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# Phylogenetic definitions for 25 higher-level clade names of birds

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ABSTRACT

Knowledge of the higher-level phylogenetic relationships of birds has grown substantially during the past two decades due to the application of genomic data. However, the nomenclature of higher-level taxa has not become more stable, due to the lack of regulation of taxon names above the level of superfamily by the ICZN, and the usage of rank-based nomenclature, which is not tied to clades in a phylogeny. Lack of regulation and the instability of rank-based nomenclature impede effective communication among systematists. We review support for higher-level avian clades using a set of 10 phylogenomic data sets, and identify clades that are supported by congruency of at least four of these. We provide formal definitions of the names of these clades based on the rules of the recently published PhyloCode. The names of 25 clades are here defined using minimum-crown-clade ($n$ = 23), minimum-clade ($n$ = 1) and maximum-crown-clade ($n$ = 1) definitions. Five new names are introduced here: *Dinocrypturi*, *Pteroclimesites*, *Musophagotides*, *Phaethoquornithes* and *Pelecanes*. We also review diagnostic apomorphies of the relevant clades, and identify known synonyms and homonyms. By establishing a formal link between higher-level taxon names and well-supported phylogenetic hypotheses, our phylogenetic definitions will provide a solid basis for the stabilization of avian higher-level nomenclature.

## 1. Introduction

Since the publication of the first comprehensive multi-locus phylogeny of birds in 2006 (Ericson et al., 2006), avian phylogenomic studies have clarified many aspects of the avian tree of life. Many higher-level relationships are now congruently supported by multiple phylogenies (Fig. 1). In contrast, the nomenclature of higher-level taxa has not become more stable. There are two main reasons for this. First, the names of higher-level taxa (i.e. above the level of superfamily) are not regulated by the International Code of Zoological Nomenclature (ICZN, 1999) and this is reflected by how such names are sometimes being introduced and used. Some names have been introduced informally without any indication of how the names should be applied in a slightly different phylogeny (e.g. 'Conglomerati', Slack et al., 2007; 'Coronaves', 'Metaves', Fain and Houde, 2004).

A second reason why instability may occur even if there is agreement about phylogenetic relationships is the use of taxonomic ranks. If a taxonomist intends to name a higher taxon using rank-based nomenclature, he/she must designate a single type taxon and provide a statement about the rank of the taxon. Rank-based names are not connected to a specified clade. Future workers are allowed to emend the content of taxa depending on their views about the appropriate rank of the relevant taxa. Thus, the inclusiveness of a taxon, and hence the meaning of the taxon name, is potentially unstable, even in situations where phylogenetic relationships are undisputed. This is illustrated in Fig. 2. The sister relationship of flamingos and grebes was first documented in 2001 (van Tuinen et al., 2001) and has been corroborated overwhelmingly by subsequent phylogenomic studies (e.g. Hackett et al., 2008; McCormack et al., 2013; Yuri et al., 2013; Jarvis et al., 2014; Prum et al., 2015; Reddy et al., 2017; Liu et al., 2018; Kimball et al., 2019; Kuhl et al., 2021). The flamingo-grebe clade was formally named *Mirandornithes* in 2005 (Sangster, 2005), but within a couple of years its nomenclature had become unstable due to the introduction and re-use of other names (Fig. 2). As a consequence of this, and the lack of restrictions to the

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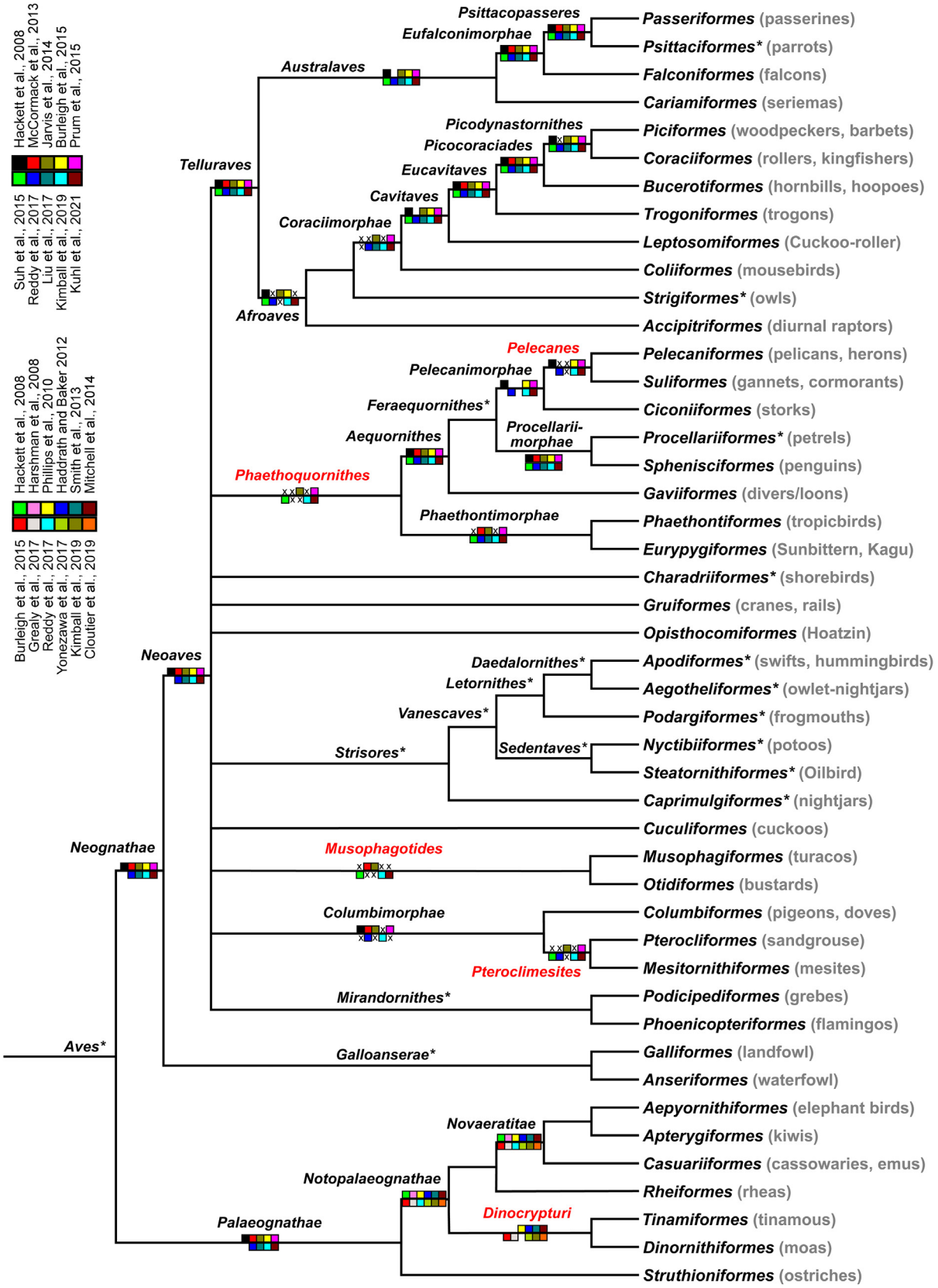


**Fig. 1.** Consensus phylogeny of birds based on phylogenomic studies. Names along branches are defined in the present paper, except those marked with an asterisk which have been defined in previous work (Clarke et al., 2020; Mindell, 2020; Sangster, 2020a, 2020b, 2020c, 2020d, 2020e, 2020f, 2020g; Chen and Field, 2020; Sangster and Mayr, 2021). Clades labelled in red are newly named in this paper. Support for clades in different studies is indicated with 10 boxed colour codes (upper legend). A cross indicates that the study did not support the clade. Note that *Notopalaeognathae*, *Novaeratitae* and *Dinocrypturi* are supported by a different set of studies and have a different (12-box) set of colour codes than the other clades (lower legend). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

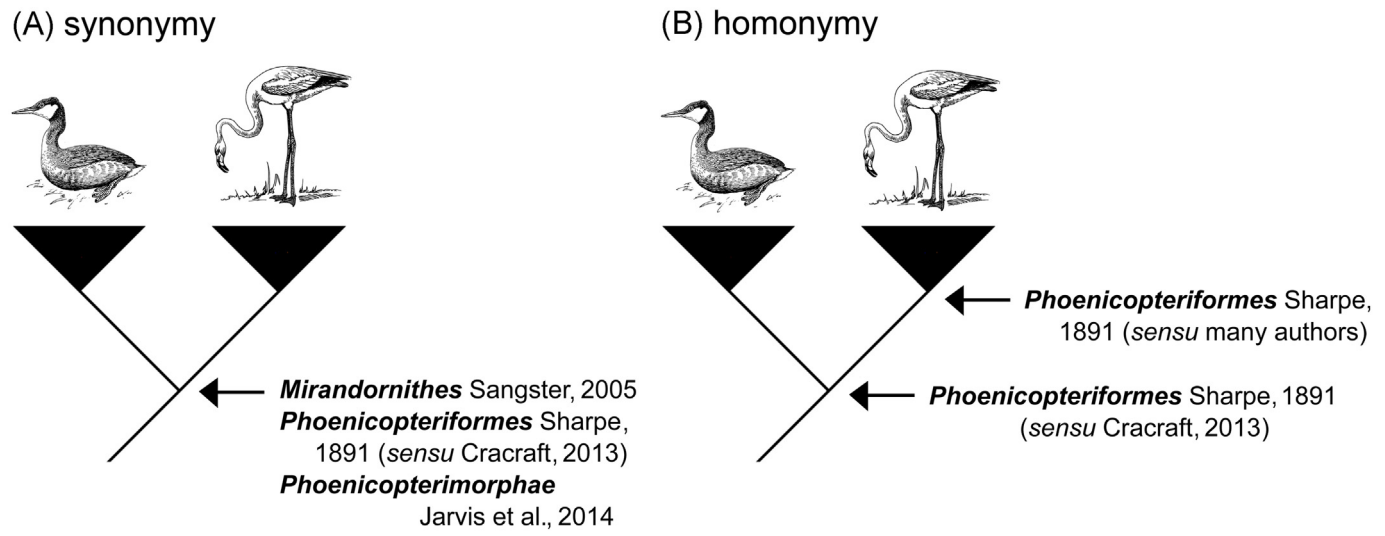


**Fig. 2.** Synonymy and homonymy. (A) synonymy, multiple names are used for the same clade, and (B) homonymy, the same name is applied to multiple clades. The bird vignettes are in the public domain (https://publicdomainvectors.org).

inclusiveness of a taxon, taxon names are more closely associated with ranks than with actual taxa.

The lack of restrictions to the inclusiveness of a taxon often leads to situations where different authors use the same name for different taxa (homonymy) and use different names for the same taxon (synonymy, Fig. 2). Homonymy is a problem because information associated with a name refers to different taxa. One has to know to which taxon the name is, or has been, applied. Failure to recognize homonymy may lead to misinterpretation of biological information. Synonymy is also a problem because a search for information about a taxon means that one has to know all names of a taxon and must repeat the search effort for all of these synonyms. Failure to recognize all synonyms of a taxon may result in relevant literature being overlooked. Synonymy and homonymy pose serious problems for information retrieval and communication in biology. These problems underscore that the rules of rank-based nomenclature do not promote explicitness, universality nor stability with regard to the phylogenetic meanings of taxon names (De Queiroz and Gauthier, 1994).

An alternative system that aims to avoid the problems of rank-based nomenclature has been developed by De Queiroz and Gauthier (1990, 1992). This system is now known as 'phylogenetic nomenclature'. Phylogenetic nomenclature has the same basic goals as rank-based nomenclature: to provide unambiguous methods for (i) applying names to taxa, (ii) selecting a single accepted name for a taxon (from multiple homonyms or synonyms), and (iii) promoting nomenclatural stability and continuity, as long as this does not contradict new systematic conclusions (De Queiroz, 2005). This system differs from rank-based nomenclature in several important ways. First and foremost, phylogenetic nomenclature is rankless. As a consequence, taxonomic names do not depend on, nor vary with, their phylogenetic position. As there are no mandatory ranks, each clade only has one valid name.

Second, taxonomic names are *explicitly* defined in terms of ancestry and descent. Each name is defined using at least *two* reference points on a cladogram (two taxa, or a taxon and an apomorphy). This means that the limits of the taxon to which the name refers are fixed. The contents of the clade to which the name refers are determined empirically, and therefore one needs a reference phylogeny to determine the meaning of the name. Each name explicitly refers to a clade; therefore, all taxa are monophyletic, and only the contents of the clade are subject to change.

The rules of phylogenetic nomenclature are codified in the *PhyloCode*, of which the printed version was officially published in spring 2020 (Cantino and De Queiroz, 2020). The starting date of the *PhyloCode* coincides with the publication of '*PhyloNyms*' (De Queiroz et al., 2020), a major volume that provides phylogenetic definitions for many widely used clade names. Names defined in *PhyloNyms* or in subsequent publications are available under the *PhyloCode*. *PhyloNyms* includes definitions of eleven clade names of birds, including four higher-level clades (*Aves*, *Galloanserae*, *Mirandornithes* and *Daedalornithes*). Several others have been published subsequently (Chen and Field, 2020; Sangster and Mayr, 2021). Names proposed before the starting date of the *PhyloCode* (e.g. Gauthier and De Queiroz, 2001) are unavailable and remain subject to instability until these are formally defined.

In this paper, we define 25 names of higher-level clades of birds that are well-corroborated by comprehensive phylogenomic studies using the rules and recommendations of the *PhyloCode*. The scope of this paper is restricted to 'supra-ordinal' names because these are almost all supported by the same set of studies.

## 2. Methods

Genomic support for phylogenetic relationships among major clades of birds was evaluated using a set of 10 phylogenomic studies published between 2008 and 2021 (Table 1). For palaeognath clades, we also consulted a set of eight other works (i.e. Harshman et al., 2008; Phillips et al., 2010; Haddrath and Baker, 2012; Smith et al., 2013; Mitchell et al., 2014; Grealy et al., 2017; Yonezawa et al., 2017; Cloutier et al., 2019; see Table 2). Relationships congruently supported by a minimum of four phylogenomic studies were used to construct a consensus phylogeny. In addition to a full consideration of these studies we also assessed relationships that were not as strongly corroborated with other studies that largely analysed published data and/or did not present a preferred cladogram (Kimball et al., 2013; Gilbert et al., 2018; Houde et al., 2019; Braun and Kimball, 2021). For these studies, we focused on what we felt were the figures that provided the most robust and distinct information (i.e., Figures 1 and 4 from Kimball et al., 2013, Figure 3a from Gilbert et al., 2018, Figure 11d from Houde et al., 2019, and Figures 4c and 5 from Braun and Kimball, 2021).

We selected the most appropriate phylogenetic definition based on the state of knowledge about the clade, and our wish to maximize the explicitness of the definition. For instance, if the relationships within a clade are well-known and its sister-taxon is also well-known, we adopted a minimum-crown-clade or minimum-clade definition because this explicitly defines the origin of the clade as that of a known clade. On the other hand, if the relationships within the clade are poorly known but its sister-taxon is well-known (e.g. *Neoaves*), we selected a maximum-crown-clade definition (Fig. 3).

**Table 1**
Phylogenomic support for 22 clade names defined in this paper. ML, maximum likelihood; PP, posterior probability; MRP, matrix representation with parsimony; 3′UTR, noncoding 3-prime untranslated region; SH-aLRT, Shimodaira-Hasegawa approximate likelihood ratio test.

| Source | Data type(s) | *Palaeognathae* | *Neognathae* | *Neoaves* | *Columbimorphae* | *Pteroclimesites* | *Musophagotides* | *Phaethoquornithes* | *Phaethontimorphae* |
|---|---|---|---|---|---|---|---|---|---|
| Hackett et al. (2008) | 19 nuclear loci | 100% ML bootstrap | 96% ML bootstrap | 96% ML bootstrap | <70% ML bootstrap | Not recovered | Not recovered | Not recovered | Not recovered |
| McCormack et al. (2013) | 1541 ultra-conserved elements | | | >0.95 PP, >70% bootstrap | >0.95 PP, >70% bootstrap | Not recovered | >0.95 PP, >70% bootstrap | Not recovered | 96% ML bootstrap |
| Jarvis et al. (2014) | 8251 exon loci, 2516 intron loci, 3769 ultra-conserved elements | 100% exaML bootstrap | 100% exaML bootstrap | 100% exaML bootstrap | 100% exaML bootstrap | 100% exaML bootstrap | 55% exaML bootstrap | 70% exaML bootstrap | 100% exaML bootstrap |
| Burleigh et al. (2015) | 25 nuclear loci, mitochondrial DNA | 95% ML bootstrap | 95% ML bootstrap | 93% ML bootstrap | Not recovered | Not recovered | Not recovered | Not recovered | Not recovered |
| Prum et al. (2015) | 259 anchored nuclear loci | 1.0 PP | 1.0 PP | 1.0 PP | 1.0 PP | 1.0 PP | Not recovered | 1.0 PP | 1.0 PP |
| Suh et al. (2015) | 2118 retroposon presence/absence loci | | | | Not recovered | 8 retroposons | 7 retroposons | 5 retroposons | 20 retroposons |
| Reddy et al. (2017) | 54 nuclear loci | ≥95% ML bootstrap | ≥95% ML bootstrap | ≥95% ML bootstrap | <70% ML bootstrap | <70% ML bootstrap | Not recovered | Not recovered | <70% ML bootstrap |
| Liu et al. (2018) | 63 nuclear protein-coding loci | 100% ML bootstrap | 100% ML bootstrap | 100% ML bootstrap | Not recovered | Not recovered | Not recovered | Not recovered | 100% ML bootstrap |
| Kimball et al. (2019) | supertree | 100% MRP bootstrap | 100% MRP bootstrap | 100% MRP bootstrap | 85% MRP bootstrap | 100% MRP bootstrap | 25% MRP bootstrap | 43% MRP bootstrap | 100% MRP bootstrap |
| Kuhl et al. (2021) | 3′UTR sequences (2.5 million analyzable patterns) | 100% (SH-aLRT) | 100% (SH-aLRT) | 100% (SH-aLRT) | Not recovered | 100% (SH-aLRT) | 100% (SH-aLRT) | 100% (SH-aLRT) | 100% (SH-aLRT) |

| Source | *Aequornithes* | *Procellariimorphae* | *Pelecanimorphae* | *Pelecanes* | *Telluraves* | *Afroaves* | *Coraciimorphae* |
|---|---|---|---|---|---|---|---|
| Hackett et al. (2008) | 89% ML bootstrap | 98% ML bootstrap | 81% ML bootstrap | 88% ML bootstrap | 98%ML bootstrap | <70%ML bootstrap | Not recovered |
| McCormack et al. (2013) | >0.95 PP, >70% bootstrap | 99% ML bootstrap | | | >0.95 PP, 66% bootstrap | Not recovered | Not recovered |
| Jarvis et al. (2014) | 100% exaML bootstrap | 100% exaML bootstrap | | | 100% exaML bootstrap | 100% exaML bootstrap | 100% exaML bootstrap |
| Burleigh et al. (2015) | Not recovered | 99% ML bootstrap | 77% ML bootstrap | 73% ML bootstrap | 49% ML bootstrap | 50% ML bootstrap | Not recovered |
| Prum et al. (2015) | 1.0 PP | 1.0 PP | 1.0 PP | 1.0 PP | 1.0 PP | Not recovered | 1.0 PP |
| Suh et al. (2015) | 16 retroposons | 212 retroposons | | | 64 retroposons | 16 retroposons | Not recovered |
| Reddy et al. (2017) | ≥95% ML bootstrap | ≥95% ML bootstrap | ≥95% ML bootstrap | ≥95% ML bootstrap | ≥95% ML bootstrap | <70% ML bootstrap | <70% ML bootstrap |
| Liu et al. (2018) | 99% ML bootstrap | 80% ML bootstrap | | | 97% ML bootstrap | Not recovered | <70% ML bootstrap |
| Kimball et al. (2019) | 100% MRP bootstrap | 100% MRP bootstrap | 100% MRP bootstrap | 100% MRP bootstrap | 100% MRP bootstrap | 100% MRP bootstrap | 72% MRP bootstrap |
| Kuhl et al. (2021) | 100% (SH-aLRT) | 100% (SH-aLRT) | 100% (SH-aLRT) | 100% (SH-aLRT) | 100% (SH-aLRT) | 100% (SH-aLRT) | 100% (SH-aLRT) |

| Source | *Cavitaves* | *Eucavitaves* | *Picocoraciae* | *Picodynastornithes* | *Australaves* | *Eufalconimorphae* | *Psittacopasserae* |
|---|---|---|---|---|---|---|---|
| Hackett et al. (2008) | 85% ML bootstrap | 71% ML bootstrap | 98% ML bootstrap | 98% ML bootstrap | 64% ML bootstrap | 73% ML bootstrap | 77% ML bootstrap |
| McCormack et al. (2013) | | >0.95 PP, >70% bootstrap | >0.95 PP, >70% bootstrap | Not recovered | | >0.95 PP, >70% bootstrap | >0.95 PP, >70% bootstrap |
| Jarvis et al. (2014) | 100% exaML bootstrap | 72% exaML bootstrap | 100% exaML bootstrap | 100% exaML bootstrap | 100% exaML bootstrap | 100% exaML bootstrap | 100% exaML bootstrap |
| Burleigh et al. (2015) | 76% ML bootstrap | 69% ML bootstrap | 89% ML bootstrap | 85% ML bootstrap | 72% ML bootstrap | 59% ML bootstrap | 47% ML bootstrap |
| Prum et al. (2015) | 1.0 PP | 1.0 PP | 1.0 PP | 1.0 PP | 1.0 PP | 1.0 PP | 1.0 PP |
| Suh et al. (2015) | 124 retroposons | 16 retroposons | 6 retroposons | 5 retroposons | 176 retroposons | 88 retroposons | 16 retroposons |
| Reddy et al. (2017) | ≥70% ML bootstrap | ≥95% ML bootstrap | ≥95% ML bootstrap | ≥95% ML bootstrap | ≥95% ML bootstrap | <70% ML bootstrap | ≥95% ML bootstrap |
| Liu et al. (2018) | 71% ML bootstrap | 93% ML bootstrap | 95% ML bootstrap | 100% ML bootstrap | <70% ML bootstrap | 85% ML bootstrap | 92% ML bootstrap |
| Kimball et al. (2019) | 100% MRP bootstrap | 100% MRP bootstrap | 100% MRP bootstrap | 100% MRP bootstrap | 100% MRP bootstrap | 100% MRP bootstrap | 100% MRP bootstrap |
| Kuhl et al. (2021) | 100% (SH-aLRT) | 100% (SH-aLRT) | 100% (SH-aLRT) | 100% (SH-aLRT) | 100% (SH-aLRT) | 100% (SH-aLRT) | 100% (SH-aLRT) |

**Table 2**
Phylogenomic, mitochondrial and morphological support for three clade names defined in this paper. ML, maximum likelihood; PP, posterior probability; MRP, matrix representation with parsimony.

| Source | Data type(s) | *Notopalaeognathae* | *Novaeratitae* | *Dinocrypturi* |
|---|---|---|---|---|
| Hackett et al. (2008) | 19 nuclear loci | 100% ML bootstrap | 96% ML bootstrap | |
| Harshman et al. (2008) | 20 nuclear loci | 100% ML bootstrap, 1.0 PP | 100% ML bootstrap, 1.0 PP | |
| Phillips et al. (2010) | mitochondrial DNA | 44% ML bootstrap, 0.99 PP | 92% ML bootstrap, 1.0 PP | 99% ML bootstrap, 1.0 PP |
| Haddrath and Baker (2012) | 27 nuclear loci | 1.0 PP | 1.0 PP | 1.0 PP |
| Smith et al. (2013) | 60 nuclear loci, mitochondrial DNA | 100% ML bootstrap, 1.0 PP | 100% ML bootstrap, 1.0 PP | 100% ML bootstrap, 1.0 PP |
| Mitchell et al. (2014) | mitochondrial DNA | 63% ML bootstrap, 1.0 PP | 87% ML bootstrap, 1.0 PP | 100% ML bootstrap, 1.0 PP |
| Burleigh et al. (2015) | 25 nuclear loci, mitochondrial DNA | 86% ML bootstrap | 100% ML bootstrap | 44% ML bootstrap |
| Grealy et al. (2017) | 154 nuclear loci, mitochondrial DNA | 80% ML bootstrap, 1.0 PP | 57% ML bootstrap, 1.0 PP | 100% ML bootstrap, 1.0 PP |
| Reddy et al. (2017) | 54 nuclear loci | ≥95% ML bootstrap | ≥95% ML bootstrap | |
| Yonezawa et al. (2017) | Morphology | 92% ML bootstrap, 0.99 PP | 100% ML bootstrap, 0.94 PP | 96% ML bootstrap, 0.99 PP |
| Cloutier et al. (2019) | 20,850 nuclear loci | 100% ML bootstrap | 100% ML bootstrap | 100% ML bootstrap |
| Kimball et al. (2019) | supertree | 100% MRP bootstrap | 100% MRP bootstrap | 100% MRP bootstrap |

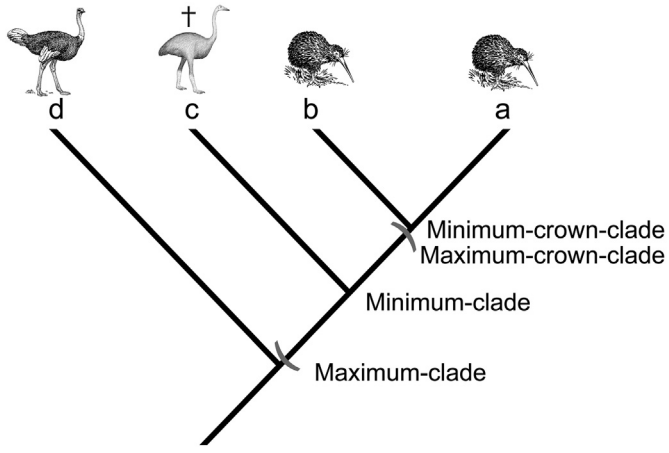


**Fig. 3.** Four types of phylogenetic definitions. A *minimum-crown-clade* is a clade defined by two or more extant taxa (in this example, the least inclusive crown clade containing species a and b). A *maximum-crown-clade* refers to a clade that includes one or more extant species and all other extant species that are closer to these than to a specified other species (e.g. the most inclusive crown clade that includes species a but not d). A *minimum-clade* is a clade defined by at least two taxa, of which at least one can be extinct (e.g. the least inclusive clade containing a and c). A *maximum-clade* refers to a clade and all other clades/lineages (known and unknown) that are closer to it than to a specified other species (e.g. the most inclusive clade that includes species a but not d). The bird vignettes are in the public domain (https://publicdomainvectors.org).

Reference phylogenies were selected based on their topology and taxonomic completeness. In most cases, we used Prum et al. (2015) and Kuhl et al. (2021).

Diagnostic apomorphies were located in the extensive morphological data set published by Livezey and Zusi (2006, 2007). We list these data 'as is'. Thus, we did not verify these data, and in some cases, we cannot vouch for their accuracy.

The accounts follow the same format as that of *Phylonyms*, except that we also include a paragraph on homonyms. All names, including five that are newly proposed in this work, are included in RegNum (https://www.phyloregnum.org), the official registry of clade names (Cellinese and Dell, 2020).

## 3. Results

A total of 25 clades met our criteria for naming. In one case (the basal relationships among *Notopalaeognathae*), two topologies were each supported by at least four studies. Although detailed evaluations of the evidence clearly supported one of these over the other (Cloutier et al., 2019, but see Simmons et al., 2022), we have refrained from naming the relevant clade. The position of elephantbirds as the sister of the kiwis was supported by only three studies (Mitchell et al., 2014; Grealy et al., 2017; Yonezawa et al., 2017), one of which is mitogenomic rather than phylogenomic data, and thus we have left the kiwi–elephantbird clade unnamed. We have also refrained from naming the *Strigiformes–Coraciimorphae* clade due to uncertainty about the position of *Strigiformes* (Braun and Kimball, 2021). The topology of the avian consensus tree used in this paper is very similar to that of Suh (2016) and differs only in the position of *Coliiformes* and the lack of sufficient support for a sister-relationship of *Cuculiformes* and (*Otidiformes* + *Musophagiformes*) (Fig. 1). The consensus tree includes a basal polytomy of ten clades. As pointed out by Suh (2016), there is strong disagreement among phylogenomic studies about the initial divergence of *Neoaves* and this may well represent a hard polytomy.

## 4. Phylogenetic nomenclature

### 4.1. *Palaeognathae Pycraft, 1900 [Sangster, Braun, Johansson, Kimball, Mayr and Suh], converted clade name*

**Registration number:** 695.

**Definition:** The least inclusive crown clade containing *Tetrao major* (now *Tinamus major*) Gmelin, 1789 (*Tinamiformes*) and *Struthio camelus* Linnaeus, 1758 (*Struthioniformes*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Tinamus major* (Gmelin, 1789) & *Struthio camelus* Linnaeus, 1758).

**Etymology:** Derived from the Greek words παλαιός (*palaios*), meaning old, ancient, and γνάθος (*gnathos*), meaning jaw, which refer to the skeletal anatomy of the palate, which is considered to be more primitive than that in *Neognathae*.

**Reference phylogeny:** For the purpose of applying the definition of *Palaeognathae*, Figure 3 in Kuhl et al. (2021) should be regarded as the primary reference phylogeny. Figure 1 in Prum et al. (2015) may be regarded as a secondary reference phylogeny.

**Composition:** *Struthioniformes* (ostriches, 2 extant species), *Rheiformes* (rheas, 2 extant species), *Apterygiformes* (kiwis, 5 extant species), *Casuariiformes* (cassowaries, 3 extant species, and Emu), and *Tinamiformes* (tinamous, 47 extant species).

This clade also includes the extinct groups *Dinornithiformes* (moas) and *Aepyornithiformes* (elephant birds). Accounts of these groups are given in Worthy and Holdaway (2002), Hume and Walters (2012), Mayr (2017), Hansford and Turvey (2018) and Torres and Clarke (2018). It is not clear if *Lithornithiformes* are part of *Palaeognathae* (Houde, 1988; Livezey and Zusi, 2007; Yonezawa et al., 2017; Nesbitt and Clarke, 2016; Worthy et al., 2017).

**Diagnostic apomorphies:** Diagnostic apomorphies are (characters

and states are indicated by their number-letter combination in Livezey and Zusi, 2006, 2007): (1) Os quadratum, processus orbitalis, articulatio pterygoideus marginalis ventralis, present (540b); (2) Os prearticulare, processus prearticularis—tuberculum (dorsale) insertii m. pseudotemporalis superficialis—present and prominent (tuberculum verae), on margo dorsalis of processus rostralis prearticulare and at approximate midpoint of margines ventralis et dorsalis mandibulae, typically medial to fenestra caudale mandibulae within fossa aditus canalis mandibulae (631b); (3) Rostrum (symphysis) mandibulae, pars symphysialis and anteriormost segment of pars intermedia, dorsoventral compression of rami producing essentially flat apex (especially obvious in rostral perspective), associated with virtual absence of crista tomialis rostrally, present (656b); (4) Ramus mandibulae, partes symphysialis et intermedia, shallow sulci indicative of rhamphothecal patterns, present (659b); (5) Articulatio metacarpophalangealis alulae, approximate position with respect to facies cranialis ossis metacarpale II (in repose), angulus diagonal (approximating 45°), alula approaching diagonality with respect to ossa metacarpalia, associated with facies articularis phalangealis spheroidal and subdiagonal to axis majoris phalangis alularis (1750b); (6) Extremitas distalis femoris, condylus lateralis, crista supracondylaris lateralis, tuberculum m. gastrocnemialis lateralis, eminentia present, vaguely indicated (2029b); (7) Junctura (articulatio) tibiofibularis, os fibulare (calcaneum), status definitivum absent by failure of os fibulare to ossify (2436c); (8) Testa, limitates stratorum primus et secundus, aprismatic (2945b).

Mayr and Clarke (2003) noted that in palaeognathous birds the mesethmoid reaches beyond the nasofrontal hinge.

**Synonyms:** The following names are approximate synonyms: *Struthioniformes* (*sensu* Garrod, 1874; Bock and Bühler, 1990), *Struthiones* (*sensu* Garrod, 1874), *Palaeognathiformes* (*sensu* Cracraft, 1981), *Eoaves* (*sensu* Sibley and Ahlquist, 1990), *Ratitae* (*sensu* Sibley et al. 1988; Sibley and Ahlquist, 1990; Kurochkin, 1995).

**Homonyms:** There are no homonyms.

**Comments:** Monophyly of the clade formed by the ostriches, rheas, kiwis, cassowaries, emus and tinamous was already supported by early molecular data sets (Ho et al., 1976; Prager and Wilson, 1976; Sibley and Ahlquist, 1990; Harshman, 1994) and analyses of morphological characters (Meise, 1963; Cracraft, 1986, 1988; Elzanowski, 1995; Kurochkin, 1995; Livezey and Zusi, 2007). Reciprocal monophyly of *Palaeognathae* and *Neognathae* is now overwhelmingly supported by phylogenomic data (Table 1).

Arguments for non-monophyly proposed by Feduccia (1985), Houde and Olson (1981) and Olson (1985) were based on differences among *Palaeognathae* (i.e. *Ratitae* and *Tinamiformes*) and the belief that the defining characters of *Palaeognathae* are primitive. The first argument is not acceptable under phylogenetic methodology and the second holds true for only some of the characteristics of palaeognathous birds.

The definition proposed here agrees with current usage of the name *Palaeognathae* (Cracraft, 1988, 2013; Cracraft and Mindell, 1989; Kurochkin, 1995; Elzanowski, 1995; Livezey and Zusi, 2007). A definition of the name *Palaeognathae* was previously given by Gauthier and De Queiroz (2001), who also used *Tinamus major* and *Struthio camelus* as internal specifiers.

In Linnean classifications, this clade has been ranked at the level of family (Garrod, 1874), cohort (Garrod, 1874; Livezey and Zusi, 2007), order (Cracraft, 1981), superorder (del Hoyo et al., 1992), infraclass (Sibley and Ahlquist, 1990; Cracraft, 2013), and parvclass (Sibley et al., 1988; Sibley and Ahlquist, 1990; Kurochkin, 1995).

A node-based (minimum-crown-clade) definition was selected because there is congruent support for the basal dichotomy within *Palaeognathae* in recent molecular analyses (Harshman et al., 2008; Phillips et al., 2010; Haddrath and Baker, 2012; Smith et al., 2013; Baker et al., 2014; Mitchell et al., 2014; Grealy et al., 2017; Yonezawa et al., 2017; Cloutier et al., 2019).

*Palaeognathae* is sometimes erroneously spelt *Paleognathae* (e.g. Gussekloo and Zweers, 1999; Baker and Pereira, 2009).

### *4.2. Notopalaeognathae Yuri, Kimball, Harshman, Bowie, Braun, Chojnowski, Han, Hackett, Huddleston, Moore, Reddy, Sheldon, Steadman, Witt and Braun (2013) [Sangster, Braun, Johansson, Kimball, Mayr and Suh], converted clade name*

**Registration number:** 696.

**Definition:** The least inclusive crown clade containing *Struthio americanus* (now *Rhea americana*) Linnaeus, 1758 (*Rheiformes*), *Tetrao major* (now *Tinamus major*) Gmelin, 1789 (*Tinamiformes*) and *Apteryx australis* Shaw, 1813 (*Apterygiformes*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Rhea americana* (Linnaeus, 1758), *Tinamus major* Gmelin, 1789 & *Apteryx australis* Shaw, 1813).

**Etymology:** The derivation of the name was given by Yuri et al. (2013) as follows: "*Notopalaeognathae* is from the Greek *notos* (southern) and Palaeognathae from the Greek word *palaios* (ancient, old) and *gnathidion* (jaw), the latter two words referring to the birds classified by Pycraft (1900) as having a "primitive" (palaeognathous) palate. *Noto* refers to the distribution of these taxa on fragments of the ancient southern supercontinent Gondwana. It also refers to the exclusion of *Struthioniformes* (ostriches) from this clade since they historically had a widespread Eurasian distribution."

**Reference phylogeny:** For the purpose of applying the definition of *Notopalaeognathae*, Figure 1A in Cloutier et al. (2019) should be regarded as the primary reference phylogeny. Figure 1 in Yonezawa et al. (2017) may be regarded as a secondary reference phylogeny.

**Composition:** *Notopalaeognathae* includes all *Palaeognathae* except the ostriches.

**Diagnostic apomorphies:** Our examination of the morphological data set of Livezey and Zusi (2006, 2007) revealed only one potential apomorphy: Acetabulum, foramen acetabuli, bilateral compression and dorsal position relative to synsacrum in combination creating dorsally deep bilateral recessi—termed recessus acetabulo-synsacralis by Livezey and Zusi (2006)—visible through acetabulae (lateral perspective) and/or between ossa coxae et synsacrum (ventral perspective), present (1773b). This character state is not found in Tinamidae.

**Synonyms:** There are no synonyms.

**Homonyms:** There are no homonyms.

**Comments:** Evidence for a clade comprising all *Palaeognathae* except ostriches was first found by Hackett et al. (2008) and Harshman et al. (2008), and subsequently corroborated by Phillips et al. (2010), Haddrath and Baker (2012), Smith et al. (2013), Baker et al. (2014), Mitchell et al. (2014), Grealy et al. (2017), Yonezawa et al. (2017) and Cloutier et al. (2019).

The position of *Rheidae* among Palaeognathae is not congruently resolved, and three alternative positions have been inferred during the past decade: (i) as the sister-group to all other *Palaeognathae*, except ostriches (Figure 1 in Harshman et al., 2008; Phillips et al., 2010; Mitchell et al., 2014; Burleigh et al., 2015; Prum et al., 2015; Grealy et al., 2017; Yonezawa et al., 2017), (ii) as the sister-group to cassowaries, Emu and kiwis (*Novaeratitae*) (Haddrath and Baker, 2012; Baker et al., 2014; Reddy et al., 2017; Cloutier et al., 2019; Kimball et al., 2019), and (iii) as the sister-group to tinamous (Figure 2 in Harshman et al., 2008) or tinamous and moas (Smith et al., 2013). As a consequence, a definition with three internal specifiers was selected.

### *4.3. Novaeratitae Yuri, Kimball, Harshman, Bowie, Braun, Chojnowski, Han, Hackett, Huddleston, Moore, Reddy, Sheldon, Steadman, Witt and Braun (2013) [Sangster, Braun, Johansson, Kimball, Mayr and Suh], converted clade name*

**Registration number:** 697.

**Definition:** The least inclusive crown clade containing *Apteryx australis* Shaw, 1813 (*Apterygiformes*) and *Struthio Casuarius* (now *Casuarius casuarius*) Linnaeus, 1758 (*Casuariiformes*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Apteryx australis*

Shaw, 1813 & *Casuarius casuarius* (Linnaeus, 1758)).

**Etymology:** *Novaeratitae* is from the Latin words *novus* (new) and *ratis* (a raft). *Novae* refers to the three regions where this clade is found, namely New Guinea (*novaeguineae*), Australia (*novaehollandiae*), and New Zealand (*novaeseelandiae*) and *ratis* refers to the unkeeled sternum of these birds (Yuri et al., 2013).

**Reference phylogeny:** For the purpose of applying the definition of *Novaeratitae*, Figure 1a in Cloutier et al. (2019) should be regarded as the primary reference phylogeny. Figure 1 in Yonezawa et al. (2017) may be regarded as a secondary reference phylogeny.

**Composition:** *Apterygiformes* (kiwis, 5 extant species) and *Casuariiformes* (cassowaries, 3 extant species, and Emu).

The clade also includes the extinct *Aepyornithiformes* (elephant birds). The latter group comprises the taxa *Mullerornis*, *Vorombe* and *Aepyornis*. Accounts of the elephant birds are given in Hume and Walters (2012), Mayr (2017), Hansford and Turvey (2018) and Torres and Clarke (2018).

**Diagnostic apomorphies:** Diagnostic apomorphies are (characters and states are indicated by their number-letter combination in Livezey and Zusi, 2006, 2007): (1) Os carpi radiale, os proprius et facies articularis metacarpalis, vestigial, meniscoid, typically substantially smaller and of reduced functionality than os carpi ulnare (1562b); (2) Os metacarpale primus (I, alulare), absent (1580e); (3) Os metacarpale secundus (II, majus), closely synchondrotic with ossa metacarpalia I et III, spatium intermetacarpale obsolete or absent (1581c); (4) Phalanges digiti I (alularis, primus) manus, zero, phalanges alulae lacking entirely (1677f); (5) Phalanges digiti minus (III, tertius), zero, despite retention of os metacarpale III, typically vestigial (1679e); (6) Phalanx proximalis digiti I (alulae, primus), absent (1693b); (7) Junctura interphalangealis (proximalis) digiti majoris manus, synchondrosis (1756d); (8) M. rhomboideus superficialis, situs origii costae vertebrales, facies laterales (2512b); (9) M. biceps brachii, insertio(nes), one, insertio radialis only (2574d); (10) M. flexor (meta)carpi ulnaris, pars (caudalis) remigialis, vestigial or absent (2611b); (11) M. interosseus dorsalis (volaris), corpus, vestigial or absent, typically associated with reduction of spatium intermetacarpale (2622c); (12) M. interosseus ventralis (palmaris), absent (2624b); (13) M. extensor brevis alulae (pollicus), absent (2628b); (14) M. abductor alulae (pollicus), vestigial or absent (2629b); (15) M. adductor alulae (pollicus), absent (2632b); (16) M. flexor digiti minoris, absent (2635b). Many of these apomorphies are related to forelimb reduction and flightlessness. Given that a close relationship between the New Zealand kiwi and the Malagasy elephant birds implies multiple origins of flightlessness in this clade, it is possible that these character states developed convergently.

**Synonyms:** There are no synonyms.

**Homonyms:** There are no homonyms.

**Comments:** The monophyly of a clade formed by kiwis, emus and cassowaries is supported by at least 11 modern studies (Hackett et al., 2008; Harshman et al., 2008; Phillips et al., 2010; Haddrath and Baker, 2012; Smith et al., 2013; Baker et al., 2014; Mitchell et al., 2014; Grealy et al., 2017; Yonezawa et al., 2017; Cloutier et al., 2019; Kimball et al., 2019). The only recent study that did not recover a kiwi-emu-cassowary clade was Prum et al. (2015); reanalysis of the Prum et al. (2015) data in a multispecies coalescent framework does yield this clade (Braun and Kimball, 2021).

A node-based (minimum-crown-clade) definition was selected because there is congruent support for the basal dichotomy within *Novaeratitae* (Phillips et al., 2010; Haddrath and Baker, 2012; Smith et al., 2013; Baker et al., 2014; Mitchell et al., 2014; Grealy et al., 2017; Yonezawa et al., 2017; Cloutier et al., 2019).

### 4.4. *Dinocrypturi Sangster, Braun, Johansson, Kimball, Mayr and Suh, new clade name*

**Registration number:** 698.

**Definition:** The smallest clade containing *Tetrao major* (now *Tinamus major*) Gmelin, 1789 (*Tinamiformes*) and *Dinornis Novae-Zealandiae* (now *Dinornis novaezealandiae*) Owen, 1843 (*Dinornithiformes*). This is a minimum-clade definition. Abbreviated definition: min ∇ (*Tinamus major* (Gmelin, 1789) & *Dinornis novaezealandiae* Owen, 1843).

**Etymology:** Derived from the Greek δεινος (*deinos*), meaning terrible, and the Greek κρυπτικός (*krypticos*), from which Pycraft's (1900) name for the tinamous (*Crypturi*) was derived. The name combines elements of the names of the two main clades.

**Reference phylogeny:** For the purpose of applying the definition of *Dinocrypturi*, Figure 1 in Yonezawa et al. (2017) should be regarded as the primary reference phylogeny. Figure 2C in Grealy et al. (2017) may be regarded as a secondary reference phylogeny.

**Composition:** *Dinocrypturi* includes the tinamous (*Tinamiformes*, 46 extant species; Gill et al., 2020) and moas (*Dinornithiformes*, 10 extinct species; Gill, 2010).

**Diagnostic apomorphies:** No unambiguous morphological apomorphies are known, but it is noted that the *Dinornithidae* and *Tinamidae* are the only palaeognathous birds in which an ossified supratendinal bridge is consistently present on the tarsometatarsus (see, however, Mayr, 2019 for the occurrence of this feature in the Eocene *Palaeotididae*).

**Synonyms:** There are no synonyms.

**Homonyms:** There are no homonyms.

**Comments:** Evidence for a sister-group relationship of tinamous and moas was first documented by Phillips et al. (2010) and subsequently corroborated by Haddrath and Baker (2012), Smith et al. (2013), Baker et al. (2014), Mitchell et al. (2014), Grealy et al. (2017), Yonezawa et al. (2017), Cloutier et al. (2019), Urantówka et al. (2020), and Gordon et al. (2021).

A node-based (minimum-crown-clade) definition was selected because there is congruent support for the basal dichotomy within *Dinocrypturi* (Phillips et al., 2010; Haddrath and Baker, 2012; Smith et al., 2013; Baker et al., 2014; Mitchell et al., 2014; Grealy et al., 2017; Yonezawa et al., 2017; Cloutier et al., 2019; Urantówka et al., 2020).

The name *Dinornis giganteus*, used in several molecular papers (Grealy et al., 2017; Yonezawa et al., 2017), is a junior synonym of *Dinornis novaezealandiae* Owen, 1843 (Gill, 2010).

### 4.5. *Neognathae Pycraft, 1900 [Sangster, Braun, Johansson, Kimball, Mayr and Suh], converted clade name*

**Registration number:** 699.

**Definition:** The least inclusive crown clade containing *Phasianus* (now *Gallus*) *gallus* (Linnaeus, 1758) (*Galliformes*) and *Fringilla domestica* (now *Passer domesticus*) Linnaeus, 1758 (*Passeriformes*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Gallus gallus* (Linnaeus, 1758 & *Passer domesticus* (Linnaeus, 1758)).

**Etymology:** Derived from the Greek words νέος (*néos*) meaning "new", and γνάθος (*gnathos*), meaning "jaw", which together refer to the skeletal anatomy of the palate, which is considered to be more advanced than that in *Palaeognathae*.

**Reference phylogeny:** For the purpose of applying the definition of *Neognathae*, Figure 3 in Kuhl et al. (2021) should be regarded as the primary reference phylogeny. Figure 1 in Prum et al. (2015) may be regarded as a secondary reference phylogeny.

**Composition:** All *Aves* except *Palaeognathae*, i.e. a total of >10,000 extant bird species (Dickinson and Remsen, 2013; Dickinson and Christidis, 2014; Gill et al., 2020).

**Diagnostic apomorphies:** Diagnostic apomorphies are (characters and states are indicated by their number-letter combination in Livezey and Zusi, 2006, 2007): (1) Sutura frontoparietalis, absent, rendered indiscernable by synostosis (213b); (2) Os quadratum, processus mandibularis quadrati, facies articularis pterygoidea (facies ventralis in those taxa having two), condylar, tubercular, or jugo-sublinear (523c); (3) Junctura interpalatina et articulatio palatino-rostroparasphenoidalis ("palatorostralis"), preclusion by medial interposition of ossa vomera throughout length of palatum osseum, absent (579b); (4) Junctura

pterygopalatina, articulatio pterygo-palatina simplex (601b); (5) Sutura costouncinata, typus ligamentosus, absent, suturae typically indiscernable and synostosis complete in adults (1096b); (6) Corpus sterni, facies muscularis sterni, lineae intermusculares (dorsomedialis), present, bilateral pair in approximate parallel with axis medianus sterni (1106b); (7) Extremitas distalis humeri, facies caudalis, sulcus tendinis m. humerotricipitalis (*sensu stricto*), present (1487c); (8) Tuberculum preacetabulare (processus pectinealis), os principalis, os ilium (1809b); (9) Synchondrosis (caudalis) ilioischiadica (et fenestra ilioischiadica definitivum), present (1953b); (10) Extremitas proximalis tibiotarsi, caput tibiae, facies articulares medialis et lateralis, distinctness of mutual delimitation by area interarticularis et fossae retrocristales, marked (2068b); (11) Extremitas proximalis tibiotarsi, caput tibiotarsi, facies articularis fibularis, present, short jugum extending distal from margo capitis et/aut distinct lateral extension of rima capitis (2108c); (12) Os tibiale (astragalus), medial extent and contribution to tibiotarsus relative to extremitas distalis tibiotarsi, condylae lateralis et medialis restricted, forming only part of tibiotarsus, extremitas distalis tibiotarsi, typically only condylus lateralis (2209b); (13) Os pretibiale, absent (2216b); (14) Os tarsi distale proprius, contribution to extremitas proximalis tarsometatarsus proprius (i.e., laminar, dorsal, subangular corona for termini proximales ossa tarsalia, present, contributes to both lamina et hypotarsus (2217b).

**Synonyms:** *Carinatae* (*sensu* Sclater, 1880; Sharpe, 1891; Gadow, 1893; Prager and Wilson, 1980) and *Neoaves* (*sensu* Sibley and Ahlquist, 1990) are approximate synonyms.

**Homonyms:** Wetmore (1960) used the name *Neognathae* for a group comprising all *Aves* except *Spheniscidae* (penguins).

**Comments:** Evidence for a close relationship of all crown group birds except Palaeognathae was presented by Pycraft (1900), and supported by studies of morphological characters (Cracraft, 1986, 1988; Kurochkin, 1995; Mayr and Clarke, 2003; Livezey and Zusi, 2007), immunological distances among transferrins (Prager and Wilson, 1976; Prager et al. 1976), α-crystallin sequences (Stapel et al., 1984; Hedges et al., 1995; Caspers et al., 1997), 12S and 16S rRNA sequences (Hedges et al. 1995) and more recently by a series of phylogenomic studies (Table 1).

A node-based (minimum-crown-clade) definition was selected because there is congruent support for the basal dichotomy within *Neognathae* in recent molecular analyses, i.e. between *Galloanserae* and *Neoaves* (Hackett et al., 2008; Jarvis et al., 2014; Burleigh et al., 2015; Prum et al., 2015; Reddy et al., 2017; Liu et al., 2018; Kimball et al., 2019; Kuhl et al., 2021). A definition of the name *Neognathae* was previously given by Gauthier and De Queiroz (2001), who used a stem-modified node-based (maximum-crown-clade) definition, with *Pluvialis apricaria* as an internal specifier and *Struthio camelus* and *Tinamus major* as external specifiers.

The definition proposed here agrees with current usage of the name *Neognathae* (Cracraft, 1988, 2013; Cracraft and Mindell, 1989; Yuri et al., 2013; Jarvis et al., 2014).

In Linnean classifications the clade defined here as Neognathae has been ranked at the level of infraclass (Sibley and Ahlquist, 1990; Cracraft, 2013), parvclass (Kurochkin, 1995), and cohort (Livezey and Zusi, 2007).

### 4.6. *Neoaves Sibley, Ahlquist and Monroe (1988) [Sangster, Braun, Johansson, Kimball, Mayr and Suh], converted clade name*

**Registration number:** 700.

**Definition:** The most inclusive crown clade including *Fringilla domestica* (now *Passer domesticus*) Linnaeus, 1758 (*Passeriformes*) but not *Phasianus gallus* (now *Gallus gallus*) Linnaeus, 1758 (*Galliformes*). This is a maximum-crown-clade definition. Abbreviated definition: max crown ∇ (*Passer domesticus* (Linnaeus, 1758) ~ *Gallus gallus* (Linnaeus, 1758)).

**Etymology:** The prefix *neo-*, from the Greek νέος (*néos*) meaning "new", and the Latin *aves*, meaning birds.

**Reference phylogeny:** For the purpose of applying the definition of *Neoaves*, Figure 3 in Kuhl et al. (2021) should be regarded as the primary reference phylogeny. Figure 1 in Prum et al. (2015) may be regarded as a secondary reference phylogeny.

**Composition:** All *Aves* except *Palaeognathae* and *Galloanserae*, i.e. a total of >9600 extant bird species (Dickinson and Remsen, 2013; Dickinson and Christidis, 2014; Gill et al., 2020).

**Diagnostic apomorphies:** Diagnostic apomorphies are (characters and states are indicated by their number-letter combination in Livezey and Zusi, 2006, 2007): (1) Extremitas omalis coracoidei, processus glenoidalis coracoidei, facies (sulcus) articularis humeralis (labrum glenoidale), primary position (dorsoventral and lateromedial dimensions) relative to processus acrocoracoideus, dorsolateral (1280c); (2) Apparatus copulationis — Mm. retractores phalli caudalis et cranialis (organa masculina) aut mm. levator cloacae et dilator cloacae (organa feminina)— absent (2502b); (3) M. entepicondylo-ulnaris, absent (2586b); (4) Epididymis, ductulus conjugens testis, absent (2893b); (5) Apparatus copulationis, phallus protrudens, basis phalli, lymphobulbus phalli, corpus vasculare phalli, glomera corporis vascularis phalli, absent (2895b); (6) Apparatus copulationis, phallus protrudens, basis phalli, vasa lymphatica cloacalia, absent (2896b); (7) Proctodeum, phallus femininus, absent (2900d).

**Synonyms:** *Plethornithae* Groth and Barrowclough 1999 is an approximate synonym.

**Homonyms:** *Neoaves* (*sensu* Sibley and Ahlquist, 1990) also included *Galloanserae*.

**Comments:** Monophyly of a clade comprising all birds except *Palaegnathae* and *Galloanserae* is well supported by several early molecular data sets (Ho et al., 1976; Prager and Wilson, 1976; Stapel et al., 1984; Mindell and Honeycutt, 1989; Sibley and Ahlquist, 1990; Cooper and Penny, 1997; Mindell et al., 1997) and is now very strongly supported by phylogenomic data sets (Table 1).

The name *Neoaves* was proposed by Sibley et al. (1988) for a clade comprising all extant birds except *Palaeognathae* and *Galloanserae*. At the time, they considered Galloanserae to be the sister-taxon of *Palaeognathae* and combined the two groups under the name *Eoaves*. The grouping of *Galloanserae* with *Palaeognathae* was later replaced (Sibley and Ahlquist, 1990) by the now well corroborated topology that places *Palaeognathae* sister to *Neognathae*, which consists of two major clades, *Galloanserae* and *Neoaves*. Unfortunately, in their revised classification, Sibley and Ahlquist (1990) did not use the familiar and widely accepted names *Palaeognathae* and *Neognathae* but used instead their own names *Eoaves* and *Neoaves* in a new sense.

Groth and Barrowclough (1999) considered that Sibley and Ahlquist's change of the meaning of the name *Neoaves* was confusing and proposed the name *Plethornithae* for the clade consisting of all extant birds except *Palaeognathae* and *Galloanserae*. However, although Sibley and Ahlquist's (1990) subsequent use of the name *Neoaves* was unfortunate and may cause confusion, it does not invalidate this name. Thus, Neoaves does not have to be replaced by *Plethornithae*. The latter name is a junior synonym of *Neoaves*.

A definition of *Neoaves* was previously given by Gauthier and De Queiroz (2001), who used a stem-modified node-based (maximum-crown-clade) definition, with *Passer domesticus* as an internal specifier and *Gallus gallus* and *Anser anser* as external specifiers.

Comprehensive phylogenomic studies show no congruent support for the basal dichotomy at the base of Neoaves (reviewed by Suh, 2016). This, in combination with evidence for incomplete lineage sorting (Suh et al. 2015; Houde et al. 2020) suggests that the base of *Neoaves* represents a hard polytomy (Suh, 2016). For this reason, a maximum-crown-clade definition was selected.

### 4.7. *Columbimorphae Cracraft, 2013 [Sangster, Braun, Johansson, Kimball, Mayr and Suh], converted clade name*

**Registration number:** 701.

**Definition:** The least inclusive crown clade containing *Columba oenas* Linnaeus, 1758 (*Columbiformes*), *Mesites variegata* (now *Mesitornis*

*variegatus*) I. Geoffroy Saint-Hilaire, 1838 (*Mesitornithiformes*) and *Tetrao* (now *Pterocles*) *alchata* Linnaeus, 1766 (*Pteroclidiformes*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Columba oenas* Linnaeus, 1758 & *Mesitornis variegatus* (Geoffroy Saint-Hilaire, 1838) & *Pterocles alchata* (Linnaeus, 1766)).

**Etymology:** Derived from the Latin *Columba*, meaning pigeon or dove, and the Greek μορφή (*morphe*), meaning shape or form.

**Reference phylogeny:** For the purpose of applying the definition of *Columbimorphae*, Figure 1 in Prum et al. (2015) should be regarded as the primary reference phylogeny. Figure 1 in Jarvis et al. (2014) may be regarded as a secondary reference phylogeny.

**Composition:** This clade includes *Columbiformes* (331 extant species), *Mesitornithiformes* (3 extant species) and *Pteroclidiformes* (16 extant species) (Gill et al. 2020).

**Diagnostic apomorphies:** *Columbiformes* and *Pteroclidiformes* share numerous derived morphological characteristics and were considered closely related by many earlier authors (e.g., Stegmann, 1968; Mayr and Clarke, 2003). It is, however, difficult to characterize a clade that also includes the *Mesitornithiformes* with derived characters. Here we note that all three taxa exhibit a notarium and a humerus with a strongly developed and proximodistally elongated tuberculum dorsale. This tubercle serves for the attachment of musculus supracoracoideus and is usually strongly developed in birds capable of powerful flight. Its occurrence in the *Mesitornithiformes* is particularly remarkable, because mesites have very poor flight capabilities.

**Synonyms:** There are no synonyms.

**Homonyms:** There are no homonyms.

**Comments:** Monophyly of *Columbiformes*, *Mesitornithiformes* and *Pteroclidiformes* was first documented by Hackett et al. (2008) and subsequently recovered in five other phylogenomic studies (Table 1). *Cuculiformes* is sometimes recovered as part of this clade; specifically, *Cuculiformes* is nested within *Columbimorphae* in several Jarvis et al. (2014) trees (Figure 4C, Figure S14B, and Figure S14D) and in the primary tree in Kuhl et al. (2021).

A node-based (minimum-crown-clade) definition was selected because there is congruent support for the basal dichotomy within *Columbimorphae* in recent molecular analyses (Jarvis et al., 2014; Prum et al., 2015; Reddy et al., 2017; Kimball et al., 2019).

### 4.8. *Pteroclimesites Sangster, Braun, Johansson, Kimball, Mayr and Suh, new clade name*

**Registration number:** 702.

**Definition:** The least inclusive crown clade containing *Mesites variegata* (now *Mesitornis variegatus*) I. Geoffroy Saint-Hilaire, 1838 (*Mesitornithiformes*) and *Tetrao* (now *Pterocles*) *alchata* Linnaeus, 1766 (*Pteroclidiformes*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Mesitornis variegatus* (Geoffroy Saint-Hilaire, 1838) & *Pterocles alchata* (Linnaeus, 1766)).

**Etymology:** Derived from the scientific names of sandgrouse and mesites, which in turn are derived from the Greek πτερός (*pteros*, feather, wing) and κλεις (*kleis*, key), and μεσί (*mesi*, middle), respectively.

**Reference phylogeny:** For the purpose of applying the definition of *Pteroclimesites*, Figure 3 in Kuhl et al. (2021) should be regarded as the primary reference phylogeny. Figure 1 in Prum et al. (2015) may be regarded as a secondary reference phylogeny.

**Composition:** This clade includes *Mesitornithiformes* (mesites, 3 extant species) and *Pteroclidiformes* (sandgrouse, 16 extant species) (Dickinson and Remsen, 2013).

**Diagnostic apomorphies:** Our examination of the morphological data set of Livezey and Zusi (2006, 2007) revealed two potential apomorphies: (1) Corpus sterni, margo caudalis sterni, trabeculae caudolateralis, intermediana, et mediana, relative caudal extents caudal to margo caudalis proprius trabecula mediana ≥ trabecula caudolateralis ≥ trabecula intermedia (1192e); this character state is otherwise only found in *Afrotis* and *Passeriformes*; (2) Scapus (corpus) pubis (dorsal perspective), pars intermedia, flexible, filamentous, extremely reduced in diameter (1932b). The latter character state is otherwise only found in some members of *Galliformes*, *Suliformes*, *Geococcyx* and *Falconidae* (Livezey and Zusi, 2006, 2007).

**Synonyms:** There are no synonyms.

**Homonyms:** There are no homonyms.

**Comments:** The phylogenetic affinities of the mesites (*Mesitornithiformes*) and sandgrouse (*Pteroclidiformes*) have long been unclear due to incongruence among studies. Mesites have been found close to *Gruiformes* (Sibley and Ahlquist, 1990; Livezey, 1998), *Cuculidae* (Mayr and Ericson, 2004), and *Turnicidae* (Tunicidae) (Livezey and Zusi, 2007), whereas sandgrouse have been associated with *Charadriiformes* (Fjeldså, 1976; Sibley and Ahlquist, 1990) or *Columbiformes* (Livezey and Zusi, 2007; Mayr and Clarke, 2003). A sister-relationship of mesites and sandgrouse was first documented by Jarvis et al. (2014) and subsequently recovered in six other phylogenomic studies (Table 1).

A node-based (minimum-crown-clade) definition was selected because there is congruent support for the basal dichotomy within *Pteroclimesites* in recent molecular analyses (Jarvis et al., 2014; Prum et al., 2015; Suh et al., 2015; Reddy et al., 2017; Kimball et al., 2019; Kuhl et al., 2021).

### 4.9. *Musophagotides Sangster, Braun, Johansson, Kimball, Mayr and Suh, new clade name*

**Registration number:** 703.

**Definition:** The least inclusive crown clade containing *Otis tarda* Linnaeus, 1758 (*Otidiformes*) and *Musophaga violacea* Isert, 1789 (*Musophagiformes*) but not *Ardea Grus* (now *Grus grus*) Linnaeus, 1758 (*Gruiformes*) or *Mesites variegata* (now *Mesitornis variegatus*) I. Geoffroy Saint-Hilaire, 1838 (*Mesitornithiformes*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Otis tarda* Linnaeus, 1758 & *Musophaga violacea* Isert, 1789 ~ *Grus grus* (Linnaeus, 1758) & *Mesitornis variegatus* (I. Geoffroy Saint-Hilaire, 1838).

**Etymology:** derived from the New Latin *muso-* (from *Musa*, *a* genus of bananas and plantains), and the Latin *phaga* (eater) and *ōtis* (bustard).

**Reference phylogeny:** For the purpose of applying the definition of *Musophagotides*, Figure 3 in Kuhl et al. (2021) should be regarded as the primary reference phylogeny. Figure 1 in Jarvis et al. (2014) may be regarded as a secondary reference phylogeny.

**Composition:** This clade includes *Otidiformes* (bustards, 26 species) and *Musophagiformes* (turacos, 23–33 species) (Dickinson and Remsen, 2013; Gill et al., 2020; Perktaş et al., 2020).

**Diagnostic apomorphies:** Our examination of the morphological data set of Livezey and Zusi (2006, 2007) revealed one potential apomorphy: (1) vomer (synostotic ossa vomeris), processus pterygoideus, vestigial (467b). This state is only shared with *Galliformes*.

**Synonyms:** There are no synonyms.

**Homonyms:** There are no homonyms.

**Comments:** *Otidiformes* has long been associated with *Gruiformes* in pre-cladistic classifications (reviewed by Sibley and Ahlquist, 1990). However, current phylogenomic studies support a close relationship with *Musophagiformes* (McCormack et al., 2013; Jarvis et al., 2014; Suh et al., 2015; Kimball et al., 2019; Kuhl et al., 2021). The phylogeny of Prum et al. (2015) implies that *Cuculiformes* is also part of *Musophagotides*.

A minimum-crown-clade definition was selected because there is congruent support for a dichotomy within *Musophagotides* in recent molecular analyses (McCormack et al., 2013; Jarvis et al., 2014; Suh et al., 2015; Kimball et al., 2019; Kuhl et al., 2021). The external specifiers *Grus grus* (*Gruiformes*) and *Mesitornis variegatus* (*Mesitornithiformes*) were selected to prevent the name from being applied to conflicting phylogenomic topologies in which *Gruiformes* (Burleigh et al., 2015, Reddy et al., 2017, Figure 5 in Braun and Kimball, 2021) or *Mesitornithiformes* (Liu et al., 2018) would be part of *Musophagotides*.

### 4.10. *Phaethoquornithes Sangster, Braun, Johansson, Kimball, Mayr and Suh, new clade name*

**Registration number:** 704.

**Definition:** The least inclusive crown clade containing *Phaëthon* (now *Phaethon*) *aethereus* Linnaeus, 1758 (*Phaethontiformes*) and *Pelecanus onocrotalus* Linnaeus, 1758 (*Pelecaniformes*) but not *Hirundo* (now *Apus*) *apus* Linnaeus, 1758 (*Strisores*), *Charadrius hiaticula* Linnaeus, 1758 (*Charadriiformes*) or *Musophaga violacea* Isert, 1789 (*Musophagiformes*) or *Fringilla domestica* (now *Passer domesticus*) Linnaeus, 1758 (*Passeriformes*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Phaethon aethereus* Linnaeus, 1758 & *Pelecanus onocrotalus* Linnaeus, 1758 ~ *Apus apus* (Linnaeus, 1758) & *Charadrius hiaticula* Linnaeus, 1758 & *Musophaga violacea* Isert, 1789) & *Passer domesticus* (Linnaeus, 1758).

**Etymology:** Derived from the Greek *Phaethon*, which in Greek mythology was an epithet or surname of Helios (the sun) but was also used as the name of a son of Helios by Clymene, the Latin noun *aequor*, meaning expanse of water, and the Greek noun ορνις (*ornis*), meaning bird.

**Reference phylogeny:** For the purpose of applying the definition of *Phaethoquornithes*, Figure 3 in Kuhl et al. (2021) should be regarded as the primary reference phylogeny. Figure 1 in Prum et al. (2015) may be regarded as a secondary reference phylogeny.

**Composition:** This clade includes *Phaethontimorphae* (5 extant species) and *Aequornithes* (315–355 extant species) (Dickinson and Remsen, 2013; Gill et al., 2020).

**Diagnostic apomorphies:** No morphological apomorphies are known.

**Synonyms:** *Natatores* (*sensu* Livezey and Zusi, 2007) included *Mirandornithes* but did not include *Eurypygiformes*.

**Homonyms:** There are no homonyms.

**Comments:** This name is coined in accordance with a specific phylogenetic hypothesis, which is reflected by our proposed definition. This name is not applicable to topologies in which this grouping is not monophyletic (Hackett et al., 2008; McCormack et al., 2013; Burleigh et al., 2015; Reddy et al., 2017; Liu et al., 2018).

A minimum-crown-clade definition was selected because there is congruent support for the basal dichotomy within *Phaethoquornithes* in recent molecular analyses (Jarvis et al., 2014; Prum et al., 2015; Suh et al., 2015; Kimball et al., 2019; Kuhl et al., 2021).

### 4.11. *Phaethontimorphae Cracraft, 2013 [Sangster, Braun, Johansson, Kimball, Mayr and Suh], converted clade name*

**Registration number:** 705.

**Definition:** The least inclusive crown clade containing *Phaëthon* (now *Phaethon*) *aethereus* Linnaeus, 1758 (*Phaethontiformes*), *Eurypyga helias* Pallas, 1781 and *Rhynochetos jubatus* J. Verreaux and Des Murs, 1860. This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Phaethon aethereus* (Linnaeus, 1758) & *Eurypyga helias* Pallas, 1781 & *Rhynochetos jubatus* J. Verreaux and Des Murs, 1860).

**Etymology:** Derived from the Greek Φαέθων (*Phaethon*), which in Greek mythology was an epithet or surname of Helios (the sun) but was also used as the name of a son of Helios by Clymene, and the Greek μορφή (*morphe*), meaning shape or form.

**Reference phylogeny:** For the purpose of applying the definition of *Phaethontimorphae*, Figure 3 in Kuhl et al. (2021) should be regarded as the primary reference phylogeny. Figure 1 in Prum et al. (2015) may be regarded as a secondary reference phylogeny.

**Composition:** This clade includes five extant species: *Phaethon aethereus* (Red-billed Tropicbird), *P. lepturus* (White-tailed Tropicbird), *P. rubricauda* (Red-tailed Tropicbird), *Eurypyga helias* (Sunbittern) and *Rhynochetos jubatus* (Kagu).

An account of the extinct group *Prophaethontidae* was given by Mayr (2017, 2022).

**Diagnostic apomorphies:** No morphological apomorphies are known (Livezey and Zusi, 2006, 2007). We also note that one of the authors of the current paper (GM) questions whether the results of current molecular studies correctly reflect the true evolutionary history of the involved taxa (see Mayr, 2017).

**Synonyms:** There are no synonyms.

**Homonyms:** There are no homonyms.

**Comments:** The phylogenetic affinities of the tropicbirds (*Phaethon*) were long unclear due to incongruence among studies (Cracraft et al., 2004; Fain and Houde, 2004; Ericson et al., 2006; Hackett et al., 2008). Modern phylogenomic studies support a close relationship to Sunbittern (*Eurypyga helias*) and Kagu (*Rhynochetos jubatus*) (McCormack et al., 2013; Yuri et al., 2013; Jarvis et al., 2014; Prum et al., 2015; Liu et al., 2018; Kimball et al., 2019; Kuhl et al., 2021).

The name *Phaethontimorphae* has not been widely adopted yet, but it has been used for this clade by Jarvis et al. (2014), Suh (2016), Liu et al. (2018), Braun et al. (2019), and Braun and Kimball (2021).

A node-based (minimum-crown-clade) definition was selected because there is congruent support for the basal dichotomy within *Phaethontimorphae* in recent molecular analyses (Jarvis et al., 2014; Prum et al., 2015; Suh et al., 2015; Reddy et al., 2017; Liu et al., 2018; Kimball et al., 2019; Kuhl et al., 2021).

### 4.12. *Aequornithes Mayr, 2011 [Sangster, Braun, Johansson, Kimball, Mayr and Suh], converted clade name*

**Registration number:** 706.

**Definition:** The least inclusive crown clade containing *Pelecanus onocrotalus* Linnaeus, 1758 (*Pelecaniformes*) and *Colymbus Immer* (now *Gavia immer*) Brünnich, 1764 (*Gaviiformes*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Pelecanus onocrotalus* Linnaeus, 1758 & *Gavia immer* (Brünnich, 1764)).

**Etymology:** Derived from from the Latin noun *aequor*, meaning expanse of water, and the Greek noun ορνις (*ornis*), meaning bird.

**Reference phylogeny:** For the purpose of applying the definition of *Aequornithes*, Figure 3 in Kuhl et al. (2021) should be regarded as the primary reference phylogeny. Figure 1 in Prum et al. (2015) may be regarded as a secondary reference phylogeny.

**Composition:** *Aequornithes* includes the divers (*Gaviidae*), storm-petrels (*Hydrobatidae*, *Oceanitidae*), albatrosses (*Diomedeidae*), petrels and diving-petrels (*Procellariidae*), penguins (*Spheniscidae*), storks (*Ciconiidae*), frigatebirds (*Fregata*), darters (*Anhinga*), cormorants (*Phalacrocoracidae*), gannets and boobies (*Sulidae*), herons (*Ardeidae*), ibises (*Threskiornithidae*), pelicans (*Pelecanidae*), Shoebill (*Balaeniceps rex*) and Hamerkop (*Scopus umbretta*). This clade comprises 315–355 extant species, listings of which are given in Dickinson and Remsen (2013) and Gill et al. (2020).

**Diagnostic apomorphies:** No morphological apomorphies are known.

**Synonyms:** *Aequornithia* Cracraft, 2013 is an approximate synonym.

**Homonyms:** There are no homonyms.

**Comments:** A clade of aquatic and semi-aquatic birds, including the divers, storm-petrels, albatrosses, petrels (including diving-petrels), penguins, storks, frigatebirds, darters, cormorants, gannets and boobies, herons, ibises, pelicans, Shoebill and Hamerkop was first documented by Ericson et al. (2006) and further supported by several phylogenomic studies (Table 1).

A node-based (minimum-crown-clade) definition was selected because there is congruent support for the basal dichotomy within *Aequornithes* (i.e. between divers and all other extant members of the clade) in recent molecular analyses (Hackett et al., 2008, McCormack et al., 2013; Jarvis et al., 2014; Burleigh et al., 2015; Kuramoto et al., 2015; Prum et al., 2015; Suh et al., 2015; Reddy et al., 2017; Liu et al., 2018; Kimball et al., 2019; Kuhl et al., 2021).

### 4.13. Procellariimorphae Livezey and Zusi, 2007 [Sangster, Braun, Johansson, Kimball, Mayr and Suh], converted clade name

**Registration number:** 707.

**Definition:** The least inclusive crown clade containing *Diomedea demersa* (now *Spheniscus demersus*) Linnaeus, 1758 (*Sphenisciformes*) and *Procellaria aequinoctialis* Linnaeus, 1758 (*Procellariiformes*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Spheniscus demersus* (Linnaeus, 1758) & *Procellaria aequinoctialis* Linnaeus, 1758).

**Etymology:** Derived from the taxonomic name *Procellaria* which is "a modern adjectival form of the Latin word for a storm (*procella*) and gives the meaning of 'creatures of the storm' as is appropriate" (Marchant and Higgins, 1990: 557), and the Greek μορφή (*morphe*, shape, form).

**Reference phylogeny:** For the purpose of applying the definition of *Procellariimorphae*, Figure 3 in Kuhl et al. (2021) should be regarded as the primary reference phylogeny. Figure 1 in Prum et al. (2015) may be regarded as a secondary reference phylogeny.

**Composition:** Includes *Spheniscidae* (penguins), *Diomedeidae* (albatrosses), *Hydrobatidae* (northern storm-petrels), *Oceanitidae* (southern storm-petrels), *Procellariidae* (petrels, shearwaters, and diving petrels).

Accounts of the extinct group *Diomedeoididae* are provided by Mayr and Smith (2012) and Mayr (2017, 2022).

**Diagnostic apomorphies**: Diagnostic apomorphies are (characters and states are indicated by their number-letter combination in Livezey and Zusi, 2006, 2007): (1) Os lacrimale, processus orbitalis, lamina medialis, perforatio laminae obliquus, present (196b); (2) Os lacrimopalatinum, present, sublinear (722b); (3) Os humerus, virtual linearity independent of relative elongation, present, linear, elongate (1347b); (4) Digitus IV pedis, phalanx proximalis, basis phalangis, tuberculum flexorium, prominently symmetrical bilobation (proximal perspective), present, tuberculum typically bilobate (2404b); (5) Aponeurosis carpo-alularis dorsalis, present, broad and robust (2630b); (6) Naris externum, ducti tubulares (bilaterally paired ostia externa), comprising ostium efferens glandulae et ostium efferens respiratorium, present in early ontogeny, absent in juvenile and definitive semaphorants (2744b); (7) Pennae auriculares, plumae auriculares rostrales et caudales, present, acoustically redirecting buttress in taxa possessing or lacking facial auditory discs (2933b).

**Synonyms:** *Austrodyptornithes* Yuri et al., 2013 is an approximate synonym.

**Homonyms:** There are no homonyms.

**Comments:** The relationships of *Sphenisciformes* and *Procellariiformes* were long uncertain due to conflicting relationships inferred from limited morphological or molecular data (Sibley and Ahlquist, 1990; Cooper and Penny, 1997; García-Moreno et al., 2003; Mayr and Clarke, 2003; Chubb, 2004; Cracraft et al., 2004; Poe and Chubb, 2004; Bourdon, 2005; Smith, 2010). Among early studies, only McKitrick (1991a, 1991b) and Livezey (2001) had found a sister-group relationship of *Sphenisciformes* and *Procellariiformes*. Modern phylogenomic data now overwhelmingly support the monophyly of *Sphenisciformes* + *Procellariiformes* (Table 1).

The name *Austrodyptornithes* was proposed by Yuri et al. (2013) but this name refers to the same clade that Livezey and Zusi (2007) had named *Procellariimorphae*. Both names are currently in use; for instance, *Procellariimorphae* was used by Cracraft (2013), Jarvis et al. (2014) and Suh (2016), and *Austrodyptornithes* was used by Ksepka and Phillips (2015), Kuramoto et al. (2015), Kimball et al. (2019) and Kooijman (2020). We have selected *Procellariimorphae* over *Austrodyptornithes* based on the (informal) priority of the former.

A node-based (minimum-crown-clade) definition was selected because there is congruent support for the basal dichotomy within *Procellariimorphae* in recent molecular analyses (Hackett et al., 2008; McCormack et al., 2013; Jarvis et al., 2014; Burleigh et al., 2015; Prum et al., 2015; Reddy et al., 2017; Liu et al., 2018; Kimball et al., 2019; Kuhl et al., 2021).

### 4.14. Pelecanimorphae Livezey and Zusi, 2007 [Sangster, Braun, Johansson, Kimball, Mayr and Suh], converted clade name

**Registration number:** 708.

**Definition:** The least inclusive crown clade containing *Pelecanus onocrotalus* Linnaeus, 1758 (*Pelecaniformes*), *Pelecanus leucogaster* (now *Sula leucogaster*) Boddaert, 1783 (*Suliformes*) and *Ardea ciconia* (now *Ciconia ciconia*) Linnaeus, 1758 (Ciconiiformes). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Pelecanus onocrotalus* Linnaeus, 1758 & *Sula leucogaster* (Boddaert, 1783) & *Ciconia ciconia* (Linnaeus, 1758)).

**Etymology:** Derived from the Greek πελεκάν (*pelecan*, pelican) and the Greek μορφή (*morphe*, shape, form).

**Reference phylogeny:** For the purpose of applying the definition of *Pelecanimorphae*, Figure 3 in Kuhl et al. (2021) should be regarded as the primary reference phylogeny. Figure 1 in Prum et al. (2015) may be regarded as a secondary reference phylogeny.

**Composition:** *Pelecanimorphae* includes the storks (*Ciconiidae*), frigatebirds (*Fregatidae*), darters (*Anhingidae*), cormorants (*Phalacrocoracidae*), gannets and boobies (*Sulidae*), herons (*Ardeidae*), ibises (*Threskiornithidae*), pelicans (*Pelecanidae*), Shoebill (*Balaeniceps rex*) and Hamerkop (*Scopus umbretta*).

**Diagnostic apomorphies:** No morphological apomorphies are known.

**Synonyms**: *Pelecaniformes* Sharpe, 1891 (*sensu* Cracraft, 2013) is an approximate synonym.

**Homonyms:** Livezey and Zusi (2007) used the name for a group that comprised *Pelagornithidae* ("*Odontopterygidae*"; now considered to be galloanserine birds; Mayr, 2017, 2022), *Balaenicipitidae*, *Phaethontidae*, *Fregatidae*, *Pelecanidae*, *Sulidae*, *Phalacrocoracidae* and *Anhingidae*, but which excluded *Ciconiidae*, *Ardeidae* and *Threskiornithidae*. Cracraft (2013) used *Pelecanimorphae* as a redundant name for his *Pelecaniformes* (see above).

**Comments:** Monophyly of a clade formed by storks, frigatebirds, cormorants, gannets, herons, ibises and pelicans is supported by congruence of multiple phylogenomic data sets (Table 1).

The name *Pelecaniformes* has long been associated with a polyphyletic group comprising the tropicbirds (*Phaethontidae*), pelicans (*Pelecanidae*), gannets and boobies (*Sulidae*), cormorants (*Phalacrocoracidae*), darters (*Anhingidae*) and frigatebirds (*Fregatidae*) (e.g. Howard & Moore 1991). After the clarification of relationships among these groups, several authors have restricted the name *Pelecaniformes* to a group comprising pelicans, Shoebill, Hamerkop, herons and ibises, have applied the name *Suliformes* to the frigatebirds, darters, cormorants, gannets and boobies, and have restricted the name *Ciconiiformes* to the storks (Yuri et al., 2013; Mayr, 2017; Kimball et al., 2019; Kuhl et al., 2021). We follow these authors here. Following Cracraft (2013), we use the name *Pelecanimorphae* for the clade comprising these three major groups.

A node-based (minimum-crown-clade) definition was selected because there is congruent support for the basal subdivision within *Pelecanimorphae* in recent molecular analyses (Hackett et al., 2008; Yuri et al., 2013; Burleigh et al., 2015; Kuramoto et al., 2015; Prum et al., 2015; Reddy et al., 2017; Kimball et al., 2019; Kuhl et al., 2021).

The name *Pelecanimorphae* is sometimes ascribed to Huxley (1867) (e.g. Livezey and Zusi, 2007) but Huxley (1867) did not actually mention this name in his work. Instead, he included the pelicans (*Pelecanidae*) with other totipalmate birds in a group called *Dysporomorphae*.

### 4.15. Pelecanes Sangster, Braun, Johansson, Kimball, Mayr and Suh, new clade name

**Registration number:** 754.

**Definition:** The least inclusive crown clade containing *Pelecanus onocrotalus* Linnaeus, 1758 (*Pelecaniformes*) and *Pelecanus leucogaster* (now *Sula leucogaster*) Boddaert, 1783 (*Suliformes*). This is a minimum-

crown-clade definition. Abbreviated definition: min crown ∇ (*Pelecanus onocrotalus* Linnaeus, 1758 & *Sula leucogaster* (Boddaert, 1783)).

**Etymology:** Derived from the Greek πελεκάν (*pelecan*, pelican).

**Reference phylogeny:** For the purpose of applying the definition of *Pelecanes*, Figure 1 in Prum et al. (2015) should be regarded as the primary reference phylogeny. Figure 3 in Kuhl et al. (2021) may be regarded as a secondary reference phylogeny.

**Composition:** *Pelecanes* includes the frigatebirds (*Fregatidae*), darters (*Anhingidae*), cormorants (*Phalacrocoracidae*), gannets and boobies (*Sulidae*), herons (*Ardeidae*), ibises (*Threskiornithidae*), pelicans (*Pelecanidae*), Shoebill (*Balaeniceps rex*) and Hamerkop (*Scopus umbretta*).

**Diagnostic apomorphies:** Our examination of the morphological data set of Livezey and Zusi (2006, 2007) revealed one potential apomorphy: Extremitas proximalis tibiotarsi, caput tibiotarsi, crista cnemialis lateralis, crista patellaris, truncate and crescentiform, imbedded within vertex lateroproximalis of unified cristae cnemiales, at obtuse angulus with corpus tibiotarsi (2105f). This character state is only shared with *Phaethon* and *Uria*. An elongated hallux may also represent a synapomorphy of *Pelecanes* (Mayr, 2017).

**Synonyms**: there are no synonyms.

**Homonyms:** there are no homonyms.

**Comments:** Monophyly of a clade formed by frigatebirds, cormorants, gannets, herons, ibises and pelicans is supported by congruence of multiple phylogenomic data sets (Table 1; see also Kuramoto et al. 2015).

A node-based (minimum-crown-clade) definition was selected because there is congruent support for the basal subdivision within *Pelecanes* in recent molecular analyses (Hackett et al., 2008; Yuri et al., 2013; Burleigh et al., 2015; Kuramoto et al., 2015; Prum et al., 2015; Reddy et al., 2017; Kimball et al., 2019; Kuhl et al., 2021).

### *4.16. Telluraves Yuri, Kimball, Harshman, Bowie, Braun, Chojnowski, Han, Hackett, Huddleston, Moore, Reddy, Sheldon, Steadman, Witt and Braun (2013) [Sangster, Braun, Johansson, Kimball, Mayr and Suh], converted clade name*

**Registration number:** 709.

**Definition:** The least inclusive crown clade containing *Falco Nisus* (now *Accipiter nisus*) Linnaeus, 1758 (*Accipitriformes*) and *Fringilla domestica* (now *Passer domesticus*) Linnaeus, 1758 (*Passeriformes*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Accipiter nisus* (Linnaeus, 1758) & *Passer domesticus* (Linnaeus, 1758)).

**Etymology:** Derived from the Latin words *telluris* (the earth, earth, land) and *aves* (birds) (Yuri et al., 2013).

**Reference phylogeny:** For the purpose of applying the definition of *Telluraves*, Figure 3 in Kuhl et al. (2021) should be regarded as the primary reference phylogeny. Figure 1 in Prum et al. (2015) may be regarded as a secondary reference phylogeny.

**Composition:** *Telluraves* comprises all members of *Afroaves* and *Australaves*.

**Diagnostic apomorphies:** No morphological apomorphies are known.

**Synonyms:** There are no synonyms.

**Homonyms:** There are no homonyms.

**Comments:** This clade was first recovered by Ericson et al. (2006) and is now strongly supported by congruence of phylogenomic data sets (Table 1).

A node-based (minimum-crown-clade) definition was selected because there is congruent support for the basal dichotomy within *Telluraves* in recent molecular analyses (Hackett et al., 2008; Jarvis et al., 2014; Burleigh et al., 2015; Prum et al., 2015; Suh et al., 2015; Reddy et al., 2017; Kimball et al., 2019; Kuhl et al., 2021).

### *4.17. Afroaves Ericson, 2012 [Sangster, Braun, Johansson, Kimball, Mayr and Suh], converted clade name*

**Registration number:** 710.

**Definition:** The least inclusive crown clade containing *Falco Nisus* (now *Accipiter nisus*) Linnaeus, 1758 (*Accipitriformes*), *Loxia colius* (now *Colius colius*) Linnaeus, 1766 (*Coliiformes*) and *Picus viridis* Linnaeus, 1758 (*Piciformes*) but not *Fringilla domestica* (now *Passer domesticus*) Linnaeus, 1758 (*Passeriformes*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Accipiter nisus* (Linnaeus, 1758) & *Colius colius* (Linnaeus, 1766) & *Picus viridis* Linnaeus, 1758) ~ *Passer domesticus* (Linnaeus, 1758).

**Etymology:** Derived from the word *Africa*, and the Latin *aves*, meaning birds. The name ('African birds') refers to the inferred African origin of the clade (Ericson, 2012).

**Reference phylogeny:** For the purpose of applying the definition of *Afroaves*, Figure 3 in Kuhl et al. (2021) should be regarded as the primary reference phylogeny. Figure 3 in Reddy et al. (2017) may be regarded as a secondary reference phylogeny.

**Composition:** Includes *Accipitriformes* (hawks and allies), *Strigiformes* (owls), *Coliiformes* (mousebirds), *Leptosomiformes* (cuckoo-rollers), *Trogoniformes* (trogons), *Bucerotiformes* (hornbills and allies), *Upupiformes* (hoopoes and allies), *Coraciiformes* (rollers and allies), and *Piciformes* (woodpeckers and allies).

The clade also includes the extinct *Teratornithidae*, a group related to hawks and allies (Mayr, 2017), the extinct *Sandcoleidae*, which are stem group representatives of mousebirds (Houde and Olson, 1992; Ksepka and Clarke, 2010; Mayr, 2017, 2022), the extinct *Ogygoptyngidae* and *Protostrigidae*, and other groups related to owls (Mayr, 2009, 2017, 2022), *Messelirrisoridae*, a group related to hoopoes and wood hoopoes (Mayr, 2017), *Primobucconidae*, *Eocoraciidae* and *Geranopteridae*, three stem group taxa related to rollers and ground-rollers (Mayr, 2017) and *Sylphornithidae*, possible stem group representatives of the *Piciformes* (Mayr, 2017, 2022).

**Diagnostic apomorphies:** No morphological apomorphies are known.

**Synonyms:** *Coracornithes* Fürbringer, 1888 is a partial synonym. *Coracornithia* Cracraft, 2013 was derived from that name and is an approximate synonym.

**Homonyms:** There are no homonyms.

**Comments:** A clade comprising hawks and allies, owls, mousebirds, cuckoo-roller, trogons, hornbills and allies, rollers and allies, and woodpeckers and allies was first recovered by Ericson et al. (2006). This clade is now overwhelmingly supported by phylogenomic data (Table 1).

The name *Afroaves* was introduced by Ericson (2012) and is now in wide use (Yuri et al., 2013; Jarvis et al., 2014; Brusatte et al., 2015; Suh, 2016). As a consequence, we have selected this name rather than *Coracornithia* Cracraft, 2013.

The basal dichotomy within *Afroaves* differs among recent molecular analyses. Most studies support a dichotomy between *Accipitriformes* and all other *Afroaves* (Hackett et al., 2008; Jarvis et al., 2014; Burleigh et al., 2015; Reddy et al., 2017; Kimball et al., 2019; Kuhl et al., 2021) but one study inferred a dichotomy between *Coliiformes* and all other *Afroaves* (Suh et al. 2015, this issue is further reviewed by Suh, 2016). A node-based (minimum-crown-clade) definition was selected that reflects both hypotheses. In two recent phylogenomic studies, *Accipitriformes* was sister to a large clade that included not only mousebirds, owls, cuckoo-roller, trogons, hornbills, rollers, woodpeckers but also Australaves (Prum et al., 2015; Liu et al., 2018).

### *4.18. Coraciimorphae Cracraft, 2013 [Sangster, Braun, Johansson, Kimball, Mayr and Suh], converted clade name*

**Registration number:** 711.

**Definition:** The least inclusive crown clade containing *Loxia* (now *Colius*) *colius* Linnaeus, 1766 (*Coliiformes*) and *Picus viridis* Linnaeus, 1758 (*Piciformes*) but not *Falco nisus* (now *Accipiter nisus*) Linnaeus, 1758 (*Accipitriformes*) or *Fringilla domestica* (now *Passer domesticus*) Linnaeus, 1758 (*Passeriformes*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Colius colius* (Linnaeus, 1766) & *Picus*

*viridis* Linnaeus, 1758) ~ *Accipiter nisus* (Linnaeus, 1758) & *Passer domesticus* (Linnaeus, 1758).

**Etymology:** From the Greek κορακίας (*korakías*), derived from κόραξ (*korax*), meaning raven or crow, and the Greek μορφή (*morphe*), meaning shape or form.

**Reference phylogeny:** For the purpose of applying the definition of *Coraciimorphae*, Figure 3 in Kuhl et al. (2021) should be regarded as the primary reference phylogeny. Figure 1 in Prum et al. (2015) may be regarded as a secondary reference phylogeny.

**Composition:** Includes *Coliiformes* (mousebirds), *Leptosomiformes* (cuckoo-rollers), *Trogoniformes* (trogons), *Bucerotiformes* (hornbills and allies), *Upupiformes* (hoopoes and allies), *Coraciiformes* (rollers and allies), and *Piciformes* (woodpeckers and allies).

The clade also includes the extinct taxa *Sandcoleidae*, a group related to mousebirds (Houde and Olson, 1992; Ksepka and Clarke, 2010; Mayr, 2017), *Ogygoptyngidae, Protostrigidae*, and other groups related to owls (Mayr, 2009, 2017), *Messelirrisoridae*, a group related to hoopoes and wood hoopoes (Mayr, 2017), *Primobucconidae*, *Eocoraciidae* and *Geranopteridae*, three stem group taxa related to rollers and ground-rollers (Mayr, 2017) and *Sylphornithidae*, a stem group related to *Piciformes* (Mayr, 2017).

**Diagnostic apomorphies:** No morphological apomorphies are known.

**Synonyms:** There are no synonyms.

**Homonyms:** There are no homonyms.

**Comments:** Monophyly of a clade formed by mousebirds, cuckoo-rollers, trogons, hornbills and allies, rollers and allies, and woodpeckers and allies is supported by congruence of multiple phylogenomic data sets (Table 1). Whereas most phylogenomic studies support a closer position of *Coliiformes* to *Coraciiformes* than to *Accipitriformes* and *Strigiformes*, two analyses placed *Coliiformes* sister to a clade that includes *Accipitriformes*, *Strigiformes* and all other *Afroaves* (the ultraconserved element tree in Jarvis et al., 2014 and the Suh et al., 2015 retroposon study). Thus, we have added the external specifier *Accipiter nisus* (*Accipitriformes*) to prevent the name from being applied to that conflicting phylogenomic topologies.

A node-based (minimum-crown-clade) definition was selected because there is congruent support for the basal dichotomy within *Coraciimorphae* in recent molecular analyses (Jarvis et al., 2014; Prum et al., 2015; Reddy et al., 2017; Liu et al., 2018; Kimball et al., 2019; Kuhl et al., 2021). This is also present in Kimball et al. (2013), Gilbert et al. (2018), and Houde et al. (2019).

### *4.19. Cavitaves Yuri, Kimball, Harshman, Bowie, Braun, Chojnowski, Han, Hackett, Huddleston, Moore, Reddy, Sheldon, Steadman, Witt and Braun (2013) [Sangster, Braun, Johansson, Kimball, Mayr and Suh], converted clade name*

**Registration number:** 712.

**Definition:** The least inclusive crown clade containing *Cuculus* (now *Leptosomus*) *discolor* Hermann, 1783 and *Picus viridis* Linnaeus, 1758 (*Piciformes*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Leptosomus discolor* (Hermann, 1783) & *Picus viridis* Linnaeus, 1758).

**Etymology:** Derived from the Latin *cavus* (hollow, hole), referring to the cavity-nesting habits of the clade, and *aves* (birds).

**Reference phylogeny:** For the purpose of applying the definition of *Cavitaves*, Figure 3 in Kuhl et al. (2021) should be regarded as the primary reference phylogeny. Figure 1 in Prum et al. (2015) may be regarded as a secondary reference phylogeny.

**Composition:** *Leptosomiformes* (cuckoo-rollers), *Trogoniformes* (trogons), *Bucerotiformes* (hornbills and allies), *Upupiformes* (hoopoes and allies), *Coraciiformes* (rollers and allies), and *Piciformes* (woodpeckers and allies).

The clade also includes the extinct taxa *Messelirrisoridae*, a group related to hoopoes and wood hoopoes (Mayr, 2017), *Primobucconidae*, *Eocoraciidae* and *Geranopteridae*, three stem group taxa related to rollers and ground-rollers (Mayr, 2017) and *Sylphornithidae*, a stem group related to *Piciformes* (Mayr, 2017).

**Diagnostic apomorphies:** No morphological apomorphies are known.

**Synonyms:** There are no synonyms.

**Homonyms:** There are no homonyms.

**Comments:** Monophyly of a clade formed by cuckoo-rollers, trogons, hornbills and allies, rollers and allies, and woodpeckers and allies is supported by congruence of multiple phylogenomic data sets (Table 1).

A node-based (minimum-crown-clade) definition was selected because there is congruent support for the basal dichotomy within *Cavitaves* in recent molecular analyses (Hackett et al., 2008; Jarvis et al., 2014; Burleigh et al., 2015; Prum et al., 2015; Suh et al., 2015; Reddy et al., 2017; Liu et al., 2018; Kimball et al., 2019; Kuhl et al., 2021).

### *4.20. Eucavitaves Yuri, Kimball, Harshman, Bowie, Braun, Chojnowski, Han, Hackett, Huddleston, Moore, Reddy, Sheldon, Steadman, Witt and Braun (2013) [Sangster, Braun, Johansson, Kimball, Mayr and Suh], converted clade name*

**Registration number:** 713.

**Definition:** The least inclusive crown clade containing *Trogon viridis* Linnaeus, 1766 (*Trogoniformes*) and *Picus viridis* Linnaeus, 1758 (*Piciformes*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Trogon viridis* Linnaeus, 1766 & *Picus viridis* Linnaeus, 1758).

**Etymology:** Derived from the Latin *cavus* (hollow, hole), refering to the cavity-nesting habits of the clade, and *aves* (birds) (Yuri et al., 2013) combined with the Greek *eu* (well, good) to indicate that this group corresponds to the core Cavitaves.

**Reference phylogeny:** For the purpose of applying the definition of *Eucavitaves*, Figure 3 in Kuhl et al. (2021) should be regarded as the primary reference phylogeny. Figure 1 in Prum et al. (2015) may be regarded as a secondary reference phylogeny.

**Composition:** *Trogoniformes* (trogons), *Bucerotiformes* (hornbills and allies), *Upupiformes* (hoopoes and allies), *Coraciiformes* (rollers and allies), and *Piciformes* (woodpeckers and allies).

The clade also includes the extinct taxa *Messelirrisoridae*, a group related to hoopoes and wood hoopoes (Mayr, 2017), *Primobucconidae*, *Eocoraciidae* and *Geranopteridae*, three stem group taxa related to rollers and ground-rollers (Mayr, 2017) and *Sylphornithidae*, a stem group related to *Piciformes* (Mayr, 2017).

**Diagnostic apomorphies:** No morphological apomorphies are known.

**Synonyms:** There are no synonyms.

**Homonyms:** There are no homonyms.

**Comments:** Monophyly of a clade formed by trogons, hornbills and allies, rollers and allies, and woodpeckers and allies is supported by congruence of multiple phylogenomic data sets (Table 1).

A node-based (minimum-crown-clade) definition was selected because there is congruent support for the basal dichotomy within *Eucavitaves* in recent molecular analyses (Hackett et al., 2008; McCormack et al., 2013; Jarvis et al., 2014; Burleigh et al., 2015; Prum et al., 2015; Suh et al., 2015; Reddy et al., 2017; Liu et al., 2018; Kimball et al., 2019; Kuhl et al., 2021).

### *4.21. Picocoraciades Mayr, 2011 [Sangster, Braun, Johansson, Kimball, Mayr and Suh], converted clade name*

**Registration number:** 714.

**Definition:** The least inclusive crown clade containing *Buceros rhinoceros* Linnaeus, 1758 (*Bucerotiformes*), *Coracias garrulus* Linnaeus, 1758 (*Coraciiformes*) and *Picus viridis* Linnaeus, 1758 (*Piciformes*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Buceros rhinoceros* Linnaeus, 1758 & *Coracias garrulus* Linnaeus, 1758 &

*Picus viridis* Linnaeus, 1758).

**Etymology:** Derived from the Latin *picus* (woodpecker), and the Greek κορακίας (*korakías*), derived from κόραξ (*korax*), meaning raven or crow.

**Reference phylogeny:** For the purpose of applying the definition of *Picocoraciades*, Figure 3 in Kuhl et al. (2021) should be regarded as the primary reference phylogeny. Figure 1 in Prum et al. (2015) may be regarded as a secondary reference phylogeny.

**Composition:** *Bucerotiformes* (hornbills and allies), *Upupiformes* (hoopoes and allies), *Coraciiformes* (rollers, kingfishers, motmots, bee-eaters, todies, ground rollers) and *Piciformes* (woodpeckers, honey-guides, toucans, barbets, puffbirds and jacamars).

The clade also includes the extinct taxa *Messelirrisoridae*, a group related to hoopoes and wood hoopoes (Mayr, 2017), *Primobucconidae*, *Eocoraciidae* and *Geranopteridae*, three stem group taxa related to rollers and ground-rollers (Mayr, 2017) and *Sylphornithidae*, a stem group related to *Piciformes* (Mayr, 2017).

**Diagnostic apomorphies:** Mayr (2014) identified a well-defined sulcus for the tendon of m. extensor longus alulae on the radial carpal as a synapomorphy. Mayr (2008a) also listed a mandible that projects beyond the upper beak in hatchlings, reduced ventral secondary coverts, and a marked medial parahypotarsal fossa in which the medial margin forms a sharp ridge as potential synapomorphies, citing Manegold (2005).

**Synonyms:** There are no synonyms.

**Homonyms:** There are no homonyms.

**Comments:** Molecular phylogenetic studies have shown that *Coraciiformes* (*sensu* Voous, 1977; del Hoyo et al. 2001) is not monophyletic and that some taxa in *Coraciiformes* are more closely related to *Piciformes* than to other taxa traditionally included in *Coraciiformes* (Ericson et al., 2006; Brown et al., 2008; Hackett et al., 2008; McCormack et al., 2013; Yuri et al., 2013; Burleigh et al., 2015; Prum et al., 2015; Reddy et al., 2017). The name *Coraciiformes* has become restricted to the bee-eaters (*Meropidae*), todies (*Todidae*), motmots (*Momotidae*), rollers (*Coraciidae*), ground rollers (*Brachypteraciidae*) and kingfishers (*Alcedinidae*), whereas the clade comprising hoopoes (*Upupidae*), woodhoopoes (*Phoeniculidae*) and hornbills (*Bucerotidae*) has become known under the names *Bucerotiformes* (Sangster et al., 2013; Yuri et al., 2013; Cracraft, 2013) and *Bucerotes* (Mayr, 2011).

A node-based (minimum-crown-clade) definition was selected because there is congruent support for the basal dichotomy within *Picocoraciae* in recent molecular analyses (Hackett et al., 2008; McCormack et al., 2013; Yuri et al., 2013; Burleigh et al., 2015; Prum et al., 2015; Suh et al., 2015; Reddy et al., 2017).

The name was spelled '*Picocoraciae*' by Mayr (2011) and subsequent authors. It is here amended to *Picocoraciades* to make it grammatically correct (Coraciades is the correct plural of Coracias).

### 4.22. *Picodynastornithes [Sangster, Braun, Johansson, Kimball, Mayr and Suh], converted clade name*

**Registration number:** 715.

**Definition:** The least inclusive crown clade containing *Coracias garrulus* Linnaeus, 1758 (*Coraciidae*), *Gracula* (now *Alcedo*) *atthis* Linnaeus, 1758 (*Alcedinidae*) and *Picus viridis* Linnaeus, 1758 (*Piciformes*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Coracias garrulus* Linnaeus, 1758 & *Alcedo atthis* (Linnaeus, 1758) & *Picus viridis* Linnaeus, 1758).

**Etymology:** Derived from the Latin *picus* (woodpecker), the Greek δυνάστης (*dynastes*, lord, master, ruler) in reference to the "king" in kingfishers (Yuri et al. 2013), and the Greek noun ορνις (*ornis*), meaning bird.

**Reference phylogeny:** For the purpose of applying the definition of *Picodynastornithes*, Figure 3 in Kuhl et al. (2021) should be regarded as the primary reference phylogeny. Figure 1 in Prum et al. (2015) may be regarded as a secondary reference phylogeny.

**Composition:** *Coraciiformes* (rollers, kingfishers, motmots, bee-eaters, todies, ground rollers) and *Piciformes* (woodpeckers, honey-guides, toucans, barbets, puffbirds and jacamars).

The clade also includes the extinct taxa *Primobucconidae*, *Eocoraciidae* and *Geranopteridae*, three stem group taxa related to rollers and ground-rollers (Mayr, 2017) and *Sylphornithidae*, a stem group related to *Piciformes* (Mayr, 2017).

**Diagnostic apomorphies:** A bifurcated scapular acromion is a potential synapomorphy of *Picodynastornithes*, although this character state is absent in *Galbulae* (Mayr, 2009, 2022).

**Synonyms:** There are no synonyms.

**Homonyms:** There are no homonyms.

**Comments:** There is strong, congruent support for a sister relationship of *Coraciiformes* and *Piciformes* (e.g. Sibley and Ahlquist, 1990; Ericson et al., 2006, Table 1).

A node-based (minimum-crown-clade) definition was selected because there is congruent support for the basal dichotomy within *Picodynastornithes* in recent molecular analyses (Hackett et al., 2008; Yuri et al., 2013; Jarvis et al., 2014; Burleigh et al., 2015; Prum et al., 2015; Suh et al., 2015; Reddy et al., 2017; Liu et al., 2018; Kimball et al., 2019; Kuhl et al., 2021).

### 4.23. *Australaves Ericson, 2012 [Sangster, Braun, Johansson, Kimball, Mayr and Suh], converted clade name*

**Registration number:** 716.

**Definition:** The least inclusive crown clade containing *Palamedea* (now *Cariama*) *cristata* Linnaeus, 1766 (*Cariamiformes*) and *Fringilla domestica* (now *Passer domesticus*) Linnaeus, 1758 (*Passeriformes*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Cariama cristata* (Linnaeus, 1766) and *Passer domesticus* (Linnaeus, 1758)).

**Etymology:** Derived from the Latin *australis*, meaning southern, and the Latin *aves*, meaning birds.

**Reference phylogeny:** For the purpose of applying the definition of *Australaves*, Figure 3 in Kuhl et al. (2021) should be regarded as the primary reference phylogeny. Figure 1 in Prum et al. (2015) may be regarded as a secondary reference phylogeny.

**Composition:** The clade comprises the extant groups *Cariamiformes* (2 extant species, seriemas), *Falconiformes* (64 species, Dickinson and Remsen, 2013), *Psittaciformes* (376 species, Dickinson and Remsen, 2013) and *Passeriformes* (6063 species, Dickinson and Christidis, 2014).

The clade also includes the extinct *Idiornithidae*, *Bathornithidae*, and *Phorusrhacidae*, which are stem group representatives of the *Cariamiformes* (Angst et al. 2013; Degrange et al., 2015; Mayr, 2017, 2022), *Quercypsittidae*, a stem-group of *Psittaciformes* (Ksepka et al., 2011; Mayr, 2017), *Halcyornithidae*, *Messelasturidae* and *Vastanavidae*, which are stem groups of *Psittaciformes* or *Psittacopasseres* or perhaps even outside the total-group of *Psittacopasseres* (Ksepka et al., 2011, 2019; Mayr, 2015, 2017, 2021), *Psittacopedidae*, which is a possible stem-group of *Passeriformes* (Ksepka et al., 2019; Mayr, 2020), and the taxon *Zygodactylidae*, which is believed to represent the extinct sister-group of passerines (Mayr, 2008b, see also Mayr, 2015, 2017).

**Diagnostic apomorphies:** No morphological apomorphies are known. Suh et al. (2011) identified two retroposons that are apomorphic for this clade. A subsequent study identified a larger number of retroposons (Suh et al., 2015).

**Synonyms:** *Passerimorphae* (*sensu* Cracraft, 2013) is an approximate synonym.

**Homonyms:** There are no homonyms.

**Comments:** The existence of a clade formed by seriemas, falcons, parrots and passerines was first documented by Ericson et al. (2006), and further supported by subsequent phylogenomic studies (Table 1, see also Wang et al. 2012). The name was originally spelled '*Australavis*' by Ericson (2012); it was emended to *Australaves* by Yuri et al. (2013). The name *Australaves* is now in wide use (e.g. Jarvis et al., 2014; Brusatte

et al., 2015; Prum et al., 2015; Suh, 2016).

A node-based (minimum-crown-clade) definition was selected because there is multiple genomic support for the basal dichotomy within *Australaves* (i.e. between *Cariamidae* and *Eufalconimorphae*) in recent molecular analyses (Hackett et al., 2008; Jarvis et al., 2014; Burleigh et al., 2015; Prum et al., 2015; Suh et al., 2015; Liu et al., 2018; Kimball et al., 2019; Kuhl et al., 2021).

### 4.24. *Eufalconimorphae Suh, Paus, Kiefmann, Churakov, Franke, Brosius, Kriegs and Schmitz (2011) [Sangster, Braun, Johansson, Kimball, Mayr and Suh], converted clade name*

**Registration number:** 717.

**Definition:** The least inclusive crown clade containing *Falco subbuteo* Linnaeus, 1758 (*Falconiformes*) and *Fringilla domestica* (now *Passer domesticus*) Linnaeus, 1758 (*Passeriformes*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Falco subbuteo* Linnaeus, 1758 and *Passer domesticus* (Linnaeus, 1758)).

**Etymology:** Derived from the Greek *eu* (well, good, true), the Latin *falco* (falcon) and the Greek μορφή (*morphe*), meaning shape or form.

**Reference phylogeny:** For the purpose of applying the definition of *Eufalconimorphae*, Figure 3 in Kuhl et al. (2021) should be regarded as the primary reference phylogeny. Figure 1 in Prum et al. (2015) may be regarded as a secondary reference phylogeny.

**Composition:** The clade comprises the extant groups *Falconiformes* (64 species, Dickinson and Remsen, 2013), *Psittaciformes* (376 species, Dickinson and Remsen, 2013) and *Passeriformes* (6063 species, Dickinson and Christidis, 2014).

The clade also includes the extinct *Quercypsittidae*, a stem-group of *Psittaciformes* (Ksepka et al., 2011; Mayr, 2017), *Halcyornithidae*, *Messelasturidae* and *Vastanavidae*, which are stem groups of *Psittaciformes* or *Psittacopasseres* or may be outside the total-group of *Psittacopasseres* (Ksepka et al., 2011, 2019; Mayr, 2015, 2017, 2021), *Psittacopedidae*, which is a possible stem-group of *Passeriformes* (Ksepka et al., 2019; Mayr, 2020), and the taxon *Zygodactylidae*, which is believed to represent the extinct sister-group of passerines (Mayr, 2008b, see also Mayr, 2017).

**Diagnostic apomorphies:** Suh et al. (2011) identified three retroposons that are apomorphic for this clade. A subsequent study identified a larger number of retroposons (Suh et al., 2015). Our examination of the morphological data set of Livezey and Zusi (2006, 2007) revealed no morphological apomorphies. However, Pyle (2013) observed that falcons and parrots share a distinctive wing molt sequence that may therefore be a synapomorphy of *Eufalconimorphae* which is lost in *Passeriformes*.

**Synonyms:** The name *Australaves* was used by Ericson (2012) for a clade that also included *Cariamidae*, the latter being depicted as the sister taxon of *Falconidae*. Under the definitions in this paper, the names *Australaves* and *Eufalconimorphae* would refer to the same clade if *Cariamidae* were indeed the sister taxon of *Falconidae* (as in Wang et al., 2012). However, all subsequent phylogenomic studies have placed *Cariamidae* as the sister to the falcon-parrot-passerine clade. As a consequence, *Eufalconimorphae* is here applied to its original clade and *Australaves* is here applied to a more inclusive clade that also includes *Cariamidae*.

**Homonyms:** There are no homonyms.

**Comments:** Evidence for this clade was first presented by Hackett et al. (2008) with moderate support. The clade received further support from a retroposon study (Suh et al., 2011) and all subsequent phylogenomic studies (Table 1).

Yuri et al. (2013) noted there is a potential for confusion due to the prior use of *Falconimorphae* for the non-monophyletic group comprising *Accipitriformes* and *Falconidae*. Yuri et al. (2013) also noted that the taxon *Eufalconimorphae* includes many non-raptorial taxa (*Psittaciformes* and *Passeriformes*) and excludes a raptorial taxon (*Cariamiformes*). They concluded that it seems inappropriate to use *Eufalconimorphae* and they instead recommended using *Australaves*. However, modern evidence shows that seriemas are not sister to falcons (*contra* Ericson, 2012; Wang et al., 2012), and that *Eufalconimorphae* and *Australaves* are not synonyms.

A node-based (minimum-crown-clade) definition was selected because there is congruent support for the basal dichotomy within *Eufalconimorphae* in recent molecular analyses (Hackett et al., 2008; Suh et al., 2011, 2015, 2015; McCormack et al., 2013; Jarvis et al., 2014; Prum et al., 2015; Kimball et al., 2019; Kuhl et al., 2021).

### 4.25. *Psittacopasseres Suh, Paus, Kiefmann, Churakov, Franke, Brosius, Kriegs and Schmitz (2011) [Sangster, Braun, Johansson, Kimball, Mayr and Suh], converted clade name*

**Registration number:** 718.

**Definition:** The least inclusive crown clade containing *Psittacus erithacus* Linnaeus, 1758 (*Psittaciformes*) and *Fringilla domestica* (now *Passer domesticus*) Linnaeus, 1758 (*Passeriformes*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Psittacus erithacus* Linnaeus, 1758 and *Passer domesticus* (Linnaeus, 1758)).

**Etymology:** Derived from the Latin *psittacus*, meaning a parrot, and the Latin *passer*, meaning a sparrow.

**Reference phylogeny:** For the purpose of applying the definition of *Psittacopasseres*, Figure 3 in Kuhl et al. (2021) should be regarded as the primary reference phylogeny. Figure 1 in Prum et al. (2015) may be regarded as a secondary reference phylogeny.

**Composition:** *Psittaciformes* (376 recent species, Dickinson and Remsen, 2013) and *Passeriformes* (6063 recent species, Dickinson and Christidis, 2014).

The clade also includes the extinct *Quercypsittidae*, a stem-group of *Psittaciformes* (Ksepka et al., 2011; Mayr, 2017), *Psittacopedidae*, which is a possible stem-group of *Passeriformes* (Mayr, 2015, 2020; Ksepka et al., 2019), and the taxon *Zygodactylidae*, which is believed to represent the extinct sister-group of passerines (Mayr, 2008b, see also Mayr, 2017). It is not clear whether *Halcyornithidae*, *Messelasturidae* and *Vastanavidae* are members of this clade (Ksepka et al., 2019; Mayr, 2015, 2017, 2021).

**Diagnostic apomorphies:** Suh et al. (2011) identified six retroposons that are apomorphic for this clade. A larger number of retroposons was identified in a subsequent study (Suh et al. 2015). Our examination of the morphological data set of Livezey and Zusi (2006, 2007) revealed no morphological apomorphies. However, a possible synapomorphy is the separation of the accessory trochlea of the fourth toe from the main body of this trochlea by a furrow, a character state that is shared between parrots and stem-*Passeriformes* but not found (i.e. likely lost) in crown *Passeriformes* (Mayr, 2015).

**Synonyms:** *Passerimorphae* (*sensu* Jarvis et al., 2014) is an approximate synonym.

**Homonyms:** There are no homonyms.

**Comments:** A clade comprising *Psittaciformes* and *Passeriformes* is supported by congruence of multiple phylogenomic data sets (Table 1). A node-based (minimum-crown-clade) definition was selected because there is congruent support for the basal dichotomy within *Psittacopasserae* in recent molecular analyses (Hackett et al., 2008; Suh et al., 2011, 2015; Wang et al., 2012; McCormack et al., 2013; Jarvis et al., 2014; Burleigh et al., 2015; Prum et al., 2015; Reddy et al., 2017; Liu et al., 2018; Kimball et al., 2019; Kuhl et al., 2021).

The name was spelled '*Psittacopasserae*' by Suh et al. (2011) and subsequent authors. It is here amended to *Psittacopasseres* to make it grammatically correct (Passeres is the correct plural of Passer).

## Ethics statement

Not applicable.

## Declaration of competing interest

The authors declare that they have no competing interests.

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## Author's contributions

GS – Conceptualization, Investigation, Writing - Original Draft; ELB, USJ, RTK, GM, AS – Validation, Writing - Review & Editing. All authors read and approved the final manuscript.

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