First genetic data for the critically endangered Cuban endemic Zapata Rail *Cyanolimnas cerverai*, and the taxonomic implications

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Abstract

The taxonomic affinity of the near-flightless Zapata Rail *Cyanolimnas cerverai*, a critically endangered and highly localized species endemic to Cuba, has long been debated. Morphological analyses have suggested that this species, which constitutes a monotypic genus, could be related either to the extinct Tahitian Cave Rails (*Nesotrochis* sp.) or to the South American rail tribe Pardirallini, i.e., the genera *Neocrex*, *Mustelirallus*, and *Pardirallus*. While pronounced phenotypic convergence—and divergence—among rails have repeatedly proven morphology-based phylogenies unreliable, thus far no attempt to sequence DNA from the enigmatic *Cyanolimnas* has succeeded. In this study, we extracted historic DNA from a museum specimen collected in 1927 and sequenced multiple short fragments that allowed us to assemble a partial sequence of the mitochondrial cytochrome oxidase I gene. Phylogenetic analyses confirm that *Cyanolimnas* belongs in tribe Pardirallini as sister to genus *Neocrex*, from which it diverged about 6 million years ago. Their divergence from *Mustelirallus* was estimated at about 9 million years ago. Based on morphology and our mitochondrial phylogeny, we conclude that it is unjustified to retain the monotypic genus *Cyanolimnas* and tentatively recommend that *C. cerverai* and the two *Neocrex* species are ascribed to genus *Mustelirallus*.

Keywords Mitochondrial phylogeny · Cytochrome oxidase I · Historic DNA · Cuba · Rallidae

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ausgestorbener tahitianischer Rallen (Nesotrochis sp.) oder mit dem südamerikanischen Rallentribus Pardirallini, d.h. denGattungen Neocrex, Mustelirallus und Pardirallus, verwandt sein könnte. Während ausgeprägte phänotypische Konvergenz und Divergenz bei Rallen wiederholt gezeigt haben, dass auf der Morphologie basierende Stammbäume unzuverlässig sind, war bislang kein Versuch, die DNA der enigmatischen Cyanolimnas zu sequenzieren, von Erfolg gekrönt. In dieser Studie haben wir historische DNA aus einem Museumspräparat aus dem Jahr 1927 extrahiert und multiple kurze Fragmente sequenziert, die uns erlaubten, eine partielle Sequenz des mitochondrialen Cytochromoxidase I-Gens zu ermitteln. Phylogenetische Analysen bestätigen, dass Cyanolimnas in den Tribus Pardirallini als Schwestergruppe der Gattung Neocrex gehört, von der die Abspaltung vor etwa sechs Millionen Jahren erfolgte. Die Abspaltung von Mustelirallus erfolgte vor geschätzt etwa neun Millionen Jahren. Auf der Grundlage der Morphologie und unseres mitochondrialen Stammbaums kommen wir zu dem Schluss, dass es nicht gerechtfertigt ist, die monotypische Gattung Cyanolimnas beizubehalten, und empfehlen, dass C. cerverai und die zwei Neocrex-Arten der Gattung Mustelirallus zugeordnet werden.

Introduction

The critically endangered Zapata Rail Cyanolimnas cerverai is endemic to Cuba and unquestionably is one of the most poorly known birds in the West Indian region (Kirwan et al. 2019; Kirkconnell et al. 2020; Taylor et al. 2020). Its declining population is apparently threatened by dry-season burning of its marsh habitat, predation by introduced small Indian Mongooses (Herpestes auropunctatus), Black Rats (Rattus rattus) and African Catfish Clarias gariepinus (Collar et al. 1992; Kirkconnell 2012; Taylor et al. 2020), and habitat change engendered by the spread of the invasive Broad-leaved Paperback (Melaleuca quinquenervia). Nowadays, this rail is known from just six closely spaced localities in the northern Ciénaga de Zapata (Matanzas province) in south mainland Cuba, based on 14 specimens collected between 1927 and 1934 (all but one in four US museums; Table S1), and a relatively small number of sight records since 1979, most recently in November 2014 (Kirkconnell et al. 2020). However, fossil material of Cyanolimnas cerverai dating from the Holocene has been identified from Cueva de Pío Domingo, Sumidero, and Cueva El Abrón, Sierra de La Guíra (Pinar del Río province), Cueva de Paredones and Cueva de Sandoval (Artémisa province), Calabazar (La Habana province), Cueva de Insuns, Cueva de Las Charcas and Cueva del Indio (all in Mayabeque province), near Jagüey Grande (Matanzas province), Cueva de Humboldt and Cueva del Salón (Sancti Spíritus province), and the Sierra de Caballos in the northern Isle of Pines (Olson 1974; Arredondo 1984; Jiménez and Valdés 1995; Rojas-Consuegra et al. 2012; Jiménez and Orihuela 2021; Suárez 2022), i.e., over a much larger area than the known modern range.

Genus Cyanolimnas Barbour and Peters, 1927, has always been considered monospecific, and was described as “A medium-sized ralline with short rounded wing; very short tail, the bars of the rectrices very sparse; tarsus stout and short, not exceeding middle toe with claw. Bill moderate, somewhat longer than head, swollen basally. … The combination of short wing and stout tarsus suggests relationships with Nesotrochis Wetmore [a genus comprising three large, flightless, extinct species from the Greater Antilles] … but the latter has a tarsus more than twice as long” (Barbour and Peters 1927). Ridgway and Friedmann (1941) proffered a detailed morphological description of this genus, and thought it was apparently flightless. However, while Cyanolimnas has reduced powers of flight, it is vol- ant (AK pers obs), and in any case, flightlessness is now known to have arisen many times in Rallidae and cannot be used as a predictor of relationships (e.g., Olson 1973; Slikas et al. 2002; Kirchman 2012; Gaspar et al. 2020; Garcia-R and Matzke 2021, although Cyanolimnas was incorrectly treated as flightless in the latter). As noted by Olson (1973) and Steadman et al. (2013), in its robust, deep-based bill Cyanolimnas is similar to the two species frequently assigned to Neocrex Sclater & Salvin, 1868, Colombian Crake N. colombiana and Paint-billed Crake N. erythropus (both of which are now often placed in an expanded Mustelirallus Bonaparte, 1856; e.g., Kirchman et al. 2021). Plumage and osteological characters are similar to either Neocrex, or less so to the latter’s sister taxon Pardirallus Bonaparte, 1856, to which genus Cyanolimnas was considered most closely related in the morphological phylogenies of Livezey (1998) and Garcia-R and Matzke (2021). Currently, all four of the global bird checklists place Cyanolimnas close to both Neocrex and Pardirallus (Dickinson and Remsen 2013; del Hoyo et al 2014; Clements et al. 2021; Gill et al. 2022).

Its ecology and natural history are virtually unknown; for example, a nest with eggs ascribed to Cyanolimnas, found in early September 1982 (Bond 1984), seems unlikely to have been identified correctly (Kirkconnell et al. 2020), and even this rail’s voice is unknown. A published sound recording, originally believed to pertain to Cyanolimnas (Reynard and Garrido 1988; Hardy et al. 1996), is now identified as belonging to Spotted Rail Pardirallus maculatus, which is a rather abundant species in the Ciénaga de Zapata (Kirkconnell et al. 2020). During November–December 1998, a survey using the published sound recording as a tool estimated a population of 70–90 individuals of Cyanolimnas (Kirkconnell et al. 1999). Subsequently, it was realized that the recording actually involved P. maculatus (Kirkconnell et al. 2005) and that the description of Cyanolimnas vocalizations in Kirkconnell et al. (1999) was erroneous. Inferences
concerning the relationships of *Cyanolimnas* based on ecology or vocalizations are consequently impossible. To date, just one molecular phylogenetic study, using ultra-conserved elements (UCEs), has attempted to ascertain the relationships of *Cyanolimnas* (using a toe pad from AMNH 300416, a female collected by P. Quintaña in April 1934), but was unsuccessful in yielding any UCEs, and consequently failed to place the species (Kirchman et al. 2021). As a result, Kirchman et al. (2021) proposed to treat *Cyanolimnas* as genus incertae sedis; the aim of the present work is to address this shortfall in knowledge.

**Methods**

**Museum specimens and sampling**

Worldwide, there are 14 Zapata Rail specimens housed in museum collections (Table S1). With written permission from the museum, we obtained a ~5 mm³ toepad sample of a Zapata Rail from the Museo de Historia Natural ‘Felipe Poey’, La Habana, Cuba (catalog no. MFP 14.000218; Fig. S1) using a clean scalpel. The specimen in question was a male collected in the Ciénaga de Zapata, Cuba, on 17 June 1927 (Table S1).

**Primer design and evaluation**

We obtained cytochrome oxidase I (COI) sequences of rallid species NCBI/GenBank (https://www.ncbi.nlm.nih.gov/nucleotide/), aligned these sequences using CLC Sequence viewer v6.0 (QIAGEN; UK) (https://digitalinsights.qiagen.com/products/clc-sequence-viewer-direct-download/) and identified regions of high similarity and roughly 50% GC content. We manually designed 21–23 bp long primers, including some degenerated sites to account for alignment sequence variation among, to produce < 200 bp fragments from the degraded DNA (Table 1; Fig. S2). We tested the primer pairs on Common Moorhen *Gallinula chloropus* and Allen’s Gallinule *Porphyrio alleni*, because DNA availability was not a restriction for these two rallid species, in order to assess the likelihood of successful amplification of a limited amount of historic DNA from the Zapata Rail. Additional primers (not listed) were tested but did not yield successful amplification/sequencing.

**Sampling and laboratory procedures**

We extracted DNA from the toepad sample MFP 14.000218 using QIAGEN QIAamp® DNA microkit, following the manufacturer’s instructions, modified for digestion overnight at 56 °C and repeated vortexing. The DNA was eluted in 80 µl Buffer AE, and quantified to 22 ng/µl on a Nanodrop spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA).

We set up 50 µl PCR reactions using 2.5 µl template DNA and 47.5 µl PCR mastermix made from 5 µl of 10× Opti-Buffer (Bioline Reagents Ltd, UK), 2.5 µl of each primer at 10 μM, 1 µl 50 mM magnesium chloride, 0.6 µl 10 mM DNT mix (Sigma, Poole, UK), 0.5 µl BIO-X-ACT short DNA polymerase (Bioline Reagents Ltd, London, UK), and 35.4 µl ddH₂O. We ran samples and negative controls in PCR programs following Hebert et al. (2004), with a low annealing temperature in first 5 cycles to accommodate potential primer–sample mismatches: denaturing 60 s at 94 °C, annealing 60 s at 45 °C, and extension 50 s at 72 °C. For the following 30 cycles, the annealing temperature was increased to 51 °C. We adopted this PCR strategy for all primer combinations.

Four µl 100-bp DNA ladder (Promega, Southampton, UK) and 40 µl of the PCR products were loaded with 5 µl Promega 6×DNA loading dye on 1.5% agarose gels

### Table 1 Primers designed for the Zapata Rail COI gene

| Amplicon name | Amplicon length (bp; excl. primers) | Primer name | Primer sequence (5’–3’) |
|---------------|-----------------------------------|-------------|-------------------------|
| 1             | 125                               | ZRCOIF1a    | CTAACCAAAAGACATCGGAAAC |
|               |                                   | ZRCOIR1     | CCGCCCATGCTTCTGTAATA   |
| 2             | 132                               | ZRCOIF2a    | TACTYCTAGCTTCCCTTACAG  |
|               |                                   | ZRCOIR2a    | TCAACTTCATCAAACCGCC    |
| 2a            | 106                               | ZRCOIF2a    | GCTATCAACTTCACTACAACCG |
|               |                                   | ZRCOIR2a    | CGCTGGCATACTACACTACT   |
| 4             | 146                               | ZRCOIF4     | CYGCCTCAGGCTTCTGTAATA  |
|               |                                   | ZRCOIR4     | TTTCCTCATCAGTAGAAGCAG  |
| 5             | 146                               | ZRCOIF5     | AGCCCTCTYATCCGAGCAG    |
|               |                                   | ZRCOIR5     | CCCAGACATAGCATTCCC     |

This table lists all the PCR primers designed to amplify the DNA sequence of the Zapata Rail’s COI gene, and details on the resulting amplicons (also see Fig. S2).
(peqGOLD universal agarose; Peqlab, Fareham, UK), stained with 1–2 µl ethidium bromide, in 1 × TAE buffer. We ran the electrophoresis at 86 V, 100 mA for 20–40 min, and inspected the gel under UV light. While PCR reactions were specific, primer dimers did form, and due to the relatively small difference in length between these and the PCR product we chose not to perform differential precipitation to purify the PCR product. Instead, we cut the bands of expected size with a scalpel and isolated the PCR product from the gel fragments with a Gel Extraction Kit (Qiagen, Manchester, UK), following the manufacturer’s instructions, and eluted in 30 µl elution buffer EB. We quantified the purified PCR product with a Nanodrop spectrophotometer and diluted the PCR products to 10 µg/µl, after which they were bidirectionally Sanger sequenced by Source Bioscience (Nottingham, UK).

**Phylogenetic analyses**

We initially scrutinized the sequences using FinchTV (Geospiza Inc.) and then assembled them to the rallid sequence set used for primer design in CLC Sequence Viewer 8 (https://www.qiagenbioinformatics.com/products/clc-sequence-viewer/). This resulted in a 558-bp consensus sequence, with one internal 11-bp and one 18-bp gap consisting of primer sequence, resulting in 529 informative nucleotides (Fig. S2). We then obtained a larger set of 450 COI sequences of extant taxa within the order Gruiformes from GenBank, and additionally included sequence data from ancient DNA of the extinct *Nesotrochis steganinos* (Oswald et al. 2021), because of its proposed close relationship to the extant taxa included in the analyses in combination with its recent extinction (Oswald et al. 2021 dated bones to 6,430 ± 30 years before present). We aligned sequences with MAFFT (Katoh and Standley 2013) in Geneious v. 10.2.6 (Kearse et al. 2012) and selected ≤ 3 per taxon based on length and quality (for taxa and accession numbers, see Table S2). We further trimmed this dataset to a 962-bp region that maximized overall sequence coverage and fully overlapped the Zapata Rail COI sequence (see “Data availability”). We employed the greedy algorithm (Lanfear et al. 2012) in PartitionFinder2 (Lanfear et al. 2016) to evaluate the full set of DNA substitution models and explore optimal partitioning with regard to codon position, using PhyML (Guindon et al. 2010). The best partitioning scheme by AICc was identified as individual substitution models per codon position: the general time-reversible (GTR; Tavaré 1986) model with the among-site rate variation following a gamma (Γ) distribution and with a proportion of invariant sites (I) for position 1, the transversion model (TVM) + Γ + I for position 2, and the transition model (TiM) + Γ + I for position 3.

We implemented the partitioning scheme in Beast v. 2.6.6 (Bouckaert et al. 2014) using the plugin SSM v. 1.1.0 and set the proportion of invariant sites to be estimated, and the Γ distribution to be estimated across four rate categories. Employing a birth–death speciation model, we set the prior for death rate to follow an exponential distribution with mean 1. We enforced monophyly of the clades Rallidae, Ralloidea, and Gruoidea, and employed dating calibration priors on Gruiformes and stem Rallidae following Chaves et al. (2020). We then ran two iterations of 10 million generations, sampling every 1000 generations, and optimized tuning parameters and operator weights to produce the final xml specification used for our analyses (see “Data availability”). We ran five replicate analyses at different seeds in Beast, sampling every 1000 generation for 40–145 million generations, until inspection in Tracer v. 1.7.1 (Rambaut et al. 2018) revealed stationarity and sufficient effective samples sizes (all parameters > 200). Some substitution model-related parameters for codon position 1 and to some degree 2 (specific substitution rates, gamma shape, and proportion invariant sites) seemed to have dual optima, with shifting within and between replicates. Thus, replicates converged in either of two groups; however, this had no impact on the topology, support, or dating of the focal clade. We calculated maximum clade credibility trees with mean node heights after discarding 5–50% as burn-in.

In addition to the Bayesian inference (BI) with Beast, we also used IQtree v. 2.1.2 (Lanfear et al. 2020) for phylogenetic analyses based on maximum likelihood (ML). We applied the partitioning and substitution model scheme determined with PartitionFinder2 and ran two separate analyses comprising 1000 ultrafast bootstrap replicates.

**Results**

All phylogenetic analyses placed *Cyanolimnas* as sister to *N. erythrops*, the pair of which was sister to the Ash-throated Crane *Mustelirallus* (formerly *Porzana*) *albicollis* (Fig. 1). These three taxa formed a sister clade to the genus *Pardirallus* (Fig. 1). There was near-full support for a *Pardirallus–Mustelirallus–Neocrex–Cyanolimnas* clade (posterior probability (PP) 1.0 in the BI analyses and 99% ultrafast bootstrap support (UBF) in the ML analyses).
The exact placement of Cyanolimnas as sister to Neocrex received full support (UFB 100%) in the ML analyses and PP 0.86 with BI (Fig. 1). There were some differences in inferred topology between BI replicates (see “Data availability”); however, none of these occurred within the focal Pardirallus–Mustelirallus–Neocrex–Cyanolimnas clade.

The inferred mean age of split between Cyanolimnas and Neocrex was 6.3 MA (95% highest posterior density 2.9–10.0 MA), between those and Mustelirallus 8.8 (4.9–13.1) MA, and between that clade and Pardirallus 11.5 (7.0–16.2) MA (Fig. 1).

In line with Oswald et al. (2021), Nesotrochis was recovered as a sister lineage to Sarothruridae (Fig. 1).

Discussion

We provide the first genetic data for Cyanolimnas, as the species has not been included or successfully sequenced by any previous molecular phylogenetic study of the Rallidae (e.g., Garcia-R et al. 2014; Garcia-R and Matzke 2021; Kirchman et al. 2021), which led Kirchman et al. (2021) to consider its placement ‘incertae sedis’. It should be stressed that the reliability of phylogenies based on single genetic markers is limited, and this is particularly true for mitochondrial markers. The fast-evolving mitochondrion occurs with multiple copies per cell and has historically been widely used for molecular phylogenies,
and further remains important for genetic barcoding. However, for several reasons the mitochondrial phylogenetic signal may be discordant from that of the nuclear genome (e.g., through introgression) and reflect an evolutionary trajectory different from ‘true’ speciation events (Toews and Brelsford 2012). In our analyses, for example, the COI tree renders Gruidae paraphyletic with respect to Arami- dae (Fig. 1). Nevertheless, mitochondrial data are relevant for a first test of presumed phylogenetic context, and yield useful relative divergence times.

Similar to the whole-mitochondrion analyses by Oswald et al. (2021), our analyses of COI placed Nesotrochis outside Rallidae, separated from Cyanolimnas by some 45 million years (Fig. 1). Our data instead provide strong support for the previous hypotheses rooted in morphological traits that have placed Cyanolimnas in what has been referred to as the ‘Aramides clade’ (Livezey 1998; Garcia-R et al. 2014; Garcia-R and Matzke 2021), better termed tribe Pardirallini sensu Kirchman et al. (2021). Within this grouping, the species appears to be most closely related to *N. erythrops* and *M. albicollis*, but less so to the three species of *Pardirallus*, in partial congruence with prior predictions (Olson 1973; Livezey 1998; Garcia-R & Matzke 2021). Although it is now rather well established that plumage is not necessarily a reliable character for inferring phylogenetic relationships within the Rallidae (e.g., Garcia-R et al. 2014; Stervander et al. 2019; Chaves et al. 2020), in the present case morphology appears to be rather informative.

The key question that arises is whether the separate monospecific genus Cyanolimnas is warranted? The age of the split between Cyanolimnas and Neocrex (6.3 MA) is comparatively young relative to many other Rallidae, a family that contains several old generic clades (e.g., Aramides 7.7 MA, Porzana 10.4 MA, Rallus 11.1 MA, Rallina 12.6 MA, Zapornia 13.8 MA, and Porphyrio 19.0 MA based our COI analyses; Fig. 1). However, some clades contain even younger taxa, for example the Eulabeornis–Cabalus–Galli- rallus–Hypotaenidia group of the Rallini (which arose 4.3 MA), all or most of which are genera accepted by some authorities (e.g., Dickinson and Remsen 2013; del Hoyo et al 2014; Kirchman et al. 2021). Nevertheless, in the latter case these four genera are sometimes treated alternatively as a single genus, for which the name Gallirallus Lafresnaye, 1841, has priority (Kirchman 2012).

We consider that the available molecular and morphologi- cal evidence in combination strongly supports that *C. cer- verai* be included in either genus Neocrex Slcater & Salvin, 1869, or Mustelirallus. Bonaparte, 1856, given that its most divergent trait from either of these two, (near-)flightlessness, is well accepted to be not taxonomically informative (Olson 1973; Slikas et al. 2002; Kirchman 2012; Gaspar et al. 2020; Garcia-R and Matzke 2021). Although *N. colombiana*, an exceptionally poorly known rallid of northwestern South America and easternmost Panama, has yet to be sampled genetically, to date, there is no indication that it is not very closely related to *N. erythrops* (Wetmore 1967; Olson 1973; Taylor 1996). Following the lead of Kirchman et al. (2021), we recommend that, for the present, the most parsimonious approach is to treat all four species—Ash-throated Crane, Paint-billed Crane, Colombian Crane and, now, Zapata Rail—as members of a single genus, for which the name Mustelirallus (masculine) has priority. The new combinations are Mustelirallus albicollis, *M. erythrops*, *M. colombianus*, and *M. cerverai*. Kirchman et al. (2021) incorrectly listed Colombian Crane as *M. colombianus*, overlooking that Bangs’ (1898) original spelling was Neocrex colombianus as noted by Dickinson and Remsen (2013).

**Supplementary Information** The online version contains supplemental material available at https://doi.org/10.1007/s10336-022-02004-0.

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**Author contributions** Conceived and managed project: GMK, JMC, and MS. Provided biological sample: AK and GMK. Designed primers, performed molecular lab work: YL, AFB, TJS, and JMC. Assembled COI sequence: AFB and TJS. Performed phylogenetic analyses: MS. Wrote the manuscript: GMK and MS.

**Data availability** The Zapata Rail COI sequence has been deposited at Genbank with accession number OL449772. Supporting material has been deposited at Zenodo and is available at https://doi.org/10.5281/zenodo.6500391. This includes Table S2 (taxon name, classification, and accession numbers for sequences included); sequence alignment nexus file; Beast xml input file; Beast output including maximum clad credibility tree files; log files and raw tree files; and IQtree consensus tree files.

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