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Original Article

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The systematics and nomenclature of the Dodo and the Solitaire (Aves: Columbidae), and an overview of columbid family-group nomina

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ABSTRACT

The Dodo and its extinct sister species, the Solitaire, are iconic exemplars of the destructive capabilities of humanity. These secondarily terrestrial columbids became extinct within a century of their first encounter with humanity. Their rapid extinction, with little material retained in natural history collections, led 18th and some early 19th century naturalists to believe that these aberrant birds were mythological. This meant that the nomenclatural publications in which their scientific nomina were established were based on accounts written before the species became extinct. As such, no type specimens were designated for either the Dodo or the Solitaire. Our in-depth historical overview of both species and associated family-group nomina found that the nominal authority of the Dodo-based family group is not what is reported in the literature. Moreover, our detailed review of the family-group nomina based on columbid genera ensures that the current columbid family-group systematization is valid. Changing nomenclatural norms between the 19th and 20th centuries had a profound impact on Dodo nomenclature; so much so that the Dodo is an example of how pervasive nomenclatural 'ripples' can be and a warning for our current world of multiple nomenclatural codes.

Keywords: Columbidae; Dodo; family group; nomenclature; *Pezophaps*; *Raphus*; validity

INTRODUCTION

The Mauritian Dodo, †*Raphus cucullatus* (Linnaeus, 1758) (Fig. 1), and the Rodrigues Solitaire, †*Pezophaps solitaria* (Gmelin, 1789) (Fig. 2), are textbook examples of evolutionary transitions and of human-made extinctions. Their morphologies were so aberrant that for a time, during the 18th and early 19th centuries, they were considered mythological (Duncan 1828, de Blainville 1835, Strickland 1844, 1848, Hume 2006; see Figs 1, 2). As said by Strickland (1848: 4): 'So rapid and so complete was their extinction that the vague descriptions given of them [Dodo and Solitaire] by early navigators were long regarded as fabulous or exaggerated, and these birds, almost contemporaries of our great-grandfathers, became associated in the minds of many persons with the Griffin and the Phœnix of mythological antiquity'. The existence of the Solitaire, in particular, was long doubted, because for several decades it was known solely from the descriptions by Leguat (1708). Strickland (1844: 324) mentioned that the Solitaire had been considered either 'fictitious, or to be founded on an imperfect description of the true Dodo'.

A series of key papers during the early 19th century 'resurrected' the Dodo and the Solitaire from the realm of the mythological to the material (Duncan 1828, de Blainville 1835, Strickland 1844). The seminal work of Strickland (1848) and Melville (1848), in their shared volume, described in detail the anatomy of specimens still found in European collections at that time, in addition to giving an authoritative account of the history

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Figure 1. Dodo (†*Raphus cucullatus*) mounted composite skeleton [NHMUK S/1988.50.1 (PV A 3302)]. A, cranial view. B, left lateral view.

of the two species. However, it was not until new expeditions to the islands of Mauritius and Rodrigues during the 1860s that new incomplete skeletons of both species were discovered. The skeletal remains discovered in the 'Mare aux Songes' marsh during 1865 (Clark 1866, Hume *et al.* 2009) allowed the Dodo to be described more fully (Owen 1866), and the Solitaire was described by Newton and Newton (1868, 1869) after the Jenner excavations of 1865 discovered skeletal remains (Parish 2013: 234; Hume *et al.* 2015).

There has been renewed interest in the biology of the Dodo and the Solitaire in the 21st century. Studies have explored Dodo body mass (Brassey *et al.* 2016, van Heteren *et al.* 2017) and bone histology (Angst *et al.* 2017), and the endocranial anatomy of both species has been reconstructed digitally from computed tomography scans (Gold *et al.* 2016). New Dodo material has been discovered from Mare aux Songes, and the ecosystem of the Mare aux Songes Lagerstätte has been studied (see Rijsdijk *et al.* 2009, 2015, Meijer *et al.* 2012). The remarkable 'Thirioux Dodos' have been described in-depth, which includes the most complete Dodo skeleton known (Claessens and Hume 2015; Claessens *et al.* 2015). There have even been attempts to reconstruct digitally how these animals would have looked (Rodríguez-Pontes 2016). With each decade, our understanding of these aberrant birds is being revolutionized. To ensure that this work is on a firm basis, we need to ensure that the alpha and beta taxonomy (and accompanying nomenclature) of both species is stable. As we will show, there are no known type specimens for either species. Moreover, given that the use of Dodo-based (i.e. †*Raphus*) family-group nomina is now accepted within columbid systematics, we need to ensure that these names are themselves valid, in order to maintain the nomenclatural stability of extant pigeons and doves. To those ends, we provide an in-depth historical overview of the Dodo, the Solitaire, and the family-group nomina based upon them. We also establish a new nomen to unite both species: †Raphina.

Terminology and nomenclatural background

Before starting our historical overview, it is worth stating that the current rules of zoological nomenclatural are 'relatively' recent and have evolved from prior rules/suggestions made during the 19th century. We wish this to be clear from the outset, in order that readers will not mistake our comments hereafter as undue criticisms of past workers. There have also been dramatic shifts in both systematics (the paradigms and methods used to hypothesize clades) and nomenclature (the establishment of names for said clades, and the rules governing those names) between the

Figure 2. Solitaire (†*Pezophaps solitaria*) mounted skeletons (on display at the Royal College of Surgeons, London, UK in 2023). A, female individual. B, male individual. Note the difference in skeleton size and robusticity between the sexes.

18th and 21st centuries. During the 18th and 19th centuries, the rules and norms of zoological nomenclature were being developed (e.g. Linnaeus 1758, Kirby 1815, Westwood 1836, 1837a, 1837b, Strickland 1837, 1878, Strickland *et al.* 1843, Dall 1878, Société Zoologique de France 1881, Douvillé 1882, American Ornithologists' Union 1886, Blanchard 1889, Bütschli *et al.* 1893), prior to their widespread formulation and promulgation during the 20th century (ICZN 1905, 1961, 1964, 1985, 1999). Moreover, the paradigms used to hypothesize taxa were distinctly different, with the transition from a pre-evolutionary paradigm to an acceptance of paraphyletic groupings and groups united based on shared similarity, which then shifted to our current paradigm based on shared common ancestry and monophyletic groups (for a general overview of thought, see Mayr 1942, 1965, 1982, Hennig 1966, Nelson 1973, de Queiroz 1988, Mishler 2009; and for some clade-specific examples, see Allard *et al.* 1999, Dornburg and Near 2021, Cotterill *et al.* 2014 and the references therein).

The current International Code of Zoological Nomenclature (the Fourth Edition, ICZN 1999, 2003, 2012, 2016; 'Zoological Code' hereafter) is a direct descendent of 'Blanchard's Code' (Blanchard 1889) via the Règles Internationales de la Nomenclature Zoologique [International Rules of Zoological Nomenclature] (ICZN 1905). Raphaël Blanchard, the 'father of International Zoological Nomenclature' (Bock 1994: 33), was the Chair of the nomenclatural committee of the International Congress of Zoology, the first President of the International Committee on Zoological Nomenclature, and the Editor of the French edition of the Règles Internationales. For the first International Congress of Zoology, he wrote an overview of zoological nomenclature and outlined what he believed would be an acceptable set of rules for the international corpus of zoologists ('Blanchard's Code'; Blanchard 1889). 'Blanchard's Code' did not exist in a vacuum, because a plethora of nomenclatural codes for zoology had been proposed during the 19th century, with the earliest comprehensive code being proposed by the British Association for the Advancement of Science ('Strickland's Code').

'Strickland's Code' (Strickland *et al.* 1843) was formulated by a committee of British zoologists and palaeontologists (including famous individuals, such as Charles Darwin and Richard Owen, in addition to Hugh Strickland, who was pivotal in our understanding of the Dodo and the Solitaire), who set down many of the norms we recognize today; norms of the so-called 'Linnean' system of nomenclature, although this is perhaps more accurately called 'Linnean–Westwoodian–Stricklandian' nomenclature (*sensu* Dubois 2011: 4–5). However, there were some important differences between 'Strickland's Code' and the current Zoological Code (ICZN 1999), such as the proposed 'start date' for zoological nomenclature, which in 'Strickland's Code' was 1766, beginning with the publication of the 12th edition of Systema Naturæ (Linnaeus 1766). The ensuing controversy over the 'start date' for zoological nomenclature cost 'Strickland's Code' support amongst zoologists (Linsley and Usinger 1959: 41), with Dall (1878: 15) noting that the starting point used by the British Association had begun 'admitting to recognition some ichthyological works printed between the dates of the tenth and twelfth editions [of Systema Naturæ]'. Other national societies began proposing their own nomenclatural codes, including the American Association for the Advancement of Science (Dall 1878), the Société Zoologique de France (Société Zoologique de France 1881), the American Ornithologists' Union (American Ornithologists' Union 1886), and the Deutsche Zoologische Gesellschaft (Bütschli *et al.* 1893), as did the Congrès international de géologie [International Congress of Geology] (Douvillé 1882). It was 'Blanchard's Code' (Blanchard 1889) and the subsequent Règles Internationales (ICZN 1905) that would begin to bring international stability to zoological nomenclature (for further details, see Linsley and Usinger 1959, Bock 1994).

Zoological nomenclature of the 18th and early 19th centuries did not adhere to the quasi-legal system in place today. The renaming of pre-existing genera and specific epithets was commonplace (particularly up to the 1840s–1850s). Therefore, readers should not be surprised that the principal of priority with regard to nominal authority was not adhered to in Dodo nomenclature during this time period or that the formulation of names does not meet the requirements on the Zoological Code as we understand it today (ICZN 1999). It is also worth noting that when the Dodo and Solitaire were first named (Linnaeus 1766, Gmelin 1789), the concept of nomenclatural types did not exist. Witteveen (2016: 156) credited Westwood (1837a) as the originator of this concept, which then became incorporated into 'Strickland's Code' (and subsequent nomenclatural codes). As such, type specimens were not designated for the Dodo or the Solitaire.

Before continuing, we also need to define the terminology we will be using. We will follow the suggestions and recommendations of Dubois and Fitzhugh. Dubois (2021: 39) noted that, 'the term ***taxonomy*** is traditionally used in two distinct senses, to designate either a scientific discipline, or any scientific classification of organisms produced by this discipline and adopted as valid by taxonomists'. In order to distinguish between both meanings, Dubois (2005: 406) erected the term ergotaxonomy for the latter ('classification used by a given author in a given work', Dubois 2006: 250). To remove any ambiguity, we use the term ergotaxonomy to refer to any 'taxonomic framework' considered valid by their proposer.

We will use the term 'systematics' rather than 'taxonomy' throughout. There is disagreement within the field of evolutionary biology regarding whether taxonomy and systematics are different subfields (e.g. Simpson 1961, Wiley and Lieberman 2011), whether taxonomy is a subdiscipline within systematics (e.g. Michener *et al.* 1970, Dubois 2006, Pavlinov 2013, Winsor 2023 and the references therein), or whether systematics is a subfield of taxonomy (e.g. Toepfer 2011). However, others, such as Mayr and Ashlock (1991) and Fitzhugh (2008), have proposed that taxonomy is a synonym of systematics. We will follow Fitzhugh (2008: 54) and use the term 'systematics' throughout.

We also use the term 'systematization' in preference to 'classification' following Fitzhugh (2008). Fitzhugh (2008: 54) defined classification as the 'segregation of objects into classes based on specified properties', whereas systematization is 'the organization of observations into a system of concepts, in the form of hypotheses, according to theory' (the definitions of these terms given by de Queiroz 1988: 241 was similar). We consider the latter to be the best description of systematics, because both species and 'higher-level' clades are explanatory hypotheses rather than objects (e.g. see Fitzhugh 2005, 2008, Mortimer *et al.* 2021).

Herein, we follow ornithological convention and capitalize English vernacular names of species (Parkes 1978; and the International Ornithological Committee World Bird List v.13.2; https://www.worldbirdnames.org/english-names/spelling-rules/). Moreover, we use the English vernacular names for columbid species that appear in the International

Ornithological Committee World Bird List v.13.2 (https://www.worldbirdnames.org/new/bow/pigeons/), but with the following exceptions: (i) *Didunculus strigirostris* (Jardine, 1845) is referred to as the Samoan Tooth-billed Pigeon, because another species (†*Didunculus placopedetes* Steadman, 2006) was present throughout the islands that constitute the Kingdom of Tonga until ~2850 years ago (Steadman 2006; Worthy and Burley 2020) and was also present on Efate Island, Vanuatu (Worthy *et al.* 2015); and (ii) we generally refer to †*Pezophaps solitaria* as the Solitaire rather than the Rodrigues Solitaire, in order that it is consistent with the use of 'the Dodo' for †*Raphus cucullatus* (i.e. not using Mauritian Dodo). We follow Dubois (2000: 39) in using the term nomen (plural nomina) for any 'scientific name' that is formulated in compliance with a nomenclatural code, which, in this case, is the Zoological Code (ICZN 1999, 2003, 2012, 2016).

Our open nomenclature and synonymy lists follow the recommendations of Richter (1948) (see: Matthews 1973, who outlined them in English, and Becker 2001, who gave a recent overview in German), Sigovini *et al.* (2016), and Horton *et al.* (2021). Finally, we use the dagger (†) symbol in front of nomenclatural nomina that denote extinct taxa (except when they appear in quotations).

MATERIALS AND METHODS

Abbreviations

NHMUK, Natural History Museum, London, UK; NMP, National Museum, Prague, Czech Republic; OUMNH, Oxford University Museum of Natural History, University of Oxford, UK; ZMUK, Royal Zoological Museum, Copenhagen, Denmark.

Nomenclatural history of the Dodo

Nominal authority

In the 10th edition of Systema Naturæ, Linnaeus (1758: 155) lists the oldest binomial for the Dodo that is available under the Zoological Code: †*Struthio cucullatus*. 'Raphus' in Möhring (1752: 58) and †*Struthio cucullatus* in Linnaeus (1758: 155) both have in their synonymy lists 'Cygnus cuculatus' Nieremberg 1635. Note that when we use 'Raphus' without italics we are citing a version of the nomen that is not available under the Zoological Code (i.e. either pre-Linnean, before 1758, or from a text suppressed for nomenclatural purposes by the Commission). Therefore, the genus 'Raphus' in Möhring (1752) and the nominal species *cucullatus* in Linnaeus (1758) are based on the same indications to earlier publications (see Duncan 1828, de Blainville 1835 and Strickland 1848 for an overview), and can therefore be treated as synonyms. Brisson (1760b: 14) followed Möhring when using the genus †*Raphus* (in the Latin genitive case: *Raphi*), as he stated in a footnote: '*Raphus*, nomen à *Moehringio* huic generi inditum' ('*Raphus*, a name given to this genus by Moehringius'). Note that Brisson (1760a, b) used both *Raphus* and *Raphi* for the generic name.

It is clear that neither the genus *Raphus* nor the specific epithet *cucullatus* originated with Linnaeus or Brisson, although under the Zoological Code both Linnaeus and Brisson are the correct nominal authorities. This is attributable to Article 3 of the Zoological Code, which states that the 'starting point' for zoological nomenclature is on 1 January 1758, and two works are deemed to have been published on that date, one of which is that of Linnaeus (1758). Therefore, the 'Raphus' in Möhring (1752: 58) and 'Cygnus cuculatus' in Nieremberg (1635: 231) are not valid under the Zoological Code (note that Nieremberg 1635 spelt 'cuculatus' with one 'l', unlike later authors who used two). The 'Raphus' that appears in the 1758 Dutch translation of Möhring (1752), (Möhring 1758: 44), is also not considered valid because that work was suppressed for nomenclatural purposes by the International Commission on Zoological Nomenclature (the 'Zoological Commission' hereafter) (see Opinion 801 of the ICZN 1967).

Opinion 241 of the ICZN (1954) stated that the Dutch translation of Möhring (1752), (= Möhring 1758) was not valid under the Règles Internationales de la Nomenclature Zoologique (ICZN 1905) and placed it on the Official Index of Rejected Works (note that this opinion was made prior to the publication of the first edition of the current Zoological Code; ICZN 1961). A new submission was made to the 'Zoological Commission' by The Standing Committee on Ornithological Nomenclature (Salomonsen *et al.* 1964) to have Möhring (1758) suppressed for nomenclatural purposes because there was disagreement regarding whether Möhring (1758) was a re-edition of Möhring (1752) or a new work with its own pagination and additions. This resulted in Opinion 801 of the ICZN (1967) and the suppression of Möhring (1758).

Linnaeus (1766), with comments on synonymy and type specimens

In the 12th edition of Systema Naturæ, Linnaeus (1766: 267) proposed a new genus and species for the Dodo: †*Didus ineptus*. In his synonymy list for the species, he listed Brisson's (1760a, b) genus *Raphus*, his previous binomial, †*Struthio cucullatus* Linnaeus, 1758, and works that pre-date 1758 (including 'Cygnus cuculatus' in Nieremberg 1635 and 'Gallus gallinaceus peregrinus' in Clusius 1605). Given the synonymy list in Linnaeus (1766: 267), we consider the following:

(i) The nomenclatural species †*Struthio cucullatus* Linnaeus, 1758 and †*Didus ineptus* Linnaeus, 1766 are objective synonyms.
(ii) The genera †*Raphus* Brisson, 1760b and †*Didus* Linnaeus, 1766 are also objective synonyms. (This opinion matches that of Allen 1910: 329, who considered both genera to be synonymous 'with the same type'.)

The synonymy lists of Linnaeus (1758: 155), Brisson (1760b: 15), and Linnaeus (1766: 267) contained three identical bibliographic references: 'Gallus gallinaceus peregrinus' in Clusius (1605: 99), 'Cygnus cuculatus' in Nieremberg (1635: 231), and Dronte in Bontius (1658: 70). Although the work by Brisson (1760b) contained more bibliographic references (including Möhring 1752), the three bibliographic references that appear in the work by Linnaeus (1758) are all present in the work by Brisson (1760b); therefore, we consider †*Struthio cucullatus* Linnaeus, 1758 and †*Raphus raphus* Brisson, 1760b to be objective synonyms.

It is worth noting that the 'starting date' of zoological nomenclature was contested during the 19th century, and that is why †*Didus ineptus* was used during the 19th century in preference to genus †*Raphus* and the species †*Struthio cucullatus*. 'Strickland's Code' (Strickland *et al.* 1843) proposed the 12th edition of Systema Naturæ (Linnaeus 1766) as the 'start date' for zoological nomenclature, i.e. 1766. This rendered both †*Struthio cucullatus* Linnaeus, 1758 and †*Raphus raphus* Brisson, 1760a, b as unavailable nomina under that nomenclatural code. The first nomenclatural code to use the 10th edition of Systema Naturæ (Linnaeus 1758) as its 'start date' was that of the American Ornithologists' Union (American Ornithologists' Union 1886). The starting date of 1758 for zoological nomenclature was also used by Blanchard (1889; 'Blanchard's Code') and was incorporated into the Règles Internationales (ICZN 1905). This explains why there was a shift to using †*Didus cucullatus* (Rothschild 1907), †*Raphus cucullatus* (Poche 1904, Oudemans 1917), and synonymizing †*Didus* with †*Raphus* (Poche 1904, Allen 1910, Ridgway 1916) during the early 20th century.

Article 72.5.6 of the Zoological Code states that: 'In the case of a nominal species-group taxon based on an illustration or description, or on a bibliographic reference to an illustration or description, the name-bearing type is the specimen or specimens illustrated or described (and not the illustration or description itself)'. Therefore, the type series of †*Struthio cucullatus*, †*Raphus raphus*, and †*Didus ineptus* are those that appear in bibliographic references: Clusius (1605: 99), Nieremberg (1635: 231), and Bontius (1658: 70). The specimens illustrated and/or described therein are therefore the type series of the three nomenclatural species and are the basis for the genera †*Raphus* and †*Didus*. The location of those specimens is unknown.

The 'Gallus gallinaceus peregrinus' of Clusius (1605: 99–100) is based on a drawing from a now lost journal that was executed in 1598 during the voyage of Jacob Cornelis van Neck to the East Indies, in addition to observations of live Dodos by the Dutch sailors of the van Neck voyage, and Clusius' own observations of a partial leg and foot of a Dodo brought back to Leiden and kept at the house of Petrus Pauwius (Hume 2006, Parish 2013). Alas, the whereabouts of the partial leg and foot has been unknown since the 17th century (see Parish 2013: 197). The 'Cygnus cuculatus' that appears in Nieremberg (1635: 231) is largely copied from Clusius (1605) (see Parish 2013: 109). The Dronte of Bontius (1658: 70–71) is a description of the Dodo based on observations from Dutch sailors of unknown Dodo specimens (interestingly, Parish 2013: 114 noted that the author of the Dodo description could in fact be Gulielmus [William] Piso). Therefore, the type series of the Dodo is composed of: (i) the lost partial leg and foot mentioned by Clusius (1605: 100); (ii) the unknown specimens that formed the basis of Bontius' or Piso's (1658: 70–71) description; and (iii) the unknown specimens seen by Dutch sailors on the van Neck voyage that helped to form the basis of Clusius' (1605: 99–100) illustrations and description.

A subsequent type designation for †*Didus ineptus* Linnaeus, 1766 comes from Gray (1870a: 24), who stated: 'The skeleton of the Dodo, forming the type specimen on which Professor Owen has written and published an elaborate memoir, has been restored'. Owen's (1866) discussion of his 'type concept' is a metaphysical one and not as a taxonomic voucher specimen (i.e. a nomenclatural type). Regardless, Gray (1870a) stating that NHMUK PV A 9040 (a composite of multiple individuals) forms the type specimen does not constitute a valid neotype designation under Article 75 of the Zoological Code. As such, the specimen later described by Owen (1872) is not the type specimen of the Dodo.

Syntypes were listed by Mlíkovský *et al.* (2011), Mlíkovský (2012), and Parish (2015). Mlíkovský *et al.* (2011: 140) and Mlíkovský (2012: 105–106) listed a cranial rostrum ('upper beak', NMP P6V-004389) as being a syntype of †*Struthio cucullatus*. Mlíkovský *et al.* (2011) and Mlíkovský (2012) stated that the bony cranial rostrum is apparently the last known element of a Dodo that was kept by Emperor Rudolf II Habsburg (1552–1612), a live individual that was stuffed, possibly around 1609. Therefore, if NMP P6V-004389 is indeed the last remaining part of Emperor Rudolf II's Dodo, it is too old to be one of the specimens forming the basis of Bontius' (1658) description. It also cannot be from the same individual as the partial leg that Clusius (1605) mentioned and described. But could Emperor Rudolf II's Dodo be one of the unknown individuals that the Dutch sailors figured and mentioned and which helped to form the basis Clusius' (1605) description? There is no direct evidence to support that contention, but it is possible.

Parish (2013: 170–171) considered the source of Emperor Rudolf II's Dodo most likely to be Hans Schuurman's fleet that returned to Texel, The Netherlands in April 1603. There are no records of live Dodos reaching Europe from previous expeditions, and the length of those journeys would suggest that Dodos might not have survived (see Parish 2013: 170–171). The source of Clusius' (1605) information were the journals of Van Neck (his first expedition) and the 1603 expedition that returned under Hans Schuurman (Parish 2013: 108). Therefore: (i) the provenance of NMP P6V-004389 is unknown, but it might be part of Emperor Rudolf II's Dodo; (ii) Emperor Rudolf II's Dodo might have been on the expedition that returned to Europe in April 1603; (iii) Clusius' (1605) information on Mauritius was derived, in part, from information on the 1603 expedition; thus (iv) Emperor Rudolf II's Dodo might have been part of the basis for Clusius' (1605) description.

Unfortunately, Clusius (1605) made no mention of a live Dodo returning to The Netherlands and, as pointed out by Parish (2013: 170), a live Dodo is not mentioned in Clusius' posthumous *Curae posteriores* published in 1611. Complicating matters is that the provenance of NMP P6V-004389 is unclear, although it appears definitively on the auction inventory of the Prague Castle collection from 3 January 1782 (see Parish 2013: 185). As such, it is impossible to state definitively that NMP P6V-004389 is, or is not, a syntype of the Dodo. What we can say is that there is no direct evidence to support that conclusion, and until there is, we cannot consider NMP P6V-004389 to be a syntype. Moreover, there is no direct evidence to link any of the oldest known Dodo specimens with a specific collector or to determine their precise time of arrival in Europe (such as the 'Oxford' or 'Tradescant' Dodo; OUMNH ZC-11605; Figs 3, 4).

Parish (2015: 215–218) also listed four syntypes (based on communication from Jan Bolding Kristensen), the first of which, ZMUK AVES-105484, is a complete pelvis discovered in the Mare aux Songes marsh. This specimen cannot be a syntype, because it was not collected until 1865 (Parish 2015: 215).

Figure 3. The Oxford Dodo (†*Raphus cucullatus*) (OUMNH ZC-11605). A, preserved skin in left lateral view. B, skull in left lateral view. C, preserved skin in right lateral view. Scale bar: 3 cm.

Figure 4. Drawings of the Oxford Dodo (†*Raphus cucullatus*) (OUMNH ZC-11605). A, preserved skin in right lateral view. B, skull in left lateral view. C, preserved skin in right lateral view. D, scleral rings. Artwork by Julian Pender Hume.

Also listed are a skull (ZMUK AVES-105485) and two casts of the 'Prague beak' (ZMUK AVES-105487 and ZMUK AVES-10588). Even if the 'Prague beak' is a syntype, its casts would not 'inherit' its type status. The origin of the Copenhagen skull (ZMUK AVES-105485) is unknown. It was rediscovered in 1840 (see Reinhardt 1842, 1843), and its provenance is disputed (see Hume 2006: 80–81; Parish 2013: 189–194). However, there is no evidence to suggest that it came to Europe in one of the two Dutch expeditions that Clusius (1605) used as the basis for his description. Therefore, none of the specimens Parish (2015) listed as syntypes are, in fact, type specimens. This means that there is not a valid type specimen for the Dodo.

Nomenclatural history of the Solitaire

Although the nomenclatural history of the Solitaire (†*Pezophaps solitaria*) is straightforward, unfortunately, like the Dodo, no type specimen has been designated. The binomial †*Didus solitarius* was established by Gmelin (1789: 728–729) for the Solitaire. The name was not based on physical specimens; instead, it was based on two bibliographic references: Leguat (1708) and Latham (1785). Latham (1785: 3–4) referred to the species as the 'Solitary Dodo', and his comments were based solely on the descriptions given by Leguat (1708: 98–104). Therefore, as noted by Strickland (1848: 46), who established the genus †*Pezophaps* for the species, 'Leguat's bird is the type of the "*Didus solitarius*" of systematists'.

François Leguat was the commander of a group of French Protestant refugees, who, in 1691, were the first humans to settle on the island of Rodrigues (Strickland 1848: 46). Leguat's observations are therefore of live birds in their natural habitat (Leguat 1708; Fig. 5). Unfortunately, the exact individuals he observed are unknown, and thus, the type specimens of the species are also unknown.

The Nazarene Dodos

The Nazarene Dodo, †*Didus nazarenus* Gmelin, 1789, has a confusing history because the nomen has been applied to individuals from both Mauritius and Rodrigues (i.e. to both the Dodo and the Solitaire). The phrase Nazarene Dodo was first used by Latham (1785: 4–5) to denote the animals François Cauche called 'Oiseaux de Nazaret' during his voyage to Mauritius (Cauche 1651) (see Parish 2012: 6, for a list of the pre-Latham names used for the Nazarene Dodo). Latham (1785: 1–3) referred to †*Didus ineptus* as the Hooded Dodo. The primary difference between the two dodo species was that the Nazarene Dodo was said by Cauche to have three pes digits, whereas the Hooded Dodo had four. Latham (1785) stated that both species were from Mauritius, whereas the Solitary Dodo (named after Leguat's 1708 'Le Solitaire') was from Rodrigues. Gmelin (1789: 728–729) created the binomials †*Didus nazarenus* for the Nazarene Dodo and †*Didus solitarius* for the Solitary Dodo. Latham (1790: 662–663) used Gmelin's binomials for the three

Figure 5. Artistic life reconstruction of the solitaire (†*Pezophaps solitaria*). This is the only known drawing of a solitaire based on living specimens in their natural habitat. Artwork from Leguat (1708).

'species' of Dodos, but otherwise the nomen †*D. nazarenus* was largely unused thereafter.

Strickland (1848: 21–22) considered †*D. nazarenus* to be a 'phantom-species', based on Cauche's conjectures and possible confusion with the Cassowary, such as the presence of three toes and the hypothesized lack of a tongue ('which latter character was at that time falsely attributed to the Cassowary'). In Strickland's (1848: 21) opinion, 'There can be no doubt that the bird described by Cauche was the Dodo'. Unfortunately, the nomen was resurrected by Bartlett (1854 [1851]) for a different animal. (Note that, although written in 1851, the volume in which Bartlett's work was contained was not published until 1854, see Duncan 1937.)

Prior to the late 19th century, there was little material of the Dodo and the Solitaire in European collections (e.g. see Duncan 1828, de Blainville 1835, Strickland 1844, 1848). As such, after the publication of 'The Dodo and its Kindred' (Melville 1848, Strickland 1848), there was confusion about the presence of two distinct morphs from Rodrigues. Based on isolated limb bones, two distinct morphologies of Rodrigues Solitaires were recognized: one large and robust, and another smaller and more gracile. Bartlett (1854: 284), however, considered there to be three species from Rodrigues: one 'which was apparently identical with the *Dodo* (*Didus ineptus*) of the Mauritius; a second, which was well described under the name of *Solitaire*; and a third, which was much larger than either of the above'. For the third, much larger species, Bartlett (1854: 284) assigned Gmelin's nomen †*D. nazarenus*. The specimens Bartlett's (1854: 283) referral was based on were figured in plate XV of Melville (1848) and Strickland (1848), and these are, indeed, the large robust morph. Bartlett's (1854: 281) belief that the true Dodo (†*Didus ineptus*) was present on both Mauritius and Rodrigues comes from his acceptance of Sir Thomas Herbert's account that the species was on both islands.

Strickland (1859: 191) came to believe that the two morphs represented distinct species. He considered the larger robust morph to be Leguat's Solitaire (= †*Didus solitarius* and †*Pezophaps solitaria*), and Strickland provisionally established the nomen †*Pezophaps minor* for the smaller morph. Note that there has been some confusion about exactly when the nomen †*Pezophaps minor* was established. The article in which Strickland provisionally erected †*P. minor* was published in August 1859. However, the nomen had been known to members of the Zoological Society of London since 1851, because it appears in a Society report dating August–December 1851 (Mitchell 1852: 19). The gap between Strickland reading to the Zoological Society and final publication explains why †*Pezophaps minor* appears in synonymy lists from before 1859 (e.g. Bonaparte 1854b in Bonaparte 1850–1865).

In the footnote accompanying †*Pezophaps minor*, Strickland discussed Bartlett (1854). Strickland (1859: 191) dismissed the possibility of three species having been present on Rodrigues, stating: 'I have, however, endeavoured to prove that they belong to *two* species only, neither of which can be referred to the Mauritian *D. ineptus*, nor to the *D. nazarenus*, which is merely a synonym of that bird, based on the erroneous description of Cauche'. Strickland (1859: 190) did consider the possibility that the two morphs were the result of sexual dimorphism. However, given that he had demonstrated earlier that the Dodo and Solitaire were pigeons (Strickland 1848), Strickland (1859: 190) noted that in extant columbids 'the males and females present very nearly the same dimensions'. Therefore, he did not consider the sexual dimorphism hypothesis likely.

This resulted in two distinct ergotaxonomies (= systematizations or 'taxonomic classifications') for the perceived 'didine' bird species of Rodrigues during the 1850s–1870s. The larger and smaller species were either referred to as †*Didus nazarenus* and †*D. solitarius*, respectively (Bartlett 1854), or as †*Pezophaps solitaria* and †*P. minor*, respectively (Strickland 1859, Owen 1872). Note that Newton (1865) followed Bartlett, but used †*Pezophaps solitaria* instead of †*D. solitarius*. Unfortunately, this resulted in the nomen †*Pezophaps solitaria* being used in both ergotaxonomies and, confusingly, for both morphs.

It was not until the Jenner excavations of 1866, during which complete skeletons of male and female Solitaires were discovered, that the confusion ended (Hume *et al.* 2015), after which, only one species of 'didine' bird from Rodrigues was recognized (Newton and Newton 1868, 1869). †*Pezophaps solitaria* was thereafter known to be a sexually dimorphic species, with adult male individuals being noticeably larger and more robust than adult female individuals (Newton and Newton 1869, Owen 1878, Newton and Clark 1879, Lydekker 1891; see Fig. 2).

The White Dodo and Réunion Solitaire

The Nazarene Dodos of Mauritius and Rodrigues were not the only species subsequently shown not to exist; there was also the White Dodo and Solitaire of Réunion Island. Hume and Cheke (2004) have already given a detailed overview of how an extinct species of quasi-flightless ibis became confused with the Dodo. In short, there was confusion about the identity of a white, large-bodied bird species, thought to be flightless, from the island of Bourbon (now called Réunion). Strickland (1848: 59) noted that 'Bourbon [Réunion] was formerly inhabited by a brevipennate bird called the solitaire, whose white or light yellow plumage and woodcock-like beak proves it to have been distinct from the dodo of Mauritius and from the so-called solitaire of Rodrigues'. Hume and Cheke (2004: 59) noted that during the 1850s, the life reconstructions of the 'Réunion White Dodo' were not actually of a Dodo, but of an animal resembling an ibis or a stork. Such reconstructions came later, in the 1860s, once the white bird of Réunion had been linked to the Dodo.

A scientific nomen for this mysterious species was established by de Sélys-Longchamps (1848: 293), who called it †*Apterornis solitarius* (alongside two more extinct bird species from the Mascarene Islands: †*Apterornis cærulescens* and †*Apterornis bonasia*). He placed †*Apterornis solitarius* within the 'Famille *Dididées*' alongside †*Didus ineptus* (the Dodo) and †*Pezophaps solitaria* (the Solitaire). Therefore, the confusion surrounding the identity of this species continued into the scientific literature. Unfortunately, the confusion became further 'tangled' during the 1850s. Schlegel (1854: 244) referred to the species as †*Didus apterornis*, and Bonaparte (1854b in 1850–1865: 2) established the genus †*Ornithaptera* to replace †*Apterornis*, because it was already preoccupied. However, Bonaparte (1854b in 1850–1865: 2) used the binomial †*Ornithaptera borbonica*. In his synonymy list for †*Ornithaptera borbonica*, Bonaparte

(1854b in 1850–1865: 2) included both †*Apterornis solitarius* de Sélys-Longchamps, 1848 and †*Didus apterornis* Schlegel, 1854.

During the 19th and 20th centuries, different authors suggested that the Réunion 'didine' was a species of Dodo or Solitaire (see the historical overviews by Mourer-Chauviré *et al.* 1995, 1999, Hume and Cheke 2004). Hachisuka (1937), however, believed that there had been two species of 'didine' birds on the island of Réunion, one a 'dodo' and another a 'solitaire'. He applied the previous name to his hypothesized Réunion Solitaire (= †*Ornithaptera solitaria*) and included it in the family †Pezophapidae [*sic*] alongside †*Pezophaps solitaria*. In his †Raphidae, Hachisuka (1937: 71) placed †*Raphus cucullatus* and a new genus and species: †*Victoriornis imperialis*. †*Victoriornis imperalis* Hachisuka, 1937 was his new nomen for the 'White Dodo of Réunion'. Hachisuka's (1937) systematization was based not on specimens but on water colour paintings and the accounts of explorers from 17th and 18th centuries.

Mourer-Chauviré *et al.* (1995, 1999) placed †*Apterornis solitarius* in the genus *Threskiornis* and demonstrated that there had never been a 'Réunion dodo or solitaire'. They instead posited that the bird described by explorers to Réunion had, in fact, been a species of ibis.

Cyanornis and the Dodo species of Schlegel

When de Sélys-Longchamps (1848: 293) established †*Apterornis solitarius*, as noted above, he also created two more nomina for extinct bird species from the Mascarene Islands: †*A. cœrulescens* and †*A. bonasia*. They were also placed in the 'Famille *Dididées*'. Bonaparte (1854b in 1850–1865: 3) established the genus †*Cyanornis* for these species and continued to place them alongside the Dodo and the Solitaire. However, †*Apterornis coerulescens* de Sélys-Longchamps, 1848 is now considered to be an extinct species of swamp hen of the extant genus *Porphyrio* (Olson 1977: 365), whereas †*A. bonasia* de Sélys-Longchamps, 1848 is an extinct species of rail of the genus †*Aphanapteryx* (Olson 1977: 357). The two Dodo species Schlegel (1854) established, †*Didus broeckei* and †*D. herbertii*, are now considered to be subjective junior synonyms of the Red Rail †*Aphanapteryx bonasia* (Olson 1977: 357).

Nomenclatural history of the Dodo family group

The first Didus-based family group

Illiger (1811: 243–244) established Columbidae (as Columbini) for the genus *Columba*, and Inepti on page 245 for the genus †*Didus*. Illiger (1811: 245) used Linnaeus' (1766) genus *Didus* for the Dodo, although he did list Brisson's (1760a, b) genus †*Raphus* as a synonym. Interestingly, instead of using the generic name as the stem for his family group, Illiger (1811) used the specific epithet of †*Didus ineptus* to form his family group for the Dodo. Under Article 11.7.1.1 of the Zoological Code, Inepti is invalid, because the stem of the family group was based not on a generic name but on a specific epithet. Therefore, the oldest known family-group nomen for the Dodo is not valid under the Zoological Code (also noted by Mlíkovský, 2000: 79). Use of Inepti as a family-group nomen did not seem to become widespread in the literature, because we can find few instances of its usage. Notable exceptions include von Eichwald (1831: 257) and Kaup (1836: 232–234).

The Didus-based family group in the 1830s and 1840s

During the 1830s and 1840s, family-group nomina specifically for the Dodo began to appear in systematic ergotaxonomies (= 'taxonomic classifications'). These were always based on Linnaeus' genus †*Didus*. The oldest occurrence we can find is by Swainson (1835: 239), with the use of †Didiadæ, and on the same page the Dodo is mentioned explicitly. This original spelling is incorrect as per the Zoological Code (Article 32.5.3.1), namely the suffix should be -idae not -iadæ. This was corrected to †Dididæ by Swainson (1836: 286). Although †*Didus* was not was included explicitly in his †Dididæ, in the index Swainson (1836: 364) stated that 'Dodo, affinities of' occurred on page 286. Therefore, we consider that to be an indication that the genus †*Didus* was indeed within †Dididæ, and therefore it fulfils Article 11.7.1.1 of the Zoological Code.

The subfamily †Didinæ, placed within Vulturidæ, was used by de la Fresnaye (1839: 193–194). The genus †*Didus* and †*Didus ineptus* were included explicitly in the subfamily. Lesson (1842: column 1036) used a different nomen based on the genus †*Didus*: †Didusideae. The genus †*Didus*, and †*Raphus* attributed to Möhring, were included explicitly, as was the species †*Didus ineptus*.

The systematizations of the 1830s and early 1840s either followed Linnaeus (1758, 1766) in placing the Dodo in the same group as the Ostrich (such as Gray 1840, Lesson 1842, Bonaparte 1842a, b) or allied the Dodo with vultures (such as Swainson 1837, de la Fresnaye 1839). Both Gray (1840: 64) and Bonaparte (1842a: 14, 89, 1842b: 65) included either †Dididae or †Didinae (family or subfamily rank) in their ergotaxonomies to contain the Dodo, and placed it within the same order as the Ostrich. Bonaparte's earlier systematic frameworks lacked a family group specifically for the Dodo (e.g. Bonaparte 1841). In their seminal shared volume, Strickland (1848) and Melville (1848) used Didinæ to contain both the Dodo and the Solitaire, and placed it within the pigeon and dove family Columbidæ. This ergotaxonomy was followed by Gray (1848: 482–483, in Gray 1844–1849), and subsequently, the inclusion of the Dodo and the Solitaire alongside pigeons has become the prevailing systematic opinion.

The †Raphus-based family group

Unfortunately, the nominal authority of the †*Raphus*-based family group is confusing. The first to use the †*Raphus*-based family group was Poche (1904: 500). Poche (1904: 500) also demonstrated that the oldest available specific epithet for the Dodo is *cucullatus* Linnaeus, 1758, and that should be used instead of *ineptus* Linnaeus, 1766 (reflecting the shift in the 'starting date' of zoological nomenclature from 1766 to 1758, as outlined above). Poche (1904) was therefore the first to recommend the binomial †*Raphus cucullatus* be used for the Dodo. Poche (1904) based his †Raphidae on the 1758 Dutch translation of the work by Möhring (1752). At that time, Möhring (1758) had not been suppressed for nomenclatural purposes by the Zoological Commission, which did not occur until the publication of Opinion 801 (see ICZN 1967).

The validity of †Raphidae Poche, 1904 has been challenged (Bock 1994), and that challenge has also been disputed (Mlíkovský 2000). Bock (1994: 94–95) argued that Poche's

†Raphidae was invalid, owing to Poche (1904: 500) basing his family group on †'Raphus' Möhring, 1752 not †*Raphus* Brisson, 1760b. Given that the former is not an available genus (because it was established prior to 1758), the associated family group would also not be valid (under Article 11.7.1.1 of the Zoological Code). However, Poche (1904: 495) discussed the 1758 Dutch translation of the work by Möhring (1752), not the 1752 work.

Article 11.7.1.5 of the Zoological Code states that family-group names when first published must 'not be based on a genus-group name that has been suppressed by the Commission'. Möhring (1758) was suppressed by the Zoological Commission (ICZN 1967), thereby making the genus †'Raphus' contained therein unavailable of nomenclatural purposes. However, when Poche (1904) established †Raphidae, the genus †'Raphus' Möhring, 1758 was available. Because Poche (1904) treated the genus and his family group as being valid, Mlíkovský (2000: 81) contended that Poche's †Raphidae is, in fact, valid under Article 11.5.2 of the Zoological Code. We disagree.

Mlíkovský's (2000: 81) interpretation of Article 11.5.2 is that because: (i) Poche (1904) used the genus †*Raphus* for a taxon he considered to be valid, and (ii) he attributed it to an earlier work with a clear bibliographic reference (Möhring 1758: 44), Poche (1904) made the genus †*Raphus* available (with Poche being the nominal authority). However, the genus †'Raphus' Möhring, 1758 was valid in 1904. It did not become invalid until 1967. Article 39 of the Zoological Code is clear that: 'The name of a family-group taxon is invalid if the name of its type genus is a junior homonym or has been totally or partially suppressed by the Commission'. This means that when †'Raphus' Möhring, 1758 was rendered invalid by Opinion 801 (ICZN 1967), †Raphidae Poche, 1904 also became invalid.

The oldest valid †*Raphus*-based family group is often quoted to be authored by Wetmore (1930: 5). However, Wetmore (1930) simply stated that †Raphidae included 'Dodos, Solitaires' and did not state whether the genus †*Raphus* Brisson, 1760b or †'Raphus' Möhring, (1752 or 1758) was stem for his family group. Although, since Peters (1937), the genus †*Raphus* Brisson, 1760b has been considered the basis for Dodo nomenclature, Oudemans (1917) also used the binomen †*Raphus cucullatus* and the family-group nomen †Raphidae. Oudemans (1917: 6) stated: 'BRISSON 1760 vindt, dat de Dodo in een apart genus moet geplaast worden: *Raphus*[2]) (de oudste genusnaam!)' ['BRISSON 1760 thinks, that the Dodo should be placed in a separate genus: *Raphus*[2]) (the oldest genus name!)']. In footnote 2, which accompanies †*Raphus*, Oudemans (1917: 6) stated: 'Ontleend aan MOEHRING 1752; dit werk heb ik niet kunnen raadplegen' ['Taken from MOEHRING 1752; I have not been able to consult this work']. On page 101, Oudemans (1917) explicitly used 'BRISS'. after †*Raphus*. As such, the †*Raphus cucullatus* and †Raphidae of Oudemans (1917) was based on Brisson (1760b), and therefore he should be considered the nominal authority of the †*Raphus*-based †Raphidae, not Wetmore (1930).

Note that Mlíkovský (2000: 81) argued that, under Article 39, precedence should be given to †Raphidae Wetmore, 1930 rather than †Raphidae Poche, 1904. This is owing to Mlíkovský's opinion that †'Raphus' Poche, 1904 is a junior homonym of †*Raphus* Brisson, 1760. However, as we outline above, Poche (1904) did not establish an available genus †*Raphus*, because Möhring (1758) and the names contained therein were not suppressed in 1904. Therefore, an appeal to Article 11.5 does not apply in this situation.

Pigeon family-group nomina

The higher-level systematics and nomenclature of pigeons, doves, the Dodo, and the Solitaire have long been in flux (see Sibley and Ahlquist 1990: 422–425, for an overview). Here, we will focus on those systematizations that included the Dodo alongside extant pigeons (also see Supporting Information, Appendix S1). Note that we retain the ligature 'æ' from the original publications rather than correcting them to 'ae'. This is done solely to preserve original formatting.

As noted above, some of the early ergotaxonomies (= systematizations or 'taxonomic classifications') united the Dodo with the struthionids/struthiones (following Linnaeus). Gray (1840: 64) provisionally included the subfamily †Didinæ in the family Struthionidæ (in the order Cursores). Extant pigeons were in the order Gyrantes, in the family Columbidæ (which contained four subfamilies: Treroninæ, Columbinæ, Turturinæ, and Gourinæ) (Gray 1840: 57–59). Bonaparte (1842a: 14, 1842b: 65) had a very similar ergotaxonomy to Gray (1840), where the family †Dididae (with the subfamily †Didinae) was within the order Struthiones. Extant pigeons were in the order Columbae, within the family Columbidae (which contained three subfamilies: Columbinae, Treroninae, and Gourinae) (Bonaparte 1842a: 13, 1842b: 64).

Bonaparte's (1854a: 139–140) later ergotaxonomies still had the Dodo and the Solitaire in a separate order from pigeons. The Dodo and the Solitaire were in the order †Inepti, with a single family, †Didídæ. Within †Didídæ he had two subfamilies: †Epyornithinæ (to contain the Réunion 'dodo and solitaire': †*Ornithaptera* and †*Cyanornis*, alongside †*Æpyornis* Geoffroy Saint-Hilaire, 1851a, b; note that the original paper was published in two different journals, with one accompanied by an additional note, Geoffroy Saint-Hilaire 1851c) and †Didinæ (containing †*Didus* and †*Pezophaps*). Extant pigeons and doves were within the order Columbæ, within which there were five families. The first family was Didunculidæ, which had the sole subfamily Didunculinæ. The second family was Treronidæ, which had three subfamilies: Treroninæ, Ptilopodinæ, and Alectraenadinæ. The third family, Columbidæ, had six subfamilies: Lopholaeminæ [*sic*], Carpophaginæ, Columbinæ (with two tribes, Columbeæ and Macropygieæ), Turturinæ, Zenaidinæ, and Phapinæ. The fourth family, Calliænadidæ [*sic*], contained the sole subfamily Calliænadinae [*sic*]. The final family, Gouridæ, included the subfamily Gourinæ.

Bonaparte (1854b in Bonaparte 1850–1865) had a similar ergotaxonomy to his earlier publication. Again, the Dodo and the Solitaire were united in the order †Inepti, with a single family, †Dididæ. Within †Dididae he had two subfamilies: Epyornithinae (now containing only †*Æpyornis*) and †Didinae (containing †*Didus* and †*Pezophaps*, in addition to the Réunion 'dodo and solitaire' †*Ornithaptera* and †*Cyanornis*). Extant pigeons and doves were again within the order Columbæ, with five families. The first family was Didunculidae, including the sole subfamily Didunculinae. The second family was Treronidae, which had four subfamilies: Treroninae, Ptilopodinae (with two tribes: Ptilopodeae and Chrysaeneae), Alectraenadinae, and Carpophaginae. The third family, Columbidae, had five subfamilies: Lopholaeminae, Columbinae (with three tribes: Palumbeae, Columbeae, and Macropygieae), Turturinae, Zenaidinae, and Phapinae (with three tribes: Phapeae, Chalcophapeae, and Geopelieae). The fourth family, Caloenadidae, contained the sole subfamily Calaenadinae [*sic*]. The final family, Gouridae, included the subfamily Gourinae.

Gray's latter ergotaxonomy (Gray, 1848 in Gray 1844–1849, 1870b) united dodos and pigeons in the order Columbæ. Within Columbidæ, he had five subfamilies: Columbinæ, Treroninæ, Gourinæ, Didunculidæ, and †Didinæ. By the 1870s, Gray's ergotaxonomy had changed slightly (Gray 1870b), whereby he raised Didunculidæ and †Didinæ to the family rank. This resulted in three families: †Dididæ (which had a sole subfamily, †Didinæ, and a sole species, the Dodo), Columbidæ (which had three subfamilies: Columbinæ, Treroninæ, and Gourinæ), and Didunculidæ (with the subfamily Didunculinæ). The systematization of Elliot (1885) was similar, with the Dodo, Solitaire, and extant pigeons united in the order Columbæ. Elliot had five families: †Didiidæ (for the Dodo and the Solitaire), Columbidæ, Carpophagidæ, Gouridæ, and Didunculidæ.

An important individual in columbid nomenclature and systematization is Reichenbach. The publication dates for Reichenbach's work are, in the words of Bock (1994: 21): 'a major nomenclatural headache'. There were numerous, undated short contributions, in addition to larger works that had sections written at different times (even different decades, see Meyer 1879, Bock 1994). The situation is complicated further by online versions of Reichenbach's work often having the wrong publication date(s). It is also worth noting that: (i) Reichenbach amended the spelling of several pigeon generic names (such as *Geopelia* to *Geopeleia*), and (ii) he used the -inae suffix for nomina at the family, subfamily, and below subfamily ranks (at what we today would call the tribe and subtribe ranks). The text and plates within the work by Reichenbach (1849–1853) were completed at different times. According to Meyer (1879), the plates with columbid nomina were published in June 1850, whereas the text was published in October 1852. At the top of plate 22 (XXII) there is Palumbinae and Treroninae, and at the top of plate 23 (XXIII) is Peristerinae. It is not possible to determine what nomenclatural rank they were established at, but we can assume that they were not meant to be at the family level, because none of them appears in the 1852 text. On plate 22, *Palumbus* Kaup, 1829 does not appear, but *Treron* Vieillot, 1816 does, while *Peristera* Swainson, 1827 appears on plate 23. However, we can assume Palumbinae was established for *Palumbus*, because the genus appears in the 1852 text. We can therefore consider Reichenbach 1851 in Reichenbach (1849–1853) as the nominal authority of the *Palumbus*-based family group. Interestingly, in his 1852 ergotaxonomy, Reichenbach united the Dodo with *Goura* Stephens, 1819, in the family Gourinae [*sic*]. Note that although both Temminck (1813: 377) and Vieillot (1816: 49) used Goura prior to Stephens (1819), they did not use it as a generic name.

Reichenbach (1862: 13–160) later created an expansive ergotaxonomy for columbids. Reichenbach (1862) also used, for what we today would call the subtribe rank, the -eae and -rae suffices. In his 1862 text, Reichenbach united dodos and pigeons in Columbariæ, alongside taxa now included in Cracidae and Megapodidae. The Dodo and Solitaire were united with modern cracids (in the family Alectorinae), while extant columbids were placed in the families Columbinae and Peristerinae. The internal ergotaxonomy of these families is complicated by Reichenbach's use of the -inae suffix at all ranks, thus, we summarize them in Supporting Information, Appendix S1.

Sundevall (1873 in Sundevall 1872–1873: 97–101) united the Dodo and pigeons in the cohors Peristeroïdeæ. He had three families: the first was Didinæ, which included the Dodo (†*Didus*) and the extant genus *Didunculus* Jardine, 1845 (for a discussion on the correct nominal authority of this genus, see Bruce and Bahr 2020). All other extant pigeons were placed in the families Columbinæ and Megapeliinæ. Salvadori (1893) united dodos and pigeons in the order Columbæ, within which Salvadori had two suborders. The first, called †Didi, contained the family †Dididæ (for the Dodo and the Solitaire). The second suborder, also called Columbæ, contained five families for extant pigeons and doves: Treronidæ (containing the subfamilies Treroninæ, Ptilopodinæ, and Carpophaginæ), Columbidæ (containing the subfamilies Columbinæ, Macropygiinæ, and †Ectopistinæ), Peristeridæ (containing the subfamilies Zenaidinæ, Turturinæ, Geopeliinæ, Peristerinæ, Phabinæ, Geotrygoninæ, and Calœnadinæ), Gouridæ, and Didunculidæ. Sharpe's (1899) systematization was identical to that of Salvadori (1893), differing only in Sharpe's use of Columbiformes rather than Columbæ for the name of the order.

Martin (1904) also united the Dodo, the Solitaire, and extant pigeons in the order Columbiformes, with the same two suborders: †Didi and Columbae. Interestingly, he had two families in his suborder †Didi, †Dididae and †Pezophabidae, for the Dodo and the Solitaire, respectively. Extant pigeons were all placed in the suborder Columbae, with five families within: Columbidae (with the subfamilies Columbinae and Caloenadinae), Peristeridae (with the subfamilies Peristerinae, Phabinae, and Ptilopodinae), Treronidae (with the subfamily Treroninae), Carpophagidae (with the subfamilies Carpophaginae, Gourinae, and Otidiphabinae), and Didunculidae (with the subfamily Didunculinae). Peters (1937) simplified the systematics and nomenclature of pigeons, uniting dodos and pigeons in the order Columbiformes, within which he had two families, †Raphidae (for the Dodo and Solitaire) and Columbidae (for all other pigeons and doves). Peters' Columbidae had four subfamilies: Treroninae, Columbinae, Goürinae [*sic*], and Didunculinae.

Verheyen (1957), however, proposed a very different systematization of pigeons. Within the order Columbiformes, he had three families. The first was Caloenididae, within which there was three subfamilies: Caloenidinae, Goürinae [*sic*], and †Raphinae (which had two tribes, †Raphini and †Pezophabini, for the Dodo and Solitaire, respectively). The second pigeon family was Duculidae, containing five subfamilies: Ptilinopinae (containing the tribes Ptilinopini and Alectroenini), Megaloprepiinae, Tréroninae [*sic*], Didunculinae, and Duculinae (containing the tribes Duculini and Hemiphagini). The final pigeon family was Columbidae, which had eight subfamilies: Columbinae (containing the tribes Columbini, Macropygiini, Chalcophabini, and Oenini), Claravisinae [*sic*], Zenaidinae, Geotrygoninae, Starnoeninae, Turturinae (containing the tribes Turturini, Phabini, Geopeliini, Ocyphabini, and Cosmopeliini), Gallicolumbinae (containing the tribes Gallicolumbini, Geophabini, Leucosarciini, and Trugonini), and Otidiphabinae. In comparison to other pigeon and dove ergotaxonomies, Verheyen's (1957) was far more extensive. It also placed the Dodo and the Solitaire directly within the flighted columbiform radiation, uniting them with the Nicobar Pigeon *Caloenas nicobarica* (Linnaeus, 1758) and the crowned pigeons (the genus *Goura*).

Although based on comparative osteology, Verheyen's ergotaxonomy was not broadly accepted. For Goodwin (1959: 3), who prefaced his comments that he did not feel competent to criticize Verheyen's work because it was based on osteology, some of Verheyen's decisions were 'so contrary to the evidence from external taxonomic characters and behaviour-patterns that I hesitate to follow his conclusions without further evidence'. Johnston (1962: 69) was also hesitant to use Verheyen's ergotaxonomy, noting that it was based on a sample size of only 20 species. Johnston (1962: 69) agreed with Goodwin (1959) and concluded that, 'I cannot accept Verheyen's taxonomy without a great deal of additional evidence'. Unfortunately, this meant that the hypothesis uniting the Dodo and the Solitaire within the flighted columbiforms, and alongside the genera *Caloenas* Gray, 1840 and *Goura* specifically, did not gain traction. This has proved to be unfortunate, because that grouping has been supported consistently by molecular-based phylogenetic analyses (see Close relatives of the Dodo and the Solitaire).

The ergotaxonomy of Brodkorb (1971) had two families within the suborder Columbae (within the order Columbiformes). †Raphidae united the Dodo and the Solitaire, while all extant volant pigeons and doves were within Columbidae (which had three subfamilies: Columbinae, Gourinae, and Ptilinopinae). In contrast, the ergotaxonomy of Wolter (1975) had eight families within the order Columbiformes. The first family was †Raphidae, containing the subfamilies †Pezophabinae (for †*Pezophaps solitaria*) and †Raphinae (for both †*Raphus cucullatus* and the 'White Dodo' †*Raphus solitarius*). The other seven families contained extant species: Caloenadidae, Gouridae, Otidiphabidae, Columbidae, Duculidae, Treronidae, and Didunculidae.

Janoo (1996: fig. 7) created a hypothetical branching diagram of columbiform relationships. Columbiformes was composed of a polytomy of Pteroclidae (the sandgrouses), †Raphidae (containing the subfamilies †Raphinae and †Pezophabinae, for the Dodo and the Solitaire, respectively), and Columbidae. Columbidae was composed of a polytomy of five subgroups: Didunculidae, Treroninae, (Columbinae + Caloenadinae), (Pha binae + Peristerinae + Ptilopodinae), and (Otidiphabinae + Ca rpophaginae + Gourinae).

Before the molecular phylogenetic revolution, the broadly accepted systematization of Columbidae (e.g. Baptista *et al.* 1997) had five extant subfamilies: Columbinae ('typical' pigeons, 181 species), Otidiphabinae (containing only the Pheasant Pigeon), Gourinae (crowned pigeons, composed of only the genus *Goura*), Didunculinae (Samoan Tooth-billed Pigeon, one species), and Treroninae (fruit doves, 123 species). The extinct Dodo and Solitaire were often placed in a separate family (†Raphidae) alongside Columbidae within Columbiformes (e.g. Wetmore 1960, Sibley and Ahlquist 1990, Janoo 1996). Others, such as Cracraft (1981: 699), placed both species within Columbidae, stating that 'the systematic problem here is to identify their close relatives within the columbids'. However, the results of modern phylogenetic analyses were not consistent with any previous ergotaxonomy (e.g. see Janoo 2000, Johnson and Clayton 2000, Shapiro *et al.* 2002, Pereira *et al.* 2007, Fulton *et al.* 2012, Heupink *et al.* 2014, Besnard *et al.* 2016, Nowak *et al.* 2019, Chen *et al.* 2022, Boyd *et al.* 2022, Oliver *et al.* 2023). The 'traditional doves' were never recovered as monophyletic; whereas the Dodo, Solitaire, the crowned pigeons, Samoan Tooth-billed Pigeon, and Pheasant Pigeon were all recovered as members of the 'fruit dove' group (Treroninae *sensu* Baptista *et al.* 1997).

Since the work of Pereira *et al.* (2007), a three-clade subdivision of Columbidae has been recognized, with those clades referred to as Columbinae, Peristerinae, and Raphinae by Dickinson and Remsen Jr (2013: 25, 36). Dickinson and Raty (2015), however, noted that Claravinae should be used instead of Peristerinae, which has been followed since (e.g. Boyd *et al.* 2022). As such, since 2013, there has been an acceptance of using a Dodo-based family-group nomen for the clade that unites species that traditionally were placed in Gourinae, Otidiphabinae, Didunclinae, and Treroninae (*sensu* Baptista *et al.* 1997). Moreover, the tribe Raphini has been used for the clade composed of the Dodo and closely related extant genera: *Caloenas*, *Goura*, *Didunculus*, *Otidiphaps* Gould, 1870, and *Trugon* Gray, 1849 (see Chen *et al.* 2022, Oliver *et al.* 2023).

Close relatives of the Dodo and the Solitaire

A close relationship between the Dodo and the Solitaire has long been suspected (e.g. Latham 1785, 1790, Gmelin 1789, Melville 1848, Strickland 1848) and has been supported by morphology-based (Janoo 2000, Livezey and Zusi 2006, 2007) and molecular-based (Shapiro *et al.* 2002, Pereira *et al.* 2007, Heupink *et al.* 2014, Besnard *et al.* 2016, Soares *et al.* 2016, Bruxaux *et al.* 2018, Oliver *et al.* 2023) phylogenetic analyses. See Livezey (1993: 279–281) for an overview of alternative hypotheses, where the Dodo and the Solitaire are not closely related. However, their relationships with other pigeons have been more contentious, ever since Strickland (1848: 40–41) first hypothesized that the Dodo was not simply 'intermediate' between pigeons and 'gallinaceous' birds (*sensu* Reinhardt), but a 'colossal, brevipennate, frugivorous Pigeon'. Note that we have not been able to find any publication where Reinhardt discusses his hypotheses regarding the 'position' of the Dodo amongst birds (e.g. Reinhardt 1842, 1843); our only conduit to his thoughts come via Strickland (1848) and Owen (1866: 18).

Molecular-based phylogenetic analyses have consistently recovered the genus *Caloenas* as the sister taxon to the Dodo + Solitaire clade (Shapiro *et al.* 2002, Pereira *et al.* 2007, Heupink *et al.* 2014, Besnard *et al.* 2016, Soares *et al.* 2016, Bruxaux *et al.* 2018, Oliver *et al.* 2023). This is true regardless of whether only the Nicobar Pigeon (*Caloenas nicobarica*) or the Nicobar Pigeon and the extinct Spotted Green Pigeon †*Caloenas maculata* (Gmelin, 1789) are included in said analyses. An early molecular-based phylogenetic analysis recovered only a Dodo + Solitaire + *Caloenas* subclade (although *Goura* spp. and *Didunculus strigirostris* were found to be relatively close to this subclade in their topology) (Heupink *et al.* 2014). Six

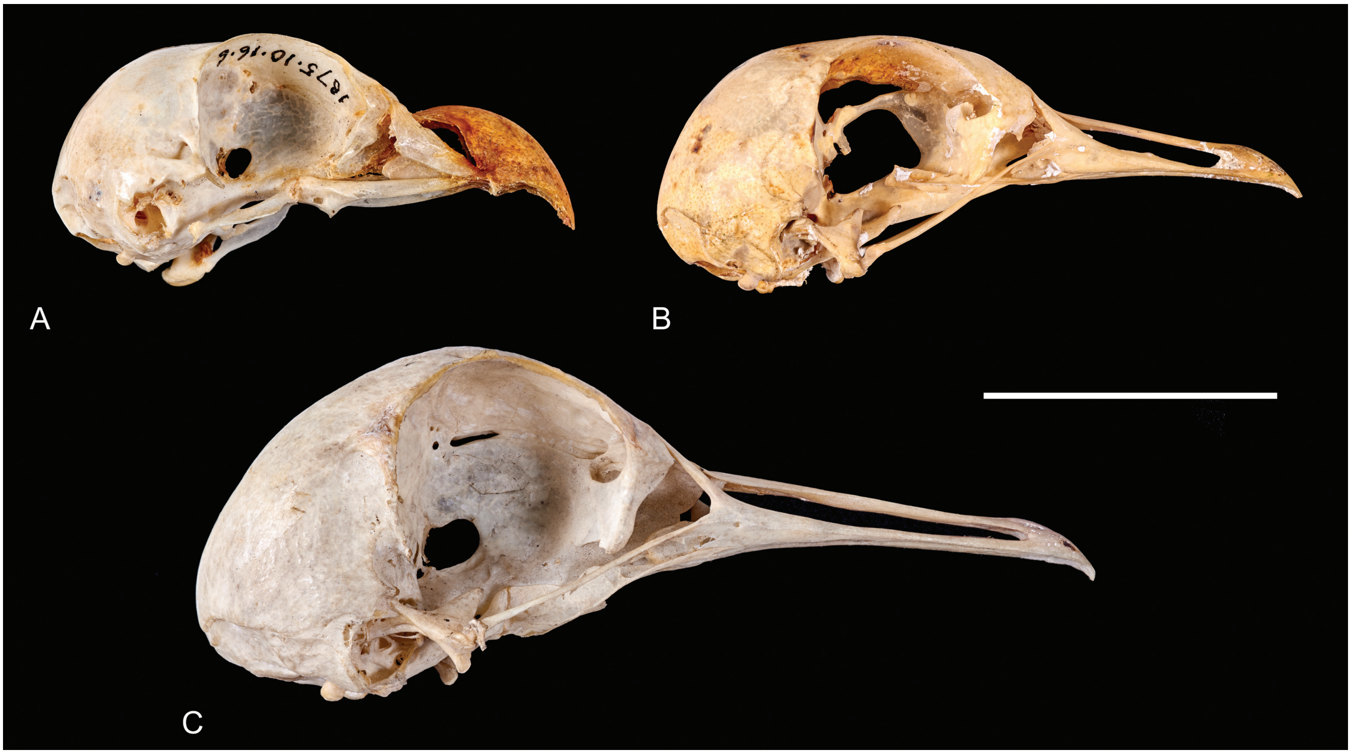

Figure 6. Skulls, in right lateral view, of extant raphine columbids closely related to the Dodo and the Solitaire. A, *Didunculus strigirostris* (NHMUK 1875.10.16.6). B, *Caloenas nicobarica* (NHMUK 1890.11.3.11). C, *Goura cristata* (NHMUK 1891.7.20.40). Scale bar: 3 cm.

studies found the Samoan Tooth-billed Pigeon (*Didunculus strigirostris*), the crowned pigeons (*Goura* spp.), the Nicobar Pigeon (*Caloenas nicobarica*), the Dodo and the Solitaire to form a clade of ground-dwelling island endemics (Shapiro *et al.* 2002, Pereira *et al.* 2007, Besnard *et al.* 2016, Soares *et al.* 2016, Bruxaux *et al.* 2018, Oliver *et al.* 2023). Chen *et al.* (2022) did not include the Solitaire (†*Pezophaps solitaria*) in their analysis, but they still recovered a Dodo + *Caloenas* clade, with *Goura* and *Didunculus* as successive sister taxa.

Interestingly, the only known morphology-based pigeon phylogeny also recovered the Dodo + Solitaire subclade as being united with the genera *Caloenas* and *Goura* (Janoo 2000). However, that analysis found the crowned pigeons (*Goura* spp.) to be the sister taxon to the Dodo and Solitaire subclade, with the Nicobar Pigeon (*Caloenas nicobarica*) being the basal-most member of the clade. The Samoan Tooth-billed Pigeon (*Didunculus strigirostris*) was not found to be closely related to the *Goura*, *Caloenas*, †*Raphus*, and †*Pezophaps* clade. The second morphology-based phylogeny that included a wide sampling of pigeons is that of Livezey and Zusi (2006, 2007). They found *Didunculus* and *Goura* to be successive sister taxa to the †*Raphus* + †*Pezophaps* subclade. The Nicobar Pigeon (*Caloenas nicobarica*) was not included in their analysis.

Regardless of whether a morphology-based or molecular-based approach is taken, every phylogenetic analysis undertaken has found †*Raphus* and †*Pezophaps* to be sister taxa. Moreover, all analyses agree that they form a subclade deep within Columbidae and are not outside of the columbid radiation. And finally, all analyses agree that the †*Raphus* + †*Pezophaps* subclade is a member of a wider clade composed of ground-dwelling island endemic pigeons (although its composition can vary, the genera *Caloenas*, *Goura*, and *Didunculus* are the most consistent close relatives; see Fig. 6).

Columbid family-group nomina

Validity of columbid family-group nomina

Given that Dodo-based family-group nomina are now accepted by columbid workers (see above), we need to ensure that the †*Raphus*-based family group is indeed the oldest available name for the subclades referred to as Raphinae and Raphini (*sensu* Dickinson and Remsen Jr 2013, Chen *et al.* 2022, Oliver *et al.* 2023). To do so, we must consult Article 11.7.1.1 of the Zoological Code (see Dubois and Ohler 2015). Article 11.7.1.1 states that, to be available, a new zoological family group must: be a noun in the nominative plural formed from the stem of an available generic name [Article 29] (indicated either by express reference to the generic name or by inference from its stem, but for family-group names proposed after 1999, see Article 16.2); and the generic name must be a name then used as valid in the new family-group taxon [Articles 63 and 64] (use of the stem alone in forming the name is accepted as evidence that the author used the generic name as valid in the new family-group taxon unless there is evidence to the contrary). Therefore, to be available, a new family-group nomen must be: (i) based on an available genus, and (ii) said genus must be within the new family group. However, new family-group nomina established after 1930 must also satisfy Article 13.1, being accompanied with a description that includes characters that purport to differentiate the taxon, or a bibliographic refence to such a published statement.

Most of the columbid family-group nomina were established before 1930, particularly between 1811 and 1862. Illiger (1811: 243–244) established the first pigeon family-group nomen for the genus *Columba* Linnaeus, 1758, which he referred to as Columbini. Note that this was before Kirby (1815) introduced the -idae (-idæ) suffix into zoological nomenclature. Leach (1819: 66) is the oldest reference to Columbidæ we can find. Therefore, the *Columba*-based family-group nomen is available. As noted above, Illiger (1811: 245) created Inepti for †*Didus ineptus*, but Inepti is not available because it was based on the specific epithet, not the stem of an available generic name (i.e. *Didus*). The valid establishment of the †*Didus*-based family group comes from †Didiadæ of Swainson (1835: 239), who later emended it to †Didіdæ (Swainson 1836: 286).

Also established in 1835 were †Ectopistinæ, Peristerinæ, and Ptilinopinæ. They were created by Selby (1835) as subfamilies within Columbidæ, alongside his use of the subfamily Columbinæ. Note that under Article 36 of the Zoological Code (Principal of Coordination applied to family-group names), when a valid family-group nomen is established, it is considered to be established simultaneously at all ranks within the family group (therefore, the nominal authority of the subfamily Columbinae is not Selby, 1835, but Illiger, 1811). Selby (1835) is the oldest instance of a subfamily rank within Columbidae we can find, because although Bonaparte (1831) is often quoted as using Columbinæ (i.e. Brodkorb 1971), Bonaparte (1831: 53) did not use any ranks below the rank of family for columbids. †Ectopistinæ was created explicitly for †*Ectopistes* Swainson, 1827 (Selby 1835: 166–168), Peristerinæ contained the genus *Peristera* (Selby 1835: 191, 193, 213), and Ptilinopinæ contained the genus *Ptilinopus* Swainson, 1825 (Selby 1835: 119–120, 124–125, 128, 192). As such, the †*Ectopistes*-based and *Ptilinopus*-based family groups are available; note that Selby (1835) used the spelling Ptilinopinæ, not Ptilonopinæ or Ptilinopodinæ (*contra* Brodkorb 1971, Bock 1994). *Contra* Bock (1994), Peristerinæ was used by Selby (1835: 191–193, 213); however, as noted by Oberholser (1899: 203), the pigeon genus *Peristera* Swainson, 1827 is a junior homonym of the mollusc genus *Peristera* Rafinesque, 1815. Under Article 39 of the Zoological Code, homonymy of the type genus renders any family-group nomina based upon it invalid. Also, there does not appear to be a Carpophaginae in Selby (1835), *contra* Bock (1994). Selby (1835: 87) used the plural noun Carpophagæ (alongside the plural noun Ptilinopi for *Ptilinopus*), but we cannot find any family-group nomen for the genus within the text. Finally, as noted by Dickinson and Raty (2015: 188), there have been several reprints of Selby (1835). The most commonly cited reprint is Selby (undated), an edition perhaps from the early 1850s, that is frequently available online. We believe we found one of the 1835 editions, but given how frequently Selby (1835) was reprinted we cannot be entirely sure.

Often, the family group based on the genus *Goura* is considered to have been established by Gray (1840: 58). However, Hodgson (1836: 160) had already used Gourinæ, alongside Columbinæ and Vinaginæ, as subfamilies within Columbidæ. It is clear from the text that he considered the genera *Goura* and *Vinago* Cuvier, 1817 to be valid (Hodgson 1836: 159). As such, the nominal authority for both the *Goura*-based and *Vinago*-based family groups should instead be Hodgson, 1836.

This means that by the end of the 1830s there were six valid family-group nomina: based on *Columba* (Illiger 1811), †*Didus* (Swainson 1835), †*Ectopistes* and *Ptilinopus* (Selby 1835), and *Goura* and *Vinago* (Hodgson 1836). Gray (1840: 57–58) created two new family-group nomina, all as subfamilies within Columbidæ: Treroninæ (Gray 1840: 57), which explicitly contained the genus *Treron*, and Turturinæ (Gray 1840: 58), which explicitly included the genus *Turtur* Boddaert, 1783. Bonaparte (1840: 26) included the subfamily Ptilophyrinae within Columbidae; although Bonaparte did not list the contents of his columbid subfamilies, we can use the stem of the family group to consider it to be based on the genus *Ptilophyrus* Swainson, 1837. Gray, 1848 in Gray (1844–1849: 480–481) established the subfamily Didunculinæ for the genus *Didunculus*. *Gnathodon*, the objective senior synonym of *Didunculus* (see Bruce and Bahr 2020), was also the basis of a family-group nomen: Gnathodontinæ, by Melville (1848: 119). The pigeon genus *Gnathodon* Jardine, 1845 is a junior homonym of the bivalve genus *Gnathodon* Sowerby, 1832 (and possibly other earlier genera, but we have been unable to confirm them ourselves), which renders the pigeon *Gnathodon*-based family group invalid under Article 39 of the Zoological Code. Interestingly, however, Melville (1848: 119) established his Gnathodontinæ specifically for *Didunculus* and not *Gnathodon*. Therefore, it is debatable whether Melville's Gnathodontinæ is valid even under Article 11.7.1.1.

During the 1850s and 1860s, more than a dozen new family-group nomina for extant columbids were established. Reichenbach (1851 in Reichenbach 1849–1853) established the *Palumbus*-based family group (as we discuss above). Le Maout (1853) used the term Lophyriens as one of two 'tribus' within Colombiens (= Columbidae). Lophyriens included only the genus *Lophyrus* Vieillot, 1816 (Le Maout 1853: 306). Under Article 11.7.2 of the Zoological Code, Lophyriens can be considered a valid family group because Bock (1994) latinized it to Lophyrinae.

Bonaparte (1853) established family-group nomina explicitly for the genera *Alectroenas* Gray, 1840 (Alectrænadinæ [*sic*]), *Caloenas* (Calænadidæ and Calænadinæ [*sic*]), *Carpophaga* Selby, 1835 (Carpophaginæ), *Lopholaimus* Gould, 1841 (Lopholaiminæ), *Phaps* Selby, 1835 (Phapinæ [*sic*]), *Ptilopus* Strickland, 1841 (Ptilopodinæ), and *Zenaida* Bonaparte, 1838 (Zenaidinæ). The next year, Bonaparte (1854a) established Macropygieæ for the genus *Macropygia* Swainson, 1837. Finally, Bonaparte (1854b in Bonaparte 1850–1865) established family-group nomina for the genera *Chalcophaps* Gould, 1848 (Chalcophapeae), *Chamaepelia* Swainson, 1827 (Chamaepelieae), *Chrysoena* Bonaparte, 1854c (Chrysaeneae), *Geopelia* Swainson, 1837 (Geopelieae), and *Starnoenas* Bonaparte, 1838 (Starnoenadeae).

Reichenbach (1862) established seven new valid nomina: *Ducula* Hodgson, 1836 (Duculinae), *Geotrygon* Gosse, 1847 (Geotrygoninae), *Myristicivora* Reichenbach, 1853 in Reichenbach (1851–1854) (Myristicivorae, not Mystricivorinae as listed by Bock 1994: 139), *Phapitreron* Bonaparte, 1854c (Phapitreroninae), *Leucotreron* Bonaparte, 1854c (Leucotreroneae), *Osmotreron* Bonaparte, 1854c (Osmotreroneae), and *Zonoenas* Reichenbach, 1853 in Reichenbach (1851–1854) (Zonoeninae). Reichenbach (1862) also created a subfamily-ranked Chlorotreroneae; however, there was no generic name included within called 'Chlorotreron', hence the family group is not valid. The earliest usage of the genus *Chlorotreron* we can find is by Salvadori (1882). Note, *contra* Bock (1994: 139), Reichenbach (1862: 13–160) did not create family-group nomina for the genera *Geophaps* Gray, 1842, *Ocyphaps* Gray, 1842, *Phalacrotreron* Bonaparte, 1854c, or *Sphenocercus* Gray, 1840. Reichenbach (1862) listed both *Geophaps* and *Ocyphaps* within Phapinae [*sic*], *Phalacrotreron* was within an unnamed subgroup of Vinagineae called 'Der Schnabel niedergedrückt' ('The beak depressed'), and *Sphenocercus* was within an unnamed subgroup of Vinagineae called 'Schwanz spitzfederig keilförmig' ('tail pointed-feathered, wedge-shaped'). Sundevall (1873 in Sundevall 1872–1873: 101) established the family Megapeliinae, in which he included the genus *Megapelia* Kaup, 1836. Note that Sundevall (1873 in Sundevall 1872–1873) used the -inae suffix for his families.

In the early 20th century, more columbid family-group nomina were established. Martin (1904: 335, 336, 348) established family-group nomina for the genera *Otidiphaps* and †*Pezophaps*, Otidiphabinae and †Pezophabidae, respectively. McGregor (1909: 42) established the subfamily Muscadivorinæ to include the genera *Muscadivores* Lesson, 1831 and *Ptilocolpa* Bonaparte, 1854c. Richmond (1909: 621) used 'Microgouridæ?' as the family that contained the extinct genus †*Microgoura* Rothschild, 1904. Although Richmond was expressing uncertainty, it was used explicitly to contain the genus †*Microgoura*. We provisionally list Richmond (1909) as the nominal authority, as we have not been able to find an earlier instance of Microgouridae. We raise this issue because Richmond (1917) had been considered the nominal authority of Claraviinae, but as shown by Dickinson and Raty (2015), it was in fact Todd (1913). Todd (1913: 512) established the family-group Claraviinae for the genus *Claravis* Oberholser, 1899, but Dickinson and Raty (2015) noted that the spelling Claravinae should instead be used.

This means that before 1930 the following columbid genera were the basis for valid family-group nomina: *Columba* (Illiger, 1811), †*Ectopistes* (Selby, 1835), *Ptilinopus* (Selby, 1835), †*Didus* (Swainson, 1835), *Goura* (Hodgson, 1836), *Vinago* (Hodgson, 1836), *Treron* (Gray, 1840), *Turtur* (Gray, 1840), *Didunculus* (Gray 1848 in Gray 1844–1849), *Ptilophyrus* (Bonaparte, 1840), *Palumbus* (Reichenbach, 1851 in Reichenbach 1849–1853), *Lophyrus* (Le Maout, 1853), *Alectroenas* (Bonaparte, 1853), *Caloenas* (Bonaparte, 1853), *Carpophaga* (Bonaparte, 1853), *Lopholaimus* (Bonaparte, 1853), *Phaps* (Bonaparte, 1853), *Ptilopus* (Bonaparte, 1853), *Zenaida* (Bonaparte, 1853), *Macropygia* (Bonaparte, 1854a), *Chalcophaps* (Bonaparte, 1854b in Bonaparte 1850–1865), *Chamaepelia* (Bonaparte, 1854b in Bonaparte 1850–1865), *Chrysoena* (Bonaparte, 1854b in Bonaparte 1850–1865), *Geopelia* (Bonaparte, 1854b in Bonaparte 1850–1865), *Starnoenas* (Bonaparte, 1854b in Bonaparte 1850–1865), *Ducula* (Reichenbach, 1862), *Geotrygon* (Reichenbach, 1862), *Myristicivora* (Reichenbach, 1862) *Phapitreron* (Reichenbach, 1862), *Leucotreron* (Reichenbach, 1862), *Osmotreron* (Reichenbach, 1862), *Zonoenas* (Reichenbach, 1862), *Megapelia* (Sundevall, 1873 in Sundevall 1872–1873), *Otidiphaps* (Martin, 1904), †*Pezophaps* (Martin, 1904), *Muscadivores* (McGregor, 1909), †*Microgoura* (Richmond, 1909), *Claravis* (Todd, 1913), and †*Raphus* (Oudemans, 1917).

After 1930, Article 13.2 of the Zoological Code adds the requirement that all available family-group nomina be accompanied by a description or bibliographic reference to such a published statement. However, Article 13.2.1 adds a complication: 'A family-group name first published after 1930 and before 1961 which does not satisfy the provisions of Article 13.1 is available from its original publication only if it was used as valid before 2000, and also was not rejected by an author who, after 1960 and before 2000, expressly applied Article 13 of the then current editions of the Code'. Although Article 13.2.1 requires that all family-group nomina published between 1930 and 1961 must be checked with the wider literature to determine whether they is valid or not, all family-group nomina established post-1961 must be accompanied by a description (including those established herein).

Luckily, the only publication we can find that established new family-group nomina post-1930 is by Verheyen (1957). As noted above, Verheyen's (1957) ergotaxonomy was extensive, including numerous family-group nomina, of which he established nine new nomina explicitly for the genera *Cosmopelia* Sundevall, 1873 in Sundevall (1872–1873) (Cosmopeliini), *Hemiphaga* Bonaparte, 1854c (Hemiphagini), *Gallicolumba* Heck, 1849 (Gallicolumbinae), *Geophaps* (Geophabini), *Leucosarcia* Gould, 1848 (Leucosarciinae), *Megaloprepia* Reichenbach, 1853 in Reichenbach (1851–1854) (Megaloprepiinae), *Ocyphaps* (Ocyphabini), *Oena* Swainson, 1837 (Oenini), and *Trugon* Gray, 1849 (Trugonini). Verheyen (1957: 30–36) provided a list of characters that defined most of the nomina he used in his ergotaxonomy, thus those nomina fulfil Article 13.2.1 of the Zoological Code. The family-group nomina based on *Cosmopelia*, *Gallicolumba*, *Geophaps*, *Leucosarcia*, *Ocyphaps*, and *Oena* explicitly had diagnostic characters listed, and characters that distinguished Megaloprepiinae from Ptilinopinae were given by Verheyen (1957: 32), thus we consider the *Megaloprepia*-based family group available as well. However, no diagnostic characters were provided for the *Trugon*-based family group (Trugonini), with Verheyen (1957: 35) stating: 'anatomie inconnue' ('anatomy unknown'). No diagnostic characters were listed for Hemiphagini either. As such, the *Trugon*- and *Hemiphaga*-based family groups do not fulfil Article 13.2.1 of the Zoological Code and are not available.

The *Claravis*-based family group

One of the consequences of our historical overview of columbid family-group nomina is the realization that within the clade Claravinae, the oldest valid family-group nomen is based on the genus *Chamaepelia* (a subjective junior synonym of *Columbina*). However, Article 35.5 of the Zoological Code allows us to retain Claravinae instead of using Chamaepeliinae. Article 35.5 states that if: 'after 1999 a name in use for a family-group taxon (e.g. for a subfamily) is found to be older than a name in prevailing usage for a taxon at higher rank in the same family-group taxon (e.g. for the family within which the older name is the name of a subfamily) the older name is not to displace the younger name'. The *Chamaepelia*-based family group was established by Bonaparte (1854b in Bonaparte 1850–1865) at a rank below the subfamily,

Table 1. List of family-group nomina validly established under the Zoological Code within Columbinae Illiger, 1811 and Claravinae Todd, 1913 (*sensu* Dickinson and Remsen Jr 2013, Dickinson and Raty 2015). Nominal authors who first used a particular rank are given, and in square brackets [ ] is how the nomen was first written. The oldest nomen within each family group, hence the nominal authority under the Zoological Code, is in bold. The nomenclatural acts written with strikethrough are unavailable.

Stem	Family	Subfamily	Below subfamily[a]
Columbinae: Columbini Illiger, 1811			
Columba	**Illiger, 1811** [Columbini]	Selby, 1835 [Columbinæ]	Bonaparte, 1854a [Columbeæ]
Palumbus		**Reichenbach, 1851**[b] [Palumbinae]	Bonaparte, 1854b [Palumbeae]
Macropygia		Salvadori, 1893 [Macropygiinæ]	**Bonaparte, 1854a** [Macropygieæ]
†*Ectopistes*		**Selby, 1835** [Ectopistinæ]	Ridgway, 1916 [Ectopisteae]
Columbinae: Zenaidini Bonaparte, 1853			
Zenaida	Burmeister, 1856 [Zenaididae]	**Bonaparte, 1853** [Zenaidinæ]	Bonaparte, 1854b [Zenaideae]
Geotrygon		**Reichenbach, 1862**[b] [Geotrygoninae]	
Claravinae Todd, 1913			
Chamaepelia[c]		Reichenbach, 1862[b] [Chamaepeleiinae]	**Bonaparte, 1854b** [Chamaepelieae]
Claravis	Richmond ,1917 [Claraviidae]	**Todd, 1913** [Claraviinae]	
~~*Peristera*~~[d]	Burmeister, 1856 [Peristerinae]	Selby, 1835 [Peristerinæ]	Bonaparte, 1854b [Peristereae]

[a] Bonaparte (1854b in Bonaparte 1850–1865) and Ridgway (1916) referred to the rank below subfamily as 'series'. They used the suffix -eæ.
[b] Reichenbach used the -inae suffix for nomina at the family, subfamily, and below subfamily ranks (at what we today would call the tribe and subtribe ranks). At what we today would call the subtribe rank, he also used the -eae and -rae suffices.
[c] *Chamaepelia* is a subjective junior synonym of *Columbina*. As we show, it does not displace the *Claravis*-based family group owing to Article 35.5 of the Zoological Code.
[d] The nomina based on the genus *Peristera* are not available.

and the *Claravis*-based family group was established (and is currently used) at the subfamily rank. Therefore, Article 35.5 applies in this situation.

The Treron-based family group

Another consequence of our historical overview of columbid family-group nomina is the realization that within the clade Treronini, the oldest valid family-group nomen is based on the genus *Vinago* (a subjective junior synonym of *Treron*). In accordance with Article 40.2 of the Zoological Code, we retain the *Treron*-based family group established by Gray (1840) rather than using the *Vinago*-based family group established by Hodgson (1836), even though the latter has priority. This is because of the conditions set out in Article 40.2, i.e. was the name replaced before 1961, and is the replacement name in prevailing usage? In this instance, both conditions are met, because since Hartert and Goodson (1918: 349) adopted *Treron* over *Vinago*, the synonymy of these two genera has not been challenged. Usage of the *Vinago*-based family group comes from the 19th century, being used by Hodgson (1836) for a subfamily-rank nomen and by Reichenbach (1862) for a below subfamily-rank nomen. The nominal authority of the *Vinago*-based family group was often given as Reichenbach, 1862 (e.g. Bock 1994); however, as we have shown, it was first used by Hodgson (1836). The *Treron*-based family group has been in prevailing usage since the 19th century (see the historical section above and Supporting Information, Appendix S1).

Following recommendation 40A, we cite the nominal authority as: Treronini Gray, 1840 (1836). Under Article 40.2, the date of priority for the *Treron*-based family group is 1836. Under standard avian taxonomic practice, Treronini can be cited as: Treronini Gray.

Ergotaxonomy of Columbidae

We can therefore confirm that the family-group nomina of the current systematization (Dickinson and Remsen Jr 2013, Chen *et al.* 2022, Oliver *et al.* 2023) of pigeons is valid (see Tables 1 and 2). Based on the consensus topology in the work by Oliver *et al.* (2023), the current ergotaxonomy of Columbidae is as follows [also see Supporting Information, Appendix S2; genera they did not recover as monophyletic are indicated with an asterisk (*)]:

Family Columbidae Illiger, 1811
  Subfamily Claravinae Todd, 1913
    Genera: *Claravis*, *Paraclaravis* Sangster *et al.*, 2018, *Columbina* von Spix, 1825, *Metriopelia* Bonaparte, 1855, and *Uropelia* Bonaparte, 1855.

Table 2. List of family-group nomina validly established under the Zoological Code within Raphinae (*sensu* Dickinson and Remsen Jr 2013, Dickinson and Raty 2015). Nominal authors who first used a particular rank are given, and in square brackets [ ] is how the nomen was first written. The oldest nomen within each family group, hence the nominal authority under the Zoological Code, is in bold. The nomenclatural acts written with strikethrough are unavailable.

Stem	Family	Subfamily	Below subfamily[a]
RAPHINI Oudemans, 1917 (1835)			
†*Didus*[b]	**Swainson, 1835** [Didiadæ]	de le Fresnaye, 1839 [Didinæ]	
†*Raphus*[b]	**Oudemans, 1917** [Raphidae]	Verheyen, 1957 [Raphinae]	Verheyen, 1957 [Raphini]
†*Pezophaps*	**Martin, 1904** [Pezophabidae]	Wolters, 1975 [Pezophabinae]	Verheyen, 1957 [Pezophabini]
†*Microgoura*	**Richmond, 1909?** [Microgouridæ]		
Goura	Reichenbach, 1852[c] [Gourinae]	**Hodgson, 1836** [Gourinæ]	
Ptilophyrus		**Bonaparte, 1840** [Ptilophyrinae]	
Lophyrus		**Le Maout, 1853** [Lophyriens]	
Megapelia	**Sundevall, 1873**[d] [Megapeliinæ]		
Didunculus	Bonaparte, 1850 [Didunculidæ]	**Gray, 1848** [Didunculinæ]	
Gnathodon[e]		**Melville, 1848** [Gnathodontinæ]	
Caloenas	Bonaparte, 1854a [Calliænadidae]	**Bonaparte, 1853** [Calænadinæ]	
Otidiphaps		**Martin, 1904** [Otidiphabinae]	
~~*Trugon*~~[f]			Verheyen, 1957 [~~Trugonini~~]
TURTURINI Gray, 1840			
Turtur		**Gray, 1840** [Turturinæ]	Verheyen, 1957 [Turturini]
Oena			**Verheyen, 1957** [Oenini]
Chalcophaps			**Bonaparte, 1854b** [Chalcophapeae]
TRERONINI Gray, 1840 (1836)			
Treron	Bonaparte, 1853 [Treronidæ]	**Gray, 1840** [Treroninæ]	Chen *et al.*, 2022? [Treronini]
Osmotreron			**Reichenbach, 1862**[c] [Osmotreroneae]
Vinago		**Hodgson, 1836** [Vinaginæ]	Reichenbach, 1862[c] [Vinagineae]
PTILINOPINI Selby, 1835			
Ptilinopus		**Selby, 1835** [Ptilinopinæ]	Verheyen, 1957? [Ptilinopini]
~~*Chlorotreron*~~[f]			Reichenbach, 1862[c] [~~Chlorotreroneae~~]
Leucotreron			**Reichenbach, 1862**[c] [Leucotreroneae]
Megaloprepia			**Verheyen, 1957** [Megaloprepiinae]
Ptilopus		**Bonaparte, 1853** [Ptilopodinæ]	Bonaparte, 1854b [Ptilopodeae]

Table 2. Continued

Stem	Family	Subfamily	Below subfamily[a]
Ducula	Verheyen, 1957? [Duculidae]	Verheyen, 1957? [Duculinae]	**Reichenbach, 1862**[c] [Duculinae]
Carpophaga	Elliot, 1885 [Carpophagidæ]	**Bonaparte, 1853** [Carpophaginæ]	Reichenbach, 1862[c] [Carpophaginae]
Myristicivora			**Reichenbach, 1862**[c] [Myristicivorae]
Zonoenas			**Reichenbach, 1862**[c] [Zonoeninae]
Muscadivores		**McGregor, 1909** [Muscadivorinæ]	
~~*Hemiphaga*~~[g]			Verheyen, 1957 [~~Hemiphagini~~]
Phapitreron			**Reichenbach, 1862**[c] [Phapitreroneae]
Lopholaimus		**Bonaparte, 1853** [Lopholaiminæ]	Reichenbach, 1862[c] [Lopholaiminae]
Alectroenas		**Bonaparte, 1853** [Alectrænadinæ]	Verheyen, 1957 [Alectroenini]
Chrysoena			**Bonaparte, 1854b** [Chrysaeneae]
PHABINI Bonaparte, 1853			
Phaps		**Bonaparte, 1853** [Phapinæ]	Bonaparte, 1854b [Phapeae]
Cosmopelia			**Verheyen, 1957** [Cosmopeliini]
Gallicolumba		**Verheyen, 1957** [Gallicolumbinae]	Verheyen, 1957 [Gallicolumbini]
Geopelia		Reichenbach, 1862[c] [Geopeleiinae]	**Bonaparte, 1854b** [Geopelieae]
Geophaps			**Verheyen, 1957** [Geophabini]
Leucosarcia			**Verheyen, 1957** [Leucosarciini]
Ocyphaps			**Verheyen, 1957** [Ocyphabini]
Starnoenas	Burmeister, 1856 [Starnoenidae]	Verheyen, 1957? [Starnoeninae]	**Bonaparte, 1854b** [Starnoenadeae]

[a] Bonaparte (1854b in Bonaparte 1850–1865) referred to the rank below subfamily as 'series'. He used the suffix -eæ.
[b] *Didus* is an objective synonym of *Raphus*.
[c] Reichenbach used the -inae suffix for nomina at the family, subfamily and below subfamily ranks (at what we today would call the tribe and subtribe ranks). At what we today would call the subtribe rank, he also used the -eae and -rae suffices.
[d] Sundevall 1873 in Sundevall (1872–1873) also used the -inae suffix for nomina at the family rank.
[e] The nomina based on the genus *Gnathodon* are not available.
[f] Reichenbach (1862) used a 'Chlorotreron'-based family-group nomen. However, he did not include a genus with that nomen. The earliest version of *Chlorotreron* we can find is Salvadori (1882).
[g] Nomen is not available as per Article 13.2.1 of the Zoological Code.

Subfamily COLUMBINAE Illiger, 1811

Tribe COLUMBINI Illiger, 1811

Genera: *Columba*, †*Ectopistes*, *Macropygia*, *Nesoenas*, *Patagioenas* Reichenbach, 1853 in Reichenbach 1851–1854, *Reinwardtoena* Bonaparte, 1854c, *Spilopelia* Sundevall, 1873 in Sundevall 1872–1873, *Streptopelia*, and *Turacoena* Bonaparte, 1854c.

Tribe ZENAIDINI Bonaparte, 1853

Genera: *Geotrygon*, *Leptotrygon* Banks *et al.*, 2013, *Leptotila* Swainson, 1837, *Zenaida*, and *Zentrygon* Banks *et al.*, 2013.

Subfamily RAPHINAE Oudemans, 1917 (1835)

Tribe PHABINI Bonaparte, 1853

Genera: *Gallicolumba*, *Geopelia*, *Geophaps*, *Henicophaps* Gray, 1862, *Leucosarcia*, *Ocyphaps*, *Pampusana* Bonaparte, 1855, *Petrophassa* Gould, 1841, and *Phaps*.

Tribe Ptilinopini Selby, 1835

Genera: *Alectroenas*, *Drepanoptila* Bonaparte, 1855, *Ducula*, *Gymnophaps* Salvadori, 1874, *Hemiphaga*, *Lopholaimus*, *Phapitreron*, and *Ptilinopus**.

Tribe Raphini Oudemans, 1917 (1835)

Genera: *Caloenas*, *Didunculus*, *Goura*, *Otidiphaps*, †*Pezophaps*, †*Raphus*, and *Trugon*.

Tribe Treronini Gray, 1840 (1836)

Genus: *Treron*.

Tribe Turturini Gray, 1840

Genera: *Chalcophaps*, *Oena*, and *Turtur*.

Note that Oliver *et al.* (2023) did not include three extant genera considered valid by the International Ornithological Committee World Bird List v.13.2 (https://www.worldbirdnames.org/new/bow/pigeons/): *Alopecoenas* Bonaparte, 1855, *Cryptophaps* Salvadori, 1893, and *Starnoenas*, the last of which is currently incertae subfamiliae. Many of the known fossil or extinct genera are likewise not included in this systematization. Based on the molecular-based supertree of Oliver *et al.* (2023, see their supplementary information for full details), the internal relationships of columbids can be summarized in parenthetical form as: Claravinae + (Columbinae + ((Treronini + Turturini) + (Phabini + (Raphini + Ptilinopini)))). Their results suggest that: (i) Claravinae is monophyletic and the sister taxon to an unnamed Columbinae + Raphinae clade; (ii) Columbinae is monophyletic and the sister taxon to Raphinae; and (iii) within Raphinae there is a deep split between the Treronini + Turturini subclade (unnamed) and the Phabini + Raphini + Ptilinopini subclade (unnamed). The analyses of Oliver *et al.* (2023) sampled Columbidae more broadly (with 250 species included) and thus differed in some respects from earlier analyses (such as Pereira *et al.* 2007, from which the three clade subdivision of Columbidae originates).

Homonymy problem

There is a homonymy problem with Raphinae/Raphidae. A *Raphium*-based Raphinae appeared in the work of Karsh (1883: 336), prior to the †*Raphus*-based Raphidae (based on Brisson 1760a, b) that first appeared in work of Oudemans (1917: 100–101). Note that under the Zoological Code, the Principal of Coordination (Article 36.1) results in the nominal authority of a family group spanning all 'ranks' of the group (in this case, Raphidae and Raphinae). *Raphium* Latreille, 1829 is a junior synonym of *Rhaphium* Meigen, 1803 (see O'Hara *et al.* 2011); the latter is still used in the dipteran literature and has its own family-group nomen, Rhaphiinae Bigot, 1852.

Under Article 35.4.1 of the Zoological Code, if a family-group nomen is established upon an unjustified emendation or incorrect spelling of the type genus it must be corrected (unless either the genus or family-group spellings are preserved under Articles 29.5 and 33.2.3.1 or 33.3.1). The correct stem for the *Raphium*-based family group is *Raphi-* not *Raph-* (as shown by the *Rhaphium*-based family-group nomen Rhaphiinae). Therefore, under Article 35.4.1 the *Raphium*-based family group should be corrected to Raphiinae, which removes the homonymy.

RESULTS

SYSTEMATIC ZOOLOGY

Aves Linnaeus, 1758

Columbiformes Latham, 1790 (as Columbæ)

Columbidae Illiger, 1811 (as Columbini)

Raphinae Oudemans, 1917 (1835)

Type genus: †*Raphus* Brisson, 1760b.

Nomenclatural note

In accordance with Article 40.2 of the Zoological Code, we retain the †*Raphus*-based family group established by Oudemans (1917) rather than use the †*Didus*-based family group established by Swainson (1835) even though the latter has priority. This is owing to the conditions set out in Article 40.2, i.e. was the name replaced before 1961, and is the replacement name in prevailing usage? In this instance, both conditions are met, because since Peters (1937: 10) adopted the use of †*Raphus* and Raphidae over †*Didus* and Dididae, the †*Raphus*-based family group has been in prevailing usage ever since (e.g. Verheyen 1957, Wetmore 1960, Brodkorb 1971, Wolters 1975, Sibley and Ahquist 1990, Witmer and Cheke 1991, Bock 1994, Mourer-Chauviré *et al.* 1995, Weber and Krell 1995, Janoo 1996, 2000, Mlíkovský 2000, Livezey and Zusi 2006, 2007, Mlíkovský *et al.* 2011, Dickinson and Remsen Jr 2013, Parish 2013, Heupink *et al.* 2014, van Grouw 2014, Byrkjedal *et al.* 2016, Gold *et al.* 2016, Rodríguez-Pontes 2016, Watanabe *et al.* 2018, Nowak *et al.* 2019, Boyd *et al.* 2022, Chen *et al.* 2022, Oliver *et al.* 2023, Szymański *et al.* 2023, Wyndham and Park 2023).

Following recommendation 40A, we cite the nominal authority as: Raphinae Oudemans 1917 (1835). Under Article 40.2, the date of priority for the †*Raphus*-based family group is 1835, thus it has priority over most other family groups within Columbidae (see above). As we noted above, the correct nominal authority of the †*Raphus*-based family group is Oudemans (1917), not Poche (1904) or Wetmore (1930). Under standard avian taxonomic practice, Raphinae can be cited as: Raphinae Oudemans.

Composition

Following Dickinson and Remsen Jr (2013: 25, 36), the †*Raphus*-based family group has been used to provide nomina for major columbid subclades. Raphinae is currently used to unite the 'traditional' subfamilies Gourinae, Otidiphabinae, Didunculinae, and Treroninae (*sensu* Baptista *et al.* 1997).

Raphini Oudemans, 1917 (1835)

Type genus: †*Raphus* Brisson, 1760b.

Nomenclatural note

As with Raphinae above, we follow recommendation 40A of the Zoological Code and cite the nominal authority of Raphini as: Raphini Oudemans 1917 (1835). Article 36 of the Zoological Code (Principal of Coordination applied to family-group nomina) states that when a name (= nomen) is established at one rank, it is simultaneously established at all other ranks in said family group. All the nomina at these various ranks retain the same nominal authority (authorship and date). Following Article 40.2, the date of priority is 1835. Under standard avian taxonomic practice, Raphini can be cited as: Raphini Oudemans.

Composition

Raphini is currently used to unite the 'traditional' subfamilies Gourinae, Otidiphabinae, and Didunculinae (*sensu* Baptista *et al.* 1997). This clade is composed of the extinct Dodo and Solitaire, alongside the extant genera *Caloenas*, *Goura*, *Didunculus*, *Otidiphaps*, and *Trugon* (see Chen *et al.* 2022, Oliver *et al.* 2023). Note that this clade is more expansive than the subclade characterized as a 'ground-dwelling island endemics' radiation (i.e. †*Raphus*, †*Pezophaps*, *Caloenas*, *Goura*, and *Didunculus*). It is possible that the extinct genera †*Microgoura* and †*Natunaornis* Worthy, 2001 also belong to this subclade.

†**Raphina subtribus nova**

- *1811* Inepti fam. nov.—Illiger, p. 245. [Invalid—stem based on a specific epithet.]
- *1835* Didiadæ fam. nov. [*sic*]—Swainson, p. 239.
- *1836* Dididæ emend. (Swainson)—Swainson, p. 286.
- *1837* Dididæ (Swainson)—Swainson, p. 200.
- *1839* Didinæ subfam. nov. (Swainson)—de la Fresnaye, p. 193–194.
- *1840* Didinæ (Swainson)—Gray, p. 64.
- *1842a* Dididæ (Swainson)—Bonaparte, p. 14, 89.
- *1842a* Didinæ (Swainson)—Bonaparte, p. 14.
- *1842b* Dididæ (Swainson)—Bonaparte, p. 65.
- *1842b* Didinæ (Swainson)—Bonaparte, p. 65.
- *1842* Didusideae fam. nov. [*sic*]—Lesson, column 1036.
- *1854a* Inepti order nov.—Bonaparte [also contained the Réunion 'dodo and solitaire'].
- *1854a* Dididæ (Swainson)—Bonaparte [also contained the Réunion 'dodo and solitaire'].
- *1862* Didinae (Swainson)—Reichenbach, p. 124.
- *1870b* Dididæ (Swainson)—Gray, p. 248.
- *1870b* Didinæ (Swainson)—Gray, p. 248.
- *1904* Raphidae fam. nov.—Poche, p. 500. [Based on Raphus Möhring, 1758—genus is contained in a work suppressed for nomenclatural purposes by the Commission. Unavailable.]
- *1916* Raphi subord. nov.—Ridgway, p. 275–277.
- *1917* Raphidae fam. nov.—Oudemans, p. VI, 98, 100, 101.
- *1971* Raphidae (Oudemans)—Brodkorb, p. 199.
- *1991* Raphidae (Oudemans)—Witmer and Cheke, p. 134.
- *1995* Raphidae (Oudemans)—Weber and Krell, p. 171. [Nominal authority cited was Wetmore 1930.]
- *2013* Raphini (Oudemans)—Parish, p. xi.
- *2014* Raphinae (Oudemans)—van Grouw, p. 300.

ZooBank registration number [urn:lsid: zoobank.org :pub:A79C5ED9-6E44-4DE7-AC70-CD77267FC655].

Type genus: †*Raphus* Brisson, 1760b.

Nomenclatural note

As with Raphinae and Raphini above, we follow recommendation 40A of the Zoological Code and cite the nominal authority of †Raphina as: †Raphina Oudemans, 1917 (1835). Note that although we formally established the new subtribe †Raphina, the correct nominal authority of †Raphina is Oudemans, 1917. This is owing to Article 36 of the Zoological Code (Principal of Coordination applied to family-group nomina). Following Article 40.2, the date of priority is 1835. Under standard avian taxonomic practice, †Raphina can be cited as: †Raphina Oudemans.

Geographical range

The islands of Mauritius and Rodrigues, Mascarene Islands.

Diagnosis

Columbids with the following unique combination of characters: large body size; sexual dimorphism of the skeleton is extreme in the Solitaire and noticeable in the Dodo; basipterygoid processes of the parasphenoid are reduced; pectoral girdle is small relative to volant columbids; pelvic girdle is large relative to volant columbids; scapulocoracoidal angle is ~100°–110°; scapula–coracoid articulation is typically not fused; modal number of sternal ribs is four to five; ulnae have conspicuous papillae remigiales caudales; sternum basin is broad and dorsally concave; sternal carina is ventrally truncated and round, with the cranial margin forming an obtuse angle with the base; the pila carinae, sulcus carinae, and crista lateralis are greatly reduced; sternal trabecula lateralis are distally reduced and essentially straight; sternal trabecula intermedia are absent; sternal fenestra medialis is absent; sternal rostrum spinae externa and interna are greatly reduced; lineae intermusculares of the sternum converge noticeably cranially to the margo caudalis; the cranial portions of the ilia are typically bowed dorsally, meeting medially in a curved arch dorsal to the crista dorsalis of the synsacrum. (The preceding characters were modified from table 2 of Livezey 1993, comparing †*Raphus cucullatus* and †*Pezophaps solitaria* with volant members of Columbidae.) Enlargement of the olfactory bulbs and Wulst. [Based on the endocranial reconstructions by Gold *et al.* (2016), comparing the Dodo and the Solitaire with volant columbids.]

Composition

†*Raphus* and †*Pezophaps*.

Comments

†Raphina is a new nomen for the clade uniting †*Raphus* and †*Pezophaps*, which historically has been referred to as Dididae, Didinae, Raphidae, Raphinae, or Raphini (see historical section above). We chose to establish a new family-group nomen rather than synonymize †*Pezophaps* with †*Raphus*, a possibility that Livezey (1993) and Janoo (2000) previously suggested. Our rationale for this is 2-fold: (ii) both genera are morphologically distinct and can be distinguished readily from one another (see

the diagnoses for both taxa below; the figures in the studies by Meville 1848, Strickland 1848, Livezey 1993, and the discussion on the differences between both taxa by Newton and Newton 1868, 1869, Owen 1872, 1878, Newton and Clark 1879); and (ii) the lack of a fossil record. At present, we cannot distinguish adequately between the following two competing hypotheses: (i) the common ancestor of the Dodo and the Solitaire was volant, with two independent transitions from powered flight to terrestrial cursoriality; or (ii) their common ancestor was also secondarily flightless. Should fossil evidence support hypothesis (i), then retaining †*Raphus* and †*Pezophaps* as distinct genera would reflect parallel evolution of a secondarily terrestrial morphotype. Molecular-based divergence estimates place the separation of †*Raphus* and †*Pezophaps* between 17.6 and 35.9 Mya, which is far older than the estimates for emergence of the islands of Mauritius and Rodrigues, both of which are <10 Mya (Shapiro *et al.* 2002). This would support hypothesis (i). However, as noted by Shapiro *et al.* (2002), other ridges of the Mascarene Plateau would have been above sea level during the divergence estimation period of the Dodo and the Solitaire. Without fossil evidence, we cannot determine raphinan modes of dispersal during this time span or when the transition(s) to secondary cursoriality occurred. However, if new fossil discoveries support hypothesis (ii), then it will be up to future workers to decide whether the genus †*Pezophaps* and our new nomen, †Raphina, are required.

We propose the English vernacular term 'Mascarene giant ground doves' for raphinans (i.e. the Dodo and the Solitaire). Our phraseology is based on that of previous workers, such as Owen (1872: 514, 515, 518), who referred to them as 'Ground-Doves', Verheyen (1957: 30), who referred to them as 'pigeons géants' [giant pigeons], and Worthy (2001: 791), who used the phrase 'Mascarene giant pigeons'. Referring to both species as dodos would be confusing, because the vernacular name 'dodo' has become engrained with †*Raphus cucullatus* in popular culture.

†*Raphus* Brisson, 1760b (as both *Raphus* and *Raphi*)

Type species: †*Raphus raphus* Brisson, 1760b. Type species by monotypy.

The use of †*Raphus raphus* (as *Raphi raphus*, where the genus had the genitive Latin suffix when appearing next to the specific epithet) first appeared in Brisson (1760b: index table). Rothschild (1907: 172–173) synonymized †*Didus ineptus* with †*Struthio cucullatus*, creating the new combination †*Didus cucullatus*. Ridgway (1916: 277) synonymized †*Didus* with †*Raphus*, creating the new combination †*Raphus cucullatus*, but Ridgway did not mention whether Brisson or Möhring was the source of the †*Raphus* he used. The first to use †*Raphus* Brisson, 1760b explicitly was Oudemans (1917: 14, 101), who also used the combination †*Raphus cucullatus*. Peters (1937: 10) synonymized †*Raphus raphus* with †*Struthio cucullatus*, using the combination †*Raphus cucullatus*. Note that Allen (1910: 329) had previously synonymized the genera †*Raphus* and †*Didus*, and stated that †*Raphus* should be used instead of †*Didus*, but he did not mention specific epithets. Allen (1910) is, we believe, the first to use †*Raphus* Brisson, 1760b as the generic name for the Dodo. Poche (1904: 500) was the first to use the binomen †*Raphus cucullatus*, but as outlined above, the genus †'Raphus' used by Poche is no longer valid. This is owing to Poche (1904) using †'Raphus' Möhring, 1758, a name that appears in a suppressed work (see Opinion 801 in ICZN 1967), and not †*Raphus* Brisson, 1760b.

Following recommendation 51G of the Zoological Code, the type species can be referred to as †*Raphus cucullatus* (Linnaeus, 1758) Oudemans, 1917. It can also be written more simply as †*Raphus cucullatus* (Linnaeus, 1758).

Etymology

According to (Jobling 2010: 331): *raphos* was the name given to the Great Bustard by Galenus (190 AD) and was 'probably a misreading of outis or ōtis'. Jobling (2010: 331) also mentioned that *rhaphos* is a 'dubious bird name mentioned by Hesychius in the plural form rhaphoi'. Parish (2012: 6, 2013: 140–141) outlined a possible etymology for *Raphus*, based on Hesychius, that derives from Rhamphios/Rhamphos, by the way of Ramphos, possibly referring to the pelican of Egypt, and in particular its large beak. The origin of the nomen *Raphus* remains unclear.

Diagnosis

Same as the only species (see below).

†*Raphus cucullatus* (Linnaeus, 1758)

(Figs 1, 3, 4)

- 1605 Gallus gallinaceus peregrinus (pre-Linnean)—Clusius, p. 99–101, figured on p. 100.
- 1635 Cygnus cuculatus (pre-Linnean)—Nieremberg, p. 231, figured on p. 231.
- *1656* Dodar (pre-Linnean)—Tradescant, p. 4.
- 1658 Dronte (pre-Linnean)—Bontius, p. 70–71, figured on p. 70.
- 1752 Raphus (pre-Linnean)—Möhring, p. 58.
- *1758* Raphus (work suppressed for nomenclatural purposes by the Commission)—Möhring, p. 44.
- *1758 Struthio cucullatus* sp. nov.—Linnaeus, p. 155.
- *1760b Raphi raphus* gen. et sp. nov.—Brisson, p. 14–15 (generic name had genitive suffix when used as a binomial).
- 1766 *Didus ineptus* gen. et sp. nov.—Linnaeus, p. 267.
- 1785 Hooded Dodo—Latham, p. 1–3, plate LXX.
- *1785* Nazarene Dodo—Latham, p. 4–5.
- *1789 Didus ineptus* Linnaeus—Gmelin, p. 728.
- *1789 Didus nazarenus* sp. nov.—Gmelin, p. 729.
- *1790 Didus ineptus* Linnaeus—Latham, p. 662.
- *1790 Didus nazarenus* Gmelin—Latham, p. 663.
- *1811 Didus ineptus* Linnaeus—Illiger, p. 245.
- 1828 *Didus ineptus* Linnaeus—Duncan, p. 554–566, figs 1–3.
- 1835 *Didus ineptus* Linnaeus—de Blainville, p. 1–36, plates 1–4.
- *1839 Didus ineptus* Linnaeus—de la Fresnaye, p. 194.
- *1840 Didus ineptus* Linnaeus—Gray, p. 64.
- *1842 Didus ineptus* Linnaeus—Bonaparte, p. 89.
- *1842 Didus ineptus* Linnaeus—Lesson, column 1036.

- *1844 Didus ineptus* Linnaeus—Strickland, p. 324.
- 1848 *Didus ineptus* Linnaeus—Strickland, p. 7–45, plates 1, 5, 6, 8, 9, 11, 12.
- 1848 *Didus ineptus* Linnaeus—Melville, p. 71–112, plates 1, 5, 6, 8, 9, 11, 12.
- 1854 *Didus ineptus* Linnaeus—Bartlett, p. 280–284, plate XLV (fig. 3). [Published in 1854.]
- *1854b Didus ineptus* Linnaeus—Bonaparte, p. 2.
- *1854b Didus nazarenus* Gmelin—Bonaparte, p. 2–3.
- 1859 *Didus ineptus* Linnaeus—Strickland, p. 187, 195–196.
- *1862 Didus ineptus* Linnaeus—Reichenbach, p. 125–128.
- *1862 Didus nazarenus* Gmelin—Reichenbach, p. 128.
- *1868 Didus ineptus* Linnaeus—Newton and Newton, p. 428–431.
- *1869 Didus ineptus* Linnaeus—Newton and Newton, p. 327, 331–350.
- *1870b Didus ineptus* Linnaeus—Gray, p. 248.
- *1878 Didus ineptus* Linnaeus—Owen, p. 87–96.
- 1872 *Didus ineptus* Linnaeus—Owen, p. 513–523, plates LXIV, LXV, LXVI (figs 8–11, 14–17).
- 1891 *Didus ineptus* Linnaeus—Lydekker, p. 129–130, fig. 31.
- *1893 Didus ineptus* Linnaeus—Sharpe, p. 632–635.
- *1904* 'Raphus' *cucullatus* (Linnaeus) comb. nov.—Poche, p. 500. ['Raphus' Möhring 1758—a work that was later suppressed by the Commission in 1967.]
- 1907 *Didus cucullatus* (Linnaeus) comb. nov.—Rothschild, p. 172–173, plate 24.
- *1916 Raphus cucullatus* (Linnaeus)—Ridgway, p. 277. [Does not state which *Raphus* was used.]
- *1917 Raphus cucullatus* (Linnaeus) comb. nov.—Oudemans, p. 14, 101. [*Raphus* Brisson, 1760b was used.]
- *1937 Raphus cucullatus* (Linnaeus)—Peters, p. 10. [*Raphus* Brisson, 1760b was used.]
- *1957 Raphus cucullatus* (Linnaeus)—Verheyen, p. 3, 6, 17, 19, 21, 24, 30.
- *1971 Raphus cucullatus* (Linnaeus)—Brodkorb, p. 199–200.
- *1975 Raphus cucullatus* (Linnaeus)—Wolters, p. 43.
- 1989 *Raphus cucullatus* (Linnaeus)—Brom and Prins, p. 233–245, plates 1–5.
- *1990 Raphus cucullatus* (Linnaeus)—Sibley and Ahquist, p. 421.
- *1991 Raphus cucullatus* (Linnaeus)—Witmer and Cheke, p. 134.
- 1993 *Raphus cucullatus* (Linnaeus)—Kitchner, p. 279–299, figs 1–3, 8–10.
- 1993 *Raphus cucullatus* (Linnaeus)—Livezey, p. 247–282, plate 1 (fig. 2a).
- 1996 *Raphus cucullatus* (Linnaeus)—Janoo, p. 57–75, figs 1–5, 7.
- 2000 *Raphus cucullatus* (Linnaeus)—Janoo, p. 323, 325–327, fig. 1.
- *2001 Raphus cucullatus* (Linnaeus)—Worthy, p. 766.
- *2002 Raphus cucullatus* (Linnaeus)—Shapiro *et al.*, p. 1683.
- 2003 *Raphus cucullatus* (Linnaeus)—Roberts and Solow, p. 245, fig. 1.
- 2005 *Raphus cucullatus* (Linnaeus)—Janoo, p. 167–178, fig. 2.
- *2006 Raphus cucullatus* (Linnaeus)—Cheke, p. 155–157.
- *2007 Raphus cucullatus* (Linnaeus)—Pereira *et al.*, p. 656–658, 660, 662, 663, 665, 667, 669.
- 2008 *Raphus cucullatus* (Linnaeus)—Cheke and Hume, p. 26, 50, 162, 400, plate.
- 2009 *Raphus cucullatus* (Linnaeus)—Rijsdijk *et al.*, p. 14, fig. 3G.
- *2011 Struthio cucullatus* Linnaeus—Mlíkovský, p. 140.
- 2012 *Raphus cucullatus* (Linnaeus)—Meijer *et al.*, p. 177, figs 4–6.
- 2012 *Raphus cucullatus* (Linnaeus)—Mlíkovský, p. 105–106, fig. 10.
- *2012 Raphus cucullatus* (Linnaeus)—Roberts, p. 1478–1480.
- 2013 *Raphus cucullatus* (Linnaeus)—Parish, [numerous occurrences].
- *2014 Raphus cucullatus* (Linnaeus)—Heupink *et al.*, p. 1, 3.
- *2014 Raphus cucullatus* (Linnaeus)—van Grouw, p. 291, 300.
- 2015 *Raphus cucullatus* (Linnaeus)—Claesson and Hume, p. 21, figs 2, 4–10.
- 2015 *Raphus cucullatus* (Linnaeus)—Claessons *et al.*, p. 29, figs 1–9, 11–65.
- 2015 *Raphus cucullatus* (Linnaeus)—Rijsdijk *et al.*, p. 4, figs 1, 3, 6–7.
- 2016 *Raphus cucullatus* (Linnaeus)—Brassey *et al.*, p. 1–3, 5, 7–14, fig. 3.
- *2016 Raphus cucullatus* (Linnaeus)—Besnard *et al.*, p. 76–78.
- *2016 Raphus cucullatus* (Linnaeus)—Byrkjedal *et al.*, p. 199.
- 2016 *Raphus cucullatus* (Linnaeus)—Gold *et al.*, p. 950–961, figs 2A, 3A, 4A, 5, 6A, 7A, 8A.
- 2016 *Raphus cucullatus* (Linnaeus)—Rodríguez-Pontes, p. 398, fig. 8.
- *2016 Raphus cucullatus* (Linnaeus)—Soares *et al.*, p. 1–3, 5.
- 2017 *Raphus cucullatus* (Linnaeus)—Angst *et al.*, p. 1–8, figs 1–5.
- 2017 *Raphus cucullatus* (Linnaeus)—van Heteren *et al.*, p. 1–15, fig. 1.
- *2018 Raphus cucullatus* (Linnaeus)—Bruxaux *et al.*, p. 250, 254.
- *2020 Raphus cucullatus* (Linnaeus)—Cheke and Parish, p. 1–12.
- 2021 *Raphus cucullatus* (Linnaeus)—Warnett *et al.*, p. 2247–2255, figs 1–6.
- *2022 Raphus cucullatus* (Linnaeus)—Chen *et al.*, p. 1005, 1011.

Type specimen

No type specimen has been designated formally for †*Raphus cucullatus* (the Mauritian Dodo, or simply the Dodo). Several syntypes have been postulated (see Mlíkovský *et al.* 2011, Mlíkovský 2012, Parish 2015), but, as discussed above, there is no direct evidence that any of those specimens form part of the original type series. Alas, we cannot locate any members of the original type series, which, as we stated above, is based upon: (i) the lost partial leg and foot brought to Europe (Clusius 1605: 100); (ii) the unknown individuals that Bontius' (1658: 70–71) description was based upon; and (iii) the unknown individuals that Dutch sailors saw during the van Neck voyage, which, in part, formed the basis of Clusius' (1605: 99–100) illustrations and description. As such, we cannot designate a lectotype.

At present, we cannot formally designate a neotype for †*Raphus cucullatus*. In order to be fully compliant with Article 75 of the Zoological Code, a neotype designation cannot be 'an end in itself, or a matter of curatorial routine, and any such neotype designation is invalid' (Article 75.2), and 'there is an exceptional need' (Article 75.3). There is no exceptional need for a neotype for the Dodo. As we have shown above, only one raphinan species is known from the Island of Mauritius, and there is no nomenclatural or systematic confusion for said species. Should fossil raphinan remains be discovered in Mauritius, it might be worth revisiting the typification of the Dodo.

Locality

Island of Mauritius, Mascarene Islands. Janoo (2005: 172) stated that the type locality was 'Type locality: Mauritius, Plaisance, Grand Port (Lydekker, 1891); Mare aux Songes (Lambrecht, 1933)'. However, no further information is presented, nor was a type specimen mentioned.

Etymology

'Hooded Dodo'. The specific epithet, *cucullatus*, is from the Late Latin for hooded (Jobling 2010: 124). The first usage of *cucullatus* for the Dodo, was as 'Cygnus cuculatus' by Nieremberg (1635), in pre-Linnean literature (hence why the binomial is not written in italics). Note, Nieremberg (1635) used one 'l' (= cuculatus) not two (= cucullatus) as later authors did.

Geographical range

Island of Mauritius, Mascarene Islands. Extinct since the 17th century, although precisely when is still subject to debate (see Roberts and Sollow 2003, Hume *et al.* 2004, Mlíkovský 2004, Cheke 2006, Cheke and Hume 2008, Roberts 2013, Cheke and Parish 2020). The IUCN Red List of Threatened Species has 1662 as the year last seen, with individuals considered to have been the last of the species killed on the islet of île d'Ambre in 1662 (BirdLife International 2016a).

Referred specimens

See Parish (2015) for a list of specimens in museum collections. Note that the specimens sent to institutions in Australia and New Zealand are not listed.

Diagnosis

Columbids with the following unique combination of characters: modest sexual dimorphism of the skeleton; the frontal processes (= processus frontales) of the premaxilla meet proximally without any space along their medial margins; distally, the premaxillary frontal processes are enlarged, gradually tapering, fusing well proximally to their distal terminus; anterior border of the nares (= apertura nasalis ossea) is slit-like; the body of the premaxilla (corpus ossis premaxillare) forms the large, porous, bulbous tip of the upper bill; the maxillary process (= processus maxillaris) of the premaxilla is vertically oriented distally, converging with the nasal process to form a slit-like nares (= apertura nasalis ossea); the distal ventral surfaces of the premaxilla are apneumatic; the distal end of the lower jaw is comparatively deep and strong; the proximal end of the lower jaw is comparatively shallow and caudally extensive, with obtuse posterior margins of the rami; the quadrate–lower jaw articulation is situated comparatively posteriorly on the cranium; the lacrimal processes of the frontal are greatly reduced; the frontal is dorsally convex and dome-shaped; the frontals extend anteromedially to the frontonasal hinge, covering the posteromedial portions of the nasals and frontal processes of the premaxillae; the orbits are relatively small; the ventral surface of the endocranial cavity forms an acute angle with the basioccipital plane; the palatines are deeply ventrally curved; the cervical vertebrae are comparatively large relative to volant columbids; the modal number of synsacral vertebrae is 17; the modal number of caudal vertebrae (excluding the pygostyle) is six; the pectoral girdle and limbs are reduced relative to volant columbids; the sternum sulcus articularis coracoideus is comparatively shallow and laterally located; the coracoid processus lateralis is well developed, curved, and pointed; the scapula blade is typically curved, especially distally; the scapula has a distinct tubercle on the cranioventral edge of the blade; the furcula is U-shaped distally; the proximal end of the humerus is displaced ventrally relative to the axis of the shaft; the humerus incisura capitis is comparatively short, broad and rounded; the humerus crista deltopectoralis is variable in morphology; the distal ends of the radii and ulnae lack exostosis; the carpometacarpus processus extensorius is more block-like than in extant (volant) columbids; the carpometacarpus and the metacarpals majus and minus are comparatively long, slender, and cylindrical, although in some specimens the metacarpal minus is somewhat flattened; carpometacarpus distal end is not deflected cranially relative to the long axes of the metacarpals; the ilia are comparatively broad, especially caudal to the acetabula; the hindlimb bones, relative to the shaft widths, are comparatively short and thick; the femur crista trochanteris has a pneumatic foramen on the craniomedial edge; the femur linea intermuscularis caudalis is distinct but not conspicuously raised; and the tarsometatarsus crista medialis hypotarsi is comparatively large. (The preceding characters were modified from table 3 of Livezey 1993, which compares the Dodo with the Solitaire.) The horizontal semicircular canal has a pronounced concavity at the mid-point of the canal. (Based on the endocranial reconstructions in Gold *et al.* 2016, comparing the Dodo with volant columbids, note that the inner ears of the Solitaire are unknown.)

†*Pezophaps* Strickland, 1848

Type species

†*Didus solitarius* Gmelin, 1789. Type species by monotypy (*contra* Peters 1937: 10, who stated that the species was the type by original designation; Strickland did not state that †*Didus solitarius* was the type species of his new genus). Strickland (1848: 69) stated: 'Leguat's bird is the type of the "*Didus solitarius*" of systematists'; there was no mention of generic type species.

Following recommendation 51G of the Zoological Code, the type species can be referred to as †*Pezophaps solitaria* (Gmelin, 1789) Strickland, 1848. It can also be written more simply as †*Pezophaps solitaria* (Gmelin, 1789).

Etymology

'Pedestrian pigeon', based on the Greek *pezós* (πεζός, 'pedestrian') and *phaps* (φάψ, 'a pigeon') (from Strickland 1848: 54). The genus is of feminine grammatical gender, hence why Strickland (1848: 46) declined the suffix of the specific epithet *solitarius* (-us) to *solitaria* (-a).

Diagnosis

Same as the only species (see below).

†*Pezophaps solitaria* (Gmelin, 1789)

(Figs 2, 5, 7–9)

- 1708 le Solitaire (pre-Linnean)—Leguat p. 98–104. Figured on the page adjacent to p. 98.
- *1785* Solitary Dodo—Latham, p. 3–4.
- *1789 Didus solitarius* sp. nov.—Gmelin, p. 728–729.
- *1790 Didus solitarius* Gmelin—Latham, p. 662–663.
- *1844 Didus solitarius* Gmelin—Strickland, p. 324–327.
- 1848 *Pezophaps solitaria* (Gmelin) gen. nov. et just. emend.—Strickland, p. 46–56, plates XIII–XV.
- 1848 *Pezophaps solitaria* (Gmelin)—Melville, p. 113–119, plates XIII–XV.
- *1852 Pezophaps solitaria* (Gmelin)—Mitchell, p. 19.
- *1852* Pezophaps minor [nomen nudum] Strickland—Mitchell, p. 19.
- 1854 *Didus nazarenus* Gmelin—Bartlett, p. 280–284, plate XLV (fig. 1). [Published in 1854.]
- 1854 *Didus solitarius* Gmelin—Bartlett, p. 280–284, plate XLV (fig. 2). [Published in 1854.]
- *1854b Pezophaps solitaria* (Gmelin)—Bonaparte, p. 3.
- *1859 Pezophaps solitaria* (Gmelin)—Strickland, p. 187–196, plate LV (figs 1–4).
- 1859 *Pezophaps minor* sp. nov.—Strickland, p. 187–196, plate LV (figs 5–7).
- *1862 Pezophaps solitaria* (Gmelin)—Reichenbach, p. 128.
- 1865 *Didus nazarenus* Gmelin—Newton, p. 199–201, plate VIII.
- *1868 Pezophaps solitaria* (Gmelin)—Newton and Newton, p. 428–433.
- 1869 *Pezophaps solitaria* (Gmelin)—Newton and Newton, p. 327 – 359, plates 15–22, 24.
- 1872 *Pezophaps minor* Strickland—Owen, p. 519, plate LXVI (figs 5–7, 12).
- 1872 *Pezophaps solitaria* (Gmelin)—Owen, p. 519, plate LXVI (figs 1–4, 13).
- 1878 *Pezophaps solitaria* (Gmelin)—Owen, p. 87–97, plates VII and VIII.
- 1879 *Pezophaps solitaria* (Gmelin)—Newton and Clark, p. 438–451, plates XLIV–L.
- *1891 Pezophaps solitaria* (Gmelin)—Lydekker, p. 128.
- *1893 Pezophaps solitarius* [*sic*] (Gmelin)—Sharpe, p. 629–632.
- 1907 *Pezophaps solitarius* [*sic*] (Gmelin)—Rothschild, p. 177–178, plates 23 and 25a (figs 1–3).
- *1916 Pezophaps solitarius* [*sic*] (Gmelin)—Ridgway, p. 277.
- *1937 Pezophaps solitaria* (Gmelin)—Peters, p. 10.
- *1957 Pezophaps solitaria* (Gmelin)—Verheyen, p. 9, 18, 21, 27, 30.
- *1971 Pezophaps solitaria* (Gmelin)—Brodkorb, p. 200.
- *1975 Pezophaps solitarius* [*sic*] (Gmelin)—Wolters, p. 43.
- *1989 Pezophaps solitaria* (Gmelin)—Brom and Prins, p. 233, 236.
- *1990 Pezophaps solitaria* (Gmelin)—Sibley and Ahquist, p. 421.
- *1991 Pezophaps solitaria* (Gmelin)—Witmer and Cheke, p. 134.
- 1993 *Pezophaps solitaria* (Gmelin)—Livezey, p. 247–282, fig. 2b.
- 1996 *Pezophaps solitaria* (Gmelin)—Janoo, p. 57, 58, 67, 69, 72, fig. 7.
- 2000 *Pezophaps solitaria* (Gmelin)—Janoo, p. 323, 325–327, fig. 1.
- *2001 Pezophaps solitaria* (Gmelin)—Worthy, p. 766.
- *2002 Pezophaps solitaria* (Gmelin)—Shapiro *et al.*, p. 1683.
- *2005 Pezophaps solitaria* (Gmelin)—Janoo, p. 177.
- *2006 Pezophaps solitaria* (Gmelin)—Cheke, p. 156.
- *2007 Pezophaps solitaria* (Gmelin)—Pereira *et al.*, p. 656–659, 662, 663, 665, 667, 669.
- 2008 *Pezophaps solitaria* (Gmelin)—Cheke and Hume, p. 30, 50, 167, 398, plate.
- 2013 *Pezophaps solitaria* (Gmelin)—Parish, [numerous occurrences].
- *2014 Pezophaps solitaria* (Gmelin)—Heupink *et al.*, p. 1, 3.
- *2014 Pezophaps solitaria* (Gmelin)—van Grouw, p. 300.
- *2015 Pezophaps solitaria* (Gmelin)—Claessons *et al.*, p. 31, 36, 184, 185–187.
- *2016 Pezophaps solitaria* (Gmelin)—Besnard *et al.*, p. 76–78.
- *2016 Pezophaps solitaria* (Gmelin)—Byrkjedal *et al.*, p. 199.
- 2016 *Pezophaps solitaria* (Gmelin)—Gold *et al.*, p. 951–957, 959–961, figs 2B, 3B, 4B, 7B, 8B.
- 2016 *Pezophaps solitaria* (Gmelin)—Rodríguez-Pontes, p. 398–413, figs 1–11.
- *2016 Pezophaps solitaria* (Gmelin)—Soares *et al.*, p. 1–3, 5.

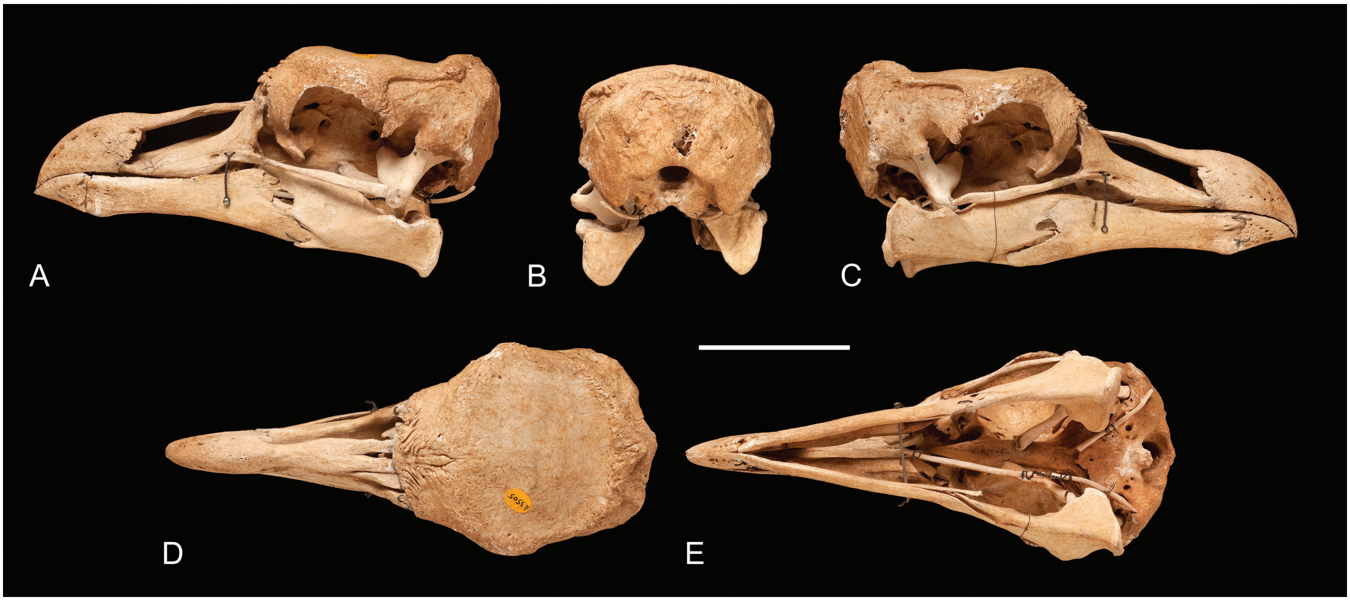

Figure 7. Solitaire (†*Pezophaps solitaria*) referred specimen (NHMUK PV A 3505). Skull in left lateral view (A), occipital view (B), right lateral view (C), dorsal view (D), and ventral view (E). Note that this is a male individual. Scale bar: 3 cm.

- *2017 Pezophaps solitaria* (Gmelin)—Angst *et al*., p. 1, 4.
- *2018 Pezophaps solitaria* (Gmelin)—Bruxaux *et al*., p. 250, 254.

Type specimen

No type specimen has been designated for †*Pezophaps solitaria* (the Rodrigues Solitaire, or simply the Solitaire). As noted by Strickland (1848: 56) the type series of †*Pezophaps solitaria* are the unknown individuals that François Leguat observed while on the island of Rodrigues. Given that they were live animals observed in their natural habitat, it is impossible to ascertain what specimens they were and whether they were ever collected. As such, we cannot locate the original syntypes, and this precludes us from designating a lectotype.

At present, we cannot formally designate a neotype for †*Pezophaps solitaria*. In order to be fully compliant with Article 75 of the Zoological Code, a neotype designation cannot be 'an end in itself, or a matter of curatorial routine, and any such neotype designation is invalid' (Article 75.2), and 'there is an exceptional need' (Article 75.3). There is no exceptional need for a neotype for the Solitaire. As we have shown above, only one raphinan species is known from the Island of Rodrigues, and there is no nomenclatural or systematic confusion for said species. Should fossil raphinan remains be discovered in Rodrigues, it might be worth revisiting the typification of the Solitaire.

Locality

Island of Rodrigues, Mascarene Islands.

Etymology

'The solitary pedestrian pigeon'. The specific epithet is based on François Leguat's name, 'le Solitaire'. As noted by Strickland (1848: 46), Leguat re-used the name 'Solitaire', which had originally been used to denote a different bird species on the island of Réunion (also part of the Mascarene Islands). This species, the Réunion or White Dodo, is, in fact, the extinct quasi-flightless ibis †*Threskiornis solitarius* (de Sélys-Longchamps, 1848) (see Hume and Cheke 2004).

Geographical range

Island of Rodrigues, Mascarene Islands. Extinct since the mid-18th century (see Cheke and Hume 2008). The IUCN Red List of Threatened Species has 1770 as the year last seen, and states that the species was reported in 1761 but was extinct by 1778 (BirdLife International 2016b). Pingré, who visited Rodrigues in 1761, did not see any Solitaires but was informed that they were still alive (Parish 2013: 65).

Referred specimens

See Parish (2015) for a list of specimens in museum collections. Note that the specimens sent to institutions in Australia and New Zealand are not listed.

Diagnosis

Columbids with the following unique combination of characters: pronounced sexual dimorphism of the skeleton; at their proximal end, the frontal processes (= processus frontales) of the premaxilla are separated by a narrow space of variable size; distally, the premaxillary frontal processes are not enlarged, fusing more distally; the caudal margin of the corpus ossis premaxillare has plate-like lateral extensions that result in the nares (= apertura nasalis ossea) being subtriangular; the upper bill tip is typically hooked; the maxillary process (= processus maxillaris) of the premaxilla tapers distally to slender splints; the premaxilla distal ventral surfaces typically have numerous neurovascular foramina in distinct depressions; the distal end of the lower jaw is comparatively shallow and weak; the proximal end of the lower jaw is comparatively deep and caudally abbreviated, with perpendicular posterior margins of the rami; the

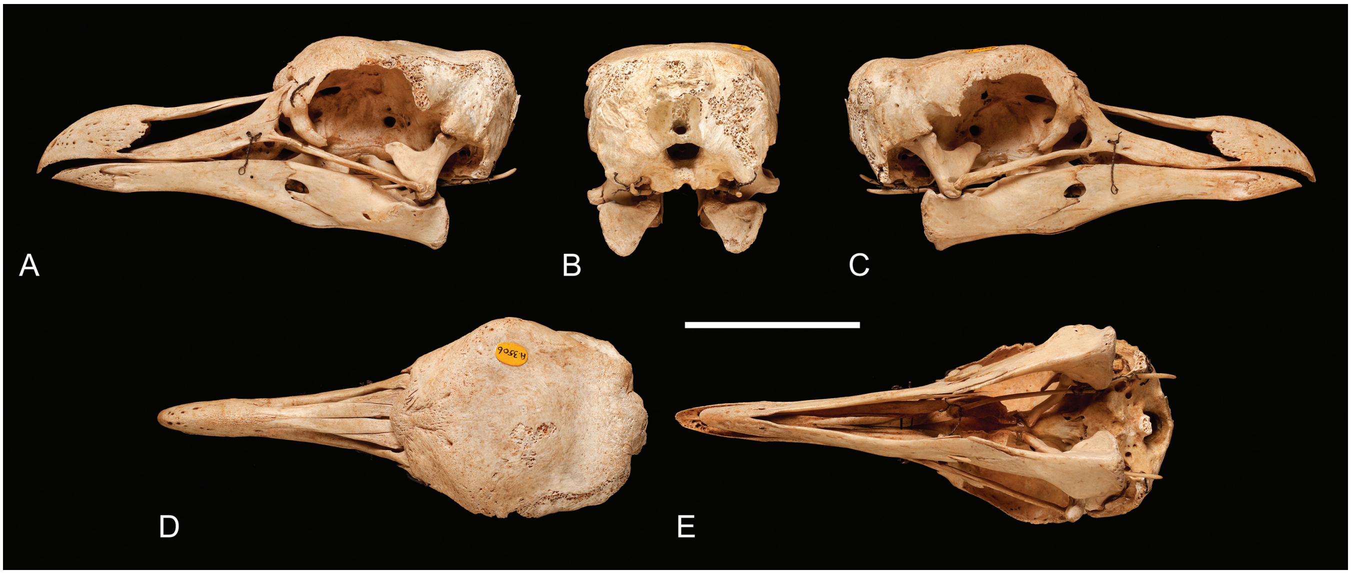

Figure 8. Solitaire (†*Pezophaps solitaria*) referred specimen (NHMUK PV A 3506). Skull in left lateral view (A), occipital view (B), right lateral view (C), dorsal view (D), and ventral view (E). Note that this is a female individual. Scale bar: 3 cm.

Figure 9. Artistic life reconstructions of the solitaire (†*Pezophaps solitaria*). A, a solitary male. B, two males engaged in intraspecific conflict. Artwork by Julian Pender Hume.

quadrate–lower jaw articulation is not situated comparatively posteriorly on the cranium; the lacrimal processes of the frontal are comparatively large; the frontal is dorsally flat; the frontals are truncated anteromedially, leaving the posteromedial portions of the nasals and frontal processes of the premaxillae exposed dorsally; the orbits are relatively large; the ventral surface of the endocranial cavity is nearly parallel with the basioccipital plane; the palatines are moderately ventrally curved; the cervical vertebrae are comparatively small; the modal number of synsacral vertebrae is 17 or 18; the modal number of caudal vertebrae (excluding the pygostyle) is five; the pectoral girdle and limbs are reduced relative to volant columbids; the sternum sulcus articularis coracoideus is comparatively deep and medially located; the coracoid processus lateralis is reduced, with the lateral margin truncated; the scapula blade is typically straight; the scapula lacks a distinct tubercle on the cranioventral edge of the blade; the furcula is essentially parabolic distally; the humerus proximal end is not displaced ventrally relative to the axis of the shaft; the humerus incisura capitis is comparatively long, with a narrow groove; the humerus crista deltopectoralis is rounded without a dorsal point; in males, the distal ends of the radii and ulnae variably are exostotic; presence of an outgrowth of the processus extensorius of the carpometacarpus (carpal knob *sensu* Hume and Steel 2013), and these exostoses can become greatly enlarged in males but can also be present in females, albeit in a much more reduced manner; the carpometacarpus and metacarpals majus and minus, are comparatively short, flat, and rectangular in cross-section; the carpometacarpus distal end is deflected cranially relative to the long axes of the metacarpals; the ilia are comparatively narrow, especially caudal to the acetabula; the hindlimb bones, relative to the shaft widths, are comparatively long and slender; the femur crista trochanteris lacks a pneumatic foramen on the craniomedial edge; the femur linea intermuscularis caudalis is comparatively raised and more prominent; the tarsometatarsus crista medialis hypotarsi is comparatively small. (The preceding characters were taken from table 3 of Livezey 1993, which compares the Solitaire with the Dodo.)

DISCUSSION

Nomenclatural 'ripples'

Our overview of the nomenclatural and systematic history of the Dodo and Solitaire has shown that even iconic species can lack type specimens. As we have demonstrated, this 'oversight' is not as surprising at it might first appear. Both species were extinct by the time their scientific nomina were established (Linneaus 1758, Gmelin 1789), and their nomina were not based on physical specimens but on written accounts of unknown live individuals and lost specimens (Clusius 1605, Nieremberg 1635, Bontius 1658, Leguat 1708). Both species had begun to fall into myth by the 18th century (Duncan 1828, de Blainville 1835, Strickland 1844, 1848, Hume 2006), and the concept of the nomenclatural type did not exist until the early 19th century (Westwood 1837a, Witteveen 2016).

Given the recent use of nomina based on the †*Raphus* family group by extant columbid workers for subclades within Columbidae (Dickinson and Remsen Jr 2013, Chen *et al.* 2022, Oliver *et al.* 2023), we undertook a historical review of columbid family-group nomina. Although most of the columbid family-group nomina are valid under the Zoological Code, we found that the *Trugon*- and *Hemiphaga*-based nomina do not fulfil Article 13.2.1 of the Zoological Code and are therefore not available. Given that most of the family-group nomina within Columbidae were established prior to 1930 and that most of the nomina in use are compliant with the Principal of Coordination for the family group (Article 36), they are not required to be accompanied by a list of characters that purport to differentiate it from other taxa (Article 13.1.1) or by a bibliographic reference to such a published statement (Article 13.1.2). However, if a new family group were to be established, any new nomina would need to be accompanied by a list of diagnostic characters.

Our review also found that Oudemans (1917), not Poche (1904) or Wetmore (1930), is the correct nominal authority of the †*Raphus*-based family group. We cannot preclude the possibility that an older undiscovered publication might alter the nominal authority again; this is owing to the early 20th century shift from using the genus †*Didus* and its family group, and the specific epithet †*ineptus* for the Dodo, to using the genus †*Raphus* and specific epithet †*cucullatus* instead (Poche 1904, Rothschild 1907, Allen 1910, Ridgway 1916, Oudemans 1917).

This shift and the nomenclatural impact it had are intriguing. The cause is a simple one: the change in the 'starting date' of zoological nomenclature. As we outlined above, during the 19th century different nomenclatural codes used different editions of Systema Naturæ as the 'start' of zoological nomenclature, with some codes preferring the 12th edition (e.g. Strickland *et al.* 1843) and others the 10th edition (American Ornithologists' Union 1886, Blanchard 1889). By the early 20th century, the international community of zoologists (ICZN 1905) had settled on using the 10th edition of Systema Naturæ (Linnaeus 1758) and a date of 1758. It was this act that impacted Dodo nomenclature so profoundly. By accepting the 10th edition of Systema Naturæ (Linnaeus 1758) as available for zoological nomenclature, and a 'starting date' of 1758, it rendered both †*Struthio cucullatus* Linnaeus, 1758 and †*Raphus raphus* Brisson, 1760a, b as available nomina.

This situation is an example of what we call herein nomenclatural 'ripples'. A seemingly small change to a nomenclatural code, or a change in which nomenclatural code is in prevailing use, can 'ripple' outwards, impacting the validity of nomina (specific, generic, and family group) and which subclade names are available to systematists when overarching analyses of the internal relationships of a clade are undertaken. The fourth edition of the Zoological Code (ICZN 1999) does have many caveats in place to prevent threats to nomenclatural stability, such as in the Dodo example herein. But this example should be used as a cautionary tale for systematists and those formulating/revising nomenclatural codes. Although the impact we described herein is restricted to an extinct species, how easily could future changes inadvertently impact the nomenclature of an endangered species and thereby detrimentally affect conservation or law-enforcement efforts?

Alas, too many zoologists/systematists who are not 'taxonomically' or 'nomenclaturally' inclined dismiss the impact that even relatively minor changes to nomenclatural codes can have.

For example, although well intentioned, the idea we can sweep away problematic nomina established during the age of colonialism (see the discussion and wider references in the works by: Bae *et al.* 2023, Ceríaco *et al.* 2023, Cheng *et al.* 2023, Guedes *et al.* 2023, Jost *et al.* 2023, Orr *et al.* 2023, Pethiyagoda 2023, Raposo *et al.* 2023) without causing nomenclatural instability is naïve. Although upsetting nomenclatural stability is not an excuse to do nothing, we must strive: (i) not to introduce unnecessary instability to our quasi-legal nomenclatural codes, because they underpin both national and international wildlife laws and regulations (especially for endangered species); and (ii) to have a reasonable idea about the potential impact that any proposed changes to the Zoological Code could have. That is the only way we can even attempt to ameliorate adverse effects (e.g. as the ICZN did with their amendments to the fourth edition of the Zoological Code to make nomenclatural acts published online available and valid, ICZN 2012).

Dear reader, if you have made it this far through our contribution, you know that addressing nomenclatural 'ripples' and other 'taxonomic tangles' is neither quick nor easy; as you can imagine, they are time intensive (not only examining specimens first hand but reading through >400 years of relevant papers, in our instance). If, as a community, we are going to address problematic nomina, taxonomic vandalism, 'nomenclatural harvesting' (*sensu* Denzer and Kaiser 2023), and other instances of using nomenclature as a weapon, there is a need for more trained taxonomists/systematists and more funding to support descriptive biology (see Boero 2010, Britz *et al.* 2020, Engel *et al.* 2021). Before we can elucidate proximate and ultimate causal relationships, we must first make observation statements on semaphoronts (which, in the 21st century, includes data gleaned from computed tomography datasets and DNA sequence alignments), formulate hypotheses based on our observations (e.g. are the semaphoronts in front of me with 'X' and 'Y' unusual characteristics a new species?), and if necessary, attach labels/nomina to those hypotheses (zoological nomenclature). To quote Mayr (1982: 70): 'It is sometimes overlooked how essential a component in the methodology of evolutionary biology the underlying descriptive work is'.

Island-dwelling and terrestrial columbids

The Mascarene giant ground pigeons (†Raphina subtribus nova) are not the only island-dwelling columbids that evolved to become secondarily terrestrial. The Fiji Giant Ground Pigeon †*Natunaornis gigoura* Worthy, 2001 is another notable example. †*Natunaornis* is known from cave deposits on the island of Viti Levu of unknown geological age, but the specimens are presumed to be from the Holocene (Worthy 2001: 767). The species is known from forelimb and hindlimb elements, the coracoid and scapula, and possibly, an isolated premaxilla. Although incompletely known, †*Natunaornis* is the third largest known columbid, behind †*Raphus* and †*Pezophaps*, and, based on the extreme size difference between the fore- and hindlimbs, it is thought to have been flightless. Based on the osteological similarities between †*Natunaornis gigoura* and the extant genus *Goura*, Worthy (2001) hypothesized that they were closely related. However, this hypothesis has never been subjected to phylogenetic analysis. If supported, there would be two instances of a secondarily terrestrial morphotype evolving from island-dwelling raphinans: the †*Raphus* and †*Pezophaps* clade (which is closely related to the extant genus *Caloenas*) and †*Natunaornis* (which might be closely related to the extant genus *Goura*).

Another large-bodied columbid presumed to be secondarily terrestrial is the Saint Helena Dove †*Dysmoropelia dekarchiskos* Olson, 1975, from the island of Saint Helena, in the South Atlantic Ocean. Lewis (2008) dated Sugar Loaf site 1, from which †*Dysmoropelia dekarchiskos* is known, to ~14 000 before present (i.e. late Pleistocene). The species is known from forelimb and hindlimb elements and the coracoid. Similar to †*Natunaornis*, the forelimb and pectoral elements of †*Dysmoropelia* Olson, 1975 are extremely reduced in size relative to the hindlimb bones, with Olson (1975: 30) noting: 'No other known columbiform bird besides the Dodos and Solitaires has evolved anything like an equivalent condition'. Olson (1975: 31) posited a *Streptopelia*-like ancestor for †*Dysmoropelia dekarchiskos* but stressed that 'the differences between the two genera are great and any relationship between them must be considered only hypothetical'. If †*Dysmoropelia* is closely related to *Streptopelia*, then it is evidence that secondarily terrestrial morphotypes evolved outside of Raphinae.

Within the raphine tribe Phabini, there are extinct species referred to the genus *Pampusana* that were either larger bodied or, possibly, secondarily terrestrial. These include †*Pampusana longitarsus* (Balouet & Olson, 1989) from New Caledonia and the possibly flightless species †*Pampusana leonpascoi* (Worthy & Wragg, 2003). Within the subfamily Columbinae, the extinct Mauritian Turtle Dove, †*Nesoenas cicur* Hume, 2011, is considered to be a terrestrial granivore (Hume 2011). Unfortunately, the lack of total-evidence phylogenetic analyses hampers our understanding of the evolutionary relationships of extinct island-dwelling columbids. It also precludes us from determining whether the flightless columbids †*Natunaornis gigoura*, †*Dysmoropelia dekarchiskos*, and †*Pampusana longitarsus* are closely related to †Raphina or are instances of convergent evolution. It is our intention to incorporate osteology and soft-tissue characters alongside molecular data in future studies in order that the relationships of subfossil, and older fossil, species can be elucidated.

CONCLUSION

The Dodo (†*Raphus cucullatus*) is an icon of conservation and a reminder of the destructive potential of humanity towards the natural world. Along with its sister species, the Solitaire (†*Pezophaps solitaria*), these aberrant columbids were named after their extinction but before the development of the 'nomenclatural type' (i.e. establishment of voucher specimens). Therefore, no type specimens have been designated previously for these iconic species. Given that there is no exceptional need for neotype designations for the Dodo or the Solitaire, we refrain from making them. We did, however, establish a new family-group nomen, †Raphina subtribus nova, to unite them.

Our historical overview of the Dodo and the Solitaire, and the family-group nomina within Columbidae, has shown that changing nomenclatural codes have had a profound impact on Dodo nomenclature. During the 19th century, when the first nomenclatural codes were being developed, the proposed 'starting date' of zoological nomenclature was based on the 12th edition of Systema Naturæ (Linnaeus 1766), using 1766 as the cut-off date for valid nomenclatural acts. This is why the genus †*Didus* was consistently preferred over †*Raphus*, why the specific epithet †*ineptus* was used over †*cucullatus*, and why the family group was †Dididae/Didinae. With the development and eventual publication of the Règles Internationales (ICZN 1905), the corpus of international zoologists adopted the 10th edition of Systema Naturæ (Linnaeus 1758) as the 'starting date' of zoological nomenclature, thereby shifting the date back to 1758. This explains the shift in Dodo nomenclature during early 20th century (e.g. Poche 1904, Rothschild 1907, Allen 1910, Ridgway 1916, Oudemans 1917).

We are again entering a period of multiple active nomenclatural codes in zoology, with the development of the fifth edition of the Zoological Code (e.g. ICZN 2014, Rheindt *et al.* 2023), proposals outlined to improve the Zoological Code by the Linz Zoocode Committee (e.g. Dubois 2006, 2011, Dubois *et al.* 2019), the now live 'PhyloCode' (Cantino and de Queiroz 2020, de Queiroz *et al.* 2020), and the proposed Biocode (Greuter *et al.* 2011). As such, we decided that it was necessary to stabilize the nomenclature and alpha taxonomy of the Dodo and its sister species, the Solitaire, and to ensure that the family-group systematization of Columbidae was valid (at least under the fourth edition of the Zoological Code).

Future workers should not underestimate the impact that rule changes within nomenclatural codes, or new codes themselves, can have. The Dodo should be a used as an example of how extensive nomenclatural 'ripples' can be, because not only was the 'correct' genus and specific epithet impacted, but also the family-group nomen. This latter issue now impacts extant species, because one of the largest subclades within Columbidae (= Raphinae) is now based on the genus †*Raphus*. Although these issues are often considered 'trivial' or 'irritating' by those not versed in nomenclature, they can have a profound impact on how we communicate our understanding of the natural world to the general public and policy-makers. In the present 'century of extinctions' (Dubois 2003), and with the 'taxonomic impediment' caused by the declining numbers of trained taxonomists/systematists (e.g. Boero 2010, Britz *et al.* 2020, Engel *et al.* 2021), the need for best practice in systematics is more important than ever.

SUPPLEMENTARY DATA

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

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AUTHOR CONTIBUTIONS

NJG and MOH obtained funding, MTY led the project, conceived the study and wrote the manuscript, JPH and NJG helped develop the project, all authors helped edit drafts and approved the final version to be published.

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DATA AVAILABILITY STATEMENT

All data are incorporated into the article and its online supplementary material.

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