**Point of View**

*Syst. Biol.* 58(5):537–543, 2009

DOI:10.1093/sysbio/syp053
Advance Access publication on August 28, 2009

# A Correction Corrected: Consensus Over the Meaning of Crocodylia and Why It Matters

CHRISTOPHER A. BROCHU[1,*], JONATHAN R. WAGNER[2], STÉPHANE JOUVE[3], COLIN D. SUMRALL[4], AND LLEWELLYN D. DENSMORE[5]

[1]*Department of Geoscience, University of Iowa, Iowa City, IA 52242, USA;*
[2]*Jackson School of Geoscience, University of Texas, Austin, TX 78712, USA;*
[3]*Département Histoire de la Terre, Muséum National d'Histoire Naturelle, CNRS UMR 5134, 8 rue Buffon, 75005 Paris, France;*
[4]*Department of Earth and Planetary Sciences, University of Tennessee, Knoxville, TN 37996, USA; and*
[5]*Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409, USA;*
**Correspondence to be sent to: Department of Geoscience, University of Iowa, Iowa City, IA 52242, USA; E-mail: chris-brochu@uiowa.edu.*

Crown clades are an important nexus of study for paleontologists and neontologists. Associating commonly used names with crown clades—the crown clade convention—draws their meanings closer to the way they are actually used by the majority of scientists. Molecular, physiological, behavioral, and soft-tissue data can usually be unambiguously optimized no deeper than the root of a crown clade, and commonly used names are applied implicitly to the crown group far more often than to larger groups including extinct relatives (Rowe 1988; Bryant 1996; Gauthier and de Queiroz 2001; Laurin 2002; Joyce et al. 2004; de Queiroz 2007).

The crown clade convention is controversial (Lee 1996; Benton 2000; Anderson 2002; Bateman and DiMichele 2003; Sereno 2005). Crown clade membership and diagnosis may differ from those of more inclusive groups historically associated with the same name. Our knowledge of phylogeny is imperfect, and changes in hypotheses may force changes in the membership and diagnosis of a group.

A recent comment by Martin and Benton (2008; hereafter Martin and Benton) suggests that the crown definition of Crocodylia—the last common ancestor of *Gavialis gangeticus* (Indian gharial), *Alligator mississippiensis* (American alligator), and *Crocodylus niloticus* (Nile crocodile) and all of its descendants—should be abandoned. They argue that crown clades might not be stable and that a consistent, stable "traditional" Crocodylia already exists. The interests of stability and continuity are best served, they argue, by reverting to this meaning. But their comment does not actually address the stability of crown Crocodylia, which has been remarkably stable since first published by Benton and Clark (1988), and literature cited in support of a consistent "traditional" meaning of Crocodylia reveals no consistency. Here, we discuss stability in the crown convention, show that one cannot identify a particular meaning of Crocodylia as "traditional," demonstrate that the crown definition has become the standard meaning for Crocodylia and is demonstrably not limited to a small number of authors, and reiterate the reasons why crown clades are highly beneficial.

## STABILITY

Martin and Benton, following Lee (1996), argue that crown clade membership and diagnosis might change if a phylogenetic hypothesis changes. This is true, but all groups (phylogenetic or Linnaean) are prone to instability as our knowledge of phylogeny changes. The crown convention (and phylogenetic nomenclature in general) tries to achieve a different kind of stability—membership and diagnosis may change but underlying meaning does not (Rowe 1986).

Martin and Benton suggest that crown clades can become unstable if one of the specifiers dies out. What would happen to Mammalia, Martin and Benton ask rhetorically, if monotremes disappeared? The answer is clear from a careful reading of the phylogenetic definitions—nothing. Crown clades are defined on the basis of living taxa but vital status is not part of the definition. There is a difference between the intent of a crown clade—to circumscribe least inclusive clades including historically living members—and the actual definition of the name, which is based only on species (Rowe and Gauthier 1992). A philosophical argument could arise over whether Crocodylia is still a crown clade if *Gavialis* becomes extinct (and if *Gavialis* is basal to other living crocodylians—this is controversial), but the kinds of nonfossilizable information we can get from living animals would be available from collections or observations made prior to extinction. The intended meaning remains unchanged.

## TRADITION

Taxonomic groupings intended to include living crocodylians, with or without extinct relatives, have been used since before 1800, but the particular meaning

Martin and Benton ascribe to Crocodylia—a group including 2 paraphyletic assemblages ("Protosuchia" and "Mesosuchia") and a monophyletic Eusuchia but excluding the paraphyletic "Sphenosuchia" (Fig. 1)—is of 20th-century vintage. Mook (1934) was the first to apply Crocodylia to a group including eusuchians, mesosuchians, protosuchians, and nothing else. This group is now called Crocodyliformes.

Protosuchians were unknown when Owen (1842; see Dundee 1989) coined the name Crocodilia. Owen included thalattosuchians (as did some earlier authors, e.g., Cuvier 1824) and *Goniopholis*—the only noncrocodylian crocodyliforms known from more than isolated teeth at the time—but he also included some fragmentary dinosaurs. Assuming Owen would have excluded these had they been better known, Crocodilia sensu Owen (1842) corresponds not with Crocodyliformes, but at most with Mesoeucrocodylia and possibly a subordinate group, such as Neosuchia, depending on how one resolves the relationships of thalattosuchians (Fig. 1).

Conversely, though Martin and Benton (p. 177) claim that "sphenosuchians have always been excluded from Crocodylia" since the early 20th century, sphenosuchians were included in most North American vertebrate paleontology textbooks written after 1960 (Romer 1966; Colbert 1980; Carroll 1988), the *Handbuch der Paläoherpetologie* series (Steel 1973; Charig et al. 1976), and several other important reviews (e.g., Kuhn 1968; Walker 1970). Indeed, this particular meaning of Crocodylia—coinciding not with Crocodyliformes, but with Crocodylomorpha—predates the meaning preferred by Martin and Benton (Nopcsa 1923).

Martin and Benton (p. 176) claim that their particular meaning of Crocodylia "was the same in standard textbooks on biological classification" but a *lack* of consensus is illustrated by the different meanings of Crocodylia in the 3 editions of the standard English-language vertebrate paleontology textbook for much of the 20th-century—A. S. Romer's *Vertebrate Paleontology*. Crocodylia corresponds with Mesoeucrocodylia in the first edition (Romer 1933), with Crocodyliformes in the second (Romer 1945), and minimally with Crocodylomorpha in the third (Romer 1966; Fig. 1). The shift from Mesoeucrocodylia to Crocodyliformes in the second edition reflects the establishment of Protosuchia (Mook 1934), but sphenosuchians were known prior to 1933. Changes between the second and third editions reflect

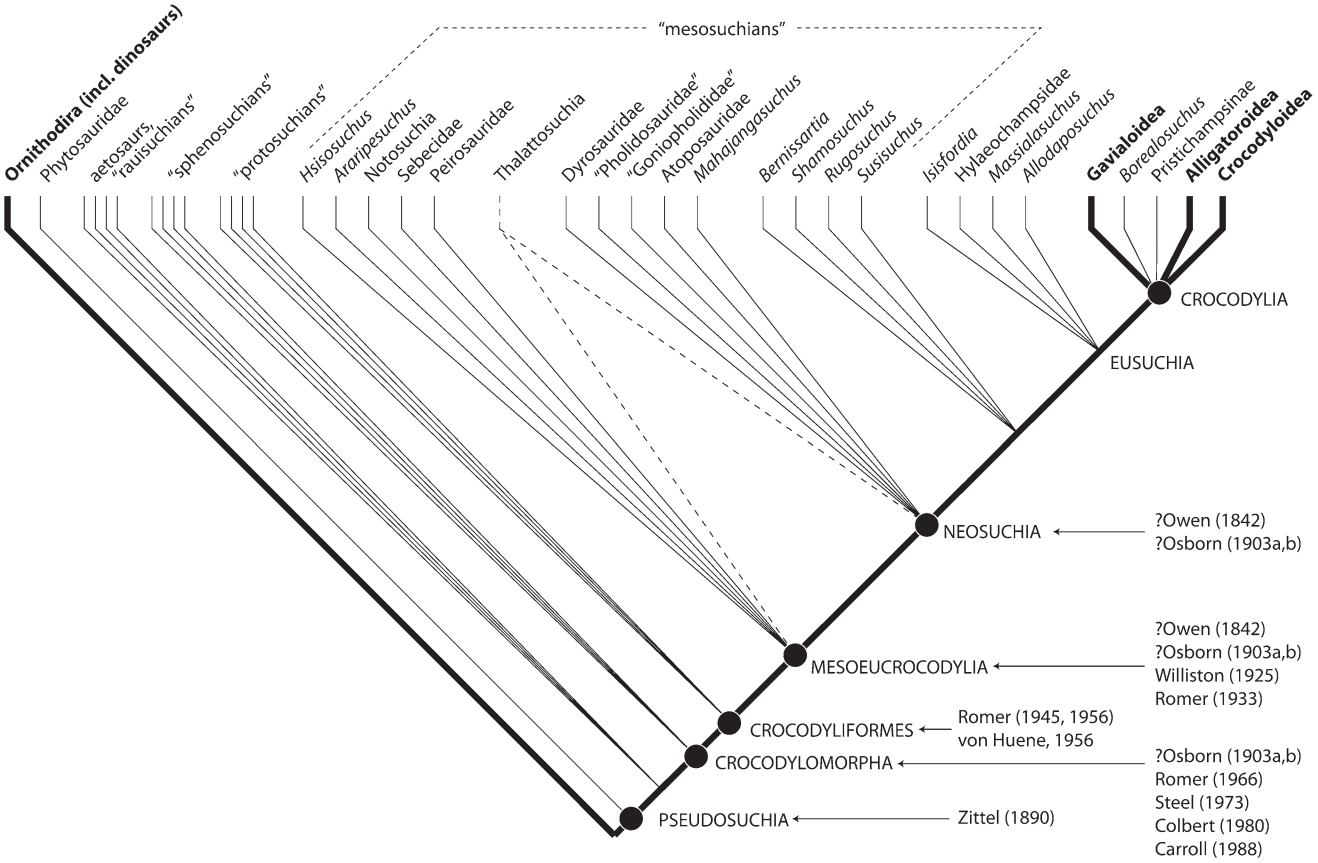


FIGURE 1. Phylogenetic relationships among pseudosuchian archosaurs showing content of Crocodylia according to various authors. Content of Crocodylia sensu Owen (1842) depends on resolution of the position of Thalattosuchia. Precise meaning sensu Osborn (1903a,b), cited by Martin and Benton as corresponding to "traditional" Crocodylia, is vague; Osborn said nothing about the content of Crocodylia other than exclusion of phytosaurs. Analyses used to construct tree are indicated in Supplementary Material (Appendix S1).

more than the rootward extension of a name to include newly described basal fossils.

In fact, it is not entirely clear what "traditional" Crocodylia means beyond "living crocodylians and some extinct relatives that look like them." Martin and Benton associate the name with Crocodyliformes, but references cited on p. 176 as following "this traditional meaning" refer to at least 4 different groups (Fig. 1). What is described as stability "even if some forms were moved in or out" (p. 176) amounts to fundamental changes in diagnosis, first appearance, and content—the very charges Martin and Benton level against the crown definition. Decisions to apply Crocodylia to a given assemblage were arbitrary and subjective, resulting in the fluctuating membership and diagnosis that left Crocodylia without a consistent meaning through the 20th century.

Martin and Benton refer to the "traditional" meanings as "stem based" (their appendix) or "total Crocodylia" (p. 173), but like most groups of organisms following the Darwinian Revolution, Crocodylia was based on a combination of relationships and similarity. It more closely approximated an apomorphy-based group. It referred to animals closely enough related to living crocodylians and sufficiently similar to avoid being exiled to some other group. This is why the "traditional" concept is vague and imprecise—no 2 experts have the same opinion of where the threshold of sufficiency is crossed. A relationship between crocodylians and sphenosuchians was understood but their inclusion or exclusion was based entirely on the significance placed on the level of similarity. The distinction was both arbitrary and subjective.

### *Priority*

Martin and Benton (p. 178) state that "Crocodyliformes is a junior synonym of Crocodylia" and apply the definition of Crocodyliformes formalized by Sereno et al. (2001) to Crocodylia. Although Martin and Benton state that their argument is not based on "legislation," "junior synonym" is an implicit reference to priority. Priority is meaningless except in the context of "legislation."

In the phylogenetic system, priority is based on definition. If 2 names refer to the same clade, the first name to be defined has priority. If a name is given 2 definitions, the first definition has priority. Thus, Crocodylia sensu Martin and Benton (2008) is a junior objective synonym of Crocodyliformes sensu Sereno et al. (2001) and a junior objective homonym of Crocodylia sensu Benton and Clark (1988). Alternative phylogenetic definitions cannot be applied to these names.

As Martin and Benton acknowledge, rules of priority under the International Code of Zoological Nomenclature do not apply because Crocodylia has usually been viewed as an order, and priority in the phylogenetic system does not formally apply until PhyloCode is officially launched (Cantino and de Queiroz 2007). But phylogenetic definitions applied to Crocodyliformes and Crocodylia have become established and remain stable. There is every reason to maintain them.

## Consensus

### *Consensus and Common Use*

Martin and Benton argue that "common usage" should be a factor in resolving taxonomic issues. As an example they cite *Sarcosuchus*, the so-called "SuperCroc" from the Cretaceous of northern Africa made famous in *National Geographic* (Sereno 2001). Media coverage followed *National Geographic* in calling *Sarcosuchus* a "crocodilian," even though it is not within the crown clade and was not referred to Crocodylia in the technical paper released at the time (Sereno et al. 2001).

One of us (C.A.B.) was involved in the discussions over what to call *Sarcosuchus* in the "National Geographic" article. The editors' decision was based on the presumption that the public would think it looks like a crocodylian. Popular magazines try to find a balance between public understanding and current systematic practice. As such, they sometimes make decisions that contradict the scientific community if, in their judgment, a nod to some sort of lay understanding is needed. Not all of these decisions are well founded. We disagree that such a nod was necessary for *Sarcosuchus*; it is a simple matter to state that *Sarcosuchus* is a close extinct relative of crocodylians—so close, and so similar, that it was once classified as a crocodylian, though we would now call it a crocodyliform.

This translates into a disassociation between nomenclatural precision and the way taxonomy is reported in the media. Martin and Benton state that Sterling Nesbitt was quoted in a newspaper describing a Triassic pseudosuchian as a "crocodilian" but this was editorial error. Nesbitt was misquoted (Nesbitt S., personal communication). Misrepresentation of what professionals say (accidental or otherwise) is perhaps not the best arbiter of systematic practice.

Scientists frequently diverge from "common usage" in the interest of accuracy and precision. For example, Benton (2004; p. 261) states that "birds are derived theropod dinosaurs" and applies the name Dinosauria on cladograms accordingly. This means, logically, that dinosaurs are not extinct. But the most recent (11th) edition of the *Merriam-Webster Dictionary* defines "dinosaur" as "any of a group of extinct long-tailed Mesozoic reptiles often of huge size." In this case, Benton appropriately disregards "common usage" for the sake of precision.

One could argue that vernacular "dinosaur" and academic "Dinosauria" are different—the latter is a clade, and the former refers to the popular beasts, mostly gigantic and (presumably) unfeathered but all toes-up, from the Mesozoic. One could also argue that including birds within Dinosauria is commonly accepted in academic circles and thus qualifies as professional "common usage." But Benton (2004) applies Osteichthyes and Sarcopterygii to monophyletic groups that include tetrapods, even though Osteichthyes historically

referred to bony fishes (which is what the name literally means) and Sarcopterygii included "lobe-finned" fishes exclusive of tetrapods. Names that meant one thing have come to mean something else. Common usage and tradition are set aside for the sake of clarity and precision.

### *Current Consensus*

Martin and Benton list 74 papers and books published between 1988 and 2006 to assess the status of the name Crocodylia. In their appendix 1, they indicate 37 using the crown definition and 36 using something more inclusive. From their list, it would appear that equal numbers of publications used a noncrown meaning of Crocodylia as did not, and numbers using different concepts of Crocodylia wax and wane over the 19-year period. Although Martin and Benton acknowledge a recent increase in use of the crown definition, there seems to be no real consensus from the list they provide. Moreover, they state, the community of crocodyliform specialists is rather small and the increase in use of the crown definition might be inflated by a handful of influential papers.

We identified an additional 383 professional books, book chapters, monographs, or journal articles published from 1988 through 2006 in which the meaning of Crocodylia could be determined. We also compiled literature published or available online through 2008 (Supplementary Material, Appendix S1; available from http://www.sysbio.oxfordjournals.org/). The crown definition accounts for more than 75% of the determinable uses of Crocodylia since 2000 and 80% during the 5-year period from 2004 through 2008 (Table 1 and Fig. 2). Only 28.6% used it from 1988 through 1999. Martin and Benton concede increasing use of the crown definition, but the magnitude of the increase was dampened by a limited literature sample.

But the critical point is this: the crown definition is widely used by evolutionary biologists, herpetologists, comparative morphologists, and paleobiologists (Larsson 1998; Blob 2000; Hutchinson 2001; Zug et al. 2001; Claessens 2004; Olmo 2005; O'Connor 2006; Tsuihiji 2007; Holliday and Witmer 2007; Sadleir and Makovicky 2008), and some of the molecular literature uses the crown definition both implicitly and explicitly (Harshman et al. 2003; Gatesy et al. 2003; Roos et al. 2007; Viola et al. 2009). These numbers do not reflect a small clique of crown enthusiasts—they demonstrate the acceptance of a particular definition in the scientific community and they disprove the suggestion that crown Crocodylia is merely in circulation within a restricted circle of crocodyliform systematists.

## WHY IT MATTERS

We name clades for precisely one reason—because we talk about them. At a certain level, the merits of a specific clade definition do not matter as long as names are used consistently in the scientific community.

TABLE 1. Numbers of professional publications (published or in press and available online) using or not using a crown definition of Crocodylia, 1988–2008

| | Noncrown | Crown | Percent crown |
|---|---|---|---|
| 1988 | 13 | 1 | 7.1 |
| 1989 | 16 | 1 | 5.9 |
| 1990 | 13 | 4 | 23.5 |
| 1991 | 15 | 2 | 11.8 |
| 1992 | 7 | 3 | 30.0 |
| 1993 | 10 | 4 | 28.6 |
| 1994 | 19 | 8 | 29.6 |
| 1995 | 9 | 4 | 30.8 |
| 1996 | 17 | 14 | 45.2 |
| 1997 | 17 | 10 | 37.0 |
| 1998 | 11 | 5 | 31.3 |
| 1999 | 15 | 9 | 37.5 |
| 2000 | 11 | 24 | 68.6 |
| 2001 | 7 | 25 | 78.1 |
| 2002 | 13 | 15 | 55.6 |
| 2003 | 10 | 17 | 63.0 |
| 2004 | 7 | 25 | 78.1 |
| 2005 | 4 | 28 | 87.5 |
| 2006 | 11 | 34 | 75.6 |
| 2007 | 7 | 38 | 84.4 |
| 2008 | 11 | 38* | 77.6* |

*Two of the papers using a crown definition were listed as "in press" at the end of 2008. Disregarding them, the percentage of papers using the crown definition drops to 76.6. The percentage from 2000 through 2006 (the last year counted by Martin and Benton) is 73.4.

What matters most is not that the crown definition is a *better* definition but that it is the *consensus* definition (Fig. 2). But in fact, the crown meaning is highly beneficial beyond its current near-universal acceptance.

### *Communication and Universality of Meaning*

Real confusion has arisen from not distinguishing different meanings of a name. For example, fossils as old as the Cretaceous have been assigned to *Crocodylus* (Steel 1973), but molecular divergence estimates suggested a Neogene split among living species (Densmore 1983). But the "conflict" had nothing to do with the data but everything to do with nomenclature: paleontological *"Crocodylus"* was a form taxon including any crocodylian

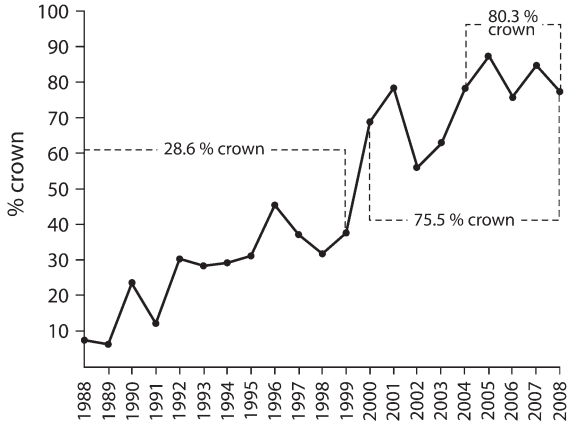


FIGURE 2. Percentage of papers in which the meaning of Crocodylia can be inferred that use a crown concept, 1988–2008.

not obviously belonging to some other genus, and few pre-Neogene fossils were thought to be within the crown genus (Brochu 2000).

This sort of confusion can have a profound impact on operations requiring knowledge of divergence timing. Olmo et al. (2002) reported anomalously low rates of chromosomal evolution in crocodylians but this was partly because the crocodylian calibration did not correspond to the crown group. Because the calibration was twice as old as the first appearance, rates were half as fast as they should have been.

The crocodylian circulatory system suggests derivation from an endothermic ancestor (Seymour et al. 2004). Summers (2005) suggested that some Jurassic "crocodilians" apparently shared similar semiaquatic ambush predator lifestyles with their modern relatives but were larger than their Triassic ancestors, possibly providing a reason for a decrease in metabolic rate—energetic costs for endotherms are greater at large body masses, especially if high levels of activity are not being maintained. Summers (2005; p. 834) then states that rates of mitochondrial evolution "from the Jurassic crocodilians" were high, suggesting a high ancestral metabolic rate. But the rates he indicates are for crown group crocodylians, not Jurassic crocodyliforms (Janke et al. 2005). Some estimates reported by Janke et al. (2005) did put the basal crocodylian divergence in the Late Jurassic, but more recent mitogenomic estimates are much closer to the fossil first appearance in the Late Cretaceous (Roos et al. 2007).

One could argue that such confusion can be avoided simply by paying attention to what an author means—in other words, by not taking taxonomy at face value. But this is true no matter what system is being used. The labels we place on species (fossil or living) change all the time whether we adopt the crown convention or not. The answer is to keep up with the literature and communicate with colleagues—something the crown convention facilitates.

### *Optimization, Prediction, and Bracketing*

We agree with Martin and Benton that crown clades may not hold any special biological importance. They might not be diagnosed by a particular feature or they might not delineate an increase in diversity. Their significance is operational—phylogeny estimates provide a clear framework for constraining predictions over the distribution of molecular, behavioral, or soft-part traits among extinct organisms, the vast majority of which cannot be directly observed in fossils (Bryant and Seymour 1990; Bryant and Russell 1992; Witmer 1995). Crown clades are not a special "class" of clade, they just happen to be bracketed by taxa that allow us to say more about their last common ancestor. Basal nodes of crown clades are the critical landmarks for these constraints, and the crown clade convention is an elegant tool for communicating them.

Martin and Benton object that characters present in all extant taxa of a crown clade, and therefore inferred to characterize their last common ancestor, likely did not arise in that ancestor. This is true (and no less problematic for the argument that commonly used names should be associated with nodes diagnosed by "significant" characters) but misses the point. Phylogenetic prediction is not intended to enumerate all taxa with a particular character state but to assess which attributes might pertain to members of a group with reasonable certainty.

Martin and Benton also object that we cannot always place an unambiguous least inclusive bound on a particular character at the root of a given crown clade. This, too, misses the point; we are qualitatively assessing predictions, not drawing fixed conclusions. The ability to clearly specify what we do not know is just as important (if not moreso) than our ability to specify what we do.

Their example of this "flaw" demonstrates our point and supports the value of the crown clade convention. Modern alligatorids (alligators and caimans) lack the salt-excreting glands found on the tongues of other living crocodylians (Taplin and Grigg 1989). Between nonpreservation in fossils and uncertainty over the relationships of gharials, we do not know whether the condition in Alligatoridae is a secondary loss or plesiomorphic absence. If a loss, we do not know where among stem alligatoroids (fossil nonalligatorids closer to Alligatoridae than to other extant crocodylian lineages) the glands were lost. We can assess neither the absence of salt glands in stem alligatoroids nor the ancestral condition for Crocodylia. But although we cannot characterize all members of one crown clade (Crocodylia) as having salt glands, we can certainly make this characterization for another (Crocodylidae) and characterize yet another (Alligatoridae) as lacking them. The crown convention lets us more precisely express not only what we can predict (presence in crocodylids, absence in alligatorids) but also what we cannot (presence or absence in basal).

Nonpreservable traits can obviously be predicted in fossils beyond phylogenetic relationships. Stable isotope geochemistry, for example, holds great promise in determining whether a fossil crocodyliform lived in fresh or salt water (Amiot et al. 2007; Wheatley and Koch 2008), which might indicate the capacity to tolerate excess environmental salt (such as lingual salt glands). Direct observation always gives greater confidence than inference. But phylogenetic bracketing, in the absence of actual preservation, provides a stronger prediction than we might make from modern analogy or raw speculation. Linking names to crown clades increases their utility for expressing the boundaries of our predictions.

## CONCLUSIONS

The crown definition of Crocodylia is the standard meaning both within and beyond the crocodyliform systematics community. It forms a robust framework around which new discoveries can be assessed and controversies can be expressed. It clarifies communication

not only of what we know but of what we do not. Martin and Benton invoke stability and tradition to uphold an alternative, but they have not demonstrated any instability with crown Crocodylia nor have they demonstrated the presence of a consistent "tradition" that gives us something tangible to stabilize. Indeed, they have not revealed any benefit to offset the risk of confusion by arbitrarily selecting one of several historical concepts and applying it in a phylogenetic framework in place of an explicit definition used widely across a broad spectrum of disciplines.

Arguments that unstable content and diagnosis are a fundamental problem with the crown convention (or with phylogenetic nomenclature in general) disregard the kind of stability phylogenetic nomenclature is trying to achieve. Of course, diagnoses, membership, and other properties will change under phylogenetic nomenclature. They will also change in the Linnaean system—this is a consequence of an imperfect understanding of the natural world. If names are defined with respect to phylogeny, we at least maintain some constancy of meaning even as our understanding of evolutionary history grows (de Queiroz and Gauthier 1990, 1992).

Any decision to name a clade is arbitrary. We can place whatever name we want at whatever node we want or we can name none of them. Selection of one "traditional" meaning out of many is no less arbitrary than the crown convention. Group names based on both relationship and similarity are reliant on subjective opinions of whether a fossil is similar enough to a living relative, or whether a particular character state is sufficiently important, to justify inclusion in a group. The "tradition" Martin and Benton wish to preserve is both arbitrary and subjective.

Ultimately, every taxonomic decision is a cost/benefit analysis. Every new name increases the volume of information we use. We gain by knowing more about the history of life but have to expend energy in both knowing and applying this information. Knowing more trumps working harder, so we accept the cost. In the case of the crown convention, we sacrifice vague traditional meanings and content, usually in the form of fossils historically classified within particular groups. But we gain universal meaning for clades that can be accessed by the full brunt of available data and discard worthless semantic discussions over trivia—which feature has enough significance to claim ownership of a name, whether it is significant enough to warrant elevation to a particular rank, and so on. Given a choice between tradition and precision, we choose precision—and based on the numbers of papers using different definitions of Crocodylia, the scientific community concurs.

We are left to ask why the particular content of Crocodylia preferred by Martin and Benton should be regarded as the traditional meaning at the expense of the many others that have been in use for more than 2 centuries. We also ask why clearly defined, precise, unambiguous, and consistent names and meanings that have become thoroughly entrenched in the literature over the past 20 years—names and meanings for which a clear and demonstrable consensus exists, such as Crocodyliformes and crown group Crocodylia, and names that bring benefits beyond their universality—should be abandoned, in spite of all we gain from their use, for the sake of a "tradition" with neither clarity nor universal meaning.

## Supplementary Material

Supplementary material can be found at: http://www.sysbio.oxfordjournals.org/.

## Funding

This work was supported financially by NSF DEB 0444133 to C.A.B. and L.D.D.

## Acknowledgements

We thank J. Sullivan for the opportunity to submit this manuscript. Many people helped locate references; we especially thank M. Spencer and E. Wilberg in this regard. J. Head, J. Anderson, Z. Gasparini, A. Turner, D. Faith, and members of the UI paleo group provided valuable advice on this manuscript. This work was supported logistically by Joe's Place I.C.

## References

Amiot R., Lécuyer C., Escarguel G., Billon-Bruyat J.-P., Buffetaut E., Langlois C., Martin S., Martineau F., Mazin J.-M. 2007. Oxygen isotope fractionation between crocodilian phosphate and water. Palaeogeogr. Palaeoclimatol. Palaeoecol. 243:412–420.

Anderson J.S. 2002. Use of well-known names in phylogenetic nomenclature: a reply to Laurin. Syst. Biol. 51:822–827.

Bateman R.M., DiMichele W.A. 2003. Genesis of phenotypic and genotypic diversity in land plants: the present as the key to the past. Syst. Biodivers. 1:13–28.

Benton M.J. 2000. Stems, nodes, crown-clades, and rank-free lists: is Linnaeus dead? Biol. Rev. 75:633–648.

Benton M.J. 2004. Vertebrate palaeontology. New York: Wiley-Blackwell.

Benton M.J., Clark J.M. 1988. Archosaur phylogeny and the relationships of the Crocodylia. In: Benton M.J., editor. The phylogeny and classification of the tetrapods. Oxford: Clarendon Press. p. 295–338.

Blob R.W. 2000. Interspecific scaling of the hindlimb skeleton in lizards, crocodilians, felids and canids: does limb bone shape correlate with limb posture? J. Zool. 250:507–531.

Brochu C.A. 2000. Phylogenetic relationships and divergence timing of *Crocodylus* based on morphology and the fossil record. Copeia. 2000:657–673.

Bryant H.N. 1996. Explicitness, stability, and universality in the phylogenetic definition and usage of taxon names: a case study of the phylogenetic taxonomy o the Carnivora (Mammalia). Syst. Biol. 45:174–189.

Bryant H.N., Russell A.P. 1992. The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. Philos. Trans. R. Soc. Lond., B. 337:405–418.

Bryant H.N., Seymour K.L. 1990. Observations and comments on the reliability of muscle reconstruction in fossil vertebrates. J. Morphol. 206:109–117.

Cantino P.D., de Queiroz K. 2007. PhyloCode: a phylogenetic code of biological nomenclature. Version 4. Available from: http://www.ohiou.edu/phylocode.

Carroll R.L. 1988. Vertebrate paleontology and evolution. New York: W. H. Freeman.

Charig A.J., Krebs B., Sues H.D., Westphal F. 1976. Handbuch der Paleoherpetologie. Vol. 13: Thecodontia. Portland, OR: Fischer-Verlag.
Claessens L.P.A.M. 2004. Archosaurian respiration and the pelvic girdle aspiration breathing of crocodyliforms. Proc. R. Soc. Lond., B. 271:1461–1465.
Colbert E.H. 1980. Evolution of the vertebrates 3rd ed. New York: Wiley-Interscience.
Cuvier G. 1824. Recherches Sur les Ossemens Fossiles, où l'On Rétablit les Caractères de Plusieurs Animaux Dont les Révolutions du Globe Ont Détruit les Espèces. In: Doufour et G., Editor. 2nd ed. Paris: D'Ocagne. p. 1–547.
de Queiroz K. 2007. Toward an integrated system of clade names. Syst. Biol. 56:956–974.
de Queiroz K., Gauthier J. 1990. Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. Syst. Zool. 39:307–322.
de Queiroz K., Gauthier J. 1992. Phylogenetic taxonomy. Ann. Rev. Ecol. Syst. 23:449–480.
Densmore L.D. 1983. Biochemical and immunological systematics of the order Crocodilia. In: Hecht M.K., Wallace B., Prance G. H., editors. Evolutionary biology. New York: Plenum Press. p. 397–465.
Dundee H.A. 1989. Higher category name usage for amphibians and reptiles. Syst. Zool. 38:389–406.
Gatesy J., Amato G., Norell M., DeSalle R., Hayashi C. 2003. Combined support for wholesale taxic atavism in gavialine crocodylians. Syst. Biol. 52:403–422.
Gauthier J., de Queiroz K. 2001. Feathered dinosaurs, flying dinosaurs, crown dinosaurs, and the name "Aves." In: Gauthier J., Gall L.F., editors. New perspectives on the origin and early evolution of birds. New Haven: Peabody Museum of Natural History. p. 7–41.
Harshman J., Huddleston C.J., Bollback J.P., Parsons T.J., Braun M.J. 2003. True and false gharials: a nuclear gene phylogeny of Crocodylia. Syst. Biol. 52:386–402.
Holliday C.M., Witmer L.M. 2007. Archosaur adductor chamber evolution: integration of musculoskeletal and topological criteria in jaw muscle homology. J. Morphol. 268:457–484.
Hutchinson J.R. 2001. The evolution of pelvic osteology and soft tissues on the line to extant birds (Neornithes). Zool. J. Linn. Soc. 131:123–168.
Janke A., Gullberg A., Hughes S., Aggarwal R.K., Arnason U. 2005. Mitogenomic analyses place the gharial *(Gavialis gangeticus)* on the crocodile tree and provide pre-K/T divergence times for most crocodilians. J. Mol. Evol. 61:620–626.
Joyce W.G., Parham J.F., Gauthier J.A. 2004. Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. J. Paleontol. 78: 989–1013.
Kuhn O. 1968. Die Vorzeitlichen Krokodile. Munich: Verlag Oeben.
Larsson H.C.E. 1998. A new method for comparing ontogenetic and phylogenetic data and its application to the evolution of the crocodilian palate. N. J. Geol. Palaeontol. Abh. 210:345–368.
Laurin M. 2002. Tetrapod phylogeny, amphibian origins, and the definition of the name Tetrapoda. Syst. Biol. 51:364–369.
Lee M.S.Y. 1996. Stability in meaning and content of taxon names: an evaluation of crown-clade definitions. Proc. R. Soc. Lond., B. 263:1103–1109.
Martin J.E., Benton M.J. 2008. Crown clades in vertebrate nomenclature: correcting the definition of Crocodylia. Syst. Biol. 57:173–181.
Mook C.C. 1934. The evolution and classification of the Crocodilia. J. Geol. 42:295–304.
Nopcsa F. 1923. Die Familien der Reptilien. Fortschr. Geol. Palaeontol. 2:1–210.
O'Connor P.M. 2006. Postcranial pneumaticity: an evaluation of soft-tissue influences on the postcranial skeleton and the reconstruction of pulmonary anatomy in archosaurs. J. Morphol. 267:1199–1226.
Olmo E. 2005. Rate of chromosome changes and speciation in reptiles. Genetica. 125:185–203.
Olmo E., Capriglione T., Odierna G. 2002. Different genomic evolutionary rates in the various reptile lineages. Gene. 295:317–321.
Osborn H.F. 1903a. On the primary division of the Reptilia into two sub-classes: Synapsida and Diapsida. Science. 17:275–276.
Osborn H.F. 1903b. The reptilian subclasses Diapsida and Synapsida and the early history of the Diaptosauria. Mem. Am. Mus. Nat. Hist. 1:449–507.
Owen R. 1842. Report on British fossil reptiles. Rep. Br. Assoc. Adv. Sci. 11:60–204.
Romer A.S. 1933. Vertebrate paleontology. 1st ed. Chicago, IL: University of Chicago Press.
Romer A.S. 1945. Vertebrate paleontology. 2nd ed. Chicago, IL: University of Chicago Press.
Romer A.S. 1956. Osteology of the reptiles. Chicago, IL: University of Chicago Press.
Romer A.S. 1966. Vertebrate paleontology. 3rd ed. Chicago, IL: University of Chicago Press.
Roos J., Aggarwal R.K., Janke A. 2007. Extended mitogenomic phylogenetic analyses yield new insight into crocodylian evolution and their survival of the Cretaceous-Tertiary boundary. Mol. Phylogenet. Evol. 45:663–673.
Rowe T. 1986. Definition and diagnosis in the phylogenetic system. Syst. Zool. 36:208–211.
Rowe T. 1988. Definition, diagnosis, and origin of Mammalia. J. Vertebr. Paleontol. 8:241–264.
Rowe T., Gauthier J. 1992. Ancestry, paleontology, and the definition of the name Mammalia. Syst. Biol. 41:372–378.
Sadleir R.W., Makovicky P.J. 2008. Cranial shape and correlated characters in crocodilian evolution. J. Evol. Biol. 21:1578–1596.
Sereno P.C. 2001. SuperCroc. Natl. Geogr. Mag. 200:84–89.
Sereno P.C. 2005. The logical basis of phylogenetic taxonomy. Syst. Biol. 54:595–619.
Sereno P.C., Larsson H.C.E., Sidor C.A., Gado B. 2001. The giant crocodyliform *Sarcosuchus* from the Cretaceous of Africa. Science. 294:1516–1519.
Seymour R.S., Bennett-Stamper C.L., Johnston S.D., Carrier D.R., Grigg G.C. 2004. Evidence for endothermic ancestors of crocodiles at the stem of archosaur evolution. Physiol. Biochem. Zool. 77:1051–1067.
Steel R. 1973. Handbuch der Paleoherpetologie. Vol. 16: Crocodylia. Portland, OR: Fischer-Verlag.
Summers A.P. 2005. Warm-hearted crocs. Nature. 434:833–834.
Taplin L.E., Grigg G.C. 1989. Historical zoogeography of the eusuchian crocodilians: a physiological perspective. Am. Zool. 29:885–901.
Tsuihiji T. 2007. Homologies of the Longissimus, Iliocostalis, and hypaxial muscles in the anterior presacral region of extant Diapsida. J. Morph. 268:986–1020.
Viola L.B., Almeida R.S., Ferreira R.C., Campaner M., Takata C.S.A., Rodrigues A.C., Paiva F., Camargo E.P., Teixeira M.M.G. 2009. Evolutionary history of trypanosomes from South American caiman *(Caiman yacare)* and African crocodiles inferred by phylogenetic analyses using SSU rDNA and gGAPDH genes. Parasitology. 136:55–65.
von Huene F. 1956. Paläontologie und Phylogenie der niederen Tetrapoden. Jena: Gustav Fischer.
Walker A.D. 1970. A revision of the Jurassic reptile Hallopus victor (Marsh), with remarks on the classification of crocodiles. Philos. Trans. R. Soc. Lond., B. 257:323–372.
Wheatley P.V., Koch P.L. 2008. Origin of salt-water tolerance in crocodylians. Geol. Soc. Am. Abstr. Prog. 40:392.
Williston S.W. 1925. The osteology of the reptiles. Cambridge, MA: Harvard University Press.
Witmer L.M. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In: Thomason J.J., editor. Functional morphology in vertebrate paleontology. New York: Cambridge University Press. p. 19–33.
Zittel K.A. 1890. Handbuch der Palaeontologie. Vol. 3. Vertebrata (Pisces, Amphibia, Reptilia, Aves). Munich: Oldenbourg.
Zug G.R., Vitt L.J., Caldwell J.P. 2001. Herpetology: an introductory biology of amphibians and reptiles. New York: Academic Press.

*Received 16 September 2008; reviews returned 18 February 2009; accepted 3 August 2009*
*Associate Editor: Dan Faith*