Gymnocrecini, Amaurornithini and Pardirallini: three new family-group names for rails, with comments on the taxonomic placement of *Zapornia akool* (Rallidae)

George Sangster, Jacob C. Blokland, Steven M.S. Gregory & Edward C. Dickinson

ABSTRACT: Multi-locus and phylogenomic studies have clarified the taxonomic limits and higher-level relationships among rails (Rallidae). A recently proposed classification of rails by Kirchman *et al.* (2021) listed nine tribes. The names of three of these (Gymnocrecini, Amaurornithini and Pardirallini) were introduced by Livezey (1998), but these names do not meet the requirements of the ICZN Code (1999) and are therefore unavailable. We formally describe these taxa and make the names available for nomenclatural purposes. In addition, we clarify the apparent incongruence among recent phylogenetic studies in the generic (and tribal) placement of *Zapornia akool*.

KEYWORDS: Gruiformes, Rallidae, *Amaurornis*, *Gymnocrex*, *Pardirallus*, *Zapornia akool*, phylogeny, new tribe.

ZOOBANK LSID for publication: 16C3C832-4BED-4023-8FFD-6831877DD6DC

The rails, crakes, gallinules and coots (Rallidae Leach, 1820) are a cosmopolitan group that includes 138 extant or recently extinct species inhabiting mostly aquatic habitats (Taylor, 1998; Dickinson & Remsen, 2013). Assessment of the relationships among rails has long been hampered by a lack of congruent phylogenetic hypotheses. During the course of the 20th century, multiple classifications have been proposed but these were not based on phylogenetic analysis (Peters, 1934; Olson, 1973; Wolters, 1975; Ripley, 1977). The first comprehensive phylogenetic analysis of rallids was carried out by Livezey (1998), who analysed a data set of 570 morphological characters and 157 species of Rallidae, several of which were additionally represented at subspecies level, and included numerous extinct species. His analyses also included other ralloid taxa, some of which were then considered as rallids (Sarothruridae and species of *Nesotrochis* Wetmore, 1918), and a broad range of other gruiform and non-gruiform birds. He proposed a classification of rails that included two subfamilies, five tribes and five subtribes. Several phylogenetic studies using molecular-based data, but relatively limited taxonomic sampling, have since further clarified the interrelationships of rails and their close relatives (e.g., Slikas *et al.*, 2002; Hackett *et al.*, 2008; Kirchman, 2012; Burleigh *et al.*, 2015).

García-R *et al*. (2014) reconstructed the phylogenetic relationships of 94 species of rails and allies using a multi-locus DNA sequence data set comprising three mitochondrial and two nuclear markers. The study identified eight major clades. The distinctive Nkulengu Rail *Himantornis haematopus* Hartlaub, 1855 was part of one of these eight clades but with weak bootstrap support (< 70%) and weak posterior probability (< 0.9).

These same eight major groups were resolved by Boast *et al.* (2019), using mitochondrial data for 104 rallid taxa. However, relationships among the eight groups differed between García-R *et al*. (2014) and Boast *et al.* (2019).

A follow-up study by García-R *et al*. (2020) included sequence data of 393 loci from 63 species. This was a different data set than that of García-R *et al*. (2014) but it reconstructed the same eight major clades. However, *Himantornis* Hartlaub, 1855 was deeply divergent and sister to Fulicini (*sensu* Kirchman *et al*., 2021), forming an additional (ninth) clade/lineage. The relationships among the nine groups differed from those in García-R *et al*. (2014) and, to a lesser degree, from Boast *et al*. (2019). As in the latter study, there was a major subdivision in Rallidae, where Rallini and 'Pardirallini' (*sensu* Kirchman *et al*., 2021) formed a clade that was sister to all other rails.

García-R and Matzke (2021) conducted a total-evidence study, including a large sample of 158 rallids (modern and recently extinct), molecular data from García-R *et al*. (2014) and García-R *et al*. (2020), and 271 of the integumentary and osteological characters of Livezey (1998). This study recovered the same nine major clades as in García-R *et al*. (2020). In addition, it resolved species of *Gymnocrex* Salvadori, 1875 as the sister taxon of *Himantornis haematopus*, which together formed the sister taxon of all other rallids. *Gymnocrex* and *Himantornis* were reconstructed as sister taxa on the basis of the morphological characters of Livezey (1998).

Kirchman *et al*. (2021) used a dataset of up to 4227 genomic ultra-conserved elements (UCEs) per taxon to study the phylogenetic placement of 82 species of rails and allies. Their phylogeny was congruent with that obtained by Boast *et al*., (2019), García-R *et al*. (2020) and García-R and Matzke (2021) in showing (*i*) the same initial divergence between the clade of Rallini + 'Pardirallini' and all other rails, and (*ii*) the same nine major clades/lineages. As in García-R *et al*. (2020), a deep divergence between *Himantornis* and Fulicini Nitzsch, 1820, was also resolved. This was the first study to include molecular data of a representative of the genus *Gymnocrex*, which was deeply divergent and was found to form a tenth major clade/lineage. The exact position of *Gymnocrex* was tested between analyses using alternative sets of taxa. In most of the analyses in which it was included, *Gymnocrex* was identified as the sister taxon of *Himantornis haematopus*, as in García-R and Matzke (2021).

Kirchman *et al*. (2021) proposed a classification in which the rails were subdivided into two subfamilies and nine tribes, the latter corresponding to the ten clades reviewed above, but with the 'Rallina' clade combined with the 'Porzana' (comprised of *Zapornia* species) clade in a single tribe Zapornini Des Murs, 1860: 521. The nine tribes recognized by Kirchman *et al*. (2021) included three family-group names introduced by Livezey (1998) as 'Tribe Gymnocrecini, new taxon' (p. 2131), 'Subtribe Amaurornithina, new rank' (p. 2135) and 'Subtribe Pardirallina, new taxon' (p. 2132). Livezey's (1998) new names appeared in his Appendix C, and were not accompanied by a diagnosis or description in words. A consequence of this is that the newly proposed names do not meet the conditions of Article 13.1.1 (ICZN, 1999: 17) which states that "every new name published after 1930 must be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon". As a result, the new names are not available for nomenclatural purposes. This also applies to 'Eulabeornithini', a fourth new taxon name established by Livezey (1998: 2131), use of which is not currently proposed.

To make family-group names available under Article 13.1.1 (ICZN, 1999: 17) and Article 16.1 (ICZN, 1999: 19), we propose:

Gymnocrecini new tribe

Diagnosis: Medium-sized (300–330 mm), long-legged forest rails with sharply tapering bills, relatively short toes, and bare facial skin surrounding and especially behind the eyes (Olson, 1973; Ripley, 1977; Taylor, 1998). The data set of Livezey (1998) includes several apomorphies of Gymnocrecini, but only one that is non-homoplasious in the context of

Gruiformes: (*i*) *maxilla*, *depressio naris*, conformation as broad and deep, contrasting blackish colouration present (character 384, state b), alluding to characteristic black colouration in the region of the nares, surrounded by an otherwise variably yellowish rostrum in adult birds. A second morphological character state, (*ii*) *lorum et regio orbitalis*, narrow unfeathered '*regio circumorbitalis*' present (character 429, state b), is an apomorphy shared by both Gymnocrecini and *Himantornis*. However, the species of Gymnocrecini further possess a more distinctive and extensive unfeathered region behind the eye, which distinguishes them from *Himantornis haematopus*. While the species of *Gymnocrex* and *Himantornis haematopus* are also similar in their foot appearance and in that they share eight rectrices, *Gymnocrex* species comparatively differ by their possession of diastataxic wings, an aftershaft, and a tufted oil gland (Chapin, 1939: 26).

Type genus: *Gymnocrex* Salvadori, 1875.

Contents: *Gymnocrex* with three species: *G. rosenbergii* (Schlegel, 1866); *G. talaudensis* Lambert, 1998; *G. plumbeiventris* (G.R. Gray, 1862) (Dickinson & Remsen, 2013; Kirchman *et al*., 2021; Gill *et al*., 2023).

ZooBank LSID for new tribe: D0F89B7D-3272-4EF2-B4AF-F0516E0E9909

Amaurornithini new tribe

Diagnosis: A group of comparatively large, 'crake-like' rallids with yellow-brown to greenish bills. The legs are a shade of yellow or brown in all species except *Megacrex inepta* which are dark brown to greyish. Most species are volant, but the clade includes the flightless *Megacrex inepta*. Our examination of the morphological data set of Livezey (1998) revealed no morphological apomorphies for this clade. In an alignment, using MUSCLE (Edgar, 2004) as implemented in MEGA7 (Kumar *et al*., 2016), of 102 DNA sequences of the mitochondrial 16S ribosomal RNA (16S rRNA) gene constructed for this study (Appendix 1), members of Amaurornithini showed (*i*) a six base pair (bp) insertion at position 705 (as delimited by MITOS; Bernt *et al*., 2013, using the 16S rRNA gene of *Gallicrex cinerea* (J.F. Gmelin, 1789), GenBank accession KP057881, as a reference); (*ii*) a one-bp insertion at position 712; and (*iii*) a one-bp insertion at position 748.

Type genus: *Amaurornis* Reichenbach, 1853.

Contents: *Poliolimnas cinereus* (Vieillot, 1819); *Megacrex inepta* D'Albertis and Salvadori, 1879; *Aenigmatolimnas marginalis* (Hartlaub, 1857); *Gallicrex cinerea*; *Amaurornis* (five species, not counting "*A*." (= *Zapornia*) *akool* (Sykes, 1832); see discussion below).

Comment: Livezey (1998) applied his name 'Amaurornithina' only to the genus *Amaurornis*.

ZooBank LSID for new tribe: CFCD1715-7FA0-4950-99E9-2DEAE7B8678D

Pardirallini new tribe

Diagnosis: A morphologically diverse group of neotropical, small, short-billed to large, long-billed rails, with red or red-brown irises and primarily yellow bills. All have reddish legs except for *Anurolimnas castaneiceps* (Sclater & Salvin, 1869) in which the legs are grey-black coloured. Our examination of the morphological data set of Livezey (1998) revealed no morphological apomorphies for this clade. In an alignment 16S rRNA sequences (n = 102) constructed for this study (Appendix 1), members of Pardirallini showed an inferred one-bp deletion at position 1151 (using the 16S rRNA gene of *Gallicrex cinerea* KP057881 as a reference) that was otherwise only found in *Rallina tricolor* G.R. Gray, 1858 (KC614032). In an alignment of 50 beta-fibrinogen intron 7 sequences of Rallidae obtained by García-R *et al*. (2014) (Appendix 1), members of Pardirallini showed an inferred one-bp deletion at position 371 (using the sequence of *Aramides axillaris* Lawrence, 1863 (KC613860) as a reference).

Type genus: *Pardirallus* Bonaparte, 1856.

Contents: *Anurolimnas castaneiceps*; *Amaurolimnas concolor* (Gosse, 1847); *Aramides* Pucheran, 1845 (eight species; Kirchman *et al*., 2021); *Mustelirallus* Bonaparte, 1856 (four species, including *M. cerverai* (Barbour & Peters, 1927), see Brown *et al*., 2022); *Pardirallus* (three species; Kirchman *et al*., 2021).

Comment: Livezey (1998) restricted his name 'Pardirallina' to *Cyanolimnas cerverai*, *Pardirallus maculatus* (Boddaert, 1783), *Ortygonax sanguinolentus* (Swainson, 1838) and *O. nigricans* (Vieillot, 1819).

ZooBank LSID for new tribe: 65E3E3E5-6211-4E81-A0DF-F467C162B255

DISCUSSION

In the classification of Rallidae proposed by Kirchman *et al*. (2021), *Zapornia akool* was placed in the genus *Amaurornis* (and Amaurornithini). This agrees with the position of this species in phylogenetic studies based on complete mitochondrial genomes (mitogenomes), which place *Z. akool* as the sister of *A. phoenicurus* (Pennant, 1769) and *Gallicrex cinerea* (see Chen *et al*., 2017; Gong *et al*., 2017; Boast *et al*., 2019; Oswald *et al*., 2021). However, these studies relied on mitogenomes of *Z. akool* (GenBank accession KJ192198 / NC_023982) and *A. phoenicurus* (KJ874440 / NC_024593) that were chimeras containing DNA fragments of both *A. phoenicurus* and *Gallinula chloropus* Linnaeus, 1758 (Sangster & Luksenburg, 2021). In the case of the published mitogenome of *Z. akool* it was not clear if the sequence included any *bona fide* DNA fragments of *Z. akool* (see Sangster & Luksenburg, 2021). Thus, these four mitogenome studies cannot be relied upon regarding the phylogenetic position of *Z. akool* and *A. phoenicurus*. Other studies, which did not use the problematic mitogenomes of *Z. akool* and *A. phoenicurus*, placed *Z. akool* in *Zapornia* Leach, 1816 with strong support (Ruan *et al*., 2012; see also García-R *et al*., 2014), and *A. phoenicurus* with *A. moluccana* (Wallace, 1865) and *G. cinerea* with strong support (Ruan *et al*., 2012; García-R *et al*., 2014). Thus, based on current evidence *Z. akool* should be placed in *Zapornia* (*cf.* Dickinson & Remsen, 2013) in the tribe Zapornini.

ACKNOWLEDGEMENTS

We are grateful to Jeremy Kirchman and an anonymous referee for their helpful suggestions which improved the clarity of the paper.

REFERENCES

Barbour T. & Peters J.L., 1927. Two more remarkable new birds from Cuba. – *Proceedings of the New England Zoological Club*, 9: 95–97.

Bernt M., Donath A., Jühling F., Externbrink F., Florentz C., Fritzsch G., Pütz J., Middendorf M. & Stadler P.F., 2013. MITOS: improved de novo metazoan mitochondrial genome annotation. – *Molecular Phylogenetics and Evolution*, 69: 313–319.

Boast A.P., Chapman B., Herrera M.B., Worthy T.H., Scofield R.P., Tennyson A.J., Houde P., Bunce M., Cooper A. & Mitchell K.J., 2019. Mitochondrial genomes from New Zealand's extinct adzebills (Aves: Aptornithidae: *Aptornis*) support a sister-taxon relationship with the Afro-Madagascan Sarothruridae. – *Diversity*, 11 (2): 24.

Boddaert P., 1783. *Table des planches enluminéez d'histoire naturelle de M. D'Aubenton: avec les denominations de M.M. de Buffon, Brisson, Edwards, Linnaeus et Latham, precedé d'une notice des principaux ouvrages zoologiques enluminés*. i–xv, 1–58. – Utrecht.

Bonaparte C.L., 1856. Excursion dans les divers Musées d'Allemagne, de Hollande et de Belgique (suite), et Tableaux paralléliques de Vordre des Échassiers (fin). – *Comptes Rendus des Séances de l'Académie des Sciences, Paris*, 43: 593–601.

Brown A.F., Lawrie Y., Shannon T.J., Collinson J.M., Kirwan G.M., Kirkconnell A. & Stervander M., 2022. First genetic data for the critically endangered Cuban endemic Zapata Rail *Cyanolimnas cerverai*, and the taxonomic implications. – *Journal of Ornithology*, 163 (4): 945–952.

Burleigh J.G., Kimball R.T. & Braun E.L., 2015. Building the avian tree of life using a large-scale, sparse supermatrix. – *Molecular Phylogenetics and Evolution*, 84: 53–63.

Chapin J.P., 1939. The birds of the Belgian Congo. Part II. – *Bulletin of the American Museum of Natural History*, 75: 1–632.

Chen Peng, Han Yuqing, Zhu Chaoying, Gao Bin & Ruan Luzhang, 2017. Complete mitochondrial genome of *Porzana fusca* and *Porzana pusilla* and phylogenetic relationship of 16 Rallidae species. – *Genetica*, 145: 559–573.

D'Albertis L.M. & Salvadori T., 1879. Catalogo declì uecelli raccolti da L. M. D'Albertis durante la 2a. e 3a. esplorazione del Fiume Fly negli anni 1876 e 1877. – *Annali del Museo Civico di storia naturale di Genova*, 14: 21–147.

Des Murs O., 1860. *Traite general d'oologie ornithologique au point de vue de la classification*. i–xix, 1–640. – F. Klincksieck, Paris.

Dickinson E.C. & Remsen J.V. (eds.), 2013. *The Howard and Moore complete checklist of the birds of the world*, vol. 1. Fourth edition. i–l, 1–461. – Aves Press, Eastbourne.

Edgar R.C., 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. – *Nucleic Acids Research*, 5: 1792–1797.

García-R J.C., Gibb G.C. & Trewick S.A., 2014. Deep global evolutionary radiation in birds: Diversification and trait evolution in the cosmopolitan bird family Rallidae. – *Molecular Phylogenetics and Evolution*, 81: 96–108.

García-R J.C., Lemmon E.M., Lemmon A.R. & French N., 2020. Phylogenomic reconstruction sheds light on new relationships and timescale of rails (Aves: Rallidae) evolution. – *Diversity*, 12 (2): 70.

García-R J.C. & Matzke N.J., 2021. Trait-dependent dispersal in rails (Aves: Rallidae): historical biogeography of a cosmopolitan bird clade. – *Molecular Phylogenetics and Evolution*, 159: 107106.

Gill F., Donsker D. & Rasmussen P. (eds.), 2023. IOC world bird list (v13.1). https://doi.org/10.14344/IOC.ML.13.1.

Gmelin J.F., 1789. *Caroli a Linné … Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, Cum Characteribus, Differentiis, Synonymis, Locis*, 13th edition. Vol. 1, Part 2. 501–1032. – Impensis Georg Emanuel Beer, Lipsiae [Leipzig].

Gong Jie, Zhao Ruoping, Huang Qingrong, Sun Xiaomin, Huang Ling & Jing Meidong, 2017. Two mitogenomes in Gruiformes (*Amaurornis akool*/*A. phoenicurus*) and the phylogenetic placement of Rallidae. – *Genes & Genomics*, 39: 987–995.

Gosse P.H., 1847. *The birds of Jamaica*. i–x, 1–447. – John van Voorst, London.

Gray G.R., 1858. A list of the birds, with descriptions of new species obtained by Mr. Alfred R. Wallace in the Aru and Ké islands. – *Proceedings of the Zoological Society of London*, 1858: 169–198.

Gray G.R., 1862. Remarks on, and descriptions of, new species of birds lately sent by Mr. A. R. Wallace from Waigiou, Mysol, and Gagie Islands. – *Proceedings of the Zoological Society of London*, 1861: 427–438.

Hackett S.J., Kimball R.T., Reddy S., Bowie R.C.K., Braun E.L., Braun M.J., Chojnowski J.L., Cox W.A., Han K.-L. & Harshman J., 2008. A phylogenomic study of birds reveals their evolutionary history. – *Science*, 320: 1763–1768.

Hartlaub G., 1855. Beschreibung einiger neuen, von Herrn H. S. Pel, holländischem Residenten an der Goldküste, daselbst gesammelten Vögelarten. – *Journal für Ornithologie*, 3 (5): 353–361.

Hartlaub G., 1857. *System der Ornithologie Westafrica's*. i–lxvi, 1–280. – C. Schünemann, Bremen.

ICZN [International Commission on Zoological Nomenclature], 1999. *International Code of Zoological Nomenclature.* Fourth edition. i–xxix, 1–306. – International Trust for Zoological Nomenclature, London.

Kirchman J.J., 2012. Speciation of flightless rails on islands: a DNA-based phylogeny of the typical rails of the Pacific. – *Auk*, 129 (1): 56–69.

Kirchman J.J., Rotzel McInerney N., Giarla T.C., Olson S.L., Slikas E. & Fleischer R.C., 2021. Phylogeny based on ultra-conserved elements clarifies the evolution of rails and allies (Ralloidea) and is the basis for a revised classification. – *Ornithology*, 138 (4): ukab042.

Kumar S., Stecher G. & Tamura K., 2016. MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. – *Molecular Biology and Evolution*, 33: 1870–1874.

Lambert F.R., 1998. A new species of *Gymnocrex* from the Talaud Islands, Indonesia. – *Forktail*, 13: 1–6.

Lawrence G.N., 1863. Descriptions of new species of birds of the families Vireonidae and Rallidae. – *Proceedings of the Academy of Natural Science Philadelphia*, 1863: 106–107.

Leach W.E., 1816. *Systematic Catalogue of the Specimens of the Indigenous Mammals and Birds that are Present in the British Museum etc*. [1–4], 5–42 [43–44]. – The trustees of the British Museum, London.

Leach W.E., 1820. Eleventh Room (pp. 65–70). In: *Synopsis of the Contents of the British Museum*, Seventeenth Edition. – British Museum, London.

Linnaeus C., 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. 10th edition. 1. 1–824. – Laurentii Salvii, Holmiae [Stockholm].

Livezey B.C., 1998. A phylogenetic analysis of the Gruiformes (Aves) based on morphological characters, with an emphasis on the rails (Rallidae). – *Philosophical Transactions of the Royal Society of London B*, 353: 2077–2151.

Nitzsch C.L., 1820. Ueber die Nafendrüfe der Vögel. – *Deutsches Archiv für die Physiologie*, 6: 234–269.

Olson S.L., 1973. A classification of the Rallidae. – *Wilson Bulletin*, 85 (4): 381–416.

Oswald J.A., Terrill R.S., Stucky B.J., LeFebvre M.J., Steadman D.W., Guralnick R.P. & Allen J.M., 2021. Ancient DNA from the extinct Haitian cave-rail (*Nesotrochis steganinos*) suggests a biogeographic connection between the Caribbean and Old World. – *Biology Letters*, 17 (3): 20200760.

Pennant T., 1769. *Indian Zoology*. 1–14, Pls. I–XII. – London.

Peters J.L., 1934. *Check-list of Birds of the World*. 2. i–xvii, 1–401. – Harvard University Press, Cambridge, Massachusetts.

Pucheran J., 1845. Notes sur quelques espèces Madécasses de l'ordre des Échassiers. *Revue Zoologique*, 8: 277–280.

Reichenbach H.G.L., 1853. *Avium Systema Naturale*. i–viii, 1–36, i–xxxi. – Friedrich Hofmeister, Leipzig.

Ripley S.D., 1977. *Rails of the World*. i–xx, 1–406. – David R. Godine, Boston.

Ruan Luzhang, Wang Yushi, Hu Jinrun & Yi Ouyang, 2012. Polyphyletic origin of the genus *Amaurornis* inferred from molecular phylogenetic analysis of rails. – *Biochemical Genetics*, 50: 959–966.

Salvadori T., 1875. Intorno a due collezioni di uccelli di Celebes, inviate al Museo Civico di Genova dal Dr. O. Beccari e dal Sig. A. A. Bruijn. – *Annali del Museo Civico di storia naturale di Genova*, 7: 641–681.

Sangster G. & Luksenburg J.A., 2021. Sharp increase of problematic mitogenomes of birds: causes, effects and remedies. – *Genome Biology and Evolution*, 13 (9): evab210.

Schlegel H., 1866. Observations zoologiques. – *Nederlands Tijdschrift voor de Dierkunde*, 3: 181–213.

Sclater P.L. & Salvin O., 1869. Synopsis of the American rails (Rallidae). – *Proceedings of the Zoological Society of London*, 1868: 442–470.

Slikas B., Olson S.L. & Fleischer R.C., 2002. Rapid, independent evolution of flightlessness in four species of Pacific Island rails (Rallidae): an analysis based on mitochondrial sequence data. – *Journal of Avian Biology*, 33: 5–14.

Swainson W., 1838. Part III. Two centenaries and a quarter of birds, either new, or hitherto imperfectly described (pp. 281–361). In: *Animals in menageries*. – Longman, Orme, Brown, Green, & Longmans, and John Taylor, London.

Sykes W.H., 1832. [Exhibition of the collection of birds formed by him in Dukhun.] – *Proceedings of the Committee of Science and Correspondence of the Zoological Society of London*, 2: 149–172.

Taylor B., 1998. *Rails, a guide to the rails, crakes, gallinules and coots of the world*. 1–600. – Pica Press, Robertsbridge.

Vieillot L.P., 1819. RALE GRIS, *Rallus cinereus* (p. 556), RALE NOIRATRE, *Rallus nigricans* (p. 560). In: *Nouveau Dictionnaire d'Histoire Naturelle*, vol. 28. – Deterville, Paris.

Wallace A.R., 1865. Descriptions of new birds from the Malay Archipelago. – *Proceedings of the Zoological Society of London*, 1865: 474–481.

Wetmore A., 1918. Bones of birds collected by Theodoor de Booy from kitchen midden deposits in the islands of St. Thomas and St. Croix. – *Proceedings of the United States National Museum*, 54 (2245): 513–522.

Wolters H.E., 1975. *Die Vogelarten der Erde Eine systematische Liste mit Verbreitungsangaben sowie deutschen und englishen Namen*. Lieferung 1. 1–80. – Paul Parey, Hamburg.

Addresses

George Sangster (✉), Naturalis Biodiversity Center, Darwinweg 2, PO Box 9517, 2300 RA Leiden, the Netherlands.
e-mail: g.sangster@planet.nl.

Jacob C. Blokland, College of Science and Engineering, Flinders University, GPO 2100, Adelaide 5001, SA, Australia.
e-mail: jacob.blokland@flinders.edu.au.

Steven M.S. Gregory, 35 Monarch Road, Northampton NN2 6EH, UK.
e-mail: sgregory.avium@ntlworld.com.

Edward C. Dickinson, Flat 19, Marlborough Court, Southfields Road, Eastbourne, East Sussex BN21 1BT, UK.
e-mail: ecdickinson13@gmail.com.

APPENDIX 1. 16S rRNA sequences used in an alignment to identify putative synapomorphies of Amaurornithini and Pardirallini. Tribe and genus designations follow Kirchman *et al.* (2021).

GenBank accession no.	Tribe	Genus	species
KC613981	Amaurornithini	*Amaurornis*	*moluccana*
KC613982	Amaurornithini	*Amaurornis*	*phoenicurus*
KF289829	Amaurornithini	*Amaurornis*	*phoenicurus*
KJ442621	Amaurornithini	*Amaurornis*	*phoenicurus*
KC613997	Amaurornithini	*Gallicrex*	*cinerea*
KP057881	Amaurornithini	*Gallicrex*	*cinerea*
KC613989	Fulicini	*Fulica*	*alai*
DQ485863	Fulicini	*Fulica*	*americana*
KC613990	Fulicini	*Fulica*	*ardesiaca*
KC613995	Fulicini	*Fulica*	*armillata*
KC613991	Fulicini	*Fulica*	*atra*
KF644582	Fulicini	*Fulica*	*atra*
KP313718	Fulicini	*Fulica*	*atra*
MN122918	Fulicini	*Fulica*	*atra*
KC613992	Fulicini	*Fulica*	*cristata*
KC613993	Fulicini	*Fulica*	*leucoptera*
KC613994	Fulicini	*Fulica*	*rufifrons*
DQ485864	Fulicini	*Gallinula*	*chloropus*
HQ896036	Fulicini	*Gallinula*	*chloropus*
KC614002	Fulicini	*Gallinula*	*tenebrosa*
KC613996	Fulicini	*Paragallinula*	*angulata*
KC613998	Fulicini	*Porphyriops*	*melanops*
DQ485862	Fulicini	*Porzana*	*carolina*
KC614016	Fulicini	*Porzana*	*fluminea*
KC614023	Fulicini	*Porzana*	*porzana*
KC613999	Fulicini	*Tribonyx*	*mortierii*
KC614003	Fulicini	*Tribonyx*	*ventralis*
KC613985	Laterallini	*Coturnicops*	*noveboracensis*
OM992117	Laterallini	*Coturnicops*	*noveboracensis*
KC614004	Laterallini	*Hapalocrex*	*exilis*
KC614009	Laterallini	*Laterallus*	*jamaicensis*
OM677841	Laterallini	*Laterallus*	*jamaicensis*
DQ485859	Laterallini	*Laterallus*	*melanophaius*
MH029238	Laterallini	*Laterallus*	*rogersi*
MN356443	Laterallini	*Laterallus*	*rogersi*
MW067132	Laterallini	*Laterallus*	*spilonota*

GenBank accession no.	Tribe	Genus	species
KC614006	Laterallini	*Rufirallus*	*fasciatus*
KC614010	Laterallini	*Rufirallus*	*viridis*
KC613978	Pardirallini	*Aramides*	*axillaris*
KC613983	Pardirallini	*Aramides*	*cajanea*
KC613980	Pardirallini	*Aramides*	*mangle*
KC613984	Pardirallini	*Aramides*	*ypecaha*
KC614018	Pardirallini	*Mustelirallus*	*albicollis*
KC614011	Pardirallini	*Mustelirallus*	*erythrops*
KC614020	Pardirallini	*Pardirallus*	*nigricans*
KC614025	Pardirallini	*Pardirallus*	*sanguinolentus*
KC614015	Porphyrionini	*Porphyrio*	*alleni*
KJ685965	Porphyrionini	*Porphyrio*	*flavirostris*
EF532934	Porphyrionini	*Porphyrio*	*hochstetteri*
KJ685958	Porphyrionini	*Porphyrio*	*madagascariensis*
KC614019	Porphyrionini	*Porphyrio*	*martinica*
KJ685957	Porphyrionini	*Porphyrio*	*melanotus*
KJ685960	Porphyrionini	*Porphyrio*	*melanotus*
KJ685963	Porphyrionini	*Porphyrio*	*melanotus*
KJ685964	Porphyrionini	*Porphyrio*	*melanotus*
KJ685961	Porphyrionini	*Porphyrio*	*poliocephalus*
DQ485858	Porphyrionini	*Porphyrio*	*porphyrio*
KF701062	Porphyrionini	*Porphyrio*	*porphyrio*
KJ685959	Porphyrionini	*Porphyrio*	*porphyrio*
KJ685962	Porphyrionini	*Porphyrio*	*pulverulentus*
KC613986	Rallini	*Crex*	*crex*
KC613987	Rallini	*Dryolimnas*	*cuvieri*
KC613988	Rallini	*Eulabeornis*	*castaneoventris*
KF644583	Rallini	*Eulabeornis*	*castaneoventris*
KC614035	Rallini	*Gallirallus*	*australis*
KF425525	Rallini	*Gallirallus*	*australis*
KF701060	Rallini	*Gallirallus*	*australis*
AP010821	Rallini	*Hypotaenidia*	*okinawae*
KC614000	Rallini	*Hypotaenidia*	*owstoni*
DQ485860	Rallini	*Hypotaenidia*	*philippensis*
KF701061	Rallini	*Hypotaenidia*	*philippensis*
KC614034	Rallini	*Hypotaenidia*	*sylvestris*
KC614012	Rallini	*Hypotaenidia*	*woodfordi*
KC614005	Rallini	*Lewinia*	*mirifica*
KC614007	Rallini	*Lewinia*	*muelleri*

GenBank accession no.	Tribe	Genus	species
KF644584	Rallini	*Lewinia*	*muelleri*
KC614008	Rallini	*Lewinia*	*pectoralis*
KC614001	Rallini	*Lewinia*	*striata*
MH219930	Rallini	*Lewinia*	*striata*
KC614027	Rallini	*Rallus*	*aquaticus*
MH229988	Rallini	*Rallus*	*aquaticus*
KC614028	Rallini	*Rallus*	*caerulescens*
KC614029	Rallini	*Rallus*	*elegans*
OM837807	Rallini	*Rallus*	*indicus*
KC614031	Rallini	*Rallus*	*limicola*
DQ485861	Rallini	*Rallus*	*longirostris*
OM992118	Rallini	*Rallus*	*obsoletus*
AP010822	Zapornini	*Rallina*	*eurizonoides*
KC614030	Zapornini	*Rallina*	*fasciata*
KC614032	Zapornini	*Rallina*	*tricolor*
MN356311	Zapornini	*Zapornia*	*atra*
KC613979	Zapornini	*Zapornia*	*flavirostra*
KC614017	Zapornini	*Zapornia*	*fusca*
KY009736	Zapornini	*Zapornia*	*fusca*
LC541456	Zapornini	*Zapornia*	*fusca*
KC614022	Zapornini	*Zapornia*	*parva*
KC614013	Zapornini	*Zapornia*	*paykullii*
MG200164	Zapornini	*Zapornia*	*paykullii*
KC614021	Zapornini	*Zapornia*	*pusilla*
KY009737	Zapornini	*Zapornia*	*pusilla*
MW043485	Zapornini	*Zapornia*	*pusilla*
KC614026	Zapornini	*Zapornia*	*tabuensis*

APPENDIX 2. Beta-fibrinogen intron 7 sequences used in an alignment to identify putative synapomorphies of Pardirallini. Tribe and genus designations follow Kirchman *et al.* (2021).

GenBank accession no.	Tribe	Genus	species
KC613863	Amaurornithini	*Amaurornis*	*phoenicurus*
KC613877	Amaurornithini	*Gallicrex*	*cinerea*
KC613868	Fulicini	*Fulica*	*alai*
KC613869	Fulicini	*Fulica*	*ardesiaca*
KC613874	Fulicini	*Fulica*	*armillata*
KC613870	Fulicini	*Fulica*	*atra*
KC613871	Fulicini	*Fulica*	*cristata*
KC613872	Fulicini	*Fulica*	*leucoptera*
KC613873	Fulicini	*Fulica*	*rufifrons*
KC613880	Fulicini	*Gallinula*	*tenebrosa*
KC613875	Fulicini	*Paragallinula*	*angulata*
KC613876	Fulicini	*Paragallinula*	*angulata*
KC613878	Fulicini	*Porphyriops*	*melanops*
KC613899	Fulicini	*Porzana*	*carolina*
KC613894	Fulicini	*Porzana*	*fluminea*
KC613902	Fulicini	*Porzana*	*porzana*
KC613881	Fulicini	*Tribonyx*	*ventralis*
KC613883	Laterallini	*Hapalocrex*	*exilis*
KC613885	Laterallini	*Laterallus*	*jamaicensis*
KC613884	Laterallini	*Rufirallus*	*fasciatus*
KC613888	Laterallini	*Rufirallus*	*viridis*
KC613860	Pardirallini	*Aramides*	*axillaris*
KC613864	Pardirallini	*Aramides*	*cajanea*
KC613862	Pardirallini	*Aramides*	*mangle*
KC613896	Pardirallini	*Mustelirallus*	*albicollis*
KC613889	Pardirallini	*Neocrex*	*erythrops*
KC613890	Pardirallini	*Neocrex*	*erythrops*
KC613898	Pardirallini	*Pardirallus*	*nigricans*
KC613904	Pardirallini	*Pardirallus*	*sanguinolentus*
KC613893	Porphyrionini	*Porphyrio*	*alleni*
KC613909	Porphyrionini	*Porphyrio*	*hochstetteri*
KC613897	Porphyrionini	*Porphyrio*	*martinica*
KC613865	Rallini	*Crex*	*crex*
KC613866	Rallini	*Dryolimnas*	*cuvieri*
KC613867	Rallini	*Eulabeornis*	*castaneoventris*
KC613911	Rallini	*Gallirallus*	*australis*

GenBank accession no.	Tribe	Genus	species
KC613910	Rallini	*Hypotaenidia*	*sylvestris*
KC613891	Rallini	*Hypotaenidia*	*woodfordi*
KC613882	Rallini	*Lewinia*	*mirifica*
KC613886	Rallini	*Lewinia*	*muelleri*
KC613887	Rallini	*Lewinia*	*pectoralis*
KC613879	Rallini	*Lewinia*	*striatus*
KC613905	Rallini	*Rallus*	*caerulescens*
KC613906	Rallini	*Rallus*	*elegans*
KC613907	Zapornini	*Rallina*	*tricolor*
KC613861	Zapornini	*Zapornia*	*flavirostra*
KC613895	Zapornini	*Zapornia*	*fusca*
KC613901	Zapornini	*Zapornia*	*parva*
KC613892	Zapornini	*Zapornia*	*paykullii*
KC613900	Zapornini	*Zapornia*	*pusilla*