A new genus-group name for *Burhinus bistriatus* (Wagler, 1829) and *Burhinus superciliaris* (Tschudi, 1843)

David Černý, Paul van Els, Rossy Natale & Steven M. S. Gregory

ABSTRACT: Recent phylogenetic findings indicate that the divergence of the Neotropical taxa *Burhinus bistriatus* (Wagler, 1829) and *Burhinus superciliaris* (Tschudi, 1843) from other thick-knees (Burhinidae) predates the split between the remaining species of *Burhinus* and the genus *Esacus*, rendering the genus *Burhinus* paraphyletic. The great age of the former divergence and potential homonymy issues stemming from treating *Esacus* Lesson, 1831 as a junior subjective synonym of *Burhinus* Illiger, 1811 suggest that the emergent paraphyly is best prevented by introducing a new genus-group name for the two New World species of *Burhinus*. Accordingly, we describe a new genus, *Hesperoburhinus* gen. nov., under Article 13.1.1 and Article 16.1 of the International Code of Zoological Nomenclature (ICZN, 1999).

Estudios filogenéticos recientes indican que la divergencia de los taxones neotropicales *Burhinus bistriatus* (Wagler, 1829) y *Burhinus superciliaris* (Tschudi, 1843) de otros alcaravanes (Burhinidae) es más antigua que la diversificación de las especies de los géneros *Burhinus* y *Esacus*, lo que hace que el género *Burhinus* sea parafilético. La gran antigüedad de las dos especies neotropicales de Burhinidae y los posibles problemas de homonimia derivados del tratamiento de *Esacus* Lesson, 1831 como un sinónimo subjetivo menor de *Burhinus* Illiger, 1811 sugieren que la parafilia emergente se previene mejor introduciendo un nuevo nombre de género para las dos especies del Nuevo Mundo. En consecuencia, se propone un nuevo género, *Hesperoburhinus* gen. nov., en cumplimiento de los Artículos 13.1.1 y 16.1 del Código Internacional de Nomenclatura Zoológica (ICZN, 1999).

KEYWORDS: Burhinidae, *Burhinus*, Double-striped thick-knee, *Esacus*, *Hesperoburhinus* gen. nov., Neotropics, paraphyly, Peruvian thick-knee, phylogeny, taxonomy, Thick-knees.

The Double-striped thick-knee was described as *Charadrius bistriatus* by Wagler (1829: 648). Gray (1844: 59) re-assigned it to the genus *Oedicnemus* Temminck, 1815, and the resulting combination *Oedicnemus bistriatus* (Wagler 1829) was widely adopted by subsequent authors (Berlepsch, 1884; Salvin, 1886; Ernst, 1887; Robinson & Richmond, 1896). The other species of Neotropical burhinid, the Peruvian thick-knee, was described as *Oedicnenus superciliaris* by Tschudi (1843: 387), with "*Oedicnenus*" representing an obvious *lapsus calami* for *Oedicnemus* Temminck, 1815.

The genus *Oedicnemus* Temminck, 1815, with *Oedicnemus crepitans* Temminck, 1815 [= *Burhinus oedicnemus* (Linnaeus, 1758)] as its type species (Table I), was later shown by Hemming (1952) to represent a junior subjective synonym of *Burhinus* Illiger, 1811. Accordingly, *Burhinus bistriatus* (Wagler, 1829) and *Burhinus superciliaris* (Tschudi, 1843) represent the accepted names of the Double-striped and Peruvian thick-knees, respectively, according to all contemporary taxonomic authorities, including *A World Checklist of Birds* (Monroe & Sibley, 1993), the *Handbook of the Birds of the World* (Hume 1996), *Avibase* (Lepage *et al.*, 2014), the *eBird/Clements Checklist of*

Table I. An exhaustive list of genera proposed for thick-knees (omitting spelling variations and *lapsus calami*) along with their type species. Genera recognized as valid by contemporary taxonomic authorities are highlighted in bold. Since none of the previously coined generic names is typified by *B. bistriatus* (Wagler, 1829) or *B. superciliaris* (Tschudi, 1843), a new name is required if the clade comprising these two species is to be separated at the genus rank.

Genus	Type species
Burhinops Roberts, 1922	*Oedicnemus capensis* Lichtenstein, 1823 　　= *Burhinus capensis* (Lichtenstein, 1823)
Burhinus Illiger, 1811	*Charadrius magnirostris* Latham, 1801 　　= *Burhinus grallarius* (Latham, 1801)
Carvanaca Hodgson, 1836	*Carvanaca grisea* Hodgson, 1836 　　= *Esacus recurvirostris* (Cuvier, 1829)
Esacus Lesson, 1831	*Oedicnemus recurvirostris* Cuvier, 1829 　　= *Esacus recurvirostris* (Cuvier, 1829)
Fedoa Leach, 1816	*Fedoa oedicnemus* (Linnaeus, 1758) 　　= *Burhinus oedicnemus* (Linnaeus, 1758)
Oedicnemus Temminck, 1815	*Oedicnemus crepitans* Temminck, 1815 　　= *Burhinus oedicnemus* (Linnaeus, 1758)
Orthorhamphus Salvadori, 1874	*Oedicnemus magnirostris* Vieillot, 1818 　　= *Esacus magnirostris* (Vieillot, 1818)
Planorhamphus Billberg, 1828	None indicated; erected as a new name for 　　*Burhinus* Illiger, 1811
Pseudops Hodgson, 1841	None indicated; erected as a new name for 　　*Carvanaca* Hodgson, 1836

Birds of the World (Clements *et al.*, 2022), the *IOC World Bird List* (Gill *et al.*, 2022), and the *Howard and Moore Complete Checklist of Birds of the World* (Dickinson & Remsen, 2013). All but the first of these taxonomies recognize two extant genera of the family Burhinidae: *Burhinus* Illiger, 1811 with *B. grallarius* (Latham, 1801) as its type species, and *Esacus* Lesson, 1831 with *E. recurvirostris* (Cuvier, 1829) as its type species (Table I).

　　To date, few phylogenetic studies have been able to corroborate the reciprocal monophyly of the two genera. The evidence from phylogenetic analyses of morphological data largely contradicts it: Chu (1995) found *Esacus* to be nested within *Burhinus*, and Livezey (2010) found the type species of *Burhinus*, *B. grallarius*, to be more closely related to *Esacus* than to its supposed congeners, prompting the author to erroneously (see Table I) reassign it to the monotypic genus *Orthorhamphus*. The evidence from molecular sequences was at first hampered by limited taxon sampling (Baker *et al.*, 2007), while later studies that sampled the Burhinidae more extensively suffered from taxonomic misidentification issues engendered by the homonymy arising between *Burhinus magnirostris* (Latham, 1801) [= *Burhinus grallarius* (Latham, 1801)] and
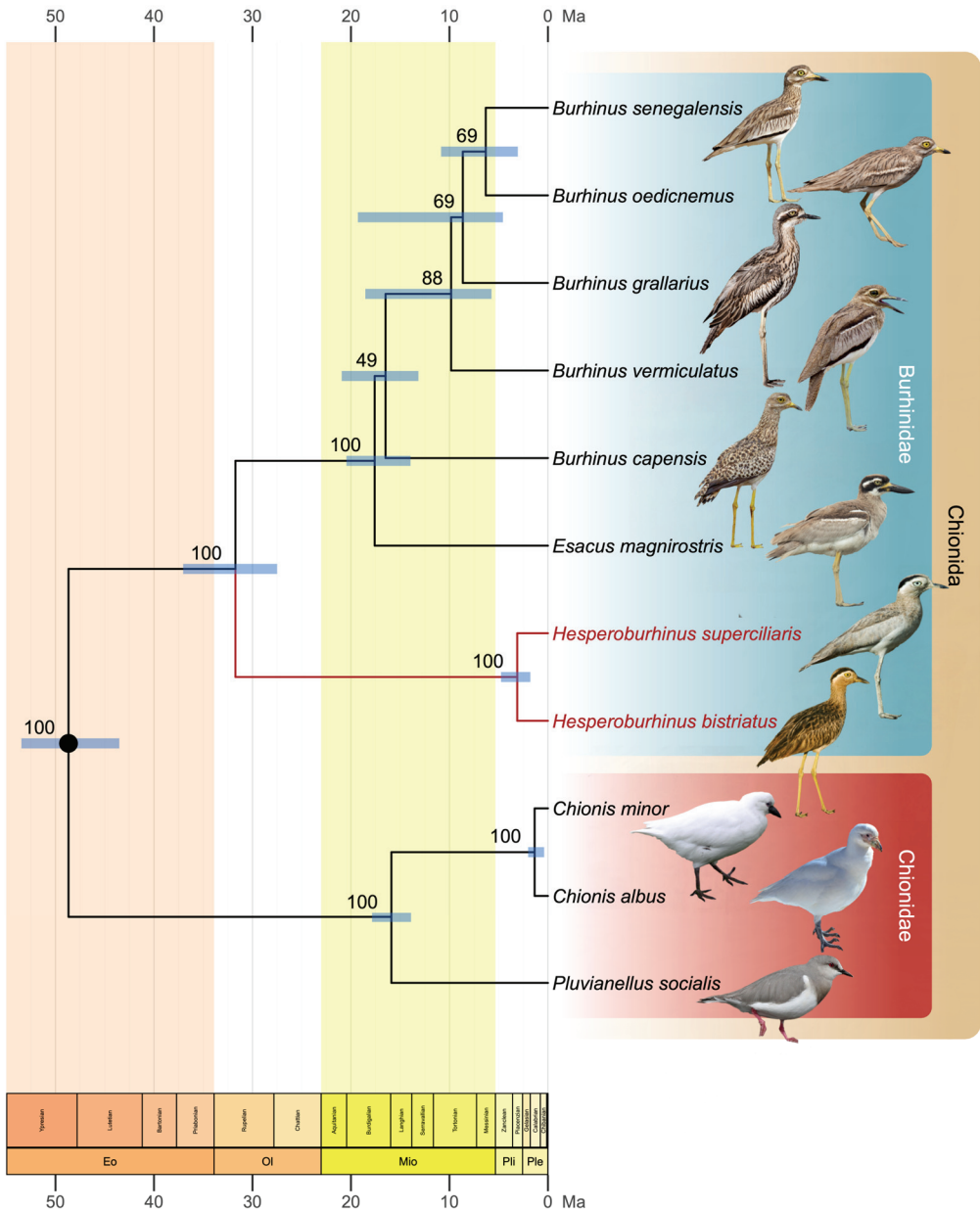
Figure 1. Time-scaled total-evidence phylogeny of thick-knees and their closest relatives, redrawn after Černý & Natale (2022). The genus *Hesperoburhinus* is highlighted with dark red branches and tip labels. Numbers above nodes indicate bootstrap support values; blue bars denote 95% node age confidence intervals derived from penalized-likelihood rate-smoothing of 1000 bootstrap pseudoreplicates. The black circle at the root denotes a fossil calibration associated with the corresponding node. Shaded tabs to the right of tip labels indicate suprageneric clades; background colours identify geochronological epochs. Abbreviations: Ma = million years ago; Eo = Eocene; Ol = Oligocene; Mio = Miocene; Pli = Pliocene; Ple = Pleistocene. Bird photo credits and licensing information from top to bottom: Frans Vandewalle (Flickr, CC BY-NC 2.0), Artemy Voikhansky (Wikimedia Commons, CC BY-SA 4.0), Cédric Larouche (Flickr, CC BY-NC-SA 2.0), Bernard Dupont (Flickr, CC BY-SA 2.0), Bernard Dupont (Flickr, CC BY-SA 2.0), John Harrison (Wikimedia Commons, CC BY-SA 4.0), Nick Athanas (Flickr, CC BY-NC-SA 2.0), Nick Athanas (Flickr, CC BY-NC-SA 2.0), "Nweider" (Wikimedia Commons, CC BY-SA 4.0), Murray Foubister (Flickr, CC BY-SA 2.0), Brendan Ryan (Flickr, CC BY-NC-SA 2.0).

Esacus magnirostris (Vieillot, 1818) in those taxonomies where the two are treated as congeneric. As recently noted by Boyd (2021), this caused the sequences of *Esacus magnirostris* to be misidentified as those of *Burhinus grallarius* in GenBank (Benson *et al.*, 2017), and in those taxonomically comprehensive phylogenies that relied on the inclusion of GenBank data (Jetz *et al.*, 2012; Burleigh *et al.*, 2015).

A recent study that took Boyd's (2021) comments into account (Černý & Natale, 2022) found the only sampled species of *Esacus* (*E. magnirostris*) to be nested within *Burhinus*, represented by a total of seven species. The earliest divergence within the Burhinidae instead consisted of the branching off of a clade comprising the Neotropical thick-knees *B. bistriatus* and *B. superciliaris* (Figure 1). The monophyly of a group uniting *Esacus magnirostris* and the Old World species of *Burhinus* received maximum support from the maximum-likelihood analysis of molecular data (bootstrap = 100%, internode certainty = 1; Černý & Natale, 2022, Appendix A: Figure A.32), the Bayesian analysis of molecular data (posterior probability = 1.0; Černý & Natale, 2022, Appendix A: Figure A.34), and the maximum-likelihood analysis of combined molecular and morphological data (bootstrap = 100%; Černý & Natale, 2022, Appendix A: Figures A.35–A.36). The sister-group relationship between the Neotropical thick-knees and a clade uniting *Esacus magnirostris* and the remaining species of *Burhinus* was supported by almost all data partitions for which the relevant taxa were sampled, including mitochondrial ribosomal RNA genes (12S, 16S; Černý & Natale, 2022, Appendix A: Figures A.3–A.4), mitochondrial protein-coding loci (COI, COIII, CytB, ND1, ND2, ND3; Černý & Natale, 2022, Appendix A: Figures A.11, A.13–A.14, A.20–A.22), and nuclear protein-coding loci (ALDOB, NTF3, RAG1; Černý & Natale, 2022, Appendix A: Figures A.6, A.27, A.29). Only the mitochondrial ND5 locus found the three taxa in a polytomy that neither supported nor contradicted the early divergence of the Neotropical taxa (Černý & Natale, 2022, Appendix A: Figure A.25), while the morphological partition yielded a contradictory topology (Černý & Natale, 2022, Appendix A: Figure A.30). Finally, when accounting for the true identity of the sequences erroneously attributed to *Burhinus grallarius* or "*Burhinus magnirostris*", the topology in question is also borne out by the phylogenies of Paton *et al.* (2003), Jetz *et al.* (2012), and Burleigh *et al.* (2015).

To avoid the paraphyly of the genus *Burhinus*, two alterations of the current taxonomy are possible. First, *Esacus* Lesson, 1831 could be treated as a junior subjective synonym of *Burhinus* Illiger, 1811 and merged into the latter genus, reducing the number of recognized genera of the Burhinidae to one, in line with some earlier taxonomies (Meinertzhagen, 1924; Condon, 1975; Monroe & Sibley, 1993). Second, the Double-striped and Peruvian thick-knees could be reassigned to another genus, increasing the number of recognized genera of the Burhinidae to three. In such a case, a new genus-group name would be required, as none of the previously proposed burhinid genera is typified by *B. bistriatus* or *B. superciliaris* (Table I). Both solutions would require altering the genus names of two recognized species: *Esacus magnirostris* and *Esacus recurvirostris* in the former case, *Burhinus bistriatus* and *Burhinus superciliaris* in the latter case.

Here, we opt for the latter solution on the following grounds. First, treating *Burhinus grallarius* (Latham, 1801) and *Esacus magnirostris* (Vieillot, 1818) as congeneric would trigger the homonomy issue reviewed in detail by Christidis & Boles (1994, 2008), Hume (1996), and Boyd (2021), which we aim to avoid. Second, although there is no widely accepted threshold above which interspecific differences merit genus-level distinction (Laurin, 2010; Avise & Liu, 2011; Hendricks *et al.*, 2014), there have been attempts to make genus delimitation less arbitrary by basing it on criteria such as estimated divergence times (e.g., Avise & Johns, 1999; Lynch Alfaro *et al.*, 2012) or rigorously quantified character change (e.g., Tschopp *et al.*, 2015), both of which support the generic separation of the Neotropical thick-knees. To demonstrate this, we pruned
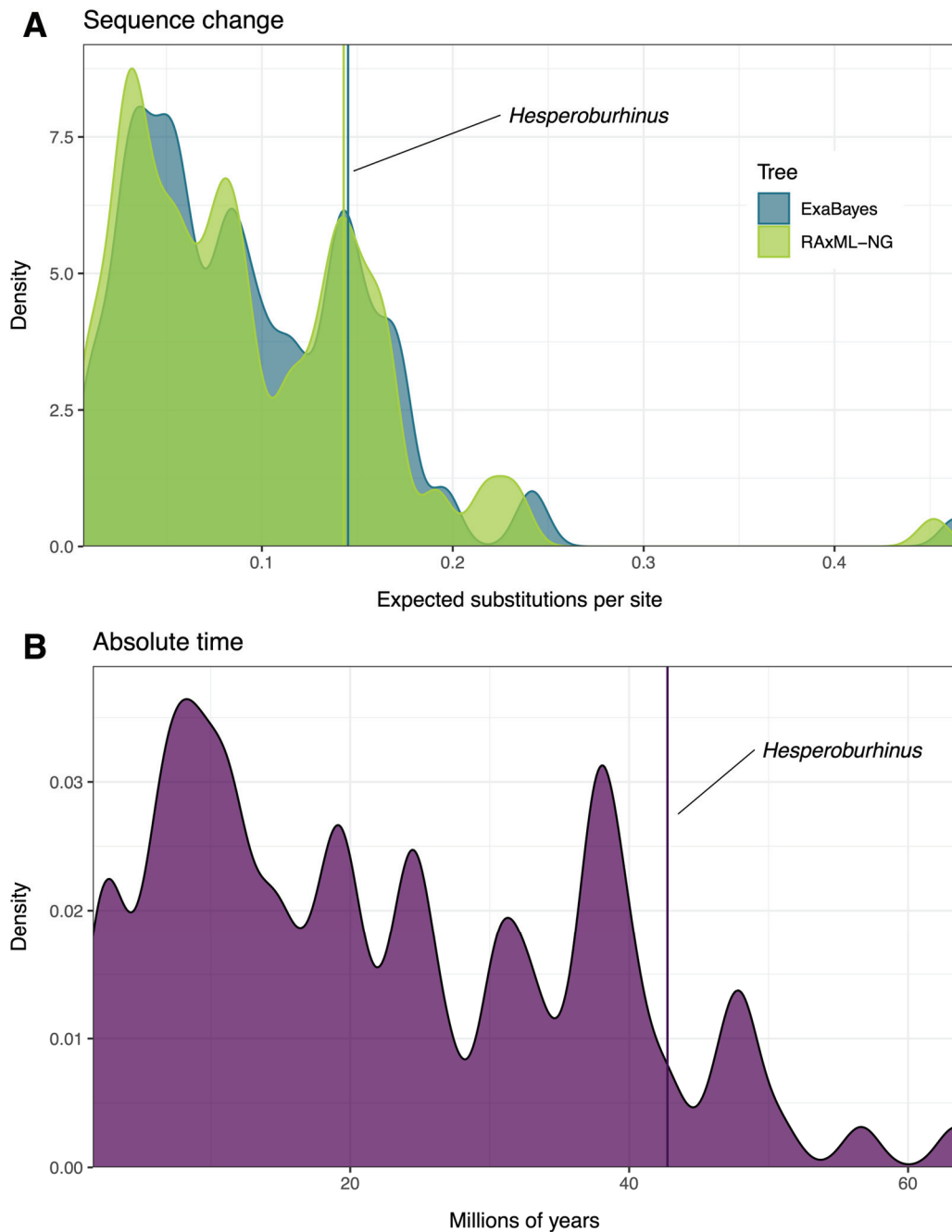
Figure 2. Kernel densities of patristic distances between individual charadriiform genera and their respective sister groups, calculated from A) phylograms with branch lengths in units of expected substitutions per site (Černý & Natale, 2022: Figure 4a, b and Appendix A, Figures A.31, A.33) and B) a time tree with branch lengths in units of calendar time (Černý & Natale 2022: Figure 6). Both metrics show *Hesperoburhinus* to be more distinctive than a majority of currently recognized genera of shorebirds.

the phylograms and the time tree of Černý & Natale (2022) at the genus level and calculated the patristic distance (sum of the lengths of the intervening branches) between each genus and its sister group (Figure 2). Specifically, using the R statistical environment (R Core Team, 2021) and the packages APE (Paradis *et al.*, 2004; Popescu *et al.*, 2012) and PHANGORN (Schliep, 2011), we retained all tips corresponding to monotypic genera, while each monophyletic genus comprising multiple species was replaced by a new tip corresponding to its most recent common ancestor (MRCA). Species and groups of species that could not be assigned to an existing genus without violating its monophyly, such as the (*"B."* *bistriatus* + *"B."* *superciliaris*) clade, were treated as representing genera of their own. Using the R package CASTOR (Louca & Doebeli, 2018), we then calculated the patristic distance between each tip and its sibling, regardless of whether the latter represented another tip (i.e., another genus-level taxon) or an internal node (i.e., the MRCA of a clade comprising multiple genera).

In the maximum-likelihood phylogram of Černý & Natale (2022), the patristic distance of the (*"B."* *bistriatus* + *"B."* *superciliaris*) node from the MRCA of *Esacus* and *Burhinus sensu stricto* (0.143 expected substitutions per site) exceeded both the mean distance (0.093 expected substitutions per site) and the distances associated with 74 of the 96 effective genera (78th percentile; Figure 2A). The results were nearly identical for the Bayesian phylogram, in which the corresponding distance (0.145 expected substitutions per site) exceeded the mean (0.095 expected substitutions per site) as well as the values for 77 of the 95 effective genera (82nd percentile; Figure 2A). The split between New World and Old World burhinids is even more pronounced when evaluated in terms of absolute time. Its age was estimated at 31.7 Ma [confidence interval (CI): 27.5–37.0 Ma] by Černý & Natale (2022), compared to 3.1 Ma (CI: 1.8–4.8 Ma) for the MRCA of *"B."* *bistriatus* and *"B."* *superciliaris*, and 17.6 Ma (CI: 13.9–20.4 Ma) for the MRCA of *Esacus* and *Burhinus sensu stricto* (Figure 1). In effect, the two clades are therefore separated by ~42.7 million years of evolutionary history, an amount almost twice as high as that separating the average charadriiform genus from its sister group (22.5 million years) and higher than the values associated with 86 of the 95 effective genera included in the time tree (92nd percentile; Figure 2B).

As taxonomic decisions based on a phylogenetic analysis of a single dataset may be unsound (Solari *et al.*, 2019), we emphasize that the great antiquity of the split between New World and Old World thick-knees has been borne out by multiple studies. Paton *et al.* (2003) dated it at 35.9 Ma (CI: 23.9–49.0 Ma), and the pseudoposterior distribution of Jetz *et al.*'s (2012) time trees show its mean age to be 33.5 Ma (credibility interval: 24.6–44.1 Ma). Together, published divergence time estimates suggest that treating all extant species of Burhinidae as members of *Burhinus sensu lato* would render the genus older than many shorebird families (Alcidae, Chionidae, Laridae, Rostratulidae, Stercorariidae, Thinocoridae) or even superfamilies (Alcoidea, Haematopodoidea) (Paton *et al.*, 2003; Jetz *et al.*, 2012; Černý & Natale, 2022). Accordingly, we prefer to underscore the great age of the split separating the Neotropical thick-knees from the rest of the clade by erecting a new genus for these taxa.

To identify potential morphological apomorphies of the new genus, we conducted a series of parsimony analyses on a large matrix of phenotypic characters assembled by Livezey (2009), which includes 9 out of 10 extant species of Burhinidae (only omitting *B. indicus*) and whose previous analysis (Livezey, 2010) recovered a clade exclusively comprising *"B."* *bistriatus* and *"B."* *superciliaris*, albeit not in a sister-group relationship to all other burhinids. We excluded all composite terminals representing supraspecific taxa (Alcidae, Larinae, Rynchopinae, Stercorariidae, Sterninae, *Turnix*), which have been shown to present considerable theoretical and empirical problems in morphological phylogenetics, including their potential to bias ancestral state estimation (Yeates, 1995; Prendini, 2001). We further removed *Afrotis*, the more
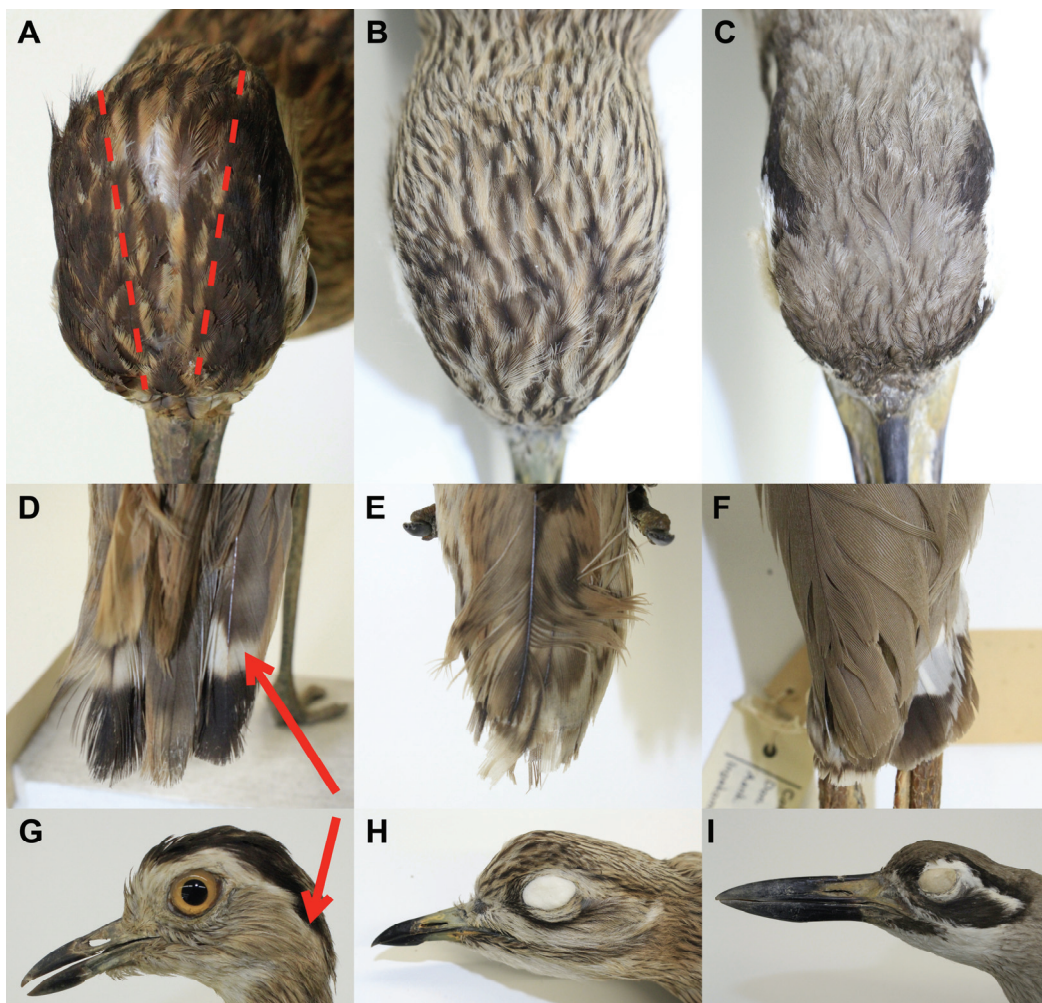
Figure 3. Diagnostic characters of the genus *Hesperoburhinus*, compared to their counterparts in *Burhinus* and *Esacus*. A) The pileum of *Hesperoburhinus bistriatus* (RMNH.AVES.226107) with black lateral stripes bordering a pale median stripe, as compared to the case in B) *Burhinus oedicnemus* (RMNH.AVES.25077) and C) *Esacus magnirostris* (RMNH.AVES.33147). D) The rectrices of *Hesperoburhinus bistriatus* (RMNH.AVES.226103) subterminally marked with a transverse bar of white, as compared to the case in E) *Burhinus oedicnemus* (RMNH.AVES.25077) and F) *Esacus magnirostris* (RMNH.AVES.33147). G) The superciliary stripe of *Hesperoburhinus bistriatus* (RMNH.AVES.226107) extending to the side of the neck, as compared to the case in H) *Burhinus oedicnemus* (RMNH.AVES.25077) and I) *Esacus magnirostris* (RMNH.AVES.33147). Abbreviations: RMNH = Rijksmuseum van Natuurlijke Historie. (Photos: Paul van Els / Naturalis Biodiversity Center, Leiden).

distant of the two non-charadriiform outgroups included in the original matrix, to reduce the risk of long-branch attraction to the outgroup (Sanderson & Shaffer, 2002). Finally, 15 of the species recognized by Livezey (2009, 2010) are considered to be subspecies or morphs of other species by all contemporary taxonomies (Dickinson & Remsen, 2013; Clements *et al.*, 2022; Gill *et al.*, 2022). These were merged with their respective conspecifics, with all differences in character coding rescored as polymorphisms. No burhinid species were affected by these

changes. The resulting matrix included 223 taxa scored for 1106 characters, of which 80 were constant and another 82 autapomorphic.

We first performed a topologically unconstrained parsimony analysis using PAUP* v4.0a168 (Swofford, 2003). Heuristic searches employing the tree bisection-reconnection (TBR) branch-swapping algorithm were run on 100 independent starting trees generated using random stepwise addition, saving a maximum of 500,000 trees. Polymorphisms were distinguished from partial uncertainties (`pset mstaxa = variable`) and 207 of the 388 multistate characters present in the matrix were treated as ordered. After completing the searches, we calculated the 50% majority-rule consensus of the resulting 300 most parsimonious trees (MPTs) with a length of 5300 steps, and subjected it to ancestral state optimization under both accelerated (ACCTRAN) and delayed (DELTRAN) transformation. The topology of the majority-rule tree was largely similar to the original results of Livezey (2010) for charadriiforms in general and identical for burhinids in particular; in both cases, it diverged drastically from the consensus established by molecular phylogenetic studies (Jetz *et al.*, 2012; Burleigh *et al.*, 2015; Černý & Natale, 2022). Nine character changes were unambiguously mapped as synapomorphies of the clade uniting "*B.*" *bistriatus* and "*B.*" *superciliaris*, which was present in the tree but did not form a sister group to the rest of the Burhinidae.

To account for this disagreement with the results of Černý & Natale (2022), we conducted another analysis under the same basic settings but with a backbone constraint comprising all 208 taxa shared between the two datasets. As a result, only 15 species were freely placed in the tree based on their morphological data, including a single burhinid (*Esacus recurvirostris*). After optimizing ancestral states on the 50% majority-rule consensus of the resulting 12 MPTs (length = 6309 steps), the two Neotropical thick-knees were found to share six unambiguous synapomorphies, which formed a strict subset of the nine synapomorphies identified by the unconstrained analysis. It is these six synapomorphies that unambiguously map onto the branch in question in both constrained and unconstrained analyses that we chose for the diagnosis of the new genus. However, an examination of the corresponding character descriptions (Livezey, 2009) revealed that some were poorly formed and did not represent mutually independent characters; we therefore merged these when appropriate. Four of the original synapomorphies (and two of the merged ones) were unique to "*B.*" *bistriatus* and "*B.*" *superciliaris* within the taxon sample of Livezey's (2009, 2010) study, and as such can be considered autapomorphies of the new genus.

In addition to characterizing the new genus using morphological apomorphies, we also followed the protocol of Burns *et al.* (2016) and identified single-nucleotide synapomorphies uniting its two constituent species. We restricted our attention to cytochrome *c* oxidase subunit I (COI) and recombination activating gene 1 (RAG1), which were sampled for the greatest number of burhinid species (6 out of 10) of all the loci used in the phylogenetic analysis of Černý & Natale (2022), and which were the only loci to be sequenced from both the double-striped and Peruvian thick-knees. We subsampled the corresponding alignments to only include the six burhinid species plus their immediate chionidan outgroups (*Chionis albus*, *Chionis minor*, and *Pluvianellus socialis*), and removed any resulting gap-only columns. We then used BioEdit (Hall, 1999) to visualize sequences so that any substitutions (and their position in the sequence) that characterize the two focal species, but not the remaining burhinid and outgroup taxa, could be identified.

Under Article 13.1.1 (ICZN, 1999: 17) and Article 16.1 (ICZN, 1999: 19), we propose a new genus-group name for *Burhinus bistriatus* (Wagler, 1829) and *Burhinus superciliaris* (Tschudi, 1843):

Hesperoburhinus   gen. nov.

Etymology: From the Greek ἕσπερος (*hésperos*), "western", in reference to the genus being the only representative of its family whose range is restricted to the Western Hemisphere; and the pre-existing name *Burhinus*, itself derived from the Greek βοῦς (*boûs*), "ox", and ῥίς, ῥινός (*rhī́s*, *rhīnós*), "nose, of the nose".

Gender: masculine.

Diagnosis: A clade of exclusively Neotropical thick-knees characterized by the following autapomorphies: (1) crown plumage coloration pattern comprised of three broad, longitudinal stripes, with black lateral stripes bordering a pale, grey median stripe that subdivides the entire pileum (Livezey, 2009: character states 551:b, 552:d, 553:b, 614:d; Figure 3A, *cf.* Figure 3B, 3C); (2) rectrices subterminally marked with a narrow transverse bar of white (Livezey, 2009: character state 914:c; Figure 3D, *cf.* Figure 3E, 3F). The genus can be further distinguished from other Burhinidae by superciliary stripes that extend caudally to the side of the neck (Livezey, 2009: character state 566:g; Figure 3G, *cf.* Figure 3H, 3I). Additionally, we have identified 55 single-nucleotide synapomorphies that unite the members of the genus and distinguish them from all other Burhinidae, as well as from outgroup species *Chionis albus*, *C. minor* and *Pluvianellus socialis*. These are, for COI: C54T, C69T, A81T, C105T, T111C, A126G, A147G, A220G, C222T, C231A, A252T, A255T, C316T, C372G, A375T, A402C, C453A, A486G, A552C, C567T, C576T, A630C, A642C, A669T; and for RAG1: G122A, T134C, G135A, A146G, T171C, T288C, T309C, G554A, T495C, T588C, A629G, T713C, A763G, C765T, C958T, G1137C, C1144T, A1371C, C1434T, A1548C, A1557G, C1677G, A1920T, A2025G, A2292G, T2343C, C2361T, T2434C, G2673A, G2793A, G2862A.

Type species, by original designation: *Charadrius bistriatus* Wagler, 1829.

Referred species: "*Oedicnenus*" (= *Oedicnemus*) *superciliaris* Tschudi, 1843.

New combinations: *Hesperoburhinus bistriatus* (Wagler, 1829); *Hesperoburhinus superciliaris* (Tschudi, 1843).

ZooBank LSID for genus: A9C859C6-090A-4734-AEEF-E91E5D105F82

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