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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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 pre-neornithean 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, diaphysis, 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 zygaphyses” and “caudal zygaphyses” 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 Queiroz 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 crowngroup 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 aegis 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 connection. 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 physiological 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-
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 at-
tendant 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 applica-
tion 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 support-
ing 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 epipophysis (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 cervicisalis
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 po-
sitions 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 “dor-
sal torus.” This draws immediate attention to the organi-
zational 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 sau-
ropods and birds, but they involve homologous elements
and likely arose as the result of a common set of develop-
mental processes that create functionally identical struc-

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 pro-
cess 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).
atures [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; hypophyses (crista ventralis corporis) and hypophyse-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.

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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 Avium and Nomina Anatomica Veterinaria) 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, hypophyse-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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