



On the Unnecessary and Misleading Taxon “Cetartiodactyla”

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Abstract

The name “Cetartiodactyla” was proposed in 1997 to reflect the molecular data that suggested that Cetacea is closely related to Artiodactyla. Since then, that taxon has spread in popularity, even outside the scientific literature. However, the implications of the name are confusing, because Cetacea and Artiodactyla are not sister-taxa. Instead, the evidence clearly shows that cetaceans are a group embedded within Artiodactyla, not a sister-taxon of equal rank. It has long been accepted practice that systematists do not modify the names of higher groups when new subgroups are added to them. For example, Owen’s original concept of Artiodactyla did not change its name when more and more disparate taxa were added to it. Dinosauria did not become “Avedinosauria” when it became clear that birds are a subgroup of dinosaurs, nor did Reptilia become “Avereptilia”. In the interests of taxonomic priority and stability, and especially because the name is inherently misleading, we recommend that the name “Cetartiodactyla” be abandoned. If one wishes to make a reference to the fact that whales are now considered to be a subgroup of artiodactyls, they could be referred to informally as “whales and other artiodactyls” or “whales and terrestrial artiodactyls” without using a formal taxonomic name that is confusing and misleading.

Keywords Cetartiodactyla · Artiodactyla · Cetaceans · Ungulates · Taxonomy

Twenty-four years ago, Montgelard et al. (1997) proposed the taxon “Cetartiodactyla” for a group that included whales

(order Cetacea) and the group of even-toed terrestrial mammals known as the order Artiodactyla. This proposal was the

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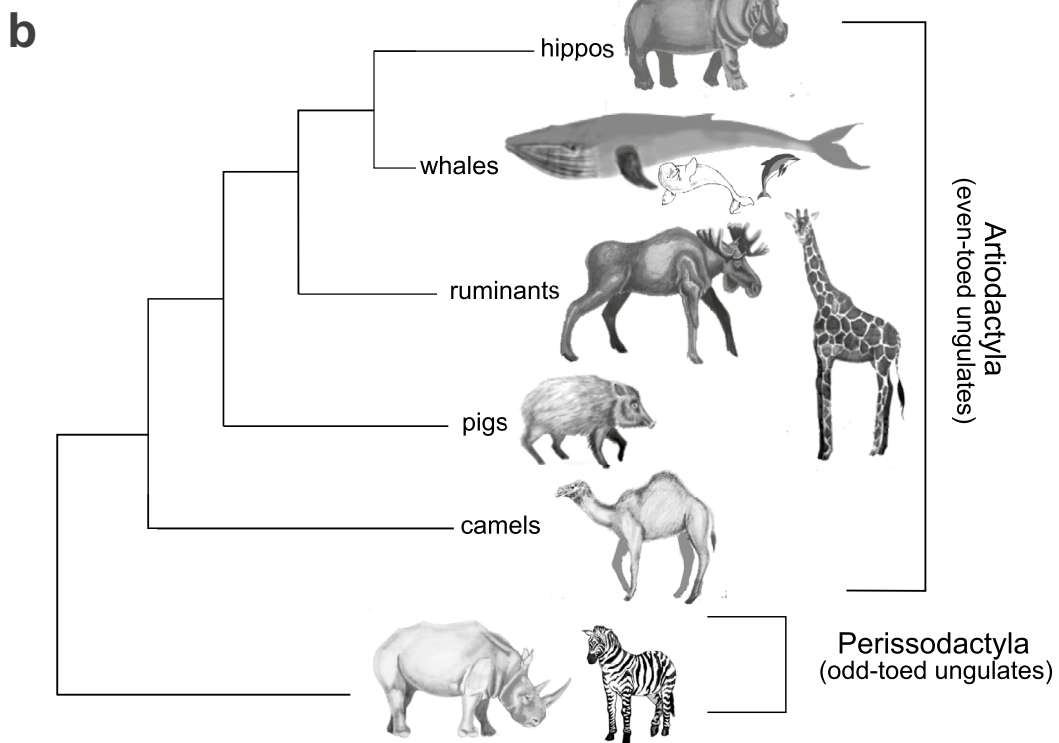
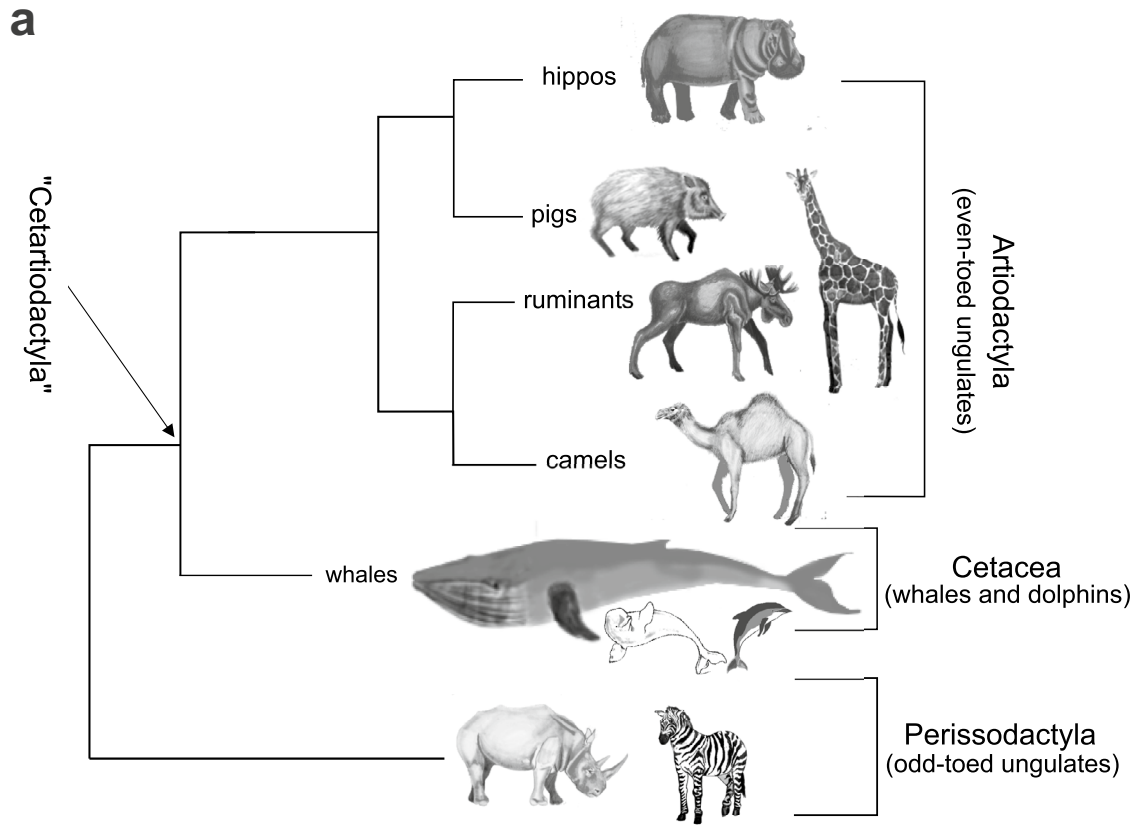


Fig. 1 Comparison of the topology and taxonomic names of the phylogenetic relationships of whales and artiodactyls. **a.** The name “Cetartiodactyla” implies that whales are the sister-taxon to the artiodactyls. **b.** The consensus topology of their relationships, showing how whales are nested within artiodactyls, not a sister-taxon to that order. (Original drawings by K.L. Mariott)

culmination of molecular phylogenetic studies that showed that cetaceans were closely related to terrestrial artiodactyls, and to the Hippopotamidae in particular (Graur and Higgins 1994; Irwin and Árnason 1994; Gatesy et al. 1996). This suggested taxon was supported by numerous molecular studies that followed (e.g., Stanhope et al. 1998; Waddell et al. 1999, 2003; Árnason et al. 2000, 2002, 2008; Murphy et al. 2007; Prasad et al. 2008). The relationship of whales to artiodactyls was confirmed paleontologically and morphologically by the discovery of the unique artiodactyl ankle structure with the “double-pulley” astragalus in two different fossil whales (Gingerich et al. 2001; Thewissen et al. 2001), and subsequently confirmed by more detailed morphological studies (Geisler and Uhen 2003, 2005; Theodor and Foss 2005; Spaulding et al. 2009; O’Leary et al. 2013). Since then, “Cetartiodactyla” has appeared in print more and more frequently, and has shown up on the internet and even in biology textbooks. According to Asher and Helgen (2010), a search on Google Scholar yielded 15,000 hits on “Artiodactyla” from 2000–2009, with only 482 hits for “Cetartiodactyla”. More recently, the same search (excluding patents and citations) yields 102,000 for Artiodactyla and 3810 for Cetartiodactyla. Even the IUCN Cetacean Specialist Group and the Taxonomy Committee of the Society for Marine Mammalogy have officially accepted Cetartiodactyla, and the name is featured on their home page (IUCN-CSG, 2021). This site further muddles the issue by frequently confusing Cetacea with Cetartiodactyla, such as listing the number of genera of Cetartiodactyla at 91, when they clearly mean the number of genera of Cetacea.

Before the name “Cetartiodactyla” becomes permanently and uncritically entrenched in the literature, it is worthwhile to examine the basis for the taxon and whether there is justification to replace the name “Artiodactyla”, which has been a universally accepted natural taxon since it was originally proposed by Richard Owen in 1848. When “Cetartiodactyla” was first proposed by Montgelard et al. (1997), the intent was to suggest that Cetacea and Artiodactyla were lumped into a larger clade of “Cetartiodactyla” (Fig. 1). This is how it was stated in their abstract (they wrote “The combined analysis of the two genes suggests a monophyletic Cetacea + Artiodactyla clade (defined as “Cetartiodactyla”)”), and they stated the same in most of their text, although in their phylogenetic tree (Fig. 1 in Montgelard et al. 1997), they showed that Cetacea is nested within Artiodactyla.

However, even as early as the studies by Irwin and Arnason (1994) and Gatesy et al. (1996), it was apparent that Cetacea is not the sister-taxon of Artiodactyla but nested deeply within Artiodactyla as the sister-taxon of the Hippopotamidae. This relationship of whales plus hippos was formalized by the taxon Whippomorpha by Waddell et al. (1999). The relationship of Cetacea and Hippopotamidae has since been confirmed by all the studies already cited and is now well established by paleontological studies that demonstrate the origin of hippos from a common ancestor with whales within the paraphyletic group Anthracotheria, which most systematists regard as the sister-group of whales and hippos. The split of the two groups, Anthracotheria (including Hippopotamidae) and Cetacea, goes as far back as the Eocene (Boisserie et al. 2005; O’Leary et al. 2013). Thus, the original purpose of having a taxon “Cetartiodactyla” (as a larger group suggesting a sister-taxon relationship between Artiodactyla and Cetacea) is no longer reflected by the current understanding of the relationships of mammals.

Despite the inappropriate basis for the name, “Cetartiodactyla” continues to be used both inside and outside the scientific community. The problems with “Cetartiodactyla” were thoughtfully reviewed by Asher and Helgen (2010). In their paper, they point out that the International Code of Zoological Nomenclature does not deal with names above the family level, so there is no formal arbiter on this issue. Instead, they argue that we need to evaluate all these new taxonomic groupings in the context of Simpson’s (1945) criteria of priority and stability. Asher and Helgen (2010, p. 2) write:

“In a nutshell, priority and stability should comprise the overriding principles by which new, high-level taxa are named. Established names for any given clade should not be altered unless the name with precedent unambiguously threatens stability. We suggest that the most appropriate will be those that are 1) the first, published name for a monophyletic group with unique content and 2) based on terms deemed familiar and logical to as many students as possible. Failure of a given taxon to meet one of these criteria does not necessarily mean it is invalid, but failure in both should.”

The proposed taxon “Cetartiodactyla” fails on both of these counts. Not only does it lack priority, because it is a junior synonym of Artiodactyla by 149 years, but it destabilizes the nomenclature rather than improving our understanding of the phylogenetic relationships of artiodactyls and cetaceans. It falsely implies that the two taxa are sister-groups, when instead one taxon is nested within the other. As Archibald (2003), Foss and Prothero (2007), and Asher and Helgen (2010) pointed out, systematists historically have not changed the name of a larger taxon when a group is placed within it. When the idea that birds are a

taxon nested within Dinosauria became widely accepted, systematists did not rename the group the “Avedinosauria,” nor did they modify the names of dinosaur groups such as Theropoda and Dromaeosauridae to “Avetheropoda” and “Avedromaeosauridae” when it became clear that birds are descended from theropods and dromaeosaurs. When phylogenetic classifications agreed that birds were a group within the Reptilia, no one proposed a taxon “Avereptilia”.

In addition, Owen’s original definition of Artiodactyla (Owen 1848: 119, 123, 131) only included a few taxa known at that time: pigs, hippos, peccaries, camels, ruminants, plus extinct Eocene taxa such as *Anthrotherium*, *Anoplotherium*, *Merycopotamus*, *Choeropotamus*, *Hippohyus*, as well as the palaeotheriid perissodactyl *Hyracotherium*, and even the primate *Adapis*. Since 1848, the content of Artiodactyla has been expanded dramatically to include animals as disparate as mouse deer, giraffes, and cattle. Yet during all those additions to the content of Artiodactyla, nobody considered renaming the group to reflect additional members.

There remains some confusion as to which clade or combination of clades should be named “Artiodactyla”, and whether there is some place where “Cetartiodactyla” could still be used. Spaulding et al. (2009) recommended that the term be restricted to the crown clade, that is all the living artiodactyls and their close fossil relatives. They wrote, “...we utilize the name Artiodactyla as a crown clade, the monophyletic group that includes the last common ancestor of cattle, antelope, deer, giraffes, musk deer, chevrotains, hippos, pigs, peccaries, and camels, and all of its descendants. Many analyses have supported the nesting of Cetacea several nodes within Artiodactyla....This prompted Montgelard et al. (1997) to rename the combined group ‘Cetartiodactyla.’ Despite our prior use of the term ‘Cetartiodactyla’, the topological change of placing Cetacea within Artiodactyla was never grounds to retire the name, Artiodactyla...”.

This last point is significant, because it reflects the important idea that there are no grounds for replacing Artiodactyla with “Cetartiodactyla”. We are not committed to any particular viewpoint on which taxa should be included in Artiodactyla, although most of the authors of this paper would prefer to define Artiodactyla as the total clade (crown group plus stem groups), so that extinct taxa that are conventionally called Artiodactyla by most paleontologists would remain in their familiar taxon.

The question about retaining the name “Cetartiodactyla” to use for a different subgroup within the Artiodactyla is an interesting one, but not central to this paper. It might replace “Whippomorpha” for the clade of cetaceans plus Hippopotamidae, but it lacks priority. In addition, this would create other problems, because most systematists who use “Cetartiodactyla” understand it to be a replacement for Artiodactyla, not a subgroup of that taxon. Árnason et al. (2000) proposed the name Cetancodonta for the clade that includes

Hippopotamidae + Cetacea because of “confusion involved in the term Whippomorpha”. Spaulding et al. (2009) followed Árnason et al. (2000) in using Cetancodonta for this group, but this just goes to show how unstable some of these clades and their names are at this point.

In addition, with the replacement of Artiodactyla with “Cetartiodactyla”, the implication that whales are just highly derived artiodactyls is lost. In other words, the polarity of the character transformation from terrestrial artiodactyls to marine artiodactyls (= whales) is no longer apparent by giving Cetacea and Artiodactyla equal billing in their name.

The only possible value of “Cetartiodactyla” is to highlight the new understanding of whales as relatives of other artiodactyls. But this does not outweigh the disadvantages of the violation of priority, the resulting instability, and especially the fact that “Cetartiodactyla” as now used falsely implies that cetaceans and artiodactyls are sister-taxa, which they are not. O’Leary et al. (2020) have made the same recommendation, so there seems to be a widespread concurrence of opinion that “Cetartiodactyla” should be abandoned.

Consequently, we recommend that the taxon name “Cetartiodactyla” should no longer be used, but the preferred name should be Artiodactyla Owen, 1848. If one wishes to convey the fact that whales are artiodactyls, one can say informally “whales and other artiodactyls” or “whales and terrestrial artiodactyls” and not use a confusing, invalid taxon to make that point.

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Declarations

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Consent to participate Not applicable.

Consent for publication Not applicable

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