Confusing Dinosaurs With Mammals: Tetrapod Phylogenetics and Anatomical Terminology in the World of Homology

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ABSTRACT

At present, three different systems of anatomical nomenclature are available to researchers describing new tetrapod taxa: a nonstandardized traditional system erected in part by Sir Richard Owen and subsequently elaborated by Alfred Romer; a standardized system created for avians, the *Nomina Anatomica Avium* (*NAA*); and a standardized system for extant (crown-group) mammals, the *Nomina Anatomica Veterinaria* (*NAV*). Conserved homologous structures widely distributed within the Tetrapoda are often granted different names in each system. The recent shift toward a phylogenetic system based on homology requires a concomitant shift toward a single nomenclatural system also based on both evolutionary and functional morphological homology. Standardized terms employed in the *NAA* and *NAV* should be perpetuated as far as possible basally in their respective phylogenies. Thus, *NAA* terms apply to nonavian archosaurs (or even all diapsids) and *NAV* terms apply to noncrown-group mammals and more basal synapsids. Taxa equally distant from both avians and crown-group mammals may maintain the traditional nonstandardized terminology until a universal anatomical nomenclature for all tetrapods is constructed.   © 2004 Wiley-Liss, Inc.

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"To the intelligent reader of every class, who may be blessed with the healthy desire for the attainment of knowledge, let it then be said: Be not dismayed with the array of 'hard words' which seems to bar your path in its acquisition. Where such words are invented or adopted by the masters in science, be assured that your acquisition and retention of their meaning will be the safest 'first steps' in the science of your choice" (Owen, 1854: p. vii).

The need for standardized terminology in anatomical studies is manifest, as evidenced by the existence of the International Committee on Veterinary Gross Anatomical Nomenclature (ICVGAN) and the International Committee on Avian Anatomical Nomenclature (ICAAN) and their resultant publications, the *Nomina Anatomica Veterinaria* (*NAV*) and *Nomina Anatomica Avium* (*NAA*), respectively (Baumel et al., 1993; ICVGAN, 1994).

Standardized terminology exists to facilitate communication between anatomists. For specialized neontologists, in this case, mammalogists and ornithologists, the terminologies outlined in their respective volumes are simple and straightforward. Since neontologists rarely, if ever, delve into the fossil record of their respective taxonomic groups, no problems have arisen historically in the application of standardized terminologies to taxa with substantially different morphologies. Even paleomammalogists and paleornithologists, for the most part, have no problem with utilizing the same terms for fossil taxa, including those with plesiomorphic or specialized morphologies not represented in the extant record. Even here, however,

some situations have demonstrated the need for further standardization (Smith and Dodson, 2003). Among paleontologists working further from extant crown-group tetrapods, the issue is not nearly as clear.

Because the only existing standardized terminologies were largely developed by neontologists (i.e., anatomists focusing on extant organisms), one may presume that they were intended specifically to target crown-group mammals [crown-group Mammalia sensu Luo et al. (2002)] and birds [Neornithes sensu Hope (2002) = Aves sensu Gauthier (1986) and Clark et al. (2002)] rather than mammals and birds sensu lato (though earlier editions of the *NAV* did encompass birds). Thus, researchers describing taxa outside those crown-group clades (generally paleontologists working with fossils) have been left without a standardized anatomical nomenclature. To some extent, it is intuitively obvious that terminology can be extended down the phylogenetic tree. For example, *NAV* terminology has been successfully employed, with only minor modification, for multituberculates by Kielan-Jaworowska et al. (2000) and, to some extent, by Kielan-Jaworowska and Gambaryan (1994). Similarly, *NAA* terminology is adequate, again with only minor modification, when describing preneornithean birds (Chiappe et al., 1999).

Further basally in their respective phylogenies (in taxa with decreasing numbers of synapomorphies and with more generalized body plans), the application of standardized terminology becomes more problematic. When large morphological gaps punctuate the fossil record of an evolutionary lineage, dividing lines between when and when not to apply a standardized terminology parallel systematic divisions. For example, prior to the discovery of numerous near-avian theropods in the Early Cretaceous of China and elsewhere, the morphological gap between "typical" theropods and *Archaeopteryx* (to say nothing of more derived birds, such as *Ichthyornis*) was substantial enough that the line dividing birds from nonbirds was easy to identify. Thus, it was consequently equally simple to decide where and where not to apply *NAA* terminology. With the discovery of very bird-like, though phylogenetically nonavian, theropods (Burnham et al., 2000; Xu et al., 2000, 2001, 2003; Norell et al., 2002), the systematic line blurred, necessitating an arbitrary definition of bird (Chiappe and Witmer, 2002; Witmer, 2002). Again in parallel, it became difficult to decide where to begin and where to cease utilizing *NAA* nomenclature. Should *NAA* terminology apply to *Archaeopteryx* but not to *Sinornithosaurus* or *Bambiraptor*, even though the latter possess numerous avian anatomical features (Xu et al., 1999, 2001; Burnham et al., 2000; Xu and Wu, 2001; Burnham, 2004) that meet definitions established in the *NAA*? If it applies to *Sinornithosaurus* and *Bambiraptor*, why not the only slightly less bird-like *Deinonychus* (Ostrom, 1969,1976; Gishlick, 2001)? And if *Deinonychus*, why not all members of the Maniraptora, or all coelurosaurians, or theropods, or, indeed, all saurischians? The argument of where to draw the line can be perpetuated ad infinitum (and, some might perceive, ad nauseum). And what of other comparative taxa?

STATEMENT OF PROBLEM

The issue of applying terminology has two facets, consisting of directional and anatomical nomenclatures. Resolving directional terminology is relatively easy: both avian (Clark, 1993) and mammalian (ICVGAN, 1994)

workers, representing disparate endpoints of the tetrapod evolutionary continuum, have abandoned the terms "anterior" and "posterior" (except in highly localized areas, such as the eyes), terms that have their origins in human anatomy and do not easily translate into the typical postures of other tetrapods. Instead, they advocate using "cranial" and "caudal," respectively, with the caveats that "proximal" and "distal" are used within the limbs and the tail and that "rostral" replaces "cranial" within the head. This convention is ubiquitous in the literature on extant tetrapods and has been broadly, though not universally, adopted in paleontological circles.

In contrast, for many paleontologists, anatomical terminology is currently in the midst of a complicated predicament. Since the fossil record of vertebrates is largely restricted to skeletal material, the following discussions and examples focus on osteological features, but the principles apply to all soft-tissue structures as well.

An established lexicon of anatomical terms has long been in use for conserved structures (e.g., centrum, prezygapophysis, diapophysis, parapophysis, etc., some of which are listed as synonyms in the *NAA*). Much or all of this terminology appears to have been established, or at least detailed, by Owen (1854) for all vertebrates and elaborated on for sauropsids and basal synapsids in particular by Romer (1956). Subsequently, these terms found broad use in descriptions of a wide variety of taxa, both fossil and extant [except humans, which again had a previously established, largely medical, nomenclature (Gray, 1901), though this induces similar problems when considering nonhuman primate anatomy]. These terms formed the orthographic and educational foundation for subsequent vertebrate anatomy. Why the Owenian terms were ignored in constructing the *NAV* and *NAA* is not explored by the authors of either volume, but may have to do with the origins of both from within the long-standing body of human anatomical nomenclature that predates Owen. In other words, it was Owen who deviated from the established system rather than vice versa, though Owen, a staunch antievolutionist, could never have foreseen the adoption of homology-based phylogenetics and the need for a unified, homology-based system of anatomical nomenclature.

Two problems arose in light of this fact. First, a number of important papers published prior to Romer (1956) applied the names of mammalian structures to, for example, dinosaur specimens. For instance, Holland (1924) identified an alisphenoid in the skull of the sauropod *Diplodocus*. The alisphenoid is a therapsid autapomorphy, but the question is how to reidentify a homologous element, if it exists, in other vertebrates [in this instance, the element was identified as the prootic by Hay (1908), but Romer (1956) specified that the plesiomorphic laterosphenoid is the correct homologue of the alisphenoid]. This issue is exacerbated by the standard dominance of mammals in basic anatomical training.

Second, and of much greater importance here, standardized and nonstandardized systems of anatomical terminology differ, sometimes significantly, both within and between higher clades, even where elements are clearly homologous. For example, the primary paired articular processes on vertebrae are historically, in the Owenian system, called "prezygapophyses" and "postzygapophyses" in essentially all fossil amniotes, but are instead called "cranial zygapophyses" and "caudal zygapophyses" in

birds (Baumel and Witmer, 1993). While this appears merely semantic and unlikely to cause much confusion should a given author opt for *NAA* terminology, the issue is further muddled by the use of "cranial articular process" and "caudal articular process" for the same, clearly homologous structures in mammals (ICVGAN, 1994). With the increasing practice of comparative morphology not only among but between higher-level clades of animals (hypothetically, comparing features of nonavian archosaurs, birds, and mammals for functional implications), this would require the application of up to three different terminologies in a single paper to refer correctly to obviously homologous structures.

Furthermore, without a common lexicon, it becomes increasingly difficult to indicate or perceive evolutionary homologies between taxa. Would a reader of a paper on, for example, sauropod dinosaur cervical anatomy necessarily recognize the similarities to avian cervical anatomy if the terminologies used in both differed?

A single all-encompassing basic terminology based on homology is the logical complement to the paradigmatic shift to a homology-based system of phylogeny (de Quieroz and Gauthier, 1990,1992). Even outside of a phylogenetic framework, a common root lexicon would greatly facilitate communication between anatomists of all specialties (for example, specialists on modern avian, modern mammalian, and dinosaurian anatomy discussing comparative aspects of muscle reconstruction and function along the vertebral column or in limb design and function). However, such a singular nomenclature remains to be established for all tetrapods (if not all vertebrates), and the question of when to cease using one nomenclatural system and begin applying another remains unanswered.

Thus, we must return to the issue of when to apply specific terminologies in taxa far removed from the crown groups for which they were originally intended. Sauropod dinosaurs present an edifying example because despite their distance from crown-group birds on the archosaur tree, they possess numerous remarkably bird-like anatomical structures, particularly in their vertebrae. Because sauropods, like all members of the Dinosauria, are phylogenetically bracketed between extant archosaurs [Crocodylia and Aves Witmer, 1995)], it is more appropriate to apply to them anatomical terminology specific to archosaurs than that of any other group. However, between crocodylians and birds, the terminology only of the latter has been standardized (Baumel et al., 1993), although detailed anatomical descriptions of the former exist (Frey, 1988; Cong, 1998; Meers, 2003). Should an internationally recognized and standardized Nomina Anatomica Crocodylium ever be issued, the debate outlined below would become further complicated unless it utilized identical terminology as the *NAA* for homologous structures, as would be reasonably expected. Ultimately, it is disingenuous to support birds within the Dinosauria based on phylogeny (as determined by homologous synapomorphies), yet maintain separate bodies of anatomical terminology for clearly homologous structures.

SOLUTIONS AND DISCUSSION

There are three possible solutions to the dilemma of when to apply a given anatomical nomenclatural system. Solution A: Ignore the conventions constructed by the ICVGAN and ICAAN and protract the traditional Owenian reptilian nomenclature. Solution B: Cease using the traditional Owenian nomenclature and apply standardized terminology whenever possible. This has the drawback of requiring a large portion of the existing population of anatomists to relearn essentially new (although very logical and certainly not difficult) terms for a portion of their vocabulary while maintaining fluency in both systems in order to read both older and newer literature. It would also entail, on occasion, the creation of new terms to describe autapomorphic features not adequately covered in the *NAV* or *NAA*. Solution C: Maintain the current distinction between crown-group and noncrown-group taxa and attempt to define a specific point along the phylogeny at which one switches from one nomenclatural system to the other.

Solution A is preferentially utilized, almost certainly unconsciously, by most current workers. Its primary weakness is that it would maintain the current polytomy of lexicons in use across a broad swath of publications. Furthermore, to its fullest logical extent, it would require the application of traditional Owenian terms to crown-group mammals and birds and concomitant disregard of much of the *NAV* and *NAA*, even for those (crown-group) animals for which they were intended. Solution C, while certainly the easiest in application, is unfeasible in the long run because, as outlined above, the required point can never be solidly drawn, even arbitrarily: new discoveries of transitional taxa with features of both crown- and non-crown-group taxa will always fall under the aegises of both (in part, this is the same reason that the Linnean hierarchical ranks have largely been dropped from phylogenetic usage). It would be counterproductive, if not confusing, to have two names for identical structures, particularly when focusing attention on the structures in order to emphasize an evolutionary or functional connections. It would unnecessarily complicate comparisons of sister taxa that happen to fall on either side of the arbitrarily drawn boundary.

Although it seems the most difficult in execution, solution B is the most rational because it is the only one that avoids the logical inconsistency of adhering to a homology-based systematic methodology but abandoning homology simply for convenience (or tradition) in its other most important application. For the sauropod example, the terminology thus should follow that of birds whenever homology between elements, either evolutionary or functional or both, is certain (or at least probable based on physiographic similarity). When elements differ substantially from their avian counterparts, terminology should follow the most commonly used (largely Owenian) terms in previous literature. These terms may then be considered standardized by breadth of historical and current application until they are formally established in some set of broader guidelines.

I acknowledge that this is currently an unpopular practice and will likely meet significant resistance. Most paleontological workers are most comfortable with the traditional Owenian terminology as evidenced by its continued dominance in, or mixture with, standardized terminology in recent papers. Oddly, even in situations where the *NAA* should apply, such as descriptions of basal, and even some derived, fossil avians, this continues to be true (Sereno, 2000; Zhang et al., 2001; Chatterjee, 2002). In scope, however, the switch is no different than either the original change in the late 1800s–early 1900s from numerous regional anatomical nomenclatural systems to a single in-
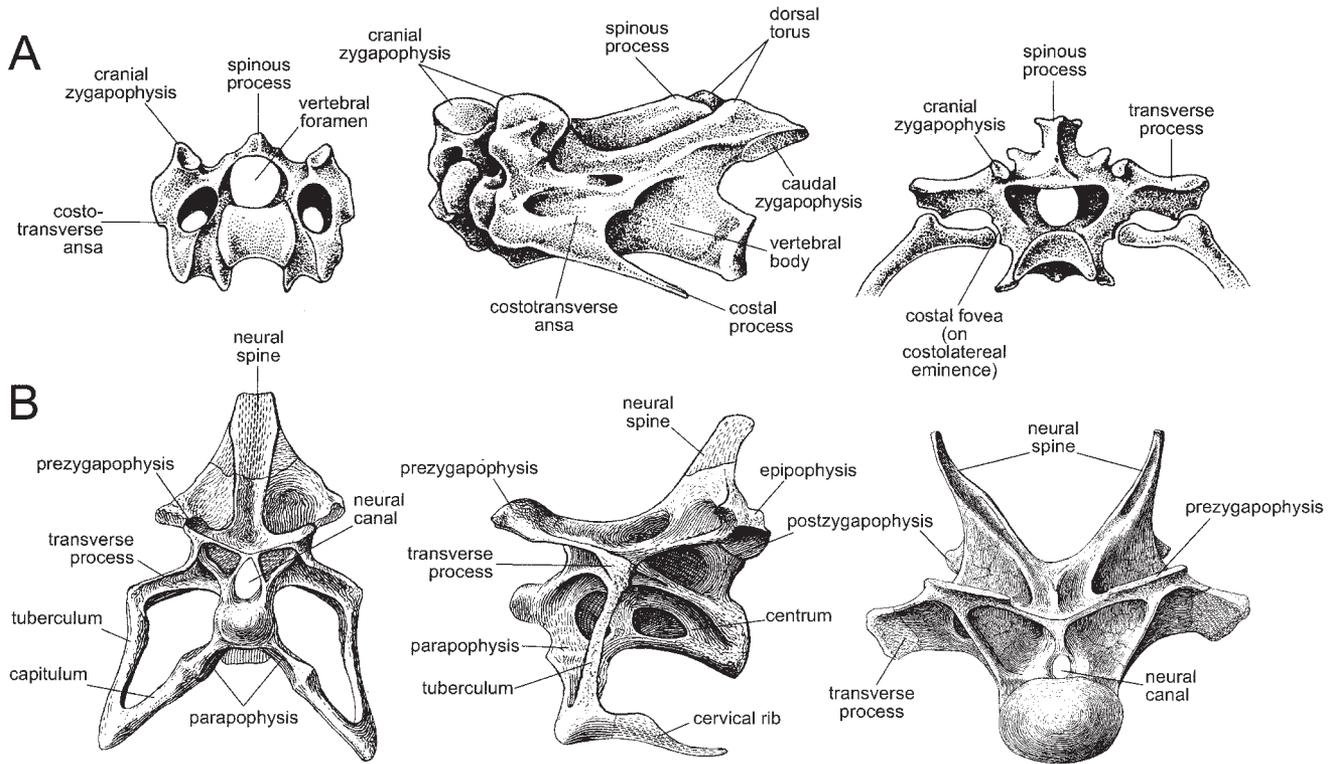
Fig. 1. Schematic comparing vertebral anatomy and terminology for identical structures in a bird (**A**) using *Nomina Anatomica Avium* terminology and the sauropod dinosaur *Apatosaurus* (**B**) using the traditional Owenian system. Cervical vertebrae in cranial (left column) and lateral (middle column) views; thoracic vertebrae (right column) in cranial view. Note that some homologous structures receive identical names (e.g., transverse process), some are only slightly different (e.g., spinous process vs. neural spine), and some are radically different (e.g., costolateral eminence vs. parapophysis). Reproduced with permission from (A) Baumel and Witmer (1993) and (B) Gilmore (1936).

ternational one (ICVGAN, 1994). More applicably, it is no different than that from the Linnean hierarchical to the modern homology-based phylogenetic system with its attendant emplacement of new and abandonment of old terminology. The broad-scale adoption of standardized terminology would require a similar grace period, but it is already underway. An example of the successful application of *NAA* terminology to a nonavian archosaur group (sauropods) appears in Wedel and Sanders (2002).

The broad-scale adoption of standardized terminology is not tacit support for a taxonomic perspective such as that of Ax (1989), in which "Mammalia" is synonymous with "Synapsida," thus making pelycosaurs mammals, and in which "Aves" is roughly synonymous with "Ornithosuchia" sensu Benton and Clark (1988) or "Archosauria" minus "Suchia" of Benton (1985), thus making sauropods (and even such radically different taxa as ankylosaurians) birds. On the contrary, it is intended only to maximize attention to homology vis-à-vis phylogenetic systematics and functional morphology while simultaneously supporting a more universal nomenclature.

What to do with structures (functional homologues) that are identical in position and function but that clearly arose separately? Continuing the sauropod example above, such a vertebral structure is the epiphysis (an Owenian term) of sauropods and the dorsal torus (an *NAA* term) of birds (Fig. 1). Both are protrusions of bone that project dorsally or caudodorsally from the caudal

(post)zygapophyseal facet (Fig. 1). In birds, these mark the insertion points for the mm. ascendens cervicalis and longus colli dorsalis; they almost certainly did the same for sauropod cervical muscles (Wedel and Sanders, 2002). Sauropod ancestors lack this structure, so its evolution is clearly convergent between the two groups. There is no way to discern if the muscles in sauropods inserting on the epipophyses were direct homologues (i.e., evolved from an identical muscle or muscle group in their most recent common ancestor) of the mm. ascendens cervicalis and longus colli dorsalis of birds. However, their identical positions in the cervical vertebrae of both taxa very strongly suggest homology of function. Even though evolutionary homology cannot be demonstrated, I suggest that their identical topographic positions in both taxa warrant the application of identical terminology, and that the term should be the standardized avian-cum-archosaurian "dorsal torus." This draws immediate attention to the organizational similarity between the two sets of organisms. Similarly, many sauropods exhibit fusion of the cervical rib to its articular surfaces on the corresponding vertebra, creating a single structure identical in position and very similar in structure to the avian ansa costotransversaria (Fig. 1). The cervical rib then becomes a costal process, also as in birds. This fusion is clearly convergent in sauropods and birds, but they involve homologous elements and likely arose as the result of a common set of developmental processes that create functionally identical struc-

tures [process homology per Hall (2003)]. They therefore warrant treatment as homologues, so the *NAA* terminology thus applies. Some of this may be alleviated by specification in future editions of the *NAA* and *NAV* of acceptable vernacular synonyms for various terms. For example, "rib" is a widely understood colloquialism, regardless of taxon, so future editions of the *Nomina* could specify that it is copacetic to refer informally to a cervical costal process as a "cervical rib."

I acknowledge that applying identical names to evolutionarily convergent but functionally and/or physiographically homologous structures does not adhere to the strictest definition and application of homology, in which only structures with a single shared evolutionary origin should bear a common name, just as evolutionary homology is the only criterion for inclusion of a taxon in a systematic clade. However, it is already common practice among vertebrates. Examples include the notarium in some birds, pterosaurs, and drepanosaurid archosaurs; hypopophyses (crista ventralis corporis) and hyposphene-hypantrum accessory vertebral articulations in several clades within the Archosauria, especially the Saurischia; the synsacrum, pygostyle, and patagia in birds and at least some pterosaurs; the rhamphotheca in numerous disparate tetrapods; and the patella of birds and mammals.

Some structures occupy a common physiographic position in the body but are not evolutionarily homologous and probably not functional homologues. The epipubis (not recognized in the *NAV*) of monotremes, marsupials, some amphibians, lizards, and turtles is an example. It appears to help support the pouch in marsupials, but nonmarsupials that have a similar structure lack pouches, so functional homology is not indicated. It is therefore an evolutionary and functional analogue but a physiographic homologue. In some taxa, a distinct term is used for a bone in this position. In pterosaurs, for example, the bone is usually termed the prepubis, though even here it has been called an epipubis by some workers (Rasskin-Gutman and Buscalioni, 2001). A case could be made for the sole use of strict evolutionary homology (regardless of functional or physiographic homology) for creating distinct terms for the structure in each taxon that possesses it, but this would create a cumbersome lexicon. Regardless, as above, this is clearly not the preferred anatomical practice. Some structures are understood as functional and/or physiographic homologues but evolutionary convergences yet retain identical names.

I emphasize that the number of changes required by a switch to a universal homology-based anatomical nomenclature is in actuality very small compared to the overall body of anatomical terminology. By far, the majority of terms already in use in papers concerning tetrapod anatomy that do not deal directly with either birds or mammals would not require any change. Features unique to noncrown-group tetrapod taxa would maintain their current names. Many other terms (e.g., transverse process) are already identical between systems (Fig. 1). A few others would require only slight modification (e.g., changing prefixes such as "centro-," "prezygo-," and "postzygo-" to "corporo-," "cranial zygo-," and "caudal zygo-," respectively). The most drastic changes only occur where the terminologies are vastly different (e.g., parapophysis vs. costolateral eminence, epipophysis vs. dorsal torus, pleurocoel vs. lateral pneumatic fossa), and this is by far the minority of cases. The proposed change to homology-based

standardized terminology is certainly neither insurmountable nor difficult but offers great rewards by facilitating communication between specialists in one or another taxon and by highlighting evolutionarily and functionally homologous structures that in turn aid in comparison, reconstruction, and evolutionary and ecological interpretation.

Homology-based phylogenetics demands a complementary standardized homology-based system of anatomical nomenclature. Such systems currently exist only for restricted groups of animals (crown-group mammals and birds), leaving workers on taxa outside those restrictions without a standardized terminology. In a broad sense, however, the standardized terminologies (*Nomina Anatomica Veterinaria* and *Nomina Anatomica Avium*) can, and should, be applied to conserved homologous structures for broader groups of synapsids and archosaurs (possibly even all diapsids), respectively, until such time as an all-encompassing Nomina Anatomica Tetrapodum is emplaced. Should such a document ever be realized, some procedure for synonymization would have to be employed to decide which terms from the Owenian system, *NAA*, or *NAV* should be made universal. In this instance, it would probably be most useful to select terms that are more easily recognized as names rather than descriptors. For example, the *NAA* "cranial-" and "caudal zygapophysis" should be preferred to the *NAV* "cranial-" and "caudal articular process" because several tetrapods, including squamates, xenarthrans, and nonavian archosaurs, possess accessory articular structures, such as zygosphene-zygantrum complexes, hyposphene-hypantrum complexes, or xenarthrous articulations, that are located at the cranial and/or caudal ends of a vertebra and thus could be described, in an adjectival sense, as "cranial-" or "caudal articular processes," thus fostering confusion with the actual, specified structures with those names.

Traditional Owenian terminology may be retained (with attendant prefixal, suffixal, or other modification as above) for structures with no homologies or whose homologies are uncertain in the crown-group taxa specifically targeted by the *NAV* and *NAA*. The creation of an all-encompassing system (a Nomina Anatomica Tetrapodum or similar regulatory entity) is vital because it would eliminate the need to expand the *NAA* and *NAV* or selectively apply Owenian terms (essentially, work downward from the top of the tetrapod phylogenetic tree) because it would establish a unified system that parallels tetrapod evolution (working from the bottom of the tree upward). Adopting standardized terminology for homologous structures is the only ingenuous practice for workers applying principles of homology to phylogeny.

I acknowledge that this solution is not comprehensive. It does not address how to treat taxa equally distant from both groups of amniotes covered by the *NAV* and *NAA* (e.g., anapsids, stem amniotes, amphibians, basal tetrapods). Here, selecting a standardized terminology to apply becomes equivocal, even though some structures are still clearly homologous (e.g., the vertebral body [centrum], the spinous process [neural spine]) and for these terms, one or another standardized system should be used. Otherwise, pending a widespread consensus on a basic nomenclature for persistent homologous structures, a worker may best be served by adhering to the traditional Owenian system. This issue

clearly highlights the need for a single unified terminology based on homology for all vertebrates.

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LITERATURE CITED

Ax P. 1989. The integration of fossils in the phylogenetic system of organisms. In: Schmidt-Kittler N, Willmann R, editors. Phylogeny and the classification of fossil and recent organisms. Hamburg: P. Parey. p 27–43.

Baumel JJ, Witmer LM. 1993. Osteologia. In: Baumel JJ, King AS, Breazile JE, Evans HE, Vanden Berge JC, editors. Handbook of avian anatomy: Nomina Anatomica Avium, 2nd ed. Cambridge: Nuttall Ornithological Club. p 45–132.

Baumel JJ, King AS, Breazile JE, Evans HE, Vanden Berge JC, editors. 1993. Handbook of avian anatomy: Nomina Anatomica Avium, 2nd ed. Cambridge: Nuttall Ornithological Club.

Benton MJ. 1985. Classification and phylogeny of the diapsid reptiles. Zool J Linn Soc 84:97–164.

Benton MJ, Clark JM. 1988. Archosaur phylogeny and the relationships of the Crocodylia. In: Benton MJ, editor. The phylogeny and classification of tetrapods, vol. 1, amphibians, reptiles, birds. Oxford: Clarendon Press. p 295–338.

Burnham DA, Derstler KL, Currie PJ, Bakker RT, Zhou Z, Ostrom JH. 2000. Remarkable new birdlike dinosaur (Theropoda: Maniraptora) from the Upper Cretaceous of Montana. Univ Kansas Paleontol Contrib 13:1–12.

Burnham DA. 2004. New information on *Bambiraptor feinbergi* (Theropoda: Dromaeosauridae) from the Late Cretaceous of Montana. In: Currie PJ, Koppelhus EB, Shugar MA, Wright JL, editors. Feathered dragons: studies on the transition from dinosaurs to birds. Bloomington: Indiana University Press. p 67–111.

Chatterjee S. 2002. The morphology and systematics of *Polarornis*, a Cretaceous loon (Aves: Gaviidae) from Antarctica. In: Zhou Z, Zhang F, editors. Proceedings of the 5th Symposium of the Society of Avian Paleontology and Evolution. Beijing: Science Press. p 125–155.

Chiappe LM, Ji S, Ji Q, Norell MA. 1999. Anatomy and systematics of the Confuciusornithidae (Theropoda: Aves) from the Late Mesozoic of northeastern China. Bull Amer Mus Nat Hist 242:1–89.

Chiappe LM, Witmer LM. 2002. Preface. In: Chiappe LM, Witmer LM, editors. Mesozoic birds: above the heads of dinosaurs. Berkeley, CA: University of California Press. p ix–xii.

Clark GA Jr. 1993. Anatomia topographica externa. In: Baumel JJ, King AS, Breazile JE, Evans HE, Vanden Berge JC, editors. Handbook of avian anatomy: Nomina Anatomica Avium, 2nd ed. Cambridge: Nuttall Ornithological Club. p 7–16.

Clark JM, Norell MA, Makovicky PJ. 2002. Cladistic approaches to the relationships of birds to other theropod dinosaurs. In: Chiappe LM, Witmer LM, editors. Mesozoic birds: above the heads of dinosaurs. Berkeley, CA: University of California Press. p 31–61.

Cong L. 1998. The gross anatomy of *Alligator sinensis* Fauvel. Beijing: China Forestry Publishing House.

de Quieroz K, Gauthier J. 1990. Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. Syst Zool 39: 307–322.

de Quieroz K, Gauthier J. 1992. Phylogenetic taxonomy. Annu Rev Ecol Syst 23:449–480.

Frey E. 1988. Anatomie des Körperstammes von *Alligator mississippiensis* Daudin. Stuttg Beitr Naturkd Ser A (Biol) 424:1–106.

Gauthier J. 1986. Saurischian monophyly and the origin of birds. In: Padian K, editor. The origin of birds and the evolution of flight. San Francisco: California Academy of Sciences. p 1–55.

Gilmore CW. 1936. Osteology of *Apatosaurus*, with special reference to specimens in the Carnegie Museum. Mem Carnegie Mus 11:175–271.

Gishlick AD. 2001. The function of the manus and forelimb of *Deinonychus antirrhopus* and its importance for the origin of avian flight. In: Gauthier J, Gall LF, editors. New perspectives on the origin and early evolution of birds. New Haven, CT: Peabody Museum of Natural History. p 301–318.

Gray H, editor. 1901. Anatomy: descriptive and surgical (Gray's anatomy), 15th ed. London: Spottiswoode.

Hall BK. 2003. Descent with modification: the unity underlying homology and homoplasy as seen through an analysis of development and evolution. Biol Rev 79:409–433.

Hay OP. 1908. Dr. W.J. Holland on the skull of *Diplodocus*. Science 28:517–519.

Holland WJ. 1924. The skull of *Diplodocus*. Mem Carnegie Mus 9:379–403.

Hope S. 2002. The Mesozoic radiation of Neornithes. In: Chiappe LM, Witmer LM, editors. Mesozoic birds: above the heads of dinosaurs. Berkeley, CA: University of California Press. p 339–388.

International Committee on Veterinary Anatomical Nomenclature. 1994. Nomina Anatomica Veterinaria, 4th ed, Nomina Histologica, rev. 2nd ed, Nomina Embryologica Veterinaria. Zürich: International Committees on Veterinary Gross Anatomical Nomenclature, Veterinary Histological Nomenclature, and Veterinary Embryological Nomenclature.

Kielan-Jaworowska Z, Gambaryan PP. 1994. Postcranial anatomy and habits of Asian multituberculate mammals. Fossils Strata 36: 1–92.

Kielan-Jaworowska Z, Novacek MJ, Trofimov BA, Dashzeveg D. 2000. Mammals from the Mesozoic of Mongolia. In: Benton MJ, Shishkin MA, Unwin DM, Kurochkin EN, editors. The age of dinosaurs in Russia and Mongolia. Cambridge: Cambridge University Press. p 573–626.

Luo Z-X, Kielan-Jaworowska Z, Cifelli RL. 2002. In quest for a phylogeny of Mesozoic mammals. Acta Palaeont Pol 47:1–78.

Meers MB. 2003. Crocodylian forelimb musculature and its relevance to Archosauria. Anat Rec 274A:891–916.

Norell M, Ji Q, Gao K, Yuan C, Zhao Y, Wang L. 2002. "Modern" feathers on a non-avian dinosaur. Nature 416:36–37.

Ostrom JH. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. Peabody Mus Nat Hist Bull 30:1–165.

Ostrom JH. 1976. On a new specimen of the Lower Cretaceous theropod dinosaur *Deinonychus antirrhopus*. Breviora 439:1–21

Owen R. 1854. The principal forms of the skeleton and of the teeth. Philadelphia: Blanchard and Lea.

Rasskin-Gutman D, Buscalioni AD. 2001. Theoretical morphology of the archosaur (Reptilia: Diapsida) pelvic girdle. Paleobiology 27: 59–78.

Romer AS. 1956. The osteology of reptiles. Chicago: University of Chicago Press.

Sereno PC. 2000. *Iberomesornis romerali* (Aves, Ornithothoraces) re-evaluated as an Early Cretaceous enantiornithine. Neues Jahrb Geol Paläont Abh 215:365–395.

Smith JB, Dodson P. 2003. A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. J Vertebr Paleontol 23:1–12.

Wedel MJ, Sanders RK. 2002. Osteological correlates of cervical musculature in Aves and Sauropoda (Dinosauria: Saurischia), with comments on the cervical ribs of *Apatosaurus*. PaleoBios 22:1–6.

Witmer LM. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In: Thomason JJ, editor. Functional morphology in vertebrate paleontology. Cambridge: Cambridge University Press. p 19–33.

Witmer LM. 2002. The debate on avian ancestry: phylogeny, function, and fossils. In: Chiappe LM, Witmer LM, editors. Mesozoic birds: above the heads of dinosaurs. Berkeley, CA: University of California Press. p 3–30.

Xu X, Wang XL, Wu XC. 1999. A dromaeosaurid dinosaur with a filamentous integument from the Yixian formation of China. Nature 401:262–266.

Xu X, Zhou Z, Wang X. 2000. The smallest known non-avian theropod dinosaur. Nature 408:705–708.

Xu X, Wu XC. 2001. Cranial morphology of *Sinornithosaurus millenii* Xu et al. 1999 (Dinosauria: Theropoda: Dromaeosauridae) from the Yixian formation of Liaoning, China. Can J Earth Sci 38:1739–1752.

Xu X, Zhou Z, Prum RO. 2001. Branched integumental structures in *Sinornithosaurus* and the origin of feathers. Nature 410:200–204.

Xu X, Zhou Z, Wang X, Kuang X, Du X. 2003. Four-winged dinosaurs from China. Nature 421:335–340.

Zhang F, Zhou Z, Hou L, Gu G. 2001. Early diversification of birds: evidence from a new opposite bird. Chin Sci Bull 46:945–949.