

Phylogenetic definitions for *Caprimulgimorphae* (Aves) and major constituent clades under the International Code of Phylogenetic Nomenclature

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Abstract

Phylogenetic nomenclature, a system of taxonomic nomenclature in which taxon names are defined based on phylogenetic relationships, has been widely adopted in recent decades, particularly by vertebrate palaeontologists. However, formal regulation of this taxonomic system had been non-existent until the recent implementation of the *International Code of Phylogenetic Nomenclature (PhyloCode)*. To fulfil the requirements of the *PhyloCode*, we explicitly establish phylogenetic definitions that we recommended in a recent phylogenetic study on the avian taxon *Caprimulgimorphae* (which includes nightjars, potoos, frogmouths, swifts, hummingbirds, and others) and many of its major constituent subclades. Two new names are coined: *Sedentaves* (for the smallest crown clade uniting *Steatornis* and *Nyctibiidae*) and *Letornithes* (for the smallest crown clade uniting *Podargidae* and *Daedalornithes*). We also briefly review the fossil record and diagnostic morphological apomorphies of caprimulgimorph clades for which relevant information is available.

Key words

Caprimulgiformes, nomenclature, phylogeny, *Strisores*, taxonomy.

Introduction

Phylogenetic nomenclature is a system of taxonomic nomenclature in which taxon names are defined based on the phylogenetic relationships among organisms (DE QUEIROZ & GAUTHIER, 1990). Although the basic tenets of phylogenetic nomenclature have been widely adopted, particularly by vertebrate palaeontologists (e.g., SERENO, 1998; CLARKE, 2004; JOYCE *et al.*, 2004; NESBITT, 2011; O'LEARY *et al.*, 2013; HENDRICKX *et al.*, 2015; EZCURRA, 2016; CHEN *et al.*, 2019; FIELD *et al.*, 2020), the establishment of taxon names and their associated definitions under this taxonomic system had not been formally regulated until recently. As of June 2020, the *International Code of Phylogenetic Nomenclature (PhyloCode)* (DE QUEIROZ & CANTINO, 2020) has gone into effect with the publication of the companion volume *Phylonyms: A Companion*

to the *PhyloCode* (DE QUEIROZ *et al.*, 2020) and the registration database *RegNum* (CELLINESE & DELL, 2020), thus providing a long-awaited framework of formal rules and guidelines for phylogenetic nomenclature. Per *PhyloCode* Recommendation 6.1A, all technical taxon names will be italicized in the present contribution.

Under *PhyloCode* Article 7.1, phylogenetic definitions recommended prior to the publication of *Phylonyms* are not considered established. To be formally recognized, all previously suggested phylogenetic definitions must be re-established in a subsequent publication fulfilling the requirements outlined by the *PhyloCode*. A recent paper we co-authored (CHEN *et al.*, 2019) proposed the first explicit phylogenetic definitions for many of the higher-order taxon names within *Caprimulgimorphae* (including the crown

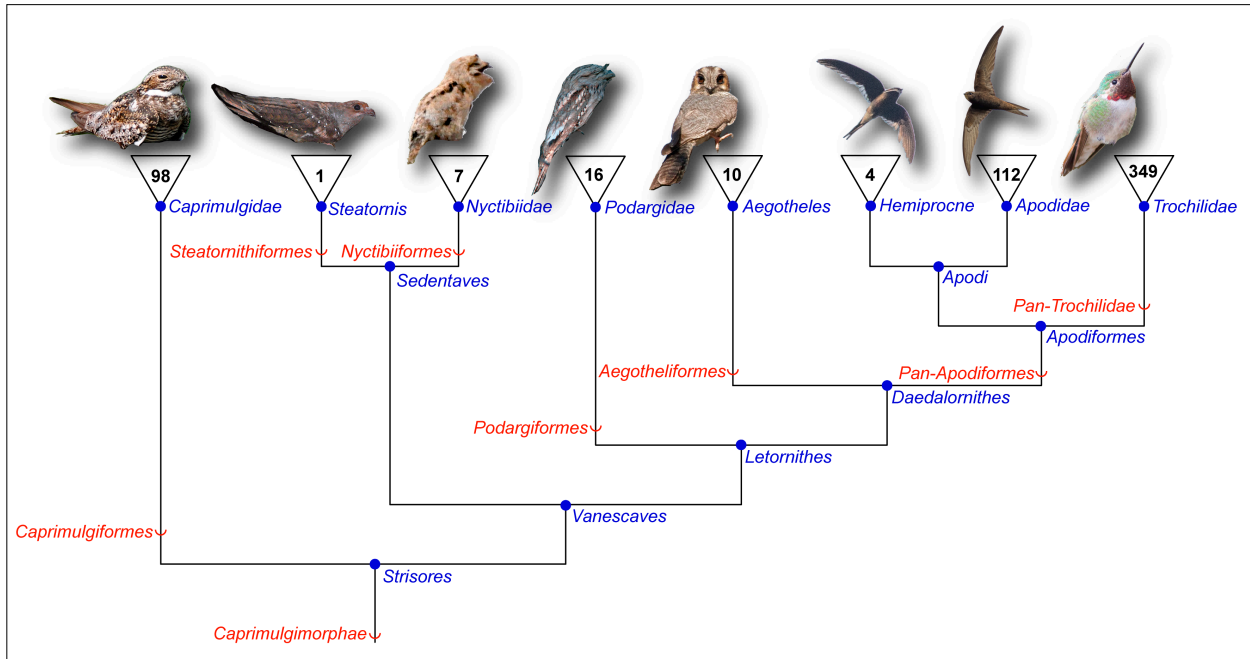


Fig. 1. Phylogenetically defined names for *Caprimulgimorphae* shown on the best-supported topology for this clade from CHEN *et al.* (2019). All definitions follow those proposed in the present contribution, except for *Daedalornithes* and *Apodiformes*, which follow SANGSTER (2020a, b), and *Pan-Trochilidae* and *Trochilidae*, which follow MCGUIRE *et al.* (2009). Closed circles at nodes denote node-based names for crown clades (associated names written in blue to the right of the relevant node), and open semi-circles denote branch-based names for the total clade comprising that branch and the crown clade it subtends (associated names written in red to the left of the relevant semi-circle). Triangles with numbers represent extant crown clade diversity of terminal taxa, with the number of extant species following version 1 of Birds of the World (BILLERMAN *et al.*, 2020). The steatornithiform crown clade contains only *Steatornis caripensis*. The names *Podargocypseli*, *Cypselomorphae*, and *Caprimulgi* are defined in the main text, but are not applicable to this tree; conversely, some of the names shown here may not be applicable to other topologies. All photos © Daniel J. Field; photographed species (L–R) are *Chordeiles minor* (*Caprimulgidae*), *Steatornis caripensis*, *Nyctibius griseus* (*Nyctibiidae*), *Podargus strigoides* (*Podargidae*), *Aegotheles cristatus*, *Hemiprocne comata*, *Apus apus* (*Apodidae*), and *Selasphorus platycercus* (*Trochilidae*).

clade *Strisores*), an avian clade that has been the subject of numerous other phylogenetic studies (MAYR, 2002, 2010a; BRAUN & HUDDLESTON, 2009; NESBITT *et al.*, 2011; KSEPKA *et al.*, 2013; WHITE & BRAUN, 2019). As the first and only authors to explicitly suggest phylogenetic definitions for most of these clade names, in this manuscript we aim to formalize these definitions, restated or modified from CHEN *et al.* (2019) following the rules of the *PhyloCode*. In addition, diagnostic morphological apomorphies are reviewed for select clades that have been adequately sampled and characterized in morphological studies.

CHEN *et al.* (2019) also proposed or listed phylogenetic definitions for the caprimulgimorph clades *Daedalornithes* and *Apodiformes*; however, those names have already been defined following *PhyloCode* requirements by SANGSTER (2020a, b), so they will not be covered here. A graphical representation of our recommended taxonomic scheme is shown in Fig. 1.

Phylogenetic nomenclature

As in CHEN *et al.* (2019), we have elected to define several names for hypothesized clades that have not been recovered by the most recent phylogenetic analyses, name-

ly *Podargocypseli*, *Cypselomorphae*, and *Caprimulgi*. Although we recognize that the balance of available evidence does not support the monophyly of these groups, we do not exclude the possibility that future research may revive support for at least some of them, given that the interrelationships within *Caprimulgimorphae* have proven challenging to disentangle definitively. Defining *Podargocypseli*, *Cypselomorphae*, and *Caprimulgi* here ensures that phylogenetically defined names are available for these hypothetical clades if they gain newfound support in the future, and also facilitates discussion about historical hypotheses of caprimulgimorph phylogeny.

Caprimulgimorphae Cracraft, 2013 [Chen & Field], converted clade name

Registration number. 383

Definition. The total clade containing *Caprimulgus europaeus* Linnaeus, 1758 (*Caprimulgidae*), *Steatornis caripensis* Humboldt, 1817 (*Steatornithidae*), *Nyctibius* (originally *Caprimulgus grandis* (Gmelin, 1789) (*Nyctibiidae*), *Podargus* (originally *Caprimulgus) strigoides* (Latham, 1801) (*Podargidae*), *Aegotheles* (originally *Capri-*

mulgus cristatus (Shaw in White, 1790) (*Aegothelidae*), and *Apus* (originally *Hirundo*) *apus* (Linnaeus, 1758) (*Apodiformes*) but not *Phoenicopterus ruber* Linnaeus, 1758 (*Mirandornithes* or *Phoenicoptermorphae*), *Columba oenas* Linnaeus, 1758 (*Columbimorphae*), *Otis tarda* Linnaeus, 1758 (*Otidimorphae*), *Musophaga* (originally *Tauraco*) *violacea* (Isert, 1788) (*Otidimorphae*), *Opisthocomus* (originally *Phasianus*) *hoazin* (Statius Müller, 1776) (*Opisthocomiformes*), *Grus* (originally *Ardea*) *grus* (Linnaeus, 1758) (*Gruiformes*), *Charadrius hiaticula* Linnaeus, 1758 (*Charadriiformes*), *Phaethon aethereus* Linnaeus, 1758 (*Phaethontimorphae*), *Procellaria aequinoctialis* Linnaeus, 1758 (*Aequornithes*), and *Vultur gryphus* Linnaeus, 1758 (*Telluraves*). This is a total-clade definition.

Abbreviated definition. Total ∇ (*Caprimulgus europaeus* Linnaeus, 1758 & *Steatornis caripensis* Humboldt, 1817 & *Nyctibius grandis* (Gmelin, 1789) & *Podargus strigoides* (Latham, 1801) & *Aegotheles cristatus* (Shaw, 1790) & *Apus apus* (Linnaeus, 1758) ~ *Phoenicopterus ruber* Linnaeus, 1758 & *Columba oenas* Linnaeus, 1758 & *Otis tarda* Linnaeus, 1758 & *Musophaga violacea* (Isert, 1788) & *Opisthocomus hoazin* (Statius Müller, 1776) & *Grus grus* (Linnaeus, 1758) & *Charadrius hiaticula* Linnaeus, 1758 & *Phaethon aethereus* Linnaeus, 1758 & *Procellaria aequinoctialis* Linnaeus, 1758 & *Vultur gryphus* Linnaeus, 1758).

Reference phylogeny. Figure 1 in PRUM *et al.* (2015) should be considered the primary reference phylogeny. Figure 1 in JARVIS *et al.* (2014) and Figure 3 in REDDY *et al.* (2017) may be regarded as secondary reference phylogenies.

Composition. *Caprimulgimorphae* includes *Strisores* and all extinct taxa more closely related to *Strisores* than to any other extant taxon. At present, no definitive members of *Caprimulgimorphae* outside of *Strisores* have been identified in the fossil record.

Comments. CRACRAFT (2013) coined *Caprimulgimorphae* as an alternative to *Strisores* (see comments on *Strisores*) to provide a name with a suitable suffix to be ranked at the level of superorder. Correspondence between assigned rank and name formulation is not of concern under the *PhyloCode* (Article 3.1) beyond the encouragement of definitions consistent with a nested hierarchy that specific prefixes or suffixes imply (Recommendation 11G). CHEN *et al.* (2019) suggested the use of *Caprimulgimorphae* for total-group *Strisores*, allowing both names to retain utility in rank-based classifications. As *Caprimulgimorphae* is the only pre-existing name that has been proposed for the total group of *Strisores*, we follow this definition here.

Given that the precise interrelationships among the major clades of neoavian birds remain unsettled, we employ multiple external specifiers representing major neoavian groups recovered as monophyletic by most

recent phylogenomic studies (JARVIS *et al.*, 2014; PRUM *et al.*, 2015; REDDY *et al.*, 2017; KIMBALL *et al.*, 2019; KUHL *et al.*, 2020).

Strisores Cabanis, 1847 [Chen & Field],
converted clade name

Registration number. 384

Definition. The smallest crown clade containing *Caprimulgus europaeus* Linnaeus, 1758 (*Caprimulgiformes*), *Steatornis caripensis* Humboldt, 1817 (*Steatornithiformes*), *Nyctibius* (originally *Caprimulgus*) *grandis* (Gmelin, 1789) (*Nyctibiiformes*), *Podargus* (originally *Caprimulgus*) *strigoides* (Latham, 1801) (*Podargiformes*), *Aegotheles* (originally *Caprimulgus*) *cristatus* (Shaw, 1790) (*Aegotheliformes*), and *Apus* (originally *Hirundo*) *apus* (Linnaeus, 1758) (*Apodiformes*). This is a minimum-crown-clade definition.

Abbreviated definition. Min crown ∇ (*Caprimulgus europaeus* Linnaeus, 1758 & *Steatornis caripensis* Humboldt, 1817 & *Nyctibius grandis* (Gmelin, 1789) & *Podargus strigoides* (Latham, 1801) & *Aegotheles cristatus* (Shaw, 1790) & *Apus apus* (Linnaeus, 1758)).

Reference phylogeny. Figure 1 in PRUM *et al.* (2015) should be considered the primary reference phylogeny. Figure 6 in CHEN *et al.* (2019) and Figure 6 in WHITE & BRAUN (2019) may be regarded as secondary reference phylogenies.

Composition. *Strisores* includes over 590 extant species (BILLERMAN *et al.*, 2020; GILL *et al.*, 2020) in the crown clades *Caprimulgidae*, *Steatornis*, *Nyctibiidae*, *Podargidae*, *Aegotheles*, and *Apodiformes*, as well as the last common ancestor of those groups and its extinct descendants. A wide variety of extinct taxa have been assigned to *Strisores* (MAYR, 2009, 2017; CHEN *et al.*, 2019).

Diagnostic apomorphies. The only identified potential morphological apomorphy shared by all examined members of the clade is an elongated *crus longum* of the ulnar carpal (MAYR, 2010a). However, other inferred apomorphies widespread within the group include a beak shorter than the rest of the skull (except in *Fluvioviridavis*, *Podargiformes*, and [*Eurotrochilus* + *Trochilidae*]), a prominent caudolateral process on the palatine (except in *Fluvioviridavis*, *Steatornis*, and *Trochilidae*), a short orbital process of the quadrate (except in *Fluvioviridavis* and *Steatornis*), a pointed mandibular symphysis (except in *Masillapodargus* and *Batrachostomus*), 18 or fewer presacral vertebrae (except in *Steatornithiformes*), and a long, deep transverse sulcus on the humerus (except in *Podargidae* and *Trochilidae*) (CHEN *et al.*, 2019).

Comments. The name *Strisores* is commonly attributed to BAIRD (1858) (including by CHEN *et al.*, 2019), but it

was in fact first coined by CABANIS (1847). Some taxonomists have instead used *Caprimulgiformes* (CRACRAFT, 2013; BRAUN *et al.*, 2019; JARVIS *et al.*, 2014; BILLERMAN *et al.*, 2020; KUHL *et al.*, 2020) as a name for this clade, occasionally in conjunction with *Caprimulgimorphae* (CRACRAFT, 2013; JARVIS *et al.*, 2014). However, we favour the application of *Strisores* here, as it has nominal priority over competing names, has seen widespread recent use in both neontological (MAYR, 2010a; YURI *et al.*, 2013; PRUM *et al.*, 2015; KIMBALL *et al.*, 2019; WHITE & BRAUN, 2019) and palaeontological (NESBITT *et al.*, 2011; MAYR, 2017; CHEN *et al.*, 2019) literature, and was originally used for a grouping that included most members of this clade other than *Podargidae* (CABANIS, 1847). In contrast, traditional usage of *Caprimulgiformes* excluded all members of *Apodiformes*. See also comments on *Caprimulgiformes*.

Podargocypseli Mayr, 2010a [Chen & Field], converted clade name

Registration number. 385

Definition. The smallest crown clade containing *Caprimulgus europaeus* Linnaeus, 1758 (*Caprimulgidae*), *Nyctibius* (originally *Caprimulgus grandis* (Gmelin, 1789) (*Nyctibiidae*)), *Podargus* (originally *Caprimulgus strigoides* (Latham, 1801) (*Podargidae*)), *Aegotheles* (originally *Caprimulgus cristatus* (Shaw, 1790) (*Aegothelidae*)), and *Apus* (originally *Hirundo apus* (Linnaeus, 1758) (*Apodiformes*)) but not *Steatornis caripensis* Humboldt, 1817 (*Steatornithidae*). This is a minimum-crown-clade definition.

Abbreviated definition. Min crown ∇ (*Caprimulgus europaeus* Linnaeus, 1758 & *Nyctibius grandis* (Gmelin, 1789) & *Podargus strigoides* (Latham, 1801) & *Aegotheles cristatus* (Shaw, 1790) & *Apus apus* (Linnaeus, 1758) ~ *Steatornis caripensis* Humboldt, 1817).

Reference phylogeny. Figure 3 in MAYR (2010a) should be considered the primary reference phylogeny.

Composition. *Podargocypseli* is hypothesized to include the crown clades *Caprimulgidae*, *Nyctibiidae*, *Podargidae*, *Aegotheles*, and *Apodiformes*, as well as the last common ancestor of those groups and its extinct descendants.

Diagnostic apomorphies. MAYR (2010a) recovered a prominent caudolateral process on the palatine and 18 or fewer presacral vertebrae as apomorphies of this group. Under the total-evidence topologies found by CHEN *et al.* (2019), *Podargocypseli* does not exist, and these features are instead optimized as apomorphies of *Strisores*. MAYR (2010a) additionally noted that the ability to enter torpor is widespread in *Podargocypseli*; it is likely that this character would also be inferred to be an apomorphy of *Strisores* in the total-evidence topologies of CHEN *et al.* (2019).

Comments. MAYR (2010a) coined this name in accordance with a specific phylogenetic hypothesis, which is reflected by our proposed definition. This name is inapplicable to topologies in which this grouping is not monophyletic (e.g., Fig. 1; HACKETT *et al.*, 2008; KSEPKA *et al.*, 2013; PRUM *et al.*, 2015; REDDY *et al.*, 2017; CHEN *et al.*, 2019; WHITE & BRAUN, 2019; KUHL *et al.*, 2020).

Cypselomorphae Huxley, 1867 [Chen & Field], converted clade name

Registration number. 386

Definition. The total clade containing *Caprimulgus europaeus* Linnaeus, 1758 (*Caprimulgidae*), *Nyctibius* (originally *Caprimulgus grandis* (Gmelin, 1789) (*Nyctibiidae*)), *Aegotheles* (originally *Caprimulgus cristatus* (Shaw, 1790) (*Aegothelidae*)), and *Apus* (originally *Hirundo apus* (Linnaeus, 1758) (*Apodiformes*)) but not *Steatornis caripensis* Humboldt, 1817 (*Steatornithidae*) and *Podargus* (originally *Caprimulgus strigoides* (Latham, 1801) (*Podargidae*)). This is a total-clade definition.

Abbreviated definition. Total ∇ (*Caprimulgus europaeus* Linnaeus, 1758 & *Nyctibius grandis* (Gmelin, 1789) & *Aegotheles cristatus* (Shaw, 1790) & *Apus apus* (Linnaeus, 1758) ~ *Steatornis caripensis* Humboldt, 1817 & *Podargus strigoides* (Latham, 1801)).

Reference phylogeny. Figure 3 in MAYR (2010a) should be considered the primary reference phylogeny. Figure 2 in KSEPKA *et al.* (2013) may be regarded as a secondary reference phylogeny.

Composition. *Cypselomorphae* is hypothesized to include the crown clades *Caprimulgidae*, *Nyctibiidae*, *Aegotheles*, and *Apodiformes*, as well as all extinct taxa more closely related to these taxa than to any other extant taxon.

Diagnostic apomorphies. MAYR (2010a) recovered a short, wide beak with narial openings extending into its tip, a reduced orbital process of the quadrate, a deep, narrow furrow separating the lateral and medial condyles of the quadrate, narrow distal mandibular rami meeting in a very short symphysis, a furcula with distinct articulation surfaces for the acrocoracoid processes of the coracoid, and a cerebellum with a reduced anterior lobe and a relatively large posterior lobe as apomorphies of this group. Under the total-evidence topologies found by CHEN *et al.* (2019), *Cypselomorphae* does not exist, and these features are instead optimized as symplesiomorphies or as apomorphies of *Strisores*.

Comments. MAYR (2004) recruited this name in accordance with a specific phylogenetic hypothesis matching the

original scope of the name ascribed by HUXLEY (1867), which is reflected by our proposed definition. This name is inapplicable to topologies in which this grouping is not monophyletic (e.g., Fig. 1; HACKETT *et al.*, 2008; PRUM *et al.*, 2015; REDDY *et al.*, 2017; CHEN *et al.*, 2019; WHITE & BRAUN, 2019; KUHL *et al.*, 2020).

Caprimulgi Ridgway, 1881 [Chen & Field], converted clade name

Registration number. 387

Definition. The smallest crown clade containing *Caprimulgus europaeus* Linnaeus, 1758 (*Caprimulgidae*) and *Nyctibius* (originally *Caprimulgus*) *grandis* (Gmelin, 1789) (*Nyctibiidae*) but not *Steatornis caripensis* Humboldt, 1817 (*Steatornithidae*), *Podargus* (originally *Caprimulgus*) *strigoides* (Latham, 1801) (*Podargidae*), *Aegotheles* (originally *Caprimulgus*) *cristatus* (Shaw, 1790) (*Aegothelidae*), and *Apus* (originally *Hirundo*) *apus* (Linnaeus, 1758) (*Apodiformes*). This is a minimum-crown-clade definition.

Abbreviated definition. Min crown ∇ (*Caprimulgus europaeus* Linnaeus, 1758 & *Nyctibius grandis* (Gmelin, 1789) ~ *Steatornis caripensis* Humboldt, 1817 & *Podargus strigoides* (Latham, 1801) & *Aegotheles cristatus* (Shaw, 1790) & *Apus apus* (Linnaeus, 1758)).

Reference phylogeny. Figure 3 in MAYR (2010a) should be considered the primary reference phylogeny. Figure 2 in KSEPKA *et al.* (2013) may be regarded as a secondary reference phylogeny.

Composition. *Caprimulgi* is hypothesized to include the crown clades *Caprimulgidae* and *Nyctibiidae*, as well as the last common ancestor of those groups and its extinct descendants.

Diagnostic apomorphies. MAYR (2010a) recovered a laterally widened palatine, strongly protruding paroccipital processes, a cone-like protrusion at the caudal margin of the optic nerve foramen, caudally flattened mandibular rami with an intramandibular joint, 17 cervical vertebrae, and an intertarsal sesamoid as apomorphies of this group. Additionally, caprimulgids and nyctibiids are the only members of *Strisores* in which the presence of a tapetum lucidum has been confirmed (BRAUN & HUDDLESTON, 2009). Under the total-evidence topologies found by CHEN *et al.* (2019), *Caprimulgi* does not exist, and many of these features are optimized as having been independently acquired by caprimulgids and nyctibiids, though it is possible that at least some of them were ancestrally present in *Strisores*.

Comments. MAYR (2010a) recruited this name in accordance with a specific phylogenetic hypothesis, which is reflected by our proposed definition. This name is in-

applicable to topologies in which this grouping is not monophyletic (e.g., Fig. 1; HACKETT *et al.*, 2008; PRUM *et al.*, 2015; REDDY *et al.*, 2017; CHEN *et al.*, 2019; WHITE & BRAUN, 2019; KUHL *et al.*, 2020).

Caprimulgiformes Shufeldt, 1904 [Chen & Field], converted clade name

Registration number. 388

Definition. The total clade containing *Caprimulgus europaeus* Linnaeus, 1758 (*Caprimulgidae*) but not *Steatornis caripensis* Humboldt, 1817 (*Steatornithidae*), *Nyctibius* (originally *Caprimulgus*) *grandis* (Gmelin, 1789) (*Nyctibiidae*), *Podargus* (originally *Caprimulgus*) *strigoides* (Latham, 1801) (*Podargidae*), *Aegotheles* (originally *Caprimulgus*) *cristatus* (Shaw, 1790) (*Aegothelidae*), and *Apus* (originally *Hirundo*) *apus* (Linnaeus, 1758) (*Apodiformes*). This is a total-clade definition.

Abbreviated definition. Total ∇ (*Caprimulgus europaeus* Linnaeus, 1758 ~ *Steatornis caripensis* Humboldt, 1817 & *Nyctibius grandis* (Gmelin, 1789) & *Podargus strigoides* (Latham, 1801) & *Aegotheles cristatus* (Shaw, 1790) & *Apus apus* (Linnaeus, 1758)).

Reference phylogeny. Figure 6 in CHEN *et al.* (2019) should be considered the primary reference phylogeny. Figure 1 in PRUM *et al.* (2015) and Figure 6 in WHITE & BRAUN (2019) may be regarded as secondary reference phylogenies.

Composition. *Caprimulgiformes* includes the crown clade *Caprimulgidae* and all extinct taxa more closely related to it than to any other extant taxon. No stem caprimulgids have yet been identified through phylogenetic analysis, though close affinities to *Caprimulgidae* have been hypothesized for some fragmentary Eocene specimens (MOURER-CHAUVIRÉ, 1988; MAYR, 2009).

Comments. *Caprimulgiformes* is typically attributed to RIDGWAY (1881), likely because he was the first to use the genus *Caprimulgus* as the basis for an ordinal-level name, which he spelled *Caprimulgi*. However, under the *PhyloCode*, names that have been subjected to such standardization should be attributed to the author who introduced the new spelling, at least in cases for which the original authorship can be ascertained (Notes 9.15A.4 and 19.5.1). The oldest use of the spelling *Caprimulgiformes* that we have been able to locate was by SHUFELDT (1904), thus we tentatively attribute nominal authorship to him here.

Traditionally, the name *Caprimulgiformes* was used to unite the nocturnal and crepuscular members of *Strisores* (*Caprimulgidae*, *Steatornithidae*, *Nyctibiidae*, *Podargidae*, and *Aegothelidae*), which in recent phylogenetic analyses have been uniformly found to constitute a paraphyletic grade with respect to *Apodiformes*. As

noted previously, many modern taxonomic authorities now use *Caprimulgiformes* to refer to a monophyletic group equivalent to *Strisores*. Although this would be justifiable under *PhyloCode* Article 10.1, we favour the use of the latter name for that clade (see comments on *Strisores*).

When used for a monophyletic group, the other most common application of *Caprimulgiformes* is to limit it to *Caprimulgidae* among extant members of *Strisores* (e.g., YURI *et al.*, 2013; PIACENTINI *et al.*, 2015; MAYR, 2017; CHEN *et al.*, 2019; CHESSER *et al.*, 2019). Under phylogenetic nomenclature, it has been customary to assign crown-clade definitions to avian clade names with the suffix “-iformes” (ranked at the level of order in Linnaean taxonomy), consistent with *PhyloCode* Recommendation 10.1B (SANGSTER, 2020b, c, d, e, f). However, clades with the suffix “-iformes” that only contain one extant taxon with the suffix “-idae” (ranked at the level of family in Linnaean taxonomy) present an unusual situation in which both the ordinal and familial names tend to be commonly used, but would refer to the same crown clade if both are given crown-clade definitions, rendering the two names synonymous under the *PhyloCode*. In cases like these, recent authors who employ phylogenetic nomenclature have often followed the spirit of Recommendation 10G (which only mentions genus names) and recommended limiting names with the suffix “-idae” to the crown group, while retaining use of the corresponding “-iformes” names for more inclusive clades encompassing all or part of the appropriate stem group (e.g., CLARKE *et al.*, 2003; KSEPKA & CLARKE, 2009; NESBITT *et al.*, 2011). We have opted to follow this recommendation here for relevant clade names such as *Caprimulgiformes* and *Caprimulgidae*, an approach that will both preserve widely used names and continue a practice established in recent literature.

Caprimulgidae Vigors, 1825 [Chen & Field], converted clade name

Registration number. 389

Definition. The smallest crown clade containing *Eurostopodus* (originally *Caprimulgus*) *mystacalis* (Temminck, 1826), *Lyncornis* (originally *Caprimulgus*) *macrotis* (Vigors in Kirby, 1831), and *Caprimulgus europaeus* Linnaeus, 1758. This is a minimum-crown-clade definition.

Abbreviated definition. Min crown ∇ (*Eurostopodus mystacalis* (Temminck, 1826) & *Lyncornis macrotis* (Vigors, 1831) & *Caprimulgus europaeus* Linnaeus, 1758).

Reference phylogeny. Figure 3 in SIGURÐSSON & CRAFT (2014) should be considered the primary reference phylogeny. Figure 2 in HAN *et al.* (2010) and Figure 4 in WHITE *et al.* (2016) may be regarded as secondary reference phylogenies.

Composition. *Caprimulgidae* includes 98 extant species (BILLERMAN *et al.*, 2020; GILL *et al.*, 2020). Potential fossil representatives have been identified, but are largely limited to Quaternary deposits (MANEGOLD, 2010).

Diagnostic apomorphies. Most morphological character states that have been optimized as apomorphies for *Caprimulgidae* have also been found in *Nyctibiiformes* (see comments on *Caprimulgi*). However, caprimulgids can be distinguished from nyctibiiforms by having a long, slender rostromedial process on the palatine as well as the longer olecranon process on their ulna (CHEN *et al.*, 2019).

Comments. See comments on *Caprimulgiformes*.

Vanescaves Chen, White, Benson, Braun, & Field, 2019 [Chen & Field], converted clade name

Registration number. 390

Definition. The smallest crown clade containing *Steatornis caripensis* Humboldt, 1817 (*Steatornithiformes*), *Nyctibius* (originally *Caprimulgus*) *grandis* (Gmelin, 1789) (*Nyctibiiformes*), *Podargus* (originally *Caprimulgus*) *strigoides* (Latham, 1801) (*Podargiformes*), *Aegothales* (originally *Caprimulgus*) *cristatus* (Shaw, 1790) (*Aegotheliformes*), and *Apus* (originally *Hirundo*) *apus* (Linnaeus, 1758) (*Apodiformes*) but not *Caprimulgus europaeus* Linnaeus, 1758 (*Caprimulgiformes*). This is a minimum-crown-clade definition.

Abbreviated definition. Min crown ∇ (*Steatornis caripensis* Humboldt, 1817 & *Nyctibius grandis* (Gmelin, 1789) & *Podargus strigoides* (Latham, 1801) & *Aegothales cristatus* (Shaw, 1790) & *Apus apus* (Linnaeus, 1758) ~ *Caprimulgus europaeus* Linnaeus, 1758).

Reference phylogeny. Figure 6 in CHEN *et al.* (2019) should be considered the primary reference phylogeny. Figure 1 in PRUM *et al.* (2015) and Figure 6 in WHITE & BRAUN (2019) may be regarded as secondary reference phylogenies.

Composition. *Vanescaves* is hypothesized to include the crown clades *Steatornis*, *Nyctibiidae*, *Podargidae*, *Aegothales*, and *Apodiformes*, as well as the last common ancestor of those groups and its extinct descendants.

Diagnostic apomorphies. This clade has primarily been recovered using molecular data (PRUM *et al.*, 2015; CHEN *et al.*, 2019; WHITE & BRAUN, 2019; KUHLE *et al.*, 2020). One morphological character state that has been identified as a potential apomorphy is a poorly developed descending process on the lacrimal (CHEN *et al.*, 2019).

Comments. CHEN *et al.* (2019) coined this name in accordance with a specific phylogenetic hypothesis, which

is reflected by our proposed definition. This name is inapplicable to topologies in which this grouping is not monophyletic (e.g., HACKETT *et al.*, 2008; MAYR, 2010a; KSEPKA *et al.*, 2013; REDDY *et al.*, 2017).

Sedentaves Chen & Field, new clade name

Registration number. 422

Definition. The smallest crown clade containing *Steatornis caripensis* Humboldt, 1817 (*Steatornithiformes*) and *Nyctibius* (originally *Caprimulgus*) *grandis* (Gmelin, 1789) (*Nyctibiiformes*) but not *Caprimulgus europaeus* Linnaeus, 1758 (*Caprimulgiformes*), *Podargus* (originally *Caprimulgus*) *strigoides* (Latham, 1801) (*Podargiformes*), *Aegotheles* (originally *Caprimulgus*) *cristatus* (Shaw, 1790) (*Aegotheliformes*), and *Apus* (originally *Hirundo*) *apus* (Linnaeus, 1758) (*Apodiformes*). This is a minimum-crown-clade definition.

Abbreviated definition. Min crown ∇ (*Steatornis caripensis* Humboldt, 1817 & *Nyctibius grandis* (Gmelin, 1789) ~ *Caprimulgus europaeus* Linnaeus, 1758 & *Podargus strigoides* (Latham, 1801) & *Aegotheles cristatus* (Shaw, 1790) & *Apus apus* (Linnaeus, 1758)).

Etymology. From Latin *sedentes* (sitting) and *aves* (birds), referring to the shortened tarsometatarsus of these birds and their habit of remaining perched for long periods of time.

Reference phylogeny. Figure 6 in CHEN *et al.* (2019) should be considered the primary reference phylogeny. Figure 1 in PRUM *et al.* (2015) and Figure 6 in WHITE & BRAUN (2019) may be regarded as secondary reference phylogenies.

Composition. *Sedentaves* is hypothesized to include the crown clades *Steatornis* and *Nyctibiidae*, as well as the last common ancestor of those groups and its extinct descendants.

Diagnostic apomorphies. This clade has primarily been recovered using molecular data (HACKETT *et al.*, 2008; PRUM *et al.*, 2015; REDDY *et al.*, 2017; CHEN *et al.*, 2019; WHITE & BRAUN, 2019; KUHLE *et al.*, 2020), but morphological character states that have been optimized as potential apomorphies include the absence of a supratendinal bridge on the tibiotarsus and an extremely short tarsometatarsus (MAYR, 2010a; CHEN *et al.*, 2019). Extant representatives of *Sedentaves* share present-day geographic distributions restricted to the Neotropics, though these may merely reflect the outcome of formerly widespread distributions that have contracted towards low latitudes throughout the Cenozoic (OLSON, 1987; MOURER-CHAUVIRÉ, 1989; MAYR, 1999, 2005, 2009; SAUPE *et al.*, 2019).

Comments. We coin this name in accordance with a specific phylogenetic hypothesis, which is reflected by our proposed definition. This name is inapplicable to topologies in which this grouping is not monophyletic (e.g., MAYR, 2010a; KSEPKA *et al.*, 2013).

Steatornithiformes Mayr, 2010a [Chen & Field], converted clade name

Registration number. 391

Definition. The total clade containing *Steatornis caripensis* Humboldt, 1817 (*Steatornithidae*) but not *Caprimulgus europaeus* Linnaeus, 1758 (*Caprimulgidae*), *Nyctibius* (originally *Caprimulgus*) *grandis* (Gmelin, 1789) (*Nyctibiidae*), *Podargus* (originally *Caprimulgus*) *strigoides* (Latham, 1801) (*Podargidae*), *Aegotheles* (originally *Caprimulgus*) *cristatus* (Shaw, 1790) (*Aegothelidae*), and *Apus* (originally *Hirundo*) *apus* (Linnaeus, 1758) (*Apodiformes*). This is a total-clade definition.

Abbreviated definition. Total ∇ (*Steatornis caripensis* Humboldt, 1817 ~ *Caprimulgus europaeus* Linnaeus, 1758 & *Nyctibius grandis* (Gmelin, 1789) & *Podargus strigoides* (Latham, 1801) & *Aegotheles cristatus* (Shaw, 1790) & *Apus apus* (Linnaeus, 1758)).

Reference phylogeny. Figure 6 in CHEN *et al.* (2019) should be considered the primary reference phylogeny. Figure 1 in PRUM *et al.* (2015) and Figure 6 in WHITE & BRAUN (2019) may be regarded as secondary reference phylogenies.

Composition. *Steatornithiformes* includes the crown clade *Steatornis* and all extinct taxa more closely related to it than to any other extant taxon. The Eocene *Prefica* has been hypothesized to be on the stem of *Steatornis* (OLSON, 1987), which has been consistently supported by phylogenetic analysis (MAYR, 2005; KSEPKA *et al.*, 2013; CHEN *et al.*, 2019). Other extinct members of this lineage might include *Euronyctibius* (MOURER-CHAUVIRÉ, 2013), *Fluvioviridavis*, and *Protocypselomorphus* (CHEN *et al.*, 2019).

Diagnostic apomorphies. Potential apomorphies include 19 or more presacral vertebrae and a tibiotarsus as long as or shorter than the carpometacarpus (CHEN *et al.*, 2019).

Comments. See comments on *Caprimulgiformes*. As noted by CHEN *et al.* (2019) and originally indicated by MAYR (2010a), this name is correctly attributed to MAYR (2010a) instead of SHARPE (1891).

Steatornis Humboldt in Humboldt & Bonpland, 1814 [Chen & Field], converted clade name

Registration number. 392

Definition. The smallest clade containing *Steatornis caripensis* Humboldt, 1817. This is a directly-specified-ancestor definition.

Abbreviated definition. Min ∇ (*Steatornis caripensis* Humboldt, 1817).

Reference phylogeny. Figure 6 in CHEN *et al.* (2019) should be considered the primary reference phylogeny. Figure 1 in PRUM *et al.* (2015) and Figure 6 in WHITE & BRAUN (2019) may be regarded as secondary reference phylogenies.

Composition. *Steatornis* includes a single extant species, *Steatornis caripensis* (BILLERMAN *et al.*, 2020; GILL *et al.*, 2020).

Comments. Per *PhyloCode* Recommendation 10G, in cases where a crown clade contains a single genus in current classifications, the genus name should preferably be converted as the name of that crown clade irrespective of whether higher-ranked taxa have been named for the same clade (in this case *Steatornithidae*, which we do not convert). This recommendation is followed here. *Steatornis* is considered a crown clade by *PhyloCode* Note 9.9.2, as we have assigned it a directly-specified-ancestor definition with an extant internal specifier, though in practice under some species concepts, this name may in fact be applied to a clade slightly more inclusive than the crown.

Nyctibiiformes Yuri, Kimball, Harshman, Bowie, Braun, Chojnowski, Han, Hackett, Huddleston, Moore, Reddy, Sheldon, Steadman, Witt, & Braun, 2013 [Chen & Field], converted clade name

Registration number. 393

Definition. The total clade containing *Nyctibius* (originally *Caprimulgus grandis* (Gmelin, 1789) (*Nyctibiidae*) but not *Caprimulgus europaeus* Linnaeus, 1758 (*Caprimulgidae*), *Steatornis caripensis* Humboldt, 1817 (*Steatornithidae*), *Podargus* (originally *Caprimulgus strigoides* (Latham, 1801) (*Podargidae*), *Aegotheles* (originally *Caprimulgus cristatus* (Shaw, 1790) (*Aegothelidae*), and *Apus* (originally *Hirundo apus* (Linnaeus, 1758) (*Apodiformes*)). This is a total-clade definition.

Abbreviated definition. Total ∇ (*Nyctibius grandis* (Gmelin, 1789) ~ *Caprimulgus europaeus* Linnaeus, 1758 & *Steatornis caripensis* Humboldt, 1817 & *Podargus strigoides* (Latham, 1801) & *Aegotheles cristatus* (Shaw, 1790) & *Apus apus* (Linnaeus, 1758)).

Reference phylogeny. Figure 6 in CHEN *et al.* (2019) should be considered the primary reference phylogeny. Figure 1 in PRUM *et al.* (2015) and Figure 6 in WHITE &

BRAUN (2019) may be regarded as secondary reference phylogenies.

Composition. *Nyctibiiformes* includes the crown clade *Nyctibiidae* and all extinct taxa more closely related to it than to any other extant taxon. The Eocene *Paraprefica* is a probable stem nyctibiid (MAYR, 2005; KSEPKA *et al.*, 2013; CHEN *et al.*, 2019).

Diagnostic apomorphies. Most morphological character states that have been optimized as apomorphies for *Nyctibiiformes* have also been found in *Caprimulgidae* (see comments on *Caprimulgi*). However, nyctibiiforms can be distinguished from caprimulgids by the more pronounced curvature of the jugal arches and mandibles, the absence of a supratendinal bridge on the tibiotarsus, and an extremely short tarsometatarsus (MAYR, 2005). As noted above, the latter two characters may be apomorphies shared between *Steatornithiformes* and *Nyctibiiformes*.

Comments. See comments on *Caprimulgiformes*.

Nyctibiidae Sharpe, 1891 [Chen & Field], converted clade name

Registration number. 394

Definition. The smallest crown clade containing *Phyllaemulor* (originally *Nyctibius bracteatus* (Gould in Yarell, 1846), *Nyctibius* (originally *Caprimulgus grandis* (Gmelin, 1789), and *Nyctibius* (originally *Caprimulgus griseus* (Gmelin, 1789)). This is a minimum-crown-clade definition.

Abbreviated definition. Min crown ∇ (*Phyllaemulor bracteatus* (Gould, 1846) & *Nyctibius grandis* (Gmelin, 1789) & *Nyctibius griseus* (Gmelin, 1789)).

Reference phylogeny. Figure 3 in WHITE *et al.* (2017) should be considered the primary reference phylogeny.

Composition. *Nyctibiidae* includes 7 extant species (BILLERMAN *et al.*, 2020; GILL *et al.*, 2020).

Diagnostic apomorphies. Morphological phylogenetic studies focusing on *Strisores* generally have not broadly sampled members of *Nyctibiidae*. However, MAYR (2005) noted that extant nyctibiids differ from the stem nyctibiid *Paraprefica* in details of the skull, coracoid, and carpometacarpus. Notably, *Paraprefica* lacks a tooth-like projection on the maxilla, which is found in all nyctibiids (COSTA & DONATELLI, 2009; COSTA *et al.*, 2018).

Comments. See comments on *Caprimulgiformes*. Under the *International Code of Zoological Nomenclature* (ICZN, 1999), this name is attributed to CHENU & DES MURS (1851) (who coined it with the spelling *Nyctibiines*). As noted under comments on *Caprimulgiformes*, however,

the *PhyloCode* treats attribution of names that have been amended to a standardized suffix under a rank-based code differently. The oldest use of the spelling *Nyctibiidae* that we have been able to locate was by SHARPE (1891), thus we tentatively attribute nominal authorship to him here.

***Letornithes* Chen & Field, new clade name**

Registration number. 423

Definition. The smallest crown clade containing *Podargus* (originally *Caprimulgus*) *strigoides* (Latham, 1801) (*Podargiformes*), *Aegotheles* (originally *Caprimulgus*) *cristatus* (Shaw, 1790) (*Aegotheliformes*), and *Apus* (originally *Hirundo*) *apus* (Linnaeus, 1758) (*Apodiformes*) but not *Caprimulgus europaeus* Linnaeus, 1758 (*Caprimulgiformes*), *Steatornis caripensis* Humboldt, 1817 (*Steatornithiformes*), and *Nyctibius* (originally *Caprimulgus*) *grandis* (Gmelin, 1789) (*Nyctibiiformes*). This is a minimum-crown-clade definition.

Abbreviated definition. Min crown ∇ (*Podargus strigoides* (Latham, 1801) & *Aegotheles cristatus* (Shaw, 1790) & *Apus apus* (Linnaeus, 1758) ~ *Caprimulgus europaeus* Linnaeus, 1758 & *Steatornis caripensis* Humboldt, 1817 & *Nyctibius grandis* (Gmelin, 1789)).

Etymology. From the Greek goddess *Leto* and *ornithes* (birds). *Leto* was the mother of both *Artemis* (goddess of the moon and the hunt) and *Apollo* (god of the sun and the arts), reflected by the membership of this clade in the nocturnal *Podargidae*, the larger species of which are known to hunt vertebrate prey (SERVENTY, 1936; BILLERMAN *et al.*, 2020), and the diurnal *Apodiformes*, in which elaborate visual and acoustic displays have evolved (CLARK & FEO, 2008; FEO & CLARK, 2010; ZUSI & GILL, 2009; CLARK, 2011; CLARK *et al.*, 2018; SIMPSON & MCGRAW, 2018; BILLERMAN *et al.*, 2020; ELIASON *et al.*, 2020). In one myth recounted by Ovid's *Metamorphoses*, *Leto* turns a group of Lycian peasants into frogs, which hearkens to the vernacular name “frogmouth” for the *Podargidae*. *Leto* was also the sister of *Asteria*, the namesake for the oldest known crown bird, *Asteriornis maastrichtensis* (FIELD *et al.*, 2020).

Reference phylogeny. Figure 6 in CHEN *et al.* (2019) should be considered the primary reference phylogeny. Figure 1 in PRUM *et al.* (2015) and Figure 6 in WHITE & BRAUN (2019) may be regarded as secondary reference phylogenies.

Composition. *Letornithes* is hypothesized to include the crown clades *Podargidae* and *Daedalornithes*, as well as the last common ancestor of those groups and its extinct descendants.

Diagnostic apomorphies. This clade has primarily been recovered using molecular data (PRUM *et al.*, 2015; RED-

DY *et al.*, 2017; CHEN *et al.*, 2019; WHITE & BRAUN, 2019; KUHLE *et al.*, 2020), but a morphological character state that has been optimized as a potential apomorphy is the absence of a distal interosseus canal on the tarsometatarsus (CHEN *et al.*, 2019). Members of this group also share the absence of basipterygoid processes (MAYR, 2010a).

Comments. We coin this name in accordance with a specific phylogenetic hypothesis, which is reflected by our proposed definition. This name is inapplicable to topologies in which this grouping is not monophyletic (e.g., HACKETT *et al.*, 2008; MAYR, 2010a; KSEPKA *et al.*, 2013).

***Podargiformes* Mathews, 1918 [Chen & Field], converted clade name**

Registration number. 395

Definition. The total clade containing *Podargus* (originally *Caprimulgus*) *strigoides* (Latham, 1801) (*Podargidae*) but not *Caprimulgus europaeus* Linnaeus, 1758 (*Caprimulgidae*), *Steatornis caripensis* Humboldt, 1817 (*Steatornithidae*), *Nyctibius* (originally *Caprimulgus*) *grandis* (Gmelin, 1789) (*Nyctibiidae*), *Aegotheles* (originally *Caprimulgus*) *cristatus* (Shaw, 1790) (*Aegothelidae*), and *Apus* (originally *Hirundo*) *apus* (Linnaeus, 1758) (*Apodiformes*). This is a total-clade definition.

Abbreviated definition. Total ∇ (*Podargus strigoides* (Latham, 1801) ~ *Caprimulgus europaeus* Linnaeus, 1758 & *Steatornis caripensis* Humboldt, 1817 & *Nyctibius grandis* (Gmelin, 1789) & *Aegotheles cristatus* (Shaw, 1790) & *Apus apus* (Linnaeus, 1758)).

Reference phylogeny. Figure 6 in CHEN *et al.* (2019) should be considered the primary reference phylogeny. Figure 1 in PRUM *et al.* (2015) and Figure 6 in WHITE & BRAUN (2019) may be regarded as secondary reference phylogenies.

Composition. *Podargiformes* includes the crown clade *Podargidae* and all extinct taxa more closely related to it than to any other extant taxon. The Eocene *Masillapodargus* is a probable stem podargid (MAYR, 1999; NESBITT *et al.*, 2011; KSEPKA *et al.*, 2013; MAYR, 2015a; CHEN *et al.*, 2019). Other potential stem podargids include *Fluviiviridavis* (NESBITT *et al.*, 2011; KSEPKA *et al.*, 2013) and *Quercypodargus* (MOURER-CHAUVIRÉ, 1989).

Diagnostic apomorphies. A large number of apomorphies differentiating *Podargiformes* from most other members of *Strisores* have been identified. These include a fossa on the ventral surface of palatine anterior to the choana, a rounded posterior edge of the articular portion of the mandible, a straight ventral margin of the mandibular ramus, a continuous lateral concavity on the mandible, a shallow transverse sulcus on the humerus, and a

distal wing skeleton shorter than the humerus (NESBITT *et al.*, 2011; CHEN *et al.*, 2019). Some of these features are also found in *Fluvioviridavis* (NESBITT *et al.*, 2011), whose assignment to this clade is debated (MAYR, 2015a; CHEN *et al.*, 2019).

Comments. See comments on *Caprimulgiformes*.

Podargidae Sclater, 1880 [Chen & Field], converted clade name

Registration number. 396

Definition. The smallest crown clade containing *Rigidipenna inexpectata* (originally *Podargus inexpectatus* Hartert in Sclater, 1901), *Podargus* (originally *Caprimulgus*) *strigoides* (Latham, 1801), and *Batrachostomus* (originally *Podargus*) *auritus* (Gray in Griffith, 1829). This is a minimum-crown-clade definition.

Abbreviated definition. Min crown ∇ (*Rigidipenna inexpectata* (Hartert, 1901) & *Podargus strigoides* (Latham, 1801) & *Batrachostomus auritus* (Gray, 1829)).

Reference phylogeny. Figure 1c in OLIVER *et al.* (2020) should be considered the primary reference phylogeny.

Composition. *Podargidae* includes 16 extant species (BIL- LERMAN *et al.*, 2020; GILL *et al.*, 2020).

Diagnostic apomorphies. Potential apomorphies include “horns” on the skull projecting posteriorly in front of the orbits and palatines fused anterior to the choanae (NESBITT *et al.*, 2011; CHEN *et al.*, 2019). *Rigidipenna* has not been sampled in morphological phylogenetic studies focusing on *Strisores*, but available osteological descriptions do not mention the absence of these characters (CLEERE *et al.*, 2007).

Comments. See comments on *Caprimulgiformes*. Under the ICZN’s Principle of Coordination (Article 36), this name is attributed to BONAPARTE (1838) (who coined *Podarginae* at the rank of subfamily). However, the *Phylo Code* ignores the ICZN’s Principle of Coordination in determining nominal authorship (Note 9.15A.3). The oldest use of *Podargidae* that we have been able to locate was by SCLATER (1880), thus we tentatively attribute nominal authorship to him here.

Batrachostomus auritus (the type species of *Batrachostomus*) was not sampled in the reference phylogeny, but three congeners were included.

Aegotheliformes Worthy, Tennyson, Jones, McNamara, & Douglas, 2007 [Chen & Field], converted clade name

Registration number. 397

Definition. The total clade containing *Aegotheles* (originally *Caprimulgus*) *cristatus* (Shaw, 1790) (*Aegothelidae*) but not *Caprimulgus europaeus* Linnaeus, 1758 (*Caprimulgidae*), *Steatornis caripensis* Humboldt, 1817 (*Steatornithidae*), *Nyctibius* (originally *Caprimulgus*) *grandis* (Gmelin, 1789) (*Nyctibiidae*), *Podargus* (originally *Caprimulgus*) *strigoides* (Latham, 1801) (*Podargidae*), and *Apus* (originally *Hirundo*) *apus* (Linnaeus, 1758) (*Apodiformes*). This is a total-clade definition.

Abbreviated definition. Total ∇ (*Aegotheles cristatus* (Shaw, 1790) ~ *Caprimulgus europaeus* Linnaeus, 1758 & *Steatornis caripensis* Humboldt, 1817 & *Nyctibius grandis* (Gmelin, 1789) & *Podargus strigoides* (Latham, 1801) & *Apus apus* (Linnaeus, 1758)).

Reference phylogeny. Figure 6 in CHEN *et al.* (2019) should be considered the primary reference phylogeny. Figure 1 in PRUM *et al.* (2015) and Figure 6 in WHITE & BRAUN (2019) may be regarded as secondary reference phylogenies.

Composition. *Aegotheliformes* includes the crown clade *Aegotheles* and all extinct taxa more closely related to it than to any other extant taxon. The Miocene *Quipollornis* has been hypothesized to be a stem aegothelid based on comparative anatomy (RICH & McEVEY, 1977). CHEN *et al.* (2019) suggested that the Eocene *Hassiavis* may also represent a stem aegothelid, though strong support for this hypothesis was only found in one of their phylogenetic analyses.

Comments. See comments on *Caprimulgiformes*. As noted by MAYR (2010a), this name is correctly attributed to WORTHY *et al.* (2007) instead of SIMONETTA (1967).

Aegotheles Vigors & Horsfield, 1827 [Chen & Field], converted clade name

Registration number. 398

Definition. The smallest crown clade containing *Aegotheles savesi* Layard & Layard, 1881, *Aegotheles insignis* Salvadori, 1875, and *Aegotheles* (originally *Caprimulgus*) *cristatus* (Shaw, 1790). This is a minimum-crown-clade definition.

Abbreviated definition. Min crown ∇ (*Aegotheles savesi* Layard & Layard, 1881 & *Aegotheles insignis* Salvadori, 1875 & *Aegotheles cristatus* (Shaw, 1790)).

Reference phylogeny. Figure 1b in DUMBACHER *et al.* (2003) should be considered the primary reference phylogeny.

Composition. *Aegotheles* includes up to 10 extant species (BILLERMAN *et al.*, 2020; GILL *et al.*, 2020). A Miocene fossil has been assigned to this genus, though its relationships to extant members of this clade remain unclear (WORTHY *et al.*, 2007).

Comments. See comments on *Steatornis*.

Pan-Apodiformes Ksepka, Clarke, Nesbitt, Kulp, & Grande, 2013 [Chen & Field], converted clade name

Registration number. 399

Definition. The total clade containing *Apus* (originally *Hirundo*) *apus* (Linnaeus, 1758) (*Apodiformes*) but not *Caprimulgus europaeus* Linnaeus, 1758 (*Caprimulgidae*), *Steatornis caripensis* Humboldt, 1817 (*Steatornithidae*), *Nyctibius* (originally *Caprimulgus*) *grandis* (Gmelin, 1789) (*Nyctibiidae*), *Podargus* (originally *Caprimulgus*) *strigoides* (Latham, 1801) (*Podargidae*), and *Aegotheles* (originally *Caprimulgus*) *cristatus* (Shaw, 1790) (*Aegothelidae*). This is a total-clade definition.

Abbreviated definition. Total ∇ (*Apus apus* (Linnaeus, 1758) ~ *Caprimulgus europaeus* Linnaeus, 1758 & *Steatornis caripensis* Humboldt, 1817 & *Nyctibius grandis* (Gmelin, 1789) & *Podargus strigoides* (Latham, 1801) & *Aegotheles cristatus* (Shaw, 1790)).

Reference phylogeny. Figure 6 in CHEN *et al.* (2019) should be considered the primary reference phylogeny. Figure 1 in PRUM *et al.* (2015) and Figure 6 in WHITE & BRAUN (2019) may be regarded as secondary reference phylogenies.

Composition. *Pan-Apodiformes* includes the crown clade *Apodiformes* and all extinct taxa more closely related to it than to any other extant taxon. The Eocene *Eocypselus* is a probable stem apodiform (MAYR, 2010b; KSEPKA *et al.*, 2013; CHEN *et al.*, 2019). Other potential stem apodiforms include the *Aegialornithidae* (MAYR, 2009, 2010b).

Diagnostic apomorphies. Potential apomorphies include an abbreviated humerus and an ossified supratendinal bridge (*arcus extensorius*) on the tarsometatarsus (MAYR, 2010b; KSEPKA *et al.*, 2013; CHEN *et al.*, 2019).

Comments. KSEPKA *et al.* (2013) attributed this name to MAYR (2010b). However, we have not been able to locate any use of the name *Pan-Apodiformes* in MAYR (2010b), who instead used *Apodiformes* for a more inclusive clade including the stem apodiform *Eocypselus*. To our knowledge, KSEPKA *et al.* (2013) were the first to use *Pan-Apodiformes* in scientific literature.

Apodi Peters, 1940 [Chen & Field], converted clade name

Registration number. 400

Definition. The smallest crown clade containing *Hemiprocne* (originally *Hirundo*) *longipennis* (Rafinesque, 1802) (*Hemiprocnidae*) and *Apus* (originally *Hirundo*) *apus* (Linnaeus, 1758) (*Apodidae*). This is a minimum-crown-clade definition.

Abbreviated definition. Min crown ∇ (*Hemiprocne longipennis* (Rafinesque, 1802) & *Apus apus* (Linnaeus, 1758)).

Reference phylogeny. Figure 6 in CHEN *et al.* (2019) should be considered the primary reference phylogeny. Figure 1 in PRUM *et al.* (2015) and Figure 6 in WHITE & BRAUN (2019) may be regarded as secondary reference phylogenies.

Composition. *Apodi* includes the crown clades *Hemiprocne* and *Apodidae*, as well as the last common ancestor of those groups and its extinct descendants.

Diagnostic apomorphies. Potential apomorphies include an elongated, narrow ventral supracondylar tubercle on the humerus, a marked tubercle on the ventral side of the radial shaft opposing the carpal tubercle of the ulna, and greatly elongated outer primary feathers (MAYR, 2010b).

Comments. This name has consistently been used in reference to the group uniting *Hemiprocne* and *Apodidae* (PETERS, 1940; HARRISON, 1984; MAYR, 2010a), which is reflected by our proposed definition. *Hemiprocne longipennis* (the type species of *Hemiprocne*) was not sampled in the reference phylogenies, but CHEN *et al.* (2019) and WHITE & BRAUN (2019) included the congener *H. mystacea* and PRUM *et al.* (2015) included the congener *H. comata*.

Hemiprocne Nitzsch, 1829 [Chen & Field], converted clade name

Registration number. 401

Definition. The largest crown clade containing *Hemiprocne* (originally *Hirundo*) *longipennis* (Rafinesque, 1802) (*Hemiprocnidae*) but not *Apus* (originally *Hirundo*) *apus* (Linnaeus, 1758) (*Apodidae*). This is a maximum-crown-clade definition.

Abbreviated definition. Max crown ∇ (*Hemiprocne longipennis* (Rafinesque, 1802) ~ *Apus apus* (Linnaeus, 1758)).

Reference phylogeny. Figure 6 in WHITE & BRAUN (2019) should be considered the primary reference phylogeny.

logeny. Figure 1 in PRUM *et al.* (2015) and Figure 6 in CHEN *et al.* (2019) may be regarded as secondary reference phylogenies.

Composition. *Hemiprocne* includes 4 extant species (BILLERMAN *et al.*, 2020; GILL *et al.*, 2020).

Comments. See comments on *Steatornis*. Given that to our knowledge no phylogenetic analysis to date has included all four extant species of *Hemiprocne*, we have opted for a maximum-crown-clade definition, ensuring that hypothetical future splits of currently recognized *Hemiprocne* species would remain within the clade *Hemiprocne*.

Apodidae Olphe-Galliard, 1887 [Chen & Field], converted clade name

Registration number. 402

Definition. The smallest crown clade containing *Cypseloides fumigatus* (originally *Hemiprocne fumigata* Streubel, 1848), *Streptoprocne* (originally *Hirundo*) *zonaris* (Shaw, 1796), *Collocalia* (originally *Hirundo*) *esculenta* (Linnaeus, 1758), *Chaetura* (originally *Hirundo*) *pelagica* (Linnaeus, 1758), and *Apus* (originally *Hirundo*) *apus* (Linnaeus, 1758). This is a minimum-crown-clade definition.

Abbreviated definition. Min crown ∇ (*Cypseloides fumigatus* (Streubel, 1848) & *Streptoprocne zonaris* (Shaw, 1796) & *Collocalia esculenta* (Linnaeus, 1758) & *Chaetura pelagica* (Linnaeus, 1758) & *Apus apus* (Linnaeus, 1758)).

Reference phylogeny. Figure 1 in PRICE *et al.* (2005) should be considered the primary reference phylogeny.

Composition. *Apodidae* includes over 110 extant species (BILLERMAN *et al.*, 2020; GILL *et al.*, 2020). Various fossil specimens dating to the Miocene onwards have been assigned to extant genera (WORTHY *et al.*, 2007), with some localities preserving an abundance of remains attributable to *Apodidae* (e.g., FIELD, 2020), but these have not been subjected to phylogenetic analysis.

Diagnostic apomorphies. Many characters that distinguish *Apodidae* from stem apodids or *Hemiprocne* have undergone considerable parallel evolution within *Apodiformes* (MAYR, 2010b, 2015b; CHEN *et al.*, 2019), but a potential apomorphy of *Apodidae* is the great shortening of the second and third phalanges of pedal digit IV (CHEN *et al.*, 2019).

Comments. *Cypseloides fumigatus* (the type species of *Cypseloides*) was not sampled in the reference phylogeny, but the congener *C. niger* was included. Another putative congener included in the reference phylogeny,

“*C. phelpsi*,” is now classified in the genus *Streptoprocne* (BILLERMAN *et al.*, 2020; GILL *et al.*, 2020).

CHEN *et al.* (2019) suggested the use of *Trochiloidea* for the total group of *Trochilidae*. However, unknown to those authors at the time, MCGUIRE *et al.* (2009) had already proposed a total-clade definition for *Pan-Trochilidae* (rendered “*Pantrochilidae*” in their paper) referring to the same clade (though *contra* MCGUIRE *et al.*, 2009, *Pan-Trochilidae* had been previously coined by MAYR & MANEGOLD, 2002). MCGUIRE *et al.* (2009) further proposed phylogenetic definitions for major constituent clades within *Trochilidae*. Neither of the authors of the present contribution were involved with the research by MCGUIRE *et al.* (2009), so we refrain from claiming authorship for their proposed definitions, but we recommend the adoption of their taxonomic scheme in future studies that employ phylogenetic nomenclature for total-group trochilids.

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