

Functional morphology in vertebrate paleontology

Edited by

Jeff Thomason

University of Guelph

**The Extant Phylogenetic Bracket and the
Importance of Reconstructing Soft Tissues
In Fossils**

Lawrence M. Witmer

1995



CAMBRIDGE
UNIVERSITY PRESS

The Extant Phylogenetic Bracket and the importance of reconstructing soft tissues in fossils

LAWRENCE M. WITMER

ABSTRACT

Fossils usually provide paleontologists with little more than bones and teeth as primary data. Because the broad aim of functional morphological analyses of extinct organisms is to breathe life into fossils, paleontologists are challenged to reconstruct those portions of the animal not normally preserved in the fossil record – in particular, soft tissues. Soft-tissue considerations are important for two major reasons: (1) Soft tissues often have morphogenetic primacy over skeletal tissues, and (2) such considerations often lie at the base of numerous paleobiological inferences. Furthermore, soft-tissue analysis can provide causal hypotheses of phylogenetic character correlation. A methodology for reconstructing soft anatomy in fossils – the Extant Phylogenetic Bracket approach – is proposed here. This method makes explicit reference to at least the first two extant outgroups of the fossil taxon of interest. It is based firmly on the relation of biological homology, provides a means of rigorously establishing the limits of our inferences, and allows construction of a hierarchy of inference. The approach can be applied to virtually any unpreserved trait of a fossil taxon with little or no modification.

INTRODUCTION

Recently, extinct organisms, in a sense, have come alive. That is, there has been renewed interest in viewing fossils not just as collections of bones but rather as living, functioning animals. This resurgence has its foundation, at least in part, in the explosion of dinosaur paleobiology in both the scientific literature (Weishampel, Dodson, & Osmólska 1990; Carpenter & Currie 1990; Halstead 1991) and the popular press (Norman 1985; Bakker 1986; Paul 1988; Benton 1989). The success of dinosaur research has led to similar popular treatments for other groups of extinct animals (Savage & Long 1986; Dixon et al. 1988; Benton 1991; Wellnhofer 1991). In fact, the proliferation of fossils fleshed out with soft tissues has even elicited a primer for illustrators for

reconstructing soft tissues (Paul & Chase 1989). It probably is of little scientific consequence whether or not robotic sauropods have trunks, and it is relatively harmless if they do. However, the question remains that, given this justifiable interest in fossils as once living organisms, what relevance do considerations of soft tissues have for the analysis and interpretation of organisms known only from fossils?

This paper seeks an answer to this question by addressing two major issues in turn. First, what importance does the study of soft anatomy hold for disciplines such as vertebrate paleontology that traditionally have bones and teeth as their primary (if not only) data? In other words, why worry about soft tissues at all? Obviously, living organisms are more than collections of bones and teeth. As a result, the evolutionary interpretation of the paleobiology of extinct organisms often *requires* explicit reference to anatomical systems other than the skeleton, that is, to those portions of the organism not normally preserved in the fossil record.

Second, since the necessary soft tissues are rarely preserved as fossils, how is this requisite information obtained? Probably because many older soft-tissue reconstructions had no explicit methodological basis, a common sentiment among paleontologists has developed that any reference to soft tissues in fossils involves little more than unsubstantiated guesswork. However, if approached correctly, more useful information can be extracted from fossils than previously has been appreciated (see Nicholls & Russell 1985; Bryant & Seymour 1990; Bryant & Russell 1992, this volume). A phylogenetically rigorous means of inferring these attributes – the Extant Phylogenetic Bracket (EPB) approach – is proposed here, based in large measure on the anatomy of the extant relatives of a fossil taxon. While speculation cannot always be eliminated, the method outlined here identifies those soft-tissue inferences that are speculative and those that are well founded. In fact,

the EPB approach provides a clear way to characterize the different sorts of speculation that must be invoked to reconstruct an extinct organism with a particular soft tissue.

The extant phylogenetic bracket approach was developed specifically for the inference of soft anatomical properties (Witmer 1992), but is generalized in the last section for the inference of any aspect of paleobiology. A very similar general approach was devised independently by Bryant and Russell (1992), and the reader is referred to their paper for an excellent and complementary discussion.

THE IMPORTANCE OF SOFT-TISSUE INFORMATION

Knowledge about the general form of soft anatomical components and their relationships to the skeleton in extinct (as well as extant) organisms is important for at least three general reasons: (1) Soft tissues largely are responsible for the existence, maintenance, and form of bones; (2) judgments about the form and actions of soft tissues are (implicitly if not explicitly) the basis for a host of paleobiological inferences; and (3), with regard to systematics, soft-tissue relationships may provide testable hypotheses on independence or nonindependence of phylogenetic characters.

The morphogenetic primacy of soft tissues

At perhaps the most fundamental level, soft tissues, not bones, may well be the proper focus of analysis. In recent years it has been recognized that skeletal tissues are largely responsive to their epigenetic systems and are correctly viewed as products of epigenetic cascades involving inductive interactions among nonosseous tissues (Hall 1983, 1988, 1990). In other words, bones do not self-differentiate (Smith & Hall 1990). Carlson (1981) noted that the inductive influence provided by the developing brain is necessary for initiation of ossification of the dermal skull roof, and that pressure from the brain and cerebrospinal fluid subsequently determines the final form of the bones. This simple, well-understood example illustrates the hierarchical nature of soft-tissue influences on bony morphology: first, the specification of the existence and spatial patterning of skeletal elements (Wolpert 1983; Wedden et al. 1988; Hall 1988), and second, the maintenance and form of these elements once present (Moss 1968, 1971; Hall 1990). The two major tiers of this hierarchy are examined in more detail below.

THE FIRST TIER: EXISTENCE AND PATTERN OF BONES. Since bones are not self-differentiating entities,

understanding the presence (or absence) and positions of bones requires some knowledge of the epigenetic system specifying their existence, for example, the nature of inductive tissue interactions, the rate and timing of cellular migrations or programmed cell death, and the pattern and size of preskeletogenic mesenchymal condensations (Oster et al. 1988; Hall 1991; Atchley & Hall 1991). Bones tend to form relatively late in ontogeny, after the differentiation of other tissues such as, in the head, the cartilaginous chondrocranium, nasal epithelium, brain, and eye. As a result, bones tend to originate in close association with particular soft tissues. Although the causal mechanisms of these associations are being worked out for a few model systems (e.g., chick scleral ossicles; Pinto & Hall 1991), in most cases, these associations remain largely phenomenological. In embryos of *Alligator mississippiensis*, for example, many of the dermal skull bones ossify next to very specific portions of the chondrocranium: the frontal bone along the *planum suprasetale* and sphenethmoidal commissure, the vomer next to the primary nasal concha, the prefrontal at the juncture of the sphenethmoidal commissure and nasal capsule, and the postorbital bone at the tip of the rostradorsal process of the quadrate cartilage (L.M. Witmer, unpublished data). The chondrocranium itself is specified even earlier in ontogeny by aspects of epithelial folding (see Born 1883, Kamal & Abdeen 1972, and Noden 1983 for the importance of nasal epithelium morphogenesis) and the rate and timing of neural crest migration (Thorogood 1988).

Thus, whether a particular bony element is present or absent probably depends more on those tissues that precede bone formation in morphogenesis than on factors intrinsic to the particular bone. For example, most of the sites of bone formation observed in alligator embryos are conserved across the major clades of vertebrates, probably because chondrocrania are so conservative (Thorogood 1988). In crocodylians, the ascending ramus of the maxilla develops after and in proximity to the *lamina transversalis rostralis* (LTR) of the chondrocranium; other sauropsid amniotes generally resemble crocodylians in this feature (de Beer 1937; Bellairs & Kamal 1981). Ornithurine birds, however, represent an exception in that they have both lost the ascending ramus of the maxilla (Cracraft 1986; Witmer 1990) and suppressed the LTR (Witmer 1992); given the situation in other sauropsids, loss of the ascending ramus in birds is probably causally associated with suppression of the LTR.

THE SECOND TIER: THE MAINTENANCE AND FORM OF BONES. Once formed, the subsequent maintenance and detailed form of bony structures are largely controlled by associated soft tissues. Hall (1990)

referred to this level of control as second-order epigenetic control. This notion has been captured effectively (although in a somewhat extreme form) in the Functional Matrix Hypothesis championed by Moss and colleagues (Moss 1968, 1971, 1972a,b; Moss & Salentijn 1969). Under the Functional Matrix Hypothesis, each specific function is performed by a particular *functional component*, which is itself composed of a *functional matrix* (which actually carries out the function and incorporates all nonskeletal tissues and “functioning spaces” that directly constrain bony morphology) and its *skeletal unit* (which responds to its particular functional matrix, playing a role in protection and/or support).

According to Moss (1981, p. 370), “the origin, growth, and maintenance of all skeletal tissue and organs are always secondary, compensatory, and obligatory responses to temporally and operationally prior events or processes that occur in specifically related nonskeletal tissues, organs, or functioning spaces (functional matrices).” Atchley and Hall (1991, p. 138) viewed Moss’s functional matrices as “the sum of the epigenetic [heritable] and environmental [nonheritable] influences that impinge on skeletal development,” and although they disagreed with Moss’s extreme stance on genomic involvement, they agreed that functional matrices are “an important component(s) of the interactive, integrative, hierarchical network that governs morphogenesis.”

No one has questioned the existence of functional matrices (even if we have difficulty characterizing them), and they have been demonstrated empirically (Moss 1972b; Ranly 1988). The now-classic example is the dramatic regression and ultimate loss of a skeletal unit (the coronoid process of the mandible) when the functional matrix (the temporalis muscle) has been eliminated via denervation or surgical resection (Schumacher & Dokládál 1968; Moss & Salentijn 1969). The profound influence of numerous soft anatomical systems on the growth and form of skeletal tissues is well documented, particularly with respect to the central nervous system (Ross 1941; Noetzel 1949; Young 1959), the jaw musculature (Scott 1957; Humphrey 1971; Spyropoulos 1977; Hall & Herring 1990), and the eye (Taylor 1939; Coulombre & Crelin 1958; Hanken 1983).

Although there may be formal problems with correctly delimiting skeletal units and functional matrices (since each is based in large measure on reference to the other), the *perspective* of the Functional Matrix Hypothesis is not only conceptually appropriate but perhaps even required for generating the correct explanations in evolutionary osteology and functional morphology. Although Moss’s (1968, p. 198) slogan – “functional matrices evolve; skeletal units respond” – is probably overstated, it properly emphasizes the primacy of soft-tissue

considerations in osteology. Thus, I see the Functional Matrix Hypothesis less as an analytical tool and more as a conceptual framework for interpreting bony morphology and evolution. Many of the well-known morphological trends documented in the fossil record clearly have their foundations in particular soft anatomical systems. An obvious example is the expansion of the bones forming the neurocranial vault of hominids associated with increasing brain size (Le Gros Clark 1964). It should be emphasized, however, that the causality vector does not point only from soft to skeletal tissues, but rather the two interact. Particular biomechanical loading regimes, for instance, often require bony buttressing to function properly. Thus, whereas the functional matrix (i.e., soft tissues) may often or even usually be a “target” of natural selection (as declared in Moss’s slogan), this need not always be the case.

Soft tissues and paleobiological inference

When paleontologists ask questions about the functional morphology of an extinct organism, they often are asking more than just “how does it work?” Often more general paleobiological information is sought, which requires a dependent sequence of questions and answers. These often start with, How does an observed anatomical structure work? and are followed by, What does this functional assessment tell us about the behavior and mode of life of the organism? What kind of paleoecological interactions did the organism have with other members of its community? and, How did this community evolve? Thus, there is a chain of inference, with each successive inference assuming accuracy of the previous one. Figure 2.1 presents such a chain of inference as an inverted pyramid, with each level (except the lowest) representing, more or less, a tier of the ecological hierarchy (sensu Eldredge & Salthe 1984; Eldredge 1986; Liem 1989). The lowest level of the pyramid (i.e., the one closest to observable data) is soft-tissue inference because it is argued here that accurate soft-tissue reconstructions often are the foundation of such paleobiological inferences as behavior, ecology, and community structure.

This point is not typically appreciated, and errors of soft-tissue reconstruction cascade up the ecological hierarchy. Thus, the pyramid in Figure 2.1 is inverted to emphasize this amplification of initial mistakes. For example, whether the jaw musculature and craniofacial biomechanics of the gigantic bird *Diatryma* point to its being an herbivore or a carnivore (Witmer & Rose 1991) bears importance beyond the functional morphology of a single taxon. These two behavioral alternatives have drastically different implications for the ecological associations

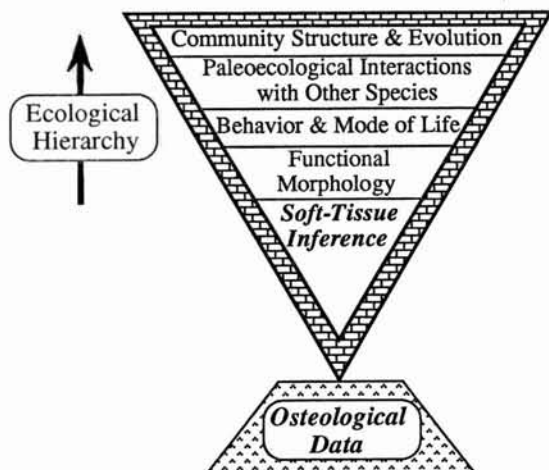


Figure 2.1. Inverted pyramid of inference. Inferences about the soft-tissue attributes of fossil organisms are often the basis for a host of paleobiological inferences. Inferences made at lower levels of the pyramid form the justification for larger-scale inferences. Pyramid is inverted to emphasize how mistakes in soft-tissue inference or at lower levels of the pyramid cascade upwards, amplifying the error. Levels of the pyramid correspond roughly to the ecological hierarchy (arrow at left).

of *Diatryma* with contemporary mammals: If it was a herbivore, *Diatryma* browsed peacefully or perhaps even competed for resources with *Hyracotherium* and *Phenacodus*, whereas if it was a carnivore, it ate them. Furthermore, larger issues are at stake, such as the guild structure of the community (sensu Van Valkenburgh 1988) to which *Diatryma* and its relatives belonged and what effect extinction of these birds had on the evolving predator-prey interactions during the Tertiary (Bakker 1983). Our interpretation of these issues would vary depending on whether we regard *Diatryma* as a herbivore or a carnivore, a determination that is at least partly founded on assessment of soft-tissue relations. Similarly, Weishampel's (1984a) treatment of the evolution of craniofacial kinesis in ornithischian dinosaurs addressed not only the musculature but also the soft anatomy of joints. Again, the deployment of different feeding strategies among ornithischians (Weishampel 1984a, 1985) and the resulting inferences regarding evolving plant-herbivore interactions throughout the Mesozoic (Weishampel 1984b; Norman & Weishampel 1985; Weishampel & Norman 1987, 1989) have soft-tissue considerations in large measure at their base.

Certainly, attention to aspects of soft anatomy and probing the nature of their relations to the skeleton rightly have held a prominent place – implicitly if not always explicitly – in several research programs, such as in biomechanics and paleoneurology. How-

ever, the structure and even the existence of a pyramid of inferences may not always be appreciated, and ignoring soft-tissue considerations amounts to making unrealized (and hence untested) assumptions of perhaps questionable validity.

Soft tissues and systematics

With the growing popularity of numerical cladistics, identifying the precise basis of comparison – “the character” – becomes a central issue. In particular, it is axiomatic that any parsimony-based system carries the fundamental assumption of statistical independence of its data points, characters in this case. Obviously, if many correlated features are counted separately, the composite of which they are a part is weighted more than independent characters, overestimating the branch length of the taxon supported by the correlated character complex. This problem is virtually identical to that emphasized recently by Harvey and colleagues (Clutton-Brock & Harvey 1977; Pagel & Harvey 1988; Harvey & Pagel 1991) with regard to the use of species as independent data points in quantitative comparisons. Character splitting may boost a consistency index to comforting levels, but it increases the likelihood of invalidating the entire analysis by violating the assumption of independence. The relevance here is that knowledge of soft tissues in some cases will help tie together correlated features into a single phylogenetic character.

Taking soft tissues into account, therefore, allows formulation of causal hypotheses of character correlation. Such a priori hypotheses are falsifiable by further cladistic analysis showing that the features are not phylogenetically correlated at all in that they do not specify a single node on a cladogram but instead occur sequentially in phylogeny (as Cracraft [1990] found for the avian “flight apparatus”). Furthermore, additional anatomical research could falsify the correlation hypothesis by demonstrating the inaccuracy of the proposed causal network in that the observed osteological features are actually associated with other aspects of soft anatomy. Alternatively, assessments of character correlation can be made a posteriori based on the pattern of character distribution, after which the causal (i.e., process-oriented) explanation of correlation may be postulated.

Summary of the importance of soft-tissue information

Evolutionary morphological analyses of bones alone are in some sense incomplete. Reconstructing (or at least considering) soft anatomy in fossils is important because skeletal tissues are largely responsive to the influence of their soft-tissue functional matrices and

thus may be only subject indirectly to natural selection. Furthermore, researchers are making assumptions (explicitly or not) about nonskeletal tissues in probing the nature of functioning anatomical systems, and indeed these soft-tissue considerations often are the foundation on which a whole suite of paleobiological inferences are based. Soft tissues even can play a role in determining the phylogenetic relationships of taxa. Thus, if features not typically preserved in fossils are so important, then considerable care must be taken in their reconstruction. It is thus surprising that there has been little attention paid to this issue in the literature until very recently (Bryant & Russell 1992).

METHODOLOGICAL CONSIDERATIONS IN SOFT-TISSUE RECONSTRUCTION

For the reasons outlined above, many questions in evolutionary biology require knowledge of the soft-tissue attributes of organisms known only as fossils. The question then becomes, what is the best way of obtaining this knowledge? Sometimes the taxon of interest may happen to be found in *Lagerstätten*, that is, in unusual preservational environments that preserve soft tissues. In these cases we may need only to observe the fossil material for the required information. Although *Lagerstätten* can provide critical clues (as described below), the vast majority of fossils are known only from hard parts, such as bones and teeth. Thus, the only soft tissues that can be reconstructed are those that may be inferred from the fossils themselves, that is, those that have osteological correlates.

The following section presents first an overview of a method for inferring soft tissues in fossils, examining its basis in phylogenetic principles, the homology relation and the importance of extant taxa. Then the method is discussed in more detail, beginning with an analysis of the causal associations of soft tissues and osteological correlates as determined by study of the extant taxa, proceeding through hypothesis formulation and testing, and finally discussing special cases where the hypothesis does not survive testing and where data from *Lagerstätten* are available.

Overview

The methods proposed here involve an application of basic cladistic principles such as outgroup comparison and parsimony (Wiley 1981; Maddison, Donoghue, & Maddison 1984; Wiley et al. 1991) and the traditional techniques of comparative anatomy. Although the question being asked seemingly is focused solely on fossil taxa, the proposed method

requires and makes explicit use of extant taxa as these are the only organisms for which we can obtain precise information about the soft tissues and their relations to the bones. The method also presupposes an existing, independently corroborated hypothesis of the phylogenetic relationships of the fossil and extant taxa.

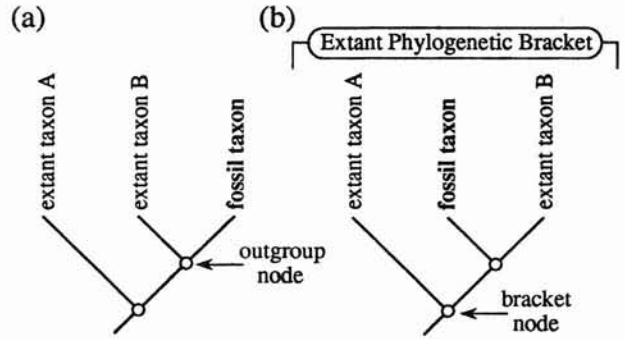
Briefly, the approach seeks to reconstruct the soft-tissue attributes of extinct vertebrate organisms (1) by determining the causal associations between soft tissues and their osteological correlates in the extant relatives of the fossil taxon, (2) by formulating a hypothesis that similarities among the extant taxa in these associations are due to inheritance from a common ancestor (i.e., the associations are homologous), and (3) by testing this hypothesis by surveying the fossil taxa for the osteological correlates. If the hypothesis survives the test and the associations are indeed causally based, then the soft tissue can be inferred in the fossil taxon with confidence.

The appropriate extant taxa are, minimally, the first two outgroups of the fossil taxon of interest having living representatives (Figure 2.2a). The character assessment of the most recent common ancestor of the fossil taxon and its first extant outgroup (i.e., its extant sister group) is critical for determining the ancestral condition of the fossil clade (see Maddison et al. 1984, who designated this hypothetical common ancestor as the outgroup node). The second, more distantly related, extant taxon serves as the outgroup to the first two together, allowing estimation of the ancestral features at the outgroup node. As always, additional extant outgroups may be necessary to resolve conflicts in situations where there is character variation between the first two outgroups (Maddison et al. 1984).

It is of some heuristic use to take advantage of the free rotation around cladogram nodes and rearrange Figure 2.2a to bring the extant outgroups to the periphery (Figure 2.2b). Thus, we may refer to the two extant outgroups as the extant phylogenetic bracket (EPB) of the fossil taxon of interest. The extant taxa in a very real sense form a "bracket" in that they constrain any inferences about the fossil taxon. For the sake of discussion, the most recent common ancestor of the extant phylogenetic bracket may be termed the bracket ancestor, which is located at the bracket node (Figure 2.2b).

Often the extant taxa are highly diverse and may vary internally with respect to the features being compared. In theory, each extant taxon used in the analysis is not a single or even several species but rather the whole monophyletic supraspecific taxon. The characters of each extant taxon are thus abstractions of its hypothetical common ancestor deduced from all subtended taxa (see Maddison et al. 1984).

Figure 2.2. (a) Phylogenetic relationships of a fossil taxon and its first two extant sister-groups. (b) Rotation around the outgroup node in (a) brings the extant taxa to the periphery, forming the Extant Phylogenetic Bracket.



The basic approach is little more than a particular application of homology determination: In order to reconstruct a particular soft-tissue attribute in a fossil taxon, the resemblances in osteological correlates between the fossil and its EPB must not only pass the test of similarity (Patterson 1982), or better, of “1:1 correspondence” (Stevens 1984), but must also pass the test of congruence (Patterson 1982) by characterizing a monophyletic group. But in addition to homology among the various osteological features, the *causal associations* of the soft and hard tissues must be homologous. Put simply, homologous soft tissues must produce homologous osteological correlates. As soft-tissue reconstructions of extinct taxa are inferential in nature, the aim of the following method is to put these inferences in the form of hypotheses that can be subjected to testing, in particular the homology tests proposed by Patterson (1982) and others.

Determination of the causal associations of soft tissues and osteological correlates in extant taxa

Routine comparative anatomical research of the extant taxa proceeds with determination of the topographical relationships and 1:1 correspondences of all of those soft tissues that are both relevant to the osteological system of interest and have clear osteological correlates that may be assessed in fossils. Osteological evidence for particular soft tissues include such typical features as tuberosities, crests, grooves, fossae, foramina, fenestrae, and septa. These features often have unambiguous relationships to the soft tissues producing them, such that the causal association is clear and can be demonstrated experimentally. For example, as discussed earlier, the mammalian temporalis muscles certainly are causally associated with coronoid processes. As another example, in *A. mississippiensis* the postvestibular recess and its pneumatic foramen are caused directly by pneumatization by an epithelial paranasal air sac; in some individuals, the air sac fails to appear during ontogeny, and in these cases the bony recess and

foramen are hence also absent (Witmer 1992). A potential hazard, however, is that there sometimes may be more than one soft-tissue system that may produce a particular feature. In these cases, it may be difficult or impossible to choose without directly studying the actual soft tissues of the extant taxa (e.g., via dissection, histology, ontogenetic analysis). For example, grooving on bones may be caused by neurovascular bundles, muscle tendons, attachment of connective-tissue sheets, pneumatic diverticula, ducts of glands, glands, or other organs and structures.

A more insidious pitfall, perhaps, is the “hole-or-the-doughnut” problem, in which it may be difficult to determine from the bones alone whether the soft tissues are directly responsible for a particular bony feature (the doughnut) or if the feature is actually an epiphenomenon (the hole) produced by the effect of other soft tissues on the area. In other words, the causal relationships are uncertain. As a general example, an elongate bony elevation could result either directly (as from muscle insertion) or may be merely the region “left over” after excavation of adjacent surfaces. Furthermore, unexpected, alternative soft-tissue systems potentially may be responsible for observed osteological features. This is more of a psychological than a methodological issue and involves over-reliance on a search image tied to the system of interest. For example, an uncritical worker may interpret all bony scars as muscle attachments, all craniofacial cavities as air sinuses, and all braincase foramina as exits for cranial nerves.

As has been emphasized throughout, the approach advocated here requires that the osteological correlates be causally related to a particular soft tissue. Ideally, the goal is to identify those soft-anatomical elements that are both necessary and sufficient to explain a particular osteological feature. That some causal relationship exists is predicted by Moss’s Functional Matrix Hypothesis and has been demonstrated by evidence that bones are products of their epigenetic systems. But as the above examples illustrate, the causal association may not be particularly apparent if only dried skeletal or fossil material is studied. The proposed causal basis of a particular

association is itself a hypothesis, perhaps requiring experimental approaches such as extirpation studies (e.g., Coulombre & Crelin 1958; Schumacher & Dokládál 1968) to be tested adequately. All of the above hazards are significantly lessened by direct comparative studies (via dissection, etc.) of the extant taxa. Comparative ontogenetic analysis also may be helpful in determining how the soft and skeletal tissues interact during morphogenesis, providing highly detailed information on the changing topographical relationships of structures.

All of the structures that are used as topographical landmarks obviously must be homologous among the extant taxa in the bracket if they are to have any bearing on the fossil taxon. As with any such hypothesis of homology, these must pass the tests of similarity (i.e., 1:1 correspondence of topographical relationships), congruence, and conjunction (i.e., putative homologs may not co-occur in a single organism) as outlined by Patterson (1982, 1988), Stevens (1984), and Rieppel (1988), among others. Additional extant outgroups will be required for this procedure, although in many cases the homologies of the soft-anatomical systems are so well established as to require little further justification.

Formulating and testing hypotheses about the bracket ancestor

Having assessed the soft tissues and their relationships to their osteological correlates in the extant taxa, it is possible to formulate hypotheses about the soft-tissue attributes of the common ancestor of the extant phylogenetic bracket. All similarities in soft tissues (and correlated osteological features) between the two extant taxa can be hypothesized to have been present (minimally at least) in their common ancestor and all its descendants, including the fossil taxon of interest (Figure 2.3: broken arrows). The assumption of this hypothesis is that the bracket ancestor had these attributes and passed them down to all its descendants, two clades of which still have living representatives. Since the hypothesis predicts that other descendants of this common ancestor also should have inherited these attributes, we may test this hypothesis by surveying these other descendants – the fossil taxa – for the osteological correlates of the soft-tissue attributes (Figure 2.3: solid arrows). If all of the fossil taxa (including the taxon of interest) exhibit the osteological correlates of the soft tissues (or clear apomorphic transformations), then we have a sound basis for inferring and reconstructing these soft tissues in the fossil taxa (Figure 2.4). In situations where one or more clades of fossil taxa lack the osteological correlates, we may appeal to parsimony to determine the fate of the initial hypothesis.

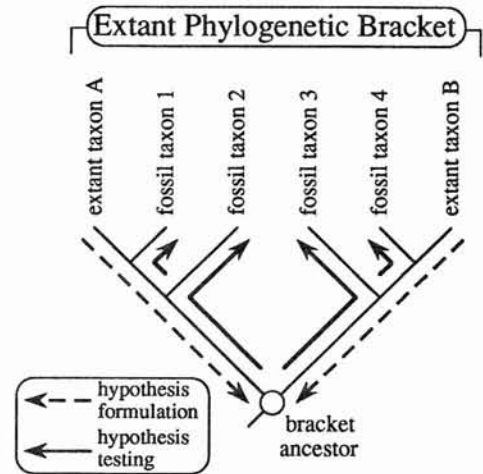


Figure 2.3. Basic scheme of hypothesis formulation and testing in the Extant Phylogenetic Bracket approach. Similarities between the components of the EPB are hypothesized as being present in the bracket ancestor (broken arrows). This hypothesis is tested for its congruence with the phylogenetic pattern by surveying the fossil taxa (solid arrows). See text.

Since osteological correlates and their presumably causally associated soft tissues are being mapped onto an existing cladogram, the EPB procedure involves the well-understood principles of a posteriori character optimization (see Swofford & Maddison 1987). The above method clearly resembles two-pass systems (Wiley et al. 1991) such as Farris optimization (Farris 1970): The downward pass involves formulating hypotheses about the bracket ancestor based on study of the extant taxa, and the upward pass involves hypothesis testing by surveying the fossil taxa for the specified osteological correlates. Optimization procedures allow determination of the character assessment at internal (ancestral) nodes, and in this case, the relevant node is the outgroup node (Figure 2.2a) because the assessment here decides whether or not the soft tissue can be inferred in the fossil taxon of interest. Three types of soft-tissue assessments at the outgroup node are possible (Figure 2.5). In the first case, both of the extant members of the bracket exhibit the soft tissue (and its causally associated bony features) that is suspected to occur in the fossil taxon; thus, the assessment at the outgroup node is decisive and positive (Figure 2.5a). In the second case, only one of the extant taxa has the suspected soft tissue and other extant outgroups lack it; here the assessment at the outgroup node is equivocal (Figure 2.5b). In the third case, neither extant taxon has the soft-tissue attribute suspected to occur in the fossil; thus, here the assessment is decisive and negative (Figure 2.5c). We will return to these three situations shortly

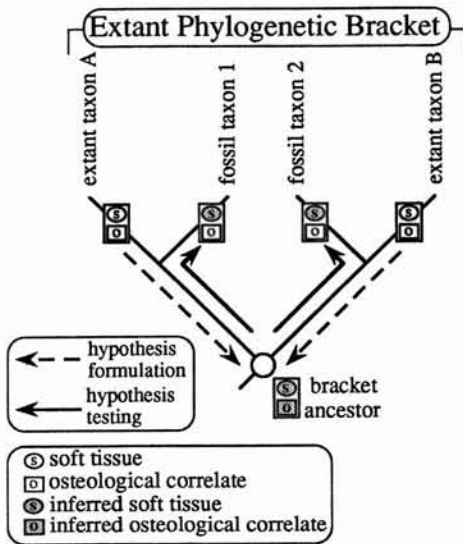


Figure 2.4. Cladogram showing the inference of soft-tissue attributes in fossil taxa using the EPB approach. Similarities in soft tissues and osteological correlates between the extant taxa are hypothesized as having been present in the bracket ancestor (broken arrows), as in Figure 2.3. Fossil taxa possess the osteological correlates, and thus the hypothesis of homology of the osteological correlates survives the congruence test. If soft tissues and osteological correlates indeed are causally associated, then soft tissue can be inferred in the fossil taxa with confidence.

because they provide a means of ordinating soft-tissue inferences.

As indicated earlier, the proposed method (and indeed optimization procedures) are based simply on the homology relation. The 1:1 correspondences within the EPB in causal associations between hard and soft tissues comprise the similarity test, allowing the formulation of a hypothesis of homology. Surveying the fossil taxa for the osteological correlates basically follows the congruence test of homology (Patterson 1982): For the hypothesis to be accepted, the 1:1 correspondences in soft and hard tissues hypothesized to be present in the bracket ancestor must be congruent with the phylogenetic structure of the EPB itself (i.e., found in the other descendants of the common ancestor). In other words, the 1:1 correspondences must characterize the monophyletic group comprised by the bracket. Even if a character passes the similarity test, if it fails to characterize a monophyletic group, then it is judged a homoplasy, not a homology. For example, the mammalian paranasal sinuses resemble somewhat those of archosaurs and so might pass the similarity test. However, paranasal pneumaticity is absent in nonarchosaurian sauropsids and basal synapsids, and thus on the basis of parsimony is judged as independent acquisitions in the clades leading to

mammals and to archosaurs because it does not characterize the monophyletic group Amniota (Witmer 1992).

For the sake of simplicity, the EPB approach will be briefly illustrated using an example in which the soft-tissue inference seems more or less obvious; the logic for more complex situations is the same (see Witmer 1992 for several examples relating to the soft-tissue relations of the antorbital cavity of archosaurs). What is the basis for inferring an eyeball in a fossil vertebrate, such as, say, *Tyrannosaurus rex*? The EPB of *T. rex* comprises birds and crocodylians. We know from numerous ontogenetic, experimental, and teratological studies that the eyeballs of extant birds and crocodylians are causally associated with specific osteological features (e.g., a complex cavity laterally within the skull communicating with the endocranial cavity via a foramen that conveys the optic nerve). The homology of these causal associations between birds and crocodylians (indeed among all vertebrates) is well established. Thus, our hypothesis is that the common (bracket) ancestor of birds and crocodylians possessed an eyeball with certain, specified osteological correlates. This hypothesis is tested by surveying other descendants of the bracket ancestor (i.e., fossil archosaurs, including *T. rex*) for these correlates. In this case, the osteological correlates are found in all fossil archosaurs, the hypothesis thus survives testing, and an eyeball may be inferred with confidence in *T. rex*. The simplicity of this example highlights the close links of the EPB approach to the homology relation and phylogenetic parsimony. The conclusion is that eyeballs and their osteological correlates are homologous in birds, crocodylians, and *T. rex*, and furthermore, since the assessment at the outgroup node is decisive and positive, it would be less parsimonious to argue differently. The stricture of causal association assures that the osteological features are indeed both necessary and sufficient to infer the soft-anatomical component in the extinct taxon.

Situations in which the initial hypothesis fails or is equivocal

The proposed method for reconstructing the soft-tissue attributes of extinct taxa may seem so rigorous that few hypotheses more complex than eyeballs in tyrannosaurs would survive. Is the method too stringent? Is there any way to save a hypothesis in which the assessment at the outgroup node is equivocal or even decisive and negative? The answer to the latter question lies in the researcher's willingness to speculate. It should be noted that the inference of soft tissues requires speculation even when the hypothesis survives all of the above tests. In many

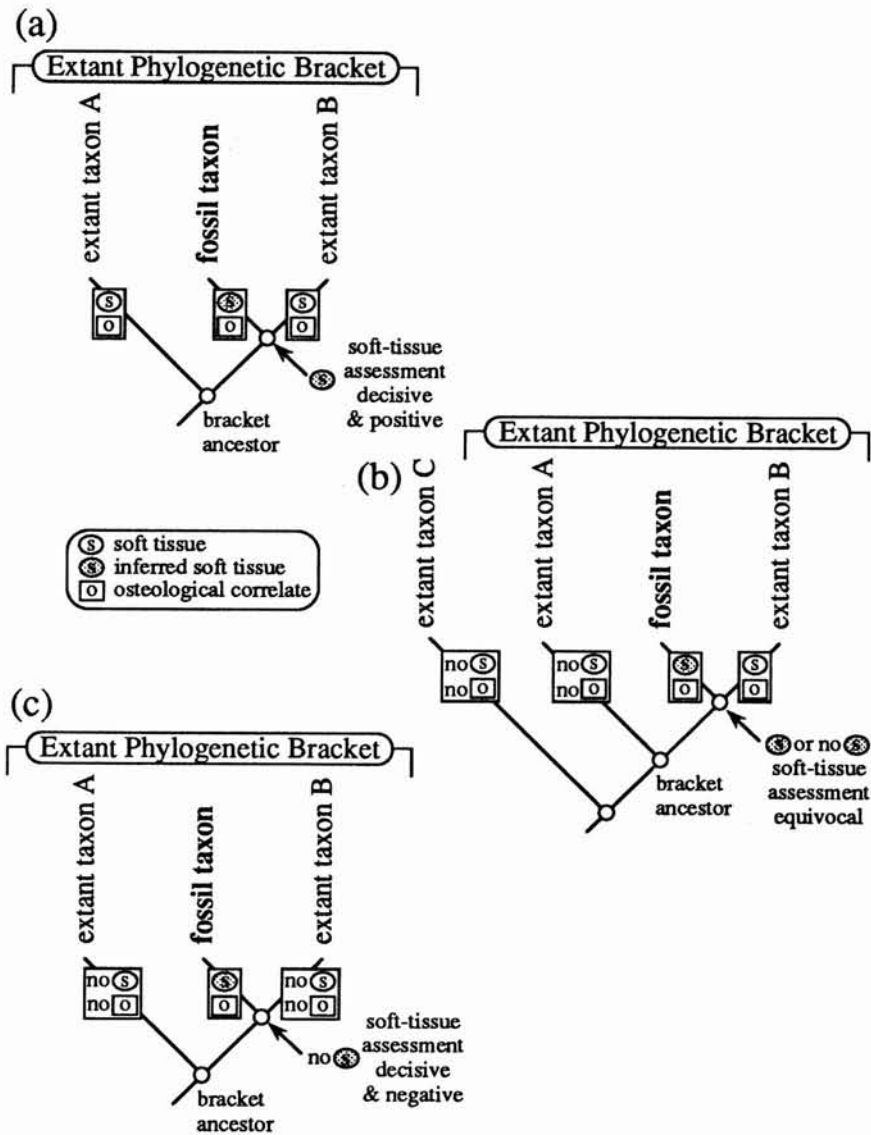


Figure 2.5. Assessment at the outgroup node and levels of inference. (a) Both extant components of the EPB possess the soft-tissue attribute (and causally associated osteological correlates) suspected to occur in a fossil taxon, leading to a decisive positive assessment at the outgroup node. (b) Only one of the extant components of the EPB has the soft-tissue attribute, leading to an equivocal assessment at the outgroup node. (c) Neither component of the EPB has the suspected soft tissue, leading to a decisive negative assessment. In (b) and (c), inference of the suspected soft tissue in the fossil may be justified if there is compelling morphological evidence. Reconstruction of the soft tissue in (a) requires a Level I inference, whereas reconstruction in (b) requires a Level II inference and in (c) a Level III inference.

respects, *any* inference of something that cannot be observed directly involves a measure of speculation (Rudwick 1964), that is, the inference of a brain within the cranial cavity of, say, *Homo erectus* is a speculation. Levels or degrees of speculation should be recognized based on the phylogenetic assessment at the outgroup node. Thus, the term speculation is not used here in its more common, pejorative sense, and implies no de facto absence of testability. One

important point of this chapter is that we need greater methodological rigor in order to determine the limits of our objective inferences – that is, to constrain, not completely eliminate, speculation. The EPB method makes the best, most economical use of the data at hand, and correctly identifies those soft-tissue inferences that are equivocal.

Furthermore, all speculation need not be idle. There are cases where the morphological clues from

hard parts are so compelling that they would seem to point to the presence of specific soft tissues regardless of the condition in outgroups; I call this an argument of compelling morphological evidence (Witmer 1992). Bryant and Russell (1992, p. 406) regard this type of approach as extrapolatory analysis because it “depends on established biological generalizations” that allow the inference of attributes of extinct organisms by extrapolating from extant taxa. Bryant and Russell’s (1992) extrapolatory analysis was explicitly intended to be separate from (but employed in parallel with) phylogenetic analysis. In the EPB approach, phylogenetics and compelling morphological evidence work together to give us a sense of the relative strength of our conclusions, that is, to ordinate our inferences.

Thus, a hierarchy of inference can be envisioned corresponding to the three possible assessments at the outgroup node that were noted earlier: (I) almost no speculation in situations where the EPB approach yields a decisive positive assessment at the outgroup node (Figure 2.5a, for example, eyeballs in tyrannosaurs), (II) more speculation when a compelling morphological evidence argument is advanced and the assessment is equivocal (Figure 2.5b), and (III) even more speculation when there is compelling morphological evidence and a decisive negative assessment (Figure 2.5c). Examples of soft-tissue inferences requiring speculations at levels II and III are presented below. In general, as long as the speculation is explicitly noted, situations involving levels II and III would seem to be admissible, and in many cases may be the only alternative short of ignoring the morphology altogether (Dodson et al. 1990). The notion of a hierarchy of inference is generalized and amplified in the Discussion.

A LEVEL II INFERENCE. This case occurs in situations where the soft tissue suspected to occur in a fossil taxon is found in its extant sister group but not in any other outgroups, leading to an equivocal assessment at the outgroup node (Figure 2.5b). In other words, the soft tissue feature indeed may characterize a monophyletic group including a living taxon but not the entire EPB of the fossil taxon. However, specific morphological attributes of the fossil may resemble those in the extant taxon so closely that, given the causal association of the attributes and soft tissues, the inference of the soft tissue in the fossil may be justified. For example, it has always been assumed that the Cretaceous bird *Ichthyornis* was feathered and capable of flight, suggesting that feathers characterize a more inclusive group than neornithine birds alone. However, applying the methodology yields an equivocal assessment with regard to feathers on *Ichthyornis* because one of

the components of its extant phylogenetic bracket, crocodylians, lacks feathers. Nevertheless, *Ichthyornis* manifests so many of the morphological attributes causally associated with feathers and flight in extant birds that we may confidently clothe *Ichthyornis* with feathers, although this inference still involves a measure of speculation. (The obvious significance of *Archaeopteryx* in this example is discussed below.)

A LEVEL III INFERENCE. In other cases, the soft tissue may have appeared independently of any extant taxon but still can be inferred in a fossil taxon with a high probability using a similar argument of compelling morphological evidence (Figure 2.5c). For example, the presence of cheeks in ornithischian dinosaurs has been postulated on the basis of, first, distinctive morphology also found in mammals (e.g., medial emargination of the maxillary and dentary dentitions), and second, the presumed functional necessity of such structures in animals that apparently masticated plant material (Galton 1973). However, application of the above methodology results in a decisive *negative* assessment because the EPB of ornithischians (birds and crocodylians) lacks cheeks, as do all other sauropsids. Nevertheless, many workers regard the morphological evidence as sufficiently compelling to reconstruct cheeks in ornithischians, probably because it is difficult to imagine how ornithischians could chew effectively without the assistance of cheeks. In fact, Galton (1973) suggested that the development of cheeks was instrumental (i.e., a key innovation) in not only the radiation of these herbivorous dinosaurs but also their competitive replacement of prosauropods. Such weighty paleobiological inferences, however, carry the *caveat* that they are founded on speculation – no matter how compelling the morphological evidence.

The significance of *Lagerstätten*

Fossil organisms known from *Lagerstätten* were mentioned earlier as often being easy cases for reconstructing soft tissues. However, they bear much greater significance for the methodology proposed here in that they can stand in some cases as “extant” taxa when composing the extant phylogenetic bracket. The method is basically the same, although the amount of morphological detail that can be extracted from fossils from *Lagerstätten* almost always will be less than for extant taxa. Nevertheless, these rare and unusual fossils can be critical in turning an equivocal assessment at the outgroup node into a decisive one. For example, the Cretaceous toothed bird *Hesperornis* has virtually no wings and was certainly a flightless diver. Despite its being part of the avian clade, what is our basis for reconstructing

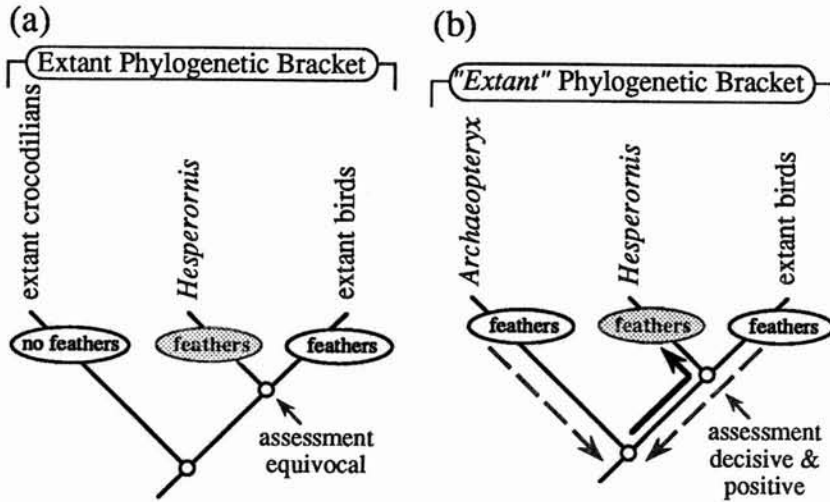


Figure 2.6. Cladograms showing the relevance of fossils known from *Lagerstätten* to the EPB approach. (a) Cretaceous flightless diving bird *Hesperornis* lacks compelling morphological evidence for the presence of feathers, and the EPB approach yields an equivocal assessment at the outgroup node. Feathers in *Hesperornis* are a Level II inference. (b) Adding *Archaeopteryx*, which is from a *Lagerstätten* and is known to have had feathers, the “E”PB approach yields a decisive positive assessment. Feathers in *Hesperornis* thus becomes a Level I inference.

Hesperornis with feathers? Given its EPB of neornithine birds and crocodilians, we have no strict basis for inferring feathers in *Hesperornis*: the presence of feathers is equivocal at the outgroup node (Figure 2.6a). If it had a good wing skeleton like its contemporary *Ichthyornis*, we might be tempted to clothe it in feathers on the basis of compelling morphological evidence (a Level II inference). Fortunately, we have *Archaeopteryx* that we know from multiple specimens from one of the most spectacular *Lagerstätten* (the Solnhofen lithographic limestone) had feathers. Thus, *Archaeopteryx* may stand as an “extant” taxon in the analysis such that the “extant” phylogenetic bracket of *Hesperornis* is *Archaeopteryx* and neornithine birds (Figure 2.6b). Proceeding through hypothesis formulation and testing, we now conclude with confidence that *Hesperornis* had feathers (i.e., a decisive positive assessment of feathers at the outgroup node – a Level I inference).

Summary of methodological considerations

An extant phylogenetic bracket allows formulation of hypotheses about the soft-tissue relations of extinct taxa that may be tested by reference to the known osteological correlates of the soft tissues in fossil taxa enclosed by the bracket. In cases where an assessment at the outgroup node is decisive and positive speculation is minimized – for example, when the two extant outgroups both exhibit the soft-

tissue attribute and form a doublet in the sense of Maddison et al. (1984). Speculation increases when the assessment is equivocal or when it is decisive and negative; in the latter case, inferring the soft tissue in the fossil may be regarded as unfounded. However, speculation may be fruitful (and even correct) if there is compelling morphological evidence for a particular soft-anatomical feature. Again, the point is to constrain speculation, not necessarily eliminate it.

DISCUSSION

The previous sections outline why paleontologists often need to look beyond fossil bones, and toward the soft-tissue functional matrices that influence bony morphology. Reconstructing the soft-anatomical properties of extinct organisms is inferential and by necessity involves a certain amount of speculation – such is the nature of historical science – and requires no apology. The EPB approach advocated here for obtaining this soft-tissue information draws heavily on the extant outgroups of the fossil taxon of interest. The next section addresses “a central worry” raised by Pagel (1991, p. 432) in a slightly different context; namely, the possibility that using extant taxa to bracket fossil taxa “guarantees that the animals that get constructed are a kind of average animal – an ‘everyanimal’ of sorts.” The final section generalizes the EPB approach for any traits not normally preserved in fossil taxa.

Pagel's "everyanimal"

For many questions in evolutionary biology, the dichotomy between paleontology and neontology is not only artificial but actually may impede an investigator's arrival at appropriate inferences. Paleontology is traditionally the domain of only hard parts, whereas neontology theoretically can examine virtually any aspect of an organism. This dichotomy presents a problem for paleontologists because critical information on soft-tissue attributes is seemingly out of reach. Thus, to interpret extinct organisms correctly, we are challenged to recover whatever relevant soft-anatomical information we can from fossils. Gauthier, Kluge, and Rowe (1988) effectively demonstrated the importance of fossils in phylogeny reconstruction. The approach advocated here is in some respects the other side of the same coin in that it emphasizes the importance of extant taxa in paleobiology.

According to the EPB approach, confidently reconstructing an extinct organism with a particular soft tissue requires (in the simplest case) that both of its extant outgroups possess both the suspected soft-tissue element and its causally associated osteological correlates. Higher levels of inference are required in cases where one or both extant outgroups lack the specified soft tissue. Thus, Pagel's (1991, p. 532) concern seems justified in this case: "use of the present to reconstruct the past condemns the past to be like the present. Worse, perhaps, the past that we get from looking backwards is a very ordinary past, an average past."

What, then, are our alternatives, since Pagel offers none? As emphasized throughout, the EPB approach seeks not only to constrain our inferences and characterize levels of inference, but also to ground these inferences in organisms for which the data are richest – those living today. The EPB approach does not bar the recognition of the novelties of extinct taxa; rather, it allows us to assess critically the empirical basis of the inference. Level I inferences such as eyeballs in tyrannosaurs are relatively safe, whereas those requiring higher levels require more caution. We *should* feel better about inferring eyeballs in tyrannosaurs than cheeks in ornithischians. No one should (or would) deny that the orbit of *T. rex* housed an eyeball, but a researcher would be justified in questioning the existence of ornithischian cheeks and certainly Galton's (1973) claims about cheeks as key innovations.

To cite a more concrete example that was in fact the impetus for developing the EPB approach, debate about the function of the antorbital cavity (an opening in the snout) of fossil archosaurs has revolved around three major hypotheses: The cavity

housed (1) a gland, (2) a jaw adductor muscle, or (3) a paranasal air sac. This is clearly a soft-tissue problem, and the EPB approach was applied to each of these hypotheses (Witmer 1992). The results showed that the bracket ancestor indeed possessed a nasal gland, a large jaw muscle, and an air sac, but only the paranasal air sinus produced osteological correlates that involved the antorbital cavity; thus, it was concluded that the function of the cavity in extinct taxa was to house an air sac (Witmer 1992). The point here is that although fossil archosaurs indeed were reconstructed to be similar to their living relatives, the EPB approach discriminated the hypothesis that most economically accounted for the data and yielded a robust result (i.e., a Level I inference). One is still free to argue for glands, muscles, or anything else, but to do so requires higher levels of inference and, since the approach is grounded in phylogenetics, more homoplasy (Witmer 1992).

The generality of the Extant Phylogenetic Bracket approach

Although the EPB approach was developed for the reconstruction of soft-tissue features of fossil taxa and soft tissues have been emphasized throughout, the approach can be generalized with little modification to any other attribute not normally preserved in the fossil record (e.g., function, behavior, some ecological parameters) but that has causally associated features (e.g., osteological correlates) that can be checked in extinct and extant animals alike. As mentioned, Bryant and Russell (1992) also presented a very similar general approach (see their paper for examples), and Weishampel (this volume) uses the EPB approach to probe functional inferences.

A special, yet important, case needs to be mentioned here. Although, the soft-tissue focus of the previous discussion emphasized the role of osteological correlates, not all attributes of organisms have reliable bony indicators. In the absence of such data, one may formulate a hypothesis about unpreserved traits on strictly phylogenetic grounds (i.e., presence of the trait in the bracket ancestor), but this hypothesis can be tested only by additional phylogenetic analysis and not by direct reference to fossil material. According to the protocol outlined earlier, inferring the trait in the bracket ancestor amounts to formulating a hypothesis of homology. Only when the trait has osteological correlates can this hypothesis of homology be tested directly for its congruence with the phylogeny of extinct and extant taxa alike. Furthermore, arguments of compelling morphological evidence obviously cannot be advanced without osteological correlates.

These limitations do not necessarily invalidate the

inference of those unpreserved traits that lack osteological correlates. However, such inferences must require additional speculation. The inference of a four-chambered heart (which lacks osteological correlates) in, say, *Hyracotherium* seems relatively safe, but strictly requires more speculation than the inference of a brain (which has such correlates). Thus, to be consistent, a hierarchy of inference parallel to the one outlined earlier can be constructed, again based on whether the assessment at the outgroup node is (I') decisive and positive, (II') equivocal, or (III') decisive and negative, but this time in the absence of osteological correlates. The levels of this hierarchy are given prime (') designations because it is not easy to ordinate all six levels. On the one hand, a Level I inference clearly is preferred to a Level I' because the former draws additional support from osteological evidence, and similarly a Level III' inference is probably untenable because it involves a decisive negative assessment and lacks osteological corroboration. On the other hand, it is unclear a priori if Level I' inferences are more robust than those at Level II, or if Level II' inferences are more robust than those at Level III. What remains clear, however, is that there are relatively rigorous means now available for inferring soft tissues and other normally unpreserved traits in extinct taxa, providing an explicit characterization of the level or amount of speculation that a researcher must invoke.

ACKNOWLEDGMENTS

Thanks are due to H.N. Bryant and A.P. Russell for friendly and productive discussion and correspondence and for supplying a preprint of their paper. Thanks are also due to D. Krause and S. Leigh for useful suggestions. The manuscript was read by D.B. Weishampel, N. Solounias, and an anonymous referee. The research presented in this chapter was part of my doctoral dissertation, undertaken at the Johns Hopkins University School of Medicine under the direction of D.B. Weishampel. I thank D.B. Weishampel, A. Walker, P. Dodson, N.C. Fraser, and R.L. Zusi for their discussions and for their critical comments on those portions of this chapter that are derived from my dissertation. Funding was provided by NSF Dissertation Improvement Grant BSR-9112070, the Alexander Wetmore Fund of the American Ornithologists' Union, Sigma Xi, and a fellowship from the Lucille P. Markey Charitable Trust.

REFERENCES

- Atchley, W.R., & Hall, B.K. 1991. A model for development and evolution of complex morphological structures. *Biological Review* 66, 101-157.
- Bakker, R.T. 1983. The deer flies, the wolf pursues: incongruencies in predator-prey coevolution. In *Coevolution*, ed. D.J. Futuyma & M. Slatkin, pp. 350-382. Sunderland: Sinauer Associates, Inc.
- Bakker, R.T. 1986. *The Dinosaur Heresies*. New York: William Morrow.
- Bellairs, A.d'A., & Kamal, A. 1981. The chondrocranium and development of the skull in Recent reptiles. In *Biology of the Reptilia*, Vol. 11, ed. C. Gans & T.S. Parsons, pp. 1-264. New York: Academic Press.
- Benton, M.J. 1989. *On the Trail of the Dinosaurs*. New York: Crescent Books.
- Benton, M.J. 1991. *The Rise of the Mammals*. London: New Burlington Books.
- Born, G. 1883. Die Nasenhöhlen und der Thränennasengang der amnioten Wirbelthiere. III. *Gegenbaurs Morphologisches Jahrbuch* 8, 188-232.
- Bryant, H.N., & Russell, A.P. 1992. The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. *Philosophical Transactions of the Royal Society of London B* 337, 405-418.
- Bryant, H.N., & Seymour, K.L. 1990. Observations and comments on the reliability of muscle reconstruction in fossil vertebrates. *Journal of Morphology* 206, 109-117.
- Carlson, B.M. 1981. Summary. In *Morphogenesis and Pattern Formation*, ed. T.G. Connelly, L.L. Brinkley, & B.M. Carlson, pp. 289-293. New York: Raven Press.
- Carpenter, K., & Currie, P.J. 1990. *Dinosaur Systematics: Approaches and Perspectives*. Cambridge University Press.
- Clutton-Brock, T.H., & Harvey, P.H. 1977. Primate ecology and social organisation. *Journal of Zoology* 183, 1-39.
- Coulombre, A.J., & Crelin, E.S. 1958. The role of the developing eye in the morphogenesis of the avian skull. *American Journal of Physical Anthropology* 16, 25-37.
- Cracraft, J. 1986. The origin and early diversification of birds. *Paleobiology* 12, 383-399.
- Cracraft, J. 1990. The origin of evolutionary novelties: pattern and process at different hierarchical levels. In *Evolutionary Innovations*, ed. M.H. Nitecki, pp. 21-44. Chicago: University of Chicago Press.
- de Beer, G.R. 1937. *The Development of the Vertebrate Skull*. London: Oxford University Press.
- Dixon, D., Cox, B., Savage, R.J.G., & Gardiner, B. 1988. *The Macmillan Illustrated Encyclopedia of Dinosaurs and Prehistoric Animals*. New York: Macmillan Publishing.
- Dodson, P., Coombs, W.P., Jr., Farlow, J.O., & Tatarinov, L.P. 1990. Dinosaur paleobiology. In *The Dinosauria*, ed. D.B. Weishampel, P. Dodson, & H. Osmólska, pp. 31-62. Berkeley: University of California Press.
- Eldredge, N. 1986. Information, economics, and evolution. *Annual Review of Ecology and Systematics* 17, 351-369.
- Eldredge, N., & Salthe, S.N. 1984. Hierarchy and evolution. In *Oxford Surveys in Evolutionary Biology*, Vol. 1, ed. R. Dawkins & M. Ridley, pp. 184-208. Oxford: Oxford University Press.
- Farris, J.S. 1970. Methods of computing Wagner trees. *Systematic Zoology* 19, 83-92.
- Galton, P.M. 1973. The cheeks of ornithischian dinosaurs. *Lethaia* 6, 67-89.
- Gauthier, J.A., Kluge, A.G., & Rowe, T. 1988. Amniote phylogeny and the importance of fossils. *Cladistics* 4, 105-209.

- Hall, B.K. 1983. Epigenetic control in development and evolution. In *Development and Evolution*, ed. B.C. Goodwin, N. Holder, & C.C. Wylie, pp. 353–379. Cambridge University Press.
- Hall, B.K. 1988. The embryonic development of bone. *American Scientist* 76, 174–181.
- Hall, B.K. 1990. Genetic and epigenetic control of vertebrate embryonic development. *Netherlands Journal of Zoology* 40, 352–361.
- Hall, B.K. 1991. What is bone growth? In *Fundamentals of Bone Growth: Methodology and Applications*, ed. A.D. Dixon, B.G. Sarnat, & D.A.N. Hoyte, pp. 605–612. Boston: CRC Press.
- Hall, B.K., & Herring, S.W. 1990. Paralysis and growth of the musculoskeletal system in the embryonic chick. *Journal of Morphology* 206, 45–56.
- Halstead, L.B. 1991. Dinosaur Studies, Commemorating the 150th Anniversary of Richard Owen's Dinosauria. *Modern Geology*, Volume 16.
- Hanken, J. 1983. Miniaturization and its effects on cranial morphology in plethodontid salamanders, genus *Thorius* (Amphibia, Plethodontidae): II. The fate of the brain and sense organs and their role in skull morphogenesis and evolution. *Journal of Morphology* 177, 255–268.
- Harvey, P.H., & Pagel, M.D. 1991. *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.
- Humphrey, T. 1971. Development of oral and facial motor mechanisms in human fetuses and their relation to craniofacial growth. *Journal of Dental Research* 50, 1428–1441.
- Kamal, A.M., & Abdeen, A.M. 1972. The development of the chondrocranium of the lacertid lizard, *Acanthodactylus boskiana*. *Journal of Morphology* 137, 289–334.
- Le Gros Clark, W.E. 1964. *The Fossil Evidence for Human Evolution*. Chicago: University of Chicago Press.
- Liem, K.F. 1989. Functional morphology and phylogenetic testing within the framework of symecomorphosis. *Acta Morphologica Neerlandoscandinavica* 27, 119–131.
- Maddison, W.P., Donoghue, M.J., & Maddison, D.R. 1984. Outgroup analysis and parsimony. *Systematic Zoology* 33, 83–103.
- Moss, M.L. 1968. A theoretical analysis of the functional matrix. *Acta Biotheoretica* 18, 195–202.
- Moss, M.L. 1971. Functional cranial analysis and the functional matrix. *American Speech and Hearing Association Reports* 6, 5–18.
- Moss, M.L. 1972a. The regulation of skeletal growth. In *Regulation of Organ and Tissue Growth*, ed. R.J. Goss, pp. 127–142. New York: Academic Press.
- Moss, M.L. 1972b. Twenty years of functional cranial analysis. *American Journal of Orthodontics* 62, 479–485.
- Moss, M.L. 1981. Genetics, epigenetics, and causation. *American Journal of Orthodontics* 80, 366–375.
- Moss, M.L., & Salentijn, L. 1969. The primary role of functional matrices in facial growth. *American Journal of Orthodontics* 55, 566–577.
- Nicholls, E.L., & Russell, A.P. 1985. Structure and function of the pectoral girdle and forelimb of *Struthiomimus altus* (Theropoda: Ornithomimidae). *Palaeontology* 28, 643–677.
- Noden, D.M. 1983. The role of the neural crest in patterning of avian cranial skeletal, connective, and muscle tissues. *Developmental Biology* 96, 144–165.
- Noetzel, H. 1949. Ueber den Einfluss des Gehirns auf die Form der benachbarten Nebenhöhlen des Schädels. *Deutsche Zeitschrift für Nervenheilkunde* 160, 126–136.
- Norman, D.B. 1985. *The Illustrated Encyclopedia of Dinosaurs*. New York: Crescent Books.
- Norman, D.B., & Weishampel, D.B. 1985. Ornithopod feeding mechanisms: their bearing on the evolution of herbivory. *American Naturalist* 126, 151–164.
- Oster, G.F., Shubin, N.H., Murray, J.D., & Alberch, P. 1988. Evolution and morphogenetic rules: the shape of the vertebrate limb in ontogeny and phylogeny. *Evolution* 42, 862–884.
- Pagel, M.D. 1991. Constructing "everyanimal." Review of *Body Size in Mammalian Paleobiology*, edited by J. Damuth & B. MacFadden, Cambridge University Press, 1990. *Nature* 351, 532–533.
- Pagel, M.D., & Harvey, P.H. 1988. Recent developments in the analysis of comparative data. *Quarterly Review of Biology* 63, 413–440.
- Patterson, C. 1982. Morphological characters and homology. In *Problems of Phylogenetic Reconstruction*, ed. K.A. Joysey & A.E. Friday, pp. 21–74. New York: Academic Press.
- Patterson, C. 1988. Homology in classical and molecular biology. *Molecular Biology and Evolution* 5, 603–625.
- Paul, G.S. 1988. *Predatory Dinosaurs of the World*. New York: Simon & Schuster.
- Paul, G.S., & Chase, T.L. 1989. Reconstructing extinct vertebrates. In *The Guild Handbook of Scientific Illustration*, ed. E.R.S. Hodges, pp. 239–256. New York: Van Nostrand.
- Pinto, C.B., & Hall, B.K. 1991. Toward an understanding of the epithelial requirement for osteogenesis in scleral mesenchyme of the embryonic chick. *Journal of Experimental Zoology* 259, 92–108.
- Ranly, D.M. 1988. *A Synopsis of Craniofacial Growth*, 2nd Edition. Norwalk: Appleton & Lange.
- Rieppel, O. 1988. *Fundamentals of Comparative Biology*. Boston: Birkhäuser Verlag.
- Ross, A.T. 1941. Cerebral hemiatrophy with compensatory homolateral hypertrophy of the skull and sinuses, and diminution of cranial volume. *American Journal of Roentgenology* 45, 332–341.
- Rudwick, M.J.S. 1964. The inference of function from structure in fossils. *British Journal for the Philosophy of Science* 15, 27–40.
- Savage, R.J.G., & Long, M.R. 1986. *Mammal Evolution: An Illustrated Guide*. New York: Facts on File.
- Schumacher, G.-H., & Dokládal, M. 1968. Ueber unterschiedliche Sekundärveränderungen am Schädel als Folge von Kaumuskelresektionen. *Acta Anatomica* 69, 378–392.
- Scott, J. H. 1957. Muscle growth and function in relation to skeletal morphology. *American Journal of Physical Anthropology* 15, 197–234.
- Smith, M.M., & Hall, B.K. 1990. Development and evolutionary origins of vertebrate skeletogenic and odontogenic tissues. *Biological Reviews* 65, 277–373.
- Spyropoulos, M.N. 1977. The morphogenetic relationship of the temporal muscle to the coronoid process in hu-

- man embryos and fetuses. *American Journal of Anatomy* 150, 395–410.
- Stevens, P.F. 1984. Homology and phylogeny: morphology and systematics. *Systematic Botany* 9, 395–409.
- Swofford, D.L., & Maddison, W.P. 1987. Reconstructing ancestral states under Wagner parsimony. *Mathematical Bioscience* 87, 199–229.
- Taylor, W.O.G. 1939. Effect of enucleation of one eye in childhood upon the subsequent development of the face. *Transactions of the Ophthalmology Society of the United Kingdom* 59, 361–371.
- Thorogood, P.V. 1988. The developmental specification of the vertebrate skull. *Development* 103 Supplement, 141–153.
- Van Valkenburgh, B. 1988. Trophic diversity in past and present guilds of large predatory mammals. *Paleobiology* 14, 155–173.
- Wedden, S.E., Ralphs, J.R., & Tickle, C. 1988. Pattern formation in the facial primordia. *Development* 103 Supplement, 31–40.
- Weishampel, D.B. 1984a. Evolution of jaw mechanisms in ornithomimid dinosaurs. *Advances in Anatomy, Embryology and Cell Biology* 87, 1–110.
- Weishampel, D.B. 1984b. Interactions between Mesozoic plants and vertebrates: fructifications and seed predation. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 167, 224–250.
- Weishampel, D.B. 1985. An approach to jaw mechanics and diversity: the case of ornithomimid dinosaurs. In *Vertebrate Morphology*, ed. H.-R. Duncker and G. Fleischer, pp. 261–263. New York: Gustav Fischer Verlag.
- Weishampel, D.B., & Norman, D.B. 1987. Dinosaur-plant interactions in the Mesozoic. In *Fourth Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*, ed. P.J. Currie & E.H. Koster, pp. 167–172. Drumheller: Occasional Paper of the Tyrrell Museum of Palaeontology 3.
- Weishampel, D.B., & Norman, D.B. 1989. Vertebrate herbivory in the Mesozoic: Jaws, plants, and evolutionary metrics. *Geological Society of America Special Paper* 238, 87–100.
- Weishampel, D.B., Dodson, P., & Osmólska, H. 1990. *The Dinosauria*. Berkeley: University of California Press.
- Wellnhofer, P. 1991. *The Illustrated Encyclopedia of Pterosaurs*. New York: Crescent Books.
- Wiley, E.O. 1981. *Phylogenetics: The Theory and Practice of Phylogenetic Systematics*. New York: John Wiley and Sons.
- Wiley, E.O., Siegel-Causey, D., Brooks, D.R., & Funk, V.A. 1991. *The Complete Cladist: A Primer of Phylogenetic Procedures*. Lawrence: University of Kansas Museum of Natural History Special Publication 19.
- Witmer, L.M. 1990. The craniofacial air sac system of Mesozoic birds (Aves). *Zoological Journal of the Linnean Society* 100, 327–378.
- Witmer, L.M. 1992. *Ontogeny, Phylogeny, and Air Sacs: The Importance of Soft-Tissue Inferences in the Interpretation of Facial Evolution in Archosauria*. Unpublished Ph.D. Dissertation. Baltimore: Johns Hopkins University School of Medicine.
- Witmer, L.M., & Rose, K.D. 1991. Biomechanics of the jaw apparatus of the gigantic Eocene bird *Diatryma*: implications for diet and mode of life. *Paleobiology* 17, 95–120.
- Wolpert, L. 1983. Constancy and change in the development and evolution of pattern. In *Development and Evolution*, ed. B.C. Goodwin, N. Holder, & C.C. Wylie, pp. 47–57. Cambridge University Press.
- Young, R.W. 1959. The influence of cranial contents on postnatal growth of the skull in the rat. *American Journal of Anatomy* 105, 383–415.