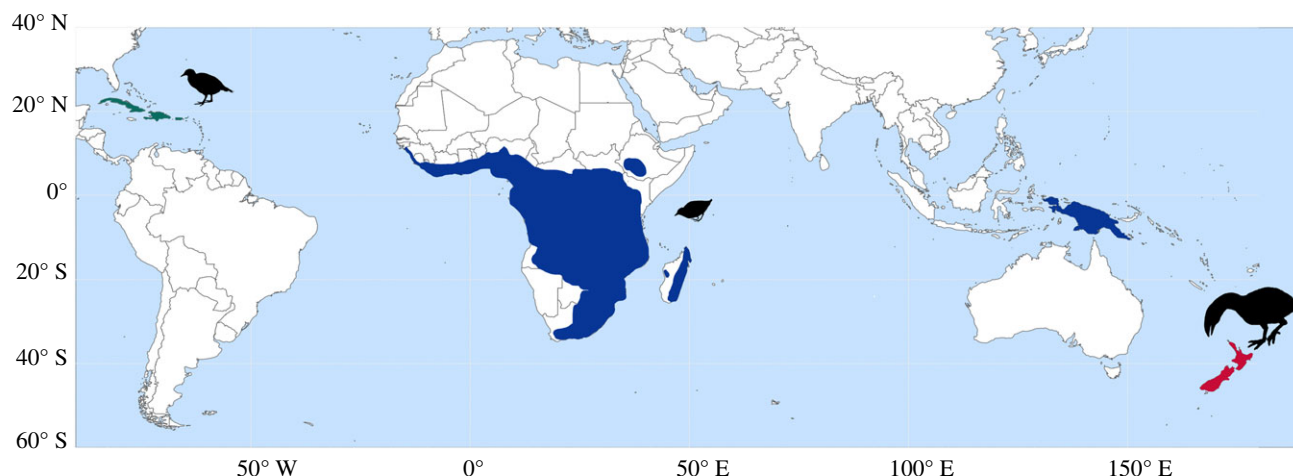


Figure 2. The distribution of *Nesotrochis* (green) within the Caribbean, Sarothruridae (blue) in Africa and New Guinea, and Aptornithidae (red) in New Zealand. Both *Nesotrochis* and Aptornithidae are extinct and are the most closely related lineages to Sarothruridae. Image credits: '*Nesotrochis*': T. Michael Keeseey and Huttu Mcphoo, <https://creativecommons.org/licenses/by-sa/3.0/>; '*Sarothrura*': Ryan S. Terrill; and *Aptornis otidiformis*: N. Tamura.

is sister to families restricted to the Old World. As such, it provides a dramatic example of human-caused extinction erasing complex biogeographic history.

(a) Biogeography of families convergent on Rallidae

The finfoots/sungrebe (Heliornithidae), adzebills (Aptornithidae), flufftails (Sarothruridae) and *Nesotrochis* clade contains many species that are morphologically convergent with rallids, with which they shared a common ancestor likely during the early Cenozoic [11,27]. Holocene extinctions have greatly diminished this clade; combined data from morphology and aDNA indicate 50% family level extinction during the Holocene (herein; [11]). Here, we briefly discuss the clade's diversity and biogeography.

Heliornithidae consists of three monotypic genera, each in a single tropical region (Neotropics—*Heliornis fulica*; Afrotropics—*Podica senegalensis*; and SE Asia—*Heliopais personatus*). The relationships among these species have not been evaluated with large-scale genomic data [35], but the family's pan-tropical distribution suggests either extinction of a more widespread temperate taxa or a highly dispersive most recent common ancestor. Aptornithidae is an extinct family from New Zealand; its fossil record extends to the Miocene [36], with divergence from the Sarothruridae conjectured during the late Eocene [11]. The two Holocene species of aptornithids were 0.8 m tall, approximately 17 kg, flightless predators until their extinction following human arrival 600 years ago [37–39].

The greatest extant diversity within the larger clade occurs in the Sarothruridae, which comprises 15 species in the genera *Sarothrura*, *Mentocrex* and *Rallacula* (*Rallina* in [26]). (*Rallina* 'rails' are likely all sarothrurids; *Rallina* 'crakes' are rallids; see [26,27]). Sarothrurids have been considered to be rallids based on morphology [19], although hypotarsal characters support the close relationship of Sarothruridae and Heliornithidae [21]. Further study may disclose that some modern and fossil taxa currently considered to be rallids are actually sarothrurids (e.g., [20]). Learning just how deeply divergent *Nesotrochis* is from the Sarothruridae will require further genetic sampling of sarothrurids and the two other species of *Nesotrochis*. If *Nesotrochis* truly is sister to the Sarothruridae, the divergence of the two lineages likely took place during the Eocene or Oligocene based on recent calibrations [11,27].

(b) Caribbean biogeography

Modern Caribbean bird diversity largely consists of New World families such as Trochilidae (hummingbirds), Mimidae (mockingbirds, tremblers), Thraupidae (tanagers) and Parulidae (wood-warblers). It also includes four endemic families: the Todidae (todies), Dulidae (palmchat), Calyptophilidae (chat-tanagers) and Phaenicophilidae (palm-tanagers). The phylogenetic relationship of *Nesotrochis* to Sarothruridae and Aptornithidae indicates a novel historical biogeographic connection between the Caribbean and the Old World. A similar hypothesis has been proposed, based on morphology, for the endemic Cuban dove *Starnoenas* [40], an idea waiting to be tested with DNA. *Nesotrochis* could be a relictual taxon that survived in the Caribbean after extinction on the adjacent mainland, or an example of long-distance dispersal from the Old World to the Caribbean.

This is the first avian Caribbean–Old World connection supported by DNA-based evidence, yet other non-avian taxa have been proposed to have dispersed from the Old World. For example, New World monkeys and caviomorph rodents arrived from Africa between or during the mid Eocene to mid Oligocene [41,42]. The enigmatic hoatzin (*Opisthocomus hoazin*) of the Amazon Basin is the last living representative of an avian order found in Europe and Africa from the late Eocene to Miocene [43–45]. The African *Ptilopachus* is the sole genus of New World quail (Odontophoridae) outside of the Americas, with a divergence that also dates to the mid Eocene to mid Oligocene [46]. Another American bird with Old World affinities is the wrenit (Paradoxornithidae), which colonized the New World in the late Miocene [47]. Others include the bushtit (Aegithalidae), verdin (Remizidae), and South American painted-snipe (Rostratulidae). For taxa with calculated divergence times, all divergences occurred well before the significant global cooling that began during the Pliocene, which suggests that warmer, less seasonal climatic conditions may have been favourable for long-distance dispersal and more widespread distributions.

5. Conclusion

Island taxa have been disproportionately affected by human-caused extinction compared with their continental relatives,

which has limited our understanding of processes shaping insular biota. Ancient DNA approaches are critical for the phylogenetic placement of extinct island taxa, which in turn supports a broader understanding of biogeography and evolution of often-enigmatic species. New insights from such research suggest that while islands can act as refugia for previously widely distributed clades, they may have also harboured unique, deeply divergent island-endemic groups such as *Nesotrochis*. As the fossil record of island vertebrates grows, we see rich opportunities for combining both morphological and molecular data within a geographically wide-open framework.

Ethics. The authors had permission from the Vertebrate Paleontology curatorial staff at the Florida Museum of Natural History to sample UF 431763 *Nesotrochis steganinos*.

Data accessibility. The UF 431763 *Nesotrochis steganinos* mitochondrial genome is available on GenBank (accession no. MW145005.1). Raw reads are available on NCBI SRA; BioProject accession number:

PRJNA680380. Individual sequencing efforts are accessioned as: SAMN16913466 (HiSeq, shotgun sequences), SAMN16913467 (MiSeq, shotgun sequences), SAMN16913468 (MiSeq, mitochondrial genome enriched sequences).

Authors' contributions. J.A.O., B.J.S., M.J.L., D.W.S., R.P.G. and J.M.A. conceived and designed the study. J.A.O. and R.S.T. performed analyses. J.A.O. and B.J.S. performed laboratory work. All authors contributed towards data interpretation and writing of the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed herein.

Competing interests. We declare we have no competing interests.

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