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Research

Genomic data reveal that the Cuban blue-headed quail-dove (*Starnoenas cyanocephala*) is a biogeographic relict

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Islands are well known for their unique biodiversity and significance in evolutionary and ecological studies. Nevertheless, the extinction of island species accounts for most human-caused extinctions in recent time scales, which have accelerated in recent centuries. Pigeons and doves (Columbidae) are noteworthy for the high number of island endemics, as well as for the risks those species have faced since human arrival. On Caribbean islands, no other columbid has generated more phylogenetic interest and uncertainty than the blue-headed quail-dove, *Starnoenas cyanocephala*. This endangered Cuban endemic has been considered more similar, both behaviourally and phenotypically, to Australasian species than to the geographically closer 'quail-dove' (*Geotrygon* s.l.) species of the Western Hemisphere. Here, we use whole genome sequencing from *Starnoenas* and other newly sequenced columbids in combination with sequence data from previous publications to investigate its relationships. Phylogenomic analyses, which represent 35 of the 51 genera currently comprising the Columbidae, reveal that the blue-headed quail-dove is the sole representative of a lineage diverging early in the radiation of columbids. *Starnoenas* is sister to the species-rich subfamily Columbinae, which is found worldwide. As a highly distinctive evolutionary lineage lacking close modern relatives, we recommend elevating the conservation priority of *Starnoenas*.

1. Introduction

Island biodiversity is shaped by ecological opportunity, dispersal and isolation, resulting in evolutionarily distinct biotic assemblages. Thus, island species have had a strong influence on the development of evolutionary and biogeographic theory (e.g. [1,2]). The colonization of islands by humans in the late Pleistocene and Holocene marked the beginning of rapid losses of biodiversity on islands that accelerated during European colonization and continues today [3–7]. Anthropogenic impacts have transformed islands from 'natural laboratories' for studying evolution and diversity into places where many native species are rare if not extinct [3,4,8]. The ongoing loss of island species compels us to try to understand the biogeography and evolution of living species, while we can.

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Bird extinctions on Caribbean islands span the avian tree of life with 80+ species lost since the late Pleistocene [6,9,10]. Despite these losses, the Caribbean still sustains approximately 175 endemic land bird species [11,12], many of which are in decline. The blue-headed quail-dove, *Starnoenas cyanocephala* (Columbiformes, Columbidae; henceforth *Starnoenas*) is endangered, morphologically unique, in a monotypic genus and endemic to Cuba (figure 1*a*). The phylogenetic relationships of *Starnoenas* within the Columbidae have long been uncertain. In both morphology (including internal and external characters) and behaviour, *Starnoenas* has a mosaic of traits that are either unique or resemble those of widespread Columbidae species, especially Australasian (Raphinae) species, rendering the taxonomic affinities of *Starnoenas* unclear [14]. Some of these characters include the absence of a uropygial gland in *Starnoenas*, similar to other genera in Raphinae (*Goura*, *Didunculus*) but is present in all Western Hemisphere doves [14]. In addition, the characteristics of the sternum of *Starnoenas* are more similar to Australian species than to any Western Hemisphere taxa [14]. Based on the many characters that *Starnoenas* shares with Australasian columbids, Olson & Wiley [14] concluded that it is more closely related to Australasian species than to any in the Western Hemisphere (figure 1*b*), suggesting that prior affiliations with Western Hemisphere quail-doves in the genera *Geotrygon*, *Zentrygon* or *Leptotrygon* (as in [13]; figure 1*b*) required re-evaluation.

Pigeons and doves are highly successful colonizers that are (or were) present on many of the world's islands. Accordingly, they have been particularly hard hit by human-caused extinctions [15,16]. These losses have affected plant communities because many columbids are important dispersers of plant propagules [16]. These extinctions also have involved unique giant and/or flightless forms such as the dodo (*Raphus cucullatus* [17]), Rodrigues solitaire (*Pezophaps solitaria* [18]), Tongan giant pigeon (*Tongoenas burleyi* [19]) and Viti Levu giant pigeon (*Natunaornis gigoura* [20]).

Insights into the deep-time biogeographic history of columbids are provided by phylogenetic data and fossils. Molecular phylogenies have placed columbids into three major clades, classified as three subfamilies [21–25]. The Columbinae includes all Western Hemisphere genera of large body size and the Eastern Hemisphere *Streptopelia*, *Aplopelia*, *Nesoenas*, *Spilophila*, *Columba*, *Macropygia*, *Turacoena* and *Reinwardtoena*. The Claravinae comprises the Western Hemisphere small ground-doves (e.g. *Columbina*, *Metriopelia*). The subfamily Raphinae comprises tropical Eastern Hemisphere species including Australian, southeast Asian and Pacific species (e.g. *Ptilinopus*, *Ducula* and *Treron*) and the African genera *Turtur* and *Oena*. The earliest substantial fossil record of columbids comes from the Early Miocene (approx. 18.5 Ma) of Florida. Represented by hundreds of specimens constituting elements from the entire skeleton, the extinct *Arenicolumba prattae* is a small species for which the endemic African genera *Oena* and *Turtur* have been proposed as the closest living genera rather than any of the Claravinae [26]. No close relatives of *Oena* or *Turtur* now occur in the Western Hemisphere. Roughly coeval columbid fossils from New Zealand and Europe are too sparse for rigorous phylogenetic interpretation [14].

Despite progress in understanding past and present diversity of doves, especially on islands, *Starnoenas* is both phylogenetically difficult to place and has traits that make it particularly vulnerable to human exploitation. In particular, it is largely ground dwelling, relatively tame and typically runs rather than flies from predators [14,27]. Ethnohistoric accounts from Cuba describe human consumption and caging of the species since the sixteenth century, if not earlier [14]. Indeed, *Starnoenas* was much more widely distributed across Cuba in the past, with much of its decline evident by the early to mid-twentieth century [28–30]. Today, the greatest threats to *Starnoenas* are habitat loss, illegal hunting for consumption, invasive species (e.g. cats) and a lack of species-specific conservation policy [31]. Estimates of the entire population of *Starnoenas* are from 600 to 1700 mature individuals [31].

Morphological change on islands, long-term isolation and human-driven extinction can confuse morphological placement of species in a phylogenetic context [32,33]. We therefore evaluated the phylogenetic relationships of *Starnoenas* by leveraging genomic data and sequencing additional Eastern Hemisphere species that represent all columbid subfamilies and 35 of the 51 recognized extant or recently extinct genera. We then used phylogenomic approaches to combine these data with whole genome sequences that we obtained from a *Starnoenas* specimen to better place this enigmatic taxon in a phylogenetic context. Of the 16 genera not included in our phylogeny, 14 are represented in published phylogenies, and their subfamilial placement was reviewed. Prior taxonomic assessments lead us to three alternative phylogenetic hypotheses regarding the phylogenetic placement of *Starnoenas*. (H1) *Starnoenas* forms a clade with *Geotrygon*, *Zentrygon*, *Zenaida* and *Leptotila* within the subfamily Columbinae. This would place *Starnoenas* with other species similar in body form also found in the Western Hemisphere (range and phylogenetic relationships of these potential relatives is shown in figure 1*b*,*c*; labelled 'H1'). (H2) *Starnoenas* is most closely related to Australasian species in the subfamily Raphinae (range and phylogenetic relationships of these potential relatives is shown in figure 1*b*,*c*; labelled 'H2'). (H3) Finally, we recognize that *Starnoenas* may represent a monotypic clade sister to one or more subfamilies that through biogeographic processes and/or extinction has become isolated within Cuba (figure 1*c*; labelled 'H3').

The distinctive morphology and behaviour of *Starnonenas* led Olson & Wiley [14] to conclude that 'It may be the most enigmatic bird not just in the West Indies, but in the entire New World'. They also noted that no molecular data existed for *Starnoenas*. In this article, we provide the missing genomic and phylogenetic contextual information needed to better evaluate the evolutionary origin of *Starnoenas*.

2. Methods

(a) Sample collection

To evaluate the phylogenetic placement of *Starnoenas*, we combined published genomic data from Boyd *et al*. [21,34] for 61 species of doves and pigeons with data from additional taxa. Specifically, we sampled and sequenced Florida Museum of

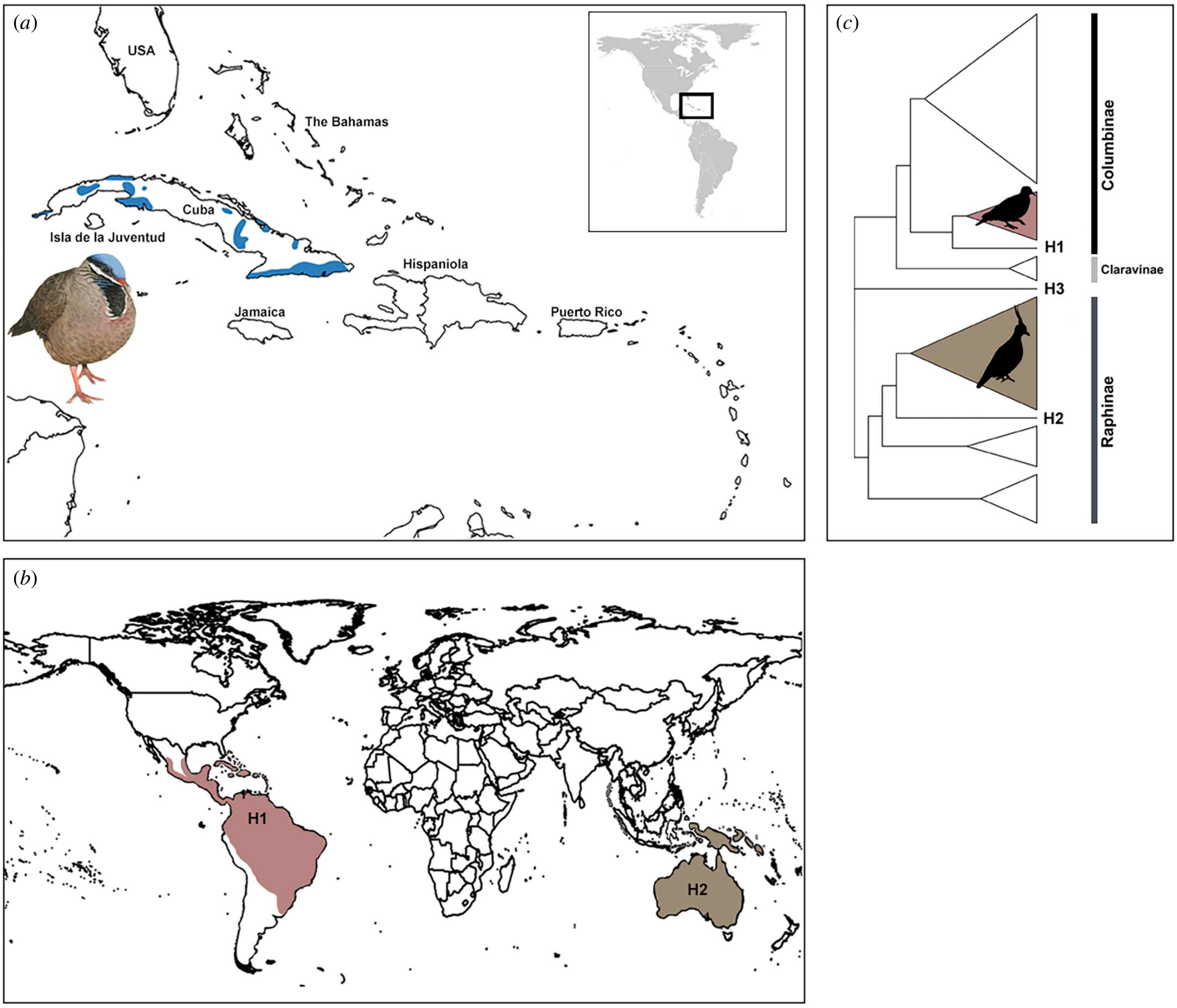

Figure 1. (*a*) Modern distribution (blue) of *Starnoenas cyanocephala* in the Caribbean. (*b*) The approximate distributions of taxa considered to be putative sister taxa to *Starnoenas*: Hypothesis 1 (H1) the Western Hemisphere quail-doves *Geotrygon*, *Zentrygon* and *Leptotrygon* [13] (pink) within the Columbinae and Hypothesis 2 (H2) various Australasian taxa (*Goura*, *Geophaps*, *Phaps*, *Didunculus*, *Leucosarcia*, etc.) within the Raphinae that share some morphological/behavioural characters with *Starnoenas* [14] (brown). Alternatively, *Starnoenas* is a divergent lineage without close relatives (Hypothesis 3 (H3); not illustrated). (*c*) Predicted phylogenetic placements of *Starnoenas*. H1: if *Starnoenas* is closely related to quail-doves (pink) then phylogenetic data will place it within the Columbinae; H2: if *Starnoenas* is closely related to Australasian species (brown) it will be within the Raphinae; or H3: alternatively, *Starnoenas* is not closely related to any taxon. Illustration credit of *S. cyanocephala* to Nils Navarro. The silhouettes in (*c*) are from phylopic.org; credit to: Danielle Alba, https://creativecommons.org/licenses/by-sa/3.0/, https://creativecommons.org/publicdomain/zero/1.0/.

Natural History, University of Florida (UF) samples UF 46675 *Goura victoria*, UF 46091 *Oena capensis*, UF 42971 *Gymnophaps albertisii*, UF 46663 *Trugon terrestris* and UF 8407 *S. cyanocephala* (electronic supplementary material, table S1). Additionally, we included NCBI Sequence Read Archive (SRA) whole genome sequencing data for *Caloenas nicobarica* (SAMN12253981) and *Ectopistes migratorius* (SAMN02688020). UF 8407 *S. cyanocephala* was collected in 1958 by A. Schwartz near Pinar del Río, Cuba. This sample is one of the most recently collected specimens from Cuba housed in institutions that participate in sharing data on vertnet.org.

Our dataset lacked only 16 genera recognized by [12]. Two are monotypic genera, the extant *Cryptophaps poecilorrhoa* (Sulawesi) and the extinct *Microgoura meeki* (Choiseul Island), which do not have available phylogenetic data. The remaining 14 genera are represented in published phylogenies based on mitochondrial genomes or a limited number of mitochondrial and/or intron loci (electronic supplementary material, table S2). These publications were reviewed to assess if missing genera are possible close relatives of *Starnoenas*. The recovered subfamilial relationship (i.e. Columbinae, Claravinae and Raphinae) is recorded in electronic supplementary material, table S2.

(b) Laboratory work

(i) Historical sample

DNA from UF 8407 *Starnoenas* toe pad was extracted using a modified protocol from [22] in a laboratory space reserved for degraded samples. Briefly, the toe pad was rinsed in ethylenediaminetetraacetic acid (pH 8.0) then placed in an extraction buffer containing ATL (Qiagen), proteinase K and 1 M dithiothreitol. The sample was incubated at 60°C for 24 h and then the resultant lysed sample was cleaned and concentrated with a Qiagen Nucleotide Removal Kit. DNA yield was quantified with a Qubit® 2.0 fluorometer.

A DNA library was produced for UF 8407 using an xGen™ Methyl-Seq DNA Library Prep Kit following the standard protocol but excluding the bisulfite conversion step. This kit is optimal for preparing DNA libraries for ancient/historical (low input) samples (see https://sg.idtdna.com/page). Amplification included 16 polymerase chain reaction (PCR) cycles. The library concentration was quantified with a Qubit® 2.0 fluorometer.

(ii) Modern samples

DNA from tissues for non-*Starnoenas* columbid taxa (electronic supplementary material, table S1) was extracted using a Qiagen DNeasy Blood & Tissue Kit following the protocol supplied by the kit. These extractions were performed in a laboratory separate from the historical sample. DNA concentration was quantified with a Qubit® 2.0 fluorometer.

DNA libraries were produced for these samples with a xGen™ DNA Lib Prep EZ. The enzymatic shearing was set to 13 min to produce 350 bp fragment sizes according to the manufacturer's guidelines. Library amplification included 16 PCR cycles.

(iii) Sequencing

Starnoenas and modern samples were cleaned, pooled and sequenced on 40% of an Illumina NovaSeq S4, using a 2 × 150 platform to recover whole genome data.

(c) Bioinformatics

(i) Identification of orthologues

Single-copy orthologues used in this study were previously identified by Boyd *et al*. [21,34]. Briefly, orthologues were identified by comparing all protein-coding sequences in *Columba livia* and all Sauropsida in OrthoDB v.8 at the time of the study [35]. Next, within-clade paralogues were identified and removed based on read sequence depth. Orthologue sequences generated by Boyd *et al.* [21] were downloaded from the associated figshare data repository [34] (raw read data associated with the assemblies are available from the SRA, organized under bioproject PRJNA318048). Additional sequences were obtained from the assembly of raw sequencing reads from additional dove and pigeon species. This included raw sequence reads that were downloaded from the SRA (https://www.ncbi.nlm.nih.gov/sra), including *C. nicobarica* (SRX6608113, SRX6608114), *Alopecoenas beccarii* (SRX6695805, SRX6695806) and *E. migratorius* (SRX554955) and newly extracted genomic DNA (gDNA), extracted from museum preserved specimens (UF42971, UF46091, UF46663, UF46675 and UF8407). Taxonomic name changes led to the erroneous addition of the *A. beccarii* (which was once also *Gallicolumba beccarii* and now *Pampusana beccarii*) sample from SRA even though this species was already represented in Boyd *et al*. [21,34]. This sample was pruned from all phylogenies.

Raw sequence reads were processed using fastp v.0.23.2 [36]. Reads from each library were then mapped to the *C. livia* orthologue sequences using Bowtie2 v.2.2.6 [37], and gene sequences were generated by taking the consensus base at each position [38] following the methods described by [21]. The newly assembled orthologues were then combined with the existing orthologue data for phylogenomic analysis (orthologue assemblies are available through figshare [34,39]). This dataset included the outgroup data for mallard (*Anas platyrhynchos*), wild turkey (*Meleagris gallopavo*), zebra finch (*Taeniopygia guttata*) and collared flycatcher (*Ficedula albicollis*). We targeted 6363 nuclear single-copy orthologous genes, with *Starneonas* yielding 5939 of these genes.

(ii) Assessing *Starnoenas* data quality

Starnoenas gDNA was obtained from a preserved toe pad from a specimen collected in 1958, which may yield poor quality gDNA and result in error-prone or otherwise compromised sequence data for assembly and phylogenetic analysis. To assess the suitability of sequence data for phylogenetic analysis, we calculated uncorrected p-distances using custom Python scripts, calculated as the total number of columns in an alignment containing a mismatch divided by the overall alignment length, following exclusion of alignment columns containing gaps or ambiguities from all orthologue pairs (alignment method described below). Using R, we compared the distribution of p-distances for species representing major clades within the Columbiformes: *Phaps elegans* (Raphinae), *Zenaida macroura* (Columbinae), *Columbina cruziana* (Claravinae) and *Starnoenas*. We sought to determine whether the distance between *P. elegans* and *Starnoenas* was substantially higher than the distances separating the other two taxa from *P. elegans*, which would indicate that the divergence with *Starnoenus* is substantially larger than the divergence across the entire tree and might indicate erroneous base calling or assembly could be influencing the phylogenetic results and would warrant further investigation to determine if this divergence was legitimate. Additionally, we manually examined a subset of orthologue alignments, for which we calculated a p-distance that was at the minimum and maximum values, providing for an additional check of sequence quality.

(iii) Orthologue alignment and supermatrix construction

Orthologue sequences were aligned as amino acid sequences using PRANK v.170427 [40] and then back translated to nucleotides. Alignment columns with >10% missing or ambiguous bases were removed from each orthologue alignment using trimAl v.1.2 [41]. Aligned orthologue sequences were then concatenated by taxon to create a supermatrix alignment using Catsequences v.1.4 [42]. In total, 10 586 851 alignment columns were available for phylogenetic analysis. To generate a partition for the supermatrix, we estimated base frequencies and rate parameters for each codon position in each orthologue alignment using RAxML v.8.2.12 [43] under the general time reversible model plus gamma parameter (GTR+G). K-means clustering was applied to group codons into seven partitions [44]. The resulting alignment supermatrix and partition are available on the figshare data repository [39].

(iv) Phylogenetic inference

A maximum-likelihood (ML) tree was inferred from a partitioned supermatrix alignment using RAxML (model = GTR+G, parsimony seed = 12 345). Support for the tree was inferred as a fraction of 100 bootstrap replicates recovering a given relationship. A species tree was inferred under the multispecies coalescent-based analysis using ASTRAL-IV (distributed within ASTER v.1.16 [45]) from individual ML gene trees inferred using RAxML. Node ages, in millions of years, were inferred using MCMCTree, implemented in PAML v.4.9 [46], given the ML tree inferred using the supermatrix. MCMCTree usage followed [21], including 5 000 000 cycles, sampling every 50 cycles, with a burnin of 50 000, rgene_gamma = 1 12.01, sigma2_gamma = 1 10. Node calibrations were restricted to the first divergence within each of the three subfamilies included in our study and divergences of the subfamilies. Our goal in calibrating the tree was not to evaluate divergence times previously reported [21], but to obtain an ultrametric tree for calculating evolutionary distinctness, given the most recent information published regarding the timing of dove and pigeon species. Therefore, calibration points were obtained from [21], restricting nodes to the median divergence time reported in fig. S3 of that study. Using the resulting time-corrected tree, evolutionary distinctness was calculated for each dove species included in the study using R v.4.2.2 [47], in particular the caper v.1.0.3 library, running ape v.5.7 to calculate branch lengths [48–50] (the second *P. beccarii* sample was excluded from this analysis; phylogenetic trees available on figshare [39]). Here, evolutionary distinctness was the sum of branch lengths with each branch divided by the total number of descendent tips between the base of the tree and each tip.

3. Results

Starnoenas represents a unique lineage that diverged early in the radiation of extant dove and pigeon species (figure 2; electronic supplementary material, figure S1). Our phylogeny revealed that *Starnoenas* is sister to all Columbinae on a distinctive long branch (figure 2). Members of Claravinae form a clade sister to *Starnoenas* + Columbinae. Newly sampled genera for this study and SRA samples (*Gymnophaps*, *Goura*, *Caloenas*, *Trugon* and *Oena*) are within the Raphinae, except the extinct passenger pigeon (*E. migratorius*), which is within the Columbinae (figure 2).

Phylogenetic inference based on a supermatrix (using RAxML) and multi-species coalescent methods (ASTRAL) yielded trees with identical topologies except for the placement of pheasant pigeon (*Otidiphaps nobilis*), a species in a monotypic genus found in New Guinea (electronic supplementary material, figure S2). The topologies recovered by ASTRAL for the clade containing pheasant pigeon had lower support (posterior probability = 0.66; electronic supplementary material, figure S2). Overall, the phylogenetic relationships in the ML tree based on the supermatrix were well supported. Most nodes have bootstrap support values of 100 except for the clade comprising *Aplopelia* and *Streptopelia* with bootstrap support of 72 (figure 2). The phylogenetic results presented here are identical to the phylogenies presented by [21], except for the pheasant pigeon being recovered in a clade composed largely of newly sampled species (figure 2).

There are 16 columbid genera that were not included in our dataset. All except two monotypic genera, *Cryptophaps* (*poecilorrhoa*) and the extinct *Microgoura* (*meeki*), have been represented in published phylogenies. The remaining 14 genera were placed within the three main dove clades (Columbinae, Claravinae and Raphinae; electronic supplementary material, table S2). This indicates that these genera are not in close phylogenetic proximity to *Starnoenas*.

A comparison of raw p-distances and manual examination of orthologue alignments do not suggest that the obtained phylogenetic patterns were dictated by erroneous base calls, as the distribution of p-distances fell within the range found for major divergences across the tree (electronic supplementary material, figures S3–S5). Evolutionary distinctness values calculated using our time-calibrated tree ranged from 0.082 to 0.448 ($M = 0.185$, s.d. = 0.079), with *Starnoenas* having the highest distinctness value (0.448), demonstrating how unique this species is within the tree (electronic supplementary material, figure S6). Additional species with comparatively high evolutionary distinctness values (0.346–0.389) also included narrowly distributed (mainly or exclusively insular) species within species-poor genera that include *Trugon terrestris*, *Otidiphaps nobilis*, *Caloenas nicobarica*, *Phapitreron leucotis*, *Goura victoria* and *Ptilinopus rivoli*, the latter belonging to a genus that was poorly represented in our study. Our dataset is missing taxa which may affect evolutionary distinctness values, e.g. *Ptilinopus*. However, because *Starnoenas* is not closely related to any other columbid taxa, relative evolutionary distinctiveness for *Starnoenus* would remain relatively unchanged with the inclusion of more dove species which would be nested within the existing clades.

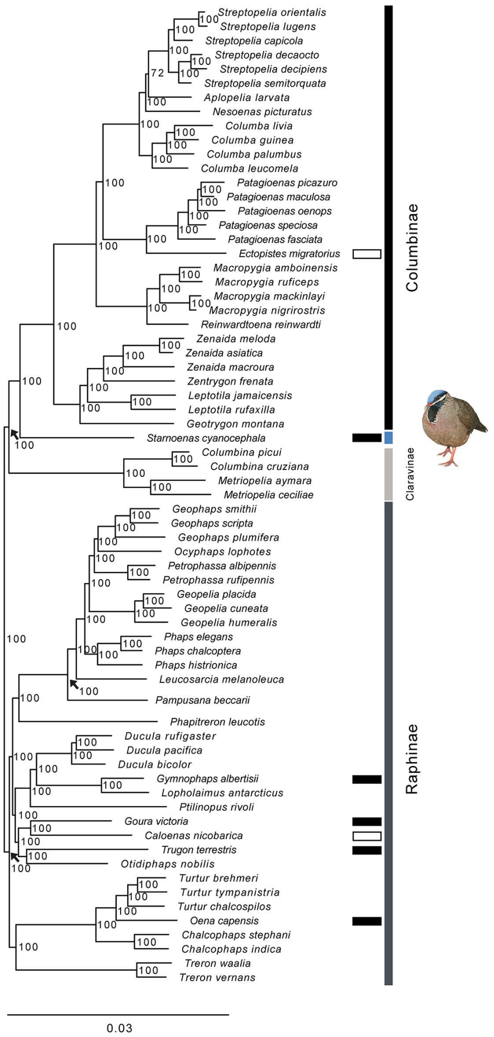

Figure 2. RAxML phylogeny of taxa from our sampling efforts (solid horizontal black bars), from NCBI Sequence Read Archive (SRA; open horizontal black bars), and Boyd *et al.* [21] based on a targeted 6363 orthologous nuclear loci. Bootstrap values are represented on the nodes. Bootstrap support values are all 100 except for the clade comprising *Aplopelia* and *Streptopelia* (bootstrap value: 72). Outgroup species include mallard (*Anas platyrhynchos*), wild turkey (*Meleagris gallopavo*), zebra finch (*Taeniopygia guttata*) and collared flycatcher (*Ficedula albicollis*) but were removed from this figure for clarity. Passenger pigeon (*Ectopistes migratorius*) is the only extinct taxon represented in our dataset. Recognized subfamilies are represented by labelled vertical bars in greyscale. *Starnoenas* is represented by the illustration and a blue bar among the vertical subfamily bars. Illustration credit of *S. cyanocephala* to Nils Navarro.

4. Discussion

The aim of our study was to elucidate the evolutionary relationships of the enigmatic Cuban endemic blue-headed quail-dove, *S. cyanocephala*. We found that *Starnoenas* is sister to the widespread subfamily Columbinae. As a distinct subfamily (following Olson & Wiley [14] and our own data), *Starnoenas* represents an ancient lineage in the Columbidae tree of life, which is reflected in its mosaic of behavioural, morphological and phenotypic characters (as reported in Olson & Wiley [14]). The deep divergence of *Starnoenas* from a larger clade provides little clarity regarding its biogeographic origins. In terms of evolutionary uniqueness and the goal of preserving phylogenetic diversity, these findings emphasize the need for the conservation of this declining relictual species.

The Caribbean, like many other insular regions, is a refugium of historical diversity [51,52]. The geology of the Caribbean across the Cenozoic is complex with regional landmasses having multiple connections and separations owing to tectonics and sea-level changes [53,54]. This is compounded further by the recent human-driven extinctions across the Holocene which can erase biogeographic connections [32].

Fossils provide no clues about the biogeography of *Starnoenas*. The fossil record of columbids is younger (approx. 20 Ma) than that of many nonpasserine families. The oldest material from Europe and New Zealand cannot be related to any modern forms [14]. The oldest columbid fossils from North America are most closely related to the African *Oena* and *Turtur* [26], providing yet another biogeographic enigma for this family with strong dispersal capabilities.

Across the late Quaternary, island floras and faunas have suffered high rates of extinction largely through human impacts that are accelerating [3,55]. The need to preserve the remaining biodiversity in these ecosystems is urgent [56]. Many insular dove species such as the extinct dodo (*R. cucullatus* [17]) and the Puerto Rican quail-dove (*Geotrygon larva* [57]) are emblematic of human-caused extinctions. In many world regions, however, islands still serve as the last refuges of relictual diversity that has been lost elsewhere, e.g. Rhynchocephalia in New Zealand [58] and Todidae in the Caribbean [51]. As a singular subfamily, genus and species that is genetically, morphologically and behaviourally unique, the endangered *S. cyanocephala* warrants protection with a goal of saving one of the last avian representatives of the unique diversity present in the Caribbean.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Raw genetic read data can be found on NCBI SRA BioProject ID: PRJNA1051637; SAMN38791721-SAMN38791725 (electronic supplementary material, table S1). Orthologue assemblies, supermatrix alignment, supermatrix partition, RAxML phylogeny, MCMCTree input phylogenies and result trees are available at [39] and online as part of the electronic supplementary material [59].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. J.A.O.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, visualization, writing—original draft, writing—review and editing; B.M.B.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, resources, supervision, validation, visualization, writing—original draft, writing—review and editing; A.R.S.: formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; M.J.L.: conceptualization, funding acquisition, supervision, writing—original draft, writing—review and editing; B.J.S.: investigation, methodology, writing—review and editing; R.P.G.: conceptualization, funding acquisition, project administration, resources, supervision, writing—review and editing; K.P.J.: conceptualization, methodology, writing—review and editing; J.M.A.: conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, writing—original draft, writing—review and editing; D.W.S.: conceptualization, investigation, project administration, resources, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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Conflict of interest declaration.

We declare we have no competing interests.

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