

## ANATOMICAL NOMENCLATURE OF FOSSIL VERTEBRATES: STANDARDIZED TERMS OR ‘LINGUA FRANCA’?

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**ABSTRACT**—Whereas the anatomy of birds, domesticated mammals, and humans is described by standardized terminology, the anatomy of most fossil vertebrates is described by nonstandardized terminology. New fossil discoveries increasingly resolve the transitions between these living groups and their fossil outgroups, diminishing morphological differences between them, and vertebrate paleontologists can easily apply more than one system of anatomical terms to such groups. This plurality of systems has led to recent proposals to standardize anatomical terminology for tetrapods, either by applying avian and mammalian anatomical terminology to their respective stem groups (Sauropsida and Synapsida) or by creating an all-encompassing terminology for Tetrapoda from a combination of existing terminologies. The main rationale for implementing standardized anatomical terminology, which requires abandoning competing terminologies, is that it reflects homology and evolutionary descent, eliminates ambiguity, and enhances interdisciplinary communication. The proposed standardized anatomical terminology, however, entails many negative consequences, including reversing character trajectories, misrepresenting complex anatomical transformations and uncertain homologies, and requiring far-reaching terminological conversions. These negative consequences result from increasing the taxonomic scope of standardized anatomical terms that were developed for a specific group, but now: (1) apply to a broader hierarchy of character states; (2) involve additional phylogenetic interpretations or assumptions; and (3) are used for basal, often more generalized conditions. In contrast, traditional non-standardized anatomical terminology, although not strictly phylogenetic, is anatomical ‘lingua franca’ that has been in usage for nearly two centuries and is consistent, ubiquitous, and descriptive.

### STANDARDIZED ANATOMICAL TERMINOLOGY

Standardized anatomical terminologies codify use of anatomical terms and orientational descriptors for specific vertebrate groups. Humans, domesticated mammals, and birds have standardized terminologies that were codified and modified by independent organizational bodies whose shared intellectual history extends back to the late 19th Century. Despite their historical connections, these three terminologies are tailored to focal taxa and need not, and often do not, agree with one another. In contrast, the extant and extinct vertebrates that share more distant evolutionary relationships with living birds, mammals, and humans have nonstandardized anatomical terminologies that are not governed by regulatory bodies. An important issue currently confronting anatomists is how we reconcile these three standardized terminologies with one another and with nonstandardized terminologies.

### Historical Overview

Perhaps not surprisingly, anatomical terminology was first standardized for humans. The Basle Nomina Anatomica (BNA) of 1895 narrowed tens of thousands of terms to a core of approximately 4,500 (Donáth, 1969). BNA terms require the orthograde (upright) positional axis for human anatomy, which was adopted as the context for dissection and illustration by Vesalius and others in the 14th Century (Singer, 1925; Fig. 1). Committees of both British and German anatomists revised BNA terms in the 1930s, resulting in the Birmingham Revision (BR) and the Jena Nomina Anatomica (JNA), respectively (Greulich et al., 1945). Importantly, the JNA revision abandoned the orthograde positional axis and adopted the pronograde (horizontal) axis, rendering its terms applicable to all vertebrates. Little progress on resolving differences between the BR and JNA occurred during the war years, but the 4th International Congress of Anatomy met in Oxford in 1950 and ap-

pointed the International Anatomical Nomenclature Committee (IANC). The IANC recommended the BNA, rather than the JNA, as the principal source from which to derive a new anatomical nomenclature for humans and, in doing so, established orthograde as the standard positional axis for human anatomy. The 5th International Congress met in Paris in 1955 and adopted the IANC-recommended list of terms, which was published in 1956 as the Paris Nomina Anatomica—later known as the Nomina Anatomica (NA). Of the approximately 5,640 NA terms, 76% were retained from the BNA, 15.6% were modified from the BNA, 4.9% were adopted from JNA, and 3.5% were new (Donáth, 1969). The NA went through five editions that were approved by the International Congress of Anatomy and the International Federation of Associations of Anatomists, but a controversial sixth edition that was published without approval of either organization led to formation of the Federative Committee on Anatomical Terminology and publication of the Terminologia Anatomica (TA) in 1998 (Whitmore, 1999).

Veterinary anatomists at the 1955 Paris congress opposed the NA because its terms were predicated on orthograde anatomical position. Following this congress, mammalian and avian veterinary anatomists split from human anatomists to form the International Association of Veterinary Anatomists, later renamed the World Association of Veterinary Anatomists (WAVA). The group met in 1957 to form the International Committee on Veterinary Anatomical Nomenclature (ICVAN) and published the first edition of the Nomina Anatomica Veterinaria (NAV) in 1968. Early ICVANs included a “subcommittee on Anatomia Avium,” but avian anatomical terms were not included in the NAV (Baumel et al., 1979:viii). This and subsequent editions of the NAV focused only on the domesticated mammals *Felis*, *Canis*, *Sus*, *Bos*, *Ovis*, *Capra*, *Oryctolagus*, and *Equus* (ICVGAN, 2005).

In 1971 WAVA set up the International Committee on Avian Anatomical Nomenclature (ICAAN), which published the

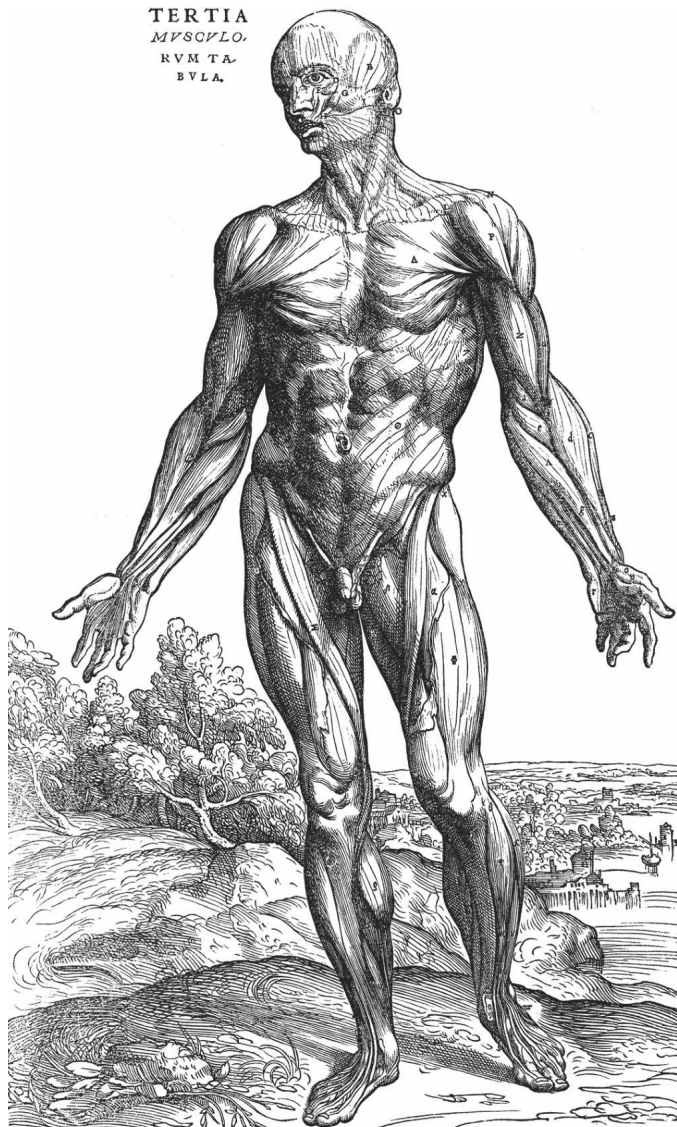


FIGURE 1. Flayed *Homo sapiens* in orthograde anatomical position, from Vesalius (1543) “Tertia Musculorum Tabula.”

Nomina Anatomica Avium (NAA) in 1979 and a second edition in 1993. In contrast to the NAV, which focuses on domesticated species, the NAA lists anatomical features common to most birds and morphological variations in particular species or higher-level groups where these can be documented (King, 1993).

The current standardized anatomical terminologies for humans, domesticated mammals, and birds descended from a single terminology that was first codified in 1895. The decision to contextualize anatomy with the orthograde positional axis resulted in a split between human (IANC) and veterinary (WAVA) anatomists half a century later. Since then, NA terms have experienced six modifications (the last in 1998). Approximately 20 years after the split between human and veterinary anatomists, the latter split into mammalian (ICVAN) and avian (ICVAN) veterinary anatomists. There have been five editions of the NAV (the last in 2005) and two editions of the NAA (the last in 1993). The IANC, ICVAN, and ICAAN maintain their intellectual independence but strive to adopt common terminological changes where possible (Schaller et al., 1973; King, 1993; ICVGN, 2005).

## The Problem

The NA, NAV, and NAA are ‘taxon-based’ anatomical terminologies that were created specifically for *Homo*, certain domesticated mammal species (see previous), and birds, respectively. Nonetheless, these standardized terminologies have been applied to species outside their taxonomic jurisdictions. For example, the NA has been applied to other hominoids (e.g., Gibbs et al., 2002)—although there has been some reluctance to apply its terms to fossil *Homo* and related taxa (Tuttle, 1988)—and the NAA has been applied to fossil members of crown-group Aves (e.g., Clarke et al., 2003; Mayr and Manegold, 2004) as well as its Mesozoic outgroups (e.g., Christiansen and Bonde, 2000; Chiappe and Witmer, 2002). The NAV was not written with crown-group mammals in mind, but it has been applied to other carnivorans, ruminants, and lagomorphs (e.g., Witmer et al., 1999; Clifford and Witmer, 2004a, b), whales (Zhu et al., 2000), primates (Smith et al., 2004), proboscideans (Weissengruber and Forstenpointner, 2004), chiropterans (Lancaster et al., 1995), and xenarthrans (Amorim et al., 2004), as well as to their fossil eutherian outgroups (e.g., Hurum, 1998; Wible et al., 2004). Despite the ease of extending coverage of taxon-based anatomical terminology to closely related species, the pitfalls of extending it to more distantly related species remain relatively unexplored.

The NAA and NAV govern anatomical nomenclature for mammals and birds, which together form the taxonomic boundaries of crown-group Amniota (e.g., Gauthier et al., 1988). Although diverse and morphologically distinct, these clades constitute less than 30% of the 50,000+ extant vertebrate species (e.g., Pough et al., 1999) and an even smaller proportion of fossil plus extant vertebrate species. Historically, inadequate sampling of the fossil record and uncertainty regarding immediate ancestry resulted in morphological gaps that isolated crown-group birds and mammals from their fossil and extant amniote relatives (Fig. 2A). Collectively referred to as “reptiles”, this paraphyletic array received its own non-standardized anatomical nomenclature popularized by Owen (1854), Williston (1925), and, most influentially, by Romer (1956). This eclectic terminology, which was shaped by tradition, common sense, and a bit of idiosyncrasy, will be referred to here as “Romerian”—although I do not suggest that it originated with or was codified by Romer. Thus, there are four anatomical nomenclatures that may apply to extant and fossil vertebrates, three standardized systems (NAA, NAV, NA) and one non-standardized system (Romerian terms), whose jurisdictions have been demarcated historically by morphological gaps (Fig. 2A). More recent fossil discoveries articulate transitions to Aves and Mammalia and raise the question of what anatomical terminology is to be used in the phylogenetically gray areas between birds, mammals, and their “reptilian” outgroups (Fig. 2B).

## A Proposed Solution

Harris (2004:1242, 1244) was the first to identify and confront this issue comprehensively, by listing four options for standardizing tetrapod anatomical nomenclature: (1) apply Romerian terms toward the tips of the tree; (2) maintain three non-overlapping systems with arbitrarily drawn boundaries; (3) apply NAA and NAV terms toward the base of the tree; or (4) develop and use a new, overarching system for all tetrapods (Fig. 3). Harris (2004) recommended implementing solutions 3 and 4 in succession.

I subsequently discuss the rationale offered for standardizing anatomical terminology, describe its negative consequences, and make the case for a fifth option—not to standardize. I recommend allowing the NAV, NAA, NA, and traditional Romerian terms to coexist as overlapping, multifaceted systems available to all vertebrate anatomists.

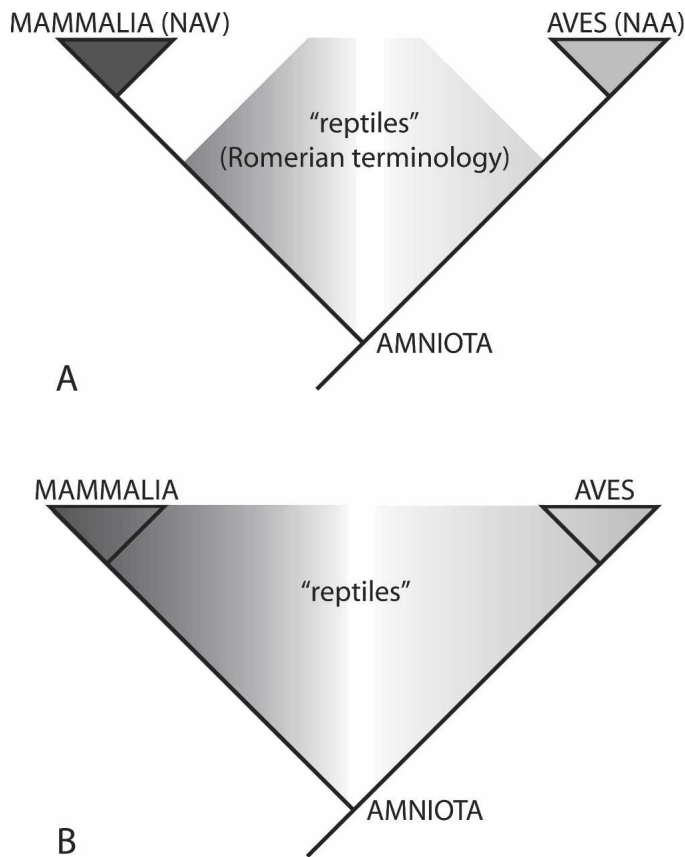


FIGURE 2. The effects of improved sampling of the fossil record on anatomical terminology. In **A**, morphological gaps delimit non-mammalian and non-avian amniotes (i.e., “reptiles”) from Mammalia and Aves, conveniently allowing use of anatomical terminologies whose jurisdictions do not overlap (Romerian terms, NAV, and NAA, respectively). This situation can be contrasted with **B**, in which discoveries of transitional fossils or resolution of phylogenetic relationships have reduced or eliminated morphological gaps that formerly separated Mammalia and Aves from “reptiles.” In the latter situation, more than one system of anatomical terminology can be applied to each taxonomic group.

### RATIONALE

Harris (2004) justified his proposed standardized anatomical terminology for fossil tetrapods as a universal system that better communicates homology, uses unambiguous anatomical language, and enhances interdisciplinary communication. Below, I examine each of these justifications with particular attention to the desirability of the qualities themselves and the ability of standardized terminology to provide them.

#### Homology-Based Anatomy

Harris (2004:1240) linked his proposed standardized anatomical terminology with the revolution in phylogenetic systematics:

“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 by the *NAA* and *NAV* should be perpetuated as far as possible basally in their respective phylogenies.”

It is true that modern phylogenetic systematics is based on homology, insofar as proximity of ancestry is established by sy-

napomorphy, which Patterson (1982) equated with homology. Within the phylogenetic paradigm, a homology (synapomorphy) refers to an anatomical structure and to the clade it diagnoses. There are two fundamental distinctions between standardized anatomical terminology and phylogenetic systematics that are relevant to this discussion.

First, taxon-based anatomical terminology focuses on the total character set of a particular species or group of species without distinguishing between structures that are autapomorphies for more exclusive clades within the focal taxon, synapomorphies for the focal taxon, and symplesiomorphies for clades more inclusive than the focal taxon (Fig. 4). Aspects of the avian syrinx and plumage, mammalian dentition, and human bipedalism are examples of features that are synapomorphic for the focal taxa of the NAA, NAV, and NA, respectively. In addition, Aves, Mammalia, and *Homo* bear many symplesiomorphies that evolved in their sauropsid ancestors (e.g., feathers, furcula) or synapsid ancestors (e.g., single temporal fenestra, squamosal–dentary joint). Still more ancient symplesiomorphies evolved in non-amniote outgroups to both Aves and Mammalia (e.g., vertebrae) and are retained in descendant taxa. Standardized anatomical nomenclature is necessarily exclusive where it refers to such plesiomorphic structures, because outgroups that possess the features are not covered by the terminology. In a truly homology-based system of anatomical nomenclature, anatomical terms describing vertebrae would be applied to all taxa descended from the common ancestor that possessed vertebrae; anatomical terms referring to specific vertebral structures not present in all vertebrates (e.g., hyposphene-hypantrum) would be applied to those taxa descendant from the common ancestor that possessed the structure. Increasing the scope of taxon-based standardized terminology to Tetrapoda, Vertebrata, or Chordata does not eliminate this fundamental distinction, because each of these groups has outgroups with which they share unique anatomical features that should be given the same anatomical name.

A second fundamental distinction between anatomical terminology and homology concerns the role of each in elucidating phylogenetic relationships. Anatomical structures are direct evidence of recent common ancestry (i.e., synapomorphies) if they pass three tests: similarity; conjunction; and congruence with other character distributions (Patterson, 1982). Comparative anatomy participates in this process by establishing topological relationships and structural similarity to satisfy the first test. However, many structures that pass the similarity test of homology fail the conjunction and/or convergence tests and, thus, are non-homologous. There is a clear distinction between similar anatomical structures (a priori conjectures of homology) and synapomorphies (a posteriori statements of homology that serve as evidence of relationship). Homology in the phylogenetic sense refers to the latter and not the former. It follows that homology-based anatomy should refer to topologically similar but incongruent structures by distinct names to reflect their hypothesized independent evolutionary origin. In other words, synapomorphies should receive the same anatomical name, but homoplasies should not. Curiously, Harris (2004:1244) did not recommend formalizing this basic distinction, but instead relied on “functional homologues” (i.e., analogues) to justify giving the same name to independently derived structures (e.g., the notarium in birds and pterosaurs). This concession reflects the fact that anatomists use anatomical terms as descriptive vocabulary rooted in topology and similarity, rather than as statements of homology that evidence relationship. Although superficially appealing, a comparison with phylogenetic systematics does not justify standardizing anatomical terms.

#### Universal System

Although he suggested broadening the scope of NAA and NAV terms to all sauropsids and synapsids as a temporary so-

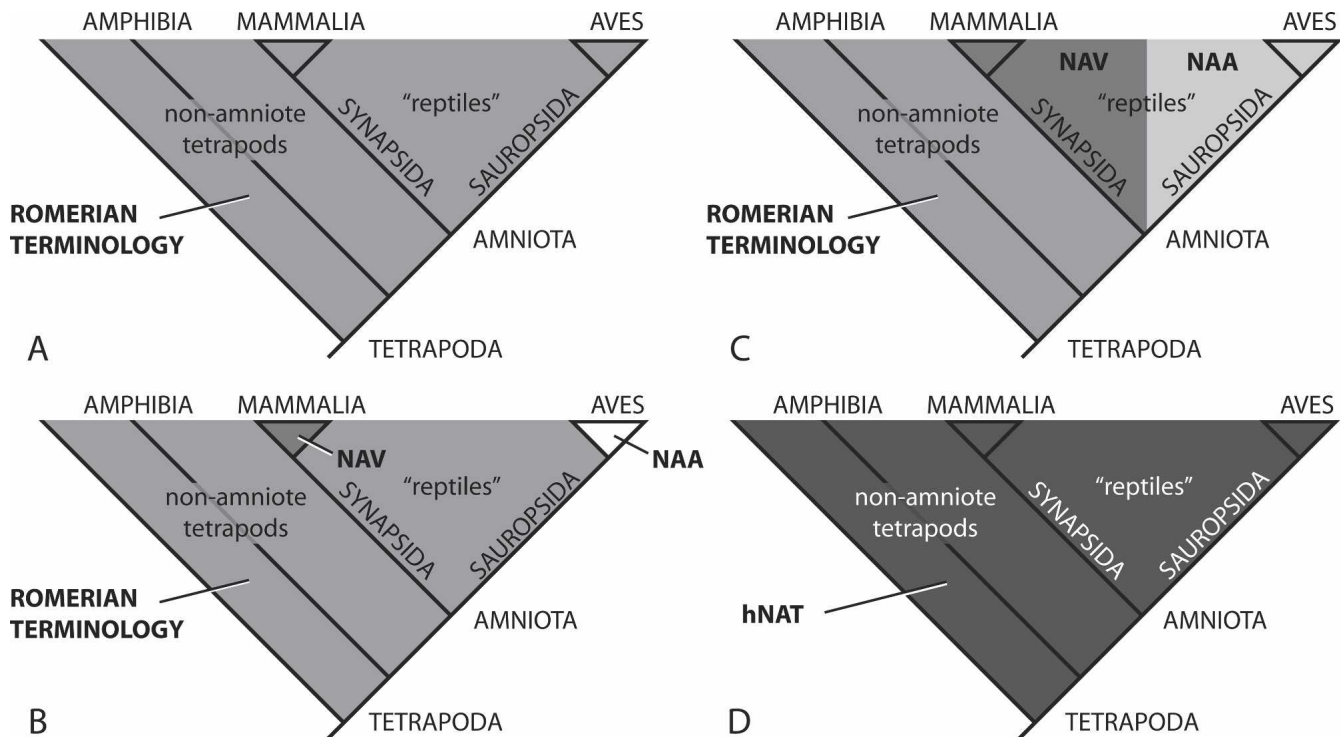


FIGURE 3. Single-system (A, D) and multiple-system (B, C) approaches to tetrapod anatomical terminology, as suggested by Harris (2004). In A, Romerian terminology is extended tipward to Mammalia and Aves, supplanting the NAV and NAA, respectively. In B, three non-overlapping systems are demarcated by arbitrarily drawn boundaries, in this case Aves, Mammalia, and all other tetrapods. In C, the jurisdiction of NAA and NAV are extended to the base of the tree to cover all sauropsids and synapsids, respectively, and Romerian terms are applied to non-amniote tetrapods. In D, a new, overarching system covers all tetrapods (hypothetical Nomina Anatomica Tetrapodum, hNAT), supplanting Romerian terms, NAA, and NAV. Weishampel et al. (1990, 2004) employed solution C in “The Dinosauria”; Harris (2004) recommended implementing solution C followed by solution D.

lution, Harris (2004:1244) outlined a long-term goal of universal anatomical terminology for all tetrapods:

“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.”

Despite the relative simplicity of applying the equivalent of a stem-based definition to anatomical terminology (i.e., extending the NAA and NAV stemward; Fig. 3C), homologous structures are often given different names in the two taxon-based systems. Synapsid and sauropsid terminologies are unambiguous for their focal taxa but sometimes differ in terminology used for structures shared by the two groups. A hypothetical Nomina Anatomica Tetrapoda (hNAT; Fig. 3D) suffers from a similar problem, because it only works “from the bottom of the tree upward” from the standpoint of tetrapods. Many transformations relevant to tetrapod evolutionary studies pertain to symplesiomorphies inherited from vertebrate and non-vertebrate outgroups that are not covered by the hNAT (Fig. 4). Thus, a subset of important anatomical terms will overlap and possibly conflict with terms used by ichthyologists, early chordate specialists, and so on. Taxon-based anatomical nomenclature cannot be truly universal because the tree of life is hierarchical and codifying terms for a focal taxon (e.g., Tetrapoda) always excludes closely related groups.

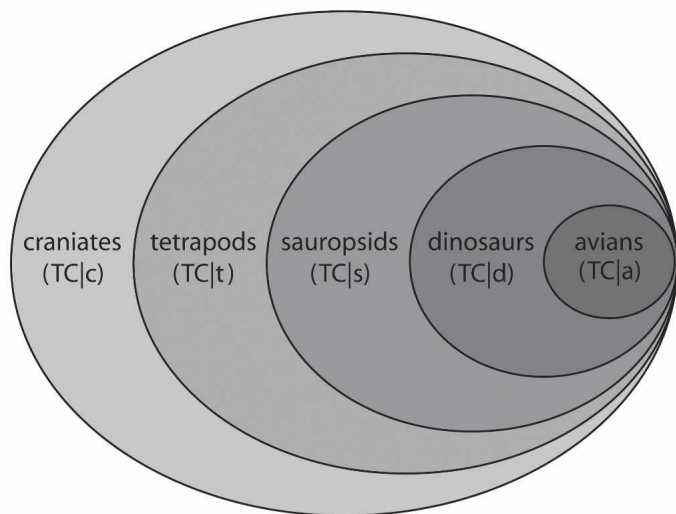
### Interdisciplinary Communication

Communication between comparative anatomists or evolutionary biologists is an oft-cited rationale for standardized terminology. For example, Smith and Dodson (2003:10) stated that “standard terminology for fossil vertebrate dentitions . . . would put the paleontological community back in the company of anthropologists, veterinary scientists, and medical and oral biologists . . . and would facilitate communication of information between these groups”. Harris (2004:1242) queried, “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?”

Three points are relevant here. First, discovery of homology through phylogenetic systematics and naming of structures through comparative anatomy are related but distinct pursuits, for reasons discussed above. It follows that discussion of homology and transformation via the language of anatomy may not entail identical terminologies. For example, the evolutionary origin of mammalian middle ear bones from jaw elements of basal synapsids is one of the best preserved anatomical transformations in the vertebrate fossil record, yet this evolutionary change is communicated without a standardized, unified terminology.

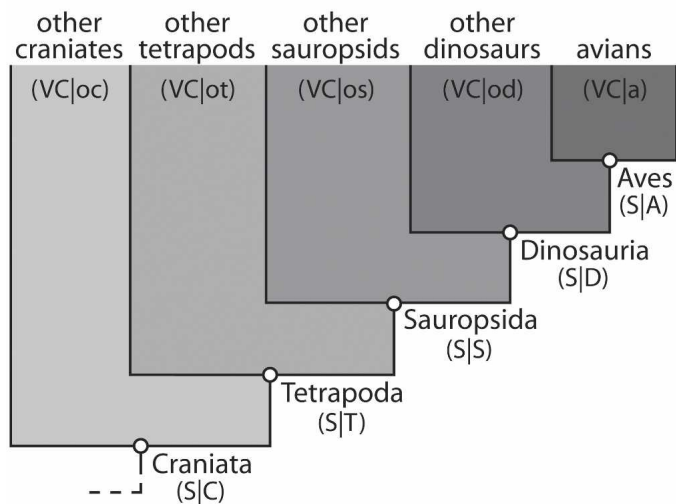
Second, it has not been demonstrated that synonymy creates confusion. Although standardized nomenclature typically strives to eliminate synonymous terms (e.g., Baumel et al., 1993; FCAT, 1998; ICVGAN, 2005), other fully functional and universally understood systems, such as the genetic code, may be both unam-

biguous (i.e., each term specifies only one structure) and degenerate (i.e., a structure can be specified by more than one term). In the status quo anatomical nomenclature for vertebrates, three standardized taxon-based terminologies (NAA, NAV, NA) co-



TAXON-SPECIFIC VIEW OF CHARACTERS

$$TC|a \not\cap TC|d \not\cap TC|s \not\cap TC|t \dots$$



HISTORICAL VIEW OF CHARACTERS

$$TC|a = VC|a + S|A + S|D + S|S + S|T \dots$$

FIGURE 4. Taxon-specific (top) and historical (bottom) views of character data. The taxon-specific view of characters, such as that implicit in standardized anatomical terminology, considers the total character set (TC) of each nested group independently. Anatomical terminologies applied to focal groups are likewise independent of one another and, consequently, characters shared by different focal taxa may be given different names in their respective terminologies. In the figure, a crossed-out intersect symbol ( $\not\cap$ ) is used to indicate, for example, that the total character set for avians (TC|a) is independent of the total character set for dinosaurs (TC|d). In contrast, the historical view of characters focuses on character distributions, which may be more, less, or as inclusive as the focal taxon. The total character set for avians (TC|a), for example, includes variable characters within avians (VC|a), synapomorphies of Aves (S|A), and synapomorphies of more inclusive clades, such as Dinosauria (S|D), Sauropsida (S|S), and so on.

exist and overlap with non-standardized Romerian terms. These overlapping terminologies function more like a vocabulary based on similarity and topology rather than as cladistic statements of homology that evidence relationship. Synonymous anatomical terms (e.g., centrum, corpus, body) and orientational descriptors (e.g., anterior, cranial) are typically not ambiguous, but those that mislead naturally fall into disuse over time. Not only do synonymous anatomical terms coexist in current and past literature with minimal confusion, it has not been demonstrated that specification of a preferred term and elimination of its synonyms facilitates communication. Nor has it been demonstrated that communication is significantly enhanced in communities using standardized anatomical nomenclature (mammalogists, ornithologists) compared to those using non-standardized terminologies (ichthyologists, herpetologists) or that differences in anatomical language obstructs communication between these groups.

Third, as discussed below (see “Presumed Homology”), aspects of the anatomy of basal and derived taxa (e.g., sauropods and birds) may be anatomically similar but evolutionarily distinct. Using anatomical terminology to communicate a message of homology pre-empts an important step in evolutionary studies, namely resolving phylogenetic relationships based on comparisons of available character distributions. Anatomy, whether standardized or not, cannot act as both an impartial description of parts and the narration of their morphological transformation.

Removing Ambiguity

In their two editions of “The Dinosauria,” Weishampel and colleagues (1990, 2004) proposed a practical rationale for standardized anatomical nomenclature. These compendia of dinosaur anatomy and systematics mandated NAA/NAV orientational terms ‘cranial,’ ‘caudal,’ ‘cranio-,’ and ‘caudo-’ in lieu of their Romerian equivalents ‘anterior,’ ‘posterior,’ ‘antero-,’ and ‘postero-’. Not surprisingly, these terms were also implemented in a comparable treatise on Mesozoic birds (Chiappe and Witmer, 2002). The rationale for this directive stems from the purported ambiguity of ‘anterior’ and ‘posterior’ associated with human standardized anatomy. By virtue of the orthograde context adopted by the NA (Fig. 1), anterior and posterior are the same as ventral and dorsal, respectively, except in the head (ICVAN, 1973:1; Weishampel et al., 1990:6–7; 2004:3).

It is true that adoption of an orthograde positional axis by the IANC proved a rift point for human and veterinary anatomists in the 1950s and that the ‘cranial-caudal’ convention adopted by the NAA and NAV served to distinguish their reference to a pronograde positional axis. Nevertheless, vertebrate paleontologists are raised on 19th, 20th, and now 21st Century monographs on non-human vertebrates that use ‘anterior’ and ‘posterior’ exclusively and unambiguously. Recommended NAA/NAV terms, despite their preferred use amongst veterinary anatomists, can introduce more confusion than their Romerian counterparts. ‘Cranial’ and ‘caudal’ are ineffective within the skull and tail, respectively, and instead require use of ‘rostral’ and ‘caudal’ within the skull and ‘proximal’ and ‘distal’ within the tail (and ‘anterior’ and ‘posterior’ within the eye). NAV and NAA orientational descriptors also lead to ambiguous phrases such as “caudal cervical vertebrae” (as noted by Gaffney, 1991: 378). These limitations are not shared by corresponding Romerian terms. At this point, there seems to be no justification for excluding either set of orientational descriptors—both should be available according to the preference of the anatomist.

NEGATIVE CONSEQUENCES

Proposed standardized anatomical terminology for fossil tetrapods entails several negative consequences that suggest it is

unfavorable to communication and misrepresents homology and the evolutionary process.

### Presumed Homology

Projecting stemward the standardized nomenclature of extant birds and mammals is a ‘top-down’ (stemward) process that goes against the natural progression of character evolution, which is directed ‘bottom-up’ (tipward). Potential difficulties arise because presumed homologous structures may be quite different due to evolutionary transformation or they may be homoplastic. Two examples illustrate this point.

The first example concerns the evolution of the mammalian middle ear. The quadrate of pelycosaur-grade synapsids is homologous to the incus of crown-group mammals (approximately at the level of Craniata), but the two structures are not identical. The quadrate of *Dimetrodon* and other non-mammalian craniates is attached to the braincase and functions in jaw suspension as the upper portion of the first gill arch, which in gnathostomes is modified into the upper jaw. In contrast, the incus of crown-group mammals is one of three middle ear bones that are detached from the skull and lower jaw and collectively function to amplify and transmit sound from the tympanum to the oval window of the braincase. The anatomical, positional, and functional transitions that led to the mammalian middle ear took place across a nested series of clades, blurring the demarcation between ‘quadrate’ and ‘incus.’ It may be best to use both terms interchangeably in transitional forms. Moreover, despite a relatively well-sampled mammalian fossil record, a single origin for the mammalian middle ear is not agreed upon (Rich et al., 2005). Regardless of whether the three hearing ossicles are resolved as having evolved once or multiple times within mammals, anatomists will likely refer to those bones as the ‘incus,’ ‘malleus,’ and ‘stapes.’ The danger of projecting derived anatomical terms stemward is that it can presuppose important anatomical, positional, and functional transformations that have not yet occurred or that cannot be resolved.

A second example of presumed homology misleading standardized terminology was cited by Harris (2004) as successful application of NAA terminology to a non-avian archosaur group. In their investigation of the osteological correlates of cervical musculature in birds and sauropods, Wedel and Sanders (2002:fig. 1) used NAA terms to label an illustration of cervical vertebrae of the paleognath *Struthio* and the sauropod *Apatosaurus*. The NAA terms ‘processus spinosus,’ ‘torus dorsalis,’ ‘tuberculum ansa,’ and ‘processus costalis’ were used in place of equivalent Romerian terms ‘neural spine,’ ‘epipophysis,’ ‘diapophysis,’ and ‘cervical process,’ respectively. In traditional anatomical practice, structural and topological correspondence between structures justifies this choice. However, the evolutionary distribution of these features amongst dinosaurs cannot be determined based on *Struthio* and *Apatosaurus* alone; they must be inferred from available character distributions and the resultant hypothesis of relationships. Wedel and Sanders (2002) identify the posteriorly projecting rib on the *Struthio* and *Apatosaurus* cervical vertebrae as the ‘processus costalis’. In birds and sauropods, the cervical ribs are morphologically similar and fuse to the cervical vertebrae early in ontogeny (i.e., vertebral processes rather than free ribs), indicating they pass the test of similarity. However, numerous characters indicate that sauropods and birds are not sister taxa and that outgroups to each bear free cervical ribs as adults. Despite the similarity and topological identity of fused cervical ribs in sauropods and birds, they are not a homologous feature present in their most recent common ancestor (Saurischia). Anatomical nomenclature that calls these structures by the same name and asserts their homology is positively misleading.

### Complex Transformations and Uncertain Homologies

A second negative consequence of standardized nomenclature for tetrapods is that it can misrepresent complex transformations or uncertain homologies. Some structures have complex evolutionary histories that involve one or more fragmentation, fusion, or transformation events. For example, the human temporal bone is a composite element that unites parts of the dermatocranium (squamous part), neurocranium (petrous and mastoid parts), and splanchnocranium (styloid process). The styloid process represents a derivative of the hyoid arch (ceratohyal) of basal gnathostomes. How can we communicate the complex relationship between the human temporal bone and its constituent elements by using a universal, taxon-based anatomical terminology or by applying crown-group terms stemward?

Still other negative consequences arise with structures whose homology is uncertain, as in the manual digits of birds and non-avian theropod dinosaurs. The manual digits have been identified as I–III in non-avian theropods based on incipient reduction in the most basal forms (e.g., Sereno and Novas, 1992), but in birds these are regarded as digits II–IV (Feduccia and Nowicki, 2002; Kundrát et al., 2002; Larsson and Wagner, 2002). Models for transformation between these two conditions have been proposed (e.g., Wagner and Gauthier, 1999; McNamara and McKinney, 2005), but there is no consensus on the homology of the individual manual digits in birds and non-avian theropods. Nonetheless, standardized anatomical terminology requires a single terminology for these digits because they are derived from a common tetrapod ancestor that shared this feature. For these and other structures of uncertain homology, applying a universal terminology that purports to represent the evolutionary process incorrectly implies that the homologies been resolved.

### Conversions

Harris (2004:1244) recommended that “standardized terminologies (Nomina Anatomica Veterinaria and Nomina Anatomica Avium) can, and should, be applied . . . until such time as an all-encompassing Nomina Anatomica Tetrapodum is emplaced.” Application of NAA and NAV terms to basal amniotes requires a nomenclatural conversion from Romerian terms to NAA/NAV terms. Adoption of a hypothetical Nomina Anatomica Tetrapodum would require a second conversion from NAA/NAV terms to hNAT terms. Each conversion requires eradicating old terms in favor of standardized terms. These nomenclatural conversions will be confusing and costly, especially because supplanted terms remain in the literature (Carrano, 2005). A resultant incongruity is that anatomists would still need to remain fluent in both Romerian and standardized terminologies to interpret prior literature, yet only use standardized terms for their current research.

The suggested parallels between the conversion to standardized anatomical terms and the conversion from traditional to cladistic characters or from traditional to phylogenetic taxonomy are superficial at best. Traditional character data, such as that from Romer, Owen, or other sources, can be converted to cladistic characters with little more than formalization of primitive and derived states. Indeed, much of the character data currently used in cladistic analyses of vertebrates has precedents in traditional studies. Similarly, in many cases Linnean taxonomy can be easily adapted to fit phylogenetic taxonomy. However, whereas both cladistic methodology and phylogenetic taxonomy constitute new paradigms for evaluating character and taxonomic data, respectively, the proposed changes suggested by Harris (2004) and Weishampel et al. (1990, 2004) do not involve new methods of evaluating anatomy. Clearly, these authors have not suggested a hierarchical system that integrates anatomy with phylogenetic hypotheses, otherwise ‘functional homologues’ and focal taxa

would not be part of their proposed standardized system. Rather than ushering in a new anatomical paradigm, standardization of tetrapod anatomical terminology will encourage papers that merely convert non-standard anatomical terms into standard terms, or coin ‘new’ terms for anatomy that has thus far not been included in the NA, NAA, or NAV.

#### ANATOMICAL ‘LINGUA FRANCA’

Standardized terminology vs. Romerian terms does not pit a modern system against an anachronistic one. Terminology utilized by Romer in “Osteology of the Reptiles” (1956) applies to the very non-mammalian synapsids and non-avian sauropsids that Weishampel et al. (1990, 2004), Harris (2004), and others target (Fig. 2). Like standardized nomenclature, Romerian terminology is not ambiguous because each term generally specifies one structure. Unlike standardized nomenclature, however, Romerian terminology tolerates synonyms—a given structure or orientation may be specified by more than one term. Although Harris (2004:1242) dismisses Romerian terminology for this degeneracy, it is this “polytomy of lexicons” that makes it the anatomical lingua franca (i.e., eclectic jargon) for vertebrate paleontologists. Two centuries of organic change has shaped this incumbent anatomical language, and an ever-growing literature lends this practice considerable historical inertia. Paleontologists working on transitional lineages leading to birds and mammals are fluent in this lingua franca as well as the NAA and NAV, despite the fact that there is no clear demarcation between the two standardized terminologies and the non-standardized terminology. In contrast, Harris’ (2004) proposed all-encompassing hNAT derived from components of existing systems currently in use is anatomical Esperanto.

I recommend retaining the status quo non-standardized system in which anatomical terminologies overlap and individuals decide which terminology best communicates to the intended audience. Romerian terms are preferred for traditional “reptiles” and non-amniote tetrapods, but they are applicable to all vertebrates. Likewise, the NAA, NAV, and NA are preferred for the avian, mammalian, and human crown groups, respectively, but their scopes may be widened to encompass more inclusive groups, with caution to the previously cited pitfalls.

#### CONCLUSION

Harris’ (2004) proposal to standardize anatomical terminology for tetrapods, whether by projecting NAA and NAV terms stemward or by creating a new all-encompassing Nomina Anatomica Tetrapodum, requires abandoning the anatomical lingua franca (i.e., Romerian terminology) currently used by vertebrate paleontologists. The rationale for this major step is that standardized terminology is homology-based, universal, interdisciplinary, and unambiguous. I have argued that standardized anatomical terminology is not preferable to traditional Romerian terminology in any of these senses. Furthermore, standardized anatomical terminology entails many negative consequences, including (1) reversing character trajectories, (2) artificially simplifying complex character transformations and uncertain homologies, (3) mandating terminological conversion, and (4) encouraging the coining of superfluous anatomical terms. The status quo anatomical lingua franca, in contrast, imposes none of these negative consequences but entails many positive ones, including simplicity, ubiquity, and the inertia of two centuries of use and modification.

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