

Ungulata C. Linnaeus 1766 [J. D. Archibald], converted clade name

Registration Number: 292

Definition: The least inclusive crown clade containing *Bos primigenius* Bojanus 1827 (= *Bos taurus* Linnaeus 1758) (*Artiodactyla*) and *Equus ferus* Boddaert 1785 (= *Equus caballus* Linnaeus 1758) (*Perissodactyla*), provided that this clade does not include *Felis silvestris* Schreber 1777 (= *Felis catus* Linnaeus 1758) (*Carnivora*), *Manis pentadactyla* Linnaeus 1758 (*Pholidota*), *Vespertilio murinus* Linnaeus 1758 (*Chiroptera*), or *Erinaceus europaeus* Linnaeus 1758 (*Lipotyphla*). This is a minimum-crown-clade definition with a qualifying clause. Abbreviated definition: min crown ∇ (*Bos primigenius* Bojanus 1827 & *Equus ferus* Boddaert 1785 ~ (*Felis silvestris* Schreber 1778 \vee *Manis pentadactyla* Linnaeus 1758 \vee *Vespertilio murinus* Linnaeus 1758 \vee *Erinaceus europaeus* Linnaeus 1758).

Etymology: “*Ungulata*” derives from the Latin *ungula* (hoof), alluding to the presence of hooves in many included taxa, including all extant species except *Cetacea*, possibly even in their most recent common ancestor.

Reference Phylogeny: For the purposes of applying this definition, Figure 1 in O’Leary et al. (2013) serves as the primary reference phylogeny. It depicts relationships among internal and external specifiers, with the exception of *Vespertilio murinus*, which is part of *Chiroptera* on that tree. *Ungulata* as defined here corresponds to *Euungulata* in O’Leary et al. (2013). See also Figure 5 (A and B) in Asher et al. (2003), Figures 1 and 2 in Beck et al. (2006), Figure 3 in Hou et al. (2009), Figure 2 in Spaulding et al. (2009), and Figure 2 in Zhou et al. (2012).

Composition: The taxa here considered to belong to *Ungulata* are currently thought to be arrayed in 341 living species grouped in 135 more inclusive taxa traditionally ranked as genera (Wilson and Reeder, 2005). McKenna and Bell (1997) list some 1,045 extinct ungulate genera. Of the two primary included crown clades, *Perissodactyla* has shown the greatest decline since its appearance in the Early Eocene, with only about 7% of the “genera” now extant. In the sister crown clade, *Artiodactyla* (this volume, including *Cetacea*), 16% of the “genera” are extant. It is also first known from the Early Eocene.

Diagnostic Apomorphies: There are no unambiguous non-molecular apomorphies for *Ungulata*. “Hooves”—thick, short, blunt and heavily keratinized structures homologous to claws and nails—have figured prominently in the traditional diagnosis of this taxon. They are present in all extant terrestrial members of both primary subclades, albeit borne on mesaxonic (*Perissodactyla*) or paraxonic (*Artiodactyla*) digits. That difference need not contradict homology, which only requires that “hooves” arose prior to these alternative modifications to the digital arch (see, for example, mesaxonic hands and paraxonic feet in the stem artiodactyl *Diacodexis pakistanensis*; Thewissen and Hussain, 1990). Hoof-like structures in afrotherian *Paenungulata*, which led some to associate them with *Ungulata* historically, are apparently non-homologous with those in ungulates.

Synonyms: Ongulogrades Normaux de Blainville 1816 (partial and approximate); *Diplarthra* Cope 1883 (partial and approximate); *Ungulata Vera* Flower and Lydekker 1891

(partial and approximate); *Euungulata* Waddell et al. 2001 (unambiguous).

Comments: Of the various names that have been used for a taxon approximating the named clade, *Ongulogrades Normaux*, *Diplarthra*, and *Ungulata Vera* are no longer used. A Google Scholar search on August 18, 2014, found 14,100 hits for “*Ungulata*” vs. 44 for “*Euungulata*”. Waddell et al. (2001) proposed the latter as a new name for this clade because whales were not traditionally included in *Ungulata*. In the phylogenetic era, whales were initially thought to be sister to artiodactyls based on fossils and morphology, but are now inferred to nest inside *Artiodactyla* based on molecular and combined datasets. *Ungulata* is clearly the name most often associated with the clade originating in the last common ancestor of crown perissodactyls and artiodactyls, and is therefore the name to be preferred. For the names of specifiers, I follow ICZN Opinion 2027 (2003) in using specific names first applied to wild forms despite earlier publication of specific names for domesticated forms, viz., for cows, horses, and cats.

Gregory (1910) provided the most comprehensive history of the use of the name *Ungulata*, at least until the early twentieth century. He stated, “the so called ‘*Ungulata Vera*,’ embracing the *Artiodactyla* and *Perissodactyla*, is almost as unnatural an assemblage as ‘the Pachydermes’ of Cuvier” (pp. 342–343). According to Gregory, Ray (1693) was the first to recognize *Ungulata* much as used here (with obvious exclusion of *Cetacea* from *Artiodactyla*). Starting with the 1735 (first) edition of his *Systema Naturae*, Linnaeus began and continued altering the names and composition of Ray’s *Ungulata*.

Many of the classifications of the nineteenth century included taxa other than artiodactyls and perissodactyls within *Ungulata*. Considering only extant taxa, notable exceptions

were de Blainville (1816; except that he referred to them as “*Ongulogrades Normaux*”), Owen (1868; except for the inclusion of an unspecified hyrax), Gill (1872), Flower and Lydekker (1891; except that they called it *Ungulata Vera* within an *Ungulata* that also included *Subungulata*), Cope (1883; except that he called it *Diplarthra* within an *Ungulata* that also included a variety of other extant and extinct taxa).

Simpson coined *Ferungulata* in 1945 to include the following extant clades traditionally ranked as orders: *Carnivora*, *Proboscidea*, *Hyracoidea*, *Sirenia*, *Perissodactyla*, and *Artiodactyla*. In 1997, McKenna and Bell did not recognize *Ferungulata*, but grouped *Proboscidea*, *Hyracoidea*, *Sirenia*, *Perissodactyla*, and *Artiodactyla* under *Ungulata* with the addition of *Tubulidentata* and *Cetacea*. *Cetacea* was linked to *Artiodactyla* by these authors within *Eparctocyona* to the exclusion of other extant placental clades. Molecular studies (see *Artiodactyla* in this volume for references) have strongly supported that *Cetacea* is not simply sister to *Artiodactyla* but is closer to *Hippopotamidae* within *Artiodactyla* (e.g., Gatesy, 1997). *Proboscidea*, *Hyracoidea*, and *Sirenia*, which have long been recognized as a clade (e.g., Simpson, 1945), usually known as *Paenungulata*, have been linked with strong support to other African clades including *Tubulidentata* (viz., Afrotheria).

The earliest known crown perissodactyls and crown artiodactyls are confidently identified from the Early Eocene onwards. The age of origin of their respective total clades, as well as the total clade of *Ungulata*, is unclear. The stems of all three clades have traditionally been sought among a diverse assemblage of Early Cenozoic placentals collectively known as “condylarths” or “archaic ungulates” (Archibald, 1998). While no clear candidates for stem *Ungulata* have emerged, possible ancestry for *Perissodactyla* may be among phenacodontid “condylarths”

(see Hooker, 2005, for a review) and for *Artiodactyla* among arctocyonid, hyopsodontid, or mioclaenid "condylarths" (see Theodor et al., 2005, for a review). A possible stem relationship to *Ungulata* was proposed for the Late Cretaceous zhelestids by Archibald (1996), but more recent phylogenetic analyses (Wible et al., 2007 and Wible et al., 2009) indicate that zhelestids are more likely stem rather than crown placentals.

Whatever else it may have contained over the years, *Ungulata* has always contained crown clades traditionally included in *Perissodactyla* and *Artiodactyla*. The definition of "*Ungulata*" proposed here is thus rooted explicitly in the *Perissodactyla* + *Artiodactyla* hypothesis, which has been supported in a recent study considering both fossil and Recent species and data from disparate morphological systems and diverse gene sequences (O'Leary et al., 2013). However, this hypothesis has been disputed by most studies based on gene sequences alone (e.g., Murphy et al., 2001; Nishihara et al., 2006; Springer et al., 2007; Matthee et al., 2007; Prasad et al., 2008). These hypotheses nest one or more major clades (traditional mammalian orders) inside the smallest clade containing all artiodactyls and perissodactyls. For this reason, the proposed definition includes external specifiers representing clades—crown chiropterans, lipotyphlans, pholidotans, and carnivorans—that, should they prove to be descended from the last ancestor of crown perissodactyls and artiodactyls, will render the name *Ungulata* inapplicable to any clade.

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Diagnosis: *Arctodactyle* Spaulding et al. (2007) listed 30 new specimens from 10 of them, *Arctodactyle* falls within *Arctodactyle*, whereas in two of the ones, *Arctodactyle* falls outside *Arctodactyle*. In morphological analysis, *Arctodactyle* is subject to *Arctodactyle* in 16 characters only. However, when we use morphological characters of *Arctodactyle* + *Galehyx* in the following four ways: (1) as a separate taxon, (2) as a separate taxon, (3) as a separate taxon, (4) as a separate taxon, (5) as a separate taxon, (6) as a separate taxon, (7) as a separate taxon, (8) as a separate taxon, (9) as a separate taxon, (10) as a separate taxon, (11) as a separate taxon, (12) as a separate taxon, (13) as a separate taxon, (14) as a separate taxon, (15) as a separate taxon, (16) as a separate taxon, (17) as a separate taxon, (18) as a separate taxon, (19) as a separate taxon, (20) as a separate taxon, (21) as a separate taxon, (22) as a separate taxon, (23) as a separate taxon, (24) as a separate taxon, (25) as a separate taxon, (26) as a separate taxon, (27) as a separate taxon, (28) as a separate taxon, (29) as a separate taxon, (30) as a separate taxon.

Synonymy: *Arctodactyle* Spaulding et al. (2007) (species only).

Comments: *Arctodactyle* has a long history of study in both phylogenetic and morphological