

Aves C. Linnaeus 1758 [J. A. Clarke, D. P. Mindell, K. de Queiroz, M. Hanson, M. A. Norell, and J. A. Gauthier], converted clade name

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Definition: The smallest crown clade containing *Struthio camelus* Linnaeus 1758 (*Palaeognathae*), *Tinamus* (originally *Tetrao*) *major* (Gmelin 1789) (*Palaeognathae/Tinamidae*), *Phasianus colchicus* Linnaeus 1758 (*Neognathae/Galloanserae/Galliformes*), and *Vultur gryphus* Linnaeus 1758 (*Neognathae/Neoaves/Accipitriformes*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Struthio camelus* Linnaeus 1758 & *Tinamus major* (Gmelin 1789) & *Phasianus colchicus* Linnaeus 1758 & *Vultur gryphus* Linnaeus 1758).

Etymology: Derived from the Latin vernacular for “birds.”

Reference Phylogeny: Figure 1 in the comprehensive molecular analysis of Prum et al. (2015). We selected specifier species from among those originally used by Linnaeus to represent uncontroversial avian subclades in order to bracket the crown clade. Because some of these specifier species are not included in the reference phylogeny, more inclusive taxa containing them are listed parenthetically in the definition to facilitate its application.

Composition: *Aves* currently contains more than 10,000 described species, but could include as many as 5,000–10,000 more depending upon reassessment of currently recognized subspecies (Barrowclough et al., 2016). These include all those listed in Brodkorb (1963, 1964, 1967, 1971, 1978), Unwin (1993), Mlíkovsky (2002), Clements (2007), Mayr (2009), del Hoyo et al. (2013), and Gill and Donsker (2018),

provided lists of many extinct members of the crown, as well as a few extinct species that are here regarded to have diverged from the avian stem.

Diagnostic Apomorphies: With respect to other extant amniotes, Huxley’s (1867: 416–417) diagnosis of *Aves* still serves (see Comments below):

1. “[E]pidermal appendages developed in sacs of the dermis, and having the structure of feathers.
2. [A] remarkably large sacrum, the vertebrae, through the intervertebral foramina of which the roots of the sacral plexus (and, consequently, of the great sciatic nerve) pass, are not provided with expanded ribs abutting against the ilium externally, and against the bodies of these vertebrae by their inner ends. [Instead, these vertebrae are connected to the ilia via] slender transverse processes, which seem to answer to those which unite with the tubercles of the ribs in the dorsal region [in other reptiles].
3. The broad and expanded part of the sternum, which immediately follows the coracoidal articular surfaces, receives all the sternal ribs.
4. The ischia never unite in a median ventral symphysis; and both pubes and ischia are directed backwards, approximately parallel with one another and with the spinal column.
5. The proximal constituent of the tarsus is ankylosed [sic] with the tibia into

one tibio-tarsal bone; the distal element of the tarsus similarly unites with the second, third, and fourth metatarsal bones, and gives rise to the tarso-metatarsal bone. The metatarsal of the hallux is shorter than the others, and does not reach the tarsus.

6. [H]ot blood ... a single aortic arch, and remarkably modified respiratory organs.”

Additional apomorphies have been listed by Cracraft (1988) and Kurochkin (1995). Currently, there are no unambiguous synapomorphies of *Aves* that will distinguish members of the crown from all known members of its stem (see Comments).

Synonyms: *Ornithurae* Haeckel 1866 (approximate); *Neornithes* Gadow 1892 (approximate); see review in Gauthier and de Queiroz (2001) and Comments below.

Comments: The ease with which *Aves* (the crown) could be diagnosed in the mid-nineteenth century depended entirely upon missing data, as does its ease of diagnosis relative to other extant taxa today. However, due both to the discovery of an array of intermediate forms (e.g., Cau, 2018), and to the fact that extinct species closest to the crown are so incompletely preserved, it is now much more difficult to distinguish members of the crown (*Aves*) from the nearest members of its stem. The poorly known extinct species most closely related to the crown were placed outside the crown when considered individually (e.g., Clarke, 2004). Nevertheless, when considered together, there was so little overlap among their preserved remains that there were no longer any unambiguously optimized morphological apomorphies for *Aves*. This remains true today.

Linnaeus proposed the name *Aves* for a group composed entirely of extant species representing

both branches of the basal split within the crown clade (Gauthier, 1986). A century later, discovery of the stem bird *Archaeopteryx lithographica* (von Meyer, 1861; Owen, 1863) with its mosaic of ancestral (e.g., teeth, long bony tail) and derived (e.g., feathers, wings) characters, engendered controversy regarding the circumscription of *Aves* (reviewed in de Beer, 1954). A consensus eventually emerged that *Archaeopteryx* should be considered part of *Aves*, as first proposed explicitly by Haeckel (1866), who also proposed *Ornithurae* to distinguish the “living ... true birds” (p. 140) from *Archaeopteryx*. A loose association between *Aves* and at least part of its stem lineage remained in steady use for more than a century following Haeckel (1866), although the exact clade to which the name applied became more varied with the discovery of additional fossil intermediates, increasing knowledge of phylogenetic relationships, and changing taxonomic philosophies. More specifically, the name *Aves* became associated with at least five different nested clades (see Gauthier and de Queiroz, 2001, for a review): (1) the total clade of birds (e.g., Patterson, 1993); (2) the clade characterized by pinnate feathers (e.g., James and Pourtless, 2009; Feduccia, 2013); (3) the clade characterized by flight (e.g., Ji and Ji, 2001; Xu et al., 2009); (4) the clade stemming from the *Archaeopteryx* node (e.g., Padian and Chiappe, 1998); and (5), the crown clade (e.g., Gauthier, 1986).

Some contemporary systematists (those adopting one of the first four uses of *Aves* listed above) prefer the name *Neornithes* Gadow 1892 for the crown. This name was proposed by Gadow (see also Gadow, 1893) as an explicit replacement name for *Ornithurae* to distinguish extant birds as well as the Cretaceous toothed birds (Marsh, 1880), which were unknown to Haeckel (1866), from *Archaeopteryx*. Subsequently, however, the associations of these names diverged. *Ornithurae* came to be applied

to a more inclusive clade than the crown, i.e., to those stem avians sharing apomorphies of the tail to which the name implicitly refers (e.g., Gauthier, 1986; Elzanowski, 1995; Gauthier and de Queiroz, 2001; Clarke, 2004; Zhou and Zhang, 2006). *Neornithes* was first applied explicitly to the crown by Walker (1981), and that practice has been followed frequently in the palaeontological literature (e.g., Thulborn, 1984; Chiappe, 1995; Dyke and van Tuinen, 2004). But palaeontologists have also used *Neornithes* for more inclusive clades, such as for the crown plus *Ichthyornithes* (e.g., Martin, 1983), or the crown and all stem birds closer to the crown than to *Enantiornithes* (e.g., Elzanowski, 1995).

Given that most published papers on birds deal only with extant species, however, the preference for *Neornithes* for the crown does not accord well with the most widespread use of the name *Aves* (Gauthier and de Queiroz, 2001). Google Scholar (Aug. 2018) yields more than one million records for searches on “*Aves*” or “avian”; by contrast, searches on “*Neornithes*” or “neornithine” (sic) yield approximately 2,500 and 800 records, respectively. Contrasting usage seems to follow disciplinary boundaries, with palaeontological authors being more likely to use *Neornithes* than ornithologists focused on extant birds. Unfortunately, some authors who have explicitly chosen to use the name *Neornithes* for the crown have not been entirely successful at avoiding inconsistent use of the name *Aves*. For example, consider the title of the paper “Phylogenetic Relationships among Modern Birds (*Neornithes*)” with the subtitle “Toward an Avian Tree of Life,” and one section of that paper entitled “The Challenge of Resolving Avian Relationships” (Cracraft et al., 2004). Similarly, authors who analyzed the “Higher-order phylogeny of modern birds (Theropoda, *Aves*: *Neornithes*)” refer to “Broad affinities of long standing among the avian orders ... that were not supported by the present analysis,”

even though they were addressing relationships within the crown (Livezey and Zusi, 2007: 42).

Despite efforts to promote the use of *Neornithes*, a preference for using *Aves* when referring to the crown remains strong. Recent landmark molecular phylogenetic studies, for example, which were necessarily restricted to the crown clade, have not used *Neornithes* or “neornithine” but referred to their topic as “avian” diversification and their target clade as *Aves* (Hackett et al., 2008; Jetz et al., 2012; Burleigh et al., 2015; Prum et al., 2015). Jarvis et al. (2014) used both *Neornithes* and “avian” when referring to the crown clade. Other studies have avoided using either *Aves* or *Neornithes* but continued to use “avian” (e.g., McCormack et al., 2013; Reddy et al., 2017).

None of the uses of the name *Aves* is optimal in all respects. Exclusion of *Archaeopteryx lithographica* from *Aves* is disruptive given that this species was included in that taxon by many authors for more than 150 years. Associating *Aves* with pinnate feathers would be even more disruptive, as such feathers are now known to diagnose a much larger clade than the *Archaeopteryx* node that includes more traditional “non-avian” theropods such as *Velociraptor* (e.g., Clarke, 2013). Applying the name to the total clade requires including even more distantly related extinct forms not traditionally included in *Aves* such as sauropodomorphs (e.g., *Brontosaurus*), ornithischians (e.g., *Triceratops*), and pterosaurs (e.g., *Rhamphorhynchus*). Linking the name *Aves* to the origin of “flight” is hard to maintain in the face of abundant discoveries that show this complex character was not a simple apomorphy diagnosing a single node (e.g., Feo et al., 2015). Additionally, the fraction of the scientific community that needs to distinguish between the origin of volant dinosaurs and the crown clade is exceeding small.

In sum, most authors continue to use “*Aves*” or “avian” to discuss aspects of bird biology—such as their genomes—that have been documented

only in extant species. Authors even use “*Aves*” or “avian” when discussing features that are known to be absent in early members of the clade to which they apply those terms (see examples in de Queiroz, 2007: 968). *Neornithes* is rarely used when discussing extant birds alone, even though that name was proposed more than a century ago. Reluctance to do so is understandable, given that precision regarding the name of the crown-clade would require that the familiar name *Aves* be supplanted by the obscure name *Neornithes*. For reasons discussed at length in Gauthier and de Queiroz (2001) and de Queiroz (2007), we have applied the best known and most frequently used name (*Aves*) to the best known and most frequently discussed clade (the crown). For those who are concerned about the status of *Archaeopteryx*, it is still a (stem) bird even if it is not part of *Aves*.

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