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Crown Clades in Vertebrate Nomenclature: Correcting the Definition of Crocodylia

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A crown group is defined as the most recent common ancestor of at least two extant groups and all its descendants (Gauthier, 1986). Despite criticism, crown-group definitions are widely used, especially for certain clades of vertebrates. As an example, crown-group Crocodylia was established by Clark (in Benton and Clark, 1988), and there has been increasing use of crown Crocodylia rather than traditional or total Crocodylia since that date. Originally, the Crocodylia embraced forms dating from the Late Triassic to the present. These were divided into three classes, Protosuchia, Mesosuchia, and Eusuchia, the first two of which were accepted as probably or certainly paraphyletic. The new convention was cemented by Brochu (2003), who gave a new definition of crown Crocodylia according to the conventions of phylogenetic nomenclature (PN), as the last common ancestor of *Gavialis gangeticus*, *Alligator mississippiensis*, and *Crocodylus niloticus*, and all of its descendants. This led to an interesting reversal in the hierarchy, so that crown-clade Crocodylia is a subset of Eusuchia, rather than the other way round, as had been the case.

Reasons for redefining the boundaries of major vertebrate groups are linked to the advent of cladistics. Such nomenclatural revisions have been accelerated by the need for clarity in the application of the principles of PN (de Queiroz and Gauthier, 1992, 1994). Many proponents of crown-clade definitions assume that crown clades are a key element of PN and the PhyloCode, but this is not the case (Cantino and de Queiroz, 2004). The assumption of a linkage arose because earlier papers by architects of the PhyloCode (e.g., de Queiroz and Gauthier, 1992) included crown clades as a part of the manifesto for change, and PhyloCode supporters generally support crown clades. This article does not aim to criticize the principles of PN (see Benton, 2000, 2007; Nixon and Carpenter, 2000;

Dyke, 2002; Forey, 2002; Monsch, 2005; Rieppel, 2006) but rather expresses dissatisfaction with the increasingly common use of crown-group definitions, with a particular focus on the use of the term Crocodylia. Names should be given to stable clades for the sake of nomenclatural stability, independent of which nomenclatural system is preferred.

Lee (1996) demonstrated that crown clades were as good as any other kinds of clades in terms of clarity of definition and biological usage. Our question is therefore the following: why is it necessary to redefine something already established and accepted for almost 250 years with a new definition that is no more stable and even more confusing than the previous one? Moreover, consistency with traditional taxonomy is recommended by the PhyloCode (e.g., Articles 10 and 11; Cantino and de Queiroz, 2003). The basis for the definition of crown clades was set up by Gauthier (1986) and Gauthier et al. (1988), who argued that crown clades possess three main advantages: (a) they allow us to reconstruct soft tissues and other unfossilizable characters of extinct members; (b) they promote stability in discussion; and (c) they conform most closely to the original concept of the name. We will develop our ideas around these three points, the aim being to survey the literature in order to determine the traditional meaning of Crocodylia.

IS A SEPARATE CLASS FOR CROWN CLADES NECESSARY?

Motivations for the usage of crown-clade definitions came with the advent of cladistics in the mid-1980s. Proponents of PN may define taxa in three ways: node-based, stem-based, and apomorphy-based definitions. A crown clade is founded on a node-based definition and it is specifically bracketed by extant taxa. Crown

clades were first defined by Hennig (1966), but the earliest proposal for their usage appears in Gauthier (1986). A key advantage of crown clades has been stated (Gauthier, 1986; Gauthier et al., 1988; Gauthier and de Queiroz, 2001) to be that inferences about the biology of contained taxa are maximized. Some authors have extended this statement to say that the number of soft-part apomorphies is maximized also, but Gauthier and de Queiroz (2001) are quite clear that this is wrong.

Rowe (1988) was the first to apply a crown-group definition to mammals. Mammalia was restricted to all taxa stemming from the most recent common ancestor of at least two extant lineages as proposed by Patterson and Rosen (1977) and Gauthier et al. (1988). Lucas (1992) expressed dissatisfaction with this practice because crown clades restrict traditional namings to more exclusive clades, and this in turn triggers further renaming through the phylogeny of the concerned group and redefinition of accepted names, and so brings confusion. As stated by Lucas (1992), and then by Bryant (1994), the use of names within the frame of codes of nomenclature allows stability and long-established names should be retained whenever possible, so avoiding conflict of usage among workers in order to avoid confusion.

Gauthier et al. (1988) argued that crown clades are superior to other clades that include at least one extinct taxon as a specifier because soft-part characters may be safely assumed, even for fossil members. However, the extant phylogenetic bracket (EPB) concept (Witmer, 1995) allows assumptions about soft-tissue characters in more inclusive clades as well. Thanks to the EPB, it is philosophically just as easy to determine unfossilizable characters in dinosaurs as in Cretaceous eusuchians. Extant crocodylians as well as birds possess a four-chambered heart (see Seymour et al., 2004, for a review). The discovery of a four-chambered heart in an ornithischian dinosaur (Fisher et al., 2000), if correct, could be said to validate the use of the EPB.

Crown clades do not differ from other kinds of clades in the confidence with which soft-part characters may be inferred. For example, the EPB approach does not allow us to determine the extent to which feathers were present in a clade wider than Aves (in the traditional sense, consisting of *Archaeopteryx* and *Passer* and everything in between). Minimally, feathers can only be demonstrated within Aves. But fossils now show that feathers were acquired much deeper in the phylogeny (Zhou and Zhang, 2007), perhaps in the wider clade Coelurosauria that includes many theropod dinosaurs as well as birds. However, a similar uncertainty applies to the soft characters of a crown clade: there is no evidence to determine that they start at the origin of that clade, and many such characters extend down the stem lineage. Feathers are unique to modern birds, and yet it would be ludicrous to claim that feathers were acquired at the node marking crown-clade Aves (= Neornithes), because feathers go much deeper in the cladogram. Similarly, no other soft character of *Struthio* and *Passer* can be marked as associated with the node they subtend; most, if not all, unique avian

characters, whether hard or soft, probably arose below the crown-clade Aves node. A further example concerns the soft characters of Rowe's (1988) crown Mammalia, which almost certainly pertain to, or originated within, larger clades—we know from fossils, for example, that mammalian hair was present into a wider group of mammals, perhaps even to traditional Mammalia (Meng et al., 2006).

A weaker argument might be that soft-tissue characters of extinct members of crown clades may be reconstructed with greater confidence than those for extinct members of total clades because there is evidence from both sides of the basal split. So, for example, soft-tissue characters of crown Archosauria must share attributes of both modern birds and modern crocodylians. It is hard though to determine why this is objectively better than bracketing total-group Archosauria by birds and crocodylians on the one hand, and lizards and snakes on the other. In both cases, there is still the uncertainty about leakage of soft characters below the node subtended by extant representatives (the example of mammalian hair above).

It may not be possible to infer soft-part characters in crown or other clades. For example, among crown-group Crocodylia, lingual salt glands are absent in extant alligatorids and present in extant crocodylids. This means that all the extinct taxa bracketed by alligatorids and crocodylids have to be coded with a question mark, demonstrating that all soft-tissue characters cannot be coded for the crown group. As a consequence, Brochu (1999) pointed out that we simply do not know whether nonalligatorid alligatoroids followed the same osmoregulatory rules as their closest living relatives. The soft-tissue argument, as originally defended by Gauthier et al. (1988), is therefore not a valid reason to make a separate class for crown clades, which in this respect are the same as all other clades.

ARE CROWN CLADES MORE STABLE?

Lee (1996) demonstrated that crown clades are no more stable than total clades, contrary to Gauthier (1986) and Gauthier et al. (1988). Crown clades are hypothesis dependent because they contain fossils, as do all other clades (Benton, 2000). Some crown clades are more stable than equivalent total clades (Gauthier, 1986), but the opposite is equally true. Aves are an example of the former: the single taxon *Archaeopteryx* lies at the base of traditional Aves and numerous fossil genera and families lie between that node and the crown-clade Aves node. Traditional Aves is then potentially unstable if new fossils below *Archaeopteryx* turn up, whereas crown Aves is marked by a split between two substantial clades (Palaeognathae, Neognathae).

In other cases, total clades are more stable than crown clades. For example, a crown definition for Gnathostomata (bracketed by sharks and *Homo*) would discard several synapomorphies present in the well-documented stem members (Placodermi and Acanthodii) included in the traditional definition. Further, crown Gnathostomata, uniting Chondrichthyes and Osteichthyes, is not

really of much evolutionary interest, whereas traditional Gnathostomata is, as the clade characterized by possession of jaws. Tetrapoda is another example of an unstable crown clade. The crown group either includes or excludes most Paleozoic amphibians, depending on the position of lissamphibians. On the other hand, traditional Tetrapoda is more stable and includes all limbed vertebrates.

In other cases, such as the clades Amniota, Chiroptera, and indeed Dinosauria, the traditional and crown definitions are not much different because few or no stem taxa occur below the first major clade split. As expected, evolution follows several different courses, and pinning clade names on nodes is a semantic, human sport. So, crown clades may emerge immediately without any stem at all, or the stem may be of variable length. Crown clades deserve names of course, as do total clades, but there is no imperative to redefine accepted names away from their normal homes.

Rowe and Gauthier (1992) presented a rather different stability argument in favor of crown clades. They underlined the potential confusion from the larger number of stem-based (seven) definitions for Mammalia versus fewer (three), but similar, versions of crown Mammalia. Clearly, the addition of crown-clade definitions simply adds to the numbers of current and available definitions, and so exacerbates the potential confusion that Rowe and Gauthier (1992) placed at the door of the supporters of traditional clade definitions. Ironically, and not predicted in 1992, there is abundant evidence that squabbles among rival teams mean that there can be just as much confusion and instability within the PN/Phylocode camp—witness the to-and-fro over nomenclature of clades within Dinosauria (Benton, 2000).

A problem with crown clades is that they only work when there are at least two extant representatives of a clade. What about Dinosauria? Birds are living dinosaurs, but Aves marks just one pole of Dinosauria. Most cladograms of Dinosauria show an early split into the major subclades Ornithischia and Saurischia, with three or four stem taxa below that split. Are these stem taxa to be excluded from crown Dinosauria, a clade marked at the major split of Ornithischia and Saurischia, or should they be included in a slightly larger total Dinosauria? If crown Dinosauria is considered, then what is the independent justification for choosing the split into Ornithischia and Saurischia? What if that split had happened in the Jurassic, after a substantial radiation of several hundred stem dinosaurian taxa? This is part of the point made by Lucas (1992) that a crown clade with more than one extant terminal taxon is a vicissitude of history. The present day has nothing unique: when Linnaeus was alive, there were many organisms alive then that are now extinct. If Mammalia today is subtended by Monotremata at one end and *Homo* at the other, what happens when the five species of platypus (*Ornithorhynchus*) and echidnas (*Tachyglossus* and *Zaglossus*) go extinct?

Mammalia would then shrink to include just marsupials and placentals and their extinct relatives. Even more

marginal is the status of crown Lepidosauria, subtended by snakes or lizards at one pole, and the tuatara, *Sphenodon*, at the other. One (or two) endangered species living on islands off New Zealand is all that stands between the current shape of crown Lepidosauria and a somewhat diminished future content.

TRADITIONAL USAGE

Gauthier (1986), Gauthier et al. (1988), Gauthier and de Queiroz (2001), and others have suggested that crown clades are preferable to total clades because the former terms more closely approximate the original usage. They note, for example, that Mammalia, according to Linnaeus (1758), included only modern taxa, and the same is true of the first presentations of many names of larger clades. This is disingenuous, of course, because the fossil record of many groups was poorly known, or entirely known, 250 years ago. Others have made the case cogently, for both birds (Chiappe, 1991; Sereno, 1999) and mammals (Lucas, 1992; Luo et al., 2002), that, as fossil taxa were discovered, contemporary naturalists had no compunction about including them within the groups established earlier by Linnaeus and others. So, *Archaeopteryx* was from the first called a bird and included in Class Aves. The same was true for the first finds of jaws and teeth of Mesozoic mammals that, from the 1820s, were included in Class Mammalia.

Here we document usage of the term Crocodylia to determine whether or not the “tradition” argument supports the crown-clade view that the term should be restricted to a clade consisting of modern forms and their immediate antecedents (Clark, 1986; Benton and Clark, 1988; Brochu, 2003). Since 1988, more and more systematists and paleontologists have adopted crown-clade Crocodylia (Fig. 1). Clark built the basis of the phylogenetic nomenclature for Crocodylia in his unpublished thesis (1986) and later, crocodylian workers expanded it, considering that the crown-group usage would be beneficial for phylogenetic nomenclature (Norell et al., 1994; Salisbury and Willis, 1996; Brochu, 1997, 1999, 2000). Proponents of the crown-clade definitions for Crocodylia recently put forward the argument that the traditional definition of Crocodylia, which includes Triassic forms, was imprecise, with a labile lower bound (Brochu, 1999, 2003). The reasons for the shift in definition of Crocodylia are not clear. Moreover, the arguments put forward do not appear to be valid, even if the new nomenclature has been widely used. The term Crocodylia was coined by Gmelin (1789) and it embraced extant forms only. Later on, a wide range of fossil crocodiles were found, and these had to be classified. Owen (1860) included the fossil forms in the classification of vertebrates, and he placed fossil crocodylians in Gmelin’s Crocodylia. From a historical standpoint, the argument that Crocodylia was first defined on extant taxa is true, but the sole reason is because fossils were not yet known, or at least they were barely known and poorly understood (contra Brochu, 1999). By 1860, then, the group Crocodylia included fossil members as old as the Early Jurassic (e.g., *Steneosaurus*, *Teleosaurus*,

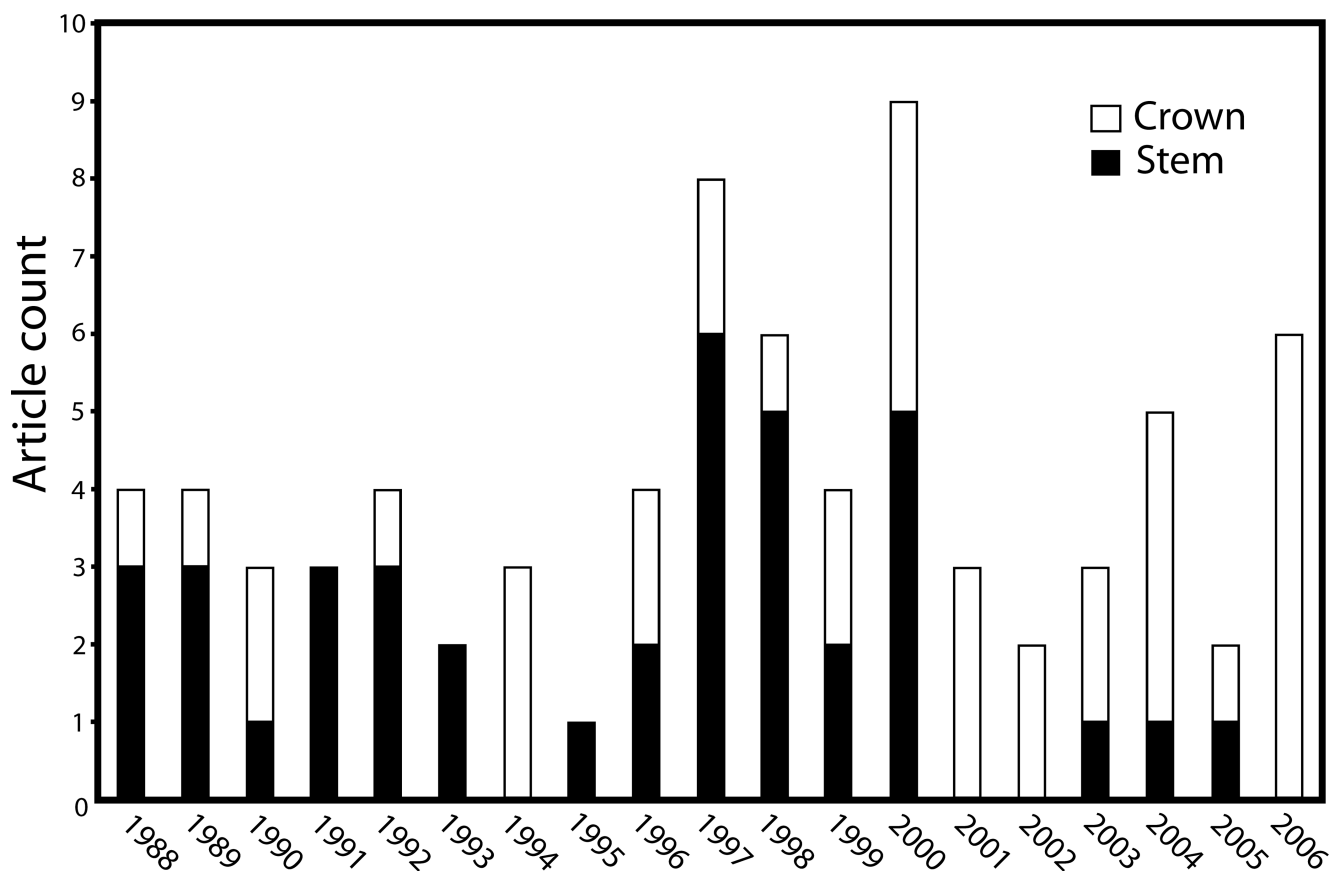


FIGURE 1. Census of the post-1988 literature indicating total count of stem-based/crown-based terms for Crocodylia per year.

Pelagosaurus). Major works reporting the current classification of Reptilia (e.g., Zittel, 1890; Osborn, 1903a, 1903b; Williston, 1925; von Huene, 1956; Romer, 1933, 1945, 1956, 1966; Steel, 1973) followed this traditional meaning, extending Crocodylia to include Late Triassic and Early Jurassic protosuchians and mesosuchians, and it was the same in standard textbooks on biological classification, which have been the references for several generations of students (Moret, 1946; 1953; Kálin in Piveteau, 1955; Grassé, 1965; Carroll in Gans, 1969; Piveteau et al., 1978). From the 20th century onwards, none of the definitions of Crocodylia has applied the term to the crown clade. Reasons for including fossil members might first be explained by the close resemblance of fossils with modern forms (e.g., the platyrostral profile with pointed teeth) but also by the ability to trace the path of palatal evolution from stem to modern members. The content of Crocodylia remained stable even if some forms were moved in or out.

Common usage of taxonomic terms further supports the traditional total-group usage. For example, the general public has heard of *Archaeopteryx* and consider it as a bird, therefore contradicting the idea that crown clades are the usual assumption. Crocodylians do not benefit from the same fame, but from time to time they appear in newspaper headlines. Recently, a few stem crocodylians have been mentioned in newspapers. The “supercroc”

Sarcosuchus imperator was presented by the BBC as a crocodile. The same happened for *Dakosaurus andiniensis* (Gasparini et al., 2006), which was also presented by the BBC as a crocodile. In early 2006, Reuters reported *Effigia okeefeae* (Nesbitt and Norell, 2006), a crocodile ancestor presented to the public as a “crocodylian” by the authors of the discovery. For nonspecialists, crocodiles are primitive and carry the erroneous reputation of having remained unchanged for several million years. Therefore, these fossils are crocodylians in traditional scientific and popular usages.

The term Crocodyliformes was coined by Clark (in Benton and Clark, 1988) to replace the traditional Crocodylia. No phylogenetic definition was presented at that time, but this was supplied later by Sereno et al. (2001): *Protosuchus richardsoni*, *Crocodylus niloticus*, and all descendants of their common ancestors. The need for the new term and the shift in meaning of Crocodylia was not explained at the time.

Clark (in Benton and Clark, 1988) only mentions that he emended the term in 1986. Brochu (2001) summarized the situation: “Crocodyliformes includes those animals conventionally called ‘crocodylians’ in the pre-phylogenetic literature, though the term ‘crocodylian’ is now restricted to the crown group.” Why is the term Crocodylia restricted to the crown group? Brochu (2003) had given the explanation: “most authorities included

'protosuchians' and 'mesosuchians', but it may or may not have included 'sphenosuchians'. The placement of 'Crocodylia' fluctuated among paleontologists, and whether or not 'sphenosuchians' or more basal animals, such as phytosaurs, should be considered 'crocodilians' was a matter of debate."

"Sphenosuchians" were included in Crocodylia by Romer (1966), Crush (1984), and Walker (1990). But this inclusion is recent and since they were first described (Haughton, 1915), sphenosuchians have always been excluded from Crocodylia. Also, their position was very recently confirmed to lie outside what is widely called Crocodyliformes (Clark et al., 2004). Parasuchia was named by Huxley (1875) as a suborder of the Crocodylia for *Stagonolepis* (an aetosaur) and *Belodon* (a phytosaur), and including the then-undescribed *Parasuchus*. Huxley (1875) presented the name in his review of crocodylian evolution, and he was clear that Parasuchia were ancestral to other crocodylian groups. Koken (1887) agreed with that concept and underlined the difference of the parasuchians *Belodon* and *Stagonolepis* from Mesozoic and Tertiary crocodylians but still included them in that group. Zittel (1890) also considered phytosaurs within Crocodylia, but from Zittel's treatise, Broili and Schlosser (1923) finally considered Parasuchia to be a reptilian order different from Crocodylia. Then, Para-

suchia, which later excluded aetosaurs, has been excluded from Crocodylia in all subsequent textbooks on reptile classification. Since the inclusion of fossil forms in Crocodylia, some time was necessary to allow distinction of crocodylian members from convergent forms. Exclusion of sphenosuchians and phytosaurs from the traditional Crocodylia has therefore been the standard view for over 80 years.

Finally, Brochu (2003) suggests that the definition of Crocodylia has never been stable: "The older applications of Crocodylia could thus apply to either Crocodyliformes or Crocodylomorpha." The stability of the name Crocodylia depends on the proposed content, whether sphenosuchians are considered or not in Crocodylia. But given that sphenosuchians were not included in the traditional Crocodylia, the older application of Crocodylia would apply to the recently created Crocodyliformes only. Walker erected Crocodylomorpha (1968) specifically for the clade that includes Crocodylia and sphenosuchians. Recent cladistic analyses have placed sphenosuchians outside what is now called Crocodyliformes (i.e., Protosuchia, Mesoeucrocodylia, and Eusuchia) (Clark et al., 2004). Therefore, the older application of Crocodylia needs to replace what is currently named Crocodyliformes, and Crocodylia + Sphenosuchia represents the subclass Crocodylomorpha.

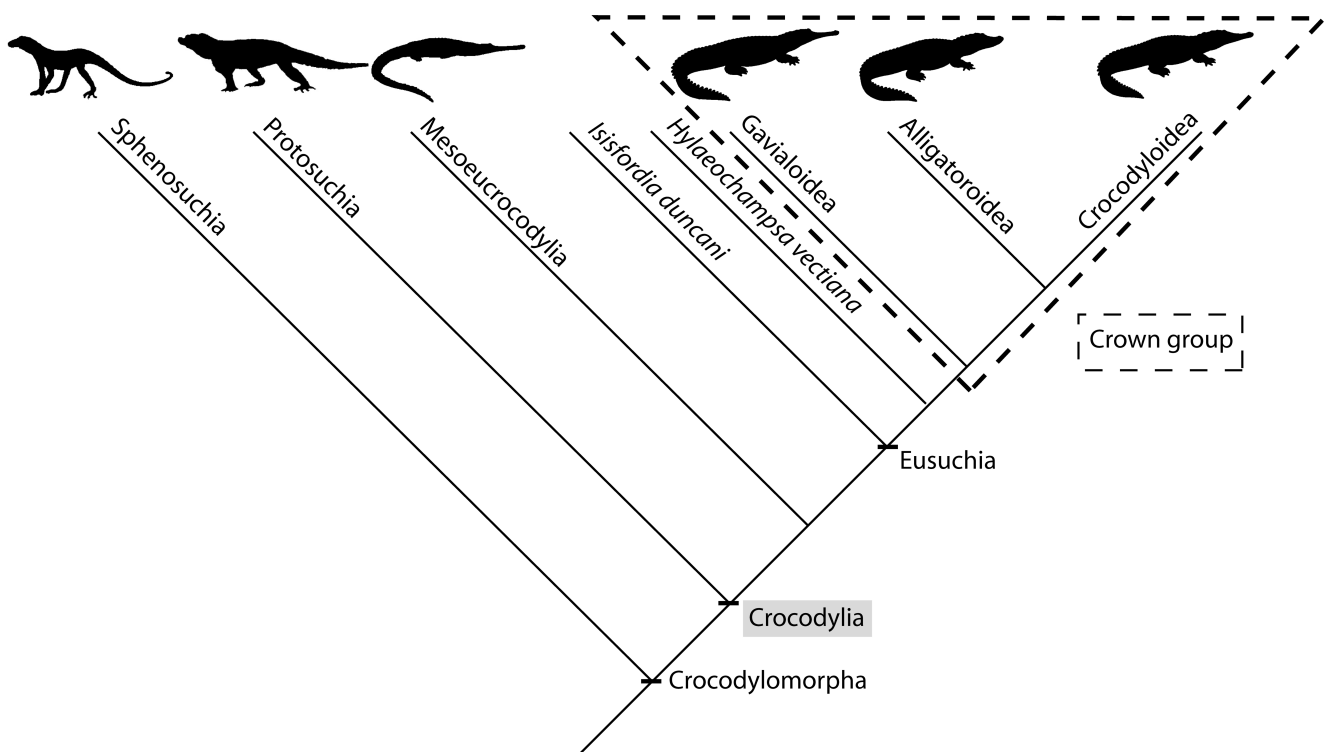


FIGURE 2. Simplified topology of the major crocodylian clades with Crocodylomorpha, which includes Sphenosuchia and Crocodylia; Crocodylia is defined as *Protosuchus richardsoni*, *Crocodylus niloticus*, and all descendants of their common ancestors. Protosuchia, according to Sereno et al. (2001): the most inclusive clade containing *Protosuchus richardsoni* (Brown, 1933) but not *Crocodylus niloticus* (Laurenti, 1768); Mesoeucrocodylia, according to Sereno et al. (2001): the most inclusive clade containing *Crocodylus niloticus* (Laurenti, 1768) but not *Protosuchus richardsoni* (Brown, 1933); Eusuchia: the least inclusive clade containing *Isisfordia duncani* (Salisbury et al., 2006) and *Crocodylus niloticus* (Laurenti, 1768).

The following statement (Brochu, 2003) referring to the reasons advanced above is unfounded: "There is thus no single traditional usage to which a phylogenetic definition could be applied." This is unfounded, because a phylogenetic definition has been applied to Crocodyliformes (Sereno, 2001): *Protosuchus richardsoni*, *Crocodylus niloticus*, and all descendants of their common ancestors (node-based definition). Given that Crocodyliformes is a junior synonym of Crocodylia, the above definition applies to Crocodylia.

The name Crocodylia that traditionally embraced members as old as the Late Triassic has been moved to the more inclusive crown-clade definition (Clark, 1986, in Benton and Clark, 1988). We now propose that the crown-clade definition, which has been used by a majority of workers for some years, is inappropriate and should replace Crocodyliformes with the phylogenetic definition of Sereno et al. (2001). For clarity, we suggest that the term Crocodylia should be used as indicated here in a hierarchical ranking (see also Fig. 2):

- Subclass CROCODYLOMORPHA Hay, 1930 (Walker, 1968)
- Order CROCODYLIA Gmelin, 1789
- Suborder Protosuchia Mook, 1934 (sensu Clark, 1994)
- Suborder Mesoeucrocodylia Whetstone and Whybrow, 1983
- Suborder Eusuchia Huxley, 1875

"Crocodylia" has been widely used in textbooks and defines exactly the same thing as Crocodylia: Protosuchia, Mesosuchia, and Eusuchia. Reasons for preferring the usage of Crocodylia over Crocodylia are expressed by Dundee (1989). Several publications refer to Gmelin (1788), but they should refer to Gmelin (1789) instead. Gmelin produced a revised edition of Linnaeus in several volumes from 1788 to 1791; the volume that presented "Crocodyli" was published in 1789.

The ICZN does not control taxonomic names above the family-level, including superfamilies (ICZN, 1999), despite efforts to effects this change (Dundee, 1989). The PhyloCode, however, extends nomenclatural rules to all taxa, without regard to hierarchy. Priority of usage under the PhyloCode applies only to definitions of terms that will be registered under the PhyloCode system and so cannot extend retrospectively to older usages. Equally, of course, systematists have generally assumed some measure of priority of usage in order to avoid a proliferation of unnecessary names. Therefore, our points about traditional usage are in the spirit of common sense rather than legislation, and those are the terms used hitherto by proponents of the crown clade concept.

CONCLUSIONS

An increasing number of articles use the crown-group definition of Crocodylia. The community of "crocodylian" paleontologists is small and is dominated in number of publications by even fewer persons who therefore are influential. Clark invented the crown-group defini-

tion for Crocodylia, which was applied in influential papers in that domain (Norell et al., 1994; Salisbury and Willis, 1996; Brochu, 1997, 1999, 2003). Other workers have been influenced and followed the same usage because it may have seemed modern to follow such new definitions, which are published in a majority of recent works by leading figures in leading journals. Nevertheless, the term Crocodylia included stem lineages back to the Early Jurassic and Late Triassic in scientific and textbook usages before 1988.

Crown clades are not superior in content, nor are they more stable than any other kinds of clades. This is not the first time that the crown-clade concept has been rejected, because it involved the redefinition of widely used terms: Aves and Mammalia (Lucas, 1992; Patterson, 1993; Lee, 1996; Rieppel, 1997; Sereno, 1998, 1999; Benton, 1999; Padian et al., 1999; Benton, 2000). For the same reasons that affected the renaming of Crocodylia, the crown-clade concept is here also rejected. Crocodyliformes then is a junior synonym of Crocodylia and Crocodylia may acquire the node-based definition applied by Sereno et al. (2001) to Crocodyliformes.

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APPENDIX 1

Literature used for the proportion count of stem-based versus crown-based usages of the term *Crocodylia* in published works concerned with crown clade crocodylian taxa from 1988 to 2006 included.

Post-1988 Literature Employing a Stem-Based Definition of *Crocodylia* (total 36)

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